Energy Management and Foraging Behaviour in Food Hoarding *Paridae*

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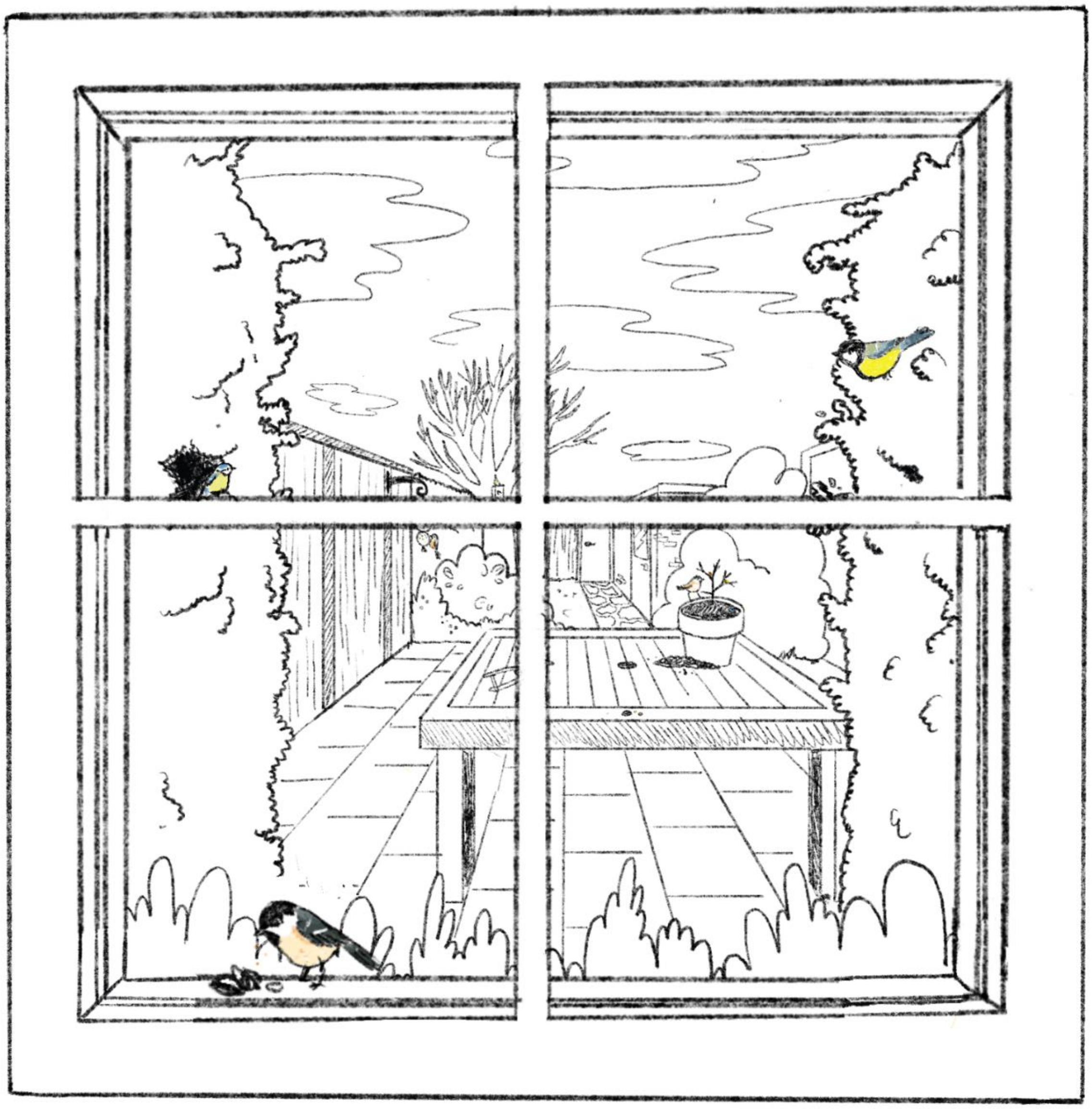

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Abstract

Winter poses significant energetic challenges for small tit species at northern latitudes, where food scarcity and shorter daylight hours limit foraging opportunities, whilst energy demands increase with dropping temperatures. Several bird species in the *Paridae* family hoard food to improve winter survival. How this behaviour is mechanistically regulated—both seasonally and in terms of foraging decision-making—is not fully understood.

This thesis investigates energy management in hoarding tit species across three projects. The first project focuses on the optimisation of energy management through fat reserves. According to Optimal Body Mass theory, hoarding birds are expected to carry less fat in winter than non-hoarders, as they have more predictable food resources. My findings show winter fattening patterns in both hoarding and non-hoarding tit species in the UK, with less pronounced patterns for hoarding birds. Furthermore, I explore the effects of temperature and day length on fattening, showing that day length is a better predictor of bird body mass than recent temperature.

My second project explores the seasonal patterns of hoarding, focusing on how food availability affects hoarding intensity during winter. I hypothesise that hoarding motivation might remain high in winter, but that birds reduce hoarding behaviour as they do not have enough food available. To gather data, I developed a large citizen science initiative where volunteers across the UK, USA and Canada reported the frequencies of hoarding and eating behaviours among birds visiting their garden feeders. Results reveal similar but slightly delayed hoarding patterns in food-supplemented birds compared to those in the wild, suggesting food supplementation was not sufficient to prevent the decline in hoarding, or that hoarding motivation is lower in winter.

My third project explores the variables influencing foraging decisions, specifically how birds decide whether to consume or hoard food. I develop agent-based models in which decision-making is based on stomach content, fat reserves or their combinations. I then explore how agents with different decision rules perform in varying environments and how this is reflected in their physiology and behaviour. The model outcomes demonstrate that simple decision rules, in which birds only hoard when there is a surplus of food and respond to information about their fat reserves, effectively replicate observed hoarding and retrieval patterns of short-term hoarding in winter.

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1.1.1 Winter Challenges

Some small passerines, such as birds from the *Paridae* family, remain at northern latitudes during winter. While many other species migrate to regions with more favourable conditions, these resident birds face long, cold nights and short days with scarce and unpredictable food sources. In northern areas, such as Scandinavia, winter temperatures often drop as low as -25°C, with daylight limited to only 5-6 hours per day. The prolonged nights and low temperatures create high energetic demands, while the short days leave limited time for foraging. Food resources are significantly reduced in winter compared to summer, as insects become scarce and difficult to find, and seeds that were plentiful in spring and summer have largely been depleted. Additionally, much of the remaining food is frequently covered by snow, making it difficult to access. These difficult circumstances cause a high winter mortality rate in resident birds. For example, winter mortality has been shown to go up to 50% in populations of tit species at northern latitudes and is mainly caused by food limitation.

1.1.2 The Importance of Fat Reserves

One of the most crucial factors in preventing starvation among small birds is body mass, and more specifically the fat reserves that are accumulated. Small birds rely on these fat reserves to survive, as the energy from food already in their digestive tract is insufficient to sustain them through the night. Instead, they have to metabolise the fat reserves they accumulated throughout the day. In winter, when nights are longer and temperatures drop, the energetic demands of staying warm increase, particularly for tit species, which lose heat more rapidly due to their high surface-to-volume ratio compared to larger animals (Brodin, 2007; Haftorn, 1972). In addition to these larger nighttime energy requirements, birds are also more likely to endure low food availability and unsuccessful foraging bouts during the daytime in winter (Desrochers et al., 1988; Jansson et al., 1981). In a field study on willow tits (*Poecile montanus*) and crested tits (*Lophophanes cristatus*), food-supplemented birds exhibited lower winter mortality rates compared to non-supplemented birds, which highlights the importance of food availability for winter survival. In summary, having access to food - and therefore being able to maintain sufficient fat reserves - is crucial for wintering passerines in order to avoid starvation.

Interestingly, birds do not carry as much fat as is physically or theoretically possible (Blem, 1976; Gosler et al., 1995; Lilliendahl et al., 1996; Lima, 1986). For instance, birds at higher latitudes maintain larger fat reserves than their southern counterparts, even without an increase in food availability (Blem, 1975). This means that the amount of fat a bird carries, is not a direct result of the food availability. Instead, studies show that birds reach their peak body mass in midwinter, coinciding with the season of highest energy expenditure and most challenging foraging conditions. If birds were always carrying the maximum amount of fat possible, we would expect opposite patterns with high body masses under the least "difficult" conditions. Instead, these findings show that it is not energetic restriction only that limits bird body mass and that birds could possibly carry larger fat reserves than they do. Therefore, there must be other factors influencing weight gain in birds (Gosler, 1996; Lima, 1986; Witter & Cuthill, 1993).

1.2 Optimal Body Mass Theory

The optimal body mass theory, originally formulated by Lima (1986), states that there is a trade-off between the risk of starvation and predation. Birds should carry large fat reserves in order to mitigate their starvation risks but on the other hand, balance the costs that come with larger fat reserves such as increased predation risks, but also increased metabolic costs (Brodin, 2001; Broggi et al., 2019; Lima, 1986; Witter & Cuthill, 1993).

1.2.1 Predation Costs

One of the main potential costs associated with larger fat reserves is the increased risk of mass-dependent predation. Birds with more substantial fat reserves may experience reduced flight performance, compromising their ability to escape from predators (Gosler et al., 1995; McNamara & Houston, 1990; Witter & Cuthill, 1993). Increased fat reserves lead to greater wing loading, which negatively impacts take-off ability by lowering ascent angles and reducing take-off velocities, which increase the success rate of predator attacks (Kullberg et al., 1996; Witter et al., 1994). However, small amounts of fat have been shown not to impair take-off ability in willow tits, suggesting that the small daily increases in their fat reserves may not significantly affect the starvation-predation trade-off (Kullberg, 1998). Nevertheless, this does not mean that this trade-off is irrelevant in preventing birds from carrying larger body masses on average. In addition, higher fat reserves can reduce manoeuvrability and in-flight velocity after take-off, making birds more susceptible to successful predation attempts whilst flying (Kullberg et al., 1996; McNamara & Houston, 1990a).

1.2.2 Metabolic Costs

In addition to mass-dependent predation risk, maintaining higher fat reserves carries a metabolic cost. Increased fat reserves—and consequently higher body mass—increase the energy required for foraging activities such as flight (McNamara & Houston, 1990a; Witter &

Cuthill, 1993). However, since birds spend only a small portion of their time in flight, this alone is unlikely to account for why fat reserves are maintained at relatively low levels (Brodin, 2001). Moreover, a rise in basal metabolic rate associated with larger fat reserves forms a substantial cost of carrying fat. Higher fat reserves result in larger flight muscles and increase basal metabolic expenditure in tissues, increasing energy consumption (Broggi et al., 2019). Consequently, birds must forage longer to sustain their energy reserves, which, in turn, heightens their overall predation risk (Brodin, 2001; Houston & McNamara, 1993; McNamara & Houston, 1990a).

1.3 Winter Fattening

Given the importance of fat reserves for winter survival, Optimal Body Mass theory suggests that birds would increase their fat stores during winter compared to other seasons. As temperatures fall and nights lengthen, the risk of starvation rises relative to predation risk, making it advantageous for birds to gain weight. This phenomenon, known as "winter fattening," has been observed in the wild, with birds increasing body mass in autumn, peaking in mid-winter, and decreasing in early spring (Gosler, 2002; Lehikoinen, 1987; Rintamaki et al., 2003).

Alongside this seasonal cycle, birds also experience daily weight gain, starting with low body mass in the morning after fasting overnight, and ending the day with higher fat reserves in preparation for roosting (Haftorn, 2000; Lehikoinen, 1987; Moiron et al., 2018; Polo & Bautista, 2002). During winter, colder and longer nights increase the risk of delayed food access upon waking and heighten energy demands overnight. As a result, birds should not only elevate their average body mass in winter but also increase their evening mass relative to their morning mass, displaying greater daily weight gain variation during these months (Lehikoinen, 1987). This combination of elevated winter average body mass and amplified daily weight gain is known as "true winter fattening" (Lehikoinen, 1987).

While the evolutionary advantage of winter fattening—reducing starvation risk during winter—is well understood, the proximate causes or triggers remain less clear. Proposed factors include day length (photoperiod) and recent temperatures. Generally, birds tend to be fatter when experiencing shorter days (Haftorn, 1989; Rintamaki et al., 2003) and show a negative relationship between temperature and body mass (Gosler, 2002; Lilliendahl et al., 1996; Rogers & Reed, 2003; Swanson & Olmstead, 1999). In Chapter 2, I will discuss this literature in more detail and investigate the factors that impact winter fattening in wild birds.

1.4 Hoarding as a solution?

Hoarding or "caching" is a behaviour in which animals do not directly eat the food items they find but hide them in their environment for later consumption (Vander Wall, 1990). Hoarding behaviour occurs across many species including rodents, primates, birds and insects and can include a wide range of behaviours. One common distinction made within hoarding behaviour is between scatter and larder hoarding (Andrews-McClymont et al., 2013; Vander Wall, 1990). In the case of larder hoarding, animals, such as hamsters and some species of woodpeckers, store their food in specific cache sites or a concentrated area in their environment. They build up food stores at these sites, returning to them when retrieval is needed. On the other hand, scatter hoarders such as birds from the *Paridae* family, fox squirrels (*Sciurus niger*) and gray jays (*Perisoreus canadensis*), will disperse their caches throughout their surroundings without forming clusters (Male & Smulders, 2007; Sherry, 1989; Vander Wall, 1990). While larder hoarders can often defend their caches from competitors, scatter hoarders benefit from dispersing their food across multiple locations, reducing the likelihood of losing all caches at once. On the other hand, the dispersal of caches makes it more difficult to memorise their location (Vander Wall, 1990).

A second distinction commonly made within hoarding behaviour is between short-term and long-term hoarding (Vander Wall, 1990). Many animals are known to store their food for only a few days or hours at the time. For example, carnivores such as pumas (*Puma concolor*) that kill prey they cannot consume at once, are known to store their food and eat it over several days (Allen et al., 2023; Vander Wall, 1990), and magpies (*Pica pica*) that will consume hoarded food items within the same day (Zinkivskay et al., 2009). On the other hand, long-term hoarders such as scrub jays (*Aphelocoma coerulescens*) will hoard food at a time it is plentiful and consume it months later when food availability is low (Fuirst et al., 2020; Vander Wall, 1990).

1.4.1 Hoarding in the Paridae Family

The *Paridae* family includes tits, chickadees and titmice which are all passerine birds that occur in the Northern hemisphere and in Africa. "Tits" refers to the species that occur in Africa, Asia and Europe, whilst birds in North America are called either chickadees (*Poecile spp*) or titmice (*Baeolophus spp*.). All chickadee and titmice species are assumed to, at least on occasion, hoard food items (Štorchová et al., 2010). For the common tit species in Europe, there is a split in hoarding and non-hoarding species. Hoarding species include willow tits (*Poecile montanus*), marsh tits (*Poecile palustris*), crested tits (*Lophophanes cristatus*), and coal tits (*Periparus ater*), which are known to regularly hoar their food. In contrast, non-hoarding species like blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) rely on immediate food availability rather than caching (Johansson et al., 2013; Štorchová et al., 2010).

Analysis of the ecological distribution of these species shows that hoarding species tend to inhabit mixed coniferous woodlands with more seasonal food availability at northern latitudes (e.g. northern Scandinavia), whilst non-hoarding species are more commonly found in open habitats in more temperate zones, where food is more abundant year round (Štorchová et al., 2010). In recent decades, blue tits and great tits have extended their ranges further north, possibly due to supplemental feeding by humans and globally increasing temperatures, which mitigate the challenges posed by harsher winters and reduced natural food sources at the northern edges of their ranges (Orell, 1989; Pakanen et al., 2018).

In titmice, hoarding can take place on both timescales; they sometimes hoard items for consumption later in the day (short-term), but there is also a seasonal pattern where hoarding behaviour peaks in autumn when birds hoard food items that are consumed during the winter months (Grubb & Pravosudov, 1994; Ludescher, 1980; Sherry, 1989).

1.4.2 Short-term Hoarding

Short-term hoarding in *Paridae* occurs when birds store food items that are retrieved and consumed later the same day or within a few days. This behaviour is thought to primarily help birds take advantage of temporarily abundant food sources (Ludescher, 1980). By caching part of a temporary food surplus, birds can consume a larger share of it than if they only ate when hungry. Storing food also prevents it from being depleted by competitors. Additionally, short-term hoarding helps buffer against short-term fluctuations in energy requirements, both within and between days (Sherry, 1989). Tit species are capable of memorizing the exact locations of their caches on a short-term basis, with research suggesting that they remember these locations for up to a few weeks (Brodin, 1994; Hitchcock & Sherry, 1990; Male & Smulders, 2007).

1.4.3 Seasonal Hoarding

Seasonal hoarding occurs primarily in autumn. During spring and summer, birds feed mostly on insects and are rarely observed storing food. As autumn approaches, their diet shifts to seeds, and hoarding intensity increases, peaking in autumn and gradually decreasing into winter (Brodin, 1994, 2005; Haftorn, 1956; Pravosudov, 2006 and sources cited therein). Although hoarding is generally low during the coldest winter months, some studies report a substantial second hoarding peak in spring, particularly in mast years when seeds are unusually abundant (Haftorn, 1956; Lange et al., 2022; Pravosudov, 1985, 2006). Birds are estimated to hoard between 45,000-150,000 food items per year, of which most are retrieved during the winter months (Brodin, 1994b; Haftorn, 1956; Pravosudov, 1985; Pravosudov & Grubb, 1997). This peak in autumn hoarding enables birds to accumulate food reserves, preparing them for the winter months when food is less accessible.

Laboratory and field studies indicate that birds do not reliably remember the exact locations of caches beyond 30 days (Brodin, 1994a; Hitchcock & Sherry, 1990; Male & Smulders, 2007). In practice, this means that the caches stored in autumn effectively become part of the birds' "food environment" in winter, as they encounter these hidden resources while foraging (Smulders, 1998).

1.4.4 Effects of Hoarding on the Energy Balance and Winter Fattening

Hoarding titmice have both short-term and long-term advantages over non-hoarding species in terms of energy management.

In the short term, hoarding allows these birds to use temporary food surpluses more effectively and structure their daily weight gain strategically. Unlike non-hoarding birds, which cannot benefit from food they find but cannot consume immediately, hoarding birds can store excess food. This behaviour creates a more predictable and accessible food supply on a short-term or within-day basis. Theoretically, this would allow hoarding birds to optimize their weight gain throughout the day. Early theoretical models investigating this, predicted that hoarding birds would maintain lower fat reserves in the morning to minimize mass-dependent costs, such as increased predation risk and metabolic expenditure. Birds would then increase their body mass in the evening using stored food to prepare for the overnight fasting period when metabolic demands are highest (McNamara, Houston, & Krebs, 1990). Some experimental data indeed show delayed daily weight gain in marsh tits and coal tits (Hurly, 1992; Polo et al., 2007). However, field data show that hoarding birds experience a peak in body mass gain rate in the early morning, unlike non-hoarders who accumulate weight more evenly throughout the day (Lilliendahl, 2002). Brodin (2000) suggested that this pattern may arise because small fat reserves have minimal effects on mass-dependent predation risk. This means that in the morning, the starvation risks are larger than predation risks, and birds will go out to forage or retrieve food items. Their access to reserves in caches allows hoarding birds to begin the day with a lower body mass, rapidly increasing their weight in the morning with the security of available food. Non-hoarders need to have larger fat reserves coming out of the night, as they cannot risk unfavourable foraging conditions in the morning (Brodin, 2000). These patterns highlight the role of hoarding in shaping the daily energy management of titmice.

Secondly, long-term hoarding behaviour has a general buffering effect on the winter food availability in hoarding tits, as seeds cached in autumn enrich the winter "food environment" (Grubb & Pravosudov, 1994; Ludescher, 1980; Sherry, 1989). If there is indeed a cost of carrying larger fat reserves, it is expected that "winter fattening" patterns would be less pronounced in hoarding birds than in non-hoarders, given the same external circumstances (predation, temperature, day length, etc.). Hoarding birds are expected to exhibit a smaller increase in average or minimum body mass during winter, as well as a smaller increase in the daily mass gain rate in winter (Broggi et al., 2003; McNamara, Houston, Krebs, et al., 1990). In line with these predictions, evidence of true winter fattening has been found in non-hoarding tit species, where an increase in mean body mass throughout autumn, peaking in winter, is well-documented (Broggi et al., 2019; Gosler, 2002; Haftorn, 1989; Lehikoinen, 1987). Some findings also show an increase in the amplitude of daily weight gain (Haftorn, 1989; Moiron et al., 2018). However, for hoarding species, evidence of true winter fattening is less consistent (Broggi et al., 2003, 2019; Cooper, 2007; Haftorn, 1989; Koivula et al., 1995). This difference between hoarding and non-hoarding species likely stems from the fact that hoarding birds cache food in their surroundings, thereby creating a more predictable food environment. As a result, they may not rely on large fat reserves in winter as a buffer against poor foraging outcomes. This adaptation allows them to maintain lower fat levels while still having access to energy resources. Chapter 2 further discusses the literature on winter fattening in hoarding and non-hoarding titmice and explores winter fattening patterns in tit species across the UK.

1.4.5 When Should Hoarding Evolve?

As mentioned above, hoarding behaviour is present in several genera within the *Paridae* family. However, evidence indicates that this behaviour is not ancestral to the family as a whole. Instead, hoarding evolved only once, in the common ancestor of the *Baelophus*, *Lophophanes*, *Periparus*, and *Poecile* group, before these species radiated across North America. This suggests that hoarding is a derived trait within the *Paridae* family, likely shaped by ecological pressures in the environment (Štorchová et al., 2010).

Early research on the evolution of hoarding and the circumstances under which it is advantageous was conducted by (Andersson & Krebs, 1978). In their seminal game-theoretic model, the authors explored the conditions under which hoarding could evolve in a group comprising both hoarding and non-hoarding *Paridae*. They demonstrated that hoarding behaviour is beneficial if it is more advantageous to hoard food than to leave it for later consumption and if hoarding birds are more likely to recover their caches than non-hoarding birds. The latter condition is crucial because, without it, non-hoarding "cheaters" could exploit caches created by hoarders, preventing the evolution of hoarding. To overcome this, hoarding birds must either remember the locations of their caches or have a higher likelihood of recovering food from individual foraging sites. (Smulders, 1998) expanded upon this framework, arguing that the strict requirement for individual benefit is not essential. Instead, hoarding can evolve if groups containing hoarders outperform groups consisting solely of non-hoarders. Similarly, (Vander Wall & Jenkins, 2003), investigated the evolution of hoarding under less restrictive conditions than those proposed by Andersson and Krebs. Their model demonstrated that even high levels of pilferage between individuals could allow hoarding to remain advantageous at a group level, provided pilfering is reciprocal. These findings align with Smulders' (1998) conclusions that groups with hoarding birds consistently outperform groups of non-hoarders.

In summary, hoarding is expected to evolve under circumstances where it is more beneficial to hoard items than to leave them for later consumption and where, at least on a group level, hoarding is more beneficial than non-hoarding (Andersson & Krebs, 1978; Brodin, 2010; Smulders, 1998). However, the drivers of hoarding behaviour on a proximate level, are less well understood (Pravosudov & Smulders, 2010).

1.5 The Motivation to Hoard

1.5.1 *Seasonal Peak in Hoarding*

As discussed above, hoarding birds show a seasonal peak in hoarding behaviour, with high hoarding intensity observed in the autumn months between September – October and sometimes additional peaks in early spring (Brodin, 1994, 2005; Haftorn, 1956; Pravosudov, 2006 and sources cited therein). Because stored food forms a large proportion of the food consumed by hoarding birds during winter and is crucial for survival (Brodin, 1994b; Grubb & Pravosudov, 1994; Haftorn, 1956; Pravosudov, 1985), it is possible that hoarding motivation evolved to be high in autumn and low during summer. Researchers have explored what may cue this change in motivation, finding that hoarding behaviour in *Paridae* species appears to be influenced by several environmental and physiological factors signalling seasonal shifts, including day length, food availability, and temperature.

Photoperiod, or the seasonal change in day length, regulates reproductive cycles in titmice as they transition through photosensitive, photostimulated, and photorefractory states throughout the year. Studies show that birds in photosensitive states hoard more than others, and that shorter days encourage hoarding; birds kept on shorter day lengths tend to hoard more than those exposed to longer day length (Krebs et al., 1995; MacDougall-Shackleton et al., 2003;

Shettleworth et al., 1995). With regards to temperature, mixed results have been found. In some studies, increased hoarding patterns were correlated with colder temperatures (Pravosudov & Grubb, 1997), whilst no effect of temperature was found in others (Clayton & Cristol, 1996). In addition, food availability has been suggested to effect hoarding motivation, as birds tend to hoard more in environments where food access is unpredictable or restricted (Hurly, 1992; Pravosudov, 2003; Pravosudov & Grubb, 1997).

Additionally, the birds' "energetic state" could play a role in regulating hoarding behaviour. Lucas and Walter (1991), using dynamic models, predicted that in high-starvation-risk settings, birds with lower body mass would consume food immediately to prevent starvation, while those with greater fat reserves might hoard to mitigate future starvation risk. Experimental evidence partly supports these predictions, showing that birds with higher fat levels are less likely to store food when it is abundant, and that hunger reduces caching frequency (Lucas et al., 1993; Lucas & Walter, 1991). This suggest that hoarding intensity is influenced by the interaction between environmental factors (such as food availability) and the bird's internal state (such as fat reserves and hunger).

Overall, evidence indicates that hoarding frequency is driven by shorter photoperiods, low food availability and predictability, lower temperatures, and the bird's energetic states. However, disentangling these factors is challenging, as environmental conditions (temperature, photoperiod, food distribution) and the bird's physiological state (hunger, fat reserves) all influence energy balance. Birds may respond to signals about their energy balance, or "energy flux" as a marker of past food availability and predictability, integrating multiple environmental influences (Lange et al., 2022; Pravosudov, 2006).

As conditions become more challenging in autumn, with longer nights and lower temperatures, the heightened energy flux could be what increases the motivation to hoard. However, despite facing similarly harsh or even worse conditions in winter, hoarding behaviour tends to be less frequent in winter (Brodin, 1994c; Pravosudov, 2006). Since food-supplemented birds reach peak hoarding intensity mid-winter, this decline may stem from limited food availability. Chapter 3 investigates this possibility further, as well as providing a broader overview of the literature on hoarding motivation.

1.5.2 Physiological Mechanisms Underlying Hoarding Motivation in Mammals

Most research on the motivation behind hoarding behaviour focuses on mammals such as squirrels (Brodin, 2010; Vander Wall, 1990) and hamsters (Keen-Rhinehart et al., 2010). Insights from this literature also suggest mechanisms through which shifts in an animal's energy balance are signalled, leading to changes in hoarding intensity. These studies often distinguish between two phases of food-related behaviour: an “appetitive” phase and a “consummatory” phase. In the appetitive phase, animals engage in behaviours that bring them into contact with food, whereas in the consummatory phase, they consume the food once it is obtained (Craig, 1918; Keen-Rhinehart et al., 2010).

1.5.2.1 Deficit Hypothesis

The “Deficit Hypothesis” is one of the primary theories on the physiological regulation of hoarding motivation. It proposes that animals begin hoarding food once their energy deficit surpasses a certain threshold, with food deprivation as the key driver of hoarding motivation (Bindra, 1947; Morgan et al., 1943). The energy deficit necessary to trigger hoarding motivation, is not thought to be the same as the shorter-term deficit which is caused by hunger. Instead, the motivation to hoard builds up across a longer time period from days to weeks (Bartness & Day, 2003; Bindra, 1947). More specifically, it has been suggested that the motivation to hoard is stimulated by shortages in fat reserves (Kennedy, 1952). However, data collected more recently, does not always match this hypothesis. The relationship between the size of adipose tissue and hoarding motivation has been shown to be more complex, as increases in hoarding intensity are not always connected to decreases in body mass. Similarly, increases in fat reserves are also not always associated with decreases in hoarding intensity, suggesting that the regulation of hoarding motivation might be regulated by smaller changes in energy metabolism (Dailey & Bartness, 2008; Keen-Rhinehart et al., 2010).

1.5.2.2 Energy flux hypothesis

An alternative to the “Deficit Hypothesis” is the “Energy-Flux Hypothesis,” proposed by Bartness and Day (2003), which addresses some issues of the deficit model. According to this hypothesis, it is not the animal’s “current” energetic state—such as the level of fat reserves—that regulates hoarding motivation. Instead, hoarding is thought to be triggered by signals from neuroendocrine factors that circulate when metabolic fuels are mobilised from storage sites (e.g., liver or adipose tissue) to locations where they are oxidised. This hypothesis helps explain why hoarding intensity can increase even when fat reserves remain constant, as it shifts the focus to the dynamic processes of energy metabolism (e.g., “energy flux”), rather than static energy stores.

1.5.2.3 Environmental factors

The Energy-Flux Hypothesis aligns well with observations in the literature on environmental influences on hoarding motivation. For instance, studies on Siberian hamsters (*Phodopus* *sungorus*), among other species, show an increase in hoarding behaviour in response to shorter day lengths (Bartness & Day, 2003; Masuda & Oishi, 1988). Furthermore, Siberian hamsters increase their hoarding intensity when exposed to colder temperatures (Masuda & Oishi, 1988), although this temperature effect is less consistent in other species, such as deer mice (*Peromyscus* spp.). In deer mice, hoarding motivation appears to be more strongly influenced by photoperiod than by temperature, though this varies across subspecies (Barry, 1976). With respect to food availability, studies indicate that Siberian hamsters increase hoarding behaviour when fasted, though similar responses are not consistently observed in other species (Bartness & Day, 2003). The impact of foraging effort has also been examined, particularly in hoarding mammals like hamsters. Experiments reveal that when foraging effort is artificially increased, animals respond by hoarding more frequently (Bartness & Day, 2003).

These findings, suggesting that shorter days, lower temperature, and higher foraging demands all increase metabolic demand, as well as increasing hoarding intensity. This supports the Energy-Flux hypothesis.

1.5.2.4 Central and Peripheral Mechanisms

The Energy-Flux Hypothesis appears to be the most plausible mechanism regulating food hoarding in hamsters and potentially other mammals. But what are the specific physiological mechanisms that signal the use of energy reserves in these animals?

In their review, Keen-Rhinehart et al. (2010) summarise the pathway through which food deprivation and increased energy consumption, along with hormonal and neural signals, influences hoarding behaviour. They describe how, in hamsters, food deprivation elevates plasma ghrelin levels, with ghrelin concentrations rising the longer the animal fasts. Ghrelin, a hormone produced in the stomach, is known to stimulate appetitive behaviours in mammals, and experimental studies have shown that artificially increasing ghrelin levels also elevates hoarding behaviour (Keen-Rhinehart & Bartness, 2005). Ghrelin will bind to the ghrelin receptors on neurons in the arcuate nucleus (hypothalamus), which will increase the release of NPY (Neuropeptide Y) and AgRP (Agouti-related protein) peptides. The latter two proteins have been experimentally shown to stimulate foraging and hoarding (Keen-Rhinehart et al., 2010).

Leptin, another key hormone, has an opposite effect on hoarding behaviour. Produced in adipose tissue, leptin inhibits appetitive behaviours. High levels of leptin have been shown to reduce foraging and hoarding motivation, thereby acting opposite to ghrelin in regulating energy balance (Keen-Rhinehart & Bartness, 2008).

Together, these hormonal mechanisms—ghrelin's stimulatory role and leptin's inhibitory role—suggest a physiological pathway through which signals from the energy metabolism could regulate hoarding behaviour in line with the Energy-Flux Hypothesis.

1.5.3 Physiological Mechanisms Underlying Hoarding Motivation in Birds

1.5.3.1 Environmental factors

As discussed in the sections above, hoarding behaviour in *Paridae* species is influenced by several environmental and physiological factors, including day length, food availability, and temperature. Similar to findings in mammals, shorter days, lower temperatures, and reduced food availability have all been linked to increased hoarding intensity in these birds. This parallel suggests that *Paridae* species may also exhibit similar adaptive responses to changes in energy metabolism. Physiological markers of these changes likely play a role in modulating hoarding behaviour, enabling birds to cope with fluctuations in food availability in their environment.

1.5.3.2 Energy Flux Hypothesis in Birds

As discussed above, it has been suggested that birds may respond not directly to environmental conditions but rather to their energy balance as an indicator of past food availability and predictability, incorporating the effects of environmental changes (Lange et al., 2022; Pravosudov, 2006). The neuroendocrine mechanisms governing this response may function similarly to those suggested for hamsters, though there are important distinctions between birds and mammals regarding the hormones and peptides involved in regulating foraging behaviour.

In both birds and mammals, ghrelin is produced in the stomach; however, unlike in mammals—where ghrelin promotes both food intake and hoarding—ghrelin generally inhibits food consumption in birds (Kaiya et al., 2009). Interestingly, circulating ghrelin levels increase during fasting in both birds and mammals, despite having opposing effects on food intake between the two groups (Kaiya et al., 2009). Furthermore, both neuropeptide Y (NPY) and agouti-related protein (AgRP) are upregulated in response to food deprivation in birds, as in mammals (Boswell & Dunn, 2015). When leptin is administered experimentally, this also inhibits food intake birds as it does in mammals (Boswell & Dunn, 2015; Kaiya et al., 2009; Lõhmus et al., 2003). However, unlike mammals, birds produce leptin in the brain, as well as other tissues, rather than in predominantly in adipose tissue, suggesting it may not reliably indicate fat reserves in birds (Friedman-Einat & Seroussi, 2019).

The differences in ghrelin's impact on food consumption, combined with the different production site and role of leptin, suggest that the regulation of appetitive behaviours may differ between mammals and birds. While few studies have explored this directly, one study found that injecting ghrelin and leptin peripherally reduced both hoarding and body mass gain in hoarding titmice (Henderson et al., 2018). This indicate that ghrelin, which is known to inhibit food consumption in birds, might also inhibit hoarding behaviour. Leptin, which inhibits food intake in both mammals and birds, might also inhibit hoarding behaviour. More research is needed to clarify the specific mechanisms that signal shifts in energy metabolism in birds and stimulate hoarding behaviour.

1.5.3.3 Suggestions for Signalling Factors

Although the exact pathways by which birds gather information about their energy flux are not yet fully understood, evidence suggests that they do rely on cues related to their energy metabolism when making foraging and hoarding decisions. Birds likely use signals that indicate how full their stomach is, or what the state of their fat reserves is.

For example, it is realistic to assume birds have information about how full their stomach is, through mechanoreceptors in the stomach (Denbow, 2015), and as discussed earlier, ghrelin has been shown to inhibit food intake (Henderson et al., 2018; Kaiya et al., 2009). Furthermore, as nutrients like lipids are absorbed and metabolized, the liver's processing rate is known to influence food intake in birds (Denbow, 1994, 1999). Finally, factors circulating in the blood during lipolysis and lipogenesis, along with the hormones that regulate these processes, likely provide birds with information about their fat metabolism and the state of their fat (Denbow, 1999; Leclercq, 1984).

The literature on these signalling factors is reviewed in a bit more detail in Chapter 4. Additionally, their potential role in the decision-making mechanisms underlying hoarding behaviour will be explored in Chapters 4 through 7.

1.6 Thesis Overview

This thesis investigates the energy management and behaviour of food-hoarding *Paridae* species, particularly examining how these processes are regulated in winter conditions.

In Chapter 2, I analyse winter fattening patterns in tit species across the UK, utilizing a large dataset on bird weight, size, and species collected by the British Trust for Ornithology. This chapter tests the hypothesis that winter fattening patterns—characterized by increased morning, mean, and evening mass, as well as a greater daily weight amplitude—will be more evident in non-hoarding species and less pronounced in hoarding titmice. Additionally, I examine how environmental factors, specifically day length and temperature, influence body mass in these birds.

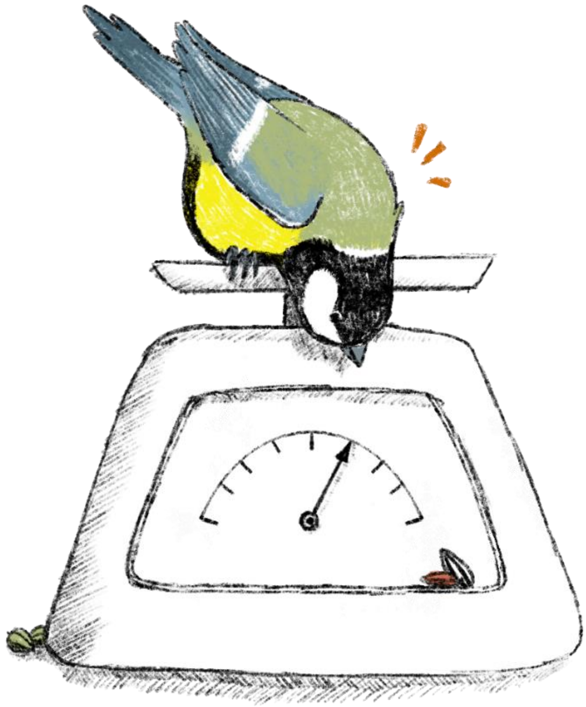
Chapter 3 focuses on hoarding motivation, with a particular interest in the seasonal peak in hoarding behaviour observed in the field. Using a citizen science approach, I investigate whether food supplementation affects the timing of the hoarding peak, shifting it toward the shortest days, when energy requirements are highest. I also analyse the effects of day length and temperature on hoarding frequencies.

The final part of this thesis, Chapters 4 through 7, involves the development of an agent-based model to simulate the decision-making mechanisms that may underlie hoarding motivation in a small wintering bird. In Chapter 4, I introduce the general structure of the model and the various model versions, where birds make decisions based on different physiological variables indicating their energetic state, as well as models with distinct hoarding strategies. Chapter 5 presents the results of models where decision-making is driven by stomach content. Chapter 6 examines models that rely on fat reserves and changes in fat reserves. Chapter 7 discusses models where decision-making is informed by a combination of stomach content and fat metabolism data.

In the general discussion, I integrate findings from the three main parts of this thesis, compare results across Chapters 5, 6, and 7, and propose hypotheses regarding the mechanisms underlying decision-making in food-hoarding birds.

Overall, this thesis seeks to advance our understanding of energy management in food-hoarding birds, particularly concerning winter fattening patterns and the regulation of hoarding motivation.

Part I: Winter Fattening



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Chapter 2. Seasonal Fluctuations of Body Mass in UK Tit Species

3.1 Abstract

Winter poses significant challenges for small tit species in northern latitudes, where food scarcity and shorter days limit foraging opportunities, and energy demands increase with dropping temperatures. To survive, these birds must optimise their energy management, primarily through the regulation of fat reserves. Larger fat reserves provide crucial insulation and fuel for overnight survival, but they also introduce trade-offs, such as increased predation risk and reduced foraging efficiency, as outlined by the Optimal Body Mass (OBM) theory. Consequently, birds are expected to carry more fat in winter and reduce it during other seasons, a process known as "winter fattening". This study examines the seasonal and daily variations in body mass among UK tit species, using citizen science data from the British Trust for Ornithology ringing scheme. I hypothesise that "true winter fattening," characterised by increased morning, mean, and evening mass, as well as a greater daily weight gain amplitude, will be observed in non-hoarding species. In contrast, hoarding species will show less pronounced fattening patterns due to their reliance on cached food. Additionally, I explore the influence of environmental cues, finding that day length, rather than temperature, primarily triggers these patterns, with birds increasing body mass in response to shorter days.

3.2 Introduction

3.2.1 Energy Management in Winter

Winter is a challenging time for small tit species that reside at northern latitudes throughout the winter. Not only is food scarcer this time of year, but birds also have less time available to forage during the shortening days. On top of these increased difficulties with finding food, the energy requirements of the birds increase due to the lower temperatures. To survive, birds need to adjust to these circumstances and adapt their energy management and behavioural strategies.

The energy management in wintering passerines is highly dependent on their fat reserves (Brodin, 2007; Mcnamara & Houston, 1990; Pravosudov & Grubb, 1997). Carrying larger fat reserves is helpful, as it allows birds to endure periods of low food availability and unsuccessful foraging bouts, which are more likely to occur in winter (Desrochers et al., 1988; Jansson et al., 1981). Moreover, body fat is crucial because it has insulating properties and serves as fuel during the long, cold winter nights when birds cannot forage and must maintain their body temperature.

However, birds do not carry as much fat as is physically or theoretically possible (Lilliendahl et al., 1996; Lima, 1986; McNamara & Houston, 1990a). According to Optimal Body Mass (OBM) theory, this is because of a trade-off where birds should carry larger fat reserves to reduce their risk of starvation, whilst balancing the costs of larger body weights (Lima, 1986; Pravosudov & Lucas, 2001b). Heavier birds face an increased predation risk, either due to increased predator exposure or reduced flying agility (Brodin, 2001; Gosler et al., 1995; Houston & McNamara, 1993; Kullberg, 1998). Besides, the metabolic rate of birds is mass-dependent and with increasing fat reserves, the rate of energy gain whilst foraging decreases (Houston & McNamara, 1993).

Therefore, in line with OBM theory, birds are predicted to carry larger fat reserves in winter when the risk of starvation is largest and reduce their adipose tissue throughout the rest of the year. From late autumn till early spring, when birds are not breeding or moulting, fluctuations in body mass are mostly due to changes in fat reserves (Chaplin, 1974; Lehikoinen, 1987; Petit et al., 2014). In this period, through a seasonal process called "winter fattening", birds start to gain body mass in autumn, which peaks in mid-winter and declines in early spring (Gosler, 2002; Lehikoinen, 1987; Rintamaki et al., 2003). On top of this seasonal cycle, bird body mass fluctuates throughout the day. Birds start the day with a low body mass after fasting for the night, which increases as they forage and reaches a maximum just before roost (Haftorn, 2000; Lehikoinen, 1987; Moiron et al., 2018; Polo & Bautista, 2002).

In winter, the short days limit the birds' foraging opportunities, whilst energy expenditure increases during the long and cold nights. To cope with this challenging combination, birds should increase both their mass gain rate and their maximum body weight at the end of the day, leading to a greater amplitude in the daily weight gain cycle during the winter months (Lehikoinen, 1987). Lehikoinen's (1987) seminal model suggests that true winter fattening is evidenced by a seasonal increase in fat reserves not only in the evening and mean body mass but also in morning mass. This increase in morning mass arises as birds need a larger safety margin from their absolute minimum mass in winter. As birds prepare for colder nights, their evening mass rises, and because they do not fully deplete their fat reserves overnight, they wake up with a higher morning mass (Figure 2.1).

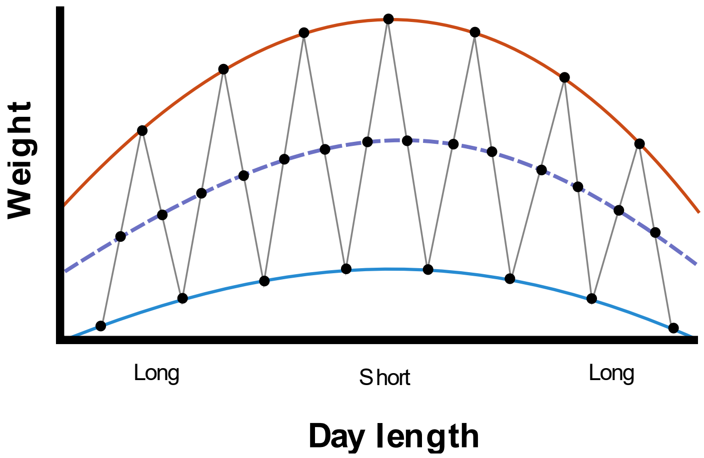

Figure 3.1. Figure adapted from (Lehikoinen, 1987). Predictions from a model of "true winter fattening", where the morning mass (blue bottom line), mean mass (purple line) and evening mass (red top line) all increase during winter, when days are shortest. The grey lines show the increase in daily weight gain amplitude, caused by the larger increase in evening mass than in morning mass.

3.2.2 Food Hoarding Paridae

Some species of *Paridae*, such as coal tits (*Periparus ater*) in the UK, can hoard food items they find, storing them for later retrieval. This behaviour allows them to use temporally abundant food sources and create a more stable and predictable food environment. Hoarding behaviour in the wild follows a seasonal pattern, where a hoarding peak is observed in autumn and sometimes in Spring in mast years (Lange et al., 2022; Pravosudov, 2006). Most seeds are retrieved in mid-winter (Brodin, 1994b; Grubb & Pravosudov, 1994; Haftorn, 1956; Pravosudov, 1985). Throughout autumn and winter, retrieval also takes place on a shorter timescale, where birds retrieve cached items within the same or a couple of days of hoarding them (Brodin, 1992).

Hoarding birds are less likely to encounter long periods without food and have a more reliable food source available than their non-hoarding counterparts, which results in an on average lower starvation risk. At the same time, hoarding birds do not need to "carry" the externally stored energy, which could reduce their predation risk and metabolic costs. Several authors have investigated how the capacity to hoard would affect the energy management of wintering tit species. Most of these studies focus on the short-term role of hoarding, such as the timing of mass gain in hoarders versus non-hoarders within a day. Hoarding birds are expected to delay their weight increase until later in the day, as they can rely on retrieval of caches and thereby circumvent the assumed costs of large fat reserves (McNamara, Houston, Krebs, et al., 1990). In contrast, non-hoarders, facing greater uncertainty, are predicted to gain weight earlier and mitigate the risks of unsuccessful foraging later in the day (McNamara, Houston, Krebs, et al., 1990). While experiments show delayed weight gain in marsh tits (Hurly, 1992) and coal tits (Polo et al., 2007), field data does not align with these predictions, showing the highest weight gain rates in the early morning for willow tits (*Poecile montanus*) and marsh tits (*Poecile palustris*), but not for great tits (*Parus major*) (Lilliendahl, 2002). Further studies on the short-term role of hoarding, have focussed on the effects of fat reserves and food predictability on hoarding intensity and timing (see Hurly, 1992; Lucas, 1994; Lucas & Walter, 1991).

Others have considered the role of hoarding in energy management on a longer, seasonal timescale. If there is indeed a cost of carrying larger fat reserves, it is expected that “winter fattening” patterns would be less pronounced in hoarding birds than in non-hoarders, given the same external circumstances (predation, temperature, day length, etc.). Hoarding birds have been suggested to rely on retrieving cached items early in the morning, which is a critical time for survival (Lucas & Walter, 1991; Pravosudov & Lucas, 2001). As a result, they may not require the buffer provided by the increased evening and morning mass to the same extent as non-hoarding birds. Therefore, hoarding birds are expected to exhibit a smaller increase in average or minimum body mass during winter, as well as a smaller increase in the daily mass gain rate in winter (Broggi et al., 2003; McNamara, Houston, Krebs, et al., 1990).

3.2.3 Evidence for True Winter Fattening

The evidence for “true winter fattening”, defined as an increase in morning and evening mass combined with a larger daily weight gain amplitude (Lehikoinen, 1987), is mixed. That passerines gain weight throughout the day and lose this overnight is well established in both hoarding (Broggi et al., 2003; Cooper, 2007; Gavrilov et al., 2013; Haftorn, 2000; Koivula et al., 1995; Lilliendahl, 2002; Moiron et al., 2018; Polo et al., 2007; Pravosudov & Grubb, 1997; Rintamaki et al., 2003) and non-hoarding tit species (Lehikoinen, 1987; Lilliendahl, 2002; Moiron et al., 2018; Rintamaki et al., 2003).

A seasonal increase in minimum, average and evening body mass is commonly observed in non-hoarding species. For example, Gosler (2002) observed a mid-winter peak in great tit fat reserves. Furthermore, great tits have been shown to increase their morning mass (Haftorn, 1989; Lehikoinen, 1987) and average mass (Haftorn, 1989; Moiron et al., 2018) in winter. Rintamaki et al. (2003) showed the same results for great tits and blue tits (*Cyanistes caeruleus*) in central Sweden and these findings were partially confirmed by Broggi et al. (2019) who found an increase in mean body mass for wintering great tits, but did not observe the same pattern in blue tits.

Evidence for the seasonal effect on average and minimum body mass in hoarding species is mixed. Koivula et al. (1995) found a small but significant increase in willow tit morning mass throughout autumn, with a peak in winter. Haftorn (1989) found a peak in morning, mean and evening mass in coal tits (*Periparus ater*), willow tits and marsh tits wintering in Norway. Similar results were shown in black-capped chickadees (*Poecile atricapillus*) at northern latitudes, which increased their body mass in winter. However, it was suggested this effect was only partly due to an increase in adipose tissue, as seasonal increases in lean tissue and water content also contributed (Nip et al., 2018; Petit et al., 2014). Mixed results were found in a study on mountain chickadees (*Poecile gambeli*) and tufted titmice (*Baelopus bicolor*), where only mountain chickadees were found to have higher fat levels in winter (Cooper, 2007). Broggi et al. (2003) also present mixed results on willow tits overwintering in Finland. They find no clear effect of photoperiod on morning mass but present some evidence that male willow tits have larger body masses on shorter days. In 2019, however, Broggi et al. did not find an effect of season on the mean body mass of willow tits.

Finally, when considering the increase in daily mass gain amplitude required for true “winter fattening”, evidence in either hoarding or non-hoarding birds is sparse. Haftorn (1989) found an increase in daily weight gain amplitude in 5 species of hoarding and non-hoarding tits wintering in Norway. Moiron et al. (2018) found that the interaction between day length and time of day causes great tits to gain weight quicker in winter. However, other studies present mixed results, such as Cooper et al. (2007) who only found an increase in daily mass gain in Mountain Chickadees, but not in the tufted titmice inhabiting the same area. Broggi et al. (2003) did not detect an effect of day in year on the daily increase of body mass in wintering Willow tits.

In summary, in non-hoarding tit species, we see clear evidence of body mass (both morning, mean, and evening) increases throughout autumn with a peak in winter, in line with true “winter fattening”. Studies on non-hoarding tits show an increase of the amplitude of their daily weight gain cycle. In hoarding species, findings are mixed both regarding the mid-winter peak in body mass and the increase in daily weight gain amplitude as predicted by true “winter fattening”.

3.2.4 Causes of Winter Fattening

Ultimately, birds exhibit winter fattening as an adaptive response to the harsh conditions they face during winter months, when short days and long nights are combined with low temperatures (Haftorn, 1989). Research has suggested various environmental cues that could trigger this seasonal process. Firstly, birds could start to increase their fat reserves based on day length, increasing their body mass as day length decreases and lowering their fat reserves when days grow longer. Notably, the timing of body mass decrease in spring is significant, as birds begin to reduce their mass in late winter, prior to the rise in temperatures, indicating that photoperiod might be a key factor in triggering this change (Haftorn, 1989; Rintamaki et al., 2003). Alternatively, temperature fluctuations might directly influence fattening, cueing birds to adjust their fat reserves based on temperatures they recently experienced. This allows for a more flexible response to changing circumstances. Most studies highlight the effects of temperature, showing that while short-term winter temperatures are generally negatively correlated with body mass, very short-term or current temperatures tend to be positively correlated (Gosler, 2002; Lilliendahl et al., 1996; Rogers & Reed, 2003; Swanson & Olmstead, 1999).

3.2.5 Study Aims

In this study, I aim to add to this body of literature, by investigating the body mass variations of wild living tits in the UK. Where most previous studies have used weights of a small number of individual birds, I use a large dataset accumulated over 19 years by the British Trust for Ornithology ringing scheme to investigate the seasonal and daily patterns of body mass variation and the occurrence of "true winter fattening".

I have the following predictions:

1. To compensate for the longer nights and colder temperatures in winter, birds show "true winter fattening". This will be visible as an increase in morning mass as well as an increase in daily weight gain amplitude throughout autumn with a peak in winter. Similar increases in the mean body mass and evening mass will follow from these patterns.
2. Hoarding birds can rely on their caches and have a lower risk of starvation. Therefore, winter fattening patterns will be less pronounced in hoarding birds. The peak morning mass and daily weight gain amplitude will be flatter in hoarding birds than in non-hoarding birds.
3. I will investigate if temperature or day length is the main driver of winter fattening patterns. First, we explore the effects of temperature using the average minimum temperature across 3 nights before capture and expect a negative relationship between temperature and body mass. For day length, I expect birds to increase their residual body mass as days shorten.

3.3 Methods

3.3.1 *BTO Ringing Scheme Data*

The bird data was collected by volunteers in the British and Irish Ringing Scheme run by the British Trust for Ornithology (BTO). Before data cleaning, the records contained a total of 1496043 captures of 486017 great tits, 861975 blue tits, and 148051 coal tits. All birds were caught in British and Irish territories between 2002 and 2021. Each record contains information about the location of the capture as well as biometric data such as species, body mass and wing length of the birds.

The data were cleaned by removing observations with missing information on species, age, weight, wing length, or location. Erroneous records were also excluded, such as instances where the English species name did not match the Euring species code or when weight or wing length values fell outside biologically plausible ranges (Euring Europe, 2023). Juvenile birds were excluded from the analysis to prevent their lighter weights in early autumn from skewing the results. Juveniles, born in the spring or summer of the same year, typically weigh less than adults during the same period. Additionally, juveniles have lower winter survival rates compared to adults (Lahti et al., 1998; Schaub & Amann, 2001). Including them in the analysis could artificially lower the observed body mass in autumn and, due to their reduced survival, create the appearance of an increase in body mass into winter. To avoid this bias, juveniles were conservatively removed from the dataset. Observations made during the breeding and moulting seasons were excluded, ensuring that only data from the period of interest (October to March) were retained. Birds captured outside the UK mainland were removed, and the dataset was filtered to include only records accurate to the hour of observation. Finally, if a bird was captured multiple times, only a single, randomly selected observation was retained to avoid the effect of correlated recaptures. See the supplementary materials for a detailed overview of the data filtering process and the number of removed observations for each filtering step.

3.3.2 *Variable Selection and Data Manipulation*

3.3.2.1 *Time and Date Stamps*

To ensure accurate and reliable time and date stamps, all time stamps were converted into UTC using the *lubridate* package in R (R Core Team, 2024; Spinu et al., 2023). The sunrise and sunset for each day and location were determined using the *Stream Metabolism* package in R (Sefick, 2023). Records made either more than 1.5 hours before sunrise or more than 1.5 hours after sunset were removed. The number of "*hours passed since sunrise*" was calculated for each observation, as well as the total "*day length*".

Then the "*proportion of day*" that has passed at the time of observation was calculated by dividing the *hours passed since sunrise* by the *day length* on the day of observation. We use this variable as a proxy for the time of capture in our analysis. By standardizing the time of capture by day length, I ensured that any observed changes in the daily weight gain rate are due to actual increases in weight gain amplitude, instead of a combined effect of shortening days and changes in amplitude.

The "*day within season*" was calculated as the number of days passed since October 1st of each season, with each season ranging from October 1st until March 31st. See supplementary materials section A for a detailed overview of the calculated variables.

3.3.2.2 Selecting a Proxy for Fat Reserves

The residual of body mass regressed on wing length was used as a proxy for the fat reserve of each bird (Labocha & Hayes, 2012; Schamber et al., 2009). Since the relationship between body mass and wing length is not linear, both variables were log-transformed prior to analysis. A linear regression was then performed to calculate the residual log(body mass) on log(wing length), ensuring that these residuals were no longer correlated with the overall body size of the bird. The regressions were conducted at the species level to account for potential differences in the relationship between body mass and wing length across species, ensuring a mean residual body mass of 0 for each species. The resulting value of the *"residual body mass*" variable greater than 0 indicates that the bird is heavier than expected for its given wing length, while a value less than 0 indicates that the bird is lighter than expected.

3.3.2.3 Weather Data

To investigate the effects of temperature on the body condition of birds, I matched each BTO record with data on the air temperature at the location and time that the observation was made. The weather records were retrieved from the Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations dataset. The MIDAS dataset used contains daily minimum and maximum air temperatures recorded at weather stations across the UK between 2002 and 2021 (Met Office, 2024). Throughout the data cleaning process, observations with missing and/or erroneous data regarding the timestamp, version, location and weather station ID were removed.

Each record in the BTO data was matched with the average minimum temperature recorded across the three days prior to the bird's capture using the *geosphere* package in R (Hijmans et al., 2022). Weather observations are logged at 09:00 in the morning, covering either a 12-hour or 24-hour period. As a result, the minimum temperature recorded at 09:00 typically occurs just before sunrise on the same day. To avoid differences in effect size based on how close in time the bird was captured to this minimum, the weather record for the day of capture was excluded from the analysis (Gosler, 2002). For example, if a bird was caught on Friday, it would be matched with the minimum temperatures logged at 09:00 on Tuesday – Thursday mornings. These represent the overnight lows between Monday night and Thursday morning.

The weather data used came from the nearest weather station up to a maximum of 50 km from the capture location. For each observation, I extracted weather data from the three previous mornings. Bird observations were only retained if weather data for at least 2 out of 3 of these mornings was available. These 2-3 nighttime minima were then averaged to produce a mean minimum temperature across the 3 nights before capture in degrees Celsius. This resulted in retaining 297,078 observations with matching temperature data. The "*temperature*" variable contains the average of the 3 (or 2) minimum overnight temperatures preceding the bird capture in degrees Celsius. See supplementary materials for a detailed overview of the weather data filtering and temperature-matching processes.

3.3.2.4 Data Subsets

Some of the analysis is conducted on subsets of the data. The "*morning data*" constitutes all observations made within 1.5 hours on either side of sunrise (N =53,445). The "*evening data*" constitutes all observations collected within 1.5 hours on either side of sunset (N = 13,757). The full data set that contains all observations after data filtering will be referred to as "*full data*" (N = 297,078).

3.3.3 Data Analysis

3.3.3.1 Fitting GAMs

To investigate the fluctuations in body mass for tit species in the UK, I fitted GAMs (Generalized Additive Models) using the *gam* function from the *mgcv* package in R (R Core Team, 2024; Wood, 2004). The following GAM parameters were set for all models: discrete = TRUE (to increase computational speed when using the *bam()* function) and gamma = 1.4 to reduce overfitting of smoothed curves (Wood, 2017).

Unless stated otherwise, the smooth terms (*day within season, proportion of day*, *temperature*, *day length*, *temperature*) were fitted with a thin plate spline with a basis size of $k = 7$. Here, k determines the complexity of the smooth. Thin plate splines are indicated with *"s()"* in the model formulas below, representing smooth, nonlinear relationships between the predictors and response variable. If the observed patterns were biologically more complex or simpler than expected, k was adjusted accordingly to allow for more or fewer basis functions, while keeping *k* constant across models for each variable. *k* was also lowered in cases where increasing the degrees of freedom did not improve model fit but increased the estimated degrees of freedom, indicating potential overfitting.

For interactions between splines or between splines and parametric coefficients (i.e. *species* was included as a categorical factor), tensor product interactions with marginal penalties were used. These interactions allow for individual interpretations of the main effects, as well as interpretation of interaction effects. They are indicated as "*ti()*" in the model equations. In these cases, *k* is set according to the *k* of the smooth term.

3.3.3.2 Patterns of True Winter Fattening

To investigate whether birds increase their fat reserves over the winter, GAMs were fitted to morning, evening, and full-day datasets. In all 3 GAMs, r*esidual body mass,* as described earlier, was used as the response variable and *day within season* as the predictor (see Models 1-3 in Table 3.1). *Day within season* was included with a thin plate spline.

To check if birds, on top of seasonal weight gain, also experience changes in their daily weight gain amplitude, two additional GAMs were fitted to the *full data (*Model 4 and Model 5 in Table 3.1*)*. Model 4 expands upon Model 3 by adding *proportion of day* as a thin plate spline with k = 5. To investigate if the daily weight gain curve changes throughout the seasons, the interaction between *proportion of day* and *day in season* was added in Model 5. This was done by expanding Model 4 with a tensor product interaction with *k*=7 for *day within year* and *k*=5 for *proportion of day*. Models 4 and 5 were also fitted with *proportion of day* as a linear predictor. Other model settings were kept the same. Models 4, 4-linear, 5 and 5-linear were compared using AIC (Akaike's Information Criterion) and "deviance explained".

3.3.3.3 Differences between Hoarders and Non-hoarders

To investigate if hoarders and non-hoarders differ in their winter fattening patterns, *species* was included in Model 6 as a factor that interacts with *proportion of day* and *day in season*. Two-way and three-way interactions between *proportion of day*, *day in season* and *species* were included as tensor product interactions. The main effect of *species* was not included, as this has been accounted for in the regression of body mass over wing length. *Day in season* was fitted with k=7, *proportion of day* with *k*=3 (see Model 6 in Table 3.1).

3.3.3.4 Drivers of Winter Fattening Patterns

To investigate if the patterns we observe are driven by day length, or if temperature directly affects the residual body mass of birds, an additional GAM was fitted. Here the *day in season* variable was replaced with the *temperature* variable which reflects the minimum temperature of the 3 nights before the day of capture. The model was fitted with thin plate splines for the main effects and tensor product interactions for the interactions. *k* was set to 3 for each term, as both *temperature* and *proportion of day* are not expected to have a complex effect (Model 7 in Table 3.1). Then, the same model was fitted but with *day length* as a covariant replacing *temperature*, with the same model settings otherwise (Model 8 in Table 3.1). AIC values and "deviance explained" were compared to understand which variable better predicts residual body mass.

3.3.3.5 Model Checks and Result Reporting

Before fitting the models, correlations between all variables were assessed to determine which could be included together. Significant correlations with values of rho > 0.4 (moderate) were observed between *day length* and *day in season*, as well as *day length* and *temperature* for the first half of the season. As a result, these variables were not included together in the models (see Supplementary materials section A for details). Diagnostic checks were conducted for all models, including visual inspections of residuals vs. fitted values to check for heteroscedasticity, QQ-plots, and evaluations of residual distributions to confirm their Gaussian nature. I also performed dimension checks to ensure that the basis dimension (k), which controls the number of basis functions used to fit smooth terms, was sufficiently high to accommodate the effective degrees of freedom (EDF) for each term while maintaining biological relevance.

In the results section below, I present the F-value and p-value for the smooth terms. A significant p-value means the smooth term has a significant effect on the outcome variable (*residual body mass*).

For R scripts of the data analysis and data cleaning process, please see https://github.com/Vera-Anne/.

3.4 Results

3.4.1 Patterns of True Winter Fattening

Model 1: Residual body mass morning ~ s(day in season): Results show a significant effect of *day in season* on the *residual mass* of birds caught in the morning ($F = 180.37, p < 0.001$). The residual morning mass increases throughout winter with a peak in late December. The explanatory power of the model is low, with only 2.0% of the variance explained. Complete model summaries for this and the following models can be found in the Supplementary materials section A.

Model 2: Residual body mass evening ~ s(day in season): Results show a significant effect of *day in season* on the *residual body mass* of birds caught in the evening ($F = 64.49, p <0.001$). The residual evening mass increases throughout winter with a peak in early January. Again, the variance explained by the model is low at 2.7%.

Model 3: Residual body mass ~ s(day in season): Results show a significant effect of *day in season* on the *residual body mass* of birds across the entire dataset (*full data*) ($F = 1{,}190.57, p <0.001$). The residual mass increases throughout winter with a peak in late December. The percentage of variance explained by this model is 2.4%.

Figure 2.2 shows the predicted values of models 1, 2 and 3, showing the peak in mean body mass that occurs in late December. Morning mass peaks slightly ahead of evening mass, with the latter peaking in early January. These results confirm a pattern of weight gain as days get shorter, in line with true winter fattening for the grouped data.

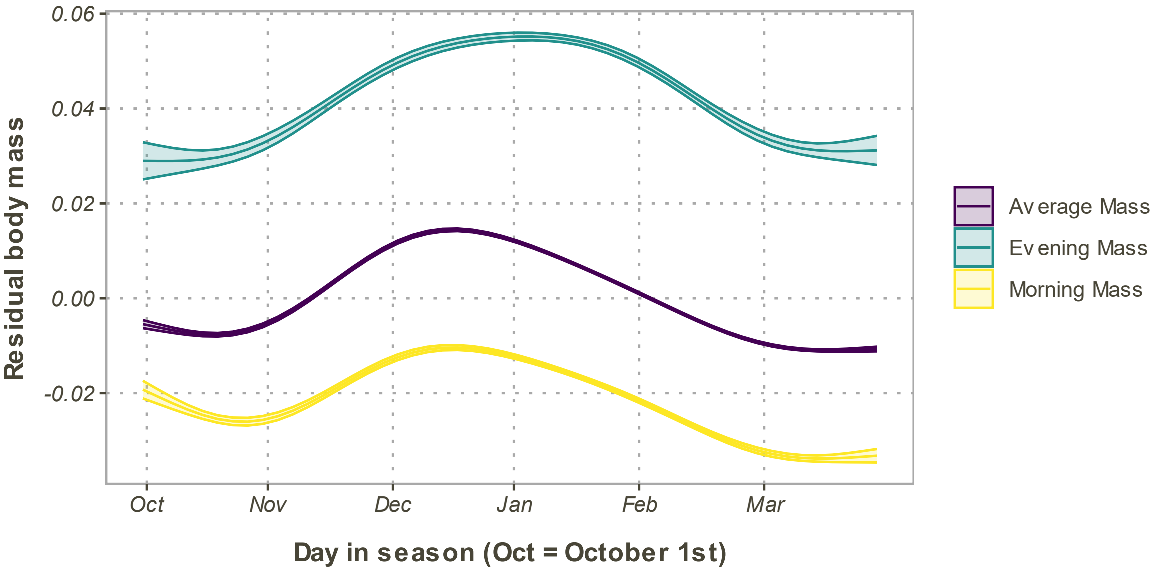

Figure 3.2. Predicted values of models 1, 2 and 3. Shaded areas show the Standard Error. Residual body mass on the y-axis and day in season on the x-axis. Vertical lines depict the start of the month they mark. Models are fitted to the 3 subsets of data as described above.

Model 4: Residual body mass mean ~ s(day in season) + s(proportion of day): Results show a significant effect of *day in season* ($F = 1{,}305.60, p <0.001$) and *proportion of day* ($F = 22{,}009.78, p < 0.001$) on the residual body mass of birds. The residual body mass peaks in mid-winter and increases gradually throughout the day. Introducing *proportion of day* into the model increases the deviance explained to 15.0%.

Table 3.1. Model overview. All interactions are fitted with a tensor product interaction. Bold indicates the best fitting model to the full dataset.

Model	***Outcome***	***Predictor(s)***	***Data set***	***AIC***	***Deviance explained***
1	Residual morning mass	s(day in season)	Morning data	-	0.020
2	Residual evening mass	s(day in season)	Evening data	-	0.027
3	Residual body mass	s(day in season)	Full data	-883161.30	0.024
4	Residual body mass	s(day in season)+ s(proportion of day)	Full data	-924254.50	0.150
4 - linear	Residual body mass	s(day in season)+ proportion of day (linear)	Full data	-924221.70	0.150
5	Residual body mass	s(day in season)+ s(proportion of day)+ ti(day in season * proportion of day)	Full data	-924609.9	0.151
5 - linear	Residual body mass	s(day in season)+ proportion of day (linear) + ti(day in season * proportion of day (linear))	Full data	-924567.2	0.151
6	Residual body mass	s(day in season)+ s(proportion of day)+ ti(day in season * proportion of day) + ti(day in season * species) + ti(proportion of day * species) + ti(day in season* proportion of day * species)	Full data	-926322.8	0.156
7	Residual body mass	s(temperature) + s(proportion of day)+ ti(temperature * proportion of day) + ti(temperature * species) + ti(proportion of day * species) + ti(proportion of day * temperature * species)	Full data	-919537.4	0.136
8	Residual body mass	s(day length) + s(proportion of day)+ ti(day length * proportion of day) + ti(day length * species) + ti(proportion of day * species) + ti(proportion of day * day length * species)	Full data	**-926331.1**	**0.156**

Model 5: Residual body mass mean ~ s(day in season) + s(proportion of day) + ti(day in season * proportion of day): Results show a significant effect of *day in season* (*F = 1,307.42, p< 0.001*), *proportion of day* (*F = 21,777.04, p <0.001*) and the interaction between *day in season* and *proportion of day* (*F = 34.12, p <0.001*) on the *residual body mass* of birds. *Residual body mass* peaks in mid-winter and increases throughout the day (Figure 2.3). The variance explained when including the interaction is slightly higher at 15.1% . Models 4 and 5 were also fitted with *proportion of day* as a linear variable. Doing so increased the AIC value and did not change or lowered the amount of variance explained (Table 2.1), therefore the non-linear smooths were kept. Details of the linear models can be found in the Supplementary Materials section A.

Model 5 has a substantially lower AIC value than Model 4 and explains slightly more variance (Table 2.1). Figure 2.3 shows the interaction effect between *proportion of day* and *day in season* from the results of Model 5. Residual body mass is low in the morning and increases throughout the day. In mid-winter (late December), both the morning body mass and the evening body mass are higher than at other times of the year.

The predicted values from Model 5 were grouped by month and daily weight gain curves were created for each set of 2 months (Figure 2.4). The highest morning mass is observed from October through to January, with lower morning masses in March and February. The highest evening mass is observed in December and January, but differences over all are small. The line for December and January is steeper than for October and November, indicating faster weight gain rates in the colder months. However, March and February show a steeper incline. Again, the effect of the interaction only increases the variance explained by 0.1%, which is significant but very small.

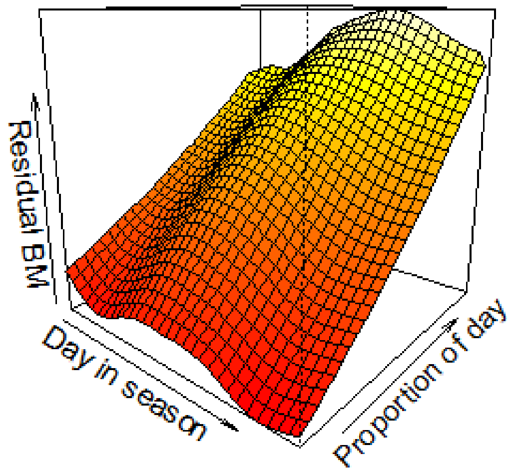

Figure 3.3. The interaction effect between "proportion of day" and "day in season" from Model 5. Yellow values indicate higher residual body masses and red values indicate lower residual body masses.

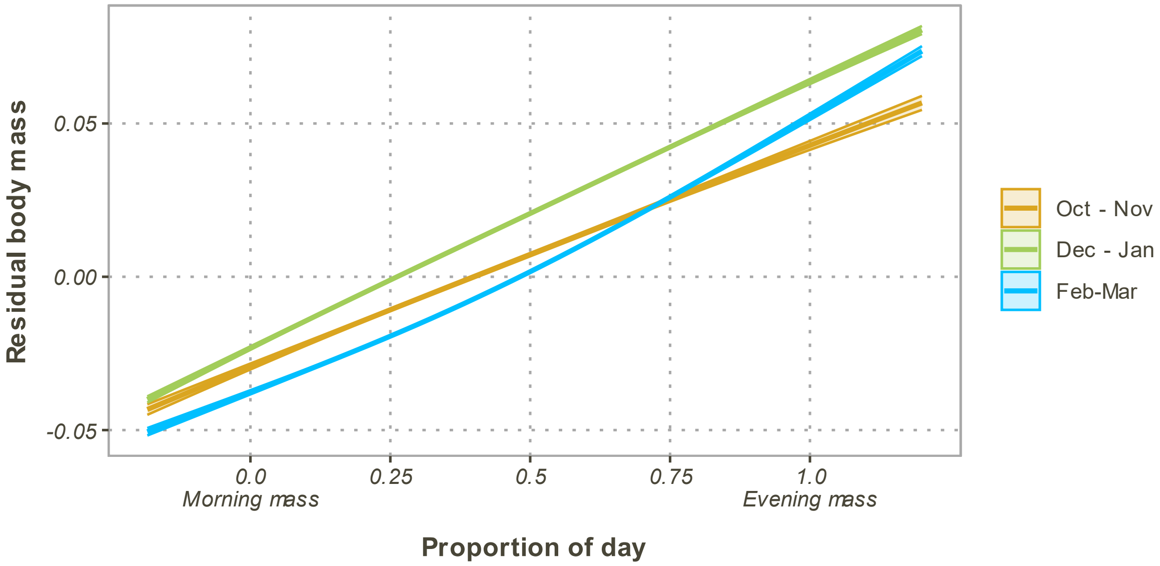

Figure 3.4. Daily weight gain curves split per month. Plotted lines are fitted values from Model 5 and CIs for the midpoint of each month. Residual body mass on the y-axis and the proportion of day on the x-axis.

3.4.2 Investigating the Differences Between Hoarders and Non-hoarders

Model 6: Residual body mass ~ s(day in season) + s(proportion of day) + ti(day in season * proportion of day)+ ti(day in season * species) + ti(proportion of day * species) + ti(proportion of day * day in season * species): In line with Model 5, Results show a significant effect of *day in season* ($F = 8.97, p < 0.001$) and of *proportion of day* ($F = 8{,}652.75, p < 0.001$). The two-way interaction between *day in season* and *proportion of day* also remains significant ($F = 13.69, p < 0.001$). This means that the effect of proportion of day is different on different days in the year.

There is a significant effect of the two-way interaction between *day in season* and *species*. The effect of *day in season* is different from the main effect of *day in season* for coal tits ($F = 7.07, p < 0.001$) and great tits ($F = 32.95, p < 0.001$), but not for blue tits. This means that the residual body mass in coal tits and great tits changes depending on the time of year in a species-specific pattern, different from the main effect of *day in season*. This is not the case for blue tits.

There is a significant effect of the two-way interaction between *proportion of day* and *species*. The effect of *proportion of day* is different from the main effect of *proportion of day* for blue tits ($F = 453.04, p < 0.001$), coal tits ($F = 27.72, p < 0.001$) and great tits ($F = 84.37, p < 0.001$). This means that the *residual body mass* in all three species changes depending on the time of year in a species-specific pattern, different from the main effect of *proportion of day*.

There is a significant effect of the three-way interaction between *day in season*, *proportion of day* and *species*. The interaction between *day in season* and *proportion of day* is significantly different from the two-way interaction between *day in season* and *proportion of day* for blue tits ($F = 6.41, p < 0.001$) and coal tits ($F = 3.31, p < 0.001$). The interaction effect between day in season and proportion of day is not significantly different from the general two-way interaction of day and proportion of day for great tits.

The current model explains 15.6% of the variance, which is more than Model 5. The AIC value for Model 6 is lower than for Model 5 (Table 2.1).

Figure 2.5 shows what the interaction effects between *day in season* and *proportion of day* look like for the three species. The larger morning mass for great tits early in the season stands out as well as the slightly lower and delayed seasonal peak in coal tits. Coal tits, also show a more concave-shaped daily weight gain curve, suggesting they gain weight later in the day.

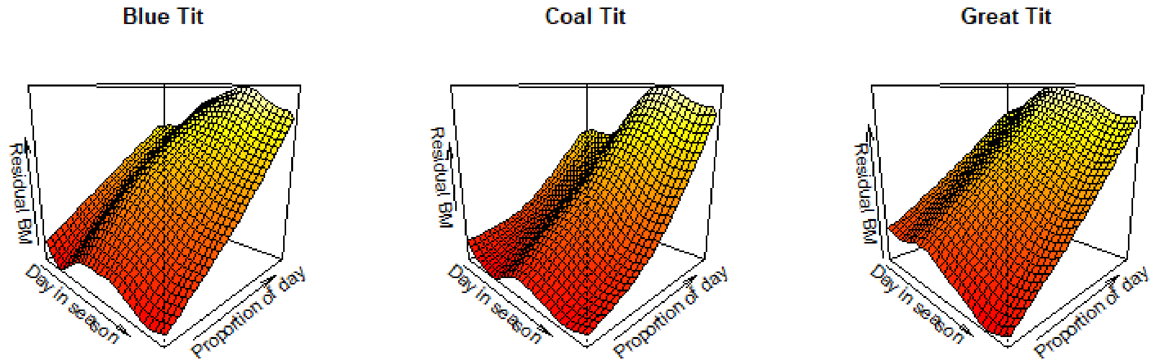

Figure 3.5. Interaction between proportion of day and day within season, split up by species (Model 6). Axes scales are the same across graphs.

Figure 2.6 shows the predicted values from Model 6, split up by species and by months of capture. Blue tits show a pattern as expected from true winter fattening, with the highest morning and evening mass in December and January and steeper slopes for the daily weight gain rates in those months as well. Coal tits stand out for their more concave daily weight gain curves, with similar morning and evening masses from December through to March. Great tits show the highest morning masses earlier in the season, with the lowest morning masses in February and March. In summary, the results from Model 6 indicate that there are differences between species regarding their winter fattening patterns, but that these are small and most variation in *residual body mass* is explained by the *proportion of day*.

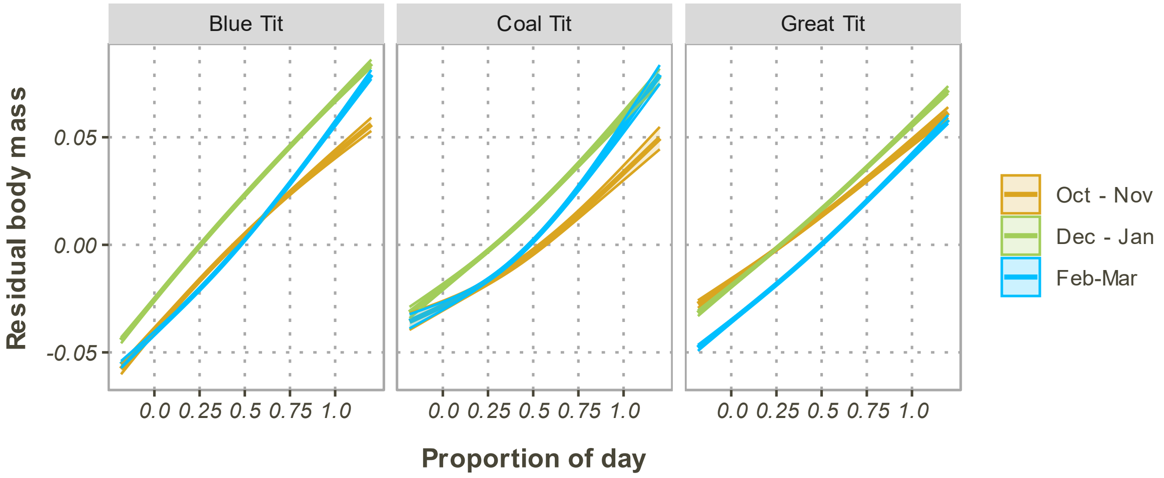

Figure 3.6. Daily weight gain curves split per month. Plotted lines are fitted values from model 6 and CIs for the midpoint of each month. Each panel includes one of the species. On the x-axes, 0.0 indicates the morning mass and 1.0 indicates the evening mass of the birds. Th residual body mass of birds is on the y-axes.

3.4.3 Drivers of Winter Fattening Patterns

Model 7: Residual body mass ~ s(temperature) + s(proportion of day) + ti(temperature * proportion of day) + ti(temperature * species) + ti(proportion of day * species) + ti(proportion of day * temperature * species): Results show a significant effect of *temperature* (*F = 465.19, p <0.001*), *proportion of day* (*F = 8,613.04, p<0.001*) and their interaction (*F = 10.47, p < 0.001*) on the residual body mass of birds. As temperatures decrease, the body mass of birds increases.

There is a significant effect of the two-way interaction between *temperature* and *species*. The effect of *temperature* on *residual body mass* is different from the main effect for blue tits (*F = 18.08, p < 0.001*), coal tits (*F = 10.30, p < 0.001*) and great tits (*F = 72.62, p < 0.001*).

There is a significant effect of the two-way interaction between the *proportion of day* and *species.* The effect of *proportion of day* on *residual body mass* is different from the main effect for blue tits (*F =449,97, p < 0.001*), coal tits (*F = 37.05, p < 0.001*) and great tits (*F = 53.71, p < 0.001*).

The three-way interaction between *proportion of day*, *temperature* and *species* is significant. The interaction between *proportion of day* and *temperature* is different from the two-way interaction effect for blue tits (*F = 4.51, p < 0.018*), coal tits (*F = 3.70, p < 0.025*) and great tits (*F = 8.62, p < 0.001*). This model explains 13.6% of the variation in residual body mass, which is less than Model 6. The AIC value for Model 7 is also higher than for Model 6.

Figure 2.7 shows a different shape interaction effect between *temperature* and *proportion of day* on the *residual body mass* of the three species. Under colder temperatures, coal tits have a lower overall *residual body mass* than other species. In addition, their daily weight gain curve is less steep and has a more concave shape than for the other two species. Blue tits and great tits show a larger daily increase in body mass with lower temperatures and a linear, steeper shape of the daily weight gain curve.

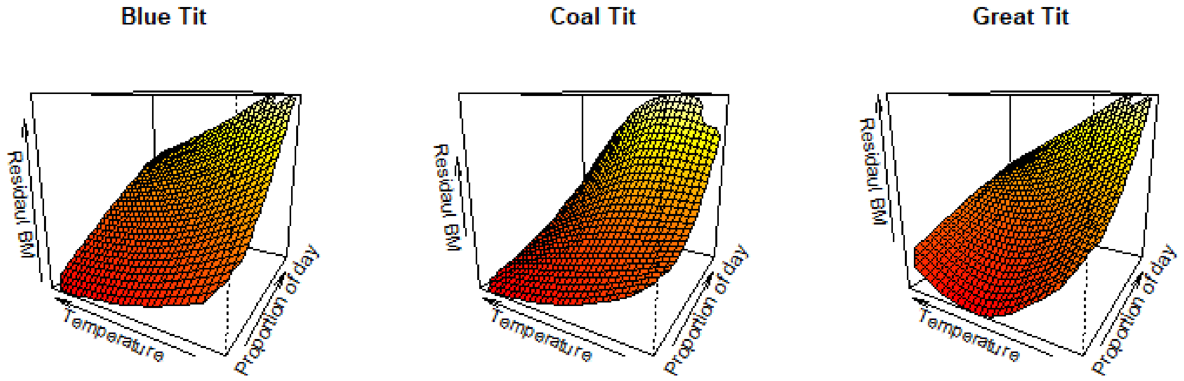

Figure 3.7. Interaction between temperature and the proportion of day, split by species (Model 7) Axes scales are the same across graphs.

Figure 2.8 further emphasises this, showing the daily weight gain curve of the different species, split up into different levels of 3-day average minima. In blue tits, the shape of the daily weight gain curve remains similar across the different temperature ranges, with higher residual body masses for lower temperatures. Coal tits, however, have more similar morning masses throughout, with steeper increases in body mass when it is colder. For great tits, the shape looks similar to that of blue tits, with the exception of the higher temperatures, under which these birds retain more weight in the morning.

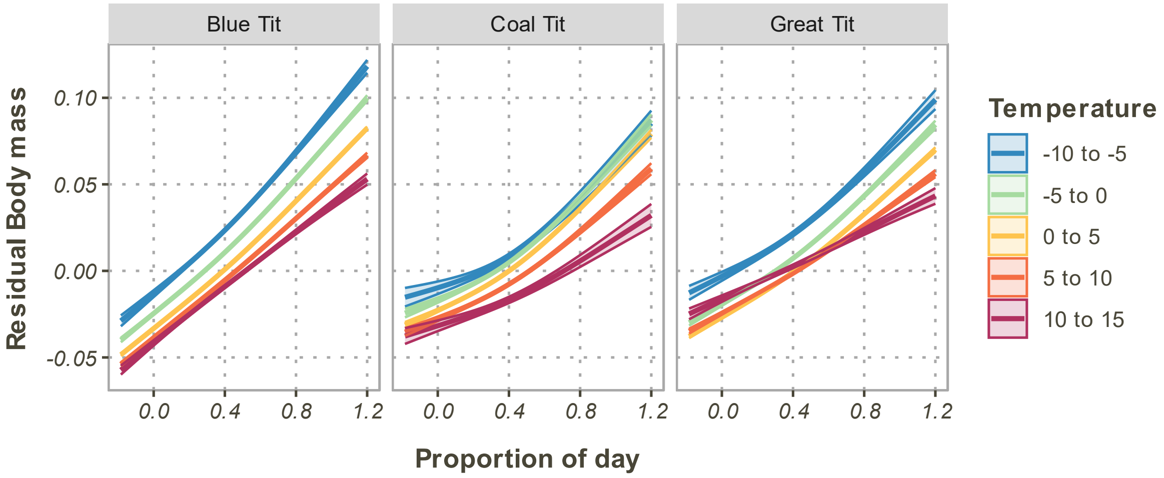

Figure 3.8. Daily weight gain curves split per temperature range. Plotted lines are fitted values from Model 7 and CIs for the midpoint of each temperature range. Each panel includes one of the species. Temperatures are in degrees Celsius. On the x-axes, 0.0 indicates the morning mass and 1.0 indicates the evening mass of the birds. The residual body mass of birds is on the y-axes.

Model 8: Residual body mass ~ s(day length) + s(proportion of day) + ti(day length * proportion of day) + ti(day length * species) + ti(proportion of day * species) + ti(proportion of day * day length, species): Results show a significant effect of *day length* ($F = 2,580.41$, $p < 0.001$), *proportion of day* ($F = 7,726.36$, $p < 0.001$) and their interaction ($F = 3.46$, $p = 0,005$) on the *residual body mass* of birds. As days get shorter, the body mass of birds increases.

The two-way interaction between *day length* and *species* has a significant effect on residual body mass. The effect of *day length* on *residual body mass* is different from the main effect of *day length* for blue tits ($F = 74.93$, $p < 0.001$), coal tits ($F = 54.58$, $p < 0.001$) and great tits ($F = 10.73$, $p = 0.009$).

The two-way interaction between the *proportion of day* and *species* has a significant effect on the residual body mass. The effect of *proportion of day* is different from the main effect of *proportion of day* for blue tits ($F = 496.41$, $p < 0.001$), coal tits ($F = 34.37$, $p < 0.001$) and great tits ($F = 84.38$, $p < 0.001$).

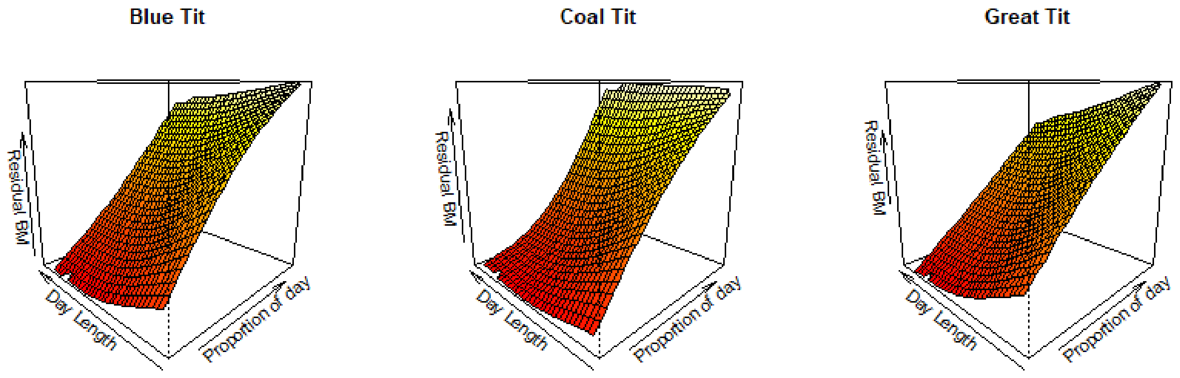

Figure 3.9. The interaction between day length and proportion of day, split by species. Predictions from Model 8. The axes scales are the same across graphs.

The three-way interaction between *proportion of day*, *day length* and *species* has a significant effect on residual body mass. The effect is different from the two-way interaction between *proportion of day* and *day length* for blue tits ($F = 5.08$, $p = 0.006$) and coal tits ($F = 4.68$, $p = 0.008$), but not for great tits ($F = 5.11$, $p = 0.050$).

Figure 2.9 shows the interaction between *day length* and *proportion of day* for each of the species. The patterns for blue tits and great tits look similar, with strong increases in morning mass when days are shorter. Coal tits, on the other hand, do not increase their *residual body* *mass* as much on shorter days. Their daily weight gain curve on short days also takes a more convex shape than the linear pattern of the other species. Figure 2.10, more specifically shows the concave shape of the daily weight gain curves on longer days in coal tits, as well as the more smaller differences in morning and evening mass for coal tits at different day lengths. blue tits and great tits show similar, more linear patterns.

Model 8 explains 15.6% of the variation in residual body mass and has the lowest AIC value of all fitted models. However, it remains important to note that the increase in variation explained after adding *proportion of day* as a variable, was extremely small.

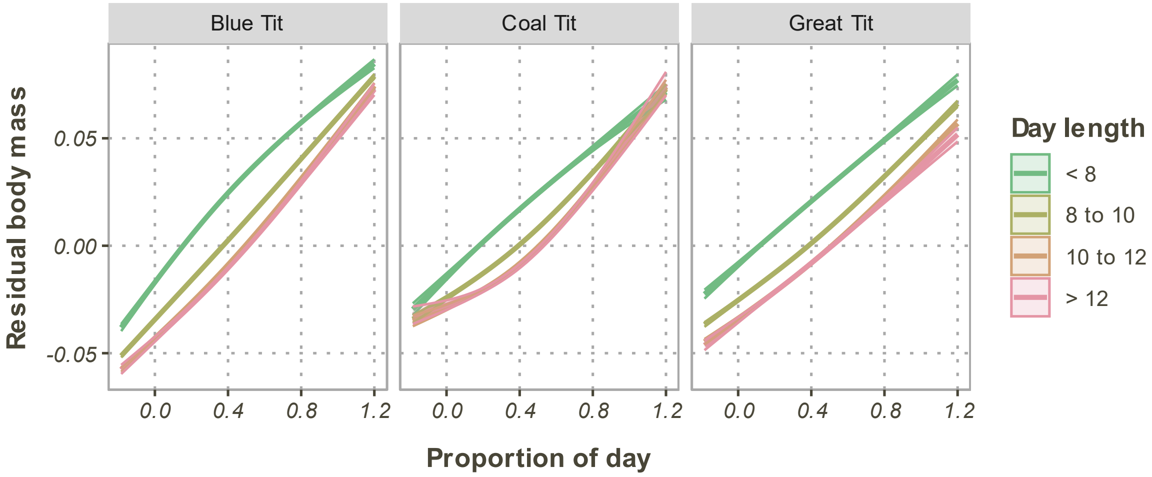

Figure 3.10. Daily weight gain curves split per day length range. Plotted lines are fitted values from Model 8 and CIs for the midpoint of each day length range. Each panel includes one of the species. On the x-axis, 0.0 indicates the birds' morning mass and 1.0 indicates the birds' evening mass.

3.5 Discussion

3.5.1 Patterns of True Winter Fattening

The results of Models 1, 2 and 3 show that, in line with my first hypothesis, birds increase their *residual body mass* in autumn, with a peak in winter and a decline towards spring. This increase is present in morning, evening and mean mass (Figure 2.2). These results are in line with the formal model of "true winter fattening" as originally suggested by Lehikoinen (1987).

Including the *proportion of day* (Model 4 and 5) into my models, substantially increased the explained variance (Table 2.1), suggesting that the variation in body mass due to daily weight gain cycles outweighs that caused by the seasonal cycle in weight gain. Both the main and interaction effects of *day within season* and *proportion of day* were significant, indicating that the shape of the daily weight gain curve changes throughout the year. Figure 3.4 indicates slightly steeper curves for the winter months, but this pattern does not remain in February and

March. Thus, my results generally align with the concept of "true winter fattening,", although the effect size of the increased winter amplitude is small.

3.5.2 Investigating Differences between Hoarders and Non-hoarders

Model 6 reveals a significant effect of species on winter fattening patterns. Coal tits display a concave-shaped daily weight gain curve, in contrast to the more linear curves observed in the other two species (Figure 3.5 and Figure 3.6). This suggests that coal tits may gain weight more rapidly later in the day, whereas non-hoarding species maintain a consistent rate of increase throughout the day. These findings align with Optimal Body Mass theory, which proposes that while larger fat reserves reduce starvation risk, they also come with costs. Coal tits, having more reliable food sources and thus a lower risk of starvation, may be able to delay weight gain until later in the day, avoiding the costs of maintaining higher fat reserves (Hurly, 1992; McNamara, Houston, Krebs, et al., 1990; Polo et al., 2007). However, these results differ from some other observations of wild birds, where hoarding species gain mass earlier in the day than non-hoarding species (Lilliendahl, 2002). It is possible that the birds in the latter study, conducted in Sweden, faced harsher conditions than those at lower latitudes in Spain, Scotland, and England (Hurly, 1992; Polo et al., 2007). The harsher environment may have driven the Swedish birds to accumulate mass earlier in the day in order to reach a higher evening mass and mitigate their higher starvation risk.

My findings also show a smaller seasonal increase in body weight for coal tits compared to the other species (Figure 2.5). This supports our prediction that coal tits may not need to increase their fat reserves as much in winter, given their reliance on food hoards. Similarly, the size of the daily weight gain amplitude is slightly smaller in coal tits than in the other species. However, the seasonal change in amplitude is not different (Figure 2.6). It is important to note that these differences are small and may not be biologically relevant. This very small effect size, together with differences in temperature and food availability between observation sites, could explain the mixed results in previous studies regarding the seasonal increase in body mass among hoarding birds (Broggi et al., 2003; Cooper, 2007; Haftorn, 1989; Nip et al., 2018; Petit et al., 2014).

In summary, despite the small effect sizes, my results generally support the hypothesis that winter fattening patterns in coal tits are less pronounced than in non-hoarding tit species, though the differences are small.

3.5.3 Drivers of Winter Fattening Patterns

Model 7 shows that *temperature* significantly affects *residual body mass*, with the relationship varying across species. Lower temperatures in the three nights preceding capture resulted in higher residual body mass (Figure 2.7 and Figure 2.8). These findings are consistent with my prediction that short to medium-term temperature negatively correlates with fat reserves. In colder temperatures, birds are likely to increase their reserves to offset higher energy expenditures during cold nights (Gosler, 2002; Lilliendahl et al., 1996; Rogers & Reed, 2003). However, this pattern is less pronounced in coal tits, whose residual body mass does not increase as much under colder conditions as it does in the other species (Figure 2.7). This finding also aligns with my expectations, as hoarding birds, with more predictable food sources, are expected to have smaller energy reserves in response to colder temperatures (McNamara, Houston, Krebs, et al., 1990; Polo et al., 2007). Coal tits also exhibit a more concave daily weight gain curve compared to the other species, in line with the results of Model 6 (Figure 2.8).

Model 8 demonstrates that *day length* significantly affects *residual body mass* and its interactions with species and the *proportion of day*. As anticipated, *day length* negatively correlates with *residual body mass*, suggesting that birds respond to shorter days by increasing their body mass. Figure 2.9 illustrates that coal tits experience less pronounced changes in morning and evening mass compared to blue tits and great tits. Similarly, the effect of *day length* on evening mass is less pronounced in coal tits than in the other two species. Figure 2.10, confirms more concave daily weight gain curves for coal tits, especially on longer days. On shorter days, when nighttime energy consumption is high, coal tits cannot delay weight gain and show more linear curves.

Day length is a slightly better predictor of residual body mass than *Day in season* (Table 2.1*)*. This may be because birds were captured across various latitudes within the UK, meaning that the same day in the season could correspond to different day lengths depending on the location. As a result, *day length* may offer a better predictor of *residual body mass* than *Day in season*.

Day length is a better predictor of *residual body mass* than *temperature* and explains more of the variation in *residual body mass* across the season (Table 2.1). These observations are in line with findings by Rintamaki et al. (2003) and Haftorn (1989), whose analyses of seasonal and diurnal body mass patterns in titmice also suggested that photoperiod is a better predictor of body mass fluctuations than temperature. My findings suggest that tits might be adapted to respond to day length cues when increasing their fat reserves for winter instead of responding to recent temperatures. The results of Model 7 suggest that birds do adjust their body mass om response to local temperatures, potentially allowing them greater flexibility in adapting to current conditions compared to relying solely on day length. However, since *temperature* and *day length* are correlated, particularly during the early months of the season, this correlation could explain the significant effect observed.

In summary, *day length* is a better predictor of *residual body mass* than *temperature* and likely shapes the overall pattern of winter fattening. At present, it remains unclear whether temperature adds additional explanatory power, as the correlation between temperature and day length prevented both variables from being included in the same model.

3.5.4 Limitations and Future Work

Unlike most studies that rely on either lab recordings or birds trained to visit specific feeders, my research used data collected by citizen scientists. While participants in the BTO ringing scheme are highly trained and experienced, data collection by multiple individuals likely led to less standardised measurements of biometrics compared to other studies in the literature. We addressed this by filtering out unreliable records, such as biologically implausible weights and wing lengths or observations made at odd hours. However, these factors may still contribute to the large unexplained variance in our models. Additional factors which we were not able to control for, such as the sex, age, and dominance status of the birds may also contribute to this variance. For instance, dominant titmice are known to have larger fat reserves than their subordinate counterparts, which may influence winter survival (Ekman & Lilliendahl, 1993; Koivula et al., 1995).

Temperature is a complex variable that can be measured across different timescales. In this study, I used a 3-day average of nightly minima to represent the temperatures recently experienced by the birds. Other studies have used different measures, such as the "current" temperature, temperatures of 5+ hours before capture, or daily averages (Bednekoff et al., 1994; Broggi et al., 2019; Gosler, 2002). Some of these, such as the “current temperature” birds are experiencing, are expected to have opposite effects on the birds’ fat reserves, such as current temperatures restricting the bird's body mass (Gosler, 2002). Averaging across longer periods may obscure short-term effects, suggesting that other temperature measures, such as daily maxima or hourly readings, might better predict residual body mass than my 3-day average.

Finally, a possible limitation of this study could be the use of residual body mass as a proxy for the fat reserves of the birds. Body mass can vary for reasons other than fat accumulation, as bird composition changes seasonally (Petit et al., 2014). Ideally, fat scores, which are taken by visually inspecting the birds' fat deposits in the furcular and abdominal areas, would be used as an index of fat reserves (British Trust for Ornithology, 2024; Kaiser, 1993). However, 83% of the cleaned dataset did not contain information about the fat scores of the birds. Alternatively, in their review of bird body mass indices, Labocha and Hayes (2012) suggest that absolute body mass is a reliable proxy for fat reserves in most bird species. To enable me to compare species, I opted to use body mass corrected for wing length as a proxy, after log transforming both variables (Labocha & Hayes, 2012; Schamber et al., 2009). An analysis of a subset of our data that does contain fat scores shows that the resulting *residual body mass* variable is more strongly correlated with fat scores than absolute body mass (see supplementary materials).

Future research should explore the parallel roles of temperature and day length, particularly in the last three months of winter, when the correlation between day length and temperature diminishes. During this period, their effects on body mass can be examined independently to determine whether responses to temperature enhance the birds' flexibility in adapting to environmental conditions, potentially reducing their risk of starvation, or if our findings can be solely explained by day length as a driving factor. Further exploration of the relationship between day length, temperature, and body mass throughout January, February, and March would be a valuable avenue for research.

3.5.5 Conclusion

From my results, I conclude that patterns of true winter fattening are observed in tit species across the UK. Fat reserves increase in the winter months, and the amplitude of the daily weight gain curve increases slightly. The largest amount of variation in body mass is, however, explained by daily weight gain changes. Differences arise between species, with hoarding coal tits displaying less pronounced patterns of winter fattening, with more concave daily weight gain curves. Finally, the results suggest that day length is more important as a driving factor behind winter fattening patterns than recent temperatures.

Part II: Hoarding Motivation

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Chapter 3. Using Citizen Science to Understand the Drivers of Hoarding Motivation in Titmice

5.1 Abstract

Winter survival poses significant challenges for small tit species at high latitudes, where colder temperatures coincide with long nights and limited foraging opportunities. Several *Paridae* species have evolved hoarding behaviour, caching surplus food during autumn to sustain themselves through the resource-scarce winter months. Research indicates that hoarding activity peaks in autumn, with a subsequent decline in intensity as winter progresses. This autumn peak may result from heightened hoarding motivation influenced by factors such as day length, photoperiodic state, food predictability, and temperature. Alternatively, it has been hypothesised that hoarding motivation remains high throughout winter but is constrained by reduced food availability. In this chapter, I test this hypothesis by examining the hoarding behaviour of titmice under food-supplemented conditions. Citizen scientists across the UK and North America contributed observations of hoarding and eating behaviours in chickadees and titmice at garden feeders. This extensive dataset of wild, food-supplemented birds was analysed to assess the influence of food availability on hoarding patterns. Additionally, I investigated whether day length and temperature affected hoarding intensity. My findings reveal an autumn peak in hoarding intensity for species in both the UK and North America. Interestingly, these peaks occurred slightly later than previously reported in studies of non-supplemented birds, suggesting that consistent food availability may shift hoarding activity closer to periods of greatest energy demand. Alternatively, the delayed peak may reflect high rates of disappearing behaviour in early autumn. A significant effect of day length on hoarding intensity was identified in the North American dataset but not in the UK data, while no significant effect of temperature was observed.

5.2 Introduction

5.2.1 Seasonal Hoarding Patterns

Winter is a challenging time for small tit species that reside at northern latitudes throughout the year. Not only is food scarcer during this time, but shorter days limit the time available for foraging. On top of these increased difficulties with finding food, the energy requirements of birds increase due to the lower temperatures. Birds have evolved energy management and behavioural strategies to survive these challenging conditions. One such strategy, which can be found in some *Paridae* species, is “food hoarding”. This behaviour allows birds to store surplus food when it is temporarily abundant and retrieve it later, providing a stable and predictable food supply during periods of scarcity.

Titmice and chickadees are two groups of hoarding *Paridae*, that cache their food and use it on two timescales. On a day-to-day basis during autumn and winter, birds recover cached items that they hoarded either the same day or a few days before (Brodin, 1992). Hoarding behaviour also follows a seasonal pattern. During spring and summer, birds primarily feed on insects and are rarely observed to store food. However, as autumn approaches, their diet shifts predominantly to seeds, and hoarding intensity increases, peaking in autumn and gradually decreasing into winter (Brodin, 1994c, 2005; Haftorn, 1956; Lange et al., 2022; Pravosudov, 2006). The exact timing of this peak in hoarding behaviour varies by location and study. For example, in Scandinavia, hoarding begins in August, peaks in September, and decreases through October and November (Brodin, 1994c). Further south, in Japan, willow tits exhibit a similar autumn peak, though slightly later in October. This study also reported some hoarding in February and March but did not collect data in December and January (Nakamura & Wako, 1988; Pravosudov, 2006). Additionally, Brodin et al. (1996) found that southern populations of willow tits peaked in hoarding later than northern populations. Birds observed in Sweden and Finland showed the highest hoarding intensities in September-October, whilst birds observed in Belgium peaked in October-November. A secondary peak in hoarding has also been reported in spring during mast years (Haftorn, 1956; Lange et al., 2022; Pravosudov, 1985, 2006). Overall, these studies indicate that hoarding birds intensify their caching efforts in autumn, with significantly less caching activity observed during the adjacent summer and winter months (e.g., June and January), although data for these periods remains limited.

The total number of food items stored by a single bird during the autumn peak ranges between 50,000 and 150,000 in mast years when food availability is high (Haftorn, 1956; Pravosudov, 1985). In non-mast years, however, the estimated number of food items stored by a single willow tit is around 46,000 (Brodin, 1994c). This large number of items cached in autumn forms an important part of the winter diet, as most are retrieved during the colder months (Brodin, 1994c; Grubb & Pravosudov, 1994; Haftorn, 1956; Pravosudov, 1985). Brodin (1994) calculated that nearly all food consumed by Swedish willow tits in December was originally stored in autumn, and about 24% of food consumed from January through March had been hoarded. These figures are expected to be even higher during colder winters, with up to 45% of all winter food coming from hoarded supplies.

Given the importance of food cached during the autumn peak for winter survival, it is plausible that hoarding motivation evolved to be high in autumn and low during summer. This raises the question: what cues drive the increased hoarding motivation in autumn?

5.2.2 Photoperiodic States and Photoperiod

One factor that has been suggested to drive hoarding behaviour, is the photoperiodic state of the birds. The reproductive cycle of *Paridae* species is regulated by photoperiod (e.g. the number of daylight hours in the day). The amount of daylight the birds are subjected to affects their behaviour and physiology throughout the year, as they cycle through three photoperiodic states. In winter and spring, birds are in a photosensitive state, where they are sensitive to the imminent increase in day length. Once day length reaches a critical length, birds become photostimulated, triggering the release of gonadotropic hormones and eventually sex hormones that stimulate reproductive behaviours. After prolonged exposure to longer days, birds enter a photorefractory state, becoming unresponsive to further increases in daylight. Here, birds no longer reproduce and moult takes place. When birds are exposed to shorter days they return to a photosensitive state (Phillmore & MacDougall-Shackleton, 2007).

Because photoperiodic state is important in the regulation of the reproductive cycle of titmice and chickadees, researchers have suggested that it could be linked to the seasonal patterns in hoarding behaviour as well. Shettleworth et al., (1995) tested this with Black-capped Chickadees captured in March. Half of the birds were subjected to short days and low temperatures. The other half was kept on longer days and high temperatures, before returning them to shorter days (mimicking the “normal” year). The group kept on long days moulted when they were back on shorter days, which indicates they entered a photorefractory state. Once on shorter days, both groups showed hoarding behaviour, but the birds that had gone through the longer days and had become photorefractory, stored more than the birds that were kept on shorter days and had not moulted. These results were corroborated by Krebs et al. (1995) and suggest that the onset of hoarding behaviour might be regulated by photoperiodic state. However, the authors did not report the photoperiodic state of the birds as indicated by the gonadal state, and temperatures varied between the long and short-day groups. This makes it difficult to conclude whether it was the photoperiod itself (e.g. number of daylight hours), the photoperiodic state of the birds, or the temperature differences causing this effect. Moreover, when the same experiment was repeated with birds captured in November, which had already started hoarding, the changes in photoperiod did not affect hoarding intensity (Shettleworth et al., 1995). In a similar experiment with marsh tits, researchers eliminated the effect of temperature and found concurrent results. Hoarding intensity was higher in birds kept on shorter days than in birds kept on longer days (Clayton & Cristol, 1996).

To further investigate if these effects are due to changes in the number of daylight hours, or the photoperiodic state of the birds, MacDougall-Shackleton et al. (2003) tested Black-capped Chickadees in a photosensitive state (short days for a long time), in a photorefractory state (long days for a long time) and birds that were switched from short to longer days (photostimulated). They found that birds kept on shorter days hoarded more than birds kept on longer daylight hours. Birds kept on long days, regardless of whether they were photostimulated or photorefractory, hoarded less intensely (MacDougall-Shackleton et al., 2003). This shows that day length, regardless of photoperiodic state might be the driver of seasonal patterns in hoarding behaviour.

5.2.3 Food Availability and Predictability

From the above studies, it is clear that the shortening of days triggers birds to store more food. These findings, however, do not necessarily mean that food storing is directly regulated by daylight. It could simply be that birds have different energy budgets on shorter days, causing them to hoard more.

For example, it has been suggested that birds have less time to forage on short days whilst having larger energy consumption during the longer nights, effectively making them food-restricted (Phillmore & MacDougall-Shackleton, 2007). Birds kept under unpredictable food regimens increase their hoarding frequency over birds kept under more predictable circumstances, even if the total amount of food available is kept constant (Hurly, 1992). This effect of food restriction and unpredictability holds up in other studies, irrespective of the bird's body condition, temperature or photoperiod that birds are exposed to (Pravosudov & Grubb, 1997). On a physiological level, mountain chickadees with artificially moderately increased corticosterone levels, a hormone normally associated with hunger or unpredictable food environments, have been shown to increase hoarding (Pravosudov, 2003). Karpouzos et al. (2005) attempted to distinguish between the effects of available foraging time and photoperiod, by keeping birds in an environment with long days and *ad libitum* food, short days with *ad libitum* food, as well as an environment with long days, but food availability for as long as during the shorter days. They found no effect of either day length or food availability on the hoarding frequency of the birds. However, it is important to note here that the birds were kept at 19 °C throughout the entire experiment, which is a high temperature for birds going through simulated autumn/winter circumstances. Therefore, it may be that although days or food access were short, the overall energy usage of the birds was low at night.

In addition, the assumption that shorter days cause more unpredictable or food-restricted circumstances is not always true. During early autumn and late spring, when peaks in hoarding are observed, birds generally have access to abundant food resources (e.g. the seeds available in autumn). If the unpredictability or lack of food is the only factor to trigger or drive hoarding behaviour, hoarding peaks would be expected in winter, when food is most unreliable, and not in autumn when it is abundant.

5.2.4 Temperature

Few studies have specifically examined the effects of temperature on hoarding intensity. In their original study on the effect of photoperiod on hoarding, Shettleworth et al. (1995), also varied temperatures, with shorter days accompanied by lower temperatures. It is possible, therefore, that the observed increase in hoarding frequency with shorter days was partly influenced by temperature changes. However, the authors noted that the hoarding patterns were very similar to other behaviours known to be regulated by photoperiod, suggesting temperature may not have played a significant role. This view was supported by Clayton & Cristol (1996), who observed that birds kept on long days began hoarding immediately after being exposed to short days, regardless of previous temperature drops. When the role of temperature was directly investigated, lower temperatures were found to correlate with higher caching rates (Pravosudov & Grubb, 1997). These findings suggest that temperature could influence hoarding behaviour, though other factors, such as photoperiod, may also contribute.

5.2.5 Energy Balance

Finally, it has been proposed that the "energetic state" of a bird plays a key role in regulating hoarding behaviour. In their model, Lucas and Walter (1991) predicted that in environments where the risk of starvation is low, lighter birds would hoard more, while heavier birds would prioritize other, non-foraging, activities. In high-risk environments, birds with lower body mass should focus on consuming food immediately, whereas birds with higher fat reserves might hoard to mitigate future starvation risk. Their experiments on Carolina chickadees supported this, showing that birds with higher fat levels were less likely to store food than lighter birds when food was abundant. While they varied the feeding schedules, no effect was found on hoarding intensity based on the frequency of feeder access. Similarly, studies on the more immediate effects of energy balance have shown that hunger reduces caching frequency in Tufted titmice (Lucas et al., 1993). These findings suggest that the bird's energetic balance, arising from the interaction between environmental factors (e.g., food availability) and the bird's internal state (e.g., fat reserves and hunger), affects hoarding intensity.

So, where does this leave us? The evidence discussed in the previous sections suggests that hoarding frequency increases with shorter photoperiods, is influenced by food availability and predictability, increases with lower temperatures, and is affected by the bird's energetic state. In practice, disentangling these factors is challenging, as environmental conditions (such as temperature, photoperiod, and food distribution) and the bird's physiological state (hunger and fat reserves) all affect its energy balance. Thus, birds may be responding to their energy balance as an indicator of past food availability and predictability, which also incorporates environmental influences (Lange et al., 2022; Pravosudov, 2006).

A possible mechanism for this has been suggested in research on hoarding mammals. In Siberian hamsters, the intensity of hoarding, or 'hoarding motivation,' is thought to respond to the animal's 'energy flux' rather than immediate indicators of starvation risk. This suggests that the triggers for hoarding behaviour are not directly tied to fat reserve levels or hunger, but are instead linked to signals from the energy being released for use in the body (Day & Bartness, 2001; Keen-Rhinehart et al., 2010). Signals for energy release may come from central neuropeptides, metabolic hormones, or other factors involved in transferring stored metabolic fuels from reserve tissues to sites of oxidation. These are, for example, hormones and peptides associated with the breakdown of glycogen into glucose before oxidation in muscles, or with triglycerides undergoing lipolysis and entering the bloodstream as free fatty acids to be transported to muscle and liver tissues. This theory explains why hamsters that reduced their body fat, were food-restricted, or those that increased foraging effort without fat loss, were shown to increase their hoarding intensity. In each case, energy is being mobilised (adipose tissue or glycogen), driving the increased motivation to hoard (Keen-Rhinehart et al., 2010).

If food hoarding motivation in *Paridae* is regulated similarly, with increased motivation during periods of high energy flux away from fat reserves, this could help explain the hoarding patterns observed in the wild. As days shorten and temperatures drop in autumn, birds require more energy to maintain their body temperature, especially at night when they cannot forage. This combination of lower temperatures and prolonged periods without foraging leads to increased mobilization of adipose tissue, increasing the 'energy flux' in the bird. This heightened energy consumption, or "flux" will lead to a greater motivation to hoard during autumn and winter. In contrast, in late spring and summer, birds have lower energy fluxes causing their hoarding motivation to drop (Lange et al., 2022). This theory might also explain the lack of response to shorter day lengths noted by Karpouzos et al. (2005). It is possible that the combination of high temperatures and ad libitum food provided, even when given in short intervals, did not create a sufficient energy flux at night to trigger a change in hoarding behaviour.

5.2.6 Why does hoarding decrease in winter?

The evidence from the captive studies discussed above suggests that hoarding motivation could be regulated by changes in the birds' energy balance. As conditions become more challenging in autumn, with longer nights and lower temperatures, the heightened energy flux increases their motivation to hoard. However, despite facing similarly harsh or even worse conditions in winter, hoarding behaviour tends to decline (Brodin, 1994c; Pravosudov, 2006). What, then, causes this decrease?

One hypothesis addressing this apparent paradox is that food availability may become a limiting factor during winter. Although birds remain highly motivated to hoard due to their elevated energy flux, they may only find small amounts of food during the short winter days. Some evidence supports this hypothesis. A study on two captive willow tits showed that, under constant food availability, birds reached their hoarding peak in November-December, around the time when nights are the longest (Ludescher, 1980). In winter under natural conditions, consuming food items takes priority over hoarding, as birds need to establish sufficient fat reserves in preparation for the long nights. This is highlighted by the fact that hoarding birds rely heavily on cached items during winter, with up to 45% of their diet coming from these stores (Brodin, 1994c; Grubb & Pravosudov, 1994; Haftorn, 1956; Pravosudov, 1985). This suggests that birds are short of food in their environments and food items found will be consumed rather than hoarded.

5.2.7 Study Aims

In this study, I aim to test the hypothesis that hoarding motivation peaks in mid-winter and that patterns observed in the wild are due to limited food availability. I do this by investigating the seasonal patterns in hoarding intensity of chickadee and titmice species under food-supplemented circumstances (Broggi et al., 2021). Where most previous studies have used either observations of wild birds (Brodin, 1994c, 2005; Haftorn, 1956; Lange et al., 2022) or experimental data from captive birds (Karpouzos et al., 2005; Krebs et al., 1995; MacDougall-Shackleton et al., 2003), I developed a citizen science project where volunteers across the UK and North America collected data about the birds that visited their garden feeders. Volunteers reported if birds were seen looking for hoarding sites, eating, or flying out of sight after picking up food items from a feeder. This resulted in a large dataset on wild birds under food-supplemented circumstances, allowing me to investigate if food availability influences hoarding behaviour in *Paridae* species.

I predict that birds that have constant access to food from feeders shift their hoarding peak to the shortest day of the year when energy consumption at night, and therefore the energy flux away from storage, is the highest. Furthermore, exploratory analyses are performed to investigate the effects of day length, temperature and latitude on seasonal hoarding patterns.

5.3 Methods

5.3.1 Ethics and GDPR

This study was approved by the Animal Welfare & Ethical Review Body (ID: 930) and the FMS ethics team (No. 17347) at Newcastle University, UK. The collection and processing of personal data in this study was carried out in accordance with the EU General Data Protection Regulation (GDPR).

5.3.2 Pilot

The pilot study for this project had two primary goals. Firstly, I sought to gather feedback on the data collection protocols and the online materials provided to volunteers. This feedback helped to refine and improve the volunteer resources for future data collection seasons. Secondly, I aimed to collect preliminary data to guide our data analysis plans and identify any potential issues related to data quality.

Volunteers for the pilot study were recruited in January 2022 in collaboration with the BTO (British Trust for Ornithology), the NHSN (Natural History Society of Northumbria) and the FeederWatch project (Cornell Lab of Ornithology). Through their newsletters, I identified volunteers able to ID and observe birds in their gardens, asking them for help to try out and refine the study protocols. In addition, an outreach video about the study was produced as part of the NSHN 1829 nature talks. A total number of 134 volunteers signed up to the pilot study of which 60 actively engaged with the materials.

Data collection took place between February and April 2022. Volunteers who signed up received the initial version of the volunteer information packs and were asked to read these and attempt to use them in their gardens. Volunteers reported species that visited their garden feeders and which behaviours they performed. The behaviours were logged as “eating” the food item that the bird found, “attempting to hoard” the item and combinations of the two. If the bird went out of sight, this was logged as “disappear”. Throughout the pilot study volunteers were able to leave feedback through an online form or via direct email. Messages were collected and compiled to inform further refinement of the study and volunteer materials. Table 5.1 shows the most commonly received feedback and which actions were taken to solve the issues.

Table 5.1. Overview of the most commonly received feedback during the pilot study, summarised by topic. For each issue, the corresponding action taken is indicated.

#	***Topic***	***Description***	***Action taken***
1	Finding coordinates	In the sign-up form, volunteers were asked to provide us with their coordinates, so I could match any observations to their location. This can be difficult for participants who are not used to Google Maps or similar software. Volunteers shared that this was difficult and that some of them ended up asking family members for help or looking it up online. This was common, especially with people using tablets or mobile phones.	Clearer instructions on how to find the coordinates in the new sign-up form were provided. Additionally, I now provided 2 sets of instructions, one for people on desktops/laptops and one for people using mobile devices/tablets. Finally, I embedded a YouTube video in the form, for participants to follow along. Finally, we provided an alternative website (https://www.maps.ie/coordinates.html) that helps volunteers look up their coordinates.
2	Not receiving information	Volunteers were put on a mailing list if they became part of the project. Some participants indicated that there were issues and that they were not receiving the emails. Outside the university network, emails from my mailing lists tended to be registered as spam.	I no longer use the mailing list system and just email the group of registered volunteers. Volunteers that unsubscribe are manually taken off this list.
3	Time spent on study	Volunteers indicated they did not know how much time they had to spend on the study. It was unclear to them how often they should log behaviours and for how long the study would run.	I updated information on how much time to spend on the study, asking volunteers to aim at 30-60 minutes per week, regularly. Start and end dates were also communicated more clearly and more often.
4	Hoarding definition	Participants indicated that they were unclear about what exactly ‘hoarding’ behaviour was and when to log it.	The definitions of ‘hoarding’ / ‘searching for hoarding spot’ were clarified further. See feedback issue #5.
5	Focus on hoarding observations	Volunteers tended to focus on hoarding behaviours and species only, whilst I was aiming to get an overview of what happens and how this might change throughout the year. They tend to only log hoarding behaviours or even tell me are leaving the study because they only see disappearing birds.	My new volunteer guidelines contain clearer instructions on the behaviours, providing more guided examples. In addition, I changed the way in which the study is presented. I now focus more on all species (hoarding and non-hoarding) and on how these birds behave at the feeders. Hoarding behaviour is now labelled as ‘searching for hoarding spots’ instead of ‘hoarding’ itself. The differences between ‘searching for a hoarding spot’ and ‘eating’

			behaviour are explained in detail. In this way, people are less focussed on hoarding but still will report behaviours that would be classified as hoarding attempts.
6	Data form design	Volunteers reported that the data form can be repetitive and take long to fill in, especially when they are observing lots of birds. Some pointed out that it is cumbersome to transfer data from the paper they write on whilst watching to the computer.	I adjusted the online data forms so that some fields could use auto-fill (date, time). For this, I switched the software from Jisc Online Surveys to Qualtrics. With help from a software developer, I also developed a mobile application, which allows volunteers to report birds directly whilst watching their feeder, without the need of a computer nearby.

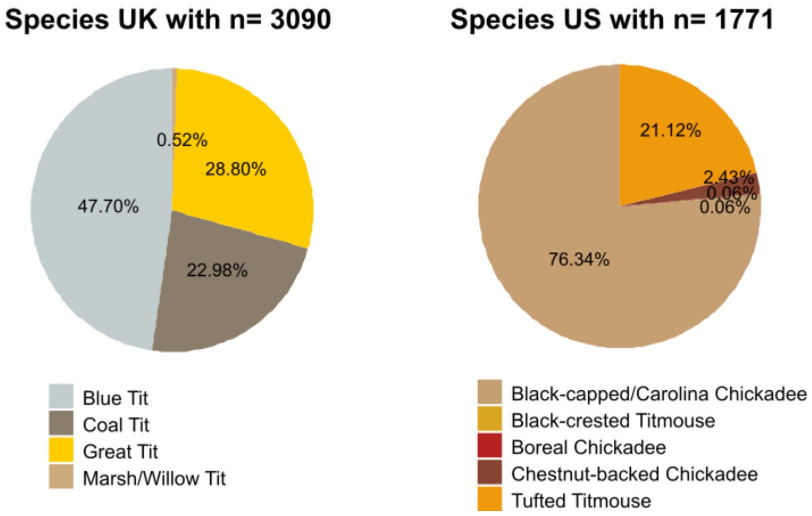


Figure 5.1. Distribution of species observed in the pilot study, for the United Kingdom on the left and North America on the right.

By the end of the pilot study, 266 submissions were received which included a total of 4861 valid observations of birds, made by 49 volunteers. A total of 3090 observations were made in the UK and 1771 observations were made in the USA. Citizen scientists, at the end of the pilot study, received a brief report outlining the results. The pilot data showed a good spread of species, which was particularly important in the UK, where I needed at least part of the data to come from less prevalent but hoarding coal tits, marsh tits and willow tits. Even though some non-hoarding birds were observed to perform "hoarding-related" behaviours, in general volunteers observed fewer of those behaviours in non-hoarding species (Figure 5.2). This indicates that volunteers correctly understood the protocols and were able to label hoarding-related behaviours correctly.

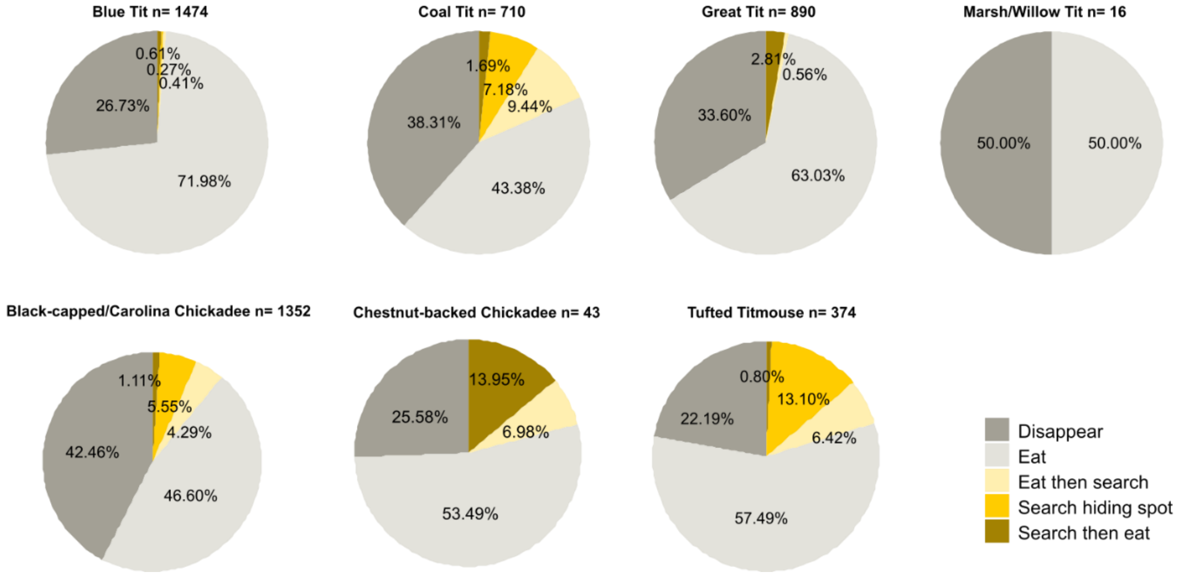


Figure 5.2. Behaviours observed in the pilot study per species. Species with fewer than 5 observations were removed. Behaviours are labelled with the "new" wording for behaviours, where "search" means that birds are looking for a spot to hide their food. Therefore, all yellow-shaded areas are hoarding-related behaviours.

5.3.3 Data Collection Seasons

5.3.3.1 Recruitment, Participants, and Volunteer Communication

Volunteer recruitment for the first data collection season took place throughout May – August 2022. For this, additional messages were sent out with newsletters of the BTO, NHSN and the FeederWatch project. Volunteers that took part in the pilot study also received an email, asking them to participate again. For the second year of data collection, volunteer recruitment took place in June-August 2023. In addition to the organisations from previous years, the study was advertised by the Durham Wildlife Trust, the Yorkshire Wildlife Trust, the Wildlife Trust for Lancashire, Manchester & North Merseyside, and the Wiltshire Wildlife Trust. Additional recruitment took place via social media, targeting birding and nature observation groups.

After signing up, volunteers received a "volunteer information pack" which included background information about the study, a description of volunteer responsibilities, a step-by-step guide to data collection, examples of observation scenarios and a bird ID guide to species relevant to their area (see Supplementary Materials section B). In addition, all materials including information packs, offline data sheets, feedback forms, Frequently Asked Questions, and information about the mobile application, were made available on https://www.staff.ncl.ac.uk/tom.smulders/research/the-evolution-of-hoarding-behaviour/volunteer-information/). During the data collection seasons from August – March, volunteers received monthly newsletters. At the end of each data collection season, a data report was distributed and individual data reports could be requested (see Supplementary Materials section B).

Recruitment resulted in a total of 616 volunteers signed up for the study, of which 396 participated actively in the study. 88 volunteers participated from the United Kingdom and 308 volunteers from the United States of America and Canada took part.

5.3.3.2 Data Collection Protocol

Data collection took place from August – March in 2022/2023 and 2023/2024. For each data collection session, volunteers were asked to watch their feeders until a bird arrived. In the USA, the species of interest were black-capped/Carolina chickadee (*Poecile atricapillus/Poecile carolinensis*), boreal chickadee (*Poecile hudsonicus*), mountain chickadee (*Poecile gambeli*), chestnut-backed chickadee (*Poecile rufescens*), Mexican chickadee (*Poecile sclateri*), grey-headed chickadee (*Poecile cinctus*), tufted titmouse (*Baeolophus bicolor*), black-crested titmouse (*Baeolophus atricristatus*), bridled titmouse (*Baeolophus wollweberi*) and juniper/oak titmouse (*Baeolophus ridgwayi/Baeolophus inornatus*). In the UK these were coal tit (*Periparus ater*), marsh/willow tit (*Poecile palustris/Poecile montanus*), great tit (*Parus major*), blue tit (*Cyanistes caeruleus*) and crested tit (*Lophophanes cristatus*). Black-capped and Carolina chickadees, juniper and oak titmice, as well as marsh tits and willow tits were grouped, as these species have overlapping ranges and are difficult to distinguish just by observing them. Two non-hoarding birds were included (blue tits and great tits), functioning as a control group to assess the possible effect of visibility and observation frequency.

Once a suitable bird picks up a seed from the feeder, volunteers begin the first observation of their session. For each observation, they note down one of 5 categories.

1. *Eat*: The bird eats the seed, or other food item, it takes from the feeder
2. *Search*: The takes the food item and is searching for a place to cache it. Both successful and unsuccessful hoarding attempts are logged in this category.
3. *Eat & search*: The bird first eats some of the seed and then attempts to hoard it
4. *Search & eat*: The bird first attempts to hoard the food item, but proceeds to eat it
5. *Disappear*: if a bird is lost out of sight after picking up a food item from the feeder. This option is also selected if the bird drops the seed or proceeds to do an unrelated behaviour (e.g., preening)

After completing an observation, volunteers fill in details such as the species, date, time, and type of food. They can choose a food item from a predefined list, which includes options such as "*sunflower hearts*", "*whole sunflower seeds*", "*peanuts (loose)", "peanuts (in shell)", "mixed* *seeds*", "*fat*", or "*I don't know*." If none of these options apply, volunteers can select "other" and manually enter the food item. They can then either proceed with their next observation or conclude their session for the day. At the end of each session, volunteers submit their data either through an online form, through the mobile application, or by providing a copy of the printed datasheet. The online forms were created using Qualtrics software and can be found at https://nclpsych.eu.qualtrics.com/jfe/form/SV_8IeSP7bixhPFUlE. The mobile application was built by Simileoluwa Aluko, hosted on Firebase, and made available for both Android and Apple OS (see Supplementary Materials section B for details on the mobile application). For each online submission, volunteers provide their email address, which functions as a volunteer ID. Volunteers can submit up to 90 observations per submission form. Observations made via the mobile app are submitted as individual observations per bird and automatically linked to the volunteer's registered email. Volunteers are asked to record bird activity for 30-60 minutes each week, maintaining regular intervals.

5.3.3.3 Data Filtering and Quality Checking

Prior to data filtering, the dataset comprised a total of 78,986 observations. I removed observations that lacked information on bird species, date and time, food type, or behaviour and flagged those submitted by email addresses not included in the registration list. Each flagged email address was individually inspected, and spelling errors were corrected where applicable. If the unregistered email address could not be verified, observations from the address were removed. The steps taken to ensure data quality—including verification of location, time and date, behaviour type, and species for each observation—are outlined below. For details on the number of observations removed at each stage, see Supplementary Materials section B.

Location

Upon registration, volunteers were required to provide the coordinates of their location. These coordinates were linked to each of their web form observations using the provided email address as a volunteer ID. Location data was automatically recorded for observations submitted via the mobile application. Both longitude and latitude were captured in decimal degrees and rounded to two decimal places. Observations from volunteers not on the sign-up list or those who failed to provide location details were excluded. The data was also checked for inaccurate locations, such as those outside the USA, Canada, or the UK, and in such cases, volunteers were contacted individually to correct the information. See Figure 5.3 for the final distribution of volunteer locations.

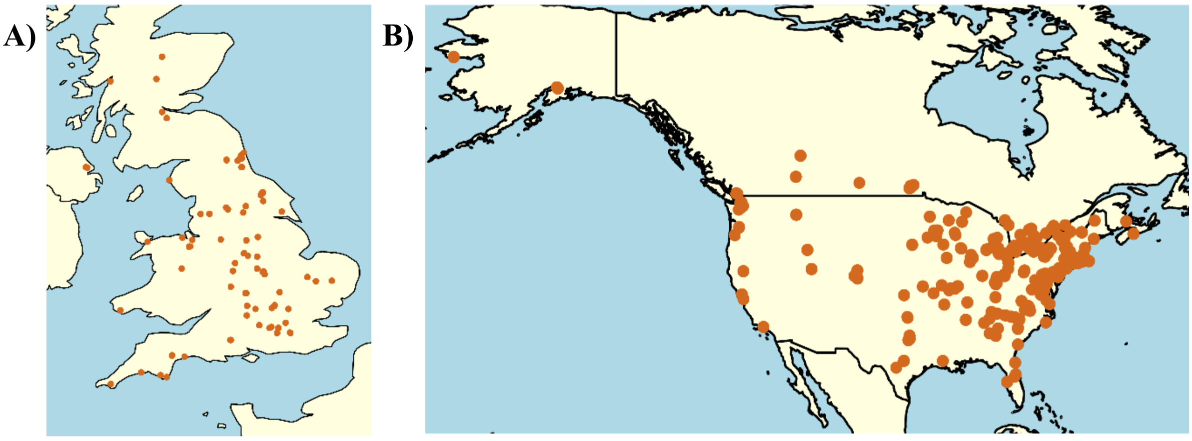


Figure 5.3. Distribution of individual volunteer locations across A) the United Kingdom and B) Northern America.

Time and date

On the web forms, volunteers could manually enter the time and date of their observations (the "*date of observation*" variable). To ensure data quality, several checks were implemented. The automated timestamp generated when volunteers submitted their online forms was used to verify whether the reported *date of observation* fell within the same data collection season as the timestamp. If a discrepancy was found, but the difference was exactly one year, the *date of observation* was manually adjusted. Adjustments were also made when volunteers individually contacted me to report errors in the submitted date. Observations where the *date of observation* did not align with the submission season and could not be otherwise verified, were filtered out. This issue did not affect data submitted via the mobile application, as it automatically generated a timestamp for each observation. Data collection seasons spanned from August 15 to March 31, and any data collected outside these dates was excluded.

Behaviour Type

The five behaviour types described above were used to identify potentially unreliable volunteers. Volunteers who contributed more than 1% of the total data were flagged for further inspection. For each of these volunteers, the distribution of hoarding-related behaviours ("*search*," "*search then eat,"* and "*eat then search*") versus non-hoarding behaviours ("*eat*" and "*disappear*") was compared to that of the overall dataset. In the full dataset (as shown in step 2 of Table B.2 in the supplementary materials), 10% of observations from the USA or Canada involved hoarding-related behaviours, as did 10% of observations from the UK for hoarding species. If a volunteer with a large number of observations (>1%) recorded more than 30% hoarding-related behaviours in the hoarding species, their data was excluded from the final dataset, as this proportion is biologically improbable.

In the UK, 2% of non-hoarding birds were reported to display hoarding behaviours. These observations were removed. Volunteers who reported non-hoarding species to “hoard”, were flagged for a further distribution check. If these flagged volunteers reported more than 30% hoarding-related behaviours in the hoarding species, their observations were removed altogether.

Food

Volunteers reported 156 different food items that birds interacted with, including the 6 items from the list above. After cleaning the text (e.g., removing punctuation, adjusting spaces, and standardising lowercase), these items were grouped into the most common categories. Observations containing "nonsense" (e.g. non-words, or odd items such as “pizza”) food items were flagged and removed. Volunteers who reported these items were further inspected to ensure the overall quality of their data. Again, the same distribution check described under "Behaviour Type" was applied for these flagged volunteers. Observations from volunteers reporting more than 30% hoarding behaviours in hoarding species, were removed. See Supplementary Materials section B for details on the number of observations removed.

Temperature

For the UK data, to investigate the effects of temperature on bird body condition, each bird record was matched with air temperature data corresponding to the location and time of the observation. The weather records were retrieved from the Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations dataset. The MIDAS dataset used contains daily minimum and maximum air temperatures recorded at weather stations across the UK between 2022 and 2024 (Met Office, 2024). Throughout the data cleaning process, observations of missing and/or erroneous data regarding the timestamp, version, location, and weather station ID were removed.

Each record in the citizen science dataset was matched with the average minimum temperature recorded across the three days prior to the bird's capture using the *geosphere* package in R (Hijmans et al., 2022). Weather observations are logged at 09:00 in the morning, covering either a 12-hour or 24-hour period. As a result, the minimum temperature recorded at 09:00 typically occurs just before sunrise on the same day. To avoid differences in effect size based on how close in time the bird was captured to this minimum, the weather record for the day of capture was excluded from the analysis (Gosler, 2002). For example, if a bird were caught on Friday, it would be matched with the minimum temperatures from Monday night, Tuesday night, and Wednesday night. The weather data used came from the nearest weather station within a 50 km radius of the capture location. Only records where at least two out of three weather observations were available within this 50 km range were included, which was the case for all 15478 observations made in the UK. The "*temperature*" variable contains the average of the 3 (or 2) recordings in degrees Celsius.

Due to time limitations, I was not able to retrieve the temperature data to match observations made in the United States of America and Canada. This will be done in future work.

Species

Any species with fewer than 3000 observations were removed from the data. The remaining species are the Carolina/black-capped chickadee and tufted titmouse for the USA and Canada and the blue tit, great tit and coal tit in the UK. See Table 5.3 for the number of observations for each species.

5.3.3.4 Variable Selection

The "*day*" variable was calculated as the number of days elapsed since August 15 of the current season for the entire dataset.

To calculate the day length on the day of observations, the sunrise and sunset timing were determined for each record using the *Stream Metabolism* package in R (Sefick, 2023). The "*day length*" in hours was calculated for each observation.

For the full dataset, the variable "*disappearing index*" was created where any observation where the bird disappeared gets a 1 and all other behaviours (*eat*, *hoard and search*, *search and hoard*, *search*) get a 0.

Then, the variable "*hoarding index*" was created, where any observation where the bird did a hoarding-related behaviour (*hoard and search, search and hoard, search*) received a 1 and "*eat*" behaviours received a 0.

The variable "*latitude group*" was created for the North American data only, with observations made above 40 degrees latitude classified as "North" and those below 40 degrees classified as "South". This threshold was chosen because it broadly splits the Black-capped and Carolina chickadees up by species. Black-capped chickadees occur mostly north of this threshold, whilst the range of Carolina chickadees is in the South (Brewer, 1963). In the North group, there are 14037 black-capped/Carolina chickadees and 5518 tufted titmice. In the South group, there are 8017 black-capped/Carolina chickadees and 5360 tufted titmice.

Temperature, as described above, is the average minimum temperature at the location where the bird was observed from the 3 days before the observation. This variable is only calculated for birds in the UK.

Volunteer ID is the unique number assigned to each volunteer.

5.3.3.5 Data Subsets

Some of the analysis is done on subsets of the data. The "*UK data*" constitutes all observations made in the United Kingdom (N =15,476). The "*North America data*" constitutes all observations collected in the United States of America and Canada (N = 32,932). For the models focussing on hoarding intensity (see below), subsets were taken of these datasets excluding all "disappear" behaviour. For the UK, any observations of non-hoarding birds were taken out as well. The "*Hoarding UK*" dataset resulted in 1332 observations. The "*Hoarding North America*" dataset resulted in 17,923 observations.

5.3.4 Data Analysis

5.3.4.1 Fitting GAMs

To understand the seasonal patterns of hoarding behaviour of titmice species under food-supplemented conditions, I fitted GAMs (Generalized Additive Models) using the *gam* function from the *mgcv* package in R (R Core Team, 2024; Wood, 2004). The following parameters were set for all models: discrete = TRUE (to increase computational speed when using the *bam()* function), gamma= 1.4 (to reduce overfitting of smoothed curves), and family = "binomial" (using a logistic link function for dichotomous variables) (Wood, 2017).

Unless stated otherwise, the smooth terms (*day*, *day length* and *temperature*) were fitted with a thin plate spline with a basis size of *k* = 4. Here, k determines the complexity of the smooth. Thin plate splines are indicated with "*s()*" in the model formulas below, representing smooth, nonlinear relationships between the predictors and response variables. If the observed patterns were biologically more complex or "simpler" than expected, *k* was adjusted accordingly to allow for more or fewer basis functions, whilst keeping *k* constant across models for each variable. *k* was also lowered in cases where increasing the degrees of freedom did not improve model fit but increased the estimated degrees of freedom, indicating potential overfitting. Categorical variables (*species* and *latitude*) were included as parametric coefficients and were not fitted with splines and thus presented without "*s()*".

For interactions between splines or between splines and parametric coefficients, tensor product interactions with marginal penalties were used. These interactions allow for individual interpretations of the main effects, as well as interpretation of interaction effects. They are indicated as "*ti()*" in the model equations. In these cases, *k* is set according to the *k* of the smooth term.

Finally, Volunteer ID was included as a random effect using a random effect smooth ("*s()*"). This approach accounted for variability across volunteers without overfitting and treated individual-level effects as random noise.

5.3.4.2 Disappearing Patterns

When birds hoard, they are more likely to fly further away from the feeder than birds that consume the seeds they find. Therefore, hoarding birds might be more likely to disappear from observation than non-hoarding birds. Additionally, I expect a higher number of "*disappear*" observations in autumn, when tree foliage provides more cover.

To examine if birds disappear less often in winter, and if there is a species effect on disappearing rates, I fitted GAMs to the "*UK data*" and "*North America data*" datasets. *Disappearing index* was used as the outcome variable and *day* and *species* were included as predictors. *Day* was included with a thin plate spline and *species* as a factor. The interaction between *day* and *species* was included to investigate if species respond differently to the seasons. This was done by adding a tensor product interaction with 4 degrees of freedom. *Volunteer ID* was included as a random effect (Models 1 and 2 in Table 5.2).

Because the onset of seasons varies across latitudes in North America, seasonal transitions will differ in their timing, as well as changes in foliage. Therefore, a third model was fitted to the North American data (Model 3 in Table 5.2), that expands on Model 2 by including the three-way interaction between *species*, *day* and *latitude*, as well as the two-way interactions between day and *latitude* and *species* and *latitude*. *Latitude* was also included as a main effect. Tensor product interactions were used for the three- and two-way interactions, apart from *species*latitude*, which was included as a factor interaction. This model was fitted to investigate if the patterns in disappearing probability differ between more northern and southern latitudes in North America, and if this effect varies between different species.

5.3.4.3 Patterns in Hoarding Intensity

To test if food-supplied birds have a hoarding peak later in the year than those observed in the literature on wild birds, two GAMs were fitted. The first model was fitted on the "*Hoarding UK*" data and included the *hoarding index* as the outcome variable, *day* as a predictor and *Volunteer ID* as a random factor (Model 4 in Table 5.2). *Day* was included as a thin plate spline.

The second model was fitted on the "*Hoarding North America*" data subset, with *hoarding index* as the outcome variable and *day* and *species* as predictors (Model 5 in Table 5.2). *Day* was included as a thin plate spline and *species* as a factor. To investigate if hoarding patterns differ by species, the interaction between *day* and *species* was included as a tensor product interaction with 4 degrees of freedom for each variable. Again, *Volunteer ID* was included as a random factor (Model 5 in Table 5.2).

The third model was fitted on the "*Hoarding North America*" data, which included the three-way interaction between *species*, *day* and *latitude bin* in order to investigate if the patterns in hoarding intensity differ between more northern and southern latitudes in North America (Model 6 in Table 5.2). This model expands on Model 4 by including the three-way interaction between *species*, *day* and *latitude*, as well as the two-way interactions between day and *latitude* and *species* and *latitude*. *Latitude* was also included as a main effect. Tensor product interactions were used for the three- and two-way interactions, apart from *species*latitude*, which was included as a factor interaction.

5.3.4.4 Exploring the Effects of Day Length and Temperature

To explore the effects of day length on hoarding intensity, three models were fitted where *day length* replaces *day* as a predictor variable. First, a model was fitted on the "UK hoarding" data with *hoarding index* as the outcome variable and *day length* as a predictor. *Day length* was added as a thin spline smooth. *Volunteer ID* was added as a random effect (Model 7 in Table 5.2).

The second model (Model 8 in Table 5.2) was fitted on the "*Hoarding North America*" data subset, with *hoarding index* as the outcome variable and *day length* and *species* as predictors. *Day length* was included as a thin plate spline and *species* as a factor. To investigate if hoarding patterns differ by species, the interaction between *day length* and *species* was included as a tensor product interaction with 4 degrees of freedom for each variable. Again, *Volunteer ID* was included as a random effect. Both *day length* models were fitted with $k = 3$ for the *day length* variable.

Finally, a model was fitted on the "*Hoarding UK*" data with *temperature* as a predictor instead of *day length* or *day* (Model 9 in Table 5.3). *Temperature* was included as a thin plate spline and *Volunteer ID* was included as a random factor. The model was fitted with $k = 3$ for the *temperature* variable. Due to time limitations, I was at this point not yet able to retrieve the weather data for the observations made in the USA and Canada

5.3.4.5 *Model Checks and Result Reporting*

Before fitting the models, correlations between all variables were assessed to determine which could be included together. All correlations were either weak or non-significant (see Supplementary Materials section B for details). Diagnostic checks were conducted for all models, including visual inspections of residuals vs. fitted values to check for heteroscedasticity, and QQ-plots of the residuals, using the *DHARMa* package in R (Hartig et al., 2024). I also performed dimension checks to ensure that the basis dimension (k), which controls the number of basis functions used to fit smooth terms, was sufficiently high to accommodate the effective degrees of freedom (EDF) for each term while maintaining biological relevance.

In the results section below, I present the F-value and p-value for the smooth terms. A significant p-value means the smooth term has a significant effect on the binary outcome variable (*disappearing-index* or *hoarding-index*). For the parametric coefficients, I present estimates, t-values and p-values. A significant p-value means there is a significant effect of the term on the outcome variable. The estimates are reported as “log odds”. I transformed these into “odds ratios” using the formula $Odds\,ratio = e^{estimate}$. In the models below, the odds ratio tells us how the levels of the factors compare to their baselines. For example, the probability of “disappearing” is x times larger for this level than for the baseline. With “x” being the odds ratio.

For R scripts of the data analysis and data cleaning process, please see https://github.com/Vera-Anne/.

Table 5.2. Model overview. All interactions are fitted with a tensor product interaction, a. AIC in bold are the best-fitting models for the "North America", "Hoarding UK" and "Hoarding North America" datasets. "s()" indicates a thin plate spine and "ti() indicates a tensor product interaction".

Model	***Outcome***	***Predictor(s)***	***Data set***	***AIC***	***Deviance explained***
1	Disappearing index	s(day) + species + ti(day * species) + s(1|volunteer ID)	United Kingdom	-	0.125
2	Disappearing index	s(day) + species + ti(day * species) + s(1|volunteer ID)	North America	37982.88	0.171
3	Disappearing index	s(day) + species + latitude + ti(day * species) + ti(day * latitude) + (latitude * species) + ti(day*latitude*species) + s(1|volunteer ID)	North America	**37938.22**	0.172
4	Hoarding index	s(day) +s (1|volunteer ID)	Hoarding UK	**1112.12**	0.207
5	Hoarding index	s(day) + species + ti(day * species) + s(1|volunteer ID)	Hoarding North America	12836.34	0.287
6	Hoarding index	s(day) + species + latitude + ti(day * species) + ti(day * latitude) + (latitude * species) + ti(day*latitude*species) + s(1|volunteer ID)	Hoarding North America	12811.40	0.289
7	Hoarding index	s(day length) + s(1|volunteer ID)	Hoarding UK	1141.514	0.168
8	Hoarding index	s(day length) + species + ti(day length* species) + s(1|volunteer ID)	Hoarding North America	**12765.44**	0.269
9	Hoarding index	s(temperature) + s(1|volunteer ID)	Hoarding UK	1157.037	0.167

5.4 Results

5.4.1 Descriptive Information

After data cleaning, the final number of observations was 48,453. Of these observations, 15,479 were made in the United Kingdom and 32,932 were made in Northern America (Figure 5.3). Of the total, 17,549 observations were made using the web form and 30,904 using the mobile application. Table 5.3 lists the number of observations made for each species, as well as the type of behaviours observed (See also Figure 5.4). Please see Supplementary Materials section B for further details on the data distribution.

Table 5.3. Number of observations per species and split per behaviour type. The "Hoarding-related" column includes behaviours labelled as "Search", "Search then Eat" and "Eat then Search".

Species	***Total***	***Eat***	***Disappear***	***Hoarding-related***
Black-capped/Carolina chickadee	22,095	9,642	9,909	2,544
Blue tit	7,888	4,656	3,232	-
Coal tit	3,230	1,072	1,898	260
Great tit	4,361	2,338	2,023	-
Tufted titmouse	10,879	4,846	5,125	908

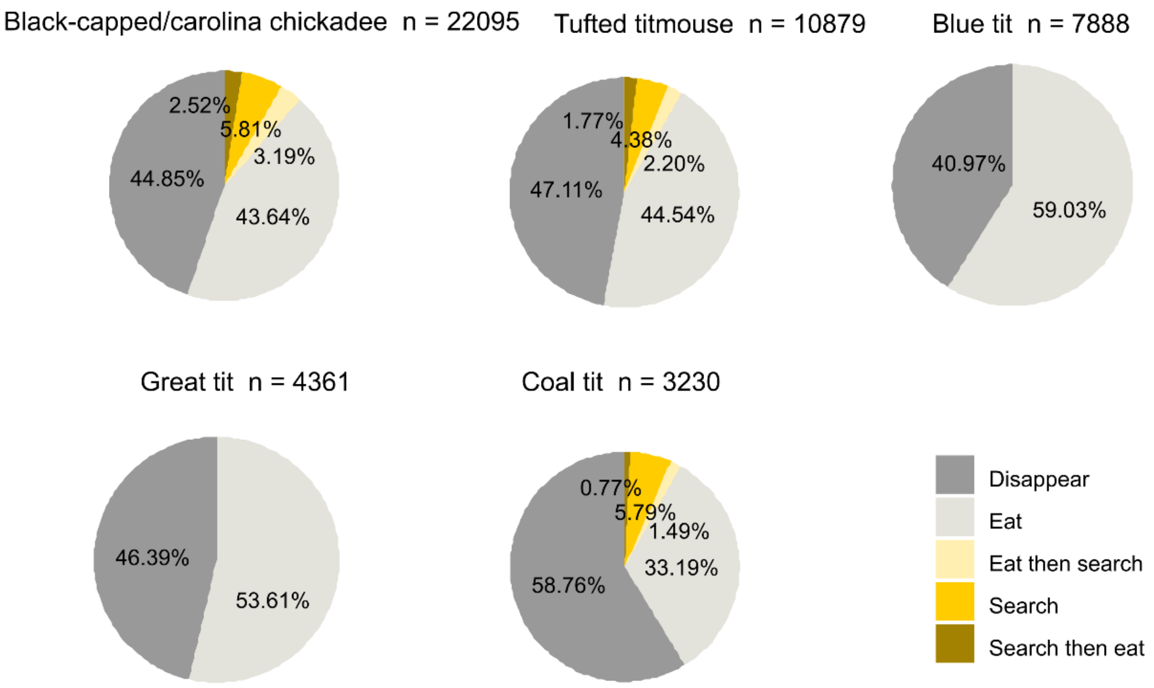


Figure 5.4. Observed behaviours by species for the cleaned dataset. N indicates the number of observations made for each species. Hoarding-related behaviours are shaded yellow.

5.4.2 Patterns in Disappearing Frequency

Model 1 – UK data: Disappearing index ~ s(day) + species + ti(day * species) + s(1|volunteer ID): Model results show a significant effect of *species*. Coal tits (*estimate = 1.24*, *t = 22.91, p < 0.001*) are significantly more likely to disappear than blue tits. The odds ratio for coal tits is 3.45, which means that coal tits are 3.45 times more likely to disappear than blue tits. Great tits (*estimate = 0.24, p <0.001*) are also more likely to disappear than blue tits, but with an odds ratio of 1.27, the difference is smaller than for coal tits. The main effect of *day* is significant but near linear, suggesting that the probability of disappearing decreases linearly throughout the data collection season (*F = 65.72, p<0.001*). The effect of *day* on the disappearing probability differs from this general effect for blue tits (*F = 35.36, p<0.001*) and coal tits (*F = 14.41, p = 0.008*), but is not significantly different from the main *day* effect for great tits. The model explains 12.4% of the variation in the data (Table 5.2). Full model summaries for this and the following models are available in the Supplementary Materials section B.

The shape of the interaction effect between the three *species* and the *day* variable is shown in Figure 5.5. Coal tits are more likely to disappear in general and disappear more often in autumn (September – November) than in the winter months (December – March). The probability of disappearing decreases more gradually throughout the season for blue tits and great tits than for coal tits.

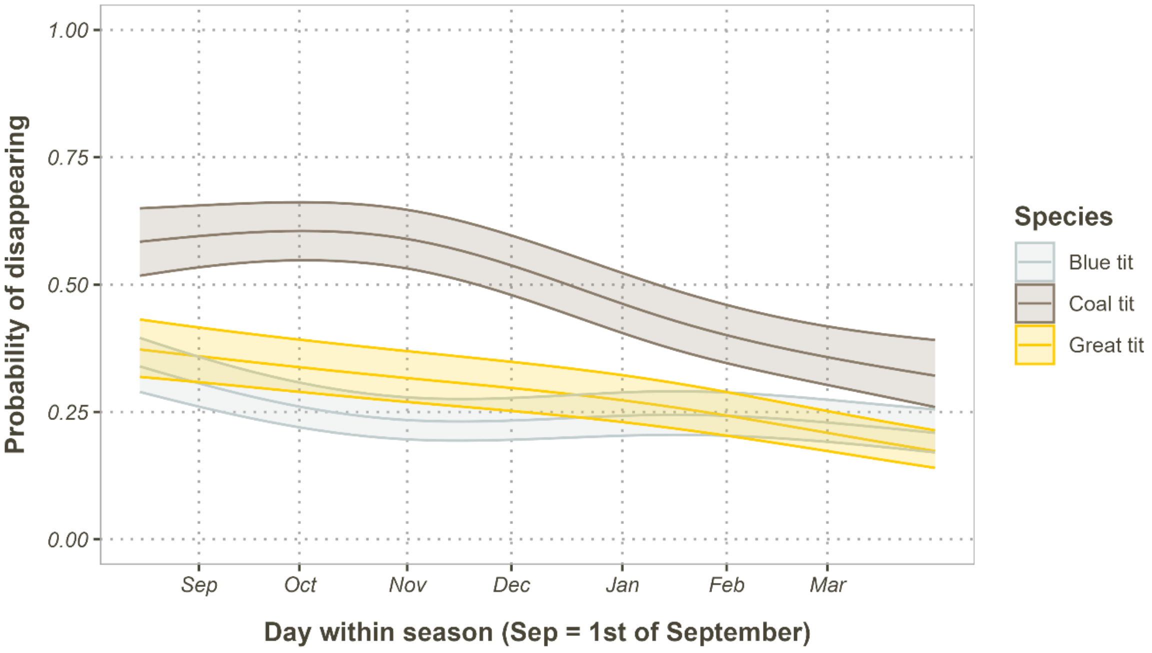


Figure 5.5. The probability of disappearing versus the day within data collection season. Plotted lines are fitted values from Model 1 averaged across volunteers and CIs are shaded.

Model 2 –North America data: Disappearing index ~ s(day) + species + ti(day * species) + s(1|volunteer_ID): Model results show a significant effect of *species*. Tufted titmice (*estimate = -0.11, t = -6.61 p =0.002*) are less likely to disappear than black-capped and Carolina chickadees. The odds ratio for tufted titmice is 0.90, which means they are 0.90 times as likely to disappear compared to black-capped/Carolina chickadees.

The effect of *day* on the probability of disappearing is significant and decreases throughout the season (*F = 23.00, p < 0.001*). The interaction effect between *species* and *day* is not significant. This indicates that there are no differences in the shape of the pattern between the species (Figure 5.6). The model explains 17.1% of the variation in the data (Table 5.2).

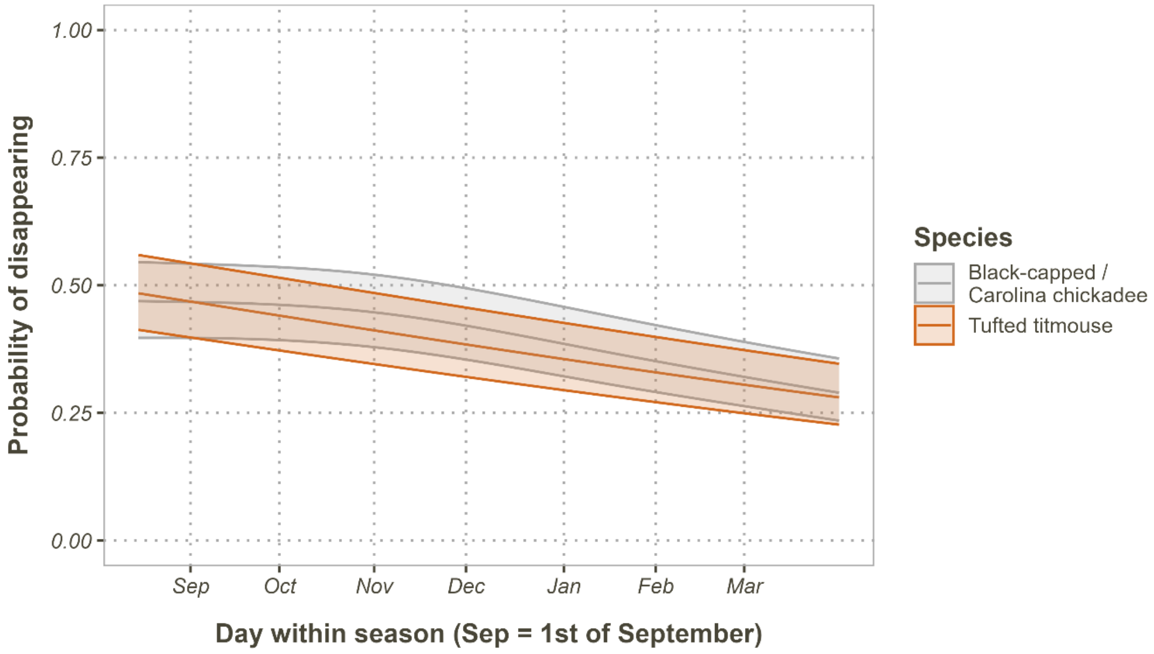


Figure 5.6. The probability of disappearing versus the day within the data collection season. Plotted lines are fitted values from model 2 averaged across volunteers and Cis are shaded.

Model 3 –North America data: Disappearing index ~ s(day) + species + latitude + ti(day * species) + ti(day * latitude) + (latitude * species) + ti(day * latitude * species) + s(1|volunteer ID):

Model results show there are no main effects of *latitude* and *day* on the disappearing probability of birds in North America. The main effect of species is significant with Titmice *(estimate = -0.10, t = -2.07, p = 0.038*) disappearing 0.90 times less often compared to black-capped/Carolina chickadees.

The two-way interactions between *day* and *species* and *latitude* and *species* are non-significant. The two-way interaction between *day* and *latitude* is significant. The effect of *day* is significant for the Northern region (*F = 18.56, p = 0.002*), but not for the South.

The three-way interaction between *species*, *latitude group* and *day* is significant. The pattern differs from the main effect of *day* for black-capped chickadees North of the 40-degree latitude (*F = 183.23, p < 0.001*), tufted titmice North of the 40-degree latitude (*F = 127.19, p<0.001*) as well as black-capped/Carolina chickadees (*F = 34.14, p<0.001*) and tufted titmice (*F = 4.47, p=0.035*) in the South. This means that the combined effect of *day* and *latitude* is different between the species. The model explains 17.2% of the variation in the data and has a lower AIC value than Model 2 (Table 5.2).

Figure 5.7 suggests that in the North, the probability of disappearing declines steeply at the start of the season for tufted titmice, whilst for black-capped/Carolina chickadees this is slightly more gradual. Titmice also disappear more often at the start of the season than black-capped/Carolina chickadees, with the opposite suggested at the end of the season. In the South, black-capped/Carolina chickadees are slightly more likely to disappear than titmice in the start of the season. Between September and November both curves plateau, to decline gradually from November onwards. The curves for the two species overlap for most of the season. In general, these results suggest that birds in the South have a more gradual decline in disappearing rates into the winter, compared to birds in the North, where disappearing rates drop more linearly.

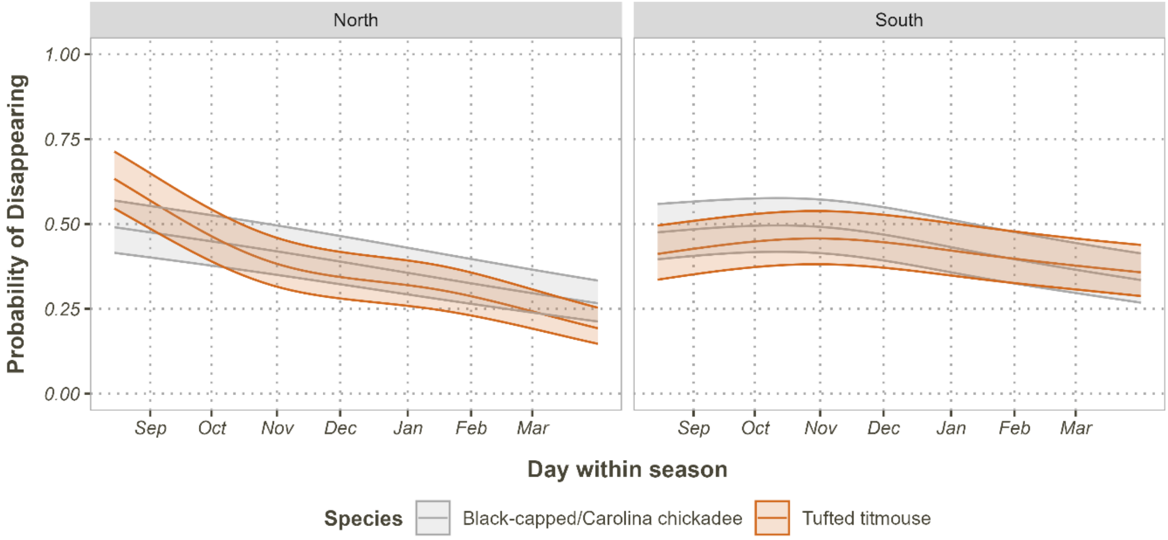


Figure 5.7. The probability of disappearing versus the day within data collection season, split up by species and latitude bin. Plotted lines are fitted values from Model 3 averaged across volunteers and CIs are shaded. Labels indicate the 1st of every month.

Model 4 – "Hoarding UK" data: Hoarding index ~ s(day)+ s(1|volunteer_ID): Model results show a significant effect of *day* on the probability of observing hoarding-related behaviour in coal tits (*F = 37.885, p<0.001*). Figure 5.8 shows a peak in the probability of observing hoarding-related behaviour in early to mid-November. The model explains 20.7% of the variation in the data (Table 5.2).

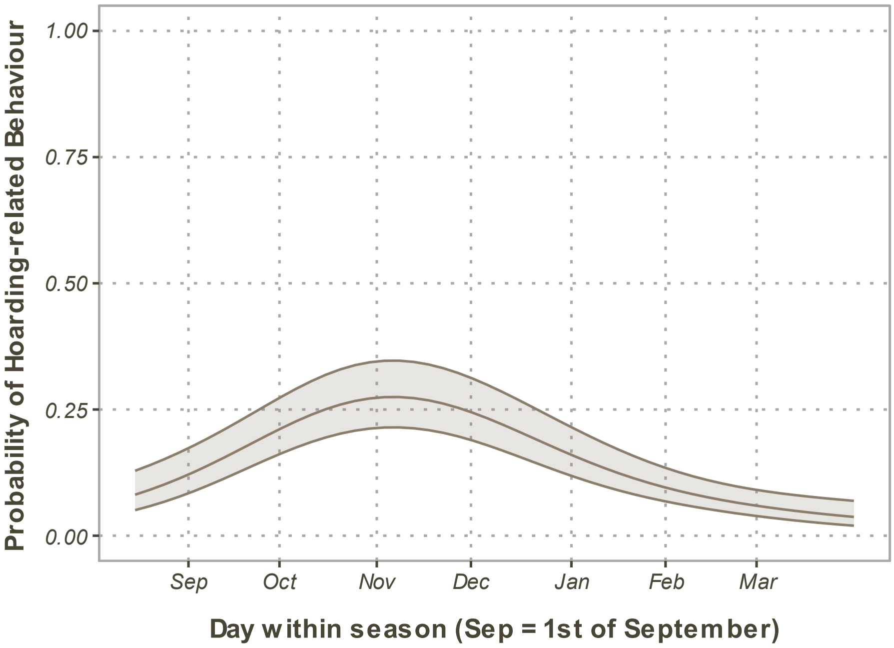


Figure 5.8. The probability of observing hoarding-related behaviour in Coal tits throughout the season. Plotted lines are fitted values from model 3 averaged across volunteers and CIs are shaded.

Model 5 – "Hoarding North America" data: Hoarding index ~ s(day) + species + ti(day * species) + s(1|volunteer ID): Model results show a significant effect of *species* with Tufted titmice (*estimate = -0.150, t = -2.62, p = 0.009*) less likely to hoard than black-capped/Carolina chickadees. The odds ratio for tufted titmice is 0.86, which means that they are 0.86 times as likely to hoard as the chickadees.

The main effect of *day* is not significant. There is a significant effect of the interaction between *day* and *species.* The effect of *day* is different from the main (non-significant) effect of *day* for both black-capped/Carolina chickadees (*F = 209.19, p <0.001*) and tufted titmice (*F = 45.57, p <0.001*). Figure 5.9 shows how the likelihood of observing hoarding-related behaviour in black-capped/Carolina chickadees peaks in early October. Tufted titmice exhibit a more linear pattern with a general decrease in the probability of observing hoarding-related behaviour between September and March. The model explains 28.7% of the variation in the data (Table 5.2).

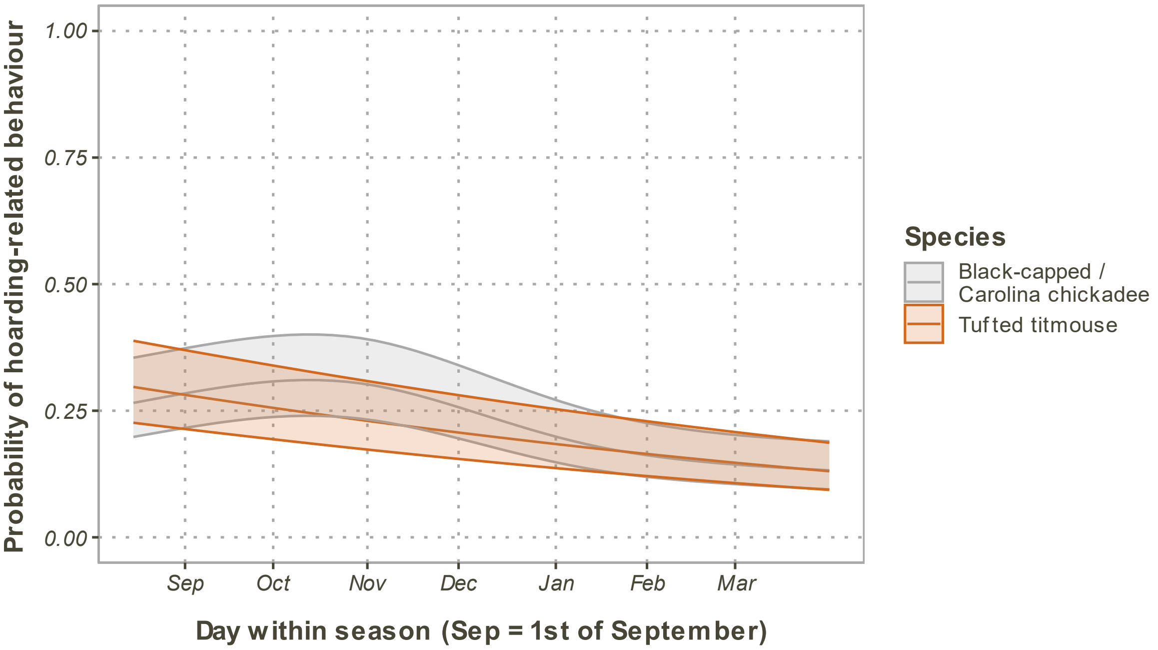


Figure 5.9. The probability of observing hoarding-related behaviour in Black-capped/Carolina chickadees and Tufted titmice throughout the season. Plotted lines are fitted values from Model 5 averaged across volunteers and CIs are shaded.

Model 6 –"Hoarding North America" data: Hoarding index ~ s(day) + species + latitude + ti(day * species) + ti(day * latitude) + (latitude * species) +ti(day * latitude * species) + s(1|volunteer ID):

Model results show a significant main effect of *latitude*, with birds in the South (*estimate* = *-0.47, t = -2.13, p = 0.028* having a lower probability of hoarding than birds in the North. More, specifically, the odds ratio for Southern birds is 0.63, meaning they are 0.63 times less likely to hoard than Northern birds. Furthermore, tufted titmice (*estimate = -0.27, t = -3.342, p<0.001)*, hoard less often than black-capped chickadees. Tufted titmice are 0.77 times as likely to hoard compared to black-capped/Carolina chickadees. There is no main effect of *day*.

The two-way iteraction between *latitude* and *species* is significant (*t = 2.19, p = 0.029*). This means that the probability of observing hoarding behaviour is different for the species at different latitudes. The effect of *day* is different from the main (non-singificant) effect of *day* for black-capped/Carolina chickadees (*F = 13.55, p = 0.008*), but not for tufted titmice. This means that for black-capped chickadees there is an effect of *day* on hoarding, but not for titmice. The two-way interaction between *latitude* and *day* is significant. The effect of *day* is significantly different from the main effect of *day* in the North (*F = 17.48, p = 0.002*) but not in the South. This indicates that there is an effect of *day* on hoarding in the North, but not in the South.

The three-way interaction between *species*, *latitude group* and *day* is significant. The effect of day is significantly different from the main effect for black-capped chickadees North of the 40-degree latitude (*F = 29.27, p < 0.001*), tufted titmice North of the 40-degree latitude (*F = 10.835, p=0.001*) as well as black-capped/Carolina chickadees (*F = 36.51, p<0.001*) and tufted titmice (*F = 15.18, p<0.001*) in the South. This means that the combined effect of *day* and *latitude* is different between the species.

Figure 5.10 indeed suggests that for black-capped/Carolina chickadees in the North, high hoarding rates occur earlier in the season, and start to decline in mid-October. In their Southern conspecifics, hoarding is lower in September, peaks in mid-October and declines into November. In tufted titmice, on the other hand, hoarding rates decline linearly in the North, whilst a peak, similar to black-capped/Carolina chickadees is shown in the South.

The model explains 28.9% of the variation in the data an has a lower AIC value than Model 5 (Table 5.2.).

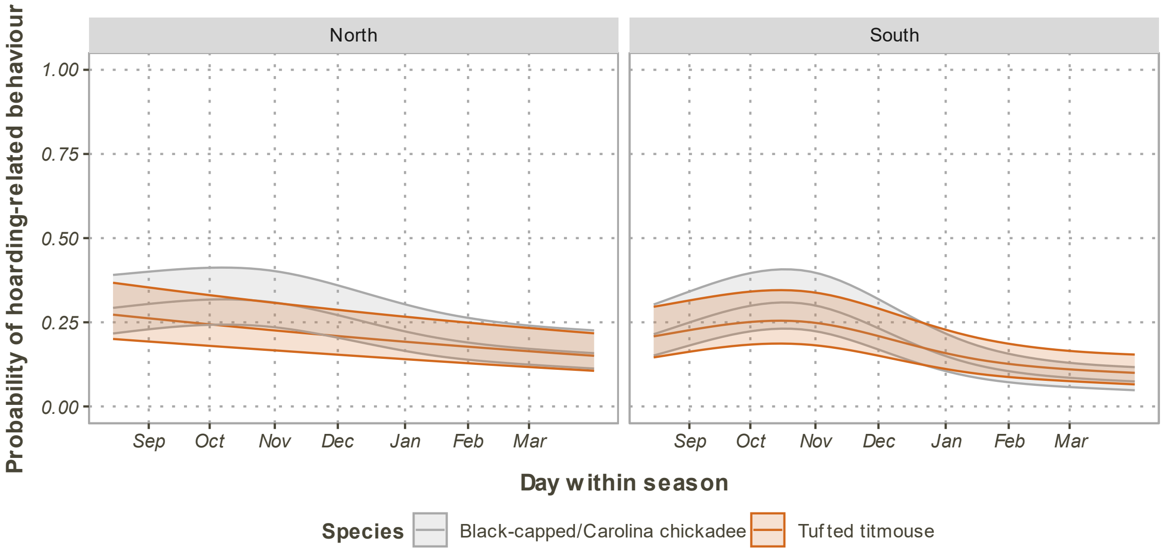


Figure 5.10. The probability of observing hoarding-related behaviour in black-capped/Carolina chickadees and tufted titmice throughout the season. Plotted lines are fitted values from Model 6 averaged across volunteers and with CI's shaded.

5.4.3 Exploratory Analysis of the Effect of Day Length and Temperature

Model 7 – "Hoarding UK" data: Hoarding index ~ s(day length) + (1|volunteer ID): Model results show no significant effect of *day length* on the probability to observe hoarding-related behaviour in coal tits (Figure 5.11).

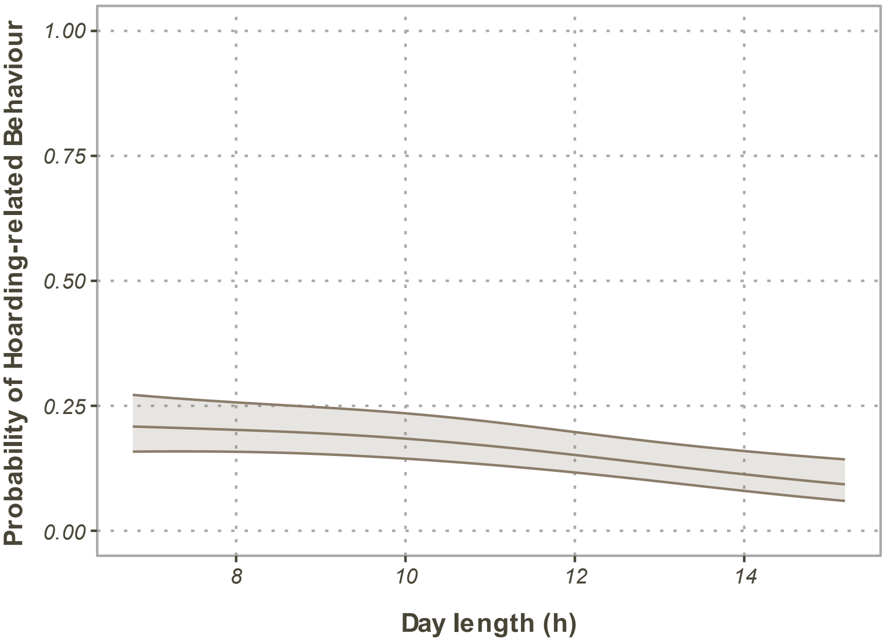


Figure 5.11. The probability of observing hoarding-related behaviour as a function of day length (hours) in Coal tits. Plotted lines are fitted values form model 5, averaged across volunteers with the CI shaded.

Model 8 – "Hoarding North America" data: Hoarding index ~ s(day length) + species + ti(day length * species) + s(1|volunteer ID): Model results show a significant main effect of *species* on the probability of observing hoarding-related behaviour. Titmice (*estimate = -0.15, t = -2.37, p = 0.018*) are 0.86 times less likely to hoard than black-capped/Carolina chickadees. There is no significant effect of *day length* on the probability of observing hoarding-related behaviour.

A significant effect of the interaction between *species* and *day length* was found. The effect of day length on hoarding probability is significant for black-capped/Carolina chickadees (*F = 5.65, p =0.039*) but not for tufted titmice.

Figure 5.12 suggests that most hoarding takes place on days with 10-11 hours of day length and least hoarding takes place on the shortest days for black-capped/Carolina chickadees. The model explains 26.9% of the variation in the data, but the AIC value is lower than in Model 6. (Table 5.2.).

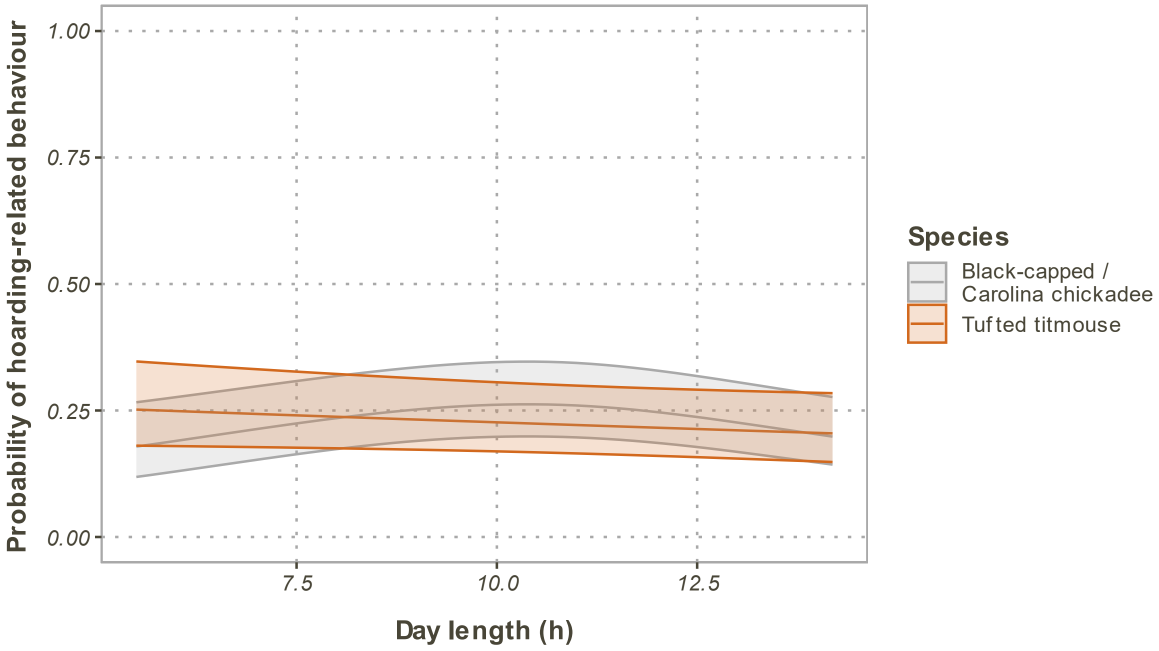


Figure 5.12. The probability of observing hoarding-related behaviour as a function of day length (hours) in black-capped/Carolina chickadees and tufted titmice. Plotted lines are fitted values from Model 8, averaged across volunteers with the CI shaded.

Model 9 – "Hoarding UK" data: Hoarding index ~ s(temperature) + s(1|volunteer ID): The model results showed no significant effect of *temperature* on the probability to observe hoarding behaviour in coal tits (Figure 5.13).

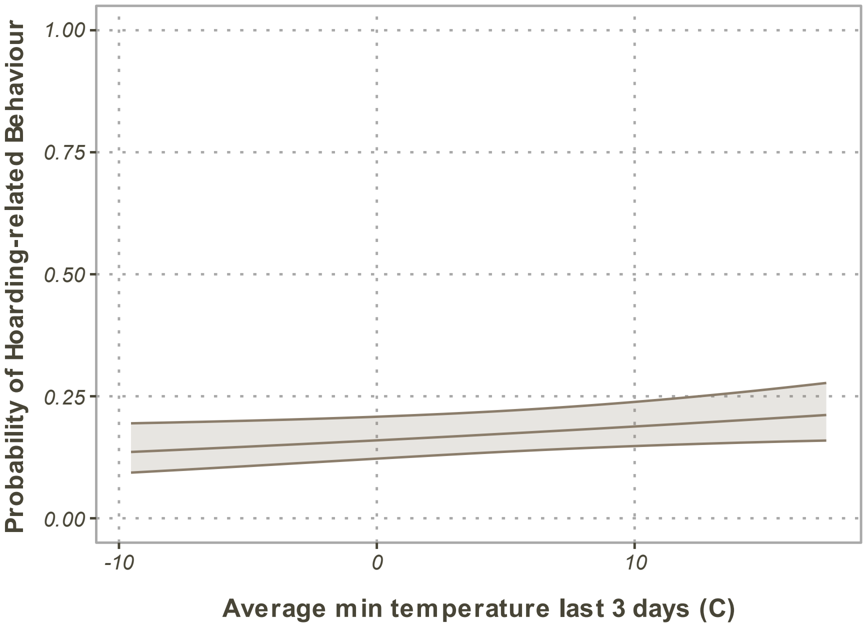


Figure 5.13. The probability of observing hoarding-related behaviour as a function of temperature in coal tits. Plotted lines are fitted values from model 9, averaged across volunteers with the CI shaded.

5.5 Discussion

5.5.1 Seasonal Variation in the Probability to "Disappear"

Results from Model 1 reveal that disappearing rates for non-hoarding birds in the UK are highest in late August, declining linearly as trees lose their foliage throughout the season. In contrast, hoarding coal tits exhibit a higher probability of disappearing, particularly during September and October, when the difference compared to non-hoarders reaches approximately 25%. From early November onward, the probability of disappearing in coal tits decreases, gradually converging with the curves for blue tits and great tits. The peak in disappearing rates for coal tits corresponds with the peak hoarding period, as anticipated from the literature (Brodin, 1992, 1994c; Brodin et al., 1996; Haftorn, 1956), suggesting that up to 50% of these "disappearances" may represent hoarding events (Figure 5.5).

In the USA and Canada, both tufted titmice and black-capped/Carolina chickadees exhibit higher disappearance rates in autumn than in winter (Model 2, Figure 5.6). This could be attributed to the decrease in foliage or a reduction in hoarding activity as winter progresses. The effect of day on disappearing probability was not different between the species. Non-hoarding species were not included in the North American data, but generalising the results from Model 1, it is likely that part of the disappearances between September and December represent "hoarding" behaviour. Because the onset of seasons varies across latitudes, I incorporated latitude into my model to investigate whether the differing timing of seasonal transitions—and consequently, variations in foliage changes—might influence disappearing rates.

Results from Model 3 indicate that the effect of day on disappearing probability varies between the two species across the two latitude groups (Figure 5.7). In general, birds in northern latitudes exhibit higher disappearing rates at the start of the season, which decline almost linearly into winter. In contrast, disappearing rates in southern latitudes plateau until mid-November, after which a gradual decline begins. The latter pattern is very similar to that of the coal tits in the UK. Additionally, tufted titmice show lower disappearing rates compared to black-capped/Carolina chickadees. This pattern may reflect the later timing of foliage loss in the South, potentially sustaining higher disappearance rates later into the season.

The ranges of black-capped chickadees and Carolina chickadees converge around 40 degrees latitude. Consequently, the observed differences between northern (black-capped chickadees) and southern (Carolina chickadees) birds in this group could potentially be attributed to species-specific differences. However, since tufted titmice also exhibit a more pronounced linear decline in the North and a plateau in the South, it is unlikely that these differences are solely due to species effects.

5.5.2 Seasonal Variation in Hoarding Intensity

Model 4 (Figure 5.8) shows that volunteers observed more hoarding behaviour in coal tits during autumn, with a peak occurring slightly later than what is typically observed in wild birds at similar latitudes (Brodin, 1992, 1994; Haftorn, 1956, but see Brodin et al., 1996). Hoarding usually peaks in September - October, followed by a decline in November and December. However, in our study, coal tits displayed a hoarding peak in early November. Two factors may explain this delayed peak. Firstly, the high disappearance rates observed in September and October could have masked an earlier peak in hoarding. If some of these disappearances are indeed hoarding events, the actual hoarding peak may have occurred earlier in the season. Alternatively, the delayed peak could be a result of food supplementation from feeders. If hoarding motivation is driven by shifts in energy balance, motivation for this behaviour may peak in winter when energy demands are highest. Under natural conditions, food scarcity in winter suppresses hoarding, as birds prioritize immediate consumption of food items they find. However, with ample food from feeders, birds may continue hoarding further into the winter months, as their motivation to hoard increases.

In North America, differences in hoarding intensity were found between the two species (Model 5, Figure 5.9). Tufted titmice have the highest hoarding probability in August and September, which declines into winter, whilst black-capped/Carolina chickadees exhibit a hoarding peak in mid-October. The timing of this peak is slightly later than field observations of black-capped chickadees in Canada, which reduced their hoarding efforts from late September onward (Brodin, 2005). Similarly, willow tits in Japan, at comparable latitudes, show a peak in hoarding in late September, followed by a decrease into winter (Nakamura & Wako, 1988). Similar to the UK data, it is challenging to determine whether the slightly later hoarding peak observed in North America is due to higher disappearance rates early in the autumn or the supplemental food provided by feeders.

To further explore whether differences in seasonal onset affect hoarding behaviour, I added latitude to the model (Model 6, Figure 5.10). The results indicate that the effect of *day* on the hoarding probability differs between the two species and the two latitude groups. In the North, the highest hoarding rates are observed between September and mid-October. tufted titmice show a linear decline into winter, whilst Chickadees have a plateau and a decline in early November. In the South, both species show a "peak" in hoarding intensity in mid-October

(Figure 5.10). This “delayed” peak in hoarding in the South could be attributed to differences in foliage, as trees lose their leaves later in southern regions, prolonging the period during which birds disappear and hoarding behaviour is “hidden”. Alternatively, the hoarding peak may take place later because of the delayed seasonal decreases in *temperature* and *day length*, which postpone the associated increase in energy demands.

5.5.3 Effects of Day Length and Temperature

Previous studies have shown that day length influences hoarding intensity, with birds tending to hoard more on shorter days (Clayton & Cristol, 1996; MacDougall-Shackleton et al., 2003; Shettleworth et al., 1995). In the current study, no significant effect of *day length* on hoarding intensity for coal tits in the UK was found (Model 7). For the North American data, a significant effect of *day length* was found for black-capped/Carolina chickadees but not for Titmice (Model 8, Figure 5.12). Birds hoarded the most during average day lengths, around 10-11 hours. Interestingly, Model 8 has the lowest AIC value across all models fitted on the “*Hoarding North America*” data. The AIC value of Model 6 is slightly higher, suggesting that Model 8 has a better fit. In contrast, however, the deviance explained is a lot higher for Model 6 (28.9%) than for Model 8 (26.9%). This is likely due to the higher number of variables included in Model 6, which are penalised when AIC values are calculated.

Regarding temperature, the literature suggests it may not play a major role in hoarding behaviour (Clayton & Cristol, 1996; Shettleworth et al., 1995), but some find increased caching rates under colder temperatures (Pravosudov & Grubb, 1997). Model 9 indicates no significant effect of temperature on the hoarding intensity of coal tits. This suggests temperature does not play a large role in regulating hoarding behaviour. However, it cannot be excluded that my measure—average minimum temperature over the three days prior to observation—may not capture the appropriate temporal window to detect an effect.

5.5.4 Limitations

It is important to acknowledge that my models explain only a small portion of the variance in the data, likely reflecting the inherent challenges of using citizen science data collected by non-expert volunteers. While participants were provided with detailed protocols, instructed to conduct regular observations, and encouraged to keep feeders filled whenever possible, full adherence to these guidelines could not be guaranteed. This may have introduced inaccuracies or potential biases, particularly toward recording hoarding-related behaviours. To address this, I did not disclose that the study's primary focus was on hoarding behaviour, instead emphasising the equal importance of logging all "disappearances." Furthermore, data from volunteers who disproportionately reported hoarding behaviours were excluded from the analysis to minimise bias. If my framework is applied in future studies, additional surveys or focus groups should be conducted to assess how well volunteers understand and follow the protocols. This would help ensure greater consistency and accuracy in data collection, improving the reliability of the findings.

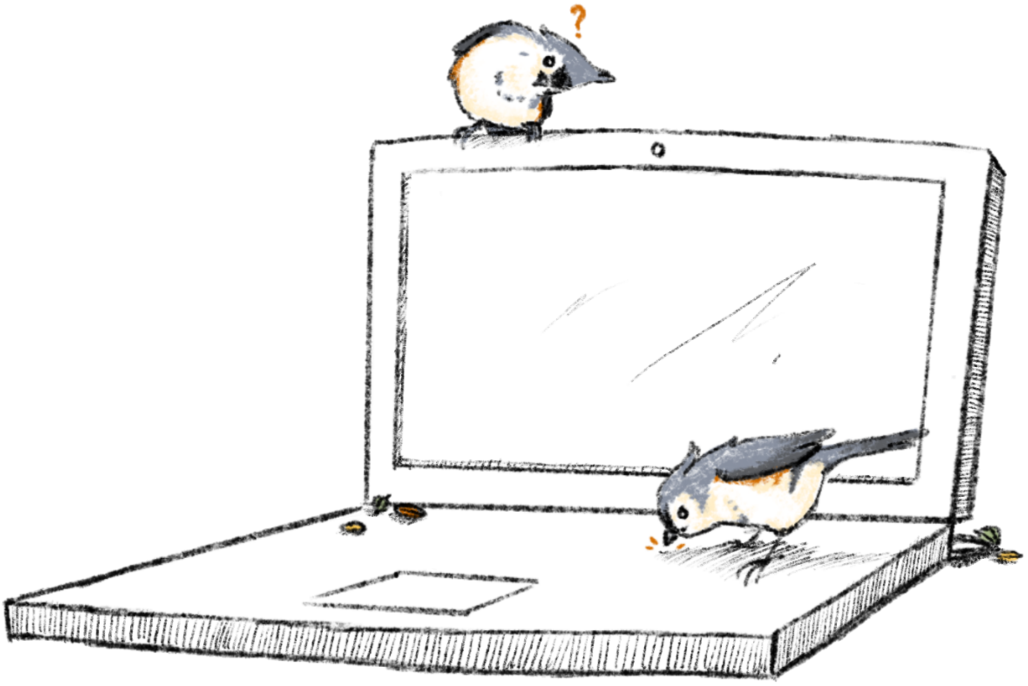
This study explored whether food availability is a limiting factor during winter, leading to a decline in hoarding intensity in late autumn, despite birds' continued motivation to store food. I hypothesised that supplementing food could shift the peak of hoarding behaviour to later in the winter. A slight shift in the hoarding peak was indeed observed, but it is difficult to determine whether this was due to hoarding behaviour being recorded as "disappear" in early autumn, making the peak appear later than it actually occurred, or if the peak genuinely took place later in the season. In addition, the slight delay in the hoarding peak observed could be attributed to annual variation in hoarding (Pravosudov, 2006). If this is the case, or if "disappearing" behaviour is obscuring earlier hoarding peaks, hoarding motivation might not necessarily be highest in winter. Instead, it may have adapted to peak in autumn, potentially regulated by other mechanisms such as photoperiod or photoperiodic state.

It is unlikely that feeders provide a truly *ad libitum* food environment, as they would need to be constantly replenished. If birds were still struggling to find sufficient food items, this could explain why a larger shift in the hoarding peak toward winter was not observed. Furthermore, wild birds are not confined to the feeder areas as in Ludescher (1980), where a shift in hoarding was observed in captive willow tits. These fully food-supplemented birds exhibited the highest hoarding intensities in mid-winter when their energy requirements were at their peak. Therefore, the current study might not have truly tested if hoarding motivation remains high in winter. Future studies should implement stricter protocols that assure true *ad libitum* food supplementation. Alternatively, field studies could compare hoarding intensities of supplemented and non-supplemented populations under similar environmental conditions.

5.5.5 Conclusion

In summary, my findings show increased hoarding probabilities in autumn for both the UK and North American titmice and chickadee species. Coal tits in the UK exhibit a hoarding peak slightly later than expected under natural circumstances, which could be due to the food supplementation, shifting the hoarding peak more towards the most energy-demanding time of year. This implies that hoarding motivation may indeed be highest in mid-winter. However, the study design has not been able to fully provide *ad libitum* food to test this hypothesis. For birds in North America, the shift in hoarding peak was less pronounced, and day length was shown to be a better predictor of hoarding behaviour, with a peak at 10-11 hours of daylight. Therefore, it could be the case that the decline in hoarding during winter is not caused by food availability, but by an alternative, unknown regulatory mechanism. While my models explain only a modest proportion of the variability, likely due to the inherent limitations of citizen science data, they are a starting point for future studies investigating the role of food availability in the suppression of hoarding behaviour in winter.

Part III: Agent-based Models of Small Birds in Winter



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Chapter 4. Agent-based Models of Small Birds in Winter: Model Description

7.1 Abstract

In this chapter, I develop the model that is used in Chapters 5-7 to investigate the decision-making mechanisms underlying food-hoarding behaviour in birds. Using agent-based models, I simulate how physiological signals—such as stomach content, fat reserves, and fluctuations in fat reserves—inform foraging and hoarding decisions. The models explore various decision rules based on these factors that indicate the bird's energetic state, as well as different hoarding strategies. Models of non-hoarding birds are incorporated, alongside various hoarding strategies, examining scenarios where hoarding and foraging are regulated together or independently. This chapter applies the ODD protocol to describe the model's framework, design, and implementation in a standardized format, including the results of my model parameterizations.

7.2 Introduction

Winter poses significant energetic challenges for small tit species at northern latitudes, where food scarcity and shorter daylight hours limit foraging opportunities, whilst energy demands increase with dropping temperatures. Several bird species in the *Paridae* family hoard food to improve winter survival. How this behaviour is regulated in terms of foraging decision making, is not fully understood (Pravosudov, 2006).

As described in the general introduction of this thesis (see Chapter 1), hoarding behaviour in birds is possibly regulated by their energetic state or "energy flux," which can provide cues about current and historical food availability in the environment. Physiological signals can inform birds about their hunger level (e.g., stomach content) and the status of their fat reserves, including whether these reserves are increasing or decreasing.

In this chapter, I use agent-based models to examine how these physiological signals may guide foraging decisions. The purpose of the modelling is to explore potential decision-making rules that birds might follow and to generate hypotheses about the mechanisms regulating hoarding behaviour. While most existing models in the literature rely on a dynamic optimization approach (Brodin, 2000, 2007; McNamara et al., 1990; Pravosudov & Lucas, 2001), where behaviours are optimised, agent-based modelling allows for simulations of food-hoarding behaviour at the decision-making level. This means that individual differences among agents and temporal correlations can be included without assuming agents have foresight regarding their future state. Therefore, my models explore how birds might make decisions based on available information at a specific moment, in contrast to optimisation models that determine ideal actions to result in optimal outcomes (Bonabeau, 2002; Grimm & Railsback, 2006). This makes agent-based modelling a suitable and realistic alternative for the purposes in this thesis.

7.2.1 Modelling the Role of "Energy Flux" in Hoarding Regulation

The literature suggests several factors influencing hoarding behaviour in titmice, including day length (Phillmore & MacDougall-Shackleton, 2007; Shettleworth et al., 1995), food distribution and availability (Karpouzos et al., 2005; Pravosudov, 2003), and temperature (Pravosudov & Grubb, 1997, also see Chapter 3). Since these factors affect the bird's energetic state in various ways, it is plausible that hoarding behaviour is regulated by the bird's energy balance. The idea that birds might use this information is inspired by the "Energy flux hypothesis" from the mammal literature, where the energy consumption of animals, and more specifically the movement of energy from storage into usable fuel, has been linked to their motivation to hoard food items (Keen-Rhinehart et al., 2010). If this also holds true for birds, decisions about whether to eat or hoard food items may be based on their physiological state.

With the current models, I explore various decision-making mechanisms that use different aspects of the birds' energy metabolism to predict bird behaviour and physiology. Specifically, I compare decision rules based on three components of their energetic system: stomach content, fat reserves, and the rate at which fat reserves change—all of which are realistically accessible sources of information for birds.

7.2.1.1 Signals about Stomach Content

It is realistic to assume birds have information about how full their stomach is. Mechanoreceptors in the stomach wall can signal fullness via the Vagus nerve (Denbow, 2015). Additionally, peptide hormones secreted by different parts of the gastrointestinal tract, such as ghrelin from the proventriculus, are secreted to different degrees depending on how full the stomach is (Henderson et al., 2018; Kaiya et al., 2009).

7.2.1.2 Signals about Fat Metabolism

When birds absorb nutrients from their food, such as lipids, these first pass the liver through the vena porta. Studies have shown that lipid absorption and liver metabolism rates can influence food intake in birds (Denbow, 1994, 1999). Additionally, circulating factors and hormones involved in lipolysis and lipogenesis likely inform birds about the state of their fat reserves. During lipolysis, triglycerides are broken down into free fatty acids and glycerol, providing energy. It is plausible that these circulating elements, along with regulatory hormones such as adrenaline, noradrenaline, and glucagon, signal the bird about decreasing fat reserves (Denbow, 1999; Leclercq, 1984).

A similar case can be made for lipogenesis, where carbohydrates are converted into fatty acids and stored as triglycerides in adipose tissue, primarily in the liver. Insulin upregulates lipogenesis, and newly synthesized lipids are transported from the liver to adipose tissues as very low-density lipoproteins (VLDL) (Denbow, 1999; Leclercq, 1984). Again, it is likely that both these factors and the hormones promoting lipogenesis signal possible increases in fat reserves.

7.2.2 Modelling the Regulation of Hoarding and Foraging

As mentioned above, the process of food ingestion includes two phases: an "appetitive" phase, where the animal searches for food, followed by a "consummatory" phase, where the food is eaten. Both foraging and hoarding behaviours are considered part of the appetitive phase in mammals (Craig, 1918; Keen-Rhinehart et al., 2010). However, this categorisation may not apply to titmice. Hamsters, for instance, are larder hoarders, storing all their food in a single location. This behaviour is supported by their ability to remember the cache's location. In contrast, scatter hoarding titmice distribute their caches across their environment and are known to forget the locations of these hoards after approximately 30 days (Brodin, 1994a; Hitchcock & Sherry, 1990; Male & Smulders, 2007). Given this tendency to forget, it is unlikely that the sequence of behaviours involved in food ingestion would be paused after hoarding (considered part of the appetitive phase) and later resumed when the food is consumed. Instead, interpreting hoarding as part of the consummatory phase seems more plausible in this context.

Historically in mammals, the motivation to hoard is thought to be regulated separately from the motivation to forage, which is caused by hunger, as they are thought to operate on different timescales and differ in the severity of energy depletion. Evidence for this has been found in several hamster species, where food hoarding intensity and food intake intensity are affected differently by food deprivation (Bartness & Day, 2003; Keen-Rhinehart et al., 2010).

On the other hand, in birds, It is known that food hoarding behaviour and food intake behaviours respond in the same way to artificially administered signals of nutritional state such as ghrelin and leptin (Boswell & Dunn, 2015; Henderson et al., 2018). This suggests that hoarding and foraging for food for consumption might be regulated in the same way.

Therefore, besides exploring the role of different physiological variables in foraging decision-making, I include several "hoarding strategies" in the different versions of my models. The “direct hoarding” models assume that hoarding is regulated independently of the motivation to forage and consume food, as seen in other food-hoarding *Paridae* models where “forage and hoard” and “forage and consume” are separate behaviours (Brodin, 2000; McNamara, Houston, & Krebs, 1990a; Pravosudov & Lucas, 2001a). The “leftover hoarding” models on the other hand, assume that foraging to eat and hoarding are regulated together, as suggested by the findings in Henderson et al. (2018). In models with this hoarding strategy, birds hoard only the food remaining after foraging and feeding until their stomach is full.

7.2.3 Study Overview and Aim

In summary, my models examine decision-making mechanisms underlying food-hoarding behaviour in two ways. Firstly, I investigate which physiological signals of the energetic state may regulate hoarding behaviour. For this purpose, I developed models assuming birds have access to information about stomach content, fat reserves, changes in fat reserves, or combinations of these two variables.

Second, I explore different configurations of these decision rules: some models regulate hoarding and foraging motivation as one behaviour, while others treat them as separate behaviours. Specifically, I include four distinct hoarding strategies: 1) “leftover hoarders,” as described above; 2) and 3) two types of “direct hoarders,” where one hoards only in high-energy states, while the other rests only in high-energy states; and 4) non-hoarding birds which function as a control group. The combination of energy indicators and hoarding strategies results in a total of 24 models.

These models will be evaluated based on their predicted winter survival and their alignment with known behavioural and physiological patterns in wild birds. Models performing best and aligning most closely with available data will be used to generate hypotheses about the decision rules that may underlie food-hoarding behaviour.

For R scripts of the full model code see https://github.com/Vera-Anne/.

7.2.4 The ODD Framework

The models will be presented following a standard framework for describing individual-based and agent-based models, originally developed by Grimm et al. (2006) and further refined in Grimm et al. (2010) and Grimm et al. (2020). This protocol, widely adopted in the field of Agent-Based Modelling (ABM) (see Grimm et al., 2020 and the list of citations therein), is known as the 'ODD protocol,' which stands for Overview, Design concepts, and Details. Table 1 outlines the structure of the ODD protocol.

In the following sections, I will describe the model developed for this thesis in accordance with the ODD protocol. The model is structured as a main framework, "the general model", comprising multiple "model versions", each with its own set of decision rules. The performance of the different model versions, described in section 4.9.8.1, will be compared in chapters 4, 5 and 6. A comparison and integration of the models in those chapters can be found in the general discussion of this thesis (see Chapter 8). As the ODD protocol is typically published as a standalone document, some overlap with other sections or chapters of this thesis may occur. For clarity, the headings below are followed with numbers in brackets, that correspond with the numbers in Table 7.1.

*Table 7.1***.** *ODD protocol outline. Image adapted from Grimm et al. (2006) and Grimm et al. (2010).*

Overview	1. Purpose and patterns	
	2. Entities, state variables and scales	
	3. Process overview and scheduling	
Design concepts	4. Design concepts	Basic principles
		Emergence
		Adaptation
		Objectives
		Learning
		Prediction
		Sensing
		Interaction
		Stochasticity
		Collectives
		Observation
Details	5. Initialization	
	6. Input data	
	7. Submodels	

7.3 Purpose and Patterns (1)

7.3.1 *Purpose*

The main purpose of my model is to theoretically explore different sets of decision rules that could be involved in food-hoarding behaviour in *Paridae* and generate hypotheses about the mechanisms underlying this behaviour. In particular, the model allows me to compare how different models, where foraging decisions are made based on variables such as stomach content, fat reserve and fat change rates, would affect survival, physiological factors and the behaviour of hoarding and non-hoarding birds across various simulated environments. Based on these comparisons, I can generate hypotheses about how hoarding motivation might be regulated in food-hoarding titmice. The model is built to reflect a "small *Parid* in winter" and does not attempt to realistically replicate any specific species or situation.

7.3.2 Patterns

The models generate patterns in three main categories; survival, physiological variables and behavioural patterns which will be used for model evaluation.

- **Pattern 1: Survival over time.** This pattern reflects how well agents survive the environments they are exposed to. This pattern was used to optimise the parameters in the decision-making rules, maximizing survival over time in standardized environments.
- **Pattern 2: Responses of physiological variables.** Birds will respond to their environment and behavioural decisions with changes in their physiological variables (stomach content and fat reserves).
- **Pattern 3: Behavioural responses**: given their decision-making rule and state variables, agents will make decisions in terms of their behaviour (e.g., resting, eating, hoarding, retrieving).

Daily patterns in variation of these variables as well as the patterns in behavioural responses can be compared to other models in the literature (Anselme et al., 2017; Brodin, 2000, 2007; Lucas & Walter, 1991; McNamara & Houston, 1990; Pravosudov & Lucas, 2001) and experimental findings (e.g., Karpouzos et al., 2005; Lilliendahl, 2002; Pravosudov & Grubb, 1997) for the purpose of hypothesis generation.

7.4 Entities, State Variables and Scales (2)

7.4.1 Entities

The model system consists of agents (birds) operating within an environment. This creates two hierarchical levels: the agents and the global environment. The birds represented by the agents are small titmice species such as coal tits (*Periparus ater*) or blue tits (*Cyanistes caeruleus*). Notably, there is no interaction between agents; each bird perceives its own stochastic environment.

7.4.2 State Variables

The global environment is described by its state variables. Table 4.2 lists each variable, its meaning, what values are possible, and in which processes it is involved. State variables 1-7 are stable throughout the simulation but vary between simulations. Variable 8 varies throughout simulated time.

The agents in the model are uniquely described by their state variables. Table 4.3 lists each variable, its meaning, what values are possible, and which process(es) it is involved in. State variable 1 is stable throughout the simulation but differs between individuals. State variables 2-18 reflect how the agent changes throughout simulated time.

7.4.3 Scales

Time steps (*TS*) in this model represent 20 minutes in real life time, which is a realistic timeframe for a bird to perform one of the behaviours of interest, without switching to another (Pravosudov & Lucas, 2001a). At the start of each simulation, one of the input parameters is the "*Days*" variable, which represents the number of days that the simulation will represent. The default for this variable is set to 30 days (2160 timesteps), representing a month in harsh winter conditions, which is a critical time of year for the bird species of interest. Spatial relationships and interactions between agents are not considered.

Table 7.2. State variables of the global environment. Meaning, range and the process in which the variable is updated are included.

#	State variable	Meaning	Range	Process
1	Simulation length**	One of the input parameters, the number of days reflected in the simulation.	Default = 30 days	None, input parameter
2	Number of agents**	The number of agents at the start of the simulation.	Default = 1000	None, input parameter
3	Food distribution**	The distribution type determines the predictability of finding food items. Food is either distributed with a Poisson distribution around the mean number of food items found at each foraging attempt, or with a more unpredictable "Bonanza" distribution with the same mean (see 4.6.9.3 for more details).	"Poisson" or "Bonanza"	None, input parameter
4	Food abundance**	Mean number of food items found at each foraging attempt.	Theoretically >=0, default range is 3-5	None, input parameter

5	Temperature range**	Ranges for the minimum and maximum temperatures are dictated by the global environment. The actual temperatures and how they fluctuate between timesteps are unique for each agent (see table 3)	The range for maximum temperatures is -3 to 13. For minimum temperatures this is -13 to 3ºC	None, input parameter
6	Day length**	The number of hours within a 24-hour day that there is day light. *	Default = 8 hours	None, input parameter
7	Decision rule**	Each bird will use a specific decision rule to determine which behaviour it will perform depending on its other state variables. Please see the *Decide behaviour* process for details on the different rules.	24 models, see Table 8	None, input parameter
8	Timestep	Timestep within the entire simulation. Each timestep reflects 20 minutes in time.	1 to (days * 72) , with days as the total number of simulated days	*Update time of day*

**Note: The number of daylight hours within the day is flexible but does not change between simulations within this thesis. Future work could investigate variation in this variable.*

*** Note: Marked state variables are input parameters set by the modeller. Therefore, these do not differ through simulated time but can differ between simulations. Therefore, technically, they are parameters, not "variables".*

Table 7.3. State variables of the agents. Meaning, Range and the process in which the variable is updated are included.

#	***State variable***	***Meaning***	***Range***	***Processes***
1	Identity	Each agent in a simulation has a number. This can be used to retrieve agent-specific state variables from the matrices. If all other state variables are the same, this number distinguishes individuals.	>=1	-
2	Life status	Each agent is either alive or dead at any given time step.	'0' for a dead bird and '1' for an alive bird.	*Update life status, Predation, Prepare for next timestep*
3	Mass	The mass of the bird at the start of the current timestep. This consists of the initial mass of the bird (allocated at initiation of the simulation), the fat reserves and the stomach content.	8.07 – 12.5	*Decide behaviour, Metabolism*

4	Fat reserve (FR)	At any given timestep, each agent has a fat-reserve in grams.	0-4 gram	*Decide behaviour, Update metabolism*
5	Stomach content (SC)	At any given timestep, each agent has a stomach-content in grams. This value is corrected for metabolic efficiency, so that it is equal to the amounts of fat a bird will gain from the contents. See 4.6.1 for further detail.	0-0.4 gram	*Decide behaviour, Update metabolism*
6	Fat loss-rate (FCR)	The amount of fat in grams that a bird has lost (-) or gained (+) over the last 2 hours.	-0.6 – 0.6 gram/2 hours	*Update FCR, Decide behaviour*
7	Number of caches	The number of caches a bird possesses. Note that this is only available for model versions with “direct-hoard” or “leftover-hoarding” decisions rules.	0-100	*Update caches, Decide behaviour, Pilferage*
8	Sleep*	Indicates if the bird was “Sleeping” in the current timestep. Note that this variable directly responds to the “Time of day” variable in the environment.	1 or 0	*Decide behaviour*
9	Rest*	Indicates if the bird performed the “Resting” behaviour in the current timestep.	1 or 0	*Decide behaviour*
10	Forage	Indicates if a bird went out to “Forage” in the current timestep. Note that this behaviour can precede “Eat”, “Eat-hoard” and “Direct-hoard” behaviours. It is, on the other hand, mutually exclusive with “Sleep”, “Rest” and “Retrieve”.	1 or 0	*Decide behaviour*
11	Find food	The number of food items found in the current timestep.	>=0, *NA* if bird did not forage.	*Decide behaviour*
12	Eat*	Indicates if the bird performed the “Eating” behaviour in the current timestep. Note that this is just for birds that ate all the food they found. If the bird hoarded the leftover food, this variable takes “0” and “Eat-hoard” will take “1”. “Eat” is always preceded by the” Forage” behaviour.	1 or 0	*Decide behaviour*

13	Eat-hoard*	Indicates if the bird performed the "Eat then hoard leftovers" behaviour in the current timestep. Note that this is only available for versions of the model with a "leftover-hoarding" decision rule.	1 or 0	*Decide behaviour*
14	Direct-hoard*	Indicates if the bird performed the "Direct-hoarding" behaviour in the current timestep. Note that this behaviour is only available for versions of the model with a "Direct- hoarding" decision rule.	1 or 0	*Decide behaviour*
15	Retrieve*	Indicates if the bird performed the "Retrieval" behaviour in the current timestep. Note that this behaviour is only available for versions of the model with "Direct-hoarding" and "Leftover-hoarding" decision rules.	1 or 0	*Decide behaviour*
16	Predation	Indicates if the bird experienced a successful predation attempt in the current timestep.	1 or 0	*Predation*
17	Cache decay	The number of caches that decayed in the current timestep. Note that this is only available for versions of the model with "Direct-hoard" and "Leftover-hoard" decision rules.	>=0	*Pilferage*
18	Temperature	The temperature at each timestep of the simulation. Note that the temperature profile is unique for each agent within the simulation. Depending on *Temperature range* input variables	Range between -13 and 13ºC	*Update temperature*

**Note: these behaviours are mutually exclusive. Only one of these can be set to "1" in each timestep.*

*** Note: Marked state variables are input parameters set by the modeller. Therefore, these do not differ through simulated time, but can differ between simulations. Therefore, technically, they are parameters, not "variables".*

7.5 Process Overview and Scheduling (3)

7.5.1 Scheduling Overview

The general model has a nested loop design where the outer loop iterates through each individual and the inner loop iterates through each timestep in the simulation. The following scheduling summary will list the processes (in ***bold italics***) and in which order they take place. These processes are described in more detail under the "submodels" section of this protocol.

1. ***General set-up:*** Parameters for both the global environment and the agents are initialised. Input parameters (*days, number of birds, day length, decision rule*) are used to calculate the (initial) values of the state variables (Table 4.2 and Table 4.3)
2. <u>Individuals-loop:</u> The outer loop iterates through all individuals in the simulation in order from 1 to *N* with *N* being the total number of initiated individuals. For each individual agent the following processes take place:
    I. ***Generate temperature profile:*** The agent-specific temperature profile for the simulation is created using the state variables form the global environment (*day length, days, temperature ranges*).
    II. ***Individual set-up***: Matrices that track the agent's state variables are initiated and state variables that change over simulated time are populated with initial values.
    III. <u>Timestep-loop</u>***:*** the inner loop iterates through all timesteps in the order of 1 to *TS* with *TS* being the number of timesteps in the current simulation. For each timestep, the following processes take place:
        i. ***Update FCR***: the *Fat change rate* is determined based on the *Fat reserves* of the bird at the end of the previous timestep (T-1) and six timesteps before that (T-7). For timesteps 1-7, previously estimated *Fat change rates* are used.
        ii. ***Update temperature***: The temperature for the current timestep is retrieved from the previously established agent-specific temperature profile.
        iii. ***Update time of day***: The global state variable for *time of day* is updated
        iv. ***Update life status:*** the *life status* of the bird is updated based on the outcome of the previous timestep.
        v. ***Decide behaviour:*** A crucial process in my models, as the different versions of the model vary in which decision rules are used to determine the behaviour that the bird performs. Decisions are made based on the hoarding type of the bird (non-hoarding, direct hoarding, leftover hoarding) and the decision-making variable(s) of the bird (*Stomach content, Fat reserve* and/or *Fat change rate*). Birds can decide to "sleep", "rest", "forage and eat", "forage, eat and hoard leftovers", "forage and hoard" or "retrieve" a food item. Behavioural *(Sleep, Rest, Forage, eat, Direct-hoard, Leftover-hoard and Retrieve*), physiological (*Stomach content, Fat reserve and Fat change rate*) and other state variables (*food items found*) are updated accordingly.

vi. ***Predation:*** Based on the birds' current *mass* and the predation risk parameter, a predation event can take place. The *life status* and *predation* state variables of the agents are updated.

vii. ***Prepare for next timestep***/ Leave loop when all timesteps are done: Saves the current agent's matrices and retrieves the next agent's matrix (go back up to #2), or ends the loop

IV. Save results

7.5.2 *Rationale*

As illustrated in Figure 4.1, the processes in my model are scheduled sequentially. The "***General set up***" process occurs before the agents or timesteps are initiated, ensuring that all parameters are correctly defined. Once the agents are initialized, their temperature profiles are generated ("***Generate temperature profile***"), which allows the model to reference the "current" temperature from this vector at each timestep. This daily variation in temperature is included because temperatures in areas where these titmice live in the wild, are known to vary throughout the day with minima just before sunrise (Gosler, 2002). Therefore, temperatures play an important role in the models, and various processes are dependent on it (e.g., ***Decide behaviour, Metabolism***).

Next, the loop that iterates through each day for each agent begins. The first process is "***Update FCR***", where the current *Fat change rate* of the bird is updated. This occurs first because the *Fat reserve* values calculated in the previous timestep must be used. Next, the *Temperature* and *Time of day* are updated for the new timestep, followed by a check to determine if the bird is alive. These three processes can theoretically occur in any order, as their outcomes are independent of each other. Only living birds proceed to the next key stage in the models, where they decide on a behaviour ("***Decide behaviour***"). Birds chose the behaviour they will engage in, which is a crucial decision as their energy expenditure and uptake are highly dependent on this process. Since this decision depends on the bird's *Stomach content*, *Fat reserves*, and *Fat change rate*, it must occur before any metabolic changes or movements of food up to the *Fat reserves.* If, during these behaviours, the bird consumes food items, its stomach content is updated immediately.

Predation is included in the model because it is known that passerines experience a starvation-predation trade-off, where their probability to be killed by predators increases with their body weight (Anselme et al., 2017; Lima, 1986; McNamara & Houston, 1990a). Therefore, the ***Predation*** process depends not only on the bird's chosen behaviour, but also on the bird's weight. It is crucial that ***Predation*** takes place before the next process, ***Metabolism***, where food is transferred from the stomach to fat reserves and metabolic rates are updated according to environmental conditions, but after the bird has (possibly) consumed food in the previous process (***Decide behaviour***),

Following ***Metabolism***, ***Pilferage*** occurs, during which some caches decay. The exact timing of ***Pilferage*** is not critical, although it must take place after the ***Decide behaviour*** process, where agents may eat from their own cache storage. The final process prepares agents for the next timestep.

7.6 Design Concepts (4)

7.6.1 Basic principles

7.6.1.1 System Level

On a system level, this model addresses questions about how food-hoarding *Paridae* make decisions about their foraging behaviours as they navigate the pressures from harsh winter environments that include long nights, low temperatures, and low food availability (Brodin, 2007; Grubb & Pravosudov, 1994; Pravosudov, 2006). It also incorporates additional processes such as mass-based predation and pilferage of hoarded caches (Bonter et al., 2013; McNamara & Houston, 1990a; Pravosudov & Grubb, 1997). The way that decision-making is modelled in my models, is different from other computational models on food-hoarding titmice. Most models in the literature have used a dynamic approach and investigated the optimal behavioural patterns that small *Paridae* in harsh winter environments should employ (Brodin, 2000, 2007; McNamara, Houston, & Krebs, 1990a; Pravosudov & Lucas, 2001a). Instead of optimizing for behavioural patterns that maximize survival rates, I am testing a series of predetermined decision rules and comparing their performance. While novel in this context, structured decision rules have been employed in other agent-based models of foraging behaviour (Anderson, 2002; Anselme et al., 2017; DeAngelis & Diaz, 2019).

7.6.1.2 Agent Level

At the agent level, birds respond to their environment in a realistic manner. The main processes reflecting this are ***Update temperature***, ***Metabolism***, ***Predation***, and ***Pilferage***. The models are partially based on dynamic models of food hoarding *Paridae*, primarily those by Pravosudov and Lucas (2001).

The temperature of the environment, as set in the ***Update temperature*** process is important to determine the *Basal Metabolic Rate* (BMR) and *Metabolic Rate* (MR) of the birds. The bird's weight, which includes *Base weight*, *Fat reserves*, and *Stomach content*, also factors into these calculations, conducted during the ***Metabolism*** process. The equations used for these calculations are consistent with the literature on small *Paridae* species in winter (Brodin, 2000; Lucas & Walter, 1991; Pravosudov & Lucas, 2001a).

During ***Metabolism***, food is transferred from the stomach to fat reserves. Following Pravosudov and Lucas (2001) and Cockcroft (2009), it is assumed that each food item provides an equivalent of 0.064 grams of fat. Food items are thus processed as "fat equivalents." Consequently, the bird's stomach capacity is adapted to hold up to 0.4 grams of "fat equivalent" food, corresponding to a maximum of six food items (0.4 / 0.064). When food is moved from the stomach to the fat reserves, further metabolization is not required, as the items are already in "fat equivalent" form. For example, 0.1 grams of "fat equivalent" food in the stomach directly contributes 0.1 grams of fat to the reserves.

The ***Predation*** process is included to account for the trade-off between starvation and predation, which influences the behavioural strategies of hoarding and non-hoarding titmice (e.g. Macleod et al., 2005; Pravosudov & Grubb, 1997). As in Pravosudov and Lucas (2001), the weight of the agent is taken into account when calculating the likelihood of surviving a predation attempt.

The ***Pilferage*** process accounts for the fact that, in the wild, birds either forget some of their caches or have them stolen by others (Hitchcock & Sherry, 1995). The equations used here follow those of Pravosudov and Lucas (2001).

To explore the possibility that birds decide whether to eat or hoard food items based on their “current” physiological state, I developed a series of model versions incorporating different foraging decision-making rules, which are reflected in the ***Decide behaviour*** process. These rules vary in terms of the physiological information available to the birds when making decisions. For instance, some models assume that birds base their decisions to rest, forage, or retrieve food on stomach content, while others use fat reserves and/or fat change rate (i.e., energy flux) as decision-making inputs. I consider these three variables, or "energy proxies," as they provide the birds with information about their energetic state and signal recent food availability, which can then influence decision-making (see 4.6.7 for details).

Additionally, the models differ in terms of the bird's behavioural strategies: some birds are non-hoarders, which may reflect the ancestral condition from which hoarding birds evolved (Johansson et al., 2013; Štorchová et al., 2010). In addition, I explore various hoarding strategies. In other models that explore the energy management of wintering titmice, hoarding is assumed to be regulated separately from the motivation to eat (Brodin, 2000; McNamara &

Houston, 1990; Pravosudov & Lucas, 2000; Pravosudov & Lucas, 2001a). The current model, however, explores various hoarding strategies that assume separate regulation (direct-hoarding models described below) and simultaneous regulation of hoarding and eating (leftover-hoarders described below). Again, this model seeks to test how these different decision rules, with different hoarding strategies, influence processes such as feeding, changes in fat reserves and hoarding behaviour.

7.6.2 Emergence

The three main model results that emerge from the simulations are 1) survival rates; 2) fluctuations in physiological variables and 3) Behaviour patterns. These emerge from a combination of the environment that is imposed on the agents (temperature, food distribution and food abundance) and the decision-making rules that the different model versions use to determine what behaviour an agent performs at each step. The latter is again dependent on state variables in the agents themselves, which fluctuate throughout time and are affected by the environment and previous decisions. Behaviour patterns and fluctuations in physiological variables are direct results of this complex integration. Survival rates emerge indirectly, through starvation and predation processes.

7.6.3 Adaptation

The adaptive behaviour of the agents involves making decisions about which behaviour to undertake at each time step. The available behaviours include sleeping, resting, foraging and eating, foraging and hoarding, retrieving and foraging, and eating and hoarding. These decisions are influenced by the energy proxies utilized in the agents' decision rules, as well as the specific hoarding strategy they employ.

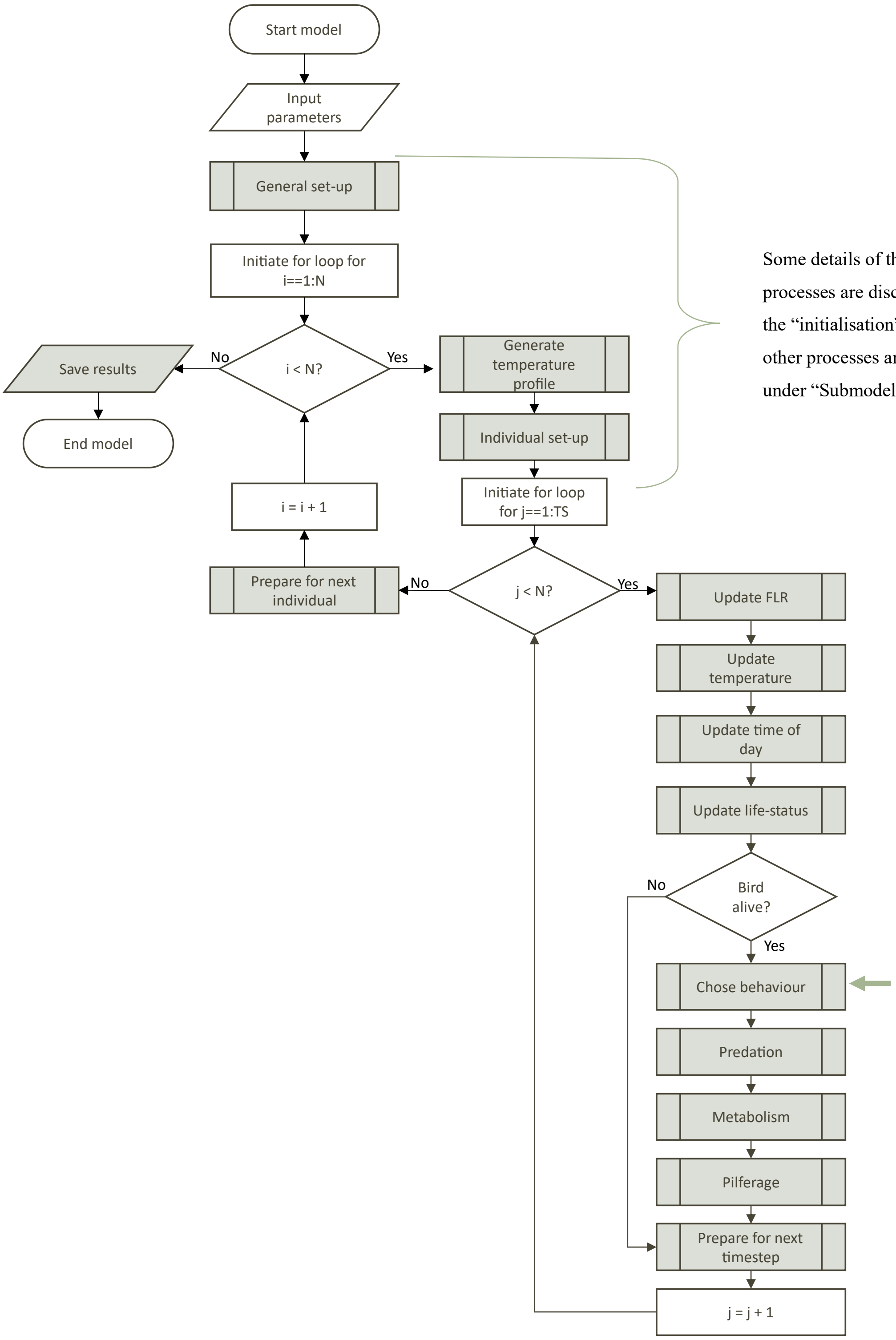
The energy proxies reflect the energetic state of the bird and include stomach content, fat reserves, and fat change rates. The hoarding strategies are categorized as non-hoarding, leftover-hoarding, and direct hoarding, with leftover-hoarding occurring in the most energy-rich state and direct hoarding incorporating resting in the most energy-rich state. A comprehensive description of the various decision rules can be found in section 4.9.8.

7.6.4 Objectives

As adaptation and fitness-seeking are not modelled, agents have no objectives.

7.6.5 Learning

There are no adaptive traits in this model, therefore they do not change over time and learning is not present.



Some details of these three processes are discussed under the "initialisation" section. All other processes are discussed under "Submodels".

This is where the "model versions" differ in their decision rules.

Figure 7.1. Overview of the general model. The model consists of 2 nested loops. Any processes are indicated with green squares. The first (outer) loop iterates through all individuals. It generates a specific temperature profile, initiates parameters, and generates some FCR values. Then, it enters the inner loop which iterates through all timesteps. For each timestep, the agent updates FCR values, temperatures, time of day and life status. A behaviour is chosen, and the predation and metabolism processes are started. After both loops have finished, the results are saved. See the "submodels" section below for details on the processes and decision rules.

7.6.6 Prediction

Agents do not predict future experiences.

7.6.7 Sensing

Agents have direct access to information about the time of day (is it day or night). They use this to decide whether to sleep (at night) or perform one of the other behaviours (during the day). This represents the circadian and hormonal mechanisms in titmice, which have a diurnal rhythm with a nocturnal sleeping period (Amlaner & Ball, 1983; Amo et al., 2011)

Agents were given access to their own *Fat reserve*, *Stomach content* and/or *Fat change rate*, depending on the decision rule (model version) used by the agent (see 4.9.8.1 for details).

It is realistic to assume birds have information about how full their stomach is. Mechanoreceptors in the wall of their stomach will inform the bird about the fullness of the stomach through the Vagus nerve (Denbow, 2015). On top of this, Ghrelin, a peptide hormone secreted by the proventriculus, inhibits food intake in birds (Boswell & Dunn, 2015; Henderson et al., 2018; Kaiya et al., 2009).

When birds absorb nutrients from their food, such as lipids, these first the liver through the vena porta. It has been shown that the rate of lipid absorption and metabolism in the liver can affect food uptake in birds (Denbow, 1994, 1999). Besides, factors that circulate in the blood when lipolysis and lipogenesis takes place, can inform birds about the state of their fat reserves. Through lipolysis, stored fat in the form of triglycerides is broken down into free fatty acids and glycerol for energy use. It is not unlikely that these circulating factors, as well as the hormones regulating this process (e.g. epinephrine, norepinephrine, glucagon), can be used to inform birds about the state of their fat reserves and the rate at which they are decreasing (Denbow, 1999; Leclercq, 1984). A similar argument can be made about lipogenesis, the metabolic process where carbohydrates are converted into fatty acids and stored in adipose tissue as triglycerides, which in birds mostly takes place in the liver. Lipogenesis is upregulated by insulin. Newly synthesised lipids are transported from the liver to adipose tissues as very low density lipoproteins (VLDL) (Denbow, 1999; Leclercq, 1984). Again, it is likely that these factors as well as the hormones upregulating lipogenesis, can inform birds about possible increases of their fat reserves.

Finally, agents have access to the number of food caches they have stored. This information is used solely when deciding whether to forage for new food items or retrieve stored ones. If the number of caches is zero, birds will not attempt to retrieve food. It is realistic to assume that birds are aware of the existence of their caches, as they are known to memorize not only the presence but also the locations of their caches over extended periods (Male & Smulders, 2007; Sherry, 1984; Shettleworth et al., 1995)

7.6.8 Interaction

Agents do not interact with each other.

7.6.9 Stochasticity

Stochasticity was introduced at several points in the models.

7.6.9.1 Initial Values

When agents are initialised in the Individual set-up process, the allocation of initial values is pseudo-randomised. The initial base weight of birds, as well as their initial *Stomach content*, *Fat reserves* and initial *number of caches* stored, are sampled from truncated normal distributions with relevant values (see 4.7 for details).

7.6.9.2 Temperature

To reflect differences in temperatures that birds at northern latitudes might experience without modelling weather specifically, each agent in each simulation experiences its own environment in terms of temperature. Whilst the minimum and maximum ranges are determined by the input parameters (#5 in Table 4.2) the exact values experienced by birds are pseudo-randomised. The exact minimum and maximum temperatures of each day are randomly sampled from the predefined ranges. See section 4.9.2 for details.

7.6.9.3 Finding Food

Whilst the mean number of food items found as well as the predictability of finding items is determined by the input parameters (#3 and #4 in Table 4.2), the chances of birds finding food items on individual foraging bouts, is stochastic. In both the “Poisson scenario” and the “Bonanza scenario” (see 4.9.8.2 for details) agents randomly sample from a distribution and find a number of food items (between 0 and 24). This stochasticity is implemented to reflect the circumstances in nature, where birds don’t always find food items when they are out foraging.

7.6.9.4 Predation

To reflect real-life predation risk without modelling complex predator-prey interactions, the ***Predation*** process is stochastic in terms of predation success. The chance of being killed by a predator (P_{kill}) is calculated based on the chance of an attack (P_{attack}) and the chance of capture ($P_{capture}$). P_{attack} is a model parameter based on the bird’s current behaviour. $P_{capture}$ is dependent on the bird's weight. P_{kill} is then compared to a random number between 0 and 1. If this number is smaller than the P_{kill}, the bird dies. See section 4.9.9 for details.

7.6.9.5 Pilferage

For each agent in each timestep, the probability of one or more caches decaying is calculated based on the number of caches the bird has. This probability is then compared to a random number between 0 and 1, if the probability of one or more items decaying is larger than this number, an item disappears from the bird's stash. This stochasticity is brought in to reflect the variation in nature where birds might forget caches or lose them to conspecifics finding them. See section 4.9.11 for more details.

7.6.10 Collectives

There are no collectives in this model, agents do not interact or group.

7.6.11 Observation

The state variables for the agents are recorded on an individual level at the end of each timestep (variables 3-18 in Table 4.3). When evaluating model outcomes, the mean value of these variables across all living birds at each timestep is used. For the *life status* variable, this is the proportion of birds that started the simulation that is still alive. For the state variables that concern behaviours (*Rest, Sleep, Direct-hoard*, etc.), the proportion of living birds that are doing the behaviour is used. Other variables, such as the physiological variables (S*tomach content*, F*at reserves* and *Fat change rate*) are averaged across all living birds.

When evaluating daily patterns in behaviours or physiological variables, these variables are aggregated across days. For example, the average proportion of surviving birds that were "E*ating*" at each timestep (first, second, etc.) is calculated across all 30 days of the simulation.

Although the means are the primary focus of the model evaluations, individual values of each variable for each agent at each timestep are recorded for completeness.

7.7 Initialisation (5)

Initialisation of the model takes place at two levels. First, the ***General set-up*** process initializes the environment and its state variables. Most state variables of the environment are assigned using the input parameters of the model, which are set by the modeller at the start of the simulation (see Table 4.4).

Table 7.4. Initial values for the environment level variables that are initialised in the "General set-up" process.

Variable	***Value***	***Meaning***	***Input parameter?***
Time of day	1	At the start of the simulation, the time of day is set to sunrise, which means birds experience daylight.	No
Timestep	1	The simulation starts at timestep 1.	No
*Simulation length**	Any integer >10	The number of days in the simulation. Set by the modeller at the start of the simulation.	Yes
*Food distribution**	Integer between 3-5	Average number of food items found per foraging bout. Set by the modeller at the start of the simulation.	Yes
*Food predictability**	"Bonanza" or "Poisson"	Food distribution setting (see 4.9.8.2 for details). Set by the modeller at the start of the stimulation.	Yes
*Minimum temperature range**	Range between 2 integers	Range in which the daily minima fall (degrees Celsius). Set by the modeller at the start of the simulation	Yes
*Maximum temperature range**	Range between 2 integers	Range in which the daily maxima fall (degrees Celsius). Set by the modeller at the start of the simulation	Yes
*Day length**	Integer	Number of daylight hours within a day. Set by the modeller at the start of the simulation.	Yes

** Note: Marked variables are input parameters set by the modeller at the start of the simulation. These do not change throughout simulated time but can differ between simulations. Therefore, technically, they are parameters, not "variables".*

The second level of initialisation takes place at the agent level in the ***Individual set-up*** process. The number of agents that is initialised depends on the input parameters and is set by the modeller at the start of the simulation. See Table 4.5 for a list of the agent state variables that are initialised in the ***Individual set-up*** process. See section 4.9.3 for more details on the process itself.

Finally, for each agent, an individual temperature profile is generated in the ***Generate temperature profile*** process, utilising the *Minimum* and *Maximum temperature range* values assigned in ***General set-up***. Details of how the temperature profile for each agent is calculated can be found in section 4.9.2.

Table 7.5. Initial values for the agent level variables which are initialised in the "Individual set-up" process.

Variable	***Value***	***Meaning***	***Reference***	***Input parameter?***
Life status	1	Each agent is either alive or dead at any given time step. Agents start the simulation alive.	-	No
Stomach content	0	At the start of the simulations, birds wake up from the night, so they are assumed to have an empty stomach.	-	No
Fat reserve	0 - 4	A random float (2 decimal points) drawn from a truncated normal distribution of minimum 0 and maximum 4, with 4 grams being the maximum fat reserve in a bird. With a mean of 2 and a standard deviation of 1.	Lucas & Walter, 1991; Pravosudov & Lucas, 2001	No
Mass	8 – 12.5	The total mass of the bird consisting of the base weight, stomach content and fat reserve of the bird. The base weight is 8 + a randomly drawn float (2 decimals) from a truncated normal distribution between 0.01 and 0.20 with a mean of 0.1 and a standard deviation of 0.01.	Lucas & Walter, 1991; Polo et al., 2007; Pravosudov & Lucas, 2001	No
*Caches***	50-100	A random integer drawn from a normal distribution between 50 and 100. Simulations reflect 30 days in winter, in which hoarding birds are assumed to have hoards from the preceding months. The mean is 75 and the standard deviation is 25.	-	No
*Decision rule**	One of 24 model versions	Each agent has a decision rule which it uses to decide what behaviour to perform in each timestep. The decision rules are described in section 4.9.8.1. Set by the modeller at the start of the simulation.	-	Yes

** Note: Marked variables are input parameters set by the modeller at the start of the simulation. These do not change throughout simulated time but can differ between simulations. Therefore, technically, they are parameters, not "variables".*

*** Note: The number of initial caches is flexible but does not change between simulations within this thesis. Future work could investigate variation in this variable.*

7.8 Input Data (6)

The model does not use input data to describe time-varying processes. It does, however, use input parameters that are set by the modeller. These have all been mentioned in the previous sections (see Table 4.2 and Table 4.3 table with state variables and Table 4.4 and Table 4.5 with initial values), but for clarity, they are repeated in Table 4.6.

Table 7.6. Input variables to be assigned by the modeller at the start of a simulation. These are taken from Tables 4.2, 4.3, 4.4 and 4.5, combined for clarity.

#	***Name***	***Meaning***	***Default value***
1	*Simulation length*	The number of days in the simulation.	30
2	*N*	The number of individuals in the simulation.	1000
3	*Food distribution*	The distribution type determines the predictability of finding food items. Food is either distributed with a Poisson distribution around the mean number of food items found at each foraging attempt, or with a more unpredictable "Bonanza" distribution with the same mean (see 4.9.8.2 for more details).	"Poisson" or "Bonanza"
4	*Food abundancy*	Mean number of food items found at each foraging attempt. Can theoretically take any integer >0.	2, 3 or 4
5	*Minimum temperature range*	Range in which the daily minima fall (degrees Celsius). Takes any two integers.	-13 to -7ºC for a "cold" environment. -3 to 3ºC for a "warm" environment.
6	*Maximum temperature range*	Range in which the daily maxima fall (degrees Celsius). Takes any two integers.	The default for a "cold" environment is -3 to 3ºC . The default for "warm" environments is 7 to 13ºC
7	*Day length*	The number of hours within a 24-hour day that there is day light.	8
8	*Decision rule*	Each agent has a decision rule which it uses to decide what behaviour to perform in each timestep. The decision rules are described in section 4.9.8.1.	No default value.

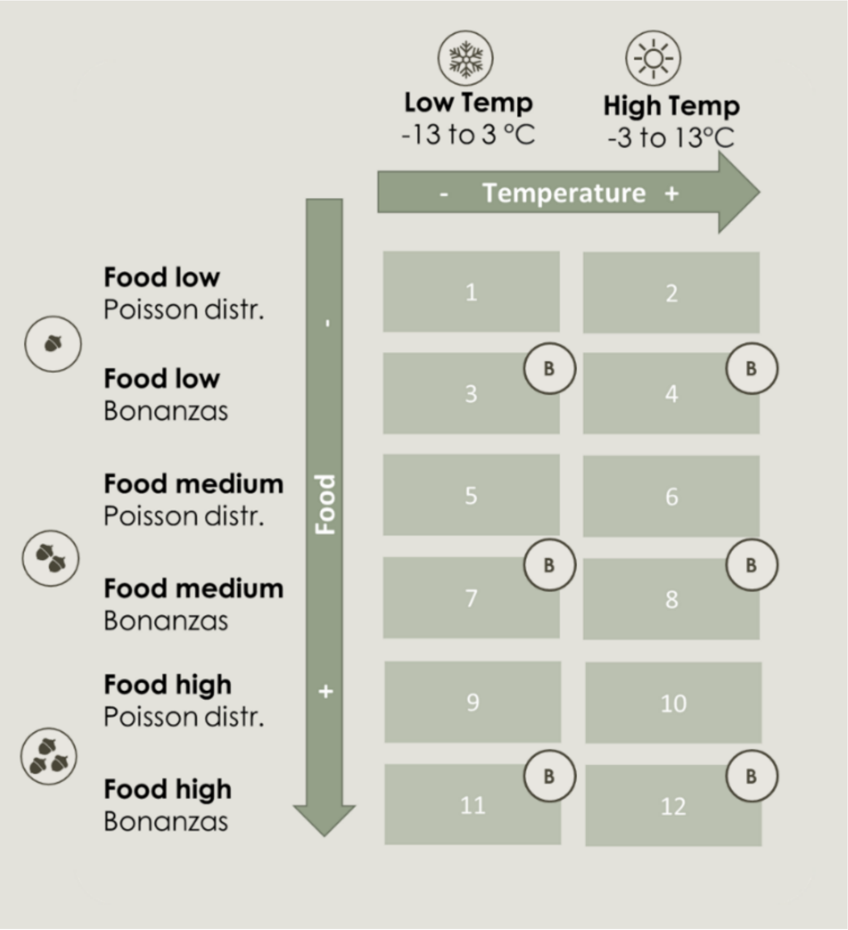


Figure 7.2. Standardized 12 environments used in model simulations. There are two levels of temperature (low and high), two types of food predictability (Poisson and Bonanza) and 3 types of food availability (low, medium, and high).

Theoretically, the values for variables 3, 4, 5, and 6 in Table 4.6 can take any of the available options. However, for simplicity, I simulate agents in standardized environments that combine default settings for food predictability, food abundance, and temperature (Figure 4.2). There are two temperature levels: low-temperature environments range from a minimum of -13ºC to a maximum of 3ºC, while high-temperature environments range from -3ºC to 13ºC. Food predictability is categorized into two types: "Poisson" and "Bonanza," with the latter representing a more unpredictable scenario (see Section 4.9.8.2 for details). Food availability is set at three levels. In low-food environments, agents find an average of 3 food items per foraging bout; in medium-food environments, this increases to 4 items; and in high-food environments, agents find an average of 5 items per bout. These standardized environments were used to optimize the decision rules, as discussed in Section 4.9.8.3.

There are 12 submodels or "processes" in the general model which are described in the following sections (Figure 4.1).

7.9 Submodels (7)

7.9.1 General Set-up

This process initialises the state variables for the environment (see 4.7 and Table 4) and defines key parameters for the subsequent processes (Table 4.7).

Table 7.7. Parameters defined in the "General set-up" process.

Variable	***Value***	***Meaning***	***Reference***
Maximum fat	4	The maximum fat reserve of a bird in gram, corrected for metabolic efficiency.	Cockcroft (2009), Pravosudov & Lucas (2001)
Minimum cache	50	The minimum number of caches a bird can have when initialising the cache number	-
Maximum cache	100	The maximum number of caches a bird can have when initialising the cache number.	-

In addition, the following parameters are calculated based on previously initiated variables:

1) **Calculate the total number of timesteps:** using the *simulation length* input variable:

$$TS = simulation\ length * 72$$

Equation 4.1

2) **Calculate timesteps in daylight:** The number of timesteps per day where daylight is present using the *day length input* variable:

$$n\ timesteps\ in\ daylight = day\ length * 3$$

Equation 4.2

After the ***General set-up*** is finished, the model will start iterating through each of the individual agents.

7.9.2 Generate Temperature Profile

This process creates a temperature profile for the agent that will be initialised in the next process (***Individual set-up***). The following steps are taken in the order presented:

1) **Create vectors with daily minima and maxima:** a vector with daily minima is created by taking random samples (as many as there are days in the simulation) from the

minimum temperature range. The same is done for a vector with daily maxima. At this point, the *Tmax* and *Tmin* of each day are known.

2) **Generate daily temperature profiles:** assuming that the maximum temperature in the day takes place at 75% of daylight hours, and the minimum temperature takes place just before sunrise, a daily temperature profile is generated for each day (Figure 1). The temperature increments are calculated as:

$$Size\ of\ intervals = \frac{\Delta\, Temperature\ (\max - \min)}{\Delta\, Time\ (\max - \min)}$$

Equation 4.3

Note that the timing of *Tmax* and *Tmin* is the same for each day in the simulations. However, the code allows for future changes in day length if simulations were to include seasons.

3) **Concatenate daily profiles:** the daily temperature profiles are concatenated, and the complete temperature is ready to be used by the agent initialised in the next process.

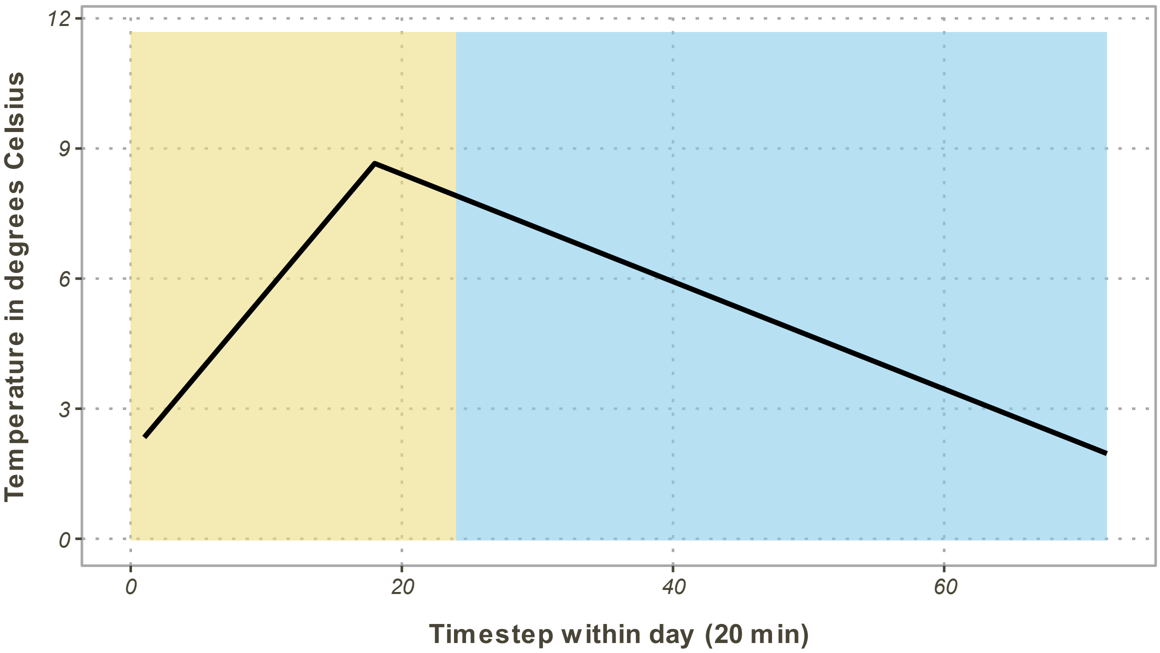


Figure 7.3. An example of a temperature profile for the default environments with "high" temperatures. The peak of the line shows the maximum, with the minimum of the day taking place at timestep 72. Timesteps in the yellow block take place in daylight. Timesteps in the blue block are in the nighttime. The steepness of the line before the maximum is determined by the minimum of the previous day.

7.9.3 Individual Set-up

This process assigns the initial values for individual agents as listed in Table 4.5. After individuals are initialised, the loop that iterates through each agent is started. The following processes take place at each timestep.

7.9.4 Update Life Status

For each agent, the life status at the previous timestep is checked. Birds that were dead previously will remain dead in the current timestep. The fat reserve of the bird is also checked. If it is equal to 0 the bird dies. Birds that are alive will execute the ***Update FCR*** process. Birds that are dead will go to ***Prepare for next timestep***.

7.9.5 Update FCR

In this process, birds update their fat change rate (FCR). This value is based on the change in fat reserves the bird experienced in the last 6 timesteps, resulting in a value expressed in grams per 2 hours. The following events take place, depending on the timestep the bird is in:

For birds in timestep 1-7:

1) **Estimate fat reserves for T_{-7} – T_{-1}:** The simulation starts at sunrise, so it is assumed that birds were sleeping during the hypothetical timesteps preceding the start. Energy expenditure during this period is calculated using the same functions as in the ***Metabolism*** process (see section 4.9.10). Using the bird's initial mass at T_1 (timestep 1) as well as the temperature at T_1, the fat reserve at T_{-1} (timestep -1) is estimated. This value, along with the same temperature, is then used to estimate the fat reserves at T_{-2}, T_{-3}, and so on.
2) **Calculate FCR for T_1 – T_7:** The fat change rate for each of the first seven timesteps can be calculated using the estimated fat reserves for T_{-7} To T_{-1}.
3) **Update current FCR:** depending on the timestep, the correct FCR is recorded.

Birds in timestep 8 onwards:

1) **Calculate FCR:** The fat change rate is calculated based on the fat reserves (FR) at T_{-7} and T_{-1} of the current timestep.

$$Current\ FCR = FR_{T-1} - FR_{T-7}$$

Equation 4.4

2) **Update current FCR**: record the FCR for the current timestep

7.9.6 Update Temperature

The temperature value for the current timestep is retrieved from the individual temperature profile generated in ***Generate temperature profile*** and recorded.

7.9.7 Update time of day

The time of day is determined using the current timestep and a modulus function:

$$base\ timestep = T \ \ mod\ 72$$

Equation 4.5

The *base timestep* represents the position of the current timestep within a day, where a day consists of 72 timesteps. Here, T is the current timestep. For example, if T =74, the *base timestep* is 2, and if *T* = 725, the *base timestep* is 5. If the *base timestep* is less than or equal to the *number of timesteps with daylight* (see ***General set-up***), the *time of day* is classified as "day" (assigned a value of 1). Otherwise, it is classified as "night" (assigned a value of 0).

7.9.8 Decide behaviour

Decide behaviour is the central process in the models, as this is where birds select the behaviour they will perform in each timestep, based on their physiological variables. As described in section 4.9, the modeller determines the *decision rule* of the agents at the start of the simulation.

Table 7.8. The 24 model versions with decision rules based on hoarding type and energy proxy The colours indicate clusters of models that are structurally similar (see section 4.9.8.1). From left to right and top to bottom: group 1, 2, 3, 4, 5, 6, 7 & 8. The first number in each cell indicates the type of energy proxy that is used (1 = Stomach content, 2 = Fat reserve, etc.). The second number indicates the hoarding strategy (1 = non-hoarder, 2 = leftover-hoarder, etc.).

		Non-hoarder	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
1 energy proxy	*Stomach content*	1.1	1.2	1.3	1.4
	Fat reserve	2.1	2.2	2.3	2.4
	Fat change rate	3.1	3.2	3.3	3.4
2 energy proxies	*Fat reserve & Fat change rate*	4.1	4.2	4.3	4.4
	Stomach content & Fat reserve	5.1	5.2	5.3	5.4
	Stomach content & Fat change rate	6.1	6.2	6.3	6.4

Decision rules vary in two main ways. Firstly, agents can have different "*hoarding types*" and can be categorized as non-hoarders, leftover-hoarders, and two types of direct hoarders. The first type of "direct hoarder" has "hoarding" as the behaviour that is selected in the highest energy state (H_{top}), the second type "rests" in this case (R_{top}). Secondly, agents can have different "*energy proxies*", that provide information about the energetic state of the bird. Birds can use either *Stomach content* (SC), *Fat reserves* (FR), *Fat change rate* (FCR), or a combination of these variables to decide which behaviour to perform. Table 4.8 lists the different model versions and how they vary in terms of hoarding type and energy proxy. The numbers in the table correspond with the numbered decision rules described in the sections below.

7.9.8.1 Decision Rule Structures

The 24 model versions listed in Table 4.8 can be grouped into 8 groups in terms of their decision rule structure. The colours in the table indicate models that are similar in structure. Models 1.1, 2.1 and 3.1 are all non-hoarding models with 1 energy proxy in their decision rule. Models 1.2, 2.2 and 3.2 are all leftover-hoarding models with 1 energy proxy in their decision rule. Models 1.3, 2.3 and 3.3 are all direct-hoarding models that have *Hoarding* as their behaviour in a high-energy state and with 1 energy proxy in their decision rule. Models 1.4, 2.4 and 3.4 are all direct-hoarding models that have *Resting* as their behaviour in a high-energy state and with 1 energy proxy in their decision rule. The same principle holds up for models starting with 4, 5 and 6, which all have 2 energy proxies in their decision rule. Below the decision tree structure is discussed for each of the 8 groups.

Group 1: Non-hoarding birds with 1 energy proxy

Submodels 1.1, 2.1 and 3.1 model a non-hoarding bird that bases its decisions on one of the 3 energy proxy variables: *Stomach content* (SC), *Fat reserves* (FR) and the *Fat change rate* (FCR) respectively. The flow chart in Figure 4.4 shows the decision-making tree for these models. The blue circles indicate where this process (***Decide behaviour***) links to the other processes in the General model. The behaviour sub-processes are indicated with green rectangles and are described in more detail in the section below (see 4.9.8.2). The *Sleep* sub-process will take place if the *Time of day* state variable is set to "night". If it is set to "day" the energy proxy, which is either *SC*, *FR* or *FCR* is compared to the threshold. The parameterisation of threshold values is described in the section below (see 4.9.8.3). If the proxy is higher than the threshold, the bird is in a relatively high energetic state and will *Rest*. Otherwise, *Forage* and *Eat* will take place before linking to the next process (***Predation***).

Group 2: Leftover-hoarding birds with 1 energy proxy

Submodels 1.2, 2.2 and 3.2 model a leftover-hoarding bird that bases its decisions on one of the 3 energy proxy variables: *Stomach content* (SC), *Fat reserves* (FR) and the *Fat change rate* (FCR) respectively. The flow chart in Figure 4.5 shows the decision-making tree for these models. The *Sleep* sub-process will take place if the *Time of day* state variable is set to “night”. If it is set to “day” the energy proxy, which is either *SC*, *FR* or *FCR* is compared to the lowest of the two thresholds and the *Number of caches* is checked. If the proxy is lower or equal to this threshold and there are more than 5 caches in the bird’s storage, the bird will *Retrieve*. Otherwise, the energy proxy is compared to the higher threshold. If the proxy is higher, the bird will *Rest,* as it is in a sufficiently high energetic state. Otherwise, *Forage* and *Eat* will take place before linking to the next process (***Predation***).

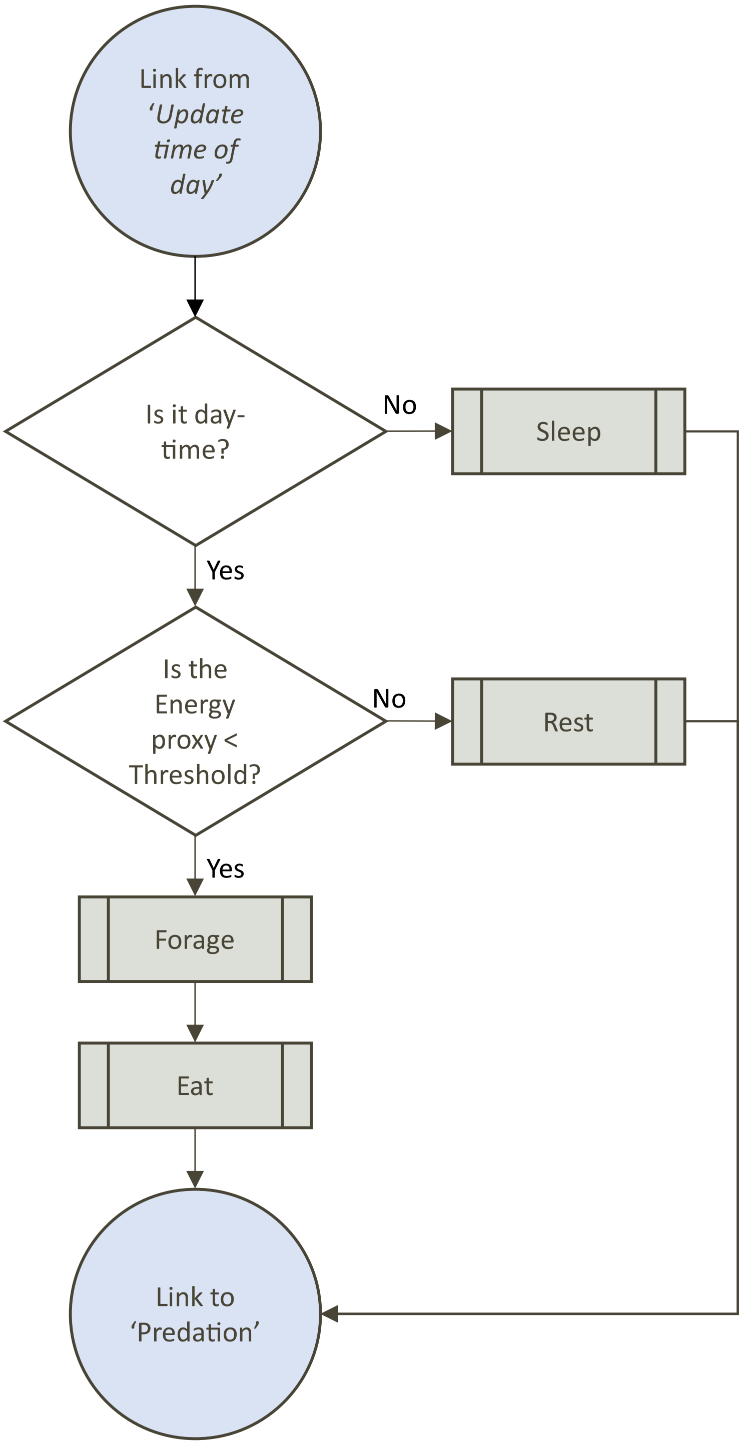


Figure 7.4. Flow chart for the "Decide behaviour" process in models of non-hoarding agents and a decision rule based on 1 energy proxy (Group 1). This proxy can be SC, FR or FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.

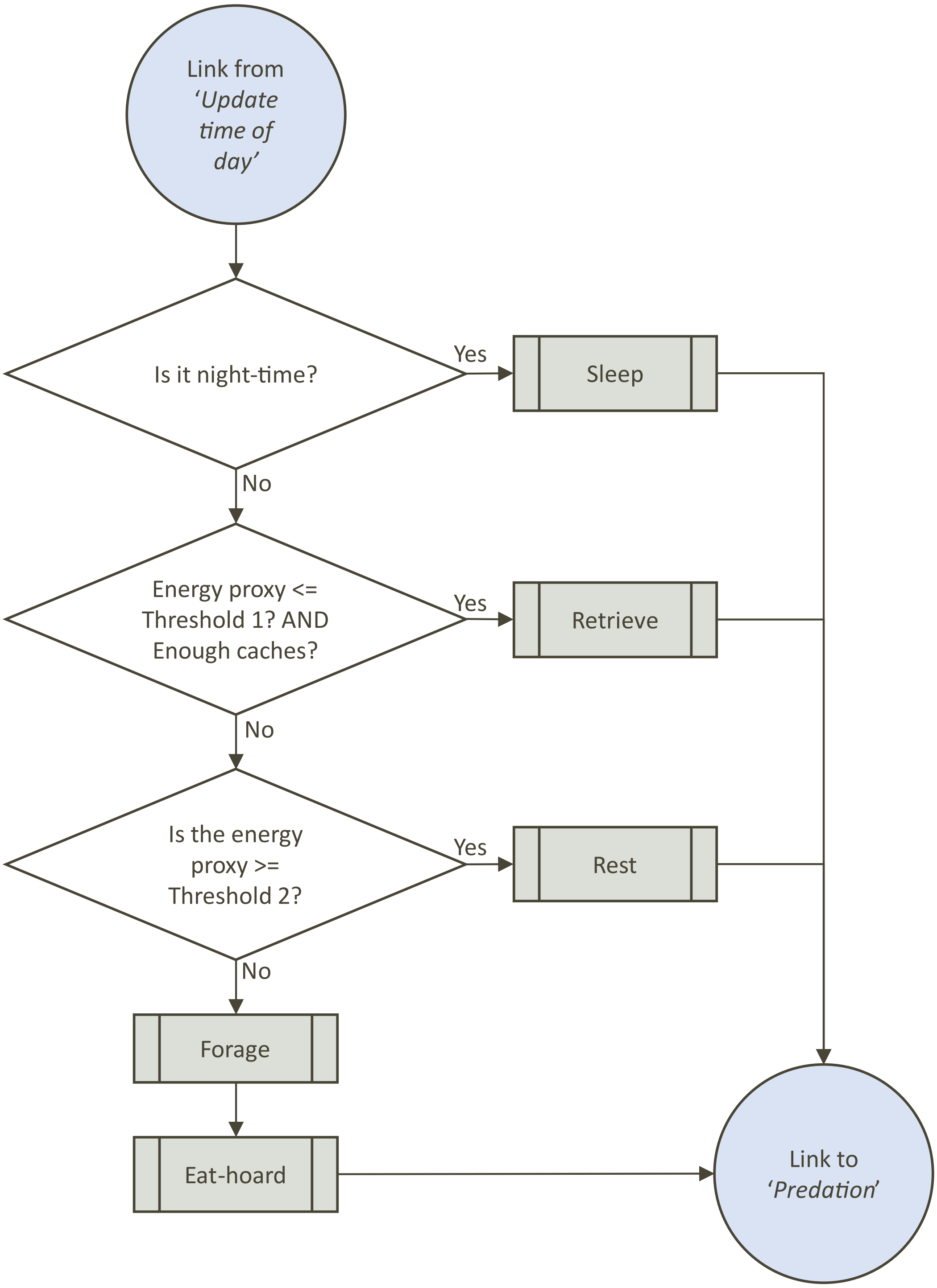


Figure 7.5. Flow chart for the "Decide behaviour" process in models of leftover-hoarding agents and a decision rule based on 1 energy proxy (Group 2). This proxy can be SC, FR or FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.

Group 3: Direct-hoarding (H_{top}) birds with 1 energy proxy

Submodels 1.3, 2.3 and 3.3 model a Direct-hoarding bird with hoarding as the behaviour when it is high in energy, and that bases its decisions on one of the 3 energy proxy variables: *Stomach content* (SC), *Fat reserves* (FR) and the *Fat change rate* (FCR) respectively. The flow chart in Figure 4.6 shows the decision-making tree for these models. The *Sleep* sub-process will take place if the *Time of day* state variable is set to "night". If it is set to "day" the energy proxy, which is either *SC*, *FR* or *FCR* is compared to the highest of the three thresholds. If the proxy is higher, the bird is in its highest energy state and will *Hoard* (hence: H_{top}). Otherwise, the middle threshold is checked. If the proxy is between the top and middle threshold, the agent will *Rest*. Finally, if the energy proxy is below the bottom threshold and there are enough caches, the bird is in its lowest energy state and will *Retrieve*. Otherwise, *Forage* and *Eat* will take place before linking to the next process (***Predation***).

Group 4: Direct-hoarding (R_{top}) birds with 1 energy proxy

Submodels 1.4, 2.4 and 3.4 model a Direct-hoarding bird with resting as the behaviour when it is high in energy, and that bases its decisions on one of the 3 energy proxy variables: stomach content (SC), fat-reserves (FR) and the fat change rate (FCR) respectively. The flow chart in Figure 7 shows the decision-making tree for these models. The *Sleep* sub-process will take place if the *Time of day* state variable is set to "night". If it is set to "day" the energy proxy, which is either SC, FR or FCR is compared to the highest of the three thresholds. If the proxy is higher, the bird is in its highest energy state and will *Rest* (hence: R_{top}). Otherwise, the middle threshold is checked. If the proxy is between the top and middle threshold, the agent will *Hoard*. Finally, if the energy proxy is below the bottom threshold and there are enough caches, the bird is in its lowest energy state and will *Retrieve*. Otherwise, *Forage* and *Eat* will take place before linking to the next process (***Predation***).

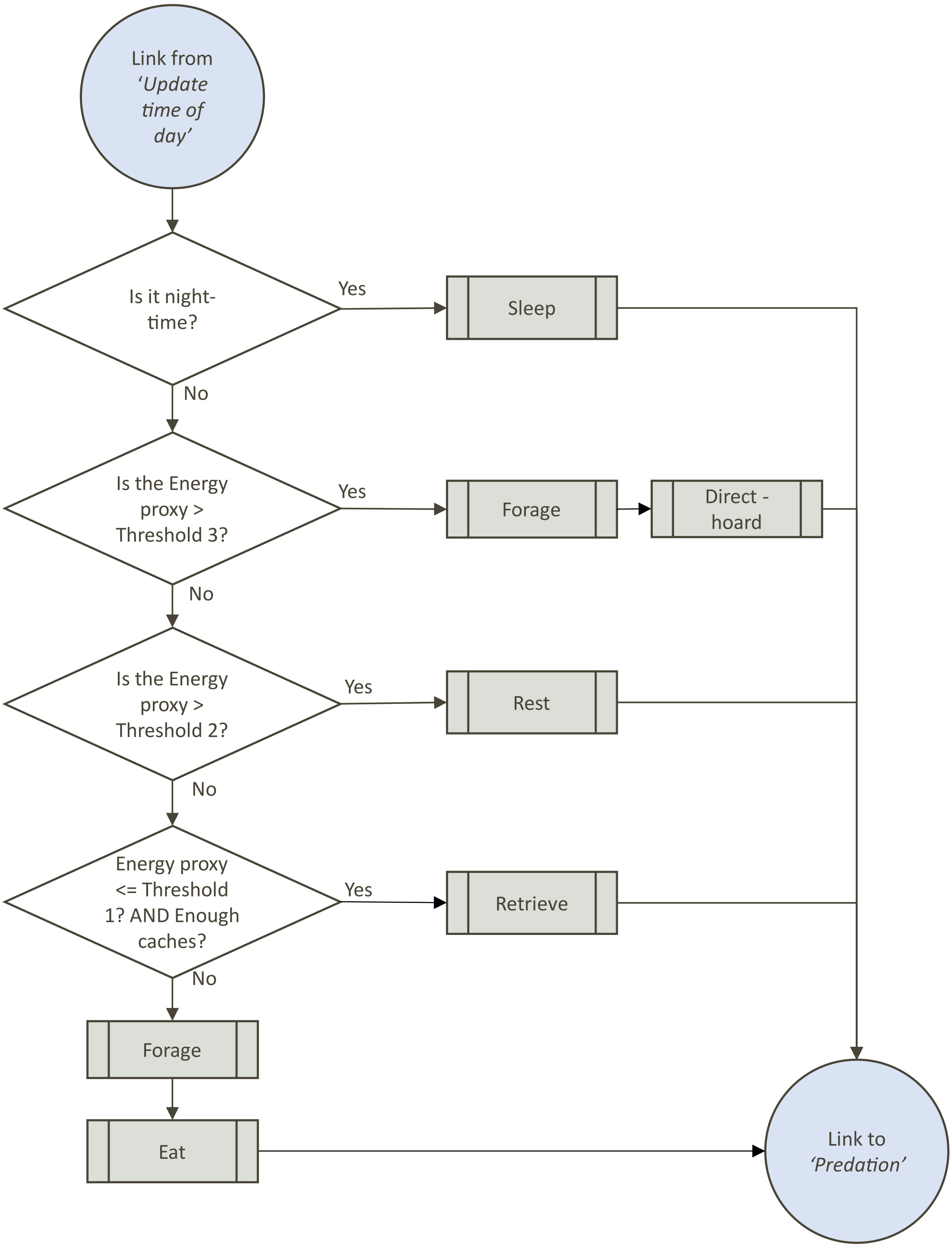


Figure 7.6. Flow chart for the "Decide behaviour" process in models of direct-hoarding (H_{top}) agents and a decision rule based on 1 energy proxy (Group 3). This proxy can be SC, FR or FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.

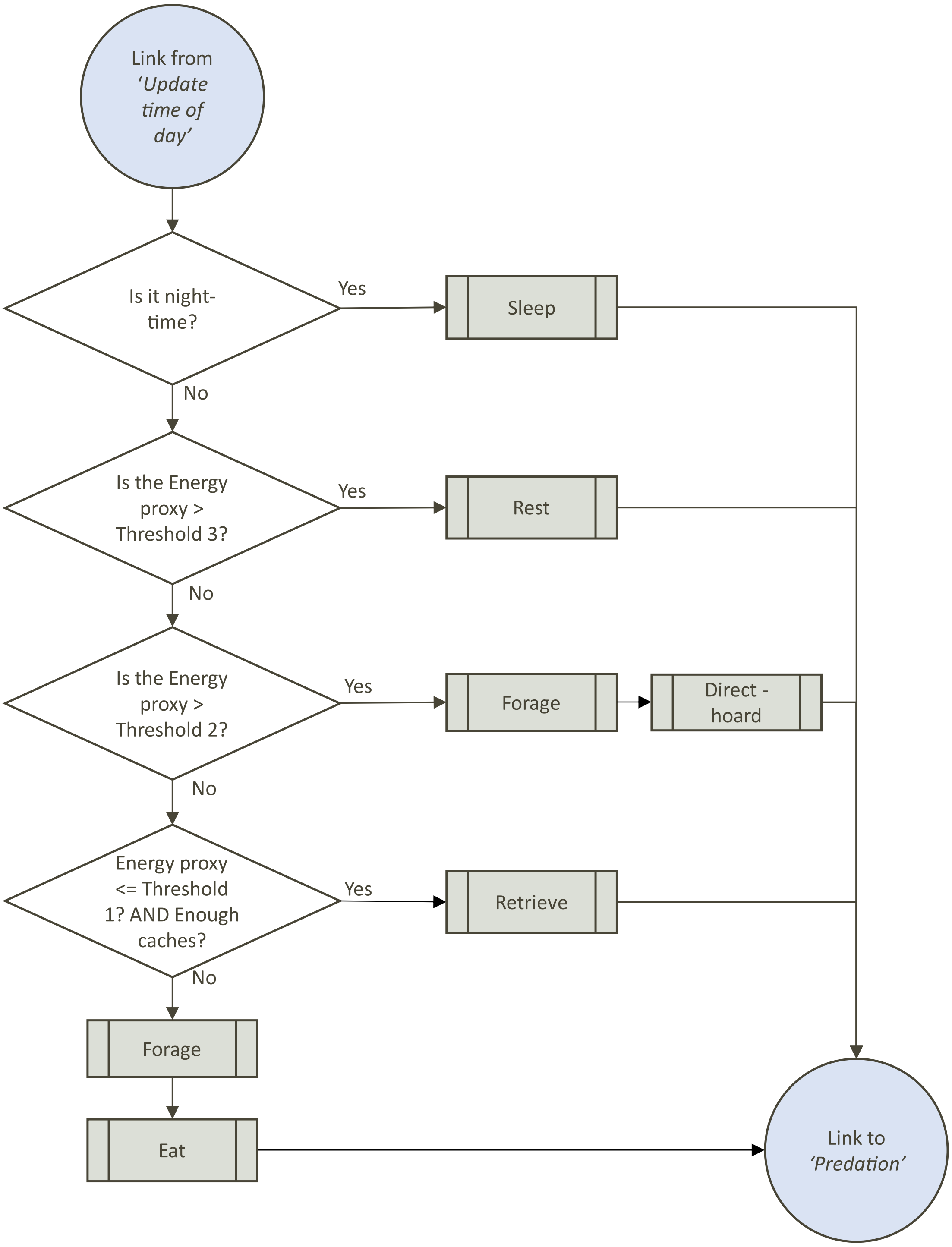


Figure 7.7. Flow chart for the "Decide behaviour" process in models of direct-hoarding (R_{top}) agents and a decision rule based on 1 energy proxy (Group 4). This proxy can be SC, FR or FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.

Group 5: Non-hoarding birds with 2 energy proxies

Submodels 4.1, 5.1 and 6.1 model a non-hoarding bird that bases its decisions on two of the 3 energy proxy variables: *FR* and *FCR*, *SC* and *FR*, and SC and *FCR* respectively. The structure of the models is similar to group one, but thresholds now need to be reached for two energy proxies. The flow chart in Figure 4.8 shows the decision-making tree for these models. The *Sleep* sub-process will take place if the *Time of day* state variable is set to "night". If it is set to "day" both energy proxies are checked to see if they are above their respective thresholds. If they both are, birds are in a high energetic state and *Rest*. Otherwise, *Forage and Eat* will take place before linking to the next process (***Predation***).

Group 6: Leftover-hoarding birds with 2 energy proxies

Submodels 4.2, 5.2 and 6.2 model a leftover-hoarding bird that bases its decisions on two of the 3 energy proxy variables: FR and FCR, SC and FR, and SC and FCR respectively. The structure of the models is similar to group two, but thresholds now need to be reached for two energy proxies. The flow chart in Figure 4.9 shows the decision-making tree for these models. The *Sleep* sub-process will take place if the *Time of day* state variable is set to "night". If it is set to "day" both energy proxies are checked to see if they are below their respective lowest thresholds. If they both are, birds are in a low energetic state and *Retrieve*. Otherwise, both energy proxies are compared to their higher thresholds. If they are both higher, the bird is in the highest energetic state and will *Rest*. Otherwise, *Forage* and *Eat* will take place before linking to the next process (***Predation***).

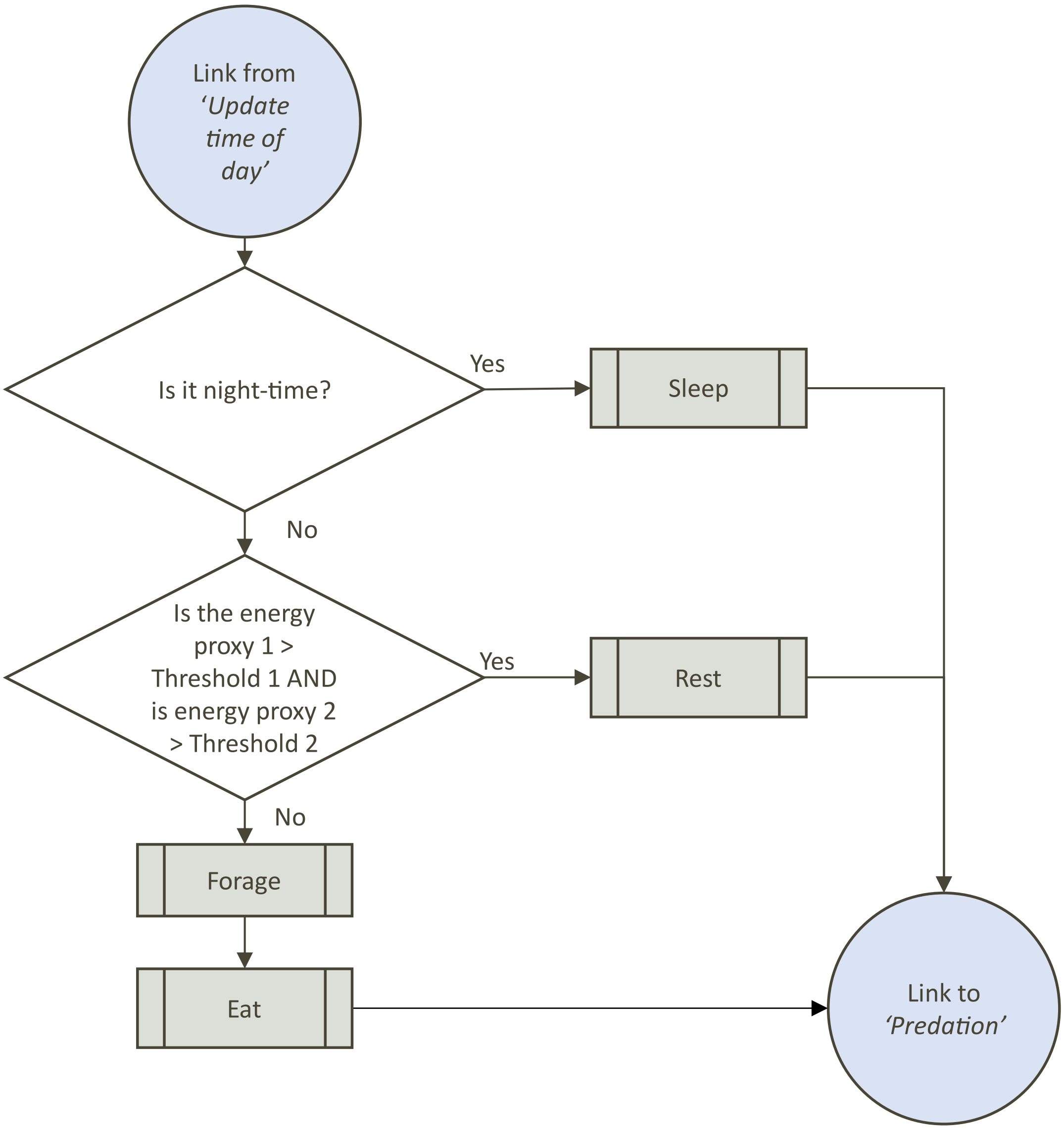


Figure 7.8. Flow chart for the "Decide behaviour" process in models of non-hoarding agents and a decision rule based on 2 energy proxies (Group 5). Either FR and FCR, SC and FR or SC and FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.

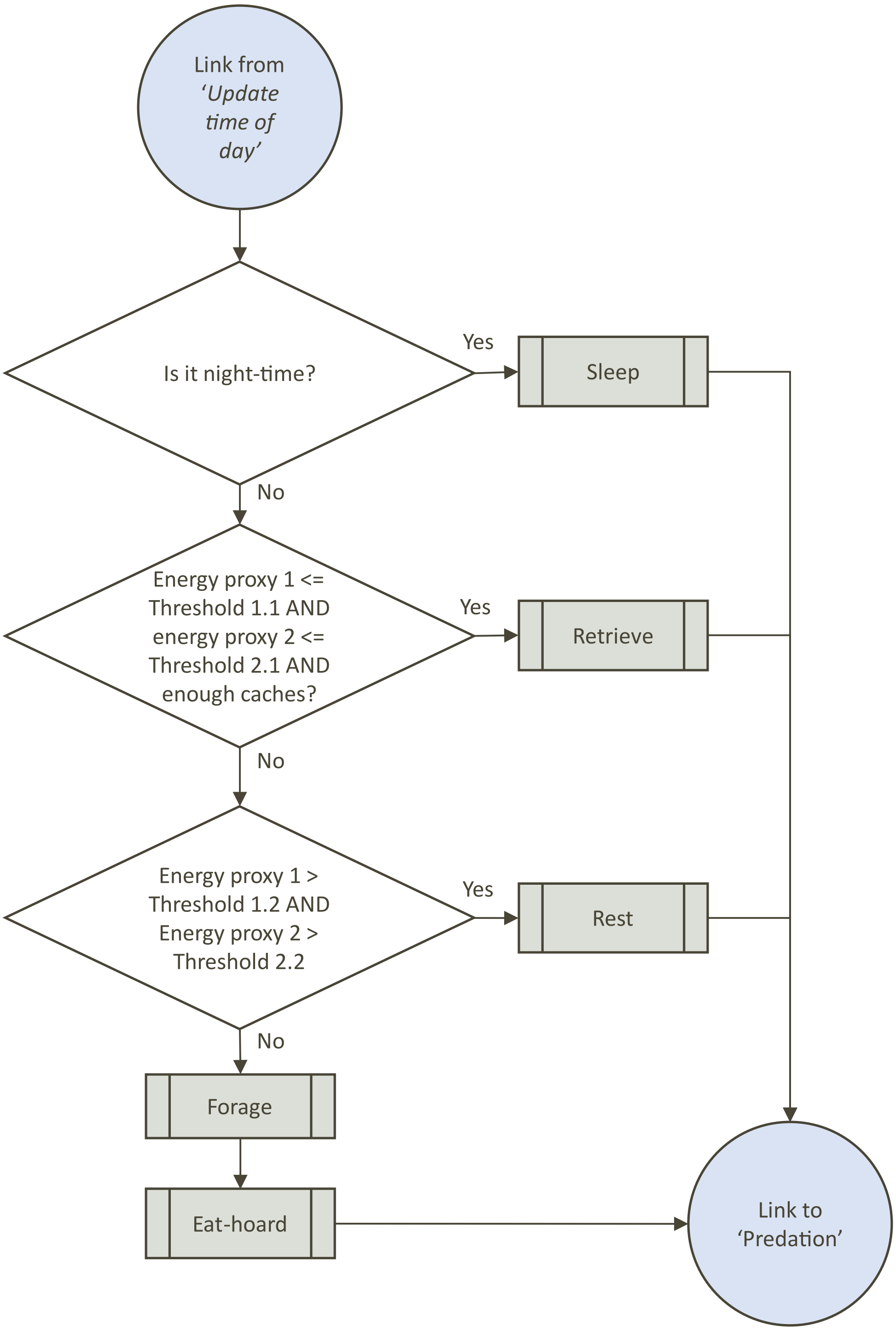


Figure 7.9. *Flow chart for the "Decide behaviour" process in models of leftover-hoarding agents and a decision rule based on 2 energy proxies (Group 6). Either FR and FCR, SC and FR or SC and FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.*

Group 7: Direct-hoarding (H_{top}) birds with 2 energy proxies

Submodels 4.3, 5.3 and 6.3 model a leftover-hoarding bird that bases its decisions on two of the 3 energy proxy variables: *FR* and *FCR*, *SC* and *FR*, and *SC* and *FCR* respectively. The structure of the models is similar to group three, but thresholds now need to be reached for two energy proxies. The flow chart in Figure 4.10 shows the decision-making tree for these models. The *Sleep* sub-process will take place if the *Time of day* state variable is set to "night". If it is set to "day" both energy proxies are checked to see if they are above their respective highest thresholds. If they both are, birds are in a high energetic state and *Hoard*. Otherwise, if either one of the energy proxies is lower than the highest threshold but higher than the middle threshold, the bird will *Rest*. This is also the case if both thresholds are higher than the middle threshold but lower than the top threshold. If both proxies are below their lowest threshold and there are enough caches, the bird will *Retrieve*. Otherwise, *Forage* and *Eat* will take place before linking to the next process (***Predation***).

Group 8: Direct-hoarding (Rtop) birds with 2 energy proxies

Submodels 4.4, 5.4 and 6.4 model a leftover-hoarding bird that bases its decisions on two of the 3 energy proxy variables: FR and FCR, SC and FR, and SC and FCR respectively. The structure of the models is similar to group three, but thresholds now need to be reached for two energy proxies. The flow chart in Figure 11 shows the decision-making tree for these models. The *Sleep* sub-process will take place if the *Time of day* state variable is set to "night". If it is set to "day" both energy proxies are checked to see if they are above their respective highest thresholds. If they both are, birds are in a high energetic state and *Rest*. Otherwise, if either one of the energy proxies is lower than the highest threshold but higher than the middle threshold, the bird will *Hoard*. This is also the case if both thresholds are higher than the middle threshold but lower than the top threshold. If both proxies are below their lowest threshold and there are enough caches, the bird will *Retrieve*. Otherwise, *Forage* and *Eat* will take place before linking to the next process (***Predation***).

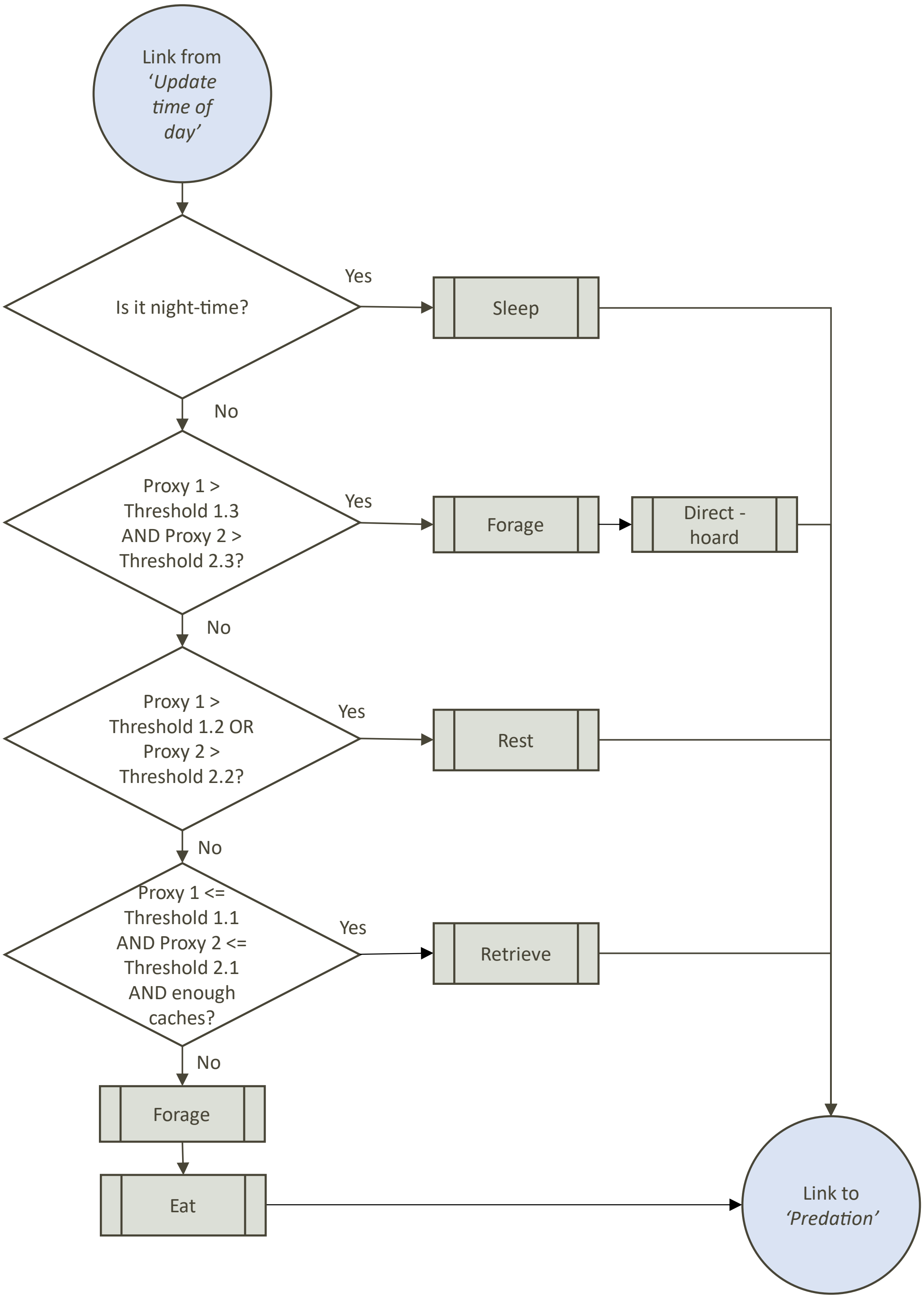


Figure 7.10. Flow chart for the "Decide behaviour" process in models of direct-hoarding (H_{top}) agents and a decision rule based on 2 energy proxies (Group 7). Either FR and FCR, SC and FR or SC and FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.

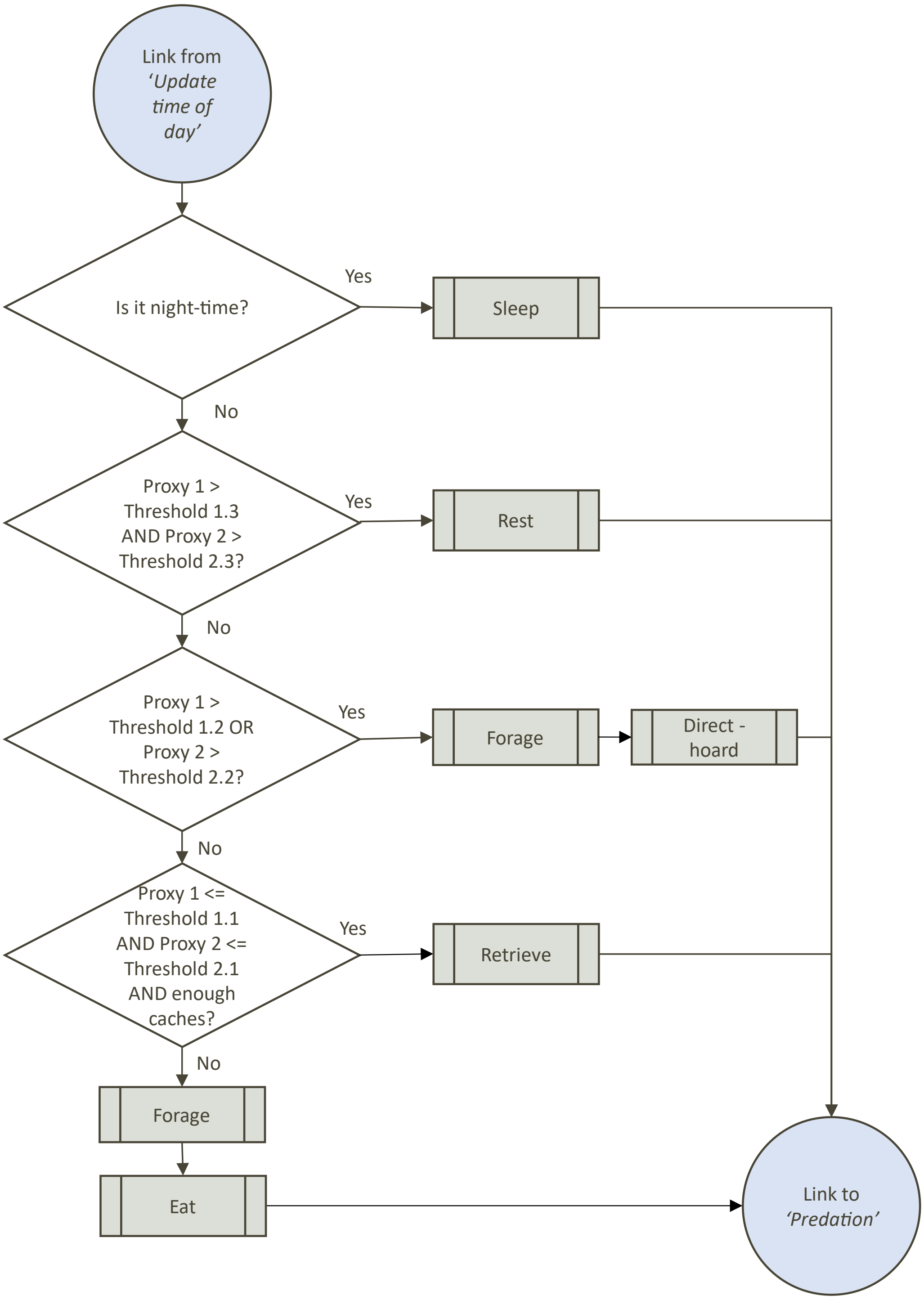


Figure 7.11. Flow chart for the "Decide behaviour" process in models of direct-hoarding (R_{top}) agents and a decision rule based on 2 energy proxies (Group 8). Either FR and FCR, SC and FR or SC and FCR. Blue circles indicate where this process links to the other processes. Green rectangles indicate behavioural sub-processes which are described in section 4.9.

7.9.8.2 Behaviour Sub-processes

The previous section described how each model version or decision rule consists of a decision tree that determines which behaviour is chosen. As outlined, not all agents have access to the same behaviours, this depends on their hoarding type. The behaviours themselves are sub-processes and are described as follows.

***Sleep*:** If the current timestep takes place at night, e.g. “time of day” is set to “0”, the agent will select “Sleep” as their behaviour. The value for “*Sleep*” is set to 1 and all other behaviours (*Forage*, *Eat*, *Eat-hoard*, *Direct-hoard* and *Retrieve*) are set to “0” for the current agent and timestep. The *Find food* state variable is set to NA.

***Rest*:** The *Rest* state variable is set to 0, and all other behaviour state variables are set to 0 (*Sleep, Eat, Eat-hoard, Direct-hoard, Retrieve*). The *Find food* state variable is set to “NA”.

***Forage*:** This behaviour precedes others that require food items, such as *Eat*, *Eat-hoard*, and *Direct-hoard*. At the start of the simulation, the modeller sets the food distribution to either "Poisson" or "Bonanza" and determines the average number of food items found during a foraging bout (*food abundance*).

In the Poisson scenario, the number of food items found during a foraging attempt is sampled from a Poisson distribution with the mean set by the *food abundance* parameter. In the Bonanza scenario, the process is more complex. A vector is created containing zeros and one “bonanza” (24 food items). The number of zeros depends on the mean *food abundance* and is calculated as:

$$Number\ of\ zeros = \frac{24 - mean\ number\ of\ food\ items\ found}{mean\ number\ of\ food\ items\ found}$$

For example, if the mean number of food items found per foraging attempt is 3, the vector will contain 7 zeros and one 24. A higher *food abundance* results in fewer zeros. In 50% of the foraging attempts in the Bonanza scenario, agents sample from this vector. In the other 50%, they sample from the Poisson distribution. This approach ensures the mean number of food items remains consistent across scenarios while varying the predictability of food availability. Including Poisson sampling in Bonanza foraging ensures the scenario remains realistic, so that birds do not always sample either 0 or 24 items.

Test simulations confirmed that both scenarios result in the expected variation in food items found, with the mean matching the *food abundance* setting. Figure 4.12 compares simulations of 1000 foraging attempts in A) a Poisson and B) a Bonanza scenario with a mean of 3 food items per bout. Repeating the simulation 1000 times for each scenario confirmed a mean of 3.00 items in both cases.

Once the number of food items found during a foraging attempt is determined, it is converted into grams of fat, adjusting for metabolic efficiency. Each food item contains 0.064 grams of fat (see 4.6.1 for details). The *Find food* state variable is set to the number of food items found. The *Forage* state variable is set to 1.

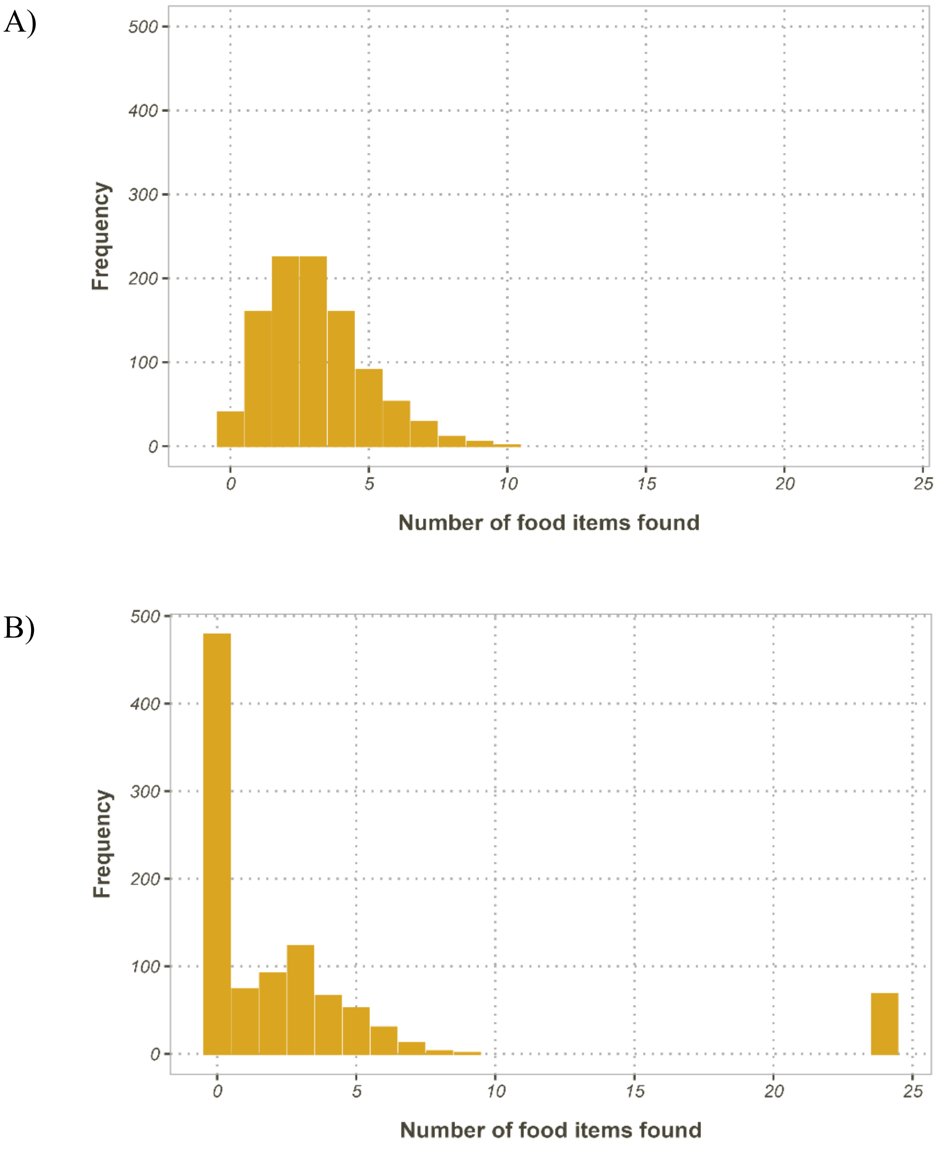


Figure 7.12. The number of food items found in a simulation of 1000 foraging attempts in A) A Poisson scenario and B) A Bonanza scenario. In both cases, the food abundancy was set to 3 items found in the average foraging bout.

Eat: If birds select to perform the *Eat* behaviour, this is always preceded by *Forage*. Once the *Forage* sub-process has taken place, the amount of food found in grams (corrected for metabolic efficiency as described in 4.6.1) is added to the stomach of the bird and the *Stomach content* state variable is updated until the stomach is full. The maximum stomach capacity is 0.4 grams. This is, again, adjusted for metabolic efficiency, so that it only reflects grams of fat that will eventually be added to the fat reserves (Cockcroft, 2009; Pravosudov & Lucas, 2001a). The *Eat* state variable is set to 1, and other behaviour state variables are set to 0 (*Eat-hoard, Direct-hoard, Sleep, Rest and Retrieve*). If the bird has an unsuccessful foraging attempt and finds 0 food items, *Eat* is set to 0 as well.

Eat-hoard: If a bird selects this behaviour, it will always be preceded by *Forage*. As in *Eat*, the food that was found is added to the *Stomach content* state variable, up until the stomach is full. In *Eat*, the leftovers would not be used. Here, the leftovers, if complete food items, can be hoarded. The surplus of whole food items is added to the *Number of caches* state variable. The *Eat-hoard* state variable is set to 1 and the other behavioural state variables are set to 0 (*Sleep, Rest, Eat, Direct-hoard, Retrieve*). If the bird did not find any food items in *Forage*, *Eat-hoard* is also set to 0. If there were no leftover items, *Eat-hoard* is set to 0 and *Eat* is set to 1.

Direct-hoard: If a bird selects this behaviour, it will always be preceded by *Forage*. The bird does not consume any of the food items it finds but hoards all of them. The number of food items found is added to the *Number of caches* state variable. The *Direct-hoard* state variable is set to 1 and the other behavioural state variables are set to 0 (*Sleep, Rest, Eat, Eat-hoard, Retrieve*).

***Retrieve*:** I assume that birds will only retrieve caches if the quantity is sufficient to justify the effort. When there are fewer than five caches, some may be located beyond the reach of other, more "unreliable" food sources that birds could forage for. Therefore, with a greater number of caches, the likelihood of finding nearby options increases, making retrieval more worthwhile. Thus, I set a minimum threshold of five caches, based on the average number retrieved within 20 minutes as calculated by Pravosudov & Lucas (2001). When an agent decides to *Retrieve*, its remaining stomach space is calculated using the *Stomach content* state variable. The number of food items retrieved is determined by dividing the remaining stomach space (in grams) by 0.064 (the fat content per food item), rounding down to the nearest integer. The *Stomach content* is then updated with the actual food consumed (retrieved items * 0.064). The *Number of caches* state variable is adjusted to reflect the items removed, and the *Retrieve* state variable is set to 1 while all other behavioural state variables (*Sleep, Rest, Eat, Eat-hoard, Direct-hoard, Forage*) are set to 0, as well as the *Find food* state variable. *Find food* only includes food found through foraging. Note that the eating that takes place under *Retrieve*, is not recorded in the *Eat* state variable.

7.9.8.3 Parameterisation of Thresholds

As discussed in section 4.9.8.1, each of the model versions has their own unique decision rule. The decision rules vary in terms of the energy proxy that they are based on as well as the hoarding strategy that the agent uses. The number of thresholds varies with the model versions, with the most basic models (e.g. 1.1, 2.1 and 3.1) only using one threshold based on 1 energy proxy. The most complex models (e.g. 4.3 and 4.4) have 6 thresholds that are based on 2 energy proxies (so 3 thresholds per proxy) (Table 4.9). Figure 4.13 and Figure 4.14 indicate where in the models these thresholds are in relation to the different behaviour options.

Table 7.9. The number of thresholds in each group of model versions

Model	***Number of thresholds***
Group 1	1
Group 2	2
Group 3	3
Group 4	3
Group 5	2
Group 6	4
Group 7	6
Group 8	6

Each threshold needs to be set to a specific value, so that the energy proxy state variables can be compared to the threshold throughout the simulation. In order to determine the optimal values of these thresholds, a parameter space that ranges across all possible values was sampled to see which generated the highest model survival. This approach was used to reflect that if birds were to follow a given decision rule, the associated threshold would have evolved to optimize survival.

Threshold Ranges: For the *Stomach content* energy proxy, the threshold is set between 0 and 0.4, corresponding to the minimum and maximum stomach content in the model. For *Fat reserves*, the range is between 0 and 4 grams, representing the model's fat reserve limits. The *Fat change rate* (FCR) range was determined through test simulations with N = 1000, *Simulation length* = 30, *Daylight hours* = 8, and *Decision rule* = 3.1. Threshold settings between -2 and 2 grams per 6 timesteps were tested across all 12 environmental settings (Figure 2). The results identified a minimum *FCR* of -0.57 grams/6 timesteps and a maximum of 0.51 grams/6 timesteps. To be conservative, the final *FCR* range was set between -0.6 and 0.6 grams/6 timesteps.

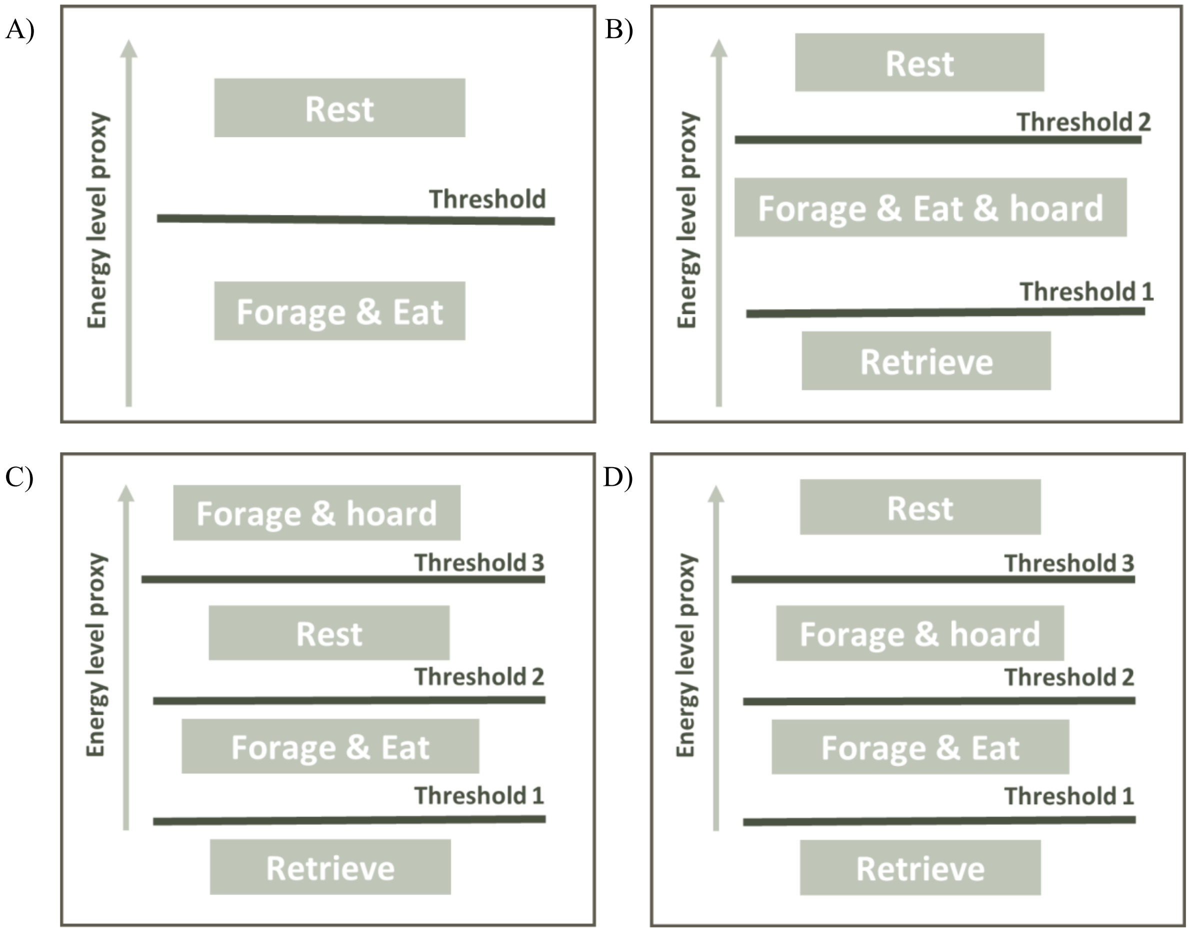


Figure 7.13. Schematics identifying the thresholds in the models with 1 energy proxy (group 1 – 4). A) Structure for Group 1 models, where birds rest in a "high" energetic state and otherwise rest B) Structure for Group 2 models, which will retrieve food items when their energy proxies are lowest C) and D) are the direct hoarding birds that separate hoarding and eating behaviour, either with Hoarding in the most energy-rich state (C) or Resting (D).

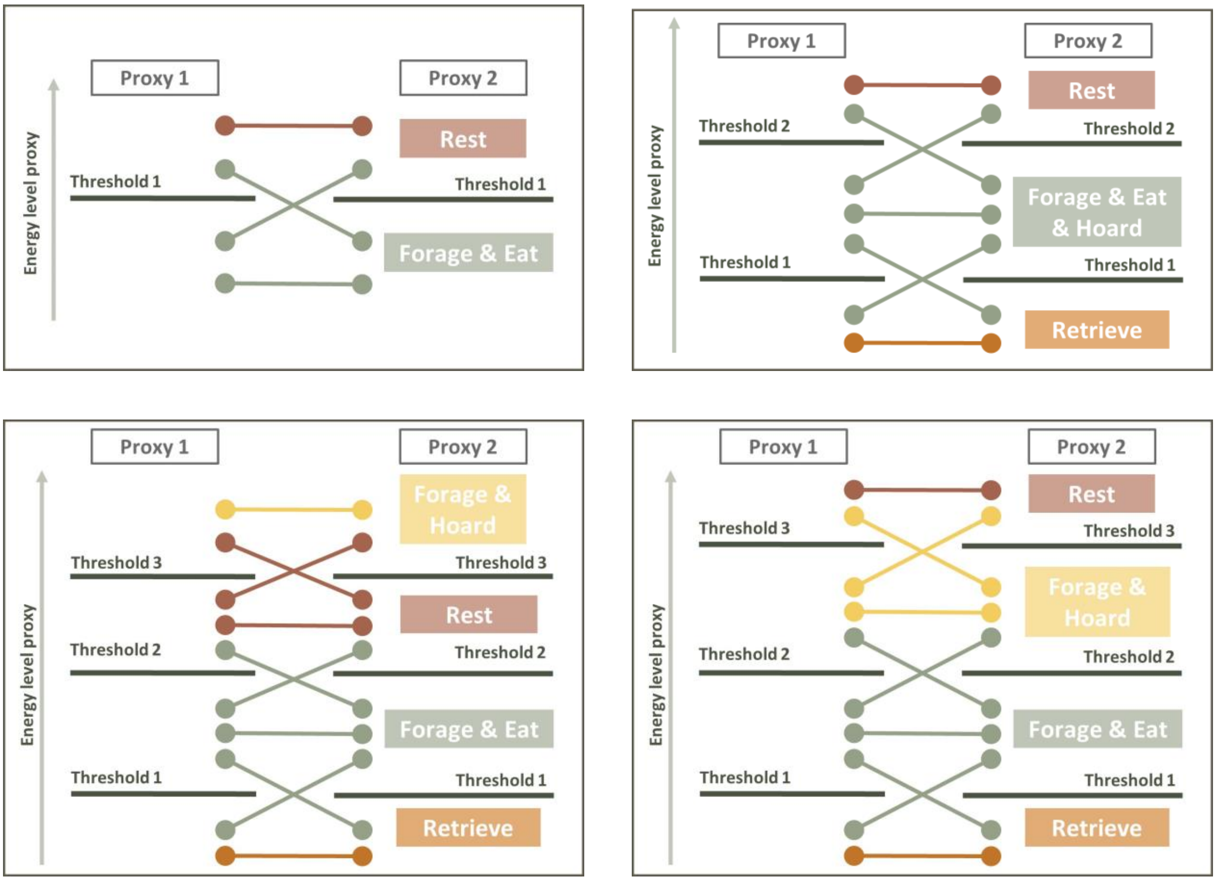


Figure 7.14. Schematics identifying the thresholds in the models with 2 energy proxies (Group 5-8). The left top corner indicates non-hoarding birds with 2 energy proxies (Group 5). The right top corner indicates leftover-hoarders with 2 energy proxies (Group 6). The bottom two are the direct-hoarding models with H_{top} on the left and R_{top} on the right (Groups 7 and 8).

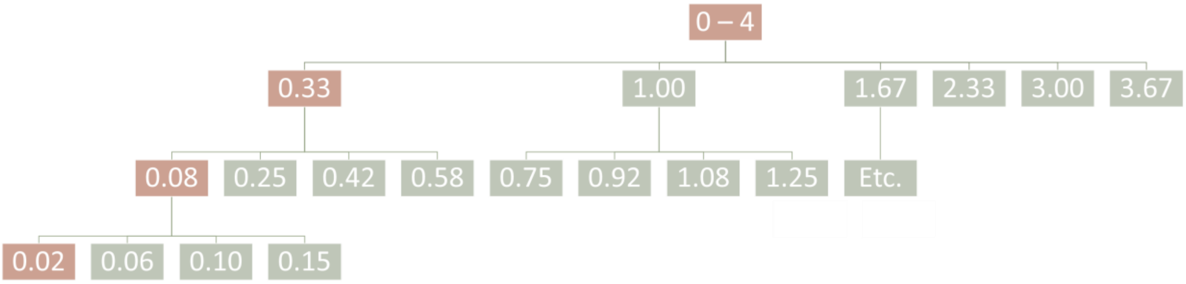


Figure 7.15. Example of the "branching" parameterisation method for model 2.1. In level 1, one out of 6 threshold values produced the best half-life survival across 12 environments and 25 simulation rounds (0.33). For level 2, 4 values around this value are selected and the process is repeated. Note that the spacing of the values for level 2 is done in a way that the full range of samples in level 2, including ones under the values from level 1 that did not perform well, sample the entire threshold space The same process is repeated for level three, with the optimal value from level 2 (0.08).

Sampling the threshold ranges: To effectively sample the entire threshold range, a "branching" approach was used, involving three levels (Figure 4.15). At the first level, six values are evenly spaced across the threshold range. For instance, with a fat reserve threshold range of 0–4, the six values would be 0.33, 1.00, 1.67, 2.33, 3,00 and 3.67. Simulations are then run for each selected threshold, with parameters set to $N = 1000$, *Simulation length* = 30 days, *Daylight hours* = 8, and the *Decision rule* specific to the model being optimized. These simulations are conducted across 12 environments (Figure 4.2), which define *Food abundance*, *Food predictability,* and *Temperature ranges*.

Survival curves from each environment are used to calculate the half-life survival—i.e., the number of timesteps by which 50% of the agents have died. This is done by fitting an exponential decay curve to the survival data using the equation:

$$y \sim a * e^{-b*t}$$

Equation 4.6

where y is the proportion of birds alive, t is the timestep, and a and b are estimated using the "stats" package in R (R Core Team, 2024). Here, using the *nls()* function, with starting values of $a = 1$ and $b = 0.0000001$, a non-linear model was fitted to the survival data by optimising a and b to minimise the residual sum of squares. The predicted half-life is determined from the fitted function for each environment, and the average half-life across all 12 environments is used to assess model performance under the given threshold. This process is repeated 25 times to account for stochastic effects, and the average half-life across all 25 repetitions is carried to the next optimization level.

At level 2, four threshold values are selected around the optimal value from level 1 and tested with the same simulation setup. Note that the spacing of the values for level 2 is done in a way so that the full range of samples in level 2, including ones that flow from level 1 values that did not perform well, sample the entire threshold space. This means that, for example for model 2.1 (Figure 4.15), there are 6*4 = 24 values possible in level 2, which are equally distanced between 0 and 4. If the best threshold value from level 1 was 0.33, only the 4 values spaced around 0.33 will be used for level 2.

At level 3, this process is repeated with four values around the level 2 optimum. The final threshold value yielding optimal survival is then incorporated into the model's decision rules. See Figure 4.17 for details.

Note that for models with multiple thresholds, the process becomes more complex as it involves combinations of thresholds. A model with two thresholds results in 36 combinations (6*6), while a model with three thresholds has 216 combinations, and the most complex models with six thresholds yield 46,656 combinations. The top threshold (e.g. threshold 2 or 3 in Figure 4.13) represents the highest energetic state for the birds and must be greater than the thresholds below it. Therefore, only combinations where threshold 3 > threshold 2 > threshold 1 are considered in the optimisation. For models with two energy proxies, this condition applies within each set of three thresholds for each proxy.

Validation of the parameterisation method: The number of initial samples in level 1 of the parameterisation was not chosen randomly; it balanced the need to sample the entire parameter space with the limitations of available computing power. The least complex models, utilising non-hoarding and leftover-hoarding strategies, were optimized using branching methods that sampled 4, 6, 8, 10, and 12 values in the parameter space. The resulting mean half-life survival rates are presented in Figure 4.16. Most decision rules demonstrated an increase in survival between branch 4 and branch 6, after which the improvement diminished. Consequently, and due to limited time and computing power, the decision was made to proceed with the 6-branch method for the more complex models with direct-hoarding strategies.

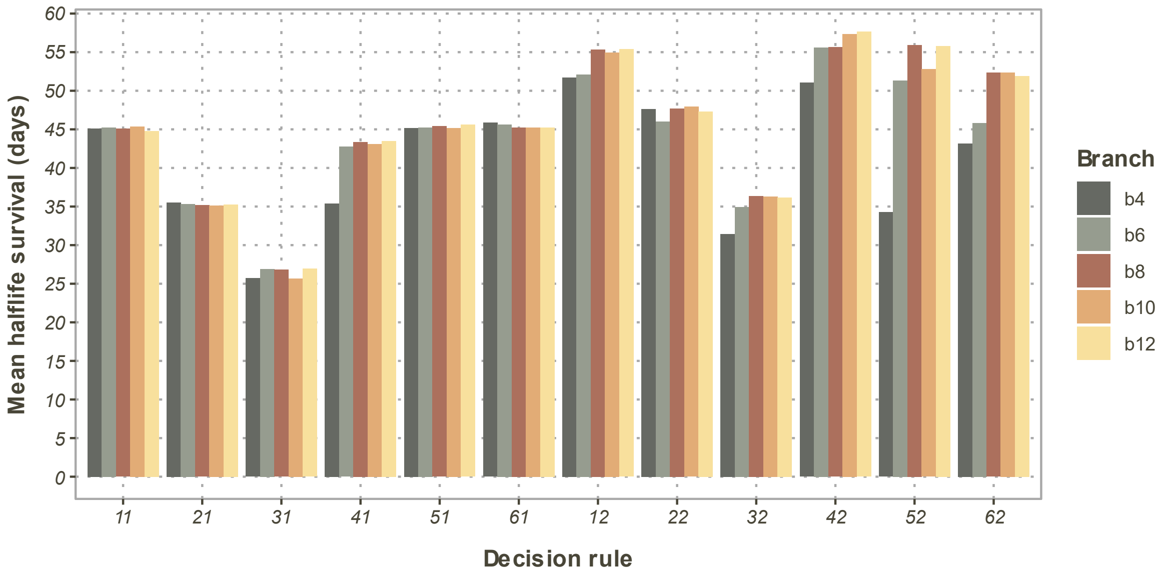


Figure 7.16. Performance of the optimised Decision rules when using different parameterisation methods. Branch "4" takes 4 samples across the parameter space in level 1 of the parameterisation process. Branch "6" takes 6 samples, etc.

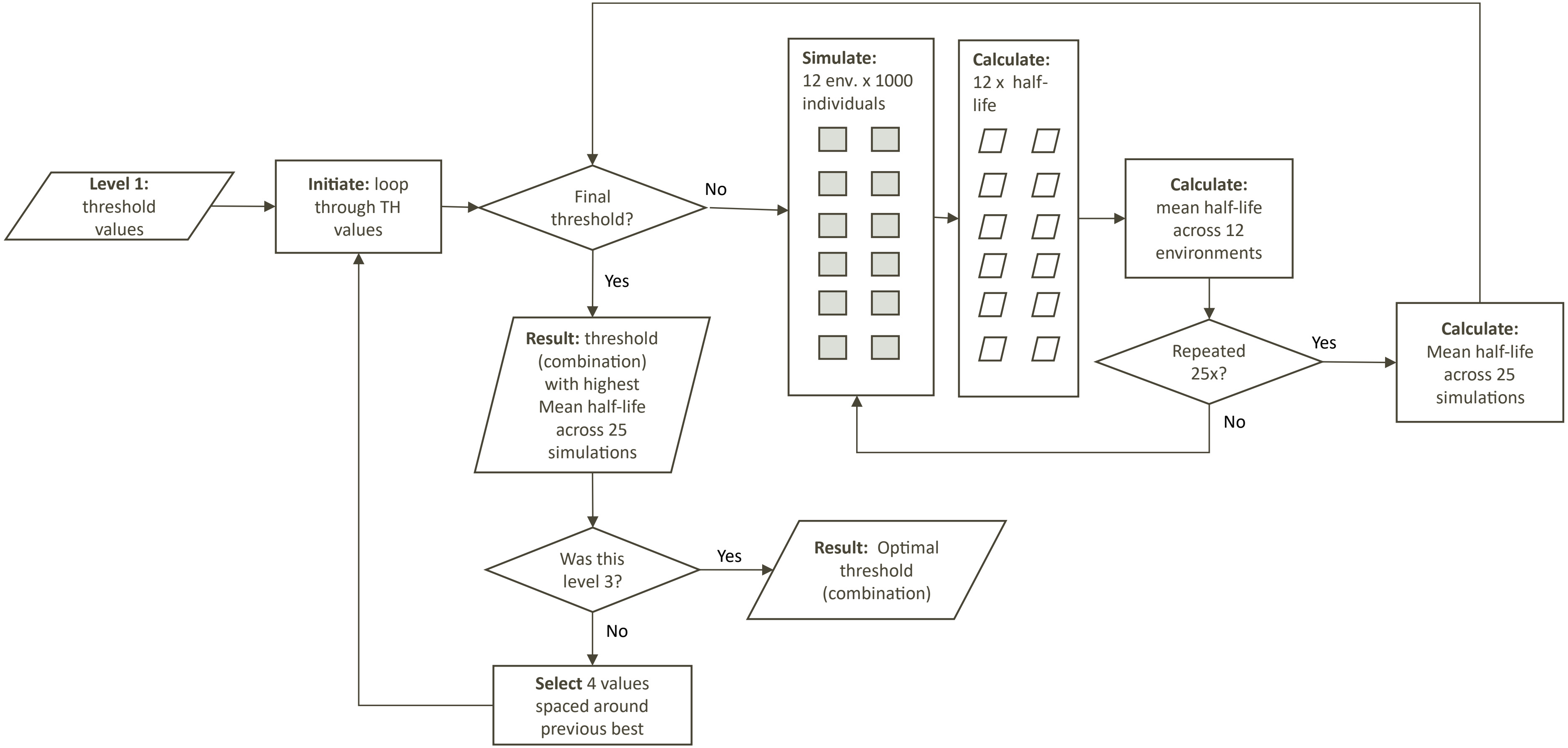


Figure 7.17. Schematic of the parameterisation method with 3 levels. At each of the 3 levels, the threshold combinations are plugged into the models for simulation across the 12 environments for 1000 individuals and 30 simulated days. This simulation is repeated 25 times, and the average half-life time is calculated across all simulations. In level 1 and 2, the best threshold (combination) is used to generate the threshold (combinations) for the next level. In level 3, the best-performing threshold (combination) is the outcome used in the final version of the models.

Resulting threshold values: The resulting threshold values for all models, generated with the Branch 6 method can be found in the tables below.

Table 7.10. Parameterisation results for models in group 1: non-hoarding birds with 1 energy proxy.

Decision rule	***Energy proxy***	***Threshold***
1.1	SC	0.003
2.1	FR	1.604
3.1	FCR	0.231

Table 7.11. Parameterisation results for models in group 2: leftover-hoarding birds with 1 energy proxy.

Decision rule	***Energy proxy***	***Threshold 1 (bottom)***	***Threshold 2 (top)***
1.2	SC	0.028	0.081
2.2	FR	1.021	1.438
3.2	FCR	-0.069	0.110

Table 7.12. Parameterisation results for models in group 3: direct-hoarding birds (H_{top}) with 1 energy proxy.

Decision rule	***Energy proxy***	***Threshold 1(bottom)***	***Threshold 2 (middle)***	***Threshold 3 (top)***
1.3	SC	0.031	0.090	0.294
2.3	FR	0.396	1.396	2.938
3.3	FCR	-0.131	0.219	0.419

Table 7.13. Parameterisation results for models in group 4: direct-hoarding birds (R_{top}) with 1 energy proxy.

Decision rule	***Energy proxy***	***Threshold 1(bottom)***	***Threshold 2 (middle)***	***Threshold 3 (top)***
1.4	SC	0.027	0.131	0.135
2.4	FR	0.396	2.229	3.813
3.4	FCR	-0.119	0.256	0.494

Table 7.14. Parameterisation results for models in group 5: non-hoarding birds with 2 energy proxies.

Decision rule	***Energy proxies***	***Threshold 1 – proxy 1***	***Threshold 1 – proxy 2***
4.1	FR & FCR	1.521	-0.006
5.1	SC & FR	0.031	0.313
6.1	SC & FCR	0.015	-0.581

Table 7.15. Parameterisation results for models in group 6: leftover-hoarding birds with 2 energy proxies.

Decision rule	***Energy proxies***	***Threshold 1 – proxy 1***	***Threshold 1 – proxy 2***	***Threshold 2 – proxy 1***	***Threshold 2 – proxy 2***
4.2	FR & FCR	1.313	-0.031	1.354	0.006
5.2	SC & FR	0.065	0.313	0.115	1.396
6.2	SC & FCR	0.052	-0.206	0.098	-0.181

Table 7.16. Parameterisation results for models in group 7: direct hoarding (H_{top}) with 2 energy proxies.

Decision rule	***Energy proxies***	***Threshold 1 – proxy 1***	***Threshold 1 – proxy 2***	***Threshold 2 – proxy 1***	***Threshold 2 – proxy 2***	***Threshold 3 – proxy 1***	***Threshold 3 – proxy 2***
4.3	FR & FCR	0.688	-0.094	1.354	0.219	3.146	0.469
5.3	SC & FR	0.006	0.729	0.085	1.563	0.318	2.104
6.3	SC & FCR	0.056	0.044	0.077	0.244	0.315	0.544

*Table 7.17***.** *Parameterisation results for models in group 8: direct hoarding (R_{top}) with 2 energy proxies.*

Decision rule	***Energy proxies***	***Threshold 1 – proxy 1***	***Threshold 1 – proxy 2***	***Threshold 2 – proxy 1***	***Threshold 2 – proxy 2***	***Threshold 3 – proxy 1***	***Threshold 3 – proxy 2***
4.4	FR & FCR	0.687	-0.044	2.354	0.281	3.438	0.419
5.4	SC & FR	0.006	0.896	0.094	2.520	0.277	3.063
6.4	SC & FCR	0.115	0.193	0.223	0.231	0.335	0.469

Resulting model performance: model performance, calculated as the mean half-life survival rates are presented in Table 4.18. Half-life survival is calculated as described in Equation 4.6, as the mean number of timesteps it takes for half of the birds in a model to die, averaged across all 12 environments used in parameterisation. In the table, these half-life timesteps are transformed into "days" for easier interpretation.

Table 7.18. Half-life survival rates for the resulting models. Half-life survival is calculated as the mean number of days that it takes for 50% of the agents in a model to die, across all 12 environments used in parametrisation. Green shades indicate longer survival, and red shades indicate shorter survival.

	Non-hoarder	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Stomach content	45	52	44	41
Fat reserve	35	46	40	29
Fat change rate	27	35	29	28
Fat reserve & Fat change rate	43	56	42	30
Stomach content & Fat reserve	45	51	73	35
Stomach content & Fat change rate	46	46	51	31

7.9.9 Predation

In this process, it is determined if an agent is killed by a predator attack. First, the probability that a bird is captured in a predation attempt is calculated (P_{apture}):

$$P_{capture} = 0.78 + 0.5 * 10^{-8} * e^{1.4 * current\ mass}$$

Equation 4.7

The current mass of the bird is calculated from the *base mass* of the bird together with the *Fat reserve* and *Stomach content* state variables. Then, the probability that a bird is actually killed in the predation attempt is calculated as:

$$P_{kill} = P_{capture} * P_{attack}$$

Equation 4.8

Where P_{attack}, the probability of a predator attack, is set based on the behaviour of the bird as selected in *Decide behaviour*. Birds that Sleep or Rest have a P_{attack} of 0. Birds that are doing one of the foraging related behaviours (Forage, Eat, Eat-hoard, Direct-hoard, Retrieve) have a probability of 0.000667 of being attacked in each 20-minute timestep. See Lima (1985) and Pravosudov and Lucas (2001) for details.

Then, the probability of survival ($P_{survival}$) is generated as a random number between 0 and 1. If $P_{survival}$ is larger than P_{kill}, the bird survives. If not, the *life status* of the bird is updated to 0 and *Predation* is set to 1. If the bird survives, *Predation* is set to 0.

7.9.10 Metabolism

The Metabolism process consists of the following steps, both contributing to the metabolization of consumed food;

First, food is moved from the stomach to the *Fat reserve*, by subtracting the stomach-clearance in grams from the current *Stomach content* and adding it to the current *Fat reserves.* The stomach clearance parameter is set to 0.132 as in Cockcroft (2009). If the *Stomach content* is smaller than this number, the full amount of food in the stomach is moved to the *Fat reserves* and the *Stomach content* is set to 0 grams. The *Stomach content* and *Fat reserve* state variables are updated accordingly.

Then, the energy expenditure of the bird is determined. The Metabolic rate (MR) and basal metabolic rate (BMR) are calculated for the temperature in the current timestep and with the weight that the bird had at the time it was doing the behaviour. See Lucas & Walter (1991) and Pravosudov and Lucas (2001) for details on the equations.

$$MR = 45.65 - (1.33 * Temperature)$$

Equation 4.9

$$BMR = 0.00616 * MR * \left(\frac{Mass}{1000}\right)^{0.66}$$

Equation 4.10

The BMR is then used to calculate the new *Fat reserve* of the agent with the equation:

$$FR_{new} = FR_{old} - (BMR * BMR_{multi})$$

Equation 4.11

where BMR_{multi} is the multiplication factor set for the behaviour the bird did in the current timestep. These values are taken from Pravosudov and Lucas (2001) and reflect the additional energy cost of foraging-related behaviours. *Sleep* and *Rest* get BMR_{multi} = 1. For *Eat*, *Direct-hoard*, *Leftover-hoard* and *Retrieve*, this is set to 8.

7.9.11 Pilferage

The ***Pilferage*** process simulates cache loss due to forgetting, decay, and consumption by other birds. I assume a cache half-life of 1440 timesteps (20 days), meaning half of the caches will disappear after this period (Brodin, 1994; Pravosudov & Lucas, 2001). The decay constant (λ) is calculated based on radioactive decay equations (Groch, 1998).

$$\lambda = \frac{\ln(2)}{1440} = 4.8 * 10^{-4}$$

Equation 4.12

At each timestep, the probability of cache decay is calculated using complement probability, ensuring the total probability across all events equals 1. The probability of k items decaying is given by:

$$P_{kDecay} = e^{-\lambda} * \frac{\lambda^k}{k!}$$

Equation 4.13

First, the probability of no decay is calculated as:

$$P_{NoDecay} = e^{-\lambda} * \frac{\lambda^0}{0!} = e^{-\lambda}$$

Equation 4.14

The probability of one or more items decaying according to complement probability is then:

$$P_{oneOrMore} = 1 - P_{NoDecay}$$

Equation 4.15

To determine if a cache decays in the current timestep, a random number between 0 and 1 is drawn. If the probability of one or more items decaying exceeds this random number, a food item decays. It is assumed that only one item decays, as the likelihood of more than one item decaying within a 20-minute timestep is negligible (Figure 18). The ***Cache decay*** and ***Cache number*** state variables are updated accordingly.

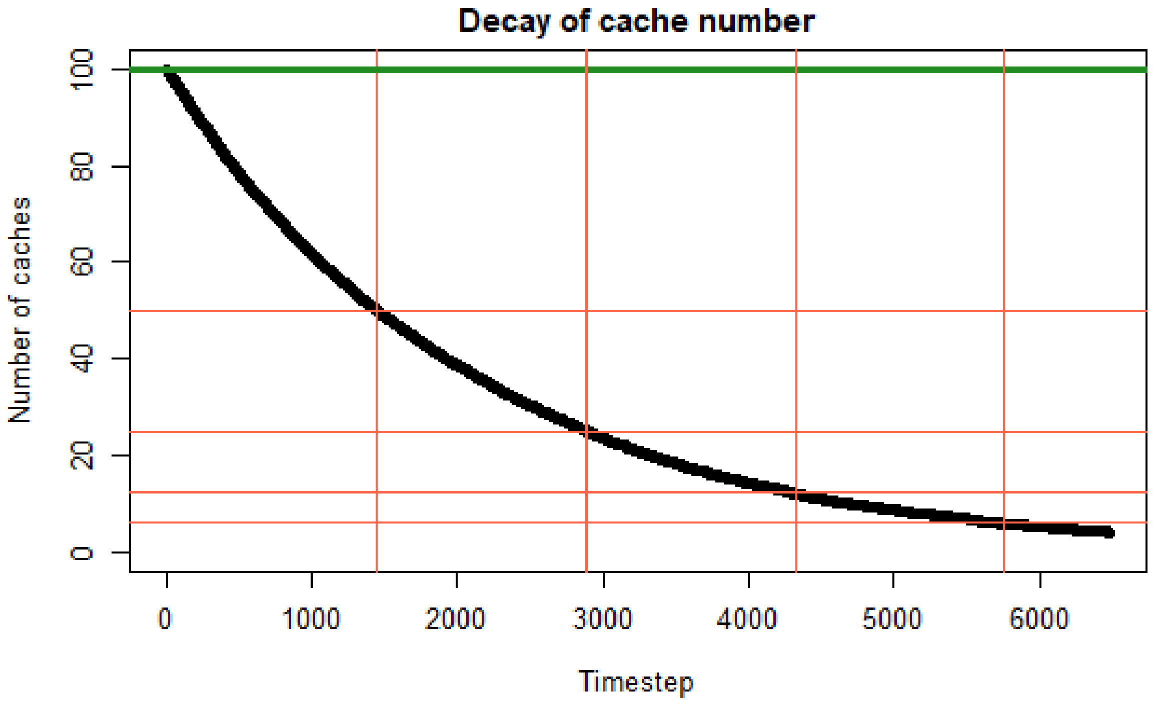


Figure 7.18. The decay curve for 100 caches (green line) simulated over 90 days (6480 timesteps). Each vertical red line indicates 20 days. Each horizontal red line indicates that the caches have been "halved".

7.9.12 Prepare for Next Timestep

The model checks if it is in the last timestep for the current individual. If so, it will go to the next process. Otherwise, the current values of the state variables are recorded. The only state variable that is not recorded here is *Fat change rate*, as this is calculated at the start of the next timestep.

7.9.13 Prepare for Next Individual

Once all timesteps for one individual have passed, the code moves on to the next individual and starts at timestep 1. Individual matrices can be saved if needed.

7.9.14 Bind and Save Mean Results

After each run, the results for all individuals are aggregated, means are calculated, and the results are saved.

Chapter 5. Agent-based Models of Small Birds in Winter: Decisions Based on Stomach Content

8.1 Abstract

This chapter presents an analysis of model versions that include decision-making rules based on *Stomach content*, as described in Chapter 4. Survival dynamics, physiological variables and behavioural patterns under various environmental circumstances are discussed. I explore how different hoarding strategies—non-hoarding, leftover-hoarding, and two types of direct-hoarders—affect survival rates across environments with high and low food predictability ("Poisson" and "Bonanza"). My findings indicate that while all models exhibit resilience in Poisson environments, challenges arise in Bonanza scenarios, particularly for non-hoarders. Leftover-hoarding birds consistently demonstrate greater survival due to their ability to maintain higher *Fat reserves* through a combination of slightly more *resting* and the use of their caches. The results of the leftover-hoarding model partly reflect real-world trends in terms of daily weight gain trajectories and patterns in hoarding intensities.

8.2 Introduction

As discussed in Chapters 1 and 4, birds likely use information about their energetic state to make decisions regarding foraging, hoarding, and eating behaviours. One aspect of the energetic system that may inform birds about their state is stomach fullness, which could be conveyed through mechanoreceptors or hormones produced in the gastrointestinal tract.

In this chapter, I use a subset of the model versions described in Chapter 4 to explore predictions generated using decision rules based on *Stomach content*. Survival outcomes, resulting energy variables and behavioural patterns of the agents are evaluated. Finally, I examine the effects of different temperatures and food distributions on these factors. The results of the *Stomach content*-specific models are discussed here. For a comprehensive comparison of all model results, see Chapter 8.

8.3 Methods

8.3.1 Recap of Model Structure

The general model in this thesis (Figure 7.1) consists of several processes, including ***Decide behaviour***, where the agent selects which behaviour to perform. This process is central to the models, as it delineates the different sets of decision rules that were implemented across model versions. Decision rules vary in two main ways. Firstly, agents can have different "*hoarding types*" and can be categorized as non-hoarders, leftover-hoarders, and two types of direct hoarders. The first type of "direct-hoarder" has "*hoarding*" as the behaviour that is selected in the highest energy state (H_{top}), the second type "rests" in this case (R_{top}). Secondly, agents can have different "*Energy proxies*" and use either *Stomach content* (SC), *Fat reserves* (FR), *Fat change rate* (FCR), or a combination of two of these variables to decide which behaviour to perform. Table 8.1 describes the different model versions and how they vary in terms of "*hoarding type*" and "*decision-making variable*". The model versions discussed in this chapter, based on *Stomach content*, are highlighted in green. The numbers align with the model versions described in Chapter 4 section 7.9.8.1. From here on, I will refer to the "model versions" as "models".

Table 8.1 Overview of the different model versions based on their decision rules. Decision rules vary in terms of hoarding type and energy proxy. The model versions discussed in the current chapter are highlighted.

Energy proxies	***Non-hoarder***	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Stomach content	1.1	1.2	1.3	1.4
Fat reserve	2.1	2.2	2.3	2.4
Fat change rate	3.1	3.2	3.3	3.4
Fat reserve & Fat change rate	4.1	4.2	4.3	4.4
Stomach content & Fat reserve	5.1	5.2	5.3	5.4
Stomach content & Fat change rate	6.1	6.2	6.3	6.4

8.3.2 "Default" Environments

When comparing models, two "default" environments were used. These are environments with "high" temperatures (between -3 and 13ºC) and "medium" food availability. The latter means that birds find on average 4 food items per foraging bout. Finally, these two environments differ in their "food predictability". In the first environment, when birds go out to forage, they sample from a Poisson distribution with a mean set by the "food availability". In the second environment, "Bonanza", birds sometimes find many food items ("bonanza") but often find nothing or a lower amount. Here, the mean probability is also set by the "food availability". Models were parameterized to include more extreme environments than the ones selected, including colder temperatures, increased food availability, and reduced food availability. For simplicity, I selected default environments that most realistically represent typical winter conditions over a 30-day period at northern latitudes, such as those found in the UK. The two environments correspond with the numbered environments 6 and 8, as discussed in Chapter 4, section 7.9.8.2. Unless stated otherwise the default input parameter settings are used (Table 8.2).

Table 8.2. Default input parameter settings.

Parameter	**Default setting**
Days	30
N	1000
Daylight hours	8

8.4 Results

8.4.1 Survival

In Table 8.3 the model performance of the models in this chapter is shown (see also Table 7.18). Half-life survival is the number of days it takes for 50% of the agents in a simulation to die, averaged across all 12 environments that were used in parameterisation (see Figure 7.2). Larger numbers indicate models with better survival. Greener shades indicate better performance. The table shows that leftover-hoarders perform better than the other models and that non-hoarders outperform direct hoarders, but with a smaller difference.

Table 8.3. Half-life survival rates for the resulting models. Half-life survival is calculated as the mean number of days that it takes for 50% of the agents in a model to die, across all 12 environments used in parametrisation.

	Non-hoarder	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Stomach content	45	52	44	41

In line with the results from Table 8.3, Figure 8.1 displays the survival curves for the four *Stomach content*-based models. In the Poisson scenario, the differences between the models are minimal. By the end of the simulation, around day 30, non-hoarding and leftover-hoarding models slightly outperform the two direct-hoarding models. In the Bonanza scenario, where food availability is less predictable, hoarding birds have an advantage over non-hoarders. Among the hoarders, leftover-hoarders exhibit better survival than direct hoarders, surviving as well as in the Poisson environment. Additionally, direct-hoarders that *Rest* before *Hoarding* outlive those that *Hoard* before *Resting*.

8.4.2 Model Selection

To streamline the discussion and maintain focus on the most relevant models, I will examine only a subset of the models presented in Figure 8.1. Across all three results chapters (Chapters 5, 6, and 7), I have applied a consistent criterion: for a model to be considered, at least 50% of birds must survive throughout the simulation, averaged across all parameterisation environments. Therefore, the half-life survival, as presented in Table 8.3 must be above 30. Additionally, hoarding models must demonstrate sustained hoarding behaviour throughout the simulation. If a hoarding model fails to exhibit such behaviour, it is excluded from further analysis as it does not fulfil its intended purpose. In contrast, all non-hoarding models are included for discussion, as they provide a valuable basis for comparison with the hoarding models.

Therefore, here, I will focus on models 1.1 (non-hoarder) and 1.2 (leftover-hoarder). Models 1.3 and 1.4 (direct-hoarders), did display a sufficiently high half-life survival (44 and 41 days respectively) but are excluded as they failed to display hoarding behaviour. Figures showing the energy variables and behavioural patterns of these models are available in Supplementary Materials, Section C.

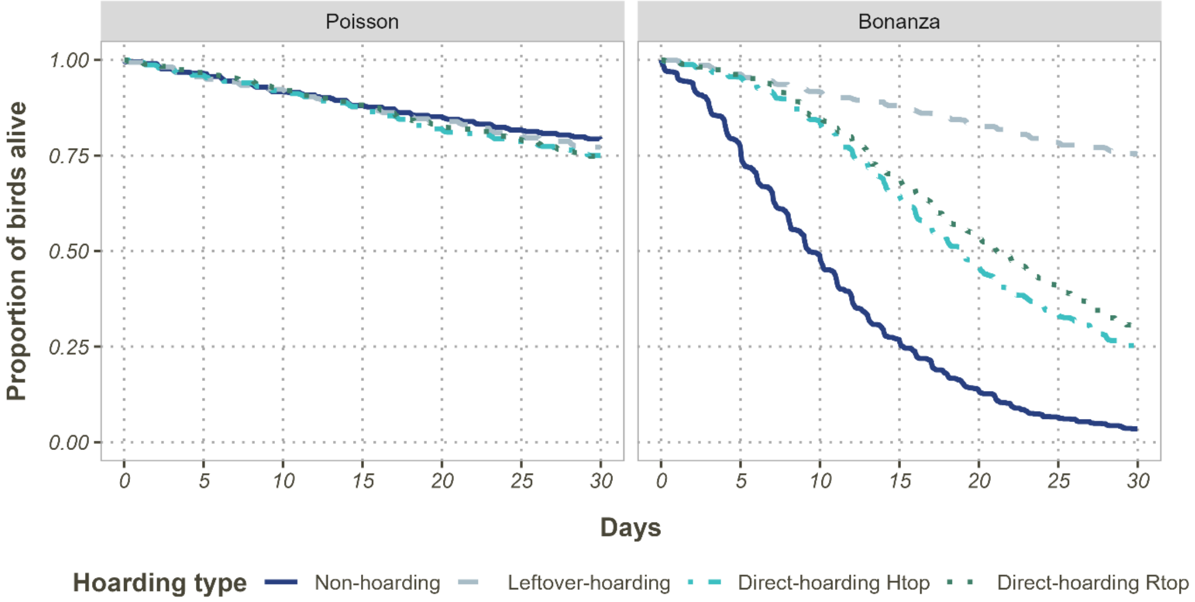


Figure 8.1. Survival rates of models 1.1, 1.2, 1.3 and 1.4 in the default environments. X-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that is alive.

8.4.3 Parameterisation Outcomes

The parameterisation results for models 1.1 (non-hoarder) and 1.2 (leftover-hoarder) are listed in Chapter 4 Table 7.10 and Table 7.11. The range of possible values for the *Stomach content* thresholds is 0 – 0.4 grams. The non-hoarding model has an optimal threshold at 0.003 grams, which results in an agent that *Rests* most of the time. The same is true for the leftover-hoarding model, which has two thresholds. The lower threshold lies at 0.028 grams, which means birds only retrieve if their stomach is almost empty. Note, a food item only has a size of 0.064 grams. The upper threshold, which decides if the bird *Rests* or *Eat-hoards*, lies at 0.081. In practice, this results in birds *Resting* unless their stomach is almost empty.

8.4.4 Energy Variables

8.4.4.1 Stomach Content

Figure 8.2 shows how the four energy variables fluctuate throughout the simulation. Note that values are averaged across the birds that are alive at each timestep. At night, the *Stomach content* of birds drops down to 0. *Stomach content* varies more at the start of simulations, due to the differences in initial values that are assigned to the agents. In the Poisson scenario, where most birds survive, "leftover-hoarding" birds and non-hoarding birds have similar values for *Stomach content*. These similarities between models are also apparent in Figure 8.3, where the values have been aggregated by the hour across days (excluding days 1-3) to allow models to stabilise after receiving initial values. Only timesteps that took place during daylight hours were plotted, as birds are otherwise asleep.

In the Bonanza scenario, after similar initial fluctuations, the pattern of *Stomach content* changes. The leftover-hoarding birds, which survive longer than the non-hoarding model in this scenario, maintain the highest *Stomach contents* during the day. Non-hoarding birds exhibit a lower *Stomach content*. These trends are again apparent in Figure 8.3. Notably, leftover-hoarding birds show greater fluctuations in *Stomach content* at the start of the day compared to the non-hoarding model, which displays more stable patterns throughout the day.

8.4.4.2 Fat Reserves and Fat Change Rates

Fat reserves are similar across both models in the Poisson scenario (Figure 8.2), with noticeable fluctuations between day and night—birds gain weight during the day and lose it overnight. Some variation is observed early in the simulation due to differences in initial values at timestep 1. In the Bonanza scenario, however, clear differences emerge between models. The leftover-hoarding model consistently maintains higher *Fat reserves* than the non-hoarding model. *Fat change rates* have different patterns between the environments and peak higher during the day in the Poisson scenario and dip lower at the start of the day in the Bonanza scenario, which is caused by the unpredictable food environment. Comparing this figure to Figure 8.1, it becomes apparent that the survival curves mirror *Fat reserve* trends: as fat reserves decline for the non-hoarding models, so does their survival.

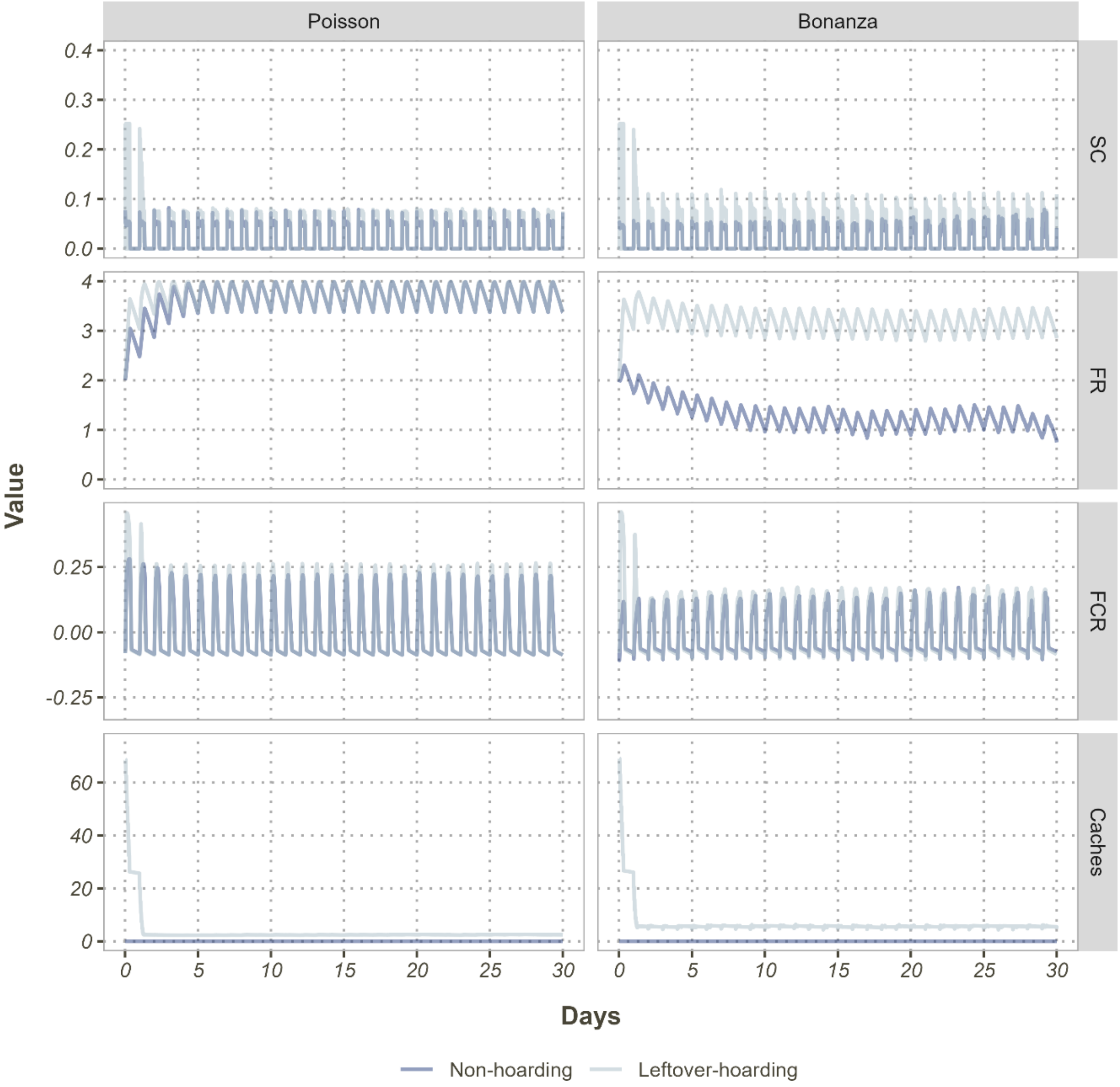


Figure 8.2. Fluctuations in Stomach content, Fat reserve, Fat change rate, and the number of caches for models 1.1 and 1.2 in the two default environments. The x-axes show the number of days in the simulation that have passed. The y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours, and the number of caches. Values were averaged across the birds that are alive at each timestep.

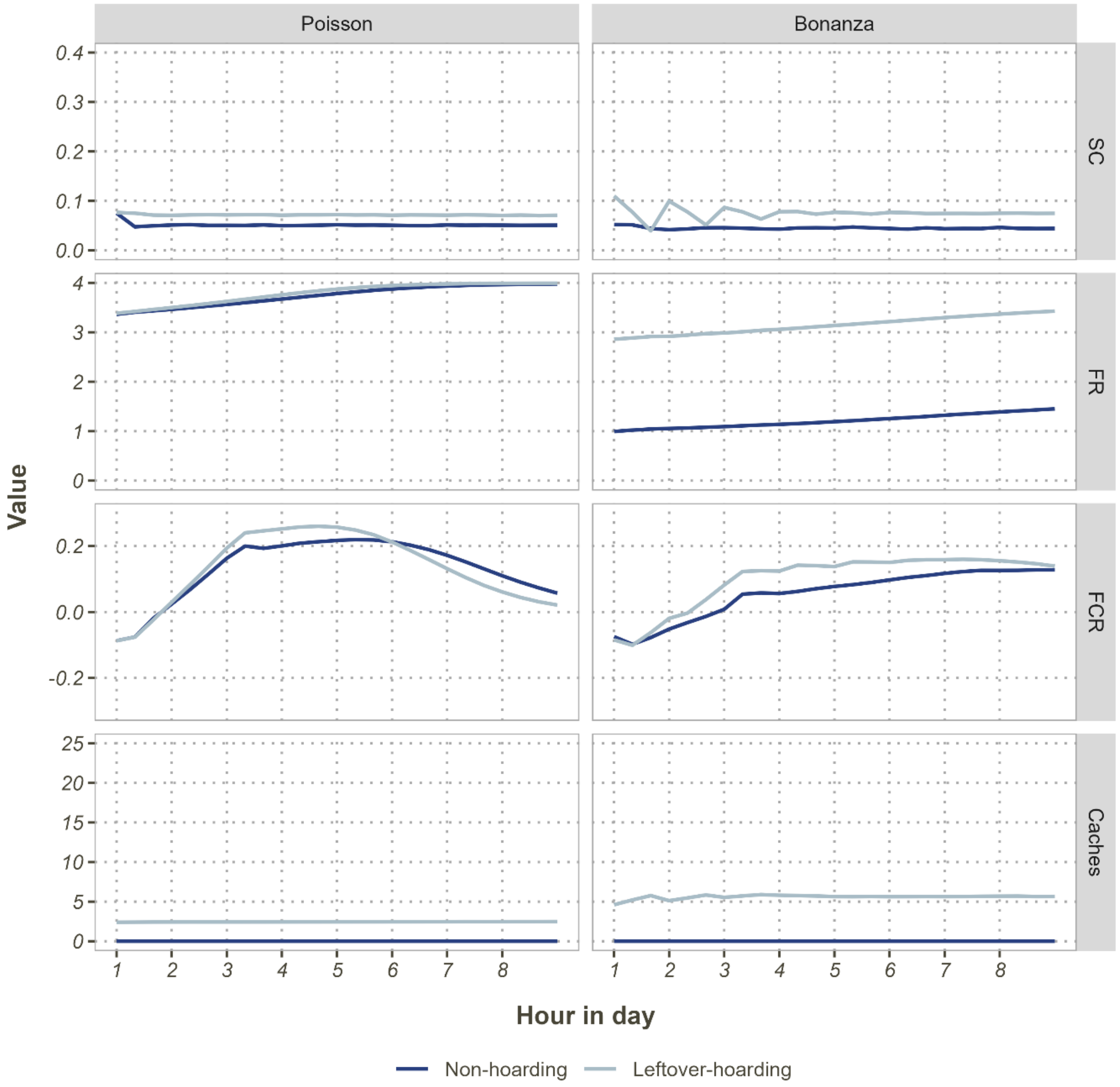


Figure 8.3. Fluctuations in Stomach content, Fat reserve, Fat change rate and number of caches for models 1.1 and 1.2 in the two default environments aggregated across days 4-30 in the simulation. The x-axes show the hours within the daylight period that have passed. Numbers indicate the start of the hour. The y-axes show the Stomach content in grams, the fat reserves in grams, the fat change rate in grams/2 hours, and the number of caches.

In Figure 8.3 the energy variables are aggregated across the days within the simulation. This further illustrates that in the Poisson scenario, where birds tend to survive, *Fat reserves* are generally higher than in the Bonanza scenario. The patterns from Figure 8.2 are reflected here as well, with the best surviving models (leftover-hoarders) exhibiting the highest *Fat reserves* in the Bonanza scenario. Additionally, daily weight gain curves are slightly more s-shaped in the Poisson scenario than in the Bonanza environment, which is reflected in the curve for the *Fat change rates*, peaking around midday in the Poisson environment and declining gradually into the night. In the Bonanza scenario, on the other hand, *Fat change rates* increase most sharply in the morning, particularly for leftover-hoarders, after which the curves stabilize and plateau throughout the day at a lower fat gain rate than in the Poisson scenario.

8.4.4.3 Number of Caches

The hoarding model begins with a relatively high number of caches, which are quickly depleted (Figure 8.2). In the Poisson scenario, cache numbers remain low throughout. In contrast, in the Bonanza scenario, leftover-hoarding birds stabilize around five items. Figure 8.3 confirms this difference in the Bonanza scenario, highlighting that leftover-hoarders maintain a stable cache level.

8.4.5 Behaviour

8.4.5.1 Eat

Figure 8.4 illustrates the differences in *Eating* behaviour between Poisson and Bonanza environments. *Eat* only includes eating behaviour that occurs within a successful foraging attempt. Non-successful foraging attempts are not included in the graphs. Eating as a result of food retrieval is plotted as *Retrieve*. Eating followed by hoarding the leftovers is recorded as *Eat-hoard*. Across both models, a higher proportion of birds engage in *Eating* behaviour throughout the day in the Poisson environment. A peak in *Eating* occurs at the start of the day in both scenarios, although this peak is more substantial in the Poisson environment. This difference is likely in part because birds are more likely to have successful foraging attempts, and therefore *Eat*, in Poisson environments. Even though the average number of food items found during a foraging bout is the same between environments, the frequency of finding 0 items, and therefore not *Eating*, is higher in a Bonanza environment.

Non-hoarding birds exhibit the highest frequency of eating, while leftover-hoarding birds eat least often. Daily patterns are shown in Figure 8.5, again displaying a peak of *Eating* behaviour in the morning, which is less pronounced in the Bonanza environment. In the Bonanza environment, leftover-hoarding birds *Eat* least often, whilst they are the best surviving model (Figure 8.1).This is due to their ability to *Retrieve* caches, which form a reliable food source.

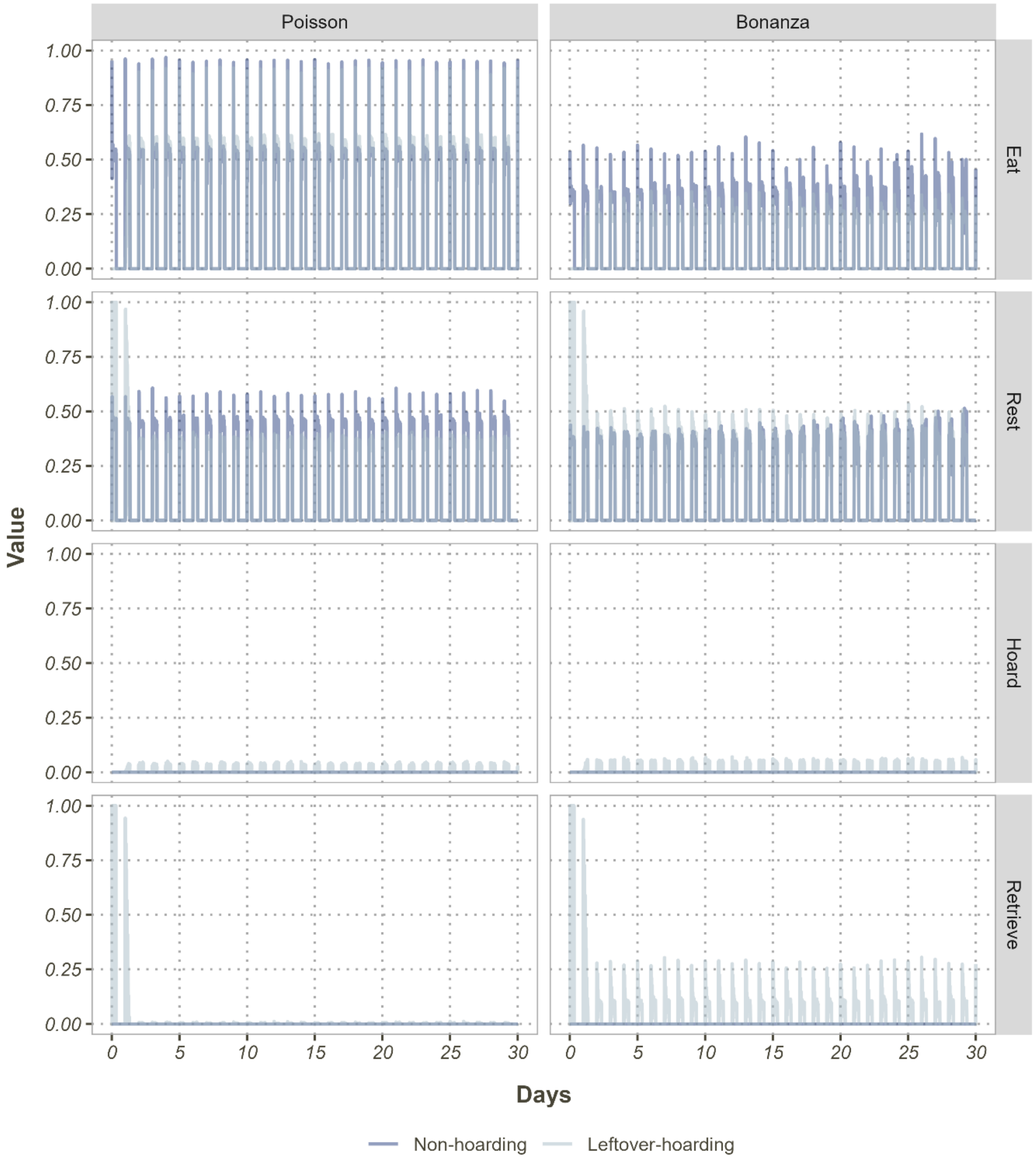


Figure 8.4. Fluctuations in Eating, Resting, Eat-hoarding, and Retrieving behaviour throughout the simulation for models 1.1 and 1.2 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of living birds exhibiting the behaviour in each timestep. Note that the "Hoard" behaviour indicates Eat-hoarding for the leftover models. When birds only "Eat" this is recorded as "Eat".

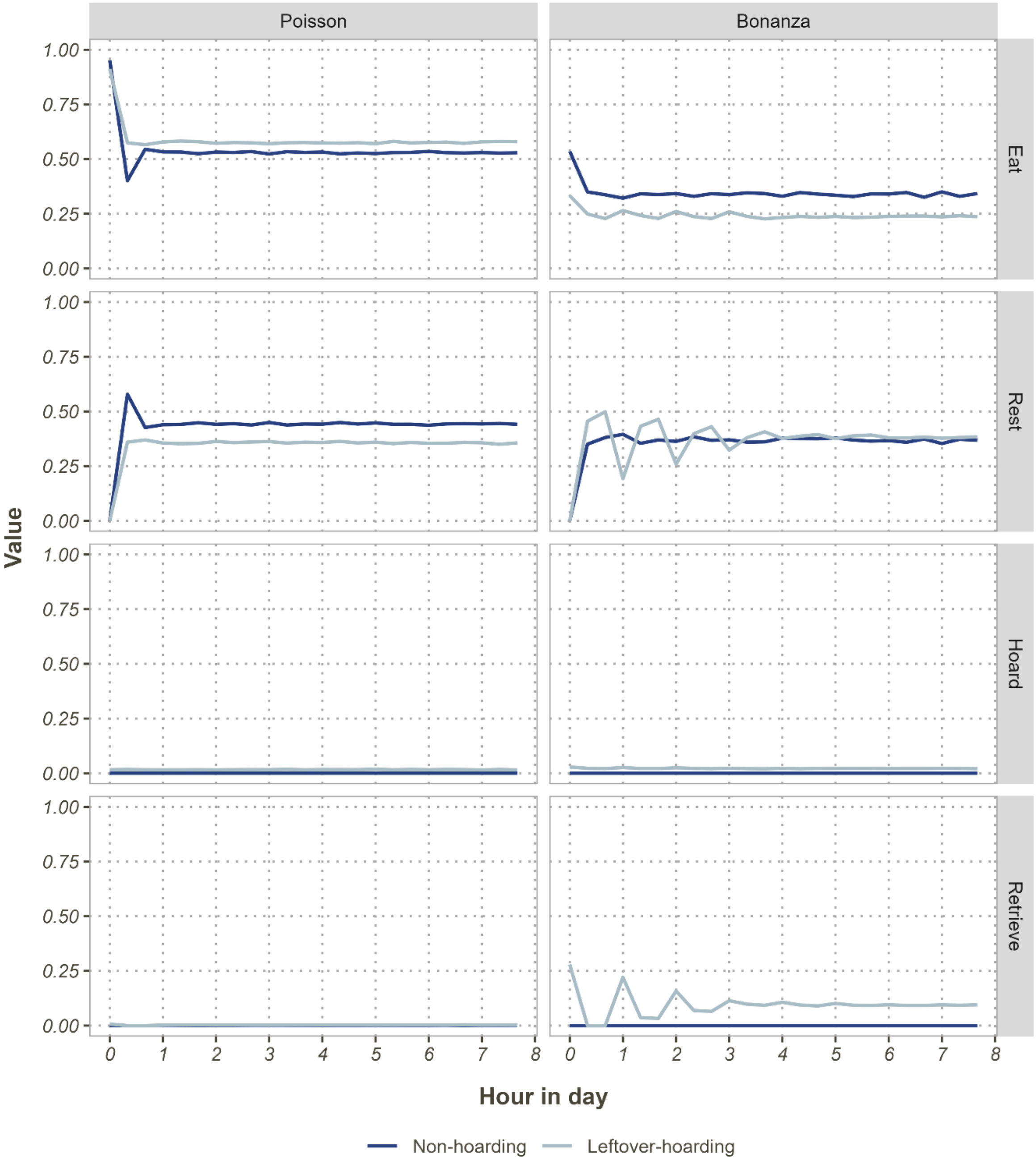


Figure 8.5. Fluctuations in Eating, Resting, Eat-hoarding, and Retrieving behaviour days for models 1.1 and 1.2 in the two default environments aggregated across days 4-30 in the simulation. The x-axes reflect the number of hours after sunrise in the day. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Note that the "Hoard" behaviour indicates eating and hoarding for the leftover-hoarding model. If the bird does not hoard but only eats, this is recorded as "Eat".

8.4.5.2 Rest

Resting patterns were similar between the Poisson and Bonanza scenarios (Figure 8.4). This again emphasizes that the lower *Eating* rates in the Bonanza scenario compared to the Poisson scenario, are not caused by a higher average number of *Resting* birds, but by unsuccessful foraging attempts. Models in which birds spend the least time *Eating,* within environments, tend to *Rest* more frequently, particularly in the non-hoarding model, where *Resting* and *Eating* are the only two available activities. Non-hoarding birds exhibit a peak in *Resting* behaviour in the morning, immediately following their peak in *Eating*.

Daily *Resting* patterns, shown in Figure 8.5, reflect similar trends, with non-hoarding birds *Resting* most frequently in Poisson environments, peaking in the early morning. In the Bonanza environment, the leftover-hoarding model shows some variation in average *Resting* proportion throughout the morning, stabilising later in the day. Notably, this model, which exhibits the highest survival rate, also shows the highest frequency of *Resting,* although the differences are small.

8.4.5.3 Hoard and Retrieve

Figure 8.4 illustrates that leftover-hoarding birds, on average, consistently engage in *Hoarding* throughout the simulation. While there is some *Hoarding* by leftover-hoarders in the Poisson scenario, this behaviour is more pronounced in the Bonanza scenario. Figure 8.5 depicts daily fluctuations, showing that leftover-hoarders consistently *Hoard* throughout the day, with up to 2% of the birds engaged in hoarding at any given time. Leftover-hoarding birds *Retrieve* food relatively frequently in the morning, and this behaviour is interspersed with *Resting* periods.

8.4.6 The Effects of Temperature and Food Distribution on Survival

Figure 8.6 illustrates how the models respond to changes in environmental conditions. The first two graphs replicate those in Figure 8.1, followed by survival results plotted for simulations with lower temperatures (as seen in environments 5 and 7 in Figure 7.2), reduced food availability (as in environments 2 and 4), and a combination of both lower food availability and lower temperatures (environments 1 and 3). Model versions within a Poisson scenario consistently demonstrate resilience to lower temperatures and reduced food availability, unless both factors are combined. In contrast, in the Bonanza scenario, bird survival decreases with lower food availability and lower temperatures, with the lowest survival observed where the two are combined. Hoarding birds are more resilient to changes in temperature and food availability than non-hoarding birds.

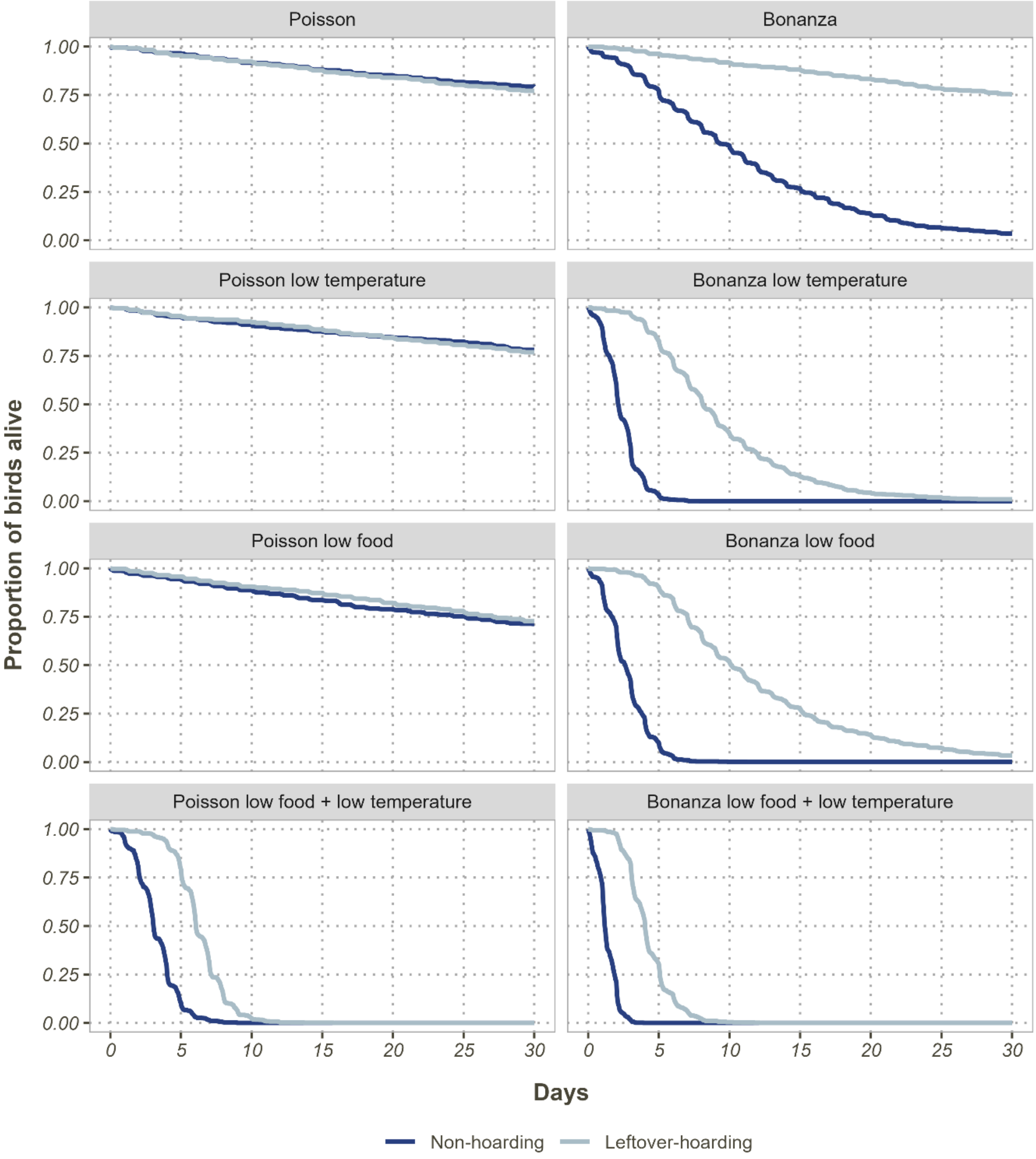


Figure 8.6. Survival rates of models 1.1 and 1.2 in the default environments, low-temperature environments, low-food environments and environments combining low food availability and low temperatures. The x-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

8.5 Discussion

8.5.1 Survival

In general, the models exhibit the best survival outcomes in a Poisson scenario with higher temperatures and at least medium food availability (Figure 8.6). Among the environmental changes, food predictability has the greatest impact on survival. In the more challenging Bonanza scenario, as expected, non-hoarding birds struggle with unpredictable conditions. Although their average *Stomach content* is not largely different from the non-hoarding models (Figure 8.3), leftover-hoarders maintain higher *Fat reserves* than non-hoarders in the Bonanza scenarios, which is crucial for night-time survival. The higher *Fat reserves* are likely due to an earlier increase in *Fat change rate* during the day, possibly because leftover-hoarders have access to a more reliable food source, buffering them from uncertainty in Bonanza environments.

This advantage is reflected in their behaviour, as leftover-hoarding birds *Eat* less, *Rest* more, and rely on *Retrieving* stored caches, allowing them to survive longer than other models. The ability to *Retrieve*, combined with increased *Resting* which conserves energy and reduces predation risk — appears to be crucial. This is also apparent in the model parameterisation, where optimised thresholds are structured to make *Resting* the most likely behaviour. At the same time, *Hoarding* behaviour in the leftover-hoarding model enables agents to use the occasional large amount of food items encountered in Bonanza environments, which further buffers them from food uncertainty.

It is important to note, however, that leftover-hoarding birds rely more on *Retrieving* existing caches than they are creating new ones, particularly at the start of the simulation. While they *Retrieve* many items early on, their hoarding and retrieval stabilise over time, reaching a balance (Figure 8.4 and Figure 8.5). *Retrieval* peaks of the leftover-hoarding model are not as high as one might expect in the morning when birds have empty stomachs. This is likely because *Retrieval* requires both *Stomach content* to be below the lowest threshold and a minimum of 5 caches. Because the leftover-hoarding model in this chapter stabilises around about 5 caches, birds will not always be able to *Retrieve* food in the early morning.

8.5.2 Daily Weight Gain Trajectories

Field data on hoarding birds indicates that the highest hourly weight gain occurs just after sunrise, with a lower, constant rate of weight gain in the afternoon (Haftorn, 1992; Lilliendahl, 2002). Most other studies report linear weight gain rates throughout the day including black-capped chickadees throughout the year in Southern Quebec (Nip et al. 2018), black-capped chickadees captured between October and March in New Jersey (Graedel & Loveland, 1995) and in experimental work on captive black-capped chickadees in Canada (Boisvert & Sherry, 2000). On the other hand, Hurly (1992), studied daily mass trajectories in hoarding marsh tits under laboratory conditions, finding that these birds often delayed weight gain until later in the afternoon. Similarly, Polo et al., (2007) found that coal tits in southern Spain tend to delay their mass gain until later in the day, whilst birds in Scotland had more linear daily weight gain curves. Hurly's experiments were conducted under mild winter conditions (temperatures above 6°C). This could indicate that birds in more favourable conditions can afford to delay their weight gain to later in the day, whilst birds in colder temperatures increase their weights throughout the day to avoid starvation.

From these studies, it is clear that birds tend to gain weight stably throughout most of the day, with some studies reporting higher rates in the morning or late afternoon. This variation could be due to differences in the level of detail recorded in the studies; these vary from hourly observations all the way to averages between birds captured on different days. In some cases, birds were recorded directly after sunrise and measured frequently, in other studies, birds were only weighed three times a day. It is possible that small increases in morning weight gain rates were not observed due to a lack of detail in the data.

My hoarding model replicates part of the pattern found by Lilliendahl (2002) and Haftorn (1992) under favourable Poisson conditions, where *Fat change rates* are higher in the morning than in the afternoon. However, the reduced *Fat change rate* observed in the evening for the models is not reflected in the field data. This dip is likely caused by the maximum *Fat reserve*, which was set to 4 grams. Because of this "forced" maximum, birds will continue to *Eat* without gaining more fat. Had this not been enforced, the daily weight gain curves would have likely been linear, as was observed in most field studies (Boisvert & Sherry, 2000; Graedel & Loveland, 1995; Nip et al., 2018). Lilliendahl (2002) found a stable weight gain rate throughout the day for non-hoarding great tits, whereas Haftorn (1992) observed a similar high early morning weight gain rate in non-hoarding as in hoarding tits. Under the Poisson condition, the non-hoarding model performs very similarly to the leftover-hoarder.

Under more challenging conditions (e.g. Bonanza), the leftover-hoarding model, which demonstrates reasonable survival, shows a more linear increase in *Fat reserves* throughout the day. These latter results align with the studies on black-capped chickadees (Boisvert & Sherry, 2000; Graedel & Loveland, 1995; Nip et al., 2018), which report similar trends.

In summary, the literature suggests that hoarding birds generally exhibit an early-day mass increase, followed by continued stable fat accumulation throughout the day. My leftover-hoarding model, which performs best in terms of survival, roughly aligns with these patterns: showing a morning mass increase in the Poisson scenario and a steady *Fat reserve* accumulation throughout the day in the Bonanza scenario. This relatively linear daily mass trajectory is likely due to the structure of the model. Since the decision-making process is based solely on *Stomach content,* birds continue to forage whenever their *Stomach content* falls below a set threshold, without factoring in their existing *Fat reserves.* This behaviour leads to continuous foraging and energy accumulation throughout the day. Chapters 6 and 7 will discuss models that include *Fat reserves* in their decision making.

8.5.3 Daily Hoarding and Retrieving Patterns

Data on daily hoarding and retrieval patterns of *Paridae* is limited and includes mixed findings. Boisvert and Sherry (2000) report preliminary data using an automated feeder system, reporting a stable hoarding pattern throughout the day for a dominant black-capped chickadee, and a delayed, late-day caching peak for a subordinate individual during winter in Canada. Brodin et al. (1994) also found no differences in hoarding intensity between the morning and afternoon in crested tits in Belgium and Sweden in autumn. In contrast, Lahti & Rytkönen (1996) observed willow tits hoarding more frequently in the morning than in the afternoon during autumn in Finland.

My leftover-hoarding model aligns closest with the findings of Boisvert and Sherry (2000) and Brodin et al. (1994), exhibiting relatively consistent *Hoarding* behaviour throughout the day, though in low amounts. The conditions of the Boisvert and Sherry (2000) study resemble mine more closely than the other two studies, as the latter focuses on autumn, a period of peak hoarding activity (e.g. Pravosudov, 2006 and sources therein), whilst my models simulated 30 days in winter. The stable *Hoarding* observed in my leftover-hoarding model is likely a result of the model's design, where foraging and *Resting* occur intermittently in response to *Stomach content* thresholds, and hoarding occurs occasionally when sufficient food is encountered. This structure explains the regular but low-intensity hoarding observed in my simulations.

The peak in *Retrieval* observed in my models during the morning aligns with predictions from other dynamic modelling studies (Pravosudov & Lucas, 2001b). While field data confirming this pattern is lacking, an experimental study by Pravosudov and Grubb (1997) does show increased cache retrieval in the morning, matching results from the leftover-hoarding model in this chapter.

8.5.4 Conclusion

In conclusion, the models presented in this chapter highlight the survival advantages of hoarding birds in environments with unpredictable food availability. Birds that have a leftover-hoarding strategy, with decision rules based on *Stomach content*, demonstrate greater performance than non-hoarding strategies, even in the more challenging Bonanza scenarios. Their behavioural pattern of intermittent *Foraging* and *Resting* allows them to conserve energy while accessing reliable food sources in their caches, resulting in higher *Fat reserves* that are crucial for survival. Additionally, weight gain trajectories observed in the leftover-hoarding model align well with existing field data, as do patterns of *Hoarding* and *Retrieval*, further validating my findings.

Chapter 6. Agent-based Models of Small Birds in Winter: Decisions Based on Fat Metabolism

9.1 Abstract

This chapter presents an analysis of model versions incorporating decision-making rules based on *Fat reserves*, *Fat change rates*, and their combination, as outlined in Chapter 4. I examine survival dynamics, physiological variables, and behavioural patterns across various environmental conditions. The impact of different hoarding strategies on survival rates is analysed within environments of high and low food predictability ("Poisson" and "Bonanza"). Findings show that while all models demonstrate resilience in Poisson environments, challenges emerge in Bonanza scenarios, especially for non-hoarders and models using direct-hoarding strategies. Leftover-hoarding birds consistently show higher survival rates than non-hoarders due to their ability to *rest* and utilise their cached food reserves. The results of the leftover-hoarding models partly mirror real-world patterns in daily weight gain trajectories and retrieval intensities.

9.2 Introduction

Birds likely use information about their energetic state to make decisions regarding foraging, hoarding, and eating behaviours (Chapter 1 and 4). One aspect of the energetic system that may inform birds about their energy balance is the state of their fat reserves or the rate at which they change. This could be conveyed through circulating factors involved in lipolysis and lipogenesis, such as regulatory hormones (e.g. glucagon, insulin) and fat metabolites (e.g. free fatty acids, glycerol and VLDLs).

In this chapter, I use a subset of the model versions described in Chapter 4 to explore predictions generated by models with decision rules based on *Fat reserves* and *Fat change rates*. The survival outcomes of these models are evaluated, along with the resulting energy variables and behavioural patterns of the agents. Finally, I examine the effects of different temperatures and food distributions on these factors. For a comprehensive comparison of all model results, see Chapter 8.

9.3 Methods

9.3.1 Recap of the Model Structure

As outlined in Chapter 4 (Figure 7.1) and as a reminder from Chapter 5, the general model in this thesis consists of several processes, one of which is the ***Decide behaviour*** process, where agents select which behaviour to perform. This process is central to the models, as it sets apart the different sets of decision rules that were implemented across the model versions. Decision rules vary in two main ways. Firstly, agents can have different "hoarding types" and can be categorized as non-hoarders, leftover-hoarders, and two types of direct-hoarders. The first type of "direct-hoarder" has "hoarding" as the behaviour that is selected in the highest energy state (H_{top}), and the second type "rests" in this case (R_{top}). Secondly, agents can have different "Energy proxies" and use either *Stomach content* (SC), *Fat reserves* (FR), *Fat change rate* (FCR), or a combination of two of these variables to decide which behaviour to perform. Table 9.1 shows the different model versions and how they vary in terms of "*hoarding type*" and "*energy proxy*". The model versions discussed in this chapter, based on *Fat reserves* and *Fat change rates*, are highlighted. The numbers align with the model versions described in Chapter 4 section 7.9.8.1. From here on, I will refer to the "model versions" as "models".

Table 9.1. Overview of the different model versions based on their decision rules. Decision rules vary in terms of hoarding type and decision-making variable. The model versions discussed in the current chapter are highlighted.

Energy proxies	***Non-hoarder***	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Stomach content	1.1	1.2	1.3	1.4
Fat reserve	2.1	2.2	2.3	2.4
Fat change rate	3.1	3.2	3.3	3.4
Fat reserve & Fat change rate	4.1	4.2	4.3	4.4
Stomach content & Fat reserve	5.1	5.2	5.3	5.4
Stomach content & Fat change rate	6.1	6.2	6.3	6.4

9.3.2 "Default" Environments

Again, as a reminder from Chapter 5, when comparing models, two "default" environments were used. These are environments with "high" temperatures (between -3 and 13ºC) and "medium" food availability. The latter means that birds find on average 4 food items per foraging bout. Finally, these two environments differ in their "food predictability". In the first environment, when birds go out to forage, they sample from a Poisson distribution with a mean set by the "food availability". In the second environment, "Bonanza", birds sometimes find many food items ("bonanza") but often find nothing or a lower amount. Here, the mean is also set by the "food availability". The models were parameterised to include more extreme environments than the ones selected — colder temperatures, increased food availability, and reduced food availability. For simplicity, I selected default environments that most realistically represent typical winter conditions over a 30-day period at northern latitudes, such as those in the UK. The two environments correspond with the numbered environments 6 and 8 (see Chapter 4, section 7.9.8.2). The default input parameter settings are used across all simulations (Table 8.2).

9.4 Results

9.4.1 Survival

In Table 6.2 the model performance of the models in this chapter is shown (see also Table 7.18). Half-life survival is the number of days it takes for 50% of the agents in a simulation to die, averaged across all 12 environments that were used in parameterisation (see Figure 7.2). Larger numbers indicate models with better survival. Greener shades indicate better performance. Direct-hoarders R_{top} have the worst model performance in general and leftover-hoarders perform the best (Table 9.2; see also Table 7.18). In general, models based solely on *Fat reserves* perform poorly. The best surviving model, a leftover-hoarder that makes decisions based on both FR and FCR, has the longest half-life of 56 days.

Table 9.2. Half-life survival rates for the resulting models. Half-life survival is calculated as the mean number of days that it takes for 50% of the agents in a model to die, across all 12 environments used in parametrisation. Green shades indicate longer survival, and red shades indicate shorter survival.

	Non-hoarder	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Fat reserve	35	46	40	29
Fat change rate	27	35	29	28
Fat reserve & Fat change rate	43	56	42	30

Figure 9.1 displays the survival curves for the 12 models based on *Fat reserves* and *Fat change rates* considered in this chapter. In the Poisson scenario, models were split into two groups based on their survival outcomes. Among the models with poorer survival, three were based on decisions using *Fat change rates* only. The only *Fat change rate* model that survived well was the leftover-hoarding strategy. Non-hoarders and both types of direct-hoarders do not perform as well. The final model in the "poorer" survival group was direct hoarding (R_{top}), based on both *Fat reserves* and *Fat change rates*. These observations are in line with the survival of the models across the 12 environments (Table 9.2).

In the Bonanza scenario, the leftover-hoarding models, regardless of the energy proxies they base their decision on, consistently outperform all other models. Among the leftover-hoarders, the combined model outperforms the *Fat loss rate*-based model, which in turn slightly outperforms the model based on *Fat reserves.* Non-hoarding models perform the worst, along with Direct Hoarding (H_{top}) models that base their decisions on *Fat change rates* and the combination of *Fat reserves* and *Fat change rates*. When comparing these survival rates to Table 9.2, which presents half-life survival across all environments used for parameterisation, leftover-hoarders still demonstrate the best performance, followed by direct-hoarders (H_{top}). However, in this specific Bonanza scenario (the default environment), the performance of direct-hoarders (R_{top}) is more similar to non-hoarders than observed in Table 9.2. Additionally, in the default environment, *Fat reserve* and *Fat change rate* leftover-hoarding models show comparable performance, and the FR leftover-hoarder slightly outperforms the FCR leftover-hoarder counterpart across all 12 environments (Table 9.2).

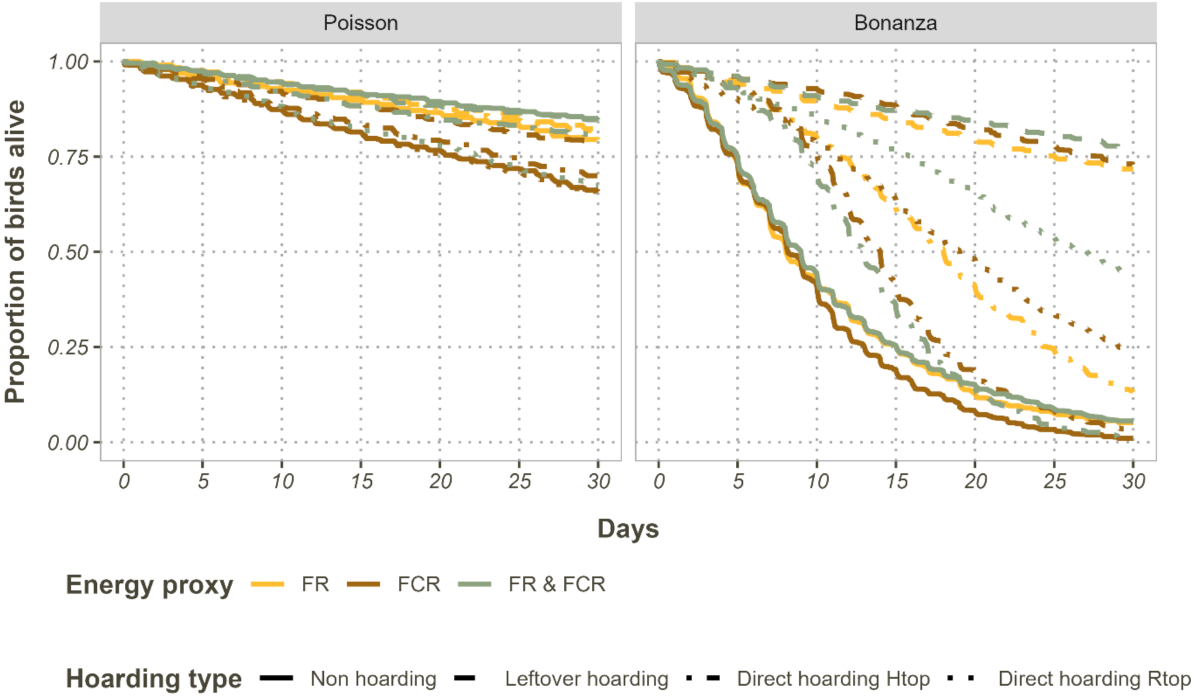


Figure 9.1. Survival rates of models with decision-making based on Fat reserves and Fat change rates in the default environments. The x-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

9.4.2 Model Selection

To streamline the discussion and maintain focus on the most relevant models, I will examine only a subset of the models presented in Table 9.1. Across all three results chapters (Chapters 5, 6, and 7), I have applied a consistent criterion; for a model to be considered, at least 50% of birds must survive throughout the simulation, averaged across all parameterisation environments. Half-life survival (Table 9.1) must exceed 30 and hoarding models must demonstrate sustained hoarding behaviour throughout the simulation. If a hoarding model fails to exhibit such behaviour, it is excluded from further analyses as it does not fulfil its intended purpose. In contrast, all non-hoarding models are included for discussion, as they provide a valuable basis for comparison with hoarding models.

Therefore, in this chapter, I will focus on non-hoarding models and leftover-hoarding models that base their decision making on FR, FCR or a combination of the two. Direct-hoarding R_{top} models, and the direct-hoarding H_{top} model that bases its decisions on *Fat change rate* only, all have a half-life survival of 30 days or less. The two other direct-hoarding models Htop, which base their decisions on only FR or FR and FCR respectively, have sufficient survival, although they lack sustained *Hoarding* behaviour throughout the simulations, and are therefore excluded. Figures showing the energy variables and behavioural patterns of the excluded models are available in Supplementary Materials, Section D.

9.4.3 Parameterisation Outcomes

The parameterisation results for models 2.2, 3.2 and 4.2 are listed in Chapter 4 (Table 7.11 and Table 7.15). The range of possible values for the *Fat reserve* thresholds is 0-4 grams. The range of possible values for the *Fat change rate* is -0.6 to 0.6 grams/2 hours.

Model version 2.2, which is a leftover-hoarding model where decisions are based on *Fat reserves*, has a bottom threshold of 1.021 grams. The top threshold, above which *Resting* takes place is at 1.438 grams, leaving only a small range in which the *Eat* or *Eat-hoard* behaviours can take place.

For model version 3.2, which is also a leftover-hoarding model, but with decisions based on *Fat change rate*, a similar story is true. Birds will *Retrieve* when they lose more than 0.069 grams/2 hours and will rest if they are gaining more than 0.110 grams of fat per 2 hours.

Model 4.2, the only model in this chapter that uses a combination of two proxies, namely *Fat reserves* and *Fat change rate is similar*. The top and bottom thresholds for *Fat reserves* (1.313 and 1.354 grams) and *Fat change rate* (-0.031 and 0.006 gram/2 hours) are very close together, leaving a small range of values in which a bird will go out to forage and *Eat* or *Eat-hoard*.

For the non-hoarding models in this chapter, the parameterisation results are in Table 7.10 and Table 7.14. For models 2.1 and 4.1, the ranges in which birds *Rest* and *Eat* are equally sized. The *Fat reserve*-based non-hoarder (2.1) has a threshold of 1.604 grams of fat. The combined model (4.1) has a 1.521-gram threshold for *Fat reserves* and a -0.006 grams/2 hours threshold for FCR. For model 3.1 on the other hand, the threshold lies at 0.231 grams/2 hours. This makes birds likely to forage and *Eat*. Interestingly, this was the best surviving non-hoarding model (see solid green line in Figure 9.1).

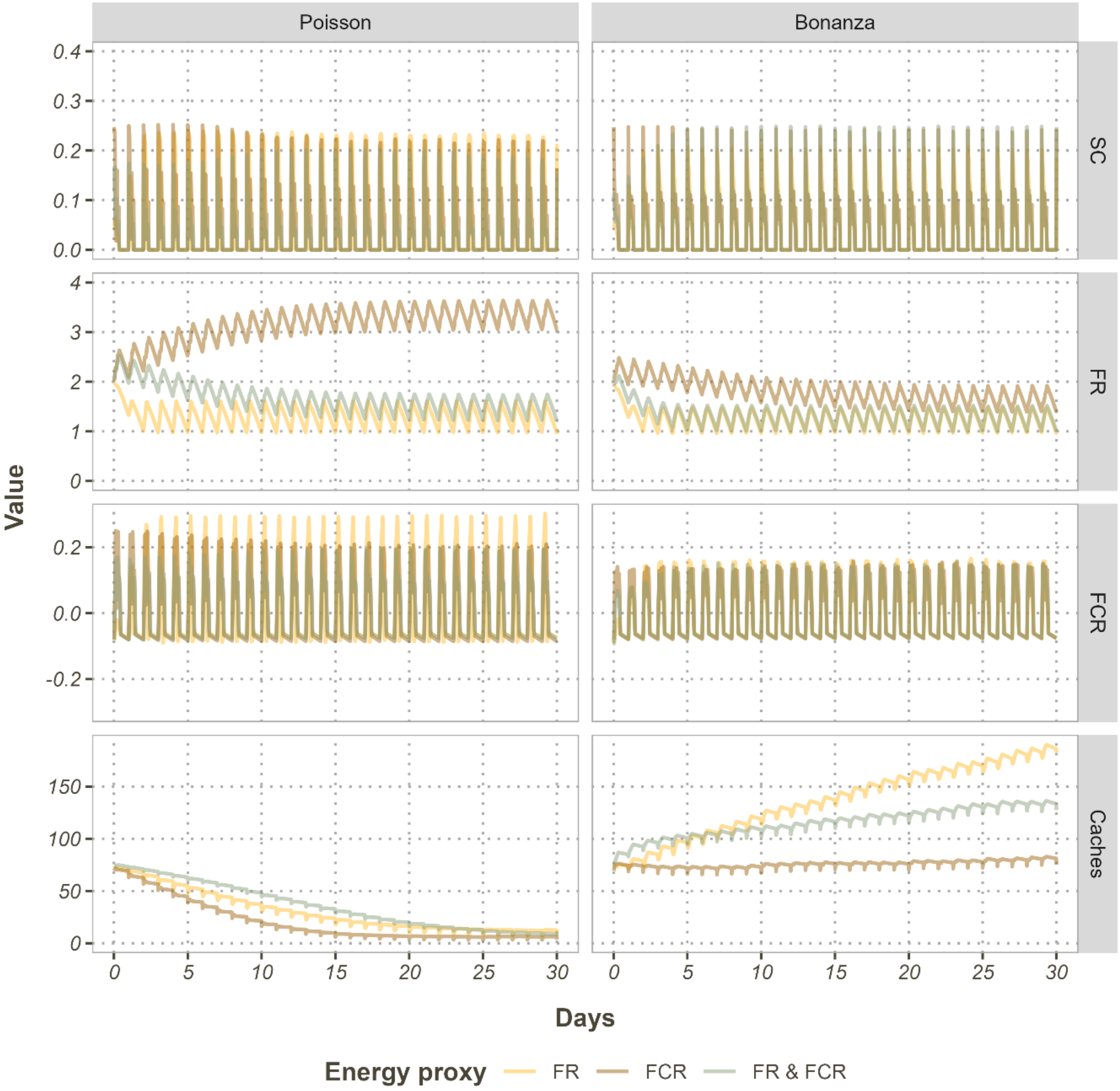


Figure 9.2. *Fluctuations in Stomach content, Fat reserve and Fat change rate for leftover-hoarding models 2.2, 3.2 and 4.2 in the two default environments. The x-axes show the number of days in the simulation that have passed. The y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches. Values are averages across all birds that are alive at each timestep.*

9.4.4 Energy Variables

9.4.4.1 Stomach Content

Figure 9.2 illustrates fluctuations in the four energy variables throughout the simulation for the leftover-hoarding models. Variables were averaged across birds that were alive at each timestep. *Stomach content* drops to zero at night and shows more variation at the start of the simulation due to differences in initial values. Similar *Stomach content* patterns emerge in both the Poisson and Bonanza scenarios throughout the simulation. Under Poisson conditions, the leftover-hoarding models using solely *Fat change rate* and *Fat reserves* as their energy proxy, reach slightly higher *Stomach content* than the combined leftover-hoarding model. In the Bonanza scenario, non-hoarding models reach generally lower *Stomach contents* than the leftover-hoarding models (Figure 9.3 and 6.2). Non-hoarders also have higher Stomach contents in the Poisson environment (Figure 9.3). As in the hoarding models, non-hoarders that use FR or FCR to make decisions, have slightly higher *Stomach contents* throughout the simulation.

Figure 9.4, shows the average value for each energy variable, averaged across days in the simulation for all birds that are alive at each time point. To allow models to stabilise after receiving initial values, days 1-3 were excluded from this aggregation. This further highlights the previous patterns: in all three leftover-hoarding models, *Stomach content* is highest at the start of the day and declines by evening. In the Poisson distribution, the combined FR and FCR model shows the earliest decrease, followed by the FCR model, which has a second peak in the afternoon, and the FR model with an S-shaped curve. In contrast, in the Bonanza environment, *Stomach content* decreases gradually throughout the day, with the *Fat reserve* and *Fat change rate* models unable to sustain the early morning plateaus they achieve under Poisson conditions. Figure 6.4 shows a flatter curve for all three non-hoarding models, with relatively stable *Stomach content* throughout the day under Bonanza conditions. Under Poisson conditions, *Stomach content* rises at the start of the day and decreases toward nighttime. Similar to the leftover-hoarding models, birds making decisions based on both *Fat reserves* and *Fat change rates* have the lowest stomach contents. These combined-model birds also exhibit the highest survival rates given their hoarding strategy (Figure 9.1). Non-hoarding birds that use only FCR in their decision making, have the highest *Stomach contents* late in the day.

9.4.4.2 Fat Reserves and Fat Change Rates

Interestingly, leftover-hoarding models here show more differences between *Fat reserve* patterns in the Poisson environment than in the Bonanza scenario (Figure 9.2). The FCR model stabilises at a higher *Fat reserve* than the other models. In the Bonanza scenario on the other hand, FCR models also start off with slightly higher *Fat reserves*, but converge to levels of the *Fat reserve*-based and combined model. The same patterns can be seen where non-hoarding models based on *Fat change rates* have higher *Fat reserves* in the Poisson scenario, but differences in the Bonanza environment are small (Figure 9.3).

Figure 9.4 further highlights these patterns, showing that models with decision-making based on *Fat change rates* maintain the highest *Fat reserves* for both leftover-hoarders and non-hoarders in the Poisson scenario. In the Bonanza scenario leftover-hoarders also have the highest *Fat reserves*, but the lines for non-hoarders are lower, hidden by the line for the combined non-hoarding model (green solid). Examining *Fat change rates* in the same figure reveals clearer differences between models. In the Poisson scenario, the FCR leftover-hoarding model exhibits two peaks in fat gain, corresponding to fluctuations in *Stomach content*. In contrast, the *Fat reserve*-based leftover-hoarding model has a single, higher peak in fat gain before dropping sharply at night. The combined leftover-hoarding model shows the lowest *Fat change rate* in the morning, followed by a plateau in the afternoon. For the FCR and the combined model, the non-hoarding models follow the hoarding models. The FCR non-hoarding model has a higher peak in *Fat change rate* than the others, which is reflected in higher *Fat reserves*.

Under Bonanza conditions, models show less variation, especially within hoarders and non-hoarders. The FCR leftover-hoarding model maintains a slightly lower fat gain rate before midday compared to the other models. Hoarding models have higher Fat change rates in the morning than their non-hoarding equivalent. For all models, there is a plateau in *Fat change rates*, starting in the late morning for hoarders and in the afternoon for non-hoarders. .

9.4.4.3 Cache Number

The number of *Caches* in all three leftover-hoarding models declines over the course of the simulation under Poisson conditions (Figure 9.2). This is likely because these models can hoard only when they have leftover food, a less frequent occurrence under Poisson than Bonanza conditions. When birds do encounter occasional Bonanza events, the number of caches either remains stable (in the FCR model), increases gradually (in the combined FR & FCR model), or rises steeply (in the FR model). Moreover, the highest cache numbers observed are in the FR model, followed by the combined model and then the FCR model (Figure 9.4). In all three models, cache numbers gradually increase throughout the day.

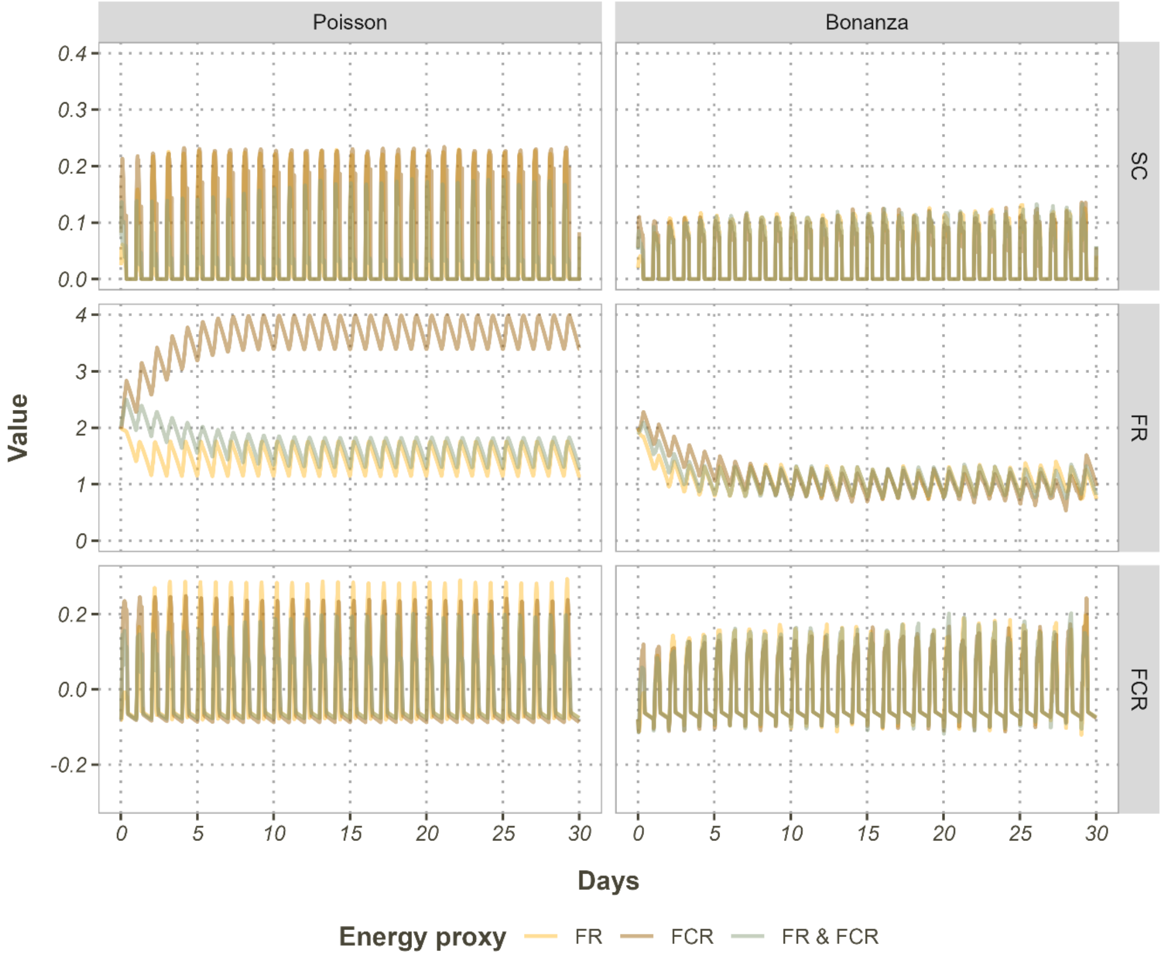


Figure 9.3. Fluctuations in Stomach content, Fat reserve and Fat change rate for non-hoarding models 2.1, 3.1 and 4.1 in the two default environments. The x-axes show the number of days in the simulation that have passed. The y-axes show the Stomach content in grams, the Fat reserves in grams and the Fat change rate in grams/2 hours. Values are averages across all birds that are alive at each timestep.

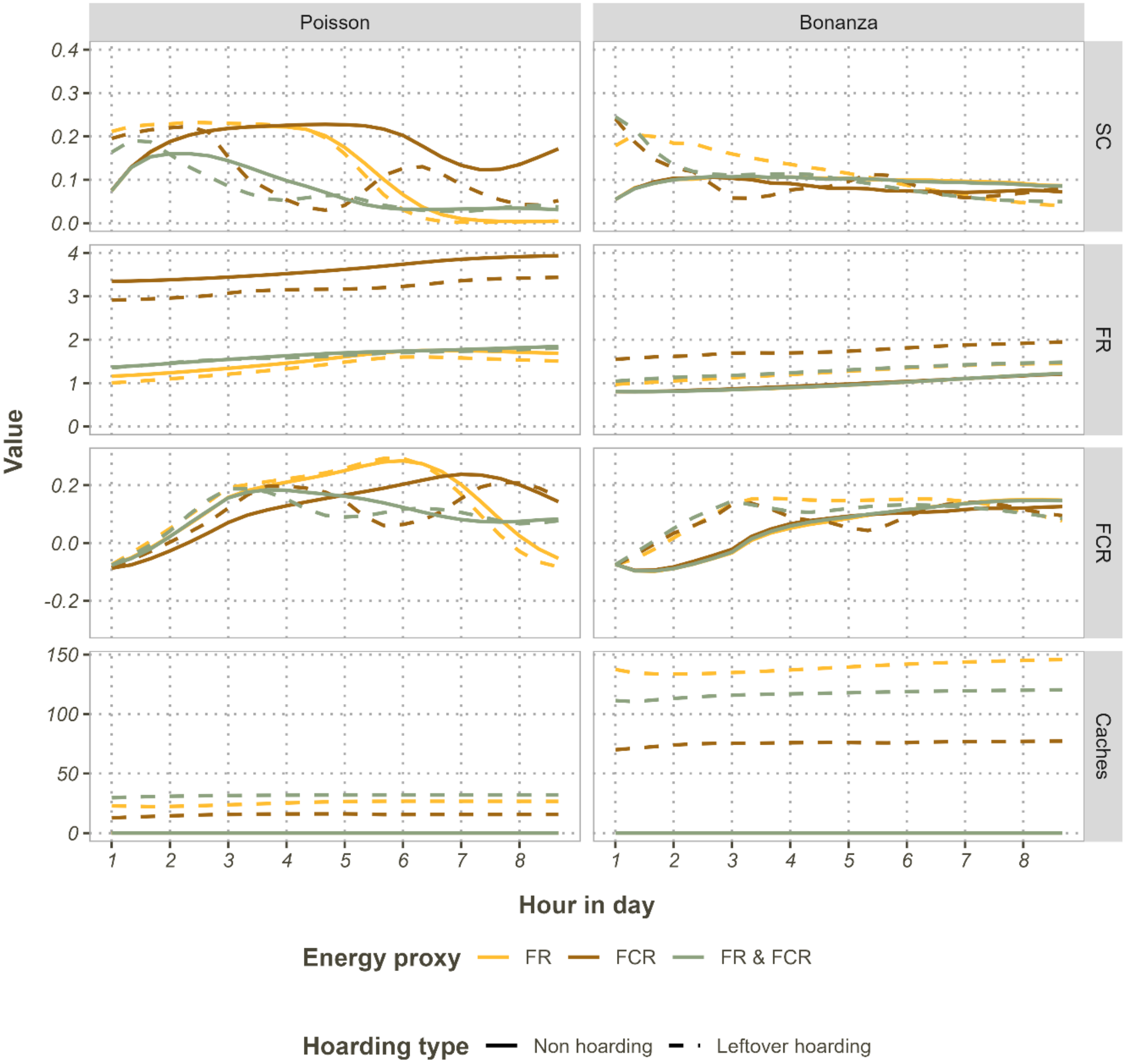


Figure 9.4. Fluctuations in Stomach content, Fat reserve, Fat change rate and cache number for leftover-hoarding models 2.2, 3.2 and 4.2 and non-hoarding models 2.1, 3.1 and 4.1 in the two default environments. The x-axes show the hours within the daylight period that have passed. Numbers indicate the start of the hour. The y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches. Values are averaged across living birds at each timestep within the day across days 4-30 in the simulation.

9.4.5 Behaviour

9.4.5.1 Eat

Figure 9.5 illustrates the differences in *Eating* behaviour between the Poisson and Bonanza environments for leftover-hoarding birds. The graphs show the proportion of living birds that is exhibiting a certain behaviour at each timestep in the simulation. Note that the "*Eat*" behaviour is what takes place when a bird has gone out to forage, found a food item and has consumed it. This behaviour does not include any items eaten as part of the "*Retrieve*" or "*Eat-hoard*" behaviours, as they are recorded separately. Non-successful foraging attempts are not included in the graphs. Across all three models, a larger proportion of birds spend their time eating at the same time in the Poisson environment than in the Bonanza environment, which could be due to larger individual differences between birds in the latter environment. The combined model (FR and FCR-based) has high peaks in *Eating* behaviour, especially at the start of the simulation. This is reflected in the higher *Fat reserves* for this model at the start of the simulation. Non-hoarding birds also show consistently lower eating rates in the Bonanza scenario (Figure 9.6).

Figure 9.7 shows the daily eating patterns for the leftover hoarders as well as their non-hoarding equivalents. The values are the proportions of a live birds that exhibit the behaviour, averaged across days in the simulation. In the Bonanza environment, the *Eating* curves are relatively stable throughout the day, with non-hoarding birds eating more often than leftover-hoarders. This is, at least partly, because some *Eating* in leftover hoarders results in "eat-hoard" behaviour. For the leftover-hoarders, both the FCR and the combined model show a small eating peak in the morning under Bonanza circumstances.

In the Poisson environment, daily patterns show more curves. Here, all three leftover-hoarding models show elevated *Eating* in the morning followed by a decrease in the afternoon. Compared to the FR-only model, the FCR and combined model have earlier peaks in *Eating*. The FCR leftover-hoarding model, as well as the combined leftover-hoarding model, have 2 Eating peaks, but the FR hoarding model has one. Non-hoarding models have the highest *Eating* rates, which are sustained into the afternoon for the FR and FCR models. The *Fat reserve*-based hoarding model barely eats in the afternoon, which is further emphasized in its non-hoarding equivalent. "*Eat*" and "*Eat-hoard*" show similar patterns, as for leftover-hoarding birds it is only the amount of food items found that determines if the bird will hoard or not.

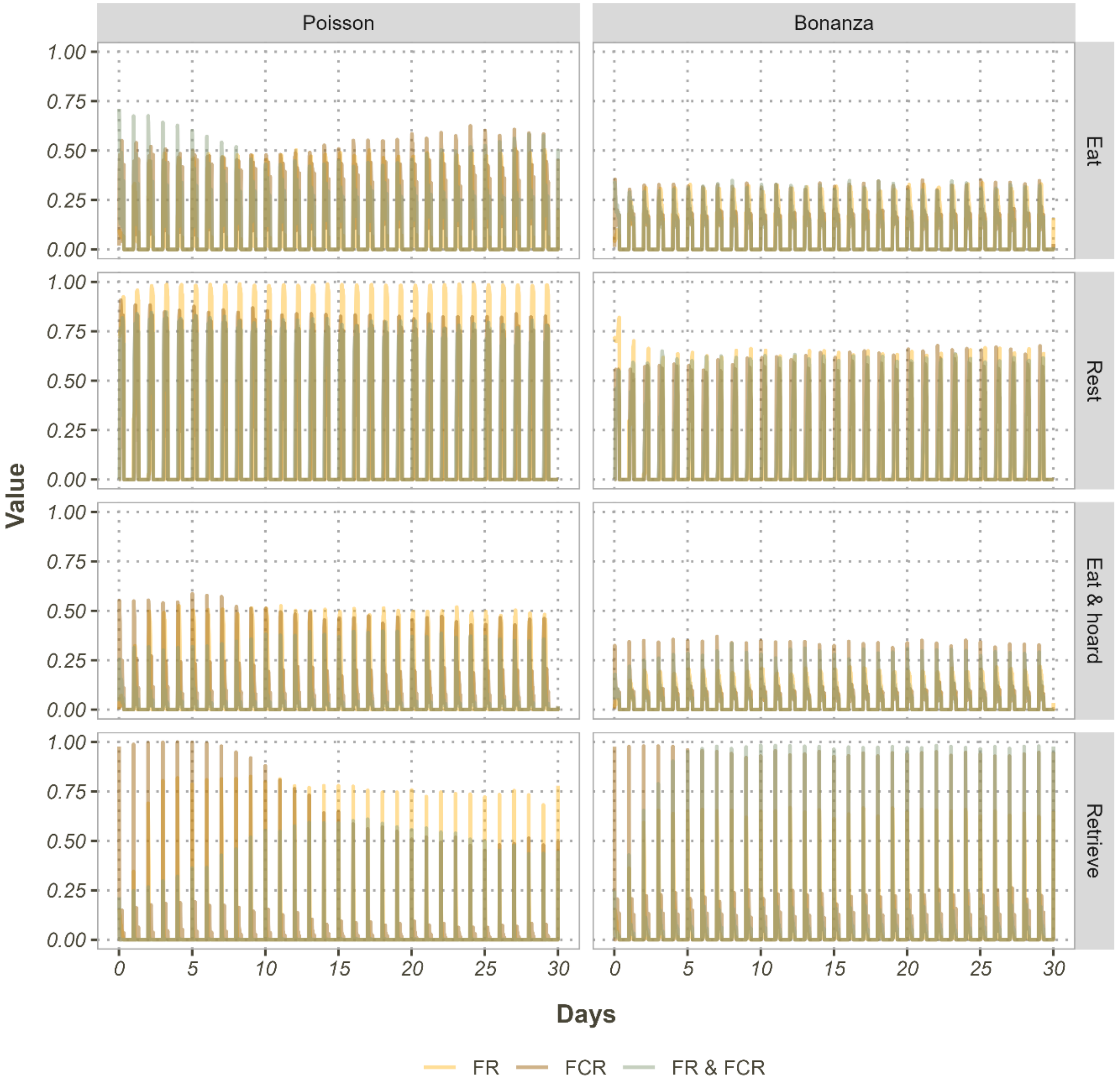


Figure 9.5. Fluctuations in Eating, Resting, Leftover-hoarding, and Retrieving behaviour throughout the simulation for leftover -hoarding models 2.2, 3.2 and 4.2 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Note that birds that "Eat" did not have any leftover items to hoard. Only birds marked as "Eat and hoard" continued to hoard after eating. These options are mutually exclusive. Values are the proportion of living birds exhibiting the behaviour at each timestep of the simulation.

9.4.5.2 Rest

The proportion of leftover-hoarding birds *Resting* at the same time is higher in the Poisson environment than in the Bonanza scenario, specifically for the model where decision making is based on *Fat reserves* (Figure 9.5). Differences between the models throughout the simulation were smaller in the Bonanza scenario. Non-hoarding birds exhibit synchronised *Resting* behaviour in Poisson scenarios, specifically the FR model (Figure 9.6). Synchronised resting proportions were generally higher for the non-hoarding FCR model under Bonanza circumstances.

Similar patterns are reflected in Figure 9.7, where birds *Rest* more on average in the Poisson scenario than in the Bonanza environment. For the *Fat reserve*-based models, most *Resting* occurs at the end of the day, with a more emphasized s-shaped curve in Poisson scenarios. In the Bonanza environment, FR leftover-hoarding models *Rest* more than non-hoarding equivalents. The combined models *Rest* throughout the day in the Poisson scenario, but show a more linear curve under the unpredictable Bonanza scenario. Again, the leftover-hoarding models can *Rest* more under unpredictable food circumstances, especially towards the end of the day. The FCR leftover-hoarding model exhibits two peaks in *Resting* in both environments. The non-hoarding FCR model has one *Resting* peak in the afternoon in Poisson, whilst gradually increasing *Resting* towards the evening in the Bonanza environment. For all six models, patterns for *Resting* and *Eating/Eat-hoarding* mirror each other. *Resting* is generally a lot lower for non-hoarding birds in the Bonanza scenario than the left-over hoarding birds in the same environment. This is reflected in the higher survival rates for the models that *Rest* more.

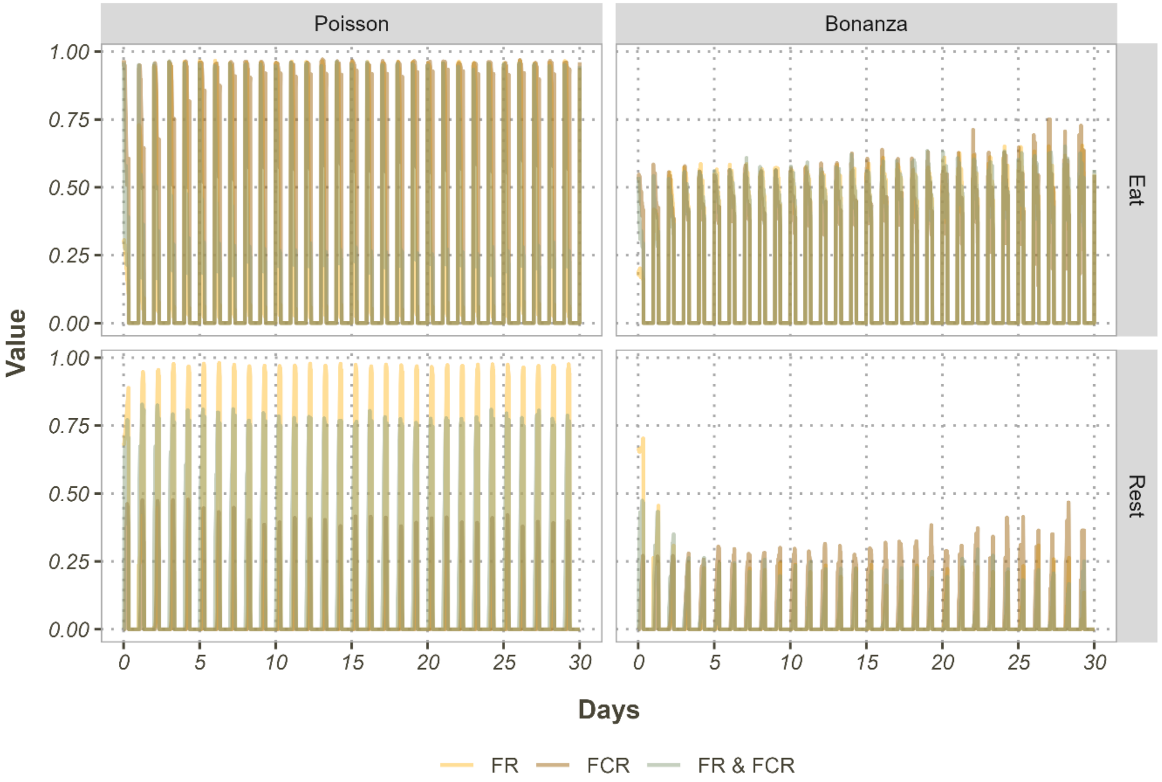


Figure 9.6. Fluctuations in Eating and Resting behaviour throughout the simulation for non-hoarding models 2.1, 3.1 and 4.1 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Values are the proportion of living birds exhibiting the behaviour at each timestep of the simulation.

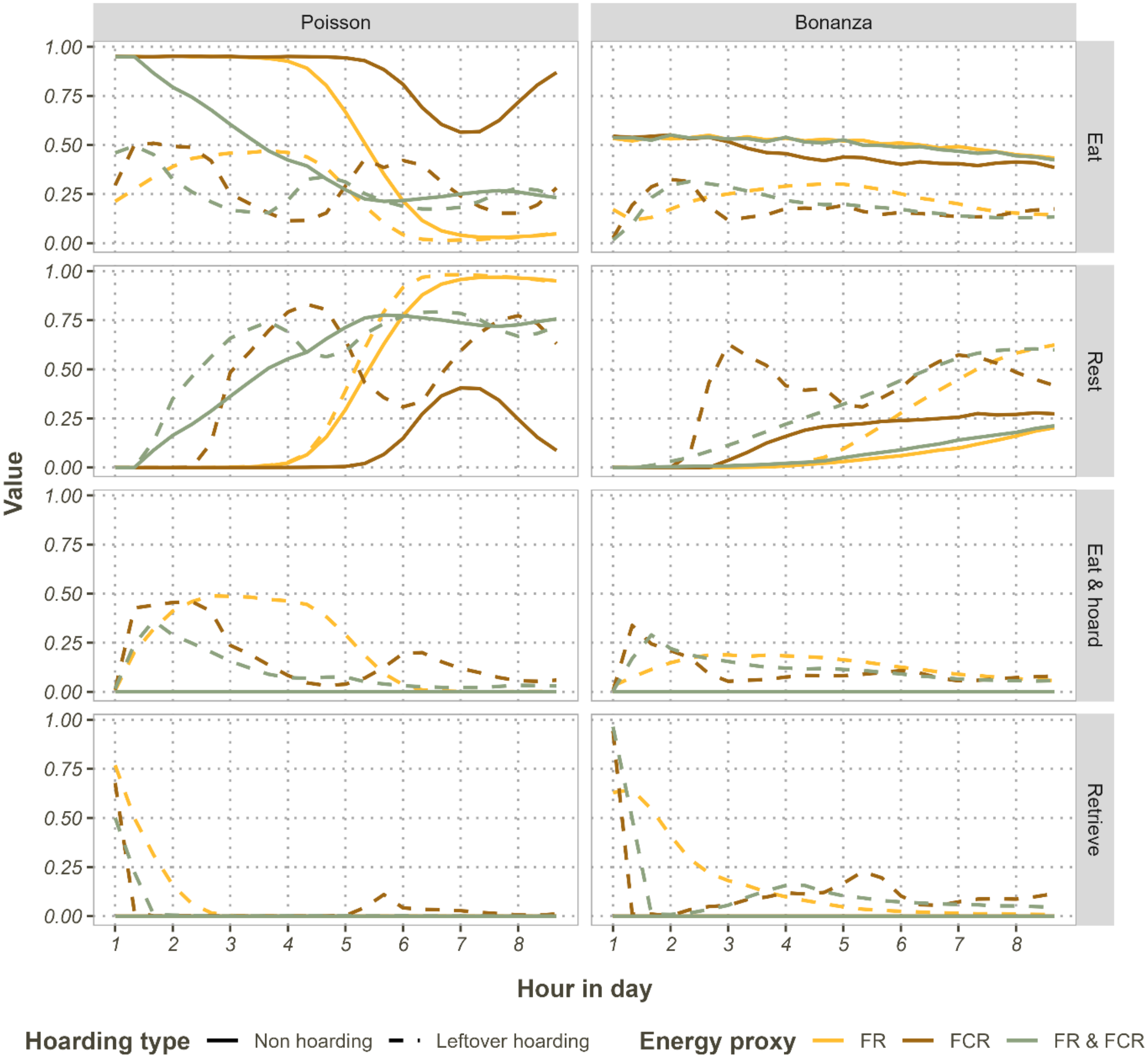


Figure 9.7. Fluctuations in Eating, Resting, Eat-hoarding, and Retrieving behaviour for leftover-hoarding models 2.2, 3.2 and 4.2 and non-hoarding models 2.1, 3.1 and 4.1 in the two default environments. The x-axes reflect the number of hours after sunrise in the day. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Note that birds that "Eat" did not have any leftover items to hoard. Only birds marked as "Eat and hoard" continued to hoard after eating. These options are mutually exclusive. Values are proportions across living birds at each timestep within the day across days 4-30 in the simulation.

9.4.5.3 Hoard and Retrieve

In the Poisson environment, *Hoarding* levels are higher throughout the simulation for birds in Poisson environments than for birds in the Bonanza environment. This is especially true for the models where decisions are based on *Fat change rates* or *Fat reserve* (Figure 9.5 and Figure 9.6). It is interesting to contrast these higher *Hoarding* rates in the Poisson scenario, with the decrease in total *Caches* seen in Figure 9.2. Birds might hoard more often under Poisson scenarios, as they find food more regularly. However, in the Bonanza environment, they will hoard more *Caches* at a time, which results in an increase in *Caches* throughout the simulation (Figure 6.2). Daily *Eat-hoarding* patterns are shown in Figure 9.7. In both the Poisson and the Bonanza environment, all models exhibit an *Eat-hoarding* peak in the morning, which coincides with peaks in *Eating*. Under Poisson circumstances, the FR-based model maintains high *Eat-hoarding* levels throughout the morning into the afternoon.

Retrieval is particularly high at the start of the simulation for the FCR model under Poisson conditions (Figure 9.5). Later in the simulation, the FR model has the highest *Retrieval* rates. The initial high *Retrieval* rates in the FCR model under Poisson circumstances may be driven by the initially high number of *Caches* available, which drops quickly as the simulation continues and birds do not hoard (Figure 9.5). In the Bonanza environment, high levels of synchronised *Retrieval* can also be seen, likely driven by high morning *Retrieval* rates. Figure 9.7 illustrates this trend, with elevated *Retrieval* rates in the mornings across both environments. FCR models display a small afternoon *Retrieval* peak, which aligned with a decrease in *Resting* behaviour. *Eat-hoarding* patterns correspond closely with eating patterns throughout the day. The morning peak in *Retrieval* was higher in the Bonanza than in the Poisson environment. This was likely because part of the birds in the Poisson environment did not have sufficient *Caches* available to them, so morning *Retrieval* was not possible.

9.4.6 The Effects of Temperature and Food Distribution on Survival

Figure 9.8 illustrates how the models respond to changes in environmental conditions. The first two graphs replicate those in Figure 9.1, followed by survival results plotted for simulations with lower temperatures (as seen in environments 5 and 7 in Figure 7.2), reduced food availability (as in environments 2 and 4), and a combination of both lower food availability and lower temperatures (environments 1 and 3). In the Poisson environment, the combined models and the models based on *Fat reserves* are fairly resilient against lower temperatures, whereas the FCR model does not survive well under these circumstances. In a Bonanza scenario, lower temperatures are almost immediately fatal for all models. The effects of reduced food availability are smaller, but again, the FCR model performs worst, even under Poisson circumstances. The combined model, which has the best survival rate in general, outperforms the FR and FCR models, but only slightly. Model survival under combined food shortage and lower temperatures is poor.

The non-hoarding models show similar responses as the leftover-hoarding models under Poisson environments. Under Bonanza environments, non-hoarding models survive worse, with the largest effect caused by lower food abundancy (Figure 9.8).

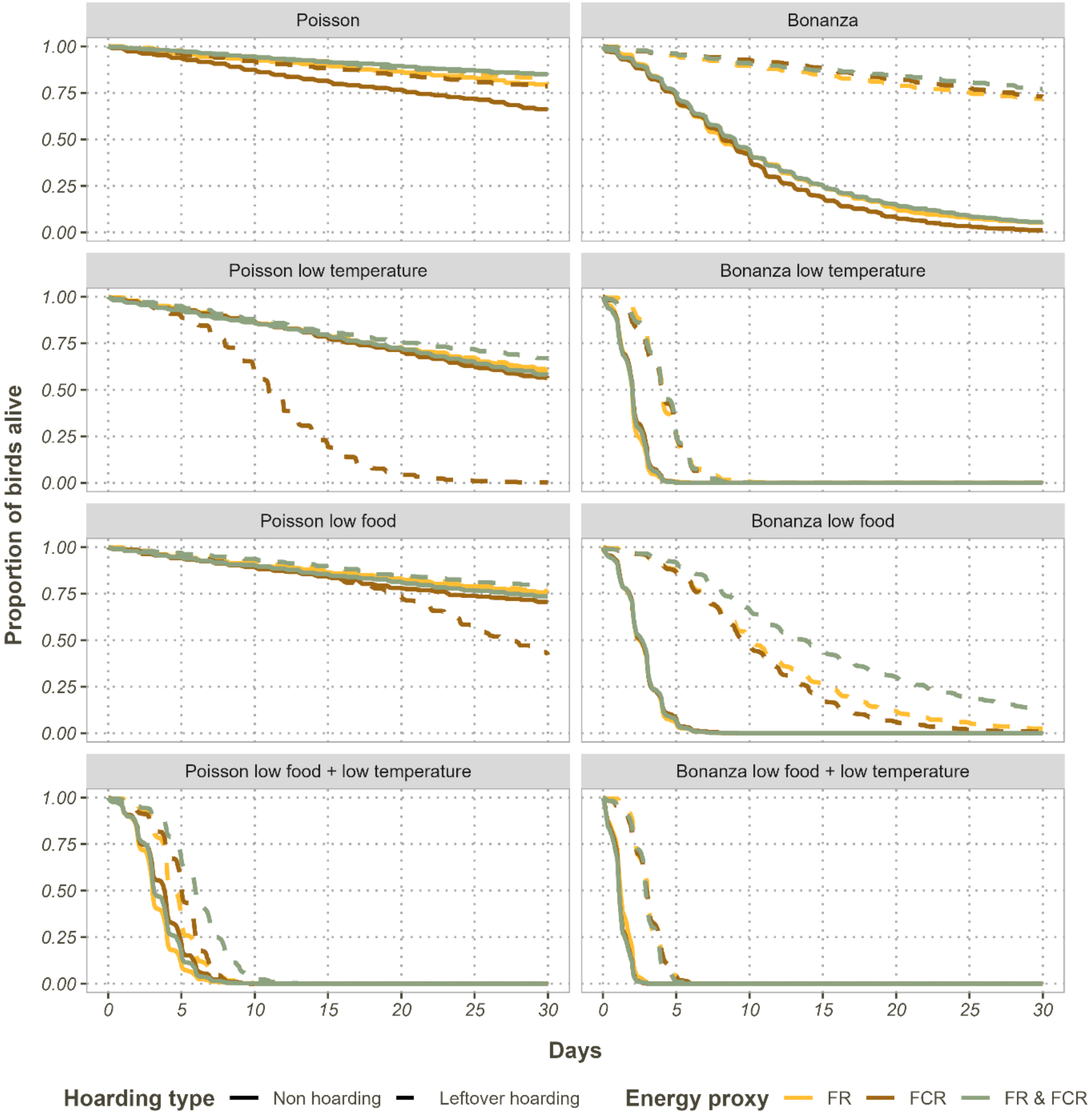


Figure 9.8. Survival rates of models 2.1, 2.2, 3.1, 3.2, 4.1 and 4.2 in the default environments, low temperature environments, low food environments and environments combining low food availability and low temperatures. The x-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that is alive.

9.5 Discussion

9.5.1 Survival

In the models discussed in this chapter, agents base their decisions on *Fat reserves*, *Fat change rates* or a combination of these two variables. In general, models show the best survival outcomes in a Poisson scenario with high temperatures and medium food availability (Figure 9.1). In the Bonanza environment, non-hoarding models survived poorly. When leftover-hoarding models were exposed to different environments (Figure 9.8), lower temperatures had a bigger effect on survival than lower food availability. The greater impact of lower temperatures can likely be attributed to the birds' *Fat reserves*, which, in this chapter, remain well below their maximum capacity. As a result, the birds lack a sufficient buffer against colder conditions, increasing their risk of nighttime starvation during such periods.

Of the leftover-hoarding models, the combined model showed the highest survival rates, followed by the FCR model and finally the *Fat reserve*-based model. Interestingly, the FCR model has the highest *Fat reserves* throughout the day, rather than the combined model. All leftover-hoarding models in the current chapter, however, did have higher *Fat reserves* than the non-hoarding models. In addition to these lower *Fat reserves*, non-hoarding models also had lower *Stomach contents* in the morning, which were sustained for a longer time. This put them at risk for starvation in the morning, after they had fasted for the night, and likely drives their poor survival. These results indicate that, whilst *Fat reserves* are important for survival as they reduce starvation risk, reserves close to the maximum are not necessary for a model to be successful.

Eat and *Eat-hoard* behaviours were similar and constant throughout the day for all hoarding models in the Bonanza scenario. Differences between the models were more emphasized in Poisson environments. This might be because Bonanza scenarios are more unpredictable, which creates larger individual differences. The more smoothened, flatter curves in those scenarios might merely reflect that there were larger differences between birds and behaviours that were less synchronised. In the Poisson environment, models differ in the timing of their *Eating* and *Eat-hoarding* peaks, which were reflected in their *Stomach content* and *Fat change rates*. The FCR leftover-hoarding model spends more time *Eating* and *Eat-hoarding* than the other two leftover models, which explains the higher *Fat reserves*. As a result, this model *Rests* less, which could explain its worse performance across all 12 environments (Table 9.2). Differences in performance between the FR and the combined model are small in the default environments, combined model has superior survival across the 12 environments together. This can be attributed to the slightly higher *Resting* rates and higher morning peaks in *Eating*.

Eat-hoarding behaviours occurs regularly for all leftover-hoarding models in both environments. Peaks occur in the morning, with stable rates subsequently in Bonanza, and higher peaks under Poisson circumstances. *Retrieval* peaks in the morning were exhibited more often in the Bonanza scenario. In Bonanza scenario, birds create more caches than they *Retrieve*, whilst under Poisson, slightly more caches were consumed than made (Figure 9.2).

Non-hoarding models, especially in Bonanza scenarios where survival is low, do not show a lot of *Resting* behaviour. This is reflected in their *Fat reserves*, which are lower than in the hoarding models, specifically under Bonanza circumstances where their survival is low. These results show that *Resting* behaviour is important for survival and that hoarding birds can successfully buffer against unpredictable food distributions.

9.5.2 Daily Weight Gain Trajectories

As reviewed in Chapter 5, hoarding birds typically display a linear increase in body mass throughout the day (Boisvert & Sherry, 2000; Graedel & Loveland, 1995; Nip et al., 2018), although some studies report a slightly higher weight gain rate in the morning, with stable rates throughout the rest of the day (Haftorn, 1992; Lilliendahl, 2002). Afternoon peaks in weight gain rate have been reported in hoarding marsh tits and coal tits under favourable conditions with relatively warm winter temperatures (Hurly, 1992; Polo et al., 2007).

In the leftover-hoarding models presented in the current chapter, linear daily weight gain trajectories are observed in the Bonanza scenario. *Fat change rates* increase during the morning and stabilise throughout the day. It is important to keep in mind that the *Fat change rates* in my models take 2 hours to "update", which is likely what is causing the relatively "low" weight gain rates in the morning. From hour "3" onwards, *Fat change rates* are stable, putting my results in line with most findings from the literature (Boisvert & Sherry, 2000; Graedel & Loveland, 1995; Nip et al., 2018).

Under the Poisson condition, however, the *Fat reserve*-based model and the FR and FCR combined model, show a sharper increase in *Fat reserves* at the start of the day, followed by a plateau towards evening. This was reflected in their *Fat change rates*, which had peaks at various levels but declined towards the evening. Whilst the peak in weight gain rate was delayed in the day, in line with findings by Hurly (1992) and Polo et al. (2007), the decrease in weight gain rate in the afternoon is not present in the literature. This is an interesting finding because, in line with optimal body mass theory, birds in predictable environments with reliable food sources should delay their weight gain until later in the day (McNamara et al., 1990).

The observed linear patterns, particularly under Bonanza conditions, stem from the models' structure. As the models based decisions on their fat metabolism, birds with high *Fat reserves* or *Fat change rates* were "forced" to *Rest*, meaning they were unlikely to reach maximum *Fat reserves* and maintain a linear daily weight gain curve. This way, by using *Fat reserves* for decision-making, birds prevented excessive weight gain and reduced the cost associated with high basal metabolic rates (BMR) and elevated predation risk.

The non-hoarding models based on fat metabolism showed a higher *Fat reserve* throughout the day in Poisson circumstances, with a slight plateau in the afternoon. This is likely because they were not able to use the external reserves that caches offer, leading them to need higher *Fat reserves* to prevent starvation. The finding that non-hoarders do not gain as much weight later in the day is in line with predictions from McNamara et al. (1990), who suggested that non-hoarders could not risk the delay in mass gain as they faced more unpredictable food environments.

9.5.3 Daily Hoarding and Retrieving Patterns

As discussed in Chapter 5, evidence on daily hoarding patterns in *Paridae* includes mixed results. Some found stable hoarding throughout the day (Boisvert & Sherry, 2000; Brodin et al., 1994), others found morning peaks (Lahti & Rytkönen, 1996). The fat metabolism-based models in this chapter align closely with findings by Lahti & Rytkönen (1996). All three of the leftover-hoarding models displayed the highest *Eat-hoard* rates in the morning, but for the *Fat reserve*-based model, these higher rates extended into the afternoon, especially in the Poisson environment. Morning hoarding peaks were more pronounced in the predictable Poisson environment than in the Bonanza scenario, likely because in the Poisson scenario, birds find food more often. Therefore, stomachs will filled up more rapidly under Poisson than under Bonanza circumstances. Because foraging continued until the *Fat reserve/Fat change rate* threshold was reached, and fuller stomachs led to more leftover hoarding, the higher peaks in the Poisson environment arose. After the peak, when thresholds were reached, birds started *Resting* and less *Eating* and *Eat-hoarding* took place.

Because the models selected for further analysis were all leftover-hoarding models, the *Eating* and *Eat-hoarding* curves were closely aligned. However, the *Eat-hoarding* peaks appear lower and slightly delayed, following the initial "*Eating*" peaks. For instance, hoarding peaks occurred in the morning but not immediately after birds woke. This delay reflects that birds wake up with empty stomachs and low energy reserves, making them more likely to either *Retrieve* cached food or consume all food items they find when foraging. Once they have met their immediate energy needs, they continue foraging, but their full stomachs lead them to hoard any surplus.

Retrieval rates were also highest in the morning across all three models. A large proportion of birds retrieved food items shortly after waking. This pattern aligns with predictions from other dynamic models (Pravosudov & Lucas, 2001b) and experimental evidence (Pravosudov & Grubb, 1997), which also indicate high retrieval rates in the early morning.

9.5.4 Conclusion

In conclusion, modelling results presented in this chapter emphasise the survival advantages of hoarding birds in environments with unpredictable food availability. Birds that employ a leftover-hoarding strategy, guided by decision rules based on *Fat reserves*, *Fat change rates*, or a combination of these variables, demonstrate greater performance compared to non-hoarding and direct-hoarding strategies, even in the more challenging Bonanza scenarios. Their regular hoarding behaviour enables them to accumulate sufficient caches, allowing for a morning retrieval peak that helps prevent starvation. This large cache buffer offers resilience against unpredictable food conditions, resulting in high survival rates even without very large *Fat reserves*. Weight gain trajectories in these models are mostly linear and align with most field observations. In more predictable Poisson environments, most weight is gained in the afternoon. Although hoarding patterns diverge from most findings in the literature, the observed morning retrieval peaks are consistent with experimental results.

Chapter 7. Agent-based Models of Small Birds in Winter: Decisions Based on Stomach Content and Fat Metabolism

10.1 Abstract

This chapter presents an analysis of model versions incorporating decision-making rules based on either *Stomach content* and *Fat reserves*, or *Stomach content* and *Fat change rates*, as outlined in Chapter 4. Survival dynamics, physiological variables, and behavioural patterns are examined across various environmental conditions. The impact of different hoarding strategies on survival rates is analysed within environments of high and low food predictability ("Poisson" and "Bonanza"). Findings show that while all models demonstrate resilience in Poisson environments, challenges emerge in Bonanza scenarios, especially for non-hoarders and models using direct-hoarding strategies with hoarding as the behaviour chosen in the most energy-rich state (H_{top}). Direct-hoarders with resting behaviour in the most energy-rich state (R_{top}) survive but show unrealistic *Resting* patterns. Leftover-hoarding birds consistently show higher survival rates due to their ability to *Rest* and utilise their cached food reserves. The results of both the leftover-hoarding models partly mirror real-world patterns in daily weight gain trajectories, hoarding and retrieval intensities.

10.2 Introduction

Birds likely use information about their energetic state to make decisions regarding foraging, hoarding, and eating behaviours (Chapter 1 and 4). Fat reserves, the rate at which they change, and their stomach content could inform birds about their energy balance. Information about fat metabolism could be conveyed through circulating factors involved in lipolysis and lipogenesis such as regulatory hormones (e.g. glucagon, insulin) and fat metabolites (e.g. free fatty acids, glycerol, very low-density lipoproteins). Information about stomach fullness could be conveyed through mechanoreceptors or hormones produced in the gastrointestinal tract.

Here, I use a subset of the model versions described in Chapter 4 to explore predictions generated by models with decision rules based on combinations of *Stomach content* and either *Fat reserves* or *Fat change rates*. The survival outcomes of these models are evaluated, along with the resulting energy variables and behavioural patterns of the agents. Finally, I examine the effects of temperature and food distribution on these factors. For a comprehensive comparison of all model results, see Chapter 8.

10.3 Methods

10.3.1 Recap of the Model Structure

As outlined in Chapter 4 (Figure 7.1) and as a reminder from Chapter 5 and Chapter 6, the general model in this thesis consists of several processes, one of which is the ***Decide behaviour*** process, where the agent selects which behaviour to perform. This process is central to the models, as it sets apart the different sets of decision rules that were implemented across the model versions. Decision rules vary in two main ways. Firstly, agents can have different "hoarding types", categorised as non-hoarders, leftover-hoarders, or two types of direct-hoarders. The first type of "direct-hoarder" has "hoarding" as the behaviour that is selected in the highest energy state (H_{top}), and the second type "rests" in this case (R_{top}). Secondly, agents can have different "Energy proxies" and use either *Stomach content* (SC), *Fat reserves* (FR), *Fat change rate* (FCR), or a combination of two of these variables to decide which behaviour to perform. Table 10.1 shows the different model versions and how they vary in terms of "hoarding type" and "energy proxy". The models discussed in this chapter, based on *Stomach content*, combined with either *Fat reserves* or *Fat change rates*, are highlighted. The numbers align with the model versions described in Chapter 4 section 7.9.8.1. From here on, I will refer to the "model versions" as "models".

Table 10.1. Overview of the different model versions based on their decision rules. Decision rules vary in terms of hoarding type and decision-making variable. The model versions discussed in the current chapter are highlighted.

Variables	***Non-hoarder***	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Stomach content	1.1	1.2	1.3	1.4
Fat reserve	2.1	2.2	2.3	2.4
Fat change rate	3.1	3.2	3.3	3.4
Fat reserve & Fat change rate	4.1	4.2	4.3	4.4
Stomach content & Fat reserve	5.1	5.2	5.3	5.4
Stomach content & Fat change rate	6.1	6.2	6.3	6.4

10.3.2 "Default" environments

Again, as a reminder from Chapter 5 and Chapter 6, when comparing models, two "default" environments were used. These are environments with "high" temperatures (between -3 and 13°C) and "medium" food availability. The latter means that birds find on average 4 food items per foraging bout. Finally, these two environments differ in their "food predictability". In the first environment, when birds go out to forage, they sample from a Poisson distribution with a mean set by the "food availability". In the second environment, "Bonanza", birds sometimes find many food items ("Bonanza") but often find nothing, or a lower amount. Here, the mean is also set by the "food availability". The models were parameterized to include more extreme environments than the ones selected—colder temperatures, increased food availability, and reduced food availability. For simplicity, default environments were selected, which most realistically represent typical winter conditions over a 30-day period at northern latitudes, such as those in the UK. The two environments correspond with the numbered environments 6 and 8, as discussed in Chapter 4, section 7.9.8.2. Unless stated otherwise the default input parameter settings are used (Table 8.2).

10.4 Results

10.4.1 Survival

In In Table 10.2 the model performance of the models in this chapter is shown (see also Table 7.18). Half-life survival is the number of days it takes for 50% of the agents in a simulation to die, averaged across all 12 environments that were used in parameterisation (see Figure 7.2). Larger numbers indicate models with better survival. Direct-hoarding models Rtop exhibit poorer survival than the other models and direct-hoarding models Htop show the best survival, especially the model based on *Stomach content* and *Fat reserve* (Table 10.2).

Table 10.2. Half-life survival rates for the resulting models. Half-life survival is calculated as the mean number of days that it takes for 50% of the agents in a model to die, across all 12 environments used in parametrisation. Green shades indicate longer survival and red shades indicate shorter survival.

	Non-hoarder	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Stomach content & Fat reserve	45	51	73	35
Stomach content & Fat change rate	46	46	51	31

Figure 10.1 illustrates the survival curves for the eight models where decision-making is based on a combination of the bird's *Stomach content* and either the *Fat reserves* or the *Fat change rate*. In the Poisson scenario, survival is generally good. Direct-hoarding birds (H_{top}) are the best-performing models, followed by the non-hoarding models, the leftover-hoarding models and the Direct-hoarding models (R_{top}). In Bonanza scenarios, the split between different hoarding strategies is even clearer. Here, leftover-hoarding birds have the best survival, followed by direct-hoarding birds (R_{top}) and direct-hoarding birds (H_{top}). Non-hoarding birds

survive the worst in the environment with unpredictable food. Whether a model uses a combination of *Stomach content* and *Fat reserves* or a combination of *Stomach content* and *Fat change rate*, does not matter as much for survival compared to the hoarding strategies. SC and FR models tend to slightly outperform the SC and FCR models.

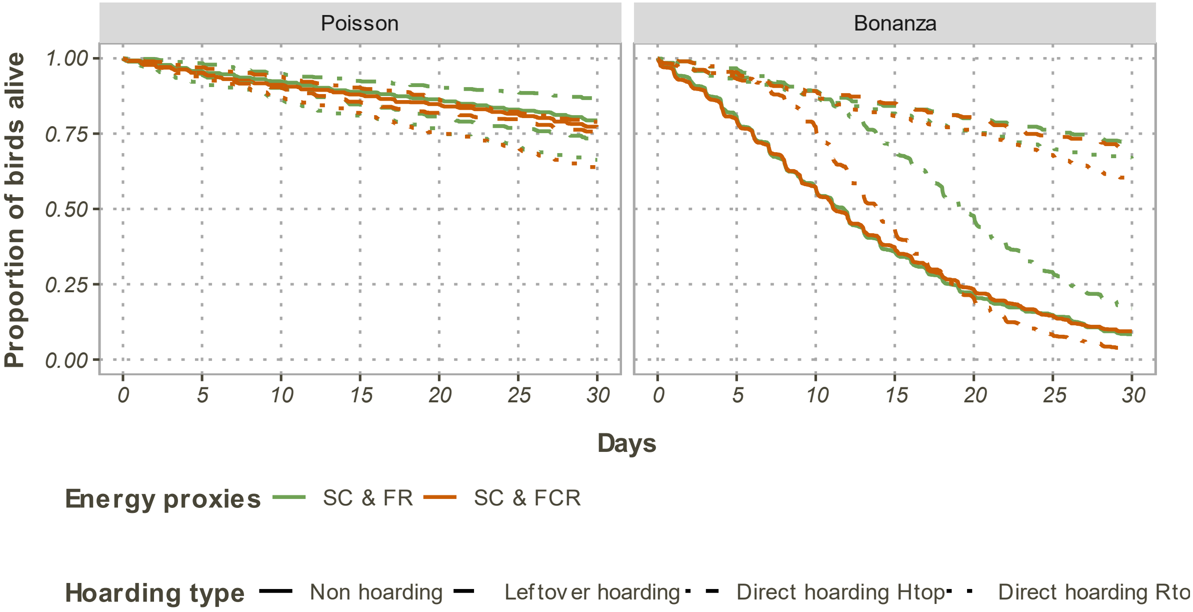


Figure 10.1. Survival rates of models with decision-making based on a combination of Stomach content and fat metabolism in the default environments. The x-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

10.4.2 Model Selection

To streamline the discussion and maintain focus on the most relevant models, I will examine only a subset of the models presented in Table 10.2. Across all three results chapters (Chapters 5, 6, and 7), I have applied a consistent criterion; for a model to be considered, at least 50% of birds must survive throughout the simulation, averaged across all parameterisation environments. This means that the half-life survival, as presented in Table 10.2 must be above 30. Additionally, hoarding models must demonstrate sustained hoarding behaviour throughout the simulation. If a hoarding model fails to exhibit such behaviour, it is excluded from further analysis as it does not fulfil its intended purpose. In contrast, all non-hoarding models are included for discussion, as they provide a valuable basis for comparison with the hoarding models.

Therefore, here, I will focus on the non-hoarding models, the leftover-hoarding models and the direct-hoarding R_{top} models that base their decisions on a combination of SC and FR or FCR.

At first sight, the H_{top} models seem to perform very well, with half-life survival of 73 and 51 days (Table 7.2), although they lack any substantial hoarding behaviour throughout the simulation, so were excluded. Figures showing the energy variables and behavioural patterns of the excluded models are available in Supplementary Materials, section E.

There is a discrepancy between survival outcomes in the default environments (Figure 10.1) and those across the 12 environments used for parameterisation (Table 10.2). While survival is consistently higher for leftover-hoarders compared to non-hoarders in both contexts, the comparison between the two types of direct-hoarders is more complex. The H_{top} models, particularly the one incorporating SC and FR in its decision-making, perform exceptionally well across all 12 environments. However, their survival in the default environments is poor. In contrast, the R_{top} models exhibit strong survival in the default environments (Table 10.1) but show lower half-life survival across the 12 environments (Table 10.2). Examining the survival curves of these models across all 12 environments reveals that H_{top} models generally outperform R_{top} models under most conditions. This can be attributed to the initial caches (50–100) provided to hoarding models at the start of simulations. The H_{top} models are effectively non-hoarding models with enhanced food availability, allowing them to survive well across the 12 environments without actively hoarding. For details on the survival of these models across all 12 environments, see Supplementary Materials, section E.

10.4.3 Parameterisation Outcomes

The parameterisation results for models 5.2, 5.4, 6.2, and 6.4 are listed in Chapter 4 Table 7.15 and Table 7.17. The range of possible values for the *Stomach content* thresholds is 0-0.4 gram. The range of possible values for the *Fat reserve* thresholds is 0-4 grams. The range of possible values for the *Fat change rate* is -0.6 to 0.6 grams/2 hours.

Model version 5.2 is a leftover-hoarding model where decisions are based on a combination of *Stomach content* (bottom threshold = 0.065 grams, top threshold = 0.115 grams) and *Fat reserves* (bottom threshold = 0.313 grams, top threshold = 1.396 grams). If both *Stomach content* and *Fat reserves* are below their bottom thresholds, the bird will *Retrieve* food. If both energy proxies are above top thresholds, birds will *Rest*. The low thresholds for *Fat reserves* make it unlikely that birds would be below the top threshold for *Fat reserves*. Therefore, in practice, birds mostly *Rest* and *Eat-hoard*, which is determined by the *Stomach content* value.

The other leftover-hoarding model in this chapter (version 6.2), uses a decision-making rule based on *Stomach content* (bottom threshold = 0.052 grams, top threshold = 0.098 grams) and

Fat change rates (bottom threshold = -0.206 grams/2 hours, top threshold = -0.181 grams/2hours). FCR needs to drop very

low for the birds to *Retrieve*, which makes it unlikely for this behaviour to take place. If the energy proxies are above both the top thresholds, birds will *Rest*. Birds tended to have positive FCR values for most of the day, meaning their *Fat change rates* were consistently above the top threshold. Again, decisions about whether to *Rest* or *Eat-hoard*, were mostly based on *Stomach content*.

Model version 5.4 (direct-hoarder R_{top}, SC and FR) has 3 thresholds for *Stomach content* (bottom = 0.006 grams, middle = 0.094 grams, top = 0.277 grams) and *Fat reserves* (bottom = 0.896 grams, middle = 2.520 grams, top = 3.063 grams). Low bottom thresholds mean that birds must have an empty stomach to *Retrieve*. If both energy proxies are above the top thresholds (where the stomach is almost full) the birds will *Rest*. If one of the energy proxies is above the top threshold and one is below, or if both energy proxies are below the top threshold but above the middle threshold, the birds forage and *Direct-hoard*. In all other cases, they forage and *Eat*. The high top threshold and low bottom threshold lead birds to *Direct-hoard* or *Eat* most of the time. Furthermore, as the middle threshold for *Fat reserve* is fairly high (2.5 grams), the value for *Fat reserves* will likely be consistently between the bottom and middle threshold. As a result, decisions in model 5.4 are largely based on the SC value, which will determine if the bird is *Direct-hoarding* or *Eating*.

Model version 6.4 (direct-hoarder R_{top}, SC and FCR) also has 3 thresholds for *Stomach content* (bottom = 0.115 grams, middle = 0.223 grams, top = 0.335 grams) and *Fat change rates* (bottom = 0.193 grams/2 hours, middle = 0.231 grams/2hours , top = 0.469 grams/2 hours). Birds do not need to be losing weight in order to start *Retrieving*, as long as their stomach is empty. If both energy proxies are above top thresholds (when the stomach is almost full) the birds will *Rest*. If one of the energy proxies is above the top threshold and one of them is below it, or if both energy proxies are below the top threshold but above the middle threshold, the birds forage and *Direct-hoard*. In all other cases, they forage and *Eat*. In practice, birds are most likely to forage and *Eat*. Again, decisions are mostly based on *Stomach content* in this model, as the FCR value is very likely to be above 0.231 during the day. Therefore, most of the time, the SC value will determine if a bird *Direct-hoards* or *Eats*.

For the non-hoarding models in this chapter, the parameterisation results are in Table 7.14. Non-hoarding models have a more basic structure. When both energy proxies are above their thresholds, birds will *Rest*. Otherwise, they will forage and *Eat* the items they find. Model 5.1

(non-hoarding, SC and FR) has a *Fat reserve* threshold of 0.313 grams, in a range between 0-4 grams. Birds are likely to be above this threshold most of the time, so decisions mostly rely on *Stomach content*. Similarly, in model 6.1 (non-hoarding, SC and FCR), *Fat change rates* need to be above -0.581 grams/2 hours, which is highly likely. Again, decisions are mostly based on variations in *Stomach content*. As a result, decisions are effectively made based on *Stomach content*, under similar thresholds for both models (lower than one food item). Models 5.1 and 6.1 therefore display similar survivorship to each other and to model 1.1 (see Chapter 5), in which decision-making is solely based on *Stomach content*.

10.4.4 Energy Variables

10.4.4.1 Stomach Content

Figure 10.2 shows fluctuations in the four energy variables throughout the simulation for the hoarding models in this chapter (both leftover-hoarding and direct-hoarding Rtop models). Values were averaged across the birds that were alive at each timestep. *Stomach content* of birds drops to zero at night. In the Poisson scenario, there is a clear difference between the Direct-hoarding (R_{top}) model that uses SC and FCR, and the other three hoarding models. The former reaches higher peaks in *Stomach content* throughout the simulation. In the Bonanza scenario, the differences between the models are smaller. At the start of the simulation, the SC-FCR direct-hoarding model still has higher *Stomach contents*, but differences disappear as time continues. These higher peaks are likely due to the initial caches that birds receive at the start of the simulation. This allows the SC and FCR direct-hoarders to *Retrieve* food items and increase their *Stomach content* until the supply runs out (day 10).

Stomach content fluctuations for the non-hoarding models are in Figure 10.3. Both models perform very similarly, which is due to the threshold values that resulted from the parameterisation process, making these models almost completely *Stomach content*-based (see above). *Stomach content* values peak slightly higher in the Poisson scenario than in the Bonanza environment, but the differences are small.

Figure 10.4 shows the value for each of the energy variables, averaged across days in the simulation for all living birds at each point in time (excluding days 1-3 to allow for stabilisation). The patterns from Figure 10.2 are further highlighted, with the direct-hoarding (R_{top}) model that uses SC and FCR maintaining the highest *Stomach content* throughout the day, in both environments. The leftover-hoarding model and the direct-hoarding model (R_{top}) that uses SC and FR follow. Non-hoarding birds have the lowest *Stomach contents*. Results are similar in the Bonanza scenario, but with both direct-hoarding models reaching higher *Stomach contents* earlier in the day.

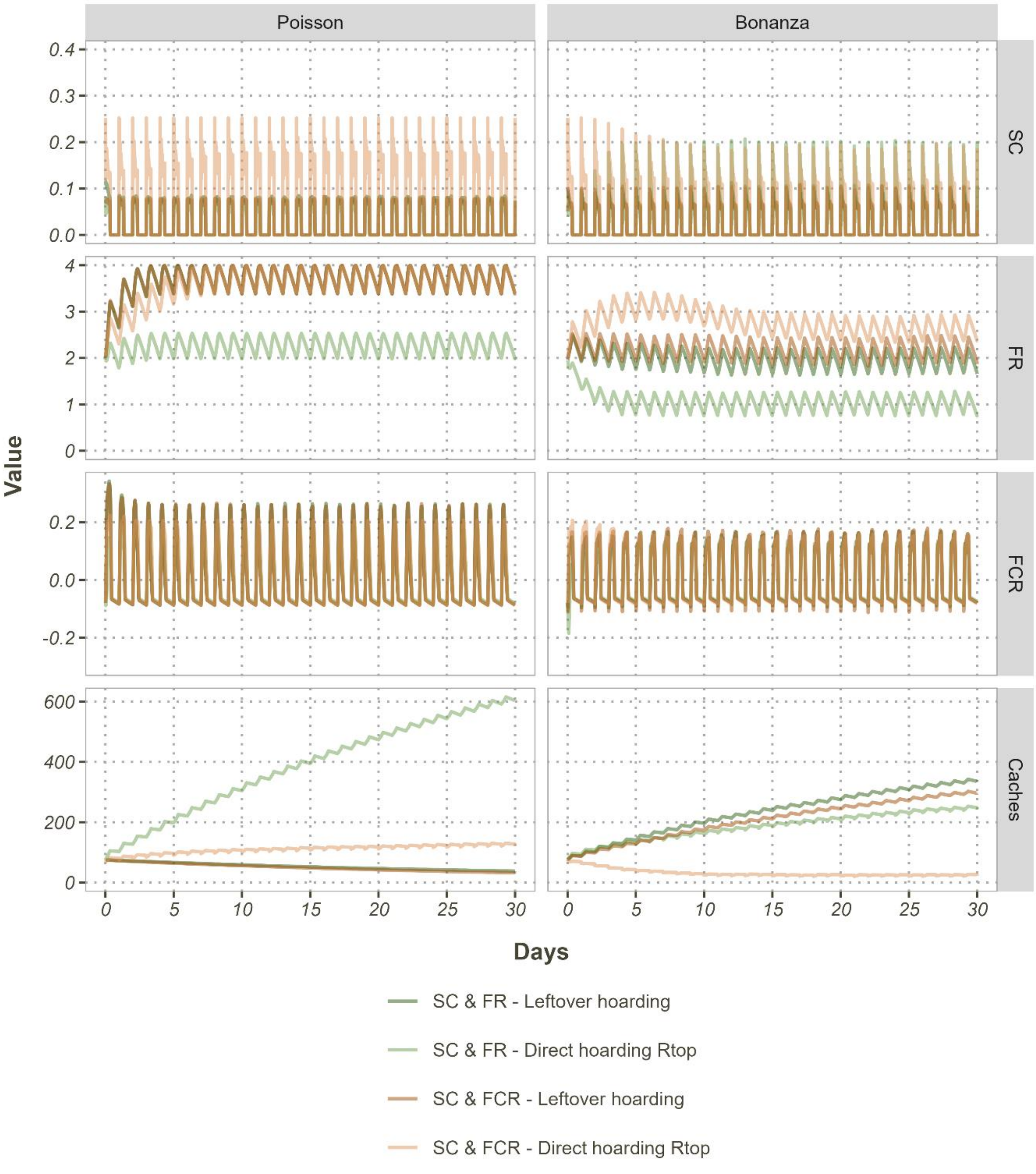


Figure 10.2. Fluctuations in Stomach content, Fat reserve and Fat change rate for leftover-hoarding models 5.2, and 6.2 and direct-hoarding models (R_{top}) 5.4 and 6.4 in the two default environments. The x-axes show the number of days in the simulation that have passed. The y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches. Values are averages across all birds that are alive at each timestep.

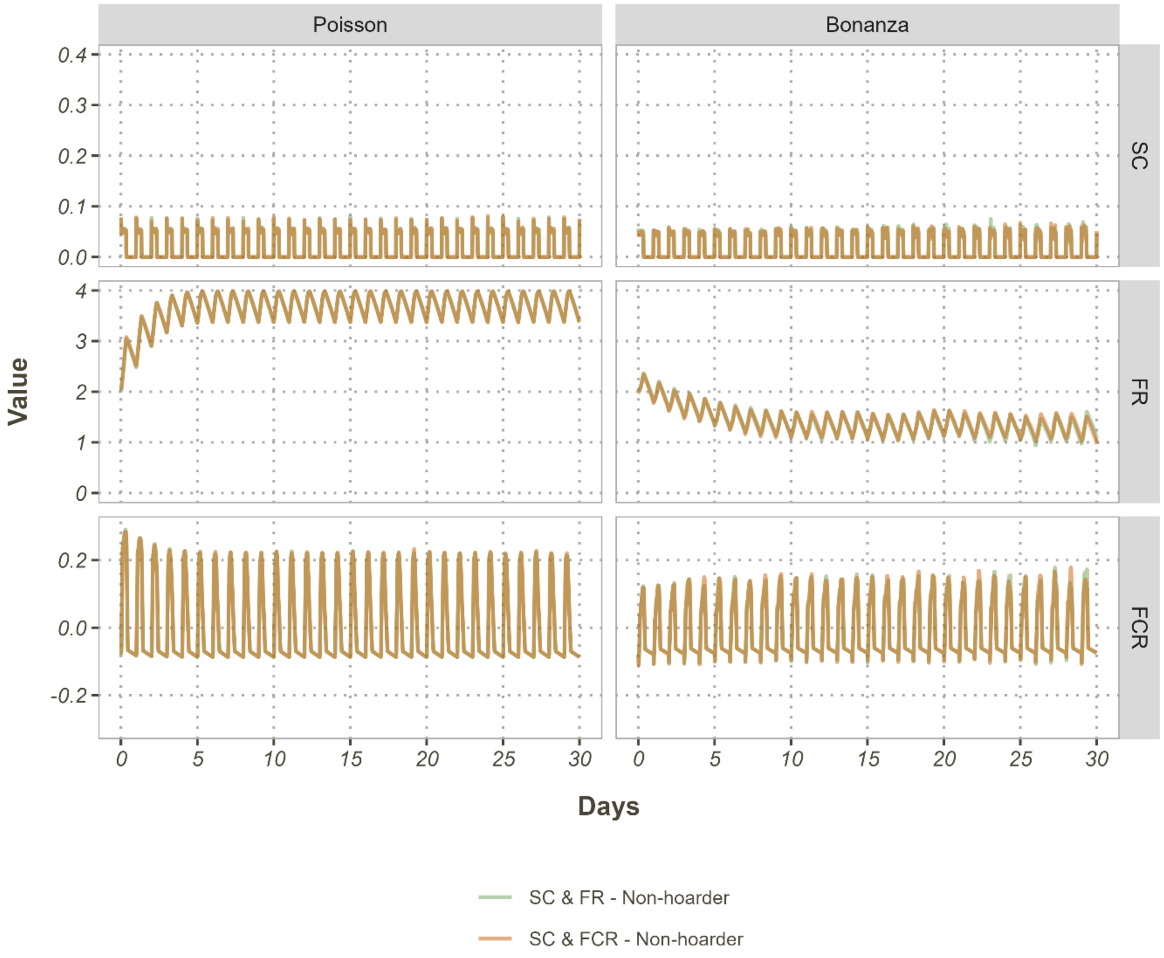


Figure 10.3. Fluctuations in Stomach content, Fat reserve and Fat change rate for non-hoarding models 5.1, and 6.1 in the two default environments. The x-axes show the number of days in the simulation that have passed. The y-axes show the Stomach content in grams, the Fat reserves in grams and the Fat change rate in grams/2 hours. Values are averages across all birds that are alive at each timestep.

10.4.4.2 Fat Reserves and Fat Change Rates

Both leftover-hoarding models—one using SC and FR, and the other using SC and FCR—exhibit similar fat metabolism patterns throughout the simulation (Figure 10.2). In the Poisson scenario, these two leftover-hoarding models show high *Fat reserves*. Interestingly, similar results were found in the direct-hoarding model (R_{top}) that bases decisions on SC and FCR, where *Fat reserves* stabilise just above 2 grams. All models exhibit lower *Fat reserves* in the Bonanza scenario than in the Poisson environment. The direct-hoarding (R_{top}) model that uses SC and FCR maintains the highest *Fat reserves*, whilst the direct-hoarding model (R_{top}), which bases decisions on SC and FR, has the lowest *Fat reserves* throughout the simulation. The leftover-hoarding models behave similarly, stabilising with *Fat reserves* of around 2 grams. *Fat change rates* are similar across all models. Figure 10.3 highlights clear differences between the Poisson and Bonanza scenarios for the non-hoarding models. *Fat reserves* are higher in the predictable environment, with higher peaks in *Fat change rates*.

Daily weight gain patterns reveal that the shape of the daily weight gain curves is consistent across models (Figure 10.4). In the Poisson scenario, *Fat reserves* increase in the morning to stabilise at the maximum in the afternoon. Only the direct-hoarding model (R_{top}) using SC and FR shows noticeably lower *Fat reserves*, which is likely imposed by the FR thresholds. *Fat change rates* peak in the late morning, with the highest peaks for the leftover-hoarders, followed by the non-hoarders and the direct-hoarders. *Fat change rates* decrease but stay above zero at the end of the day.

In the Bonanza scenario, *Fat reserves* increase linearly throughout the day (Figure 10.4). The direct-hoarding model (R_{top}) using SC and FCR retains the highest *Fat reserves*, followed by the leftover-hoarding models and then non-hoarding models. *Fat change rates* are very similar across models and show an initial increase in the morning followed by a plateau in the afternoon. The highest *Fat change rates* occur in the evening.

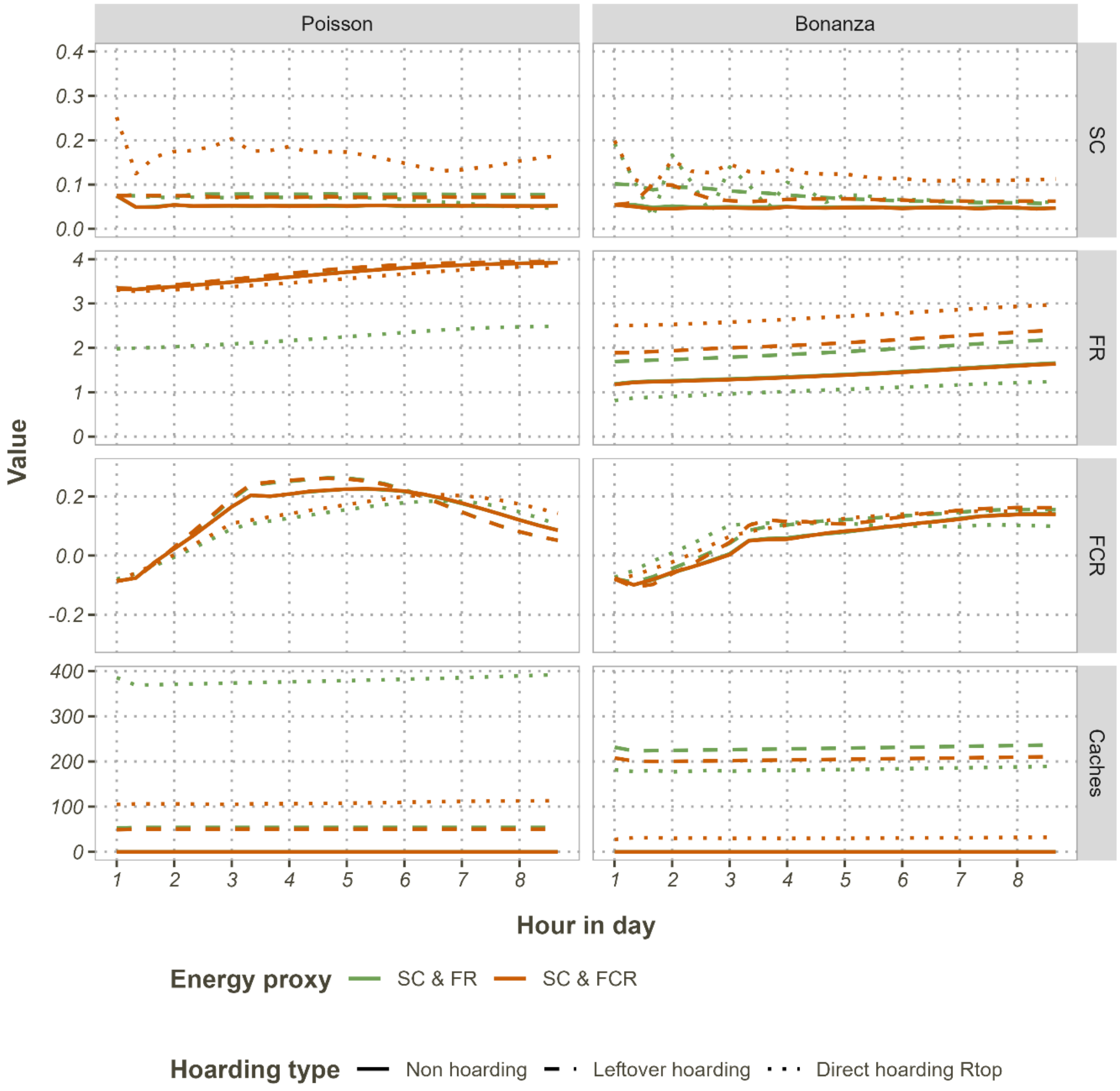


Figure 10.4. Fluctuations in Stomach content, Fat reserve, Fat change rate and cache number for leftover-hoarding models 5.2 and 6.2, direct-hoarding models (R_{top}) 5.4 and 6.4, and non-hoarding models 5.1 and 6.1 in the two default environments. The x-axes show the hours within the daylight period that have passed. Numbers indicate the start of the hour. The y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches. Values are averaged across living birds at each timestep within the day across days 4-30 in the simulation.

10.4.4.3 Cache Number

Under Poisson conditions, the cache numbers for leftover-hoarding models slowly decline throughout the simulation (Figure 10.2). The direct-hoarding models, especially the one that uses SC and FCR in the decision-making process, increase their number of caches throughout the simulation. In the Bonanza environment, a different pattern can be observed. Apart from the SC and FCR direct-hoarding model, which decreases its caches over time, all models increase their number of caches throughout the simulation. The daily patterns, shown in Figure 10.4, reflect these differences as well. Models that increase their number of caches throughout the simulation, also have increasing numbers of caches throughout the day.

10.4.5 Behaviour

10.4.5.1 Eat

Figure 10.5 illustrates the differences in *Eating* behaviour between the Poisson and Bonanza environments for the hoarding models in this chapter. The graphs show the proportion of living birds that are exhibiting a certain behaviour at each timestep in the simulation. Note that the "*Eat*" behaviour is what takes place when a bird has gone out to forage, found a food item and has consumed it. If the bird went out to forage but did not find a food item, this is not included. The "*Eat*" behaviour does also not include any instances where items were consumed as part of the "*Retrieve*" or "*Eat-hoard*" behaviours, as they are recorded separately.

Across all four models, and especially for the direct-hoarding model that uses SC and FCR in decision-making, a larger proportion of birds spend their time *Eating* at the same time in the Poisson environment than in the Bonanza environment (Figure 10.5). Non-hoarding birds also show consistently lower *Eating* rates in the Bonanza scenario (Figure 10.6).

As discussed in previous chapters, these lower *Eating* rates in the Bonanza scenario are at least partly caused by food distribution, instead of the number of foraging birds. In a Bonanza environment, individuals are more likely to find zero food items in a single foraging bout than in the Poisson environment. If food items are found, birds are likely to find more food items under Bonanza circumstances. Therefore, all else equal, birds will have more "unsuccessful" foraging attempts in Bonanza scenarios, resulting in lower *Eating* frequencies.

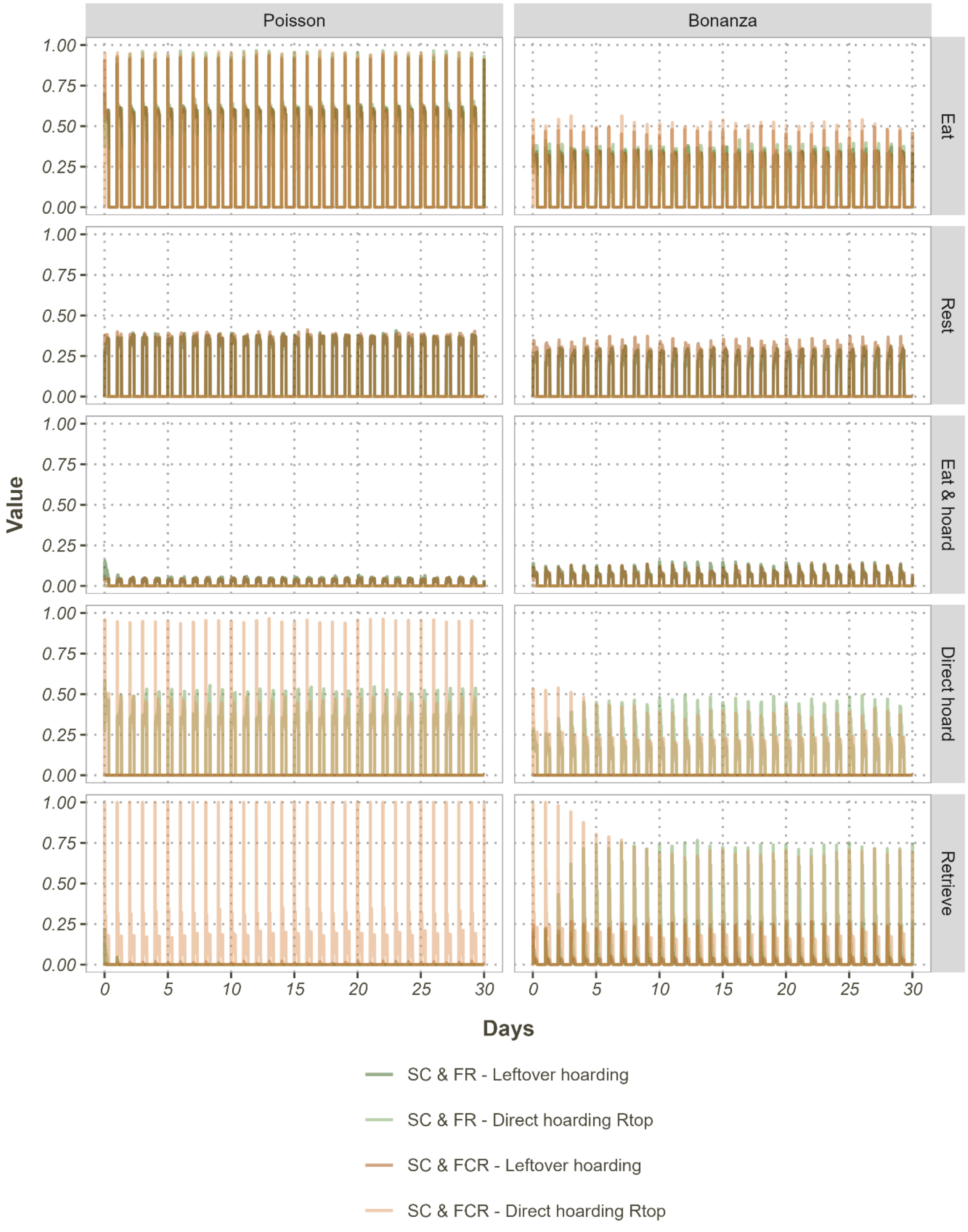


Figure 10.5. Fluctuations in Eating, Resting, Leftover-hoarding, Direct-hoarding, and Retrieving behaviour throughout the simulation for leftover-hoarding models 5.2 and 6.2 and direct-hoarding models (R_{top}) 5.4 and 6.4 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Note that leftover-hoarding birds that "Eat" did not have any leftover items to hoard. Only birds marked as "Eat and hoard" continued to hoard after eating. These options are mutually exclusive for leftover-hoarders. Values are the proportion of living birds exhibiting the behaviour at each timestep of the simulation. Foraging attempts where no food was found are not included.

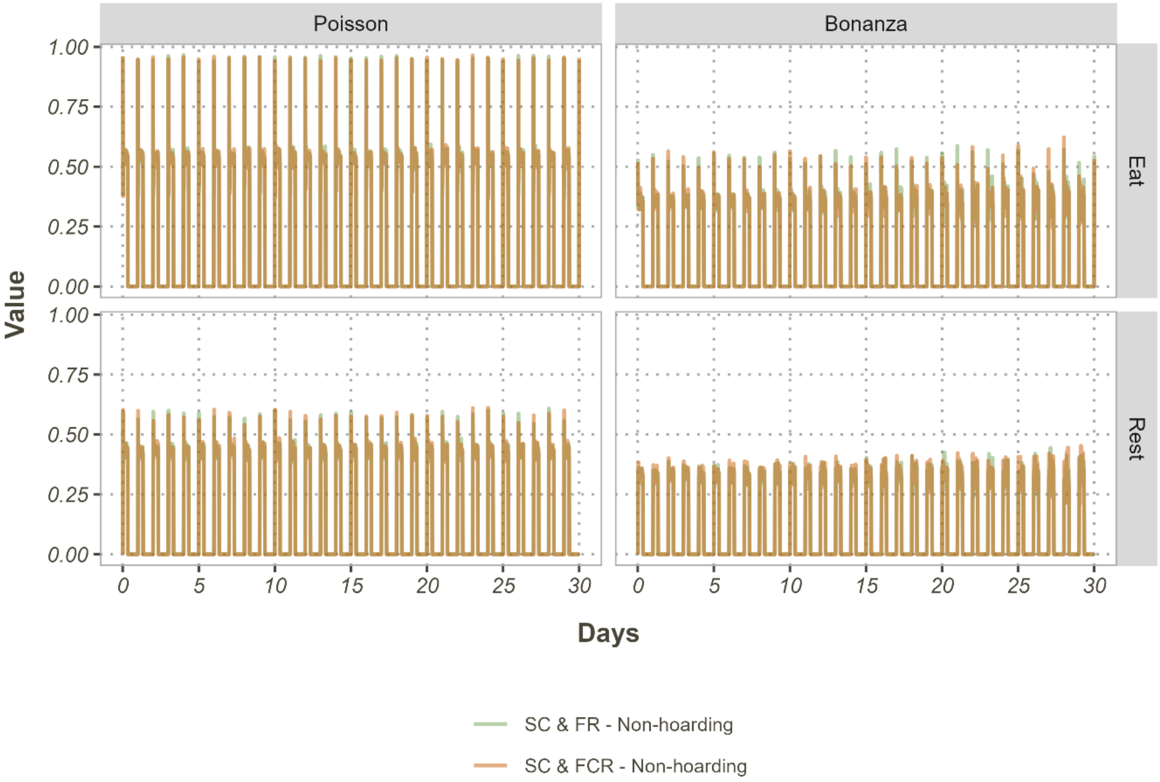


Figure 10.6. Fluctuations in Eating and Resting behaviour throughout the simulation for non-hoarding models 5.1, and 6.1 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Values are the proportion of living birds exhibiting the behaviour at each timestep of the simulation.

Figure 10.7 illustrates the daily *Eating* patterns for all 6 models in this chapter. In the Poisson environment, some variation is observed in the morning, with most models showing a clear peak in *Eating* behaviour at the very start of the day. The direct-hoarding model (R_{top}) that bases decisions on FR and FCR exhibits a slight delay in this peak, which is likely due to high early morning *Retrieval* rates (see below). Throughout the rest of the day, the lines are more stable. Note that, in this figure "D*irect-hoarding*" and "*Eat-hoard*" are grouped together. This means that some *Eating* behaviour for the leftover-hoarding models is included in the "*hoard*" behaviour. In the Bonanza scenario, the models have similar curves. Direct-hoarding models have the lowest *Eating* rates in the morning, followed by leftover-hoarders. Non-hoarders have the highest peaks, which is necessary as they cannot *Retrieve*.

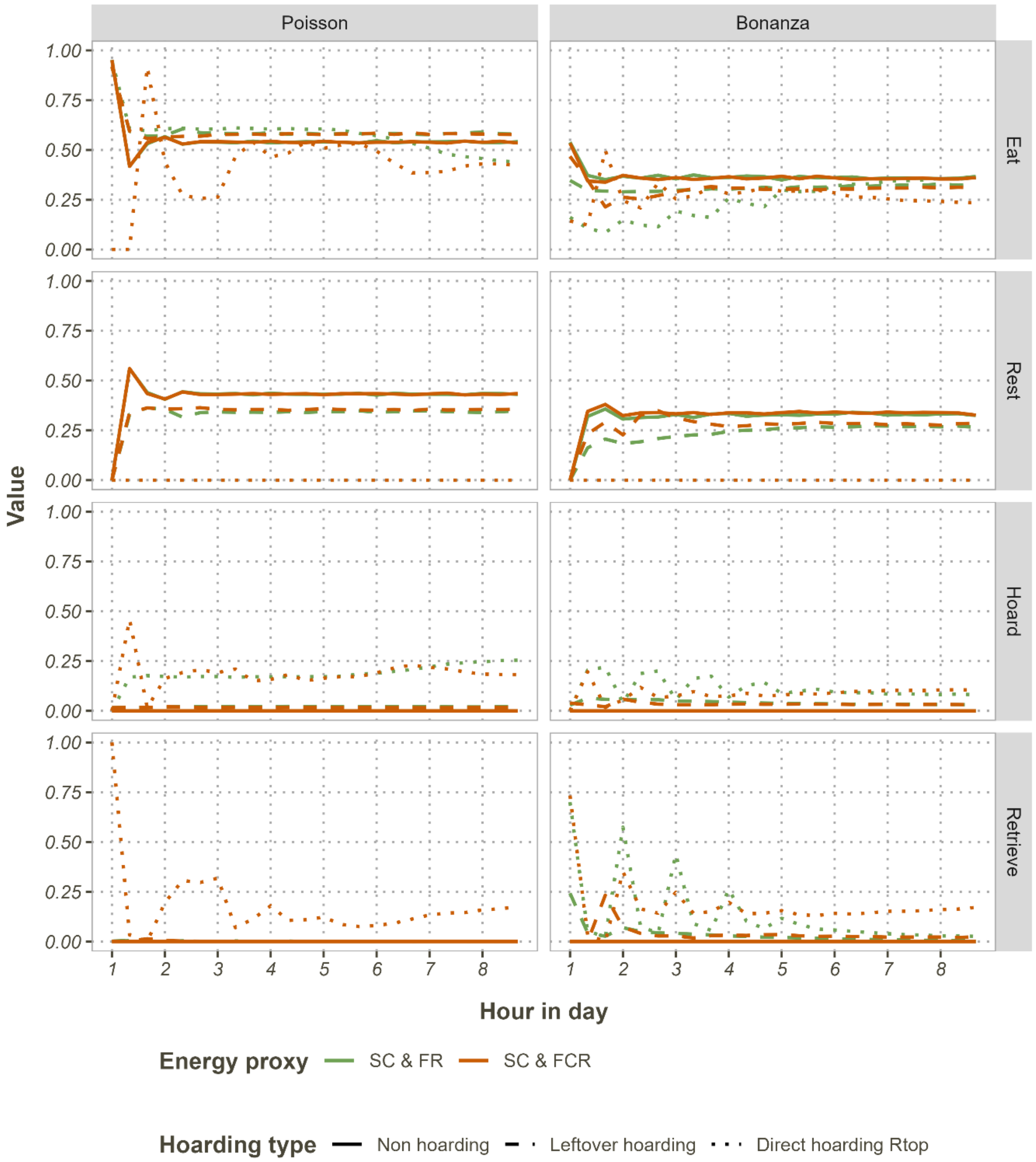


Figure 10.7. Fluctuations in Eating, Resting, Leftover-hoarding, Direct-hoarding and Retrieving behaviour throughout the simulation for leftover-hoarding models 5.2 and 6.2 and direct-hoarding models (Rtop) 5.4 and 6.4 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Note that birds that "Eat" did not have any leftover items to hoard. Only birds marked as "Eat and hoard" continued to hoard after eating. These options are mutually exclusive. Values are the proportion of living birds exhibiting the behaviour at each timestep of day 4-30 in the simulation.

10.4.5.2 Rest

The proportion of hoarding birds that *Rest* at the same time is similar between Poisson and Bonanza environments (Figure 10.5). *Resting* is very low throughout both direct hoarding models. In non-hoarding birds, slightly more *Resting* takes place in the Poisson environment than in the Bonanza scenario on average through the 30-day simulation (Figure 10.6) and on a daily level (Figure 10.7). For all models, the average proportion of birds *Resting* is slightly higher under Poisson conditions than in the Bonanza environment. This further emphasises that it is the number of successful foraging bouts, rather than increased *Resting*, that is responsible for the higher *Eating* rates in the Poisson environment. The opposite is true in Poisson environments, where birds *Rest* more and *Eat* more often. Whilst in Bonanza environments, birds *Rest* less and *Eat* less frequently, but eat more per *Eating* occasion.

Again, direct-hoarding models do not exhibit any *Resting* behaviour. Non-hoarding models *Rest* more often than leftover-hoarding models. Apart from a small peak in the morning for non-hoarding models, *Resting* behaviour is stable throughout the day.

10.4.5.3 Hoard and Retrieve

Hoarding patterns throughout the simulation vary largely between leftover-hoarding and direct-hoarding models (Figure 10.5). In Figure 10.5 "*Eat-hoard*" and "*Direct-hoard*" behaviours are split up so that the lines are easy to distinguish from each other. The leftover-hoarding models show low but sustained levels of *Eat-hoarding* behaviour throughout the simulation. Whether these models *Eat-hoard* or just *Eat* is dependent on the number of food items found, which is why hoarding levels are higher in Bonanza scenarios. In these environments, birds are more likely to find larger numbers of food items at once in successful foraging bouts.

The SC and FCR direct-hoarding model exhibits high proportions of birds *Hoarding* in the Poisson scenario, but not in the Bonanza environment (Figure 10.5). Again, this lack of synchronised *Direct-hoarding* might be due to the more unpredictable Bonanza environments, as foraging attempts, no matter if they are for *Direct-hoarding* or *Eating* purposes, are more likely to be unsuccessful under Bonanza circumstances. The direct-hoarding model that uses SC and FR shows more similar curves between the Bonanza and Poisson environments but still has higher *Direct-hoarding* proportions under Poisson circumstances.

In the Poisson environment, the only model with significant *Retrieval* behaviour throughout the simulation is the direct-hoarding model that uses SC and FR in decision-making (Figure 10.5). Under Bonanza conditions, all hoarding models show *Retrieval* behaviour, but peaks are highest for the two direct-hoarding models.

In Figure 10.7 "*Eat-hoard*" and "*Direct-hoard*" behaviours were grouped as "*Hoard*" to make a comparison of the models more straightforward. In the Poisson scenario, daily *Eat-hoarding* rates were low for the leftover-hoarders, but not zero. The direct-hoarding models both *Hoard*, with a peak for the SC and FCR-based model in the morning. In the Bonanza scenario, leftover-hoarders eat-hoard slightly more than in the Poisson environment, whilst *Hoarding* was less common for the direct-hoarding models. The latter exhibited more variation in *Hoarding* proportions in the morning than they showed in the Poisson environment.

The only model exhibiting *Retrieval* behaviour under Poisson conditions was *Direct-hoarding* that used both SC and FCR in decision-making (Figure 10.7). The SC and FR direct-hoarder does not *Retrieve.* Under Bonanza conditions, however, all four hoarding models exhibited *Retrieval* behaviour. Whilst all hoarding models exhibited a morning *Retrieval* peak, the highest peaks were shown in the two direct-hoarding models. This high *Retrieval* peak explains why direct-hoarders did not *Eat* as much in the early morning.

10.4.6 The Effects of Temperature and Food Distribution on Survival

Figure 10.8 illustrates how the models respond to changes in environmental conditions. The first two graphs replicate those in Figure 10.1, followed by survival results for simulations under specific conditions; lower temperatures (as seen in environments 5 and 7 in Figure 7.2) reduced food availability (as in environments 2 and 4), and a combination of both reduced food availability and lower temperatures (environments 1 and 3).

In Poisson environments, both the non-hoarding and leftover-hoarding models demonstrated considerable resilience to either lower temperatures or reduced food availability alone. However, when these conditions were combined, survival rates declined. In contrast, the SC and FCR direct-hoarders (R_{top}) were more affected by lower temperatures than by lower food availability. This might be because the SC and FR direct-hoarding models barely *Retrieve* under Poisson circumstances and colder temperatures increase nighttime expenditure (Figure 10.7).

In Bonanza environments, only the leftover-hoarding models that based decisions on SC and FR display some resilience to lower temperatures and reduced food availability, but survival is worse in general. Among the direct-hoarding models, survival is somewhat sustained, especially in the model using SC and FR, while the non-hoarding models exhibit the poorest survival rates. For direct-hoarders, this increased resilience is likely due to the model's high FR thresholds. Under challenging circumstances, birds rely heavily on *Retrieval* behaviour, using more caches than they produce. In contrast, the leftover-hoarder model had low FR thresholds, resulting in a tendency to spend significant time *Resting* even under energetically demanding conditions, which might leave them without sufficient *Fat reserves*. Differences in the effects of reduced temperatures and lower food availability were less distinct in the Bonanza environments.

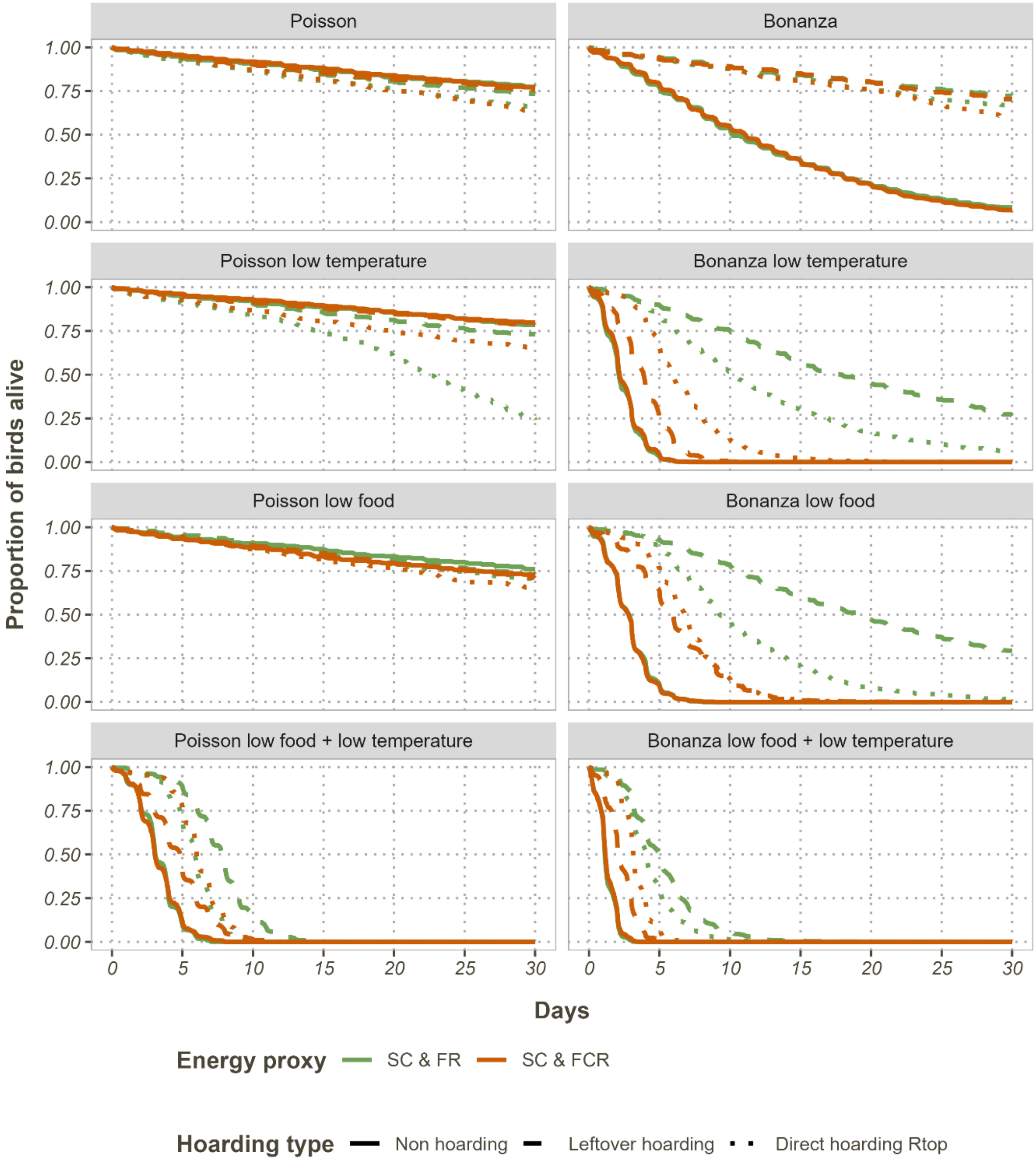


Figure 10.8. Survival rates of models 5.1, 5.2, 5.4, 6.1, 6.2 and 6.4 in the default environments, low-temperature environments, low food environments and environments combining low food availability and low temperatures. The x-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

10.5 Discussion

10.5.1 Survival

In the models discussed in this chapter, agents base their decisions on combinations of either *Stomach content* and *Fat reserves* or *Stomach content* and *Fat change rates*. In general, models exhibited the best survival outcomes in a Poisson scenario with higher temperatures and medium food availability (Figure 10.1 and Figure 9.1). Differences in survival between the two hoarding strategies (leftover-hoarding and direct-hoarding R_{top}) were minimal. As expected, non-hoarding birds struggled more with the unpredictable conditions in Bonanza environments than hoarding models.

Of the hoarding models included, the direct-hoarders exhibited the lowest survival rates in the default environments (Figure 10.1). Their poorer survival compared to leftover-hoarders might be caused by their lack of *Resting* behaviour, forcing birds to forage or *Retrieve* more often, resulting in high energetic costs. The absence of *Resting* behaviour was driven by high thresholds for *Resting* in these models, as a result of the parameterisation process. Whilst we know that "real life" birds rest during the day, these models are meaningful, as they show that high *Resting* rates are not crucial for survival.

The leftover-hoarders in this chapter demonstrate high survival (Figure 10.1). Their survival is supported by regular, albeit low, *Hoarding* rates and use of cache *Retrieval* under Bonanza circumstances. This is reflected in their number of caches, which is higher than in other hoarding models in the Bonanza environment. However, both *Hoarding* and *Retrieval* rates are very low in the Poisson environment, making them behaviourally equivalent to non-hoarding models under "favourable" circumstances.

Non-hoarding models survive as well as leftover-hoarders in the Poisson scenario, but survival is substantially worse in the Bonanza scenario. This is likely caused by the differences in *Fat reserves* that non-hoarders are able to sustain in the Poisson versus the Bonanza environment. The lower *Fat reserves* in the Bonanza environment, combined with unreliable caches, increase the risk of overnight starvation.

Across all models, survival is better in Poisson environments than in Bonanza environments, which is supported by slightly higher *Resting* rates and *Fat reserves* in Poisson environments. This allows birds to sustain higher *Fat reserves*, without the extra metabolic cost of foraging or the increased predation risk.

10.5.2 Daily Weigh Gain Trajectories

As reviewed in Chapter 5, hoarding birds typically display a linear increase in body mass throughout the day (Boisvert & Sherry, 2000; Graedel & Loveland, 1995; Nip et al., 2018), although some studies report a slightly higher weight gain rate in the morning, with stable rates throughout the rest of the day (Haftorn, 1992; Lilliendahl, 2002). Afternoon peaks in weight gain rate have been reported in hoarding Marsh Tits and Coal Tits under favourable conditions with relatively warm winter temperatures (Hurly 1992; Polo et al., 2007).

Under favourable Poisson conditions, the leftover-hoarding models replicated part of the patterns found by Lilliendahl (2002) and Haftorn (1992), where *Fat change rates* were higher in the morning than in the afternoon. However, the observed evening decrease in *Fat change rate* in the models is not reflected in field experiments. This dip is likely caused by the maximum *Fat reserve*, which was set to 4 grams in the models. Because of this “forced” maximum, birds will continue to *Eat* without gaining more fat. Had this not been enforced, daily weight gain curves would have likely been linear, as was observed in most field studies (Boisvert & Sherry, 2000; Graedel & Loveland, 1995; Nip et al., 2018). The direct-hoarding model that bases its decisions on SC and FCR exhibited similar patterns of *Fat reserve levels* to the leftover-hoarders (Figure 10.4). However, the SC and FR direct-hoarder model maintains lower *Fat reserves* under Poisson conditions. Both direct-hoarders had their peak in weight gain occurring slightly later in the day compared to the other models, whilst still showing a dip in FCR at the end of the day. The fairly stable FCR rates throughout the day put these models in line with the linear daily weight gain curves observed in the literature (Boisvert & Sherry, 2000; Graedel & Loveland, 1995; Nip et al., 2018).

In the Bonanza environment, increases in *Fat reserves* were linear for all models. When inspecting the *Fat change rates*, these increased throughout the day, with a plateau in the evening. Because the plateau was not fully flat, the highest *Fat change rates* were observed at the end of the day. However, this small “evening peak” was not as pronounced as those found by Hurly (1992), who observed that marsh tits tend to delay weight gain until later in the day.

Lilliendahl (2002) found a stable weight gain rate throughout the day for non-hoarding great tits, whereas Haftorn (1992) observed a similar high early morning weight gain rate in non-hoarding as in hoarding tits. Under the Poisson condition, the non-hoarding model performs very similarly to the leftover-hoarders. In the Bonanza scenario, non-hoarders peak slightly later in their *Fat change rates,* in line with findings by Lilliendahl (2002).

The findings in this chapter are very similar to the results from Chapter 5, because the models here were most strongly governed by *Stomach content* in decision-making. This comparison is further discussed in Chapter 8.

10.5.3 Daily Hoarding and Retrieving Patterns

Evidence on daily hoarding patterns in *Paridae* includes mixed results (Chapter 5). Some find stable hoarding throughout the day (Boisvert & Sherry, 2000; Brodin et al., 1994), while others find morning peaks (Lahti & Rytkönen, 1996).

The direct-hoarding models in this chapter exhibit peaks in *Hoarding* behaviour in the morning, consistent with findings by Lahti & Rytkönen (1996). However, these models lack *Resting* behaviour, making them less realistic than other versions discussed in previous chapters. The leftover-hoarding models show stable hoarding behaviour throughout the day, aligning with results from Boisvert & Sherry (2000) and Brodin et al. (1994). Interestingly, a minor morning peak in *Eat-hoarding* was observed for the SC and FCR leftover-hoarder model just after the peak in feeding behaviour. This was likely caused by the need for birds to forage in the morning due to low *Fat reserves* and *Stomach contents*. As leftover-hoarders only hoarded once they found enough food and had full stomachs, a slight increase in *Eat-hoarding* behaviour may appear immediately after a feeding peak. At that point, their stomach was full, but they were still out foraging and therefore likely to hoard. This effect was less prominent in the Poisson environment, where birds encounter fewer simultaneous food items and lack the "bonanza" opportunities that could be hoarded.

In all hoarding models, *Retrieval* behaviour also predominantly occurred in the morning. As previously discussed, leftover-hoarders did not *Retrieve* in the Poisson environment and barely performed *Hoard* behaviour, making them functionally similar to non-hoarding birds. The direct-hoarding model based on SC and FCR showed some *Retrieval*, with a pronounced morning peak. Under Bonanza conditions, all models demonstrated higher *Retrieval* activity in the morning, followed by a stable rate throughout the day. These morning peaks align with predictions from other dynamic models (Pravosudov & Lucas, 2001b) and experimental evidence (Pravosudov & Grubb, 1997), which also indicate high retrieval rates in the early morning. The high early-morning *Retrieval* peaks were made possible by the birds' ability to generate enough caches for early-morning access. A minimum of five caches was required for *Retrieval*, and the birds maintained more than sufficient stores to support this morning retrieval pattern. Leftover-hoarders exhibited smaller *Retrieval* peaks in the morning, because their bottom thresholds for FR and FCR were very low, and birds were less likely to *Retrieve*.

10.5.4 Conclusion

In conclusion, the models presented here highlight the survival advantages for hoarding birds in environments where food availability is unpredictable. Birds that used a direct-hoarding strategy (R_{top}) did not exhibit realistic behavioural patterns, as they lacked any *Resting* behaviour. In contrast, individuals employing a leftover-hoarding strategy, guided by decision rules based on *Stomach content* and fat metabolism, performed better than non-hoarders, especially in Bonanza scenarios. Their regular *Eat-hoarding* behaviour enabled them to build up cache reserves, which they could *Retrieve* in the morning to avoid starvation when *Fat reserves* were depleted overnight. This strategy was reflected in their ability to maintain higher *Fat reserves* compared to non-hoarding models. The weight gain trajectories for leftover-hoarding models were linear in Bonanza environments, aligning with most field observations. In more predictable Poisson environments, birds gained more weight in the morning. Furthermore, the patterns of *Hoarding* and *Retrieval* were consistent with findings in the literature, as both show morning peaks.

Chapter 8. General Discussion

11.1 Survival - Which models have the highest fitness?

In Table 11.1 the model performance of all 24 model versions is shown (see also Table 7.18). Half-life survival is the number of days it takes for 50% of the agents in a simulation to die, averaged across all 12 environments that were used in parameterisation (see Table 7.2). Larger numbers indicate models with better survival. From this table, it is evident that leftover-hoarding models tend to perform better than the direct-hoarding models. Direct-hoarding models with *Resting* as their most energy-rich behaviour generally perform the worst. Leftover-hoarding models often do better than non-hoarding models in general, which is expected, as these half-life survival rates are calculated across Poisson and Bonanza scenarios. Leftover-hoarders can store and retrieve their food, which makes them more resilient in the more unpredictable Bonanza environments (see section 11.3 for more details).

Models that include *Stomach content* in their decision-making mechanism generally survive better than other models. These include models that base their decisions solely on *Stomach content* (top row), but also models where *Stomach content* and fat metabolism are combined (bottom two rows). The best fat metabolism-based model is the one that uses both *Fat reserve* and *Fat change rate* in its decision-making. These are followed by the medium performance of *Fat reserve*-only models. Models that base their decisions on *Fat change rate* only survive poorly.

Table 11.1. Half-life survival rates for the resulting models. Half-life survival is calculated as the mean number of days that it takes for 50% of the agents in a model to die, across all 12 environments used in parametrisation. Green shades indicate longer survival and red shades indicate shorter survival. Numbers between brackets indicate the chapter that includes the model version.

	Non-hoarder	***Leftover hoarder***	***Direct hoarder H_{top}***	***Direct hoarder R_{top}***
Stomach content (5)	45	52	44	41
Fat reserve (6)	35	46	40	29
Fat change rate (6)	27	35	29	28
Fat reserve & Fat change rate (6)	43	56	42	30
Stomach content & Fat reserve (7)	45	51	73	35
Stomach content & Fat change rate (7)	46	46	51	31

Chapters 5, 6 and 7 discuss the models in detail, focussing on their performance in two default environments. In Chapter 5, I demonstrated that birds making decisions based on *Stomach content* generally perform well in Poisson scenarios. However, only the leftover-hoarding model exhibited strong survival in the Bonanza scenario. The direct-hoarding models in this chapter were excluded as they did not exhibit hoarding behaviour.

Similarly, Chapter 6 focused on models relying on *Fat reserves*, *Fat change rate*, or a combination of the two. Again, the leftover-hoarding birds performed best, while direct-hoarding birds failed to exhibit either sufficient half-life survival or sustained hoarding throughout the simulation. The leftover-hoarding models that combine FR and FCR are the best-performing models across all chapters.

In Chapter 7, the analysis was extended to models incorporating both *Stomach content* and fat metabolism. While leftover-hoarding models continued to perform well, I also examined two direct-hoarding models where *Resting* was designated as the most energy-rich behaviour (R_{top}). These models exhibited *Hoarding* and *Retrieval* behaviour but did not *Rest*. According to the results from Table 11.1, the H_{top} models outperform all other models in Chapter 7. However, as described in section 10.4.2, these models do not exhibit any *direct-hoarding* behaviour and the improved survival is due to the initial cache store that birds receive at the start of simulations.

In summary, the hoarding strategy that generates the best overall survival across all energy proxies is the leftover-hoarder. Models that base decisions on either *Stomach Content* or a combination of *Fat reserves* and *Fat change rates* have good survival rates. Having excluded any “hoarding” models that do not exhibit hoarding behaviour, the best-performing of the remaining models, in terms of survival, is the leftover-hoarding model that relies on the combination of *Fat reserves* and *Fat change rates* for decision-making.

11.2 Non-hoarding models – Comparing Energy Proxies

In total, six non-hoarding models were investigated, their survival curves in the default environments are shown in Figure 11.1. All non-hoarding models struggle in the Bonanza environment as they struggle to cope with the infrequency at which they encounter food. The worst-performing model is the model where decision-making is based on *Fat change rates* only. The best surviving model across both environments is the SC and FR-based model (dark green), followed by the model that makes decisions based on *Stomach content* and *Fat change rates* (orange). The model that uses a combination of both FR and FCR also performs well across the two environments (Figure 11.1), as well as across all 12 parameterisation environments (Table 11.1).

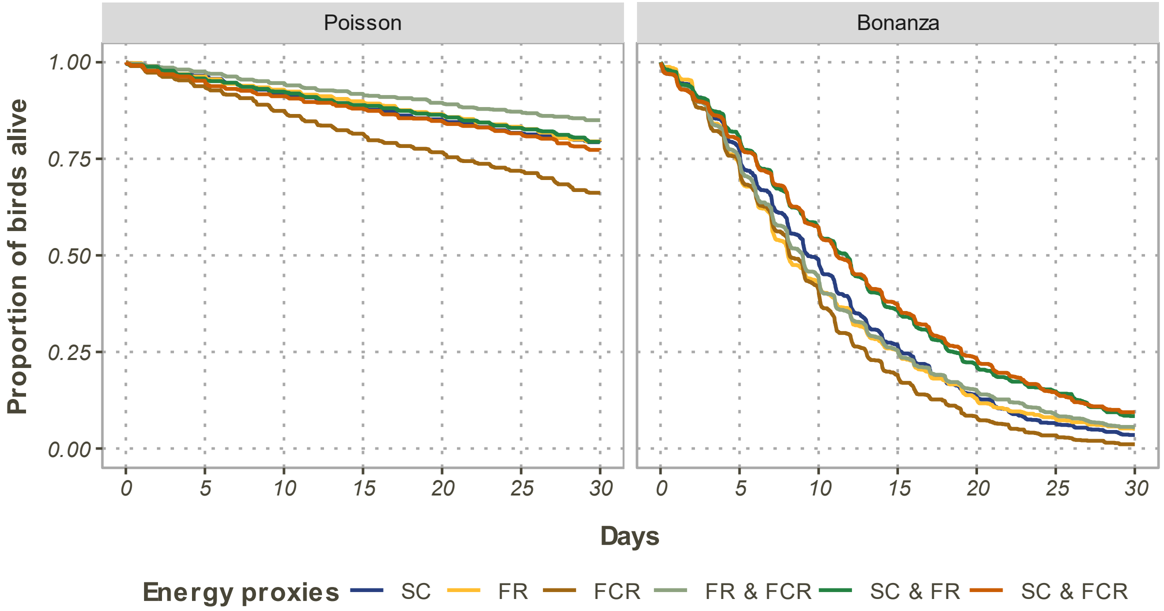


Figure 11.1. Survival rates of the non-hoarding models in the default environments. X-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

Note that two of the best-performing models (orange and dark green) are versions where decision-making is based on a combination of *Stomach content* and one of the fat-related variables (*Fat reserves* or *Fat change rates*). These non-hoarding models have two thresholds: one for *Stomach content* and another for *Fat reserves* or *Fat change rates*. As discussed in Chapter 7, these models have very low thresholds for *Fat reserves* and *Fat change rates*, respectively. Consequently, the *Fat reserves* and *Fat change rates* of birds in these models are almost always above their threshold, making decision-making primarily dependent on *Stomach content*. This makes them very similar to the non-hoarding model where decisions are based solely on *Stomach content*.

This is reflected in the daily curves of energy variables and behaviour patterns, which look very much alike for these three models. *Eating* and *Resting* proportions are stable throughout the day, with a peak in *Eating* in the morning. Note that both *Eating* and *Resting* rates are lower in Bonanza scenario. This lower *Eating* rate is because birds in Bonanza scenarios have more unsuccessful foraging bouts, which are not included in "*Eat*". Birds in a Poisson scenario, on the other hand, might find the same amount of food on average but are unlikely to be completely unsuccessful in their foraging attempt. Birds in bonanza environments also *Rest* less, because they go out to forage more often than in Poisson environments. In the latter, birds are able to keep their *Fat reserves* high and survive. The two combination models perform slightly better than the *Stomach content*-only model, which could be attributed to their slightly higher *Eating* rates, resulting in increased *Fat reserves*.

When non-hoarding models encounter more challenging environments, their survival decreases. The three models primarily driven by *Stomach content* demonstrate resilience to lower temperatures and reduced food availability in a Poisson environment (Figure 8.6 and Figure 10.8). However, in a Bonanza scenario, where initial survival is already low, all birds perish within the first five days when temperatures drop, or food availability declines further. Similar patterns are seen in the non-hoarding models from Chapter 6, where decision-making is based on either FR, FCR or a combination of the two. The models perform slightly worse in a Poisson environment with lower temperatures and similar to the default environment when faced with lower mean food availability. A combination of the two, even in a Poisson environment, is detrimental. Again, in Bonanza circumstances, either low temperatures or lower food availability assures birds die within the first few days.

It is important to note that while the mean number of food items available in the Bonanza scenario is equal to that in the Poisson scenario, non-hoarding birds do not have access to the same quantity of food. In the Bonanza environment, these birds cannot consume or hoard the surplus food items they frequently encounter. As a result, the total amount of food they can actually “utilize” is lower in the Bonanza environment compared to the Poisson environment.

In summary, the models of non-hoarding birds perform well under predictable food availability, even if temperatures are lowered or less food is available on average. Under unpredictable food availability survival is low. For the best survival across all environments combined, the decision rule needs to include *Stomach content*. Furthermore, the non-hoarding model based on a combination of *Fat reserves* and *Fat change rate* performs reasonably well too, but models that use FR or FCR only do not survive.

11.3 The Benefits of Hoarding

Throughout the chapters, I have only discussed hoarding models where at least 50% of the birds were alive at the end of the simulation across all 12 parameterisation environments. On top of this, hoarding models were only discussed if they showed *Hoarding* behaviour throughout the simulation. Otherwise, they were considered not representative of a hoarding bird. In practice, this leaves all leftover-hoarding models across the chapters, as well as the direct-hoarding (R_{top}) models in Chapter 7.

11.3.1 Hoarding vs Non-hoarding

In general, across Chapters 5, 6 and 7, the discussed hoarding models outperform non-hoarding models in the Bonanza environment (also see Figure 11.1, Figure 11.2 and Figure 11.3). In Poisson environments, we see smaller differences between hoarding and non-hoarding birds. Hoarding models, and more specifically the leftover-hoarding models, show consistently good survival in Bonanza scenarios (Figure 11.2). The only two direct-hoarding models that exhibited hoarding behaviour and where the average half-life across the 12 parameterisation environments was above 30 days, were those from Chapter 7. These direct-hoarders base their decision-making on a combination of SC and FR or FCR with *Rest* as the behaviour for the most energy-rich state (R_{top}).

As expected, the ability of food-hoarding models to cache and later retrieve food items provides a buffer against the unpredictability of the Bonanza environment. Food hoarding enhances bird survival in two ways. Firstly, hoarding behaviour allows birds to use all food items they find if a "bonanza" comes along, whilst non-hoarding birds would lose the items they cannot consume. This increases the number of caches, and therefore the total number of food items available for consumption throughout the simulation. Secondly, food hoarding buffers against environmental unpredictability, independent of the energy value of the cached items (Hitchcock & Houston, 1994). By caching, birds create an environment where they can always reliably find food, mitigating the risks of an unsuccessful foraging attempt, which are common in Bonanza environments. This reliability is especially critical in the morning when birds' fat reserves are at their lowest, and replenishing energy reserves is vital. The model results reflect this, as retrieval behaviour tends to peak during the early hours of the day (for more details, see section 11.4.4).

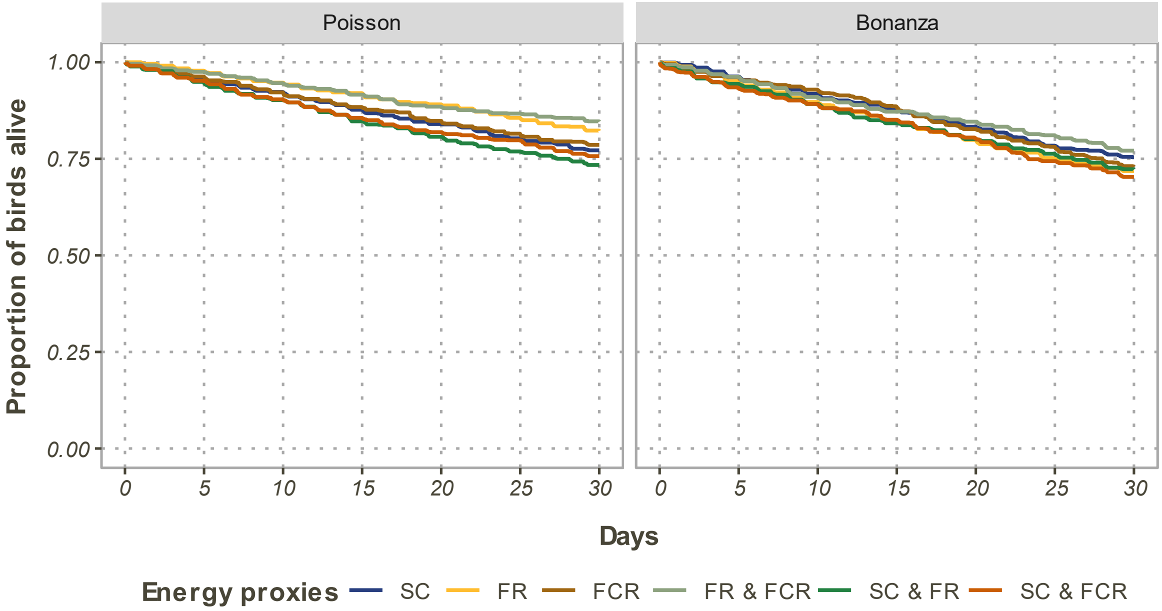


Figure 11.2. Survival rates of the leftover-hoarding models in the default environments. X-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

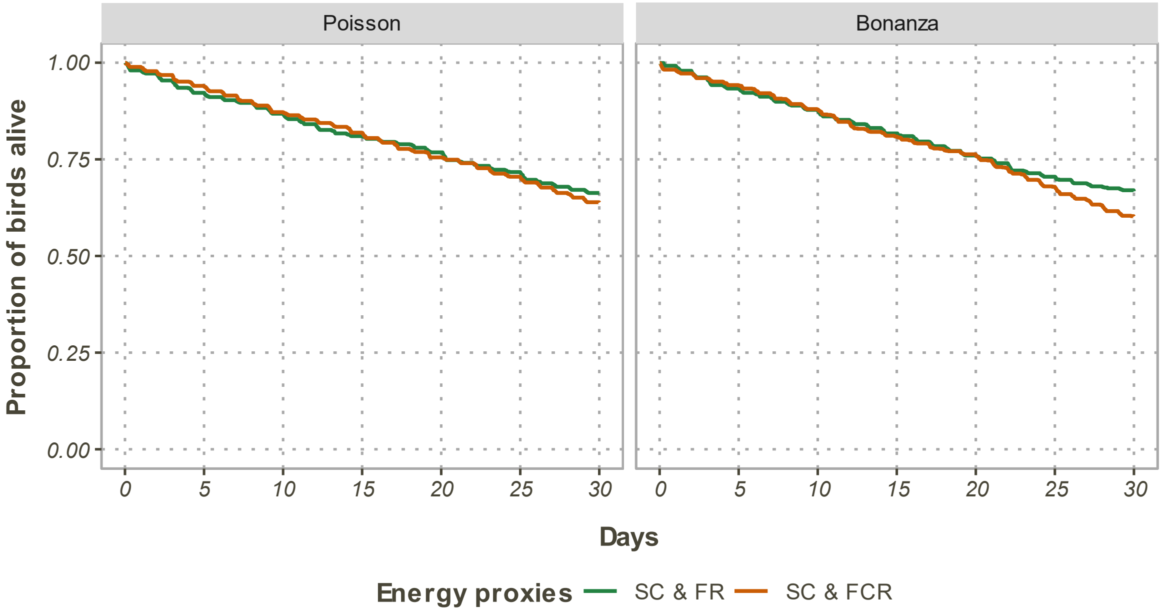


Figure 11.3. Survival rates of the direct-hoarding models in Chapter 7 in the default environments. X-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

11.3.2 Different Hoarding Strategies

Two distinct hoarding strategies were incorporated in this study. In the first, named the "leftover-hoarder," birds hoard food items only when they have foraged and found more food than they can immediately consume. This means that leftover-hoarding birds forage primarily with the motivation to eat, with hoarding occurring as a secondary outcome. In this strategy, the motivations for eating and hoarding are not independently regulated. In contrast, the direct-hoarding models reflect birds that "decide" between two actions: "forage and hoard" or "forage and eat." This approach assumes that the motivations for "foraging to hoard" and "foraging to eat" are regulated separately. Within the direct-hoarding strategy, I consider two variants: H_{top} and R_{top}. These differ in the behaviour expressed when the birds are in their most energy-rich state: *Hoarding* or *Resting*.

Across Chapters 5, 6, and 7, I examine a total of six leftover-hoarding models (Figure 11.2). Specifically, the FR and FCR-based model performs well in both default environments, which is consistent with the parameterisation results (Table 11.1). It is noteworthy that all leftover-hoarding models in practice are, at least indirectly, basing their decisions on *Stomach content*. The energy proxy on which their decisions are based, which can be SC, determines whether they are *Resting*, *Retrieving,* or going out to forage. Once foraging, the *Stomach content*, and whether it is full, determines if *Eat* or *Eat-hoard* behaviour takes place. The best-performing leftover hoarding model bases its decisions on FR and FCR, meaning that all 3 energy proxies are included in the decision-making for this model.

The only direct-hoarding models with both sufficient survival and hoarding behaviour are the R_{top} models in Chapter 7, which base their decisions on a combination of SC and FR or FCR. Their survival curves are shown in Figure 11.3. However, as indicated in Table 11.1, the R_{top} models do not perform well overall. This is likely because these models lack daily *Resting* behaviour, causing the birds to spend most of their time foraging (see Figure 10.7). This increases energy expenditure, making it harder to accumulate adequate *Fat reserves* for the night, while also elevating the risk of predation.

Leftover-hoarding models, on average, outperform the non-hoarders and direct-hoarders in both the Poisson and Bonanza environments. It is interesting that the direct-hoarding models in this study did not perform as well as the leftover-hoarding models, since other computational models in the literature often use a version of direct-hoarding. For instance, the seminal model by McNamara et al. (1990), explores optimal behavioural routines for storage and retrieval, and distinguishes between separate "behaviours" for "forage and eat" and "forage and hoard."

Similarly, models developed by Pravosudov and colleagues (e.g., Pravosudov & Lucas, 2000; Pravosudov & Lucas, 2001), are partially based on this framework and also differentiate between hoarding and eating behaviours. These models assume that the motivations to forage for hoarding and to forage for eating are regulated independently. Brodin (2000) makes the same assumption, with the addition that some food is not storable. It is unclear if food found for hoarding purposes is eaten on these occasions. Considering these studies, my findings raise the question; which type of hoarding strategy is most realistic?

In the hamster literature, as described in Chapter 1, foraging to hoard and foraging to eat are considered to both be appetitive behaviours, whereas eating is seen as consummatory (Bartness & Day, 2003). These three behaviours—foraging, hoarding, and eating—are treated as part of a behavioural sequence, with a potentially long delay between hoarding and eating. In this framework, hoarding motivation and eating motivation occur in sequence, each regulated by separate mechanisms. "Eating" can also take place immediately after foraging, if the energetic state of the animal requires this.

Alternatively, it could be argued that "hoarding" and "eating hoarded items" are not part of the same behavioural sequence. This seems more plausible for hoarding titmice, which store food for extended periods and are known to forget cache locations after about a month (Brodin, 1994a; Hitchcock & Sherry, 1990; Male & Smulders, 2007). This makes it unlikely that the behavioural sequence is "paused" between hoarding and retrieving the item. Instead, "foraging and eating" and "foraging and hoarding" likely represent distinct behavioural sequences, each ending in its own consummatory behaviour. In this scenario, retrieval is a separate behaviour, not linked to the initial hoarding event. The latter interpretation aligns with both my direct-hoarding models and similar models from the literature, which treat *Hoarding*, *Eating*, and *Retrieving* as separate behaviours, each governed by distinct regulatory mechanisms.

My leftover-hoarding models propose a third possibility, where hoarding is not a primary behaviour but rather a secondary consequence of eating. In this model, hoarding only occurs when a bird encounters an excess of food. This approach assumes no additional regulation of hoarding beyond the condition of food surplus. Interestingly, our results indicate that this simple decision rule generates the best-surviving models, where agents exhibit both *Hoarding* and *Retrieval* behaviours. This suggests that, at least in the short term, leftover-hoarding could account for much of the behaviour observed in the wild.

11.3.3 The Importance of Resting Time

In addition to the benefits of *hoarding* and *retrieval* already discussed (i.e., the ability to “use” occasional bonanzas, as well as creating more predictable environments), being a hoarding bird offers another significant advantage: increased *resting* time. The most successful models—specifically the leftover-hoarding models from Chapter 6—demonstrate that hoarding birds *Rest* more frequently than their non-hoarding counterparts, especially in Bonanza environments (Figure 9.7). *Resting* provides two critical benefits: it reduces both the risk of predation and the bird’s overall energy expenditure. Birds with more reliable food sources, as hoarders tend to have, are afforded more opportunities to *Rest*.

In contrast, the leftover-hoarding models in Chapters 5 and 7 show little difference in *Resting* frequency compared to their non-hoarding equivalents. Note that, in Chapter 7, leftover-hoarding birds rely on a combination of SC and FR or FCR to guide their behaviour. However, similar to the non-hoarding models that use SC and FR/FCR (see section 11.2), the thresholds for FR and FCR are very low. Again, this results in birds almost always having *Fat reserves* or *Fat change rates* higher than the top threshold, so the birds' decisions are predominantly based on *Stomach content*. As a result, these models are very similar to the leftover-hoarding model in Chapter 5, which is reflected in their behavioural outcomes.

This difference in *Resting* frequency between the fat metabolism-based (Chapter 6) and *Stomach content*-based (Chapters 5 and 7) models may be explained by the "speed" at which birds in these models receive information about their energetic state. The models in Chapters 5 and 7 rely at least partially on *Stomach content* to guide decisions, providing a short-term indicator of energy status. By comparison, the models in Chapter 6 base decisions on *Fat reserves*, a more long-term measure that responds more gradually to food consumption. This lag occurs because food must first pass through the stomach before contributing to *Fat reserves*. Additionally, the time required for birds to "build up" to a threshold based on *Stomach content* differs from thresholds based on *Fat reserves* or *Fat change rate*. During a single foraging bout, a bird can theoretically fill its stomach (7 food items). However, reaching the higher FR/FCR thresholds (up to 3 grams) typically requires multiple highly successful foraging bouts. In practical terms, models using *Stomach content* tend to show birds alternating between *Resting* and *Eating*, as their decisions are more immediately informed by recent food intake. This results in a lower proportion of birds engaging in the same behaviour at the same time. By contrast, the reliance on *Fat reserves* in Chapter 6 models allows for more sustained resting periods, as birds are less influenced by short-term fluctuations in *Stomach content*.

Note that the direct-hoarding models (R_{top}) discussed in Chapter 7, which make decisions based on SC and FR/FCR, do not exhibit any *Resting* behaviour at all (Figure 9.7). This is not a realistic representation of wild bird behaviour. The lack of resting clearly reduces survival but does not prevent it completely (Table 11.1 and Figure 11.3). These direct-hoarding models have the lowest half-life rates across the hoarding models I discussed. Creating sufficient *Fat reserves*, as well as having stored food, are most important for survival. In leftover-hoarders these reserves are partly achieved by high *Resting* rates, which help avoid metabolic costs and predation risk. In the direct-hoarding models, high *Fat reserves* are achieved by *Resting* less and *Foraging* more.

11.4 Daily Patterns

11.4.1 Daily Patterns of Stomach Content

For *Stomach content*-based models (Chapters 5 and 7), the average *Stomach content* across all birds that are alive is stable throughout the day (Figure 8.3 and Figure 10.4). The patterns look similar between Poisson and Bonanza environments. As discussed above, the non-hoarding and leftover-hoarding models from Chapter 7, which technically use FR or FCR in their decision-making, are very similar to models from Chapter 5, which only consider SC. This is due to the extreme threshold values for the FR and FCR energy proxies. The same is true for the direct-hoarding models in Chapter 7 (see section 0 for details). Therefore, variation in *Stomach content* will be most important in determining if birds are *Hoarding*, *Eating* or *Retrieving*.

The reason why the *Stomach content*-based models have a relatively stable *Stomach content* is related to the "speed" at which birds receive information about their energetic state. As discussed previously, *Stomach content* serves as a "short-term" variable, providing birds with immediate feedback on recently consumed food. In theory, *Stomach content* thresholds can always be reached within a single timestep, leading to birds frequently "switching" back and forth across a threshold. For leftover-hoarders, this typically involves alternating between the *Eat-hoarding* and *Resting* states (see Figure 8.5 and Figure 10.7). For the direct-hoarders described in Chapter 7, birds mostly alternate their SC above and below the second threshold, so that they *Eat* and *Hoard*. However, in these models, the bottom two thresholds are so close together that *Retrieving* also occurs regularly (see Table 7.17 and Figure 10.7).

In contrast, the models in Chapter 6 integrate fat metabolism into decision-making, basing their choices on the broader energy balance rather than recent food intake. As discussed, the "delay" in response to recent food intake is partly because *Fat reserves* and *Fat change rates* require at least one timestep to update, causing the delay as food transitions from the stomach to reserves

Additionally, thresholds for *Fat reserves* and *Fat change rates* often cannot be reached within a single foraging bout. Consequently, unlike *Stomach content*-based models, where behaviours frequently "switch" around thresholds, fat-based models exhibit longer periods of sustained *Foraging* followed by extended *Resting* phases. This dynamic leads to more variable *Stomach content* levels in fat-based models, especially under the Poisson condition (Figure 9.4). Foraging behaviour, driven by the slower-responding *Fat reserve* and *Fat change rate variables*, persists even when the stomach is full. Daily patterns of *Stomach content* show higher values in the morning, dipping later in the day, with some models exhibiting a second peak. In the fat-based models, a difference between hoarders and non-hoarders can be observed. The leftover-hoarding models tend to have higher *Stomach contents* in the morning, likely due to their ability to retrieve items and *Eat* more reliably in the morning.

11.4.2 Daily Patterns of Fat Gain

The *Stomach content*-based leftover-hoarding and non-hoarding models (Chapter 5 and Chapter 7) have different patterns for their daily weight gain curves between Poisson and Bonanza scenarios but are similar to each other. In the Poisson scenario, birds tend to have an increase in their *Fat reserves* at the start of the day, with a plateau in the afternoon and evening. The *Fat change rate* curves reflect this, showing the largest gain in the middle of the day, decreasing in the evening (Figure 8.3 and Figure 10.4). Note that the maximum *Fat reserve* (4 grams) is reached in these cases, which means that birds will continue to go out and forage, whilst they can no longer gain *Fat reserves*, “forcing” the plateau. In the Bonanza environment, the daily weight gain curves are more linear, with the highest *Fat change rates* at the end of the day. In the Poisson scenario, it is likely that had I not implemented the maximum *Fat reserves*, birds would have kept increasing their *Fat reserves* further, in a linear manner.

The direct-hoarding models that base their decisions on *Stomach content* and FCR (Chapter 7), show similar patterns to the SC-based leftover-hoarders in terms of the *Fat change rates* and the values of their *Fat reserves* (Figure 10.4). However, the SC and FR direct-hoarder R_{top}, retains lower *Fat reserves* under Poisson circumstances, with a peak in weight gain slightly further towards the end of the day than the other models. The plateau in *Fat reserves* for this model is not due to the maximum but can be attributed to the FR thresholds. This plateau, together with the lower absolute levels of *Fat reserves* shows that at least part of the decision-making happens based on FR. Simultaneously, the SC and FR direct-hoarder, exhibits a lot of *Direct-hoarding* behaviour, but barely any *Retrieving*, which means it spends energy hoarding items, but does not use the caches it has made to increase reserves at a later time. Under Bonanza circumstances, the SC and FR direct-hoarder behaves similarly to the other models in Chapters 5 and 7.

In the Poisson environment, four of the models from Chapter 6, in which decision-making is based on fat metabolism, show a plateau in *Fat reserves* at the end of the day, without reaching the maximum *Fat reserves* (Figure 9.4). The FR models and the FR and FCR models plateau just below 2 grams of fat, which is reflected in a lower *Fat change rate* at the end of the day. This shows that plateaus in *Fat reserves* can be reached without reaching maximum *Fat reserves*. The plateauing models have an upper *Fat reserve* threshold set just below 1.5 grams, which ensures that the birds transition to *Resting* behaviour as soon as their reserves reach this level, provided the *Fat change rate* is sufficiently high in the combined model. These thresholds are the primary factor responsible for the observed plateaus in *Fat reserves* under Poisson circumstances. In contrast, the two models based on FCR have higher *Fat reserves*, which plateau at or just below 4 grams in the Poisson environment. Under Bonanza environments, daily weight gain curves are linear for all six models and *Fat reserves* reach a maximum of 2 grams at the end of the day. *Fat change rates* are the highest at the end of the day for all models in Chapter 6. The hoarding models will have higher *Fat change rates* earlier in the day than non-hoarding birds, but end the day at similar levels of 0.15 grams/2 hours.

To summarise, on a mechanistic level, *Stomach content*-based birds tend to have higher *Fat reserves* than their fat metabolism-based equivalents. The reason for this is that SC-based models tend to switch between *Eating* and *Resting*, whilst slowly increasing their *Fat reserves*. Fat-based models tend to have longer periods of *Resting* and foraging, resulting in higher *Fat change rates* in the mornings with a dip in the evening.

From the literature on optimal body mass theory and the predation-starvation trade-off, we know that hoarding birds could be expected to delay their weight gain until later in the afternoon, whereas non-hoarding birds should increase their body mass linearly throughout the day (McNamara et al., 1990). This allows the hoarding birds to avoid the additional costs of mass-related predation risk and additional metabolic costs. Some studies have supported this, such as Hurly (1992) finding that captive marsh tits delay their weight gain until late in the day, which was confirmed by Polo et al. (2007) who found that coal tits, specifically at lower latitudes, delay their weight gain until later in the day. Accordingly, my results from Chapter 2, from the study on winter fattening patterns, showed a slightly more concave daily weight gain curve for hoarding coal tits than for non-hoarding great tits and blue tits. This, in line with optimal body mass theory and the findings by Hurly (1992) and Polo et al. (2007), suggest that coal tits in the UK delay their weight gain until later in the day, possibly prioritising predation risk over starvation risk. As the climate in the United Kingdom is relatively mild, this might be why hoarding birds “risk” to delay their weight gain. In comparison, none of my models exhibited a clear peak in *Fat change rate* in the evening. In some models, such as the *Stomach content and FCR/FR*-based ones, *Fat change rates* are the highest in the evening. However, they tend to be at this high level for most of the day and therefore do not exhibit a clear evening “peak” in line with optimal body mass theory.

In contrast to the evening peak in weight gain, field studies under harsher conditions (further north, lower temperatures, and/or shorter days), tend to find linear weight gain curves or the highest weight gain rates in the morning. For example, black-capped chickadees and tufted titmice in New York displayed linear feeding rates (Bonter et al., 2013). These results align with field observations made on black-capped chickadees in New Jersey and Quebec (Graedel & Loveland, 1995; Nip et al., 2018), as well as laboratory experiments on clack-capped chickadees (Boisvert & Sherry, 2000), which report similar trends. Hoarding willow tits and marsh tits in central Sweden, as well as non-food supplemented willow tits in Finland, have larger increases in weight gain in the early morning than non-hoarding great tits in the same area (Koivula et al., 2002; Lilliendahl, 2002). These findings from more northern areas are in line with the “risk spreading theorem” which states that birds should forage until they reach a body mass which is sufficient to survive the night, prioritising avoiding starvation risk (Bednekoff & Houston, 1994; Bonter et al., 2013). This would result in either linear weight gain curves, or high weight gain rates in the mornings, as hoarding birds retrieve their caches.

The results from my *Stomach content*-based models (Chapters 5 and 7) display a linear mass gain pattern throughout the day for hoarding and non-hoarding birds alike. The plateau observed under Poisson conditions is likely due to the "forced" maximum *Fat reserves*. It is likely that, had I not implemented a maximum *Fat reserve*, birds would have kept increasing their Fat reserves, resulting in a linear mass gain curve. Accordingly, *Fat change rates* are the lowest at the start of the day, but increase towards the end, with a plateau for most of the day. These findings fit with the literature suggesting similar *Fat change rates* throughout the day, resulting in linear weight gain curves (Boisvert & Sherry, 2000; Bonter et al., 2013; Graedel & Loveland, 1995; Nip et al., 2018). If anything, hoarding birds show more stable FCR throughout the day than non-hoarders, which have the highest mass gain rates in the evening. This is the opposite of what is expected under OBM theory, which suggests that it is hoarders who should delay their mass gain more than non-hoarders (McNamara, Houston, & Krebs, 1990a).

Lilliendahl (2002) report higher morning weight gain rates for hoarding willow tits than for non-hoarding great tits in the same area. Hoarding birds, which can rely on stored food, are better able to increase their body mass in the morning than non-hoarders, which have to forage and find new food items. In line with this concept, my *Stomach content-based* leftover-hoarding models (see Figure 8.3 and Figure 10.4) have slightly higher weight gain rates in the morning than their non-hoarding equivalents. However, in the study by Lilliendahl, weight gain rates were observed just after birds woke up, whilst I observed the higher *Fat change rates* in the late morning.

Meanwhile, the hoarding models based on FR and FR and FCR exhibit a plateau in *Fat reserves* under Poisson conditions, without reaching the maximum *Fat reserve* levels. By the end of the day, their *Fat change rate* declines. The highest *Fat change rates* for these models occur in the afternoon, in line with findings by Hurly (1992) and Polo et al. (2007). However, the dip in weight gain rate at the end of the day, associated with the plateau in *Fat reserves*, is not reflected in the literature. The FCR-only models increase to higher *Fat reserves* in a more linear pattern but also show a small decline in *Fat change rate* at the end of the day. Under Bonanza conditions, on the other hand, the *Fat reserve* pattern is linear for all models, and *Fat change rates* tend to plateau, with a small decrease in the evening. These linear weight gain patterns are what is generally reported in the literature (Boisvert & Sherry, 2000; Bonter et al., 2013; Graedel & Loveland, 1995; Nip et al., 2018).

In summary, fat metabolism-based models tend to have higher weight gain rates early in the morning, and lower weight gain rates in the evening, compared to the S*tomach content*-based models, which have linear daily weight gain curves. An evening decrease in mass gain rate has not been found in the field but does align with ideas about “risk spreading theorem”, where birds should gain weight as early as possible, avoiding starvation risk (Bednekoff & Houston, 1994; Bonter et al., 2013). *Stomach content*-based models, on the other hand, might be more realistic, as they tend to increase their *Fat reserves* linearly throughout the day in line with most findings from the field (Boisvert & Sherry, 2000; Bonter et al., 2013; Graedel & Loveland, 1995; Nip et al., 2018).

11.4.3 Daily Patterns of Hoarding

As reviewed in Chapter 5, the literature on daily hoarding patterns presents mixed findings with some reporting stable hoarding patterns throughout the day (Boisvert & Sherry, 2000; Brodin et al., 1994; Brotons, 2000), but others reported morning (Lahti & Rytkönen, 1996) or afternoon (Boisvert & Sherry, 2000) peaks in caching intensity.

The hoarding patterns exhibited by the models vary across different model versions, reflecting differences in their decision-making mechanisms. Consistent with much of the literature, which finds no effect of time of day on hoarding intensity, the leftover-hoarding model discussed in Chapter 5—based solely on *Stomach content*—demonstrates low but steady hoarding behaviour throughout the day (Boisvert & Sherry, 2000; Brodin et al., 1994; Brotons, 2000). Similar results are observed in Chapter 7, where leftover-hoarding models that combine *Stomach content* with *Fat reserves* or *Fat change rates* also show consistent and low hoarding frequencies throughout the day. In all 3 of these SC-based models, birds alternate between foraging to *eat-hoard* and *resting* based on SC thresholds, with hoarding occurring occasionally when sufficient food is encountered. As mentioned previously, this alternation between *Resting* and *Eat-hoarding* takes place because SC is a "fast" responding variable. Stomachs can be filled up within 1 timestep, but also be emptied within 1 timestep. Because individual birds do not often eat twice in a row, birds do not often fill their stomachs and are left with food, which leads to low *Hoarding* intensities.

In contrast, the results in Chapter 6, where leftover-hoarders base their decisions on fat metabolism, reveal distinct hoarding peaks in the morning, occurring shortly after the retrieval peak (see below). These findings align with those of Lahti and Rytkönen (1996), who observed that willow tits cache more intensively in the morning than in the afternoon. The morning hoarding peaks in the leftover-hoarding models from Chapter 6 are driven by increased foraging activity, during which birds inadvertently encounter and store surplus food. Foraging does not stop if the stomach is full, increasing the probability that birds will hoard. This reflects how the models are responding to a slightly "longer-term" energy state, as fat metabolism provides a more gradual and sustained indicator of energy balance. Unlike *Stomach content*, which updates immediately after food consumption, *Fat reserves* and *Fat change rates* respond slightly later, allowing birds to continue foraging whilst their stomach is full. This has the benefit of the increased number of caches but does cost metabolic energy. Again, note that even though the leftover-hoarders in Chapter 6 base their decisions on FR and FCR, *Stomach content* does play a role in deciding whether the bird will *Eat* or *Eat-hoard.*

The direct-hoarding models from Chapter 7, where decisions are based on both SC and FR/FCR, show lower, but comparable, morning hoarding peaks to those observed in Chapter 6. In the Chapter 7 models, hoarding peaks occur as birds, after *foraging* and reaching sufficient energy reserves, transition to *Hoarding* behaviour. This shift typically follows successful retrievals earlier in the morning (see below). The higher hoarding activity in the morning may explain the slightly lower *Fat change rates* observed in the morning for the direct-hoarding models under Poisson conditions compared to the leftover-hoarding models in Chapter 7. When birds engage in direct-hoarding, they forego eating, resulting in slightly lower *Fat reserve* increases in the morning.

Morning peaks in hoarding behaviour are also predicted by the models of Pravosudov and Lucas (2001). Under stable predation risk, their dynamic models predict hoarding during the first hours of the day, with no hoarding in the afternoon. This pattern arises from the starvation-predation trade-off, suggesting that birds should avoid carrying large fat reserves in the morning to reduce their predation risk throughout the day. Morning hoarding aligns with this strategy, as it allows birds to rapidly gain weight later in the day. Similarly, Brodin's (2000) dynamic model also predicts morning peaks in hoarding behaviour, when assuming that predation risk increases with body mass in the same way it was implemented in the Pravosudov and Lucas models.

Where these dynamic models provide predictions on how birds should behave, given the suggested trade-off between starvation and predation, my models in Chapter 6 suggest possible decision-making mechanisms for how this peak in morning hoarding could be achieved. Since hoarding is a secondary behaviour in these models, the morning peaks are driven by increased foraging and eating behaviour during the early hours of the day.

Furthermore, in both dynamic modelling studies, hoarding patterns shift when predation risk changes throughout the day or when the relationship between mass and predation risk is removed at low fat reserves (Brodin, 2000; Pravosudov & Lucas, 2001). My current model incorporates predation risk similarly to the Pravosudov and Lucas model. Future work could explore how altering the relationship between body mass and predation risk, as well as varying actual predation risk, might influence model performance in terms of survival.

11.4.4 Daily Patterns of Retrieval

In terms of daily retrieval patterns, all models display elevated levels of retrieval in the morning, followed by lower levels throughout the rest of the day. The size of the morning retrieval peak, as well as the stable retrieval levels later in the day, varies between model versions.

Pravosudov & Grubb, (1997) investigated daily hoarding and retrieval patterns in captive tufted titmice and found that birds had the highest retrieval rates in the early morning after they had woken up. This morning retrieval peak is in line with some of the predictions from the dynamic model by Pravosudov & Lucas (2001), which suggests birds should retrieve in the early morning to avoid the starvation risk when they have just come out of the night. Brodin's (2000) dynamic model also predicts a small increase in retrieval in the evening, but not for the morning. Morning peaks in retrieval were only achieved by increasing the effect of mass-dependent predation, specifically at low levels of fat reserves. The predicted retrieval peaks in the evening, just before roosting, are not observed in any of my models or in wild bird observations.

The hoarding models in my study display large differences in the size of the morning *Retrieval* peak. For example, the *Fat reserve* and *Fat change rate*-based models from Chapter 6 have morning *Retrieval* peaks where almost 100% of the birds is *Retrieving* at the first timestep of the day. The same is true for the direct-hoarding models form Chapter 7 (using SC and FR/FCR), where about 75% of the birds will *Retrieve* in this first timestep. The leftover-hoarding models from Chapter 5 and Chapter 7, however, have lower peaks with about 25% of the birds *Retrieving* at the same time.

So why do the other hoarding models not *Retrieve* as much in the early morning? The low morning retrieval peak exhibited by the *Stomach content*-based leftover-hoarders in Chapter 5, is caused by their low *Hoarding* frequencies. As previously discussed, birds need at least five caches in their "storage" in order to select the *Retrieval* behaviour. Because the *Stomach content*-based leftover-hoarders will often have fewer than five caches, the proportion of birds *Retrieving* first thing in the morning is lower than in other models. The leftover-hoarding models in Chapter 7, which base their decisions on a combination of *Stomach content* and *Fat reserve* or *Fat change rate*, show a similar, low retrieval peak in the morning. These models do create a larger collection of caches, which means their lower *Retrieval* peaks are due to their thresholds for *Retrieval* being low, whilst *Fat reserves* remain very high for these birds. This makes it unlikely for birds to have both their *Stomach content* and their *Fat reserves* or *Fat change rate* at sufficiently low levels for *Retrieval* to occur. This contrasts with the models discussed in Chapter 6, where birds hoard enough to maintain sufficient caches, and energy proxies are consistently low in the mornings, resulting in the high retrieval peaks.

11.5 Effects of Food Availability and Temperature

For each of the discussed models, I investigated how they respond to changes in environments, including lower temperatures, lower food abundancy and a combination of the two. The leftover-hoarding *Stomach content* -based models across Chapters 5 and 7, are generally resilient against lower temperatures and lower food availability in Poisson environments (Figure 8.6 and Figure 10.8). Under Bonanza circumstances, survival lowers significantly in both cases, with the strongest response to lower temperatures. When both are combined, this is detrimental for birds, even under Poisson conditions. The only leftover-hoarding model that stands out here, is the SC and FR-based model, this outperforms other leftover-hoarding SC-based models under lower temperatures and lower food availability in Bonanza scenarios. The two direct-hoarding models (R_{top}) from Chapter 7 differ slightly in their responses. The SC and FR model responds strongly to lowering in temperatures in the Poisson environment but outdoes the other models when it faces low temperatures and lower food in a Bonanza environment. Figure 10.8 clearly illustrates that the SC and FR models, both for leftover-hoarding and direct-hoarding R_{top}, exhibit greater resilience compared to their SC and FCR counterparts. For direct-hoarders, this increased resilience is likely due to the model's very high FCR thresholds. Under challenging circumstances, these birds rely heavily on *Retrieval* behaviour and will use up more caches than they produce. In contrast, the leftover-hoarder model has very low FCR thresholds, which results in a tendency to spend significant time *Resting* even under energetically demanding conditions—which is not advantageous for survival.

With regard to changes in environments, fat-based models show similar responses to lower temperature and lower food availability as their *Stomach content*-based equivalents when in a Poisson environment. They are relatively resilient against both lower temperatures and lower food availability, but a combination of the two is detrimental. Under Bonanza environments, however, they show a very strong response against lower temperatures, especially compared to the *Stomach content*-based models. This is likely because models based on fat metabolism tend to carry lower *Fat reserves*, which gives them less of a buffer against colder nighttime temperatures, leading to starvation before they can feed again in the morning.

11.6 Long-term Hoarding and Energy Management

11.6.1 Seasonal Hoarding

Seasonal patterns in “long-term” hoarding intensity have been observed across species, with a peak in autumn and a gradual decrease into winter (Brodin, 2005; Brodin et al., 1994; Haftorn, 1956; Lange et al., 2022; Pravosudov, 2006). Long-term hoarding means that birds cache food items in autumn to retrieve them months later in the winter when their food availability is low. It has been suggested that birds respond to their energy balance when they make foraging/hoarding decisions, which provides indicators of past food availability and predictability as well as incorporates environmental influences (Lange et al., 2022; Pravosudov, 2006). According to the energy-flux hypothesis, birds that are generally using more energy are thought to increase their hoarding intensity. Such a mechanism could explain the increase in hoarding intensity at the end of autumn and the start of winter. As nights get longer and colder, birds use up more fat stores overnight and need to build these back up during the shorter days, which results in a larger “energy-flux”. In line with this theory, the dip in hoarding behaviour in winter is suggested to take place because birds simply do not have enough food available to provide for their energetic needs as well as hoarding. Short-term hoarding that occurs in winter, could be explained as behaviour that occurs occasionally when there are temporally sufficient food sources. Alternatively, short-term hoarding and long-term hoarding could be regulated differently, requiring different decision-making mechanisms for each time of year.

In Chapter 3, I used a novel citizen science framework to investigate if food supplementation of hoarding Paridae species would increase hoarding intensity in winter or move the peak in hoarding intensity towards shorter days, in line with the energy-flux hypothesis. I found that an autumn peak in hoarding behaviour persists, even when birds are food-supplemented with feeders. The peak occurred slightly later than expected from the literature but did not move to the shortest day of the year. This finding either indicates that hoarding motivation is lower in winter, in contrast to the predictions of the energy-flux hypothesis, or that feeders do not supplement birds sufficiently. Further research should investigate if hoarding motivation is downregulated in winter, or if decision-making remains the same and birds are simply responding to changes in circumstances (e.g. higher energy flux, lower food availability).

Currently, my models only include “short-term hoarding”. The cache store that birds retrieve from is assumed to be a “short-term” hoarding storage, that birds have absolute knowledge of. The environments in the simulation reflect 30 days in winter. It is interesting to consider if one of my models could generate a decrease in hoarding behaviour under winter circumstances, with higher hoarding intensity in an “autumn” environment. An autumn-like environment would have increased food availability and predictability, much like my Poisson food distributions, but with a higher mean. Therefore, a model that demonstrates elevated hoarding behaviour under Poisson conditions would be a strong candidate. By default, leftover-hoarding models would be promising here, as they inherently increase hoarding as food availability rises. In line with this, my fat metabolism-based models, particularly the leftover-hoarder based on FR, exhibit higher peaks in hoarding under Poisson conditions. This aligns with the prediction of increased hoarding rates under more "autumn"-like circumstances.

For future work, it would be interesting to investigate how these well-performing fat metabolism-based models perform across the seasons. By simulating dynamic environments with changing temperature, day length, and food availability, the models could be exposed to simulated autumn, winter, and spring. This would allow an exploration of whether these decision-making rules produce the expected patterns of high hoarding intensity in autumn and reduced hoarding frequency in winter, or if separate decision rules are necessary. Fluctuations in daily and seasonal weight gain could be investigated in this way as well.

However, it is important to note that in autumn, birds hoard a very large number of items in a short period (Brodin, 1994b; Haftorn, 1956; Pravosudov, 1985). It seems unlikely that a leftover-hoarding strategy alone could explain such intense caching activity. Thus, the “true” decision rules may lie somewhere between leftover-hoarding and direct-hoarding. A plausible alternative is that birds employ both "forage-eat" and "forage-hoard" behaviours, while also opportunistically hoarding leftover food when encountered. The decision-making process might involve sequential steps, with birds first determining whether to hoard based on their *Fat reserves* or *Fat change rates*. When these are extremely low, birds should *Retrieve*. When these are high, birds should *Hoard*. If *Fat reserves/Fat change rates* are between both thresholds, the bird will either *Rest* or *Eat-hoard*, based on how full the stomach is (Figure 11.4). This rule is similar to the direct-hoarding model H_{top}, but the sequential nature assures that *Stomach content* is only used if *Fat reserves* are not depleted or very high. Therefore, hoarding behaviour is more likely to take place (an issue with the current H_{top} models). This decision rule also implies that hoarding can function as a distinct behaviour but may also arise opportunistically when birds encounter surplus food. A future study implementing this decision rule into my general model could provide further insights into which form of hoarding strategy is more realistic in a longer-term environment.

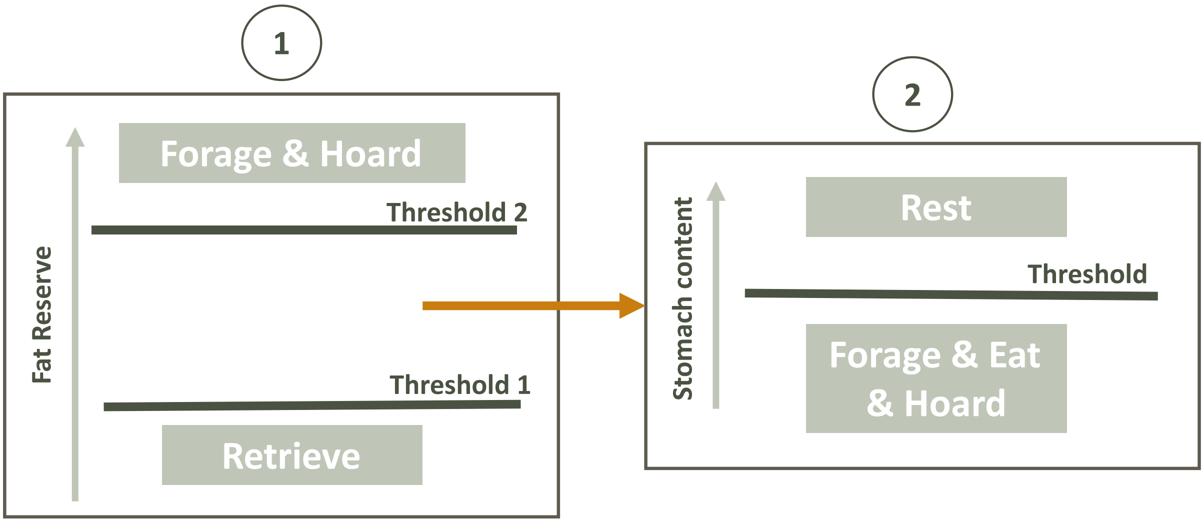


Figure 11.4. Schematic for a suggested future model with a sequential decision-making rule. In stage 1, the agent determines if Fat reserves are high enough to Direct-hoard or low enough to Retrieve. If reserves are in between the two thresholds, the agent decides whether it will Rest or Eat-hoard, based on the Stomach content.

11.6.2 Energy Management

Aside from seasonal patterns in hoarding, titmice are known to have seasonal increases in their body mass. This concept, named "winter fattening" is observed in non-hoarding birds, both in terms of seasonal weight gain (e.g., Gosler, 2002; Haftorn, 1989; Moiron et al., 2018) and an increase in daily amplitude (e.g., Haftorn, 1989; Moiron et al., 2018). In hoarding titmice, findings in the literature are mixed both with regard to the increase in average body mass in winter, as well as the increase in daily weight gain amplitude (Broggi et al., 2003; Cooper, 2007). In Chapter 2, I describe winter fattening patterns as observed in tit species across the UK, using ringing scheme data from the British Trust for Ornithology. I show that fat reserves increase in the winter months and that the amplitude of the daily weight gain curve increases slightly for great tits, blue tits and coal tits.

Furthermore, this study demonstrated that coal tits exhibit less pronounced patterns of winter fattening compared to the non-hoarding great tits and blue tits. This suggests that hoarding birds do not need to increase their fat reserves to the same extent as non-hoarders, given their access to reliable food caches. These findings align with predictions from optimal body mass theory, which proposes that birds must balance the benefits of larger fat reserves—such as reducing the risk of starvation—with the associated costs, including increased predation risk and higher metabolic demands. Hoarding birds are less likely to face starvation due to their dependable food caches, allowing them to maintain lower fat reserves during winter. This could explain why hoarding birds do not exhibit pronounced winter-fattening patterns.

In my models, specifically the fat metabolism-based models, I observe higher *Fat reserves* for non-hoarding birds than for leftover-hoarding birds in the Poisson environment. This pattern is opposite in Bonanza scenarios, where hoarding birds carry more fat, as they are able to use the bonanzas more efficiently. These results show that, how much fat birds carry in practice, is highly dependent on the environment. Under more predictable circumstances my fat-based models predict higher *Fat reserves* for non-hoarding birds than for hoarding birds in a winter environment, in line with Optimal body mass theory and my findings from Chapter 2.

Interestingly, the seasonal patterns in fattening observed in the UK tit populations in Chapter 2 align closely with the hoarding behaviour of coal tits described in Chapter 3. Hoarding activity at feeders peaks in early November, coinciding with the start of the rise in body mass, which itself peaks slightly later, in early to mid-December. Hypothetically, it could be possible that hoarding and eating are both upregulated in autumn, which causes the peak in hoarding as well as the start of winter fattening. As winter ends, temperatures increase and days get longer, the motivation to hoard will go down. The new decision model, which I proposed in the previous section, could be a way to further explore how winter fattening occurs. In autumn, with a lot of food available, birds will exhibit both hoarding and leftover-hoarding behaviours, generating a peak in hoarding. Under the model with fixed thresholds (as all my models are), birds would only hoard a lot of they reached very high *Fat reserves* in Autumn. Then, as days get shorter, their *Fat reserves* drop and therefore do not cross the top threshold. They stop *Direct-hoarding*, and as the food supply goes down, left-over hoarding is also reduced. The problem with this story is that it predicts higher *Fat reserves* in the Autumn than in the winter, which we know is not the case. To make the model produce seasonal patterns of both hoarding and fat reserves, it may be necessary to build in moving thresholds into the model. Birds could be changing the "set point" of where their fat reserves should lie, depending on the season or their photoperiodic state (Biebach, 1996; Cornelius et al., 2013). If the thresholds for *Fat reserves* and for *Stomach contents* increase into winter, birds would be less likely to do any *Direct-hoarding* and would gain more fat. During winter, with less food available, very little *Leftover-hoarding* would occur. Once winter comes to an end, the thresholds could come down again, letting birds lose weight and start hoarding again, as soon as food is available. That would fit the occasional Spring hoarding peaks which have been observed in some studies.

11.7 Future Studies

11.7.1 Expanding "Pilferage"

If the model is expanded to include longer timeframes, the pilferage process should be reviewed as well. Currently, the pilferage process in the general model assumes a half-life of 20 days. This means that, within 20 days, half of the caches stored by each bird will have disappeared. This rate accounts for various factors, including losses due to pilferage by other birds, memory decay, and food spoilage rendering caches inedible. However, pilferage rates for long-term hoards have been estimated to range between 2–30% per day based on studies using artificial caches and field observations (Brodin, 1993; Vander Wall & Jenkins, 2003). The half-life time of 20 days in my models is on the very low end of this range. Therefore, it could be interesting to increase the pilferage rate in future studies.

Furthermore, it would be interesting to split the current "pilferage" half-life into a true pilferage process where food items disappear, and a memory component, where birds forget their caches. Caches that are forgotten could be added to the general food availability in the environment and can then be found by a bird that goes out to forage for new food items. The latter is likely what takes place in long-term hoarding and retrieval. Birds enrich their food availability in winter by hoarding a large number of caches in autumn. They do not remember the location of the caches exactly but are more likely to find food in their own environment (Brodin, 2005).

Finally, the current model does not incorporate social dynamics. Birds do not interact with one another, nor do they influence each other's food availability or cache storage. Increasing the pilferage rate in the model could simulate an environment where birds steal a larger proportion of each other's caches, with higher pilferage levels representing higher bird densities. To include the benefit of other hoarding birds in the environment, the model could be set up so, that caches from other birds are added to the general food environment.

11.7.2 Tests of the Model

Determining which energy proxies are most likely used by birds to guide their foraging decisions remains challenging. If birds based their decisions on stomach content, as predicted by my models from Chapters 5 and 7, they would exhibit relatively stable stomach fill levels throughout the day and achieve the highest mass gain rates in the evening. Behaviourally, these birds would alternate between resting and eating, occasionally hoarding leftover food items. On the other hand, if decisions were driven by fat metabolism, birds would engage in longer, sustained periods of eating and resting, with more stable mass gain rates distributed evenly throughout the day. As previously discussed, some field data on feeding patterns exist, but findings are mixed depending on environmental conditions. An experimental study that records both weight gain and feeding rates under varying food predictability could provide valuable insights into these mechanisms.

Additionally, my fat metabolism-based models predict daily peaks in hoarding activity, whereas models driven by stomach content predict more stable hoarding frequencies throughout the day. While the literature predominantly reports stable hoarding patterns across the day (Boisvert & Sherry, 2000; Brodin, 1994a), experimental data might be able to verify how hoarding patterns differ under varying food availability.

11.7.3 Exploring the Energy Flux Hypothesis Further

The “energy-flux hypothesis,” suggests that birds may base their hoarding decisions on information about their energy balance. Where my current models are only looking at the possible role of signalling factors about the energetic state of birds, future work could investigate this hypothesis more specifically.

For instance, information about the “energy balance” could be incorporated in the decision-making rules of my models. Instead of basing foraging decisions on current *Fat reserves*, *Fat* *change rates* and *Stomach content*, agents could use the "energy expenditure" over the last 24 hours to base their decisions on.

Furthermore, to test this hypothesis experimentally, one could artificially increase birds' energy consumption and look for a corresponding increase in hoarding motivation. A particularly intriguing approach would be to conduct a study similar to that of Day & Bartness (2001)with hamsters. In their experiment, hamsters were trained to "forage" using a running wheel in exchange for food pellets, allowing researchers to easily manipulate the foraging effort (i.e., the number of revolutions required to earn a pellet). Their results showed that at low foraging levels, increases in effort led to greater food consumption and higher hoarding intensity. However, at the highest foraging efforts, hamsters did not further increase hoarding but instead maintained a stable body weight. In the latter case, food that was foraged was eaten instead of hoarded in order to maintain the higher energy needs.

A similar experiment with birds could provide valuable insights. For example, in an experimental set-up, titmice could be allowed to forage and hoard from a feeder, with the energy requirements for foraging manipulated. The foraging effort could be adjusted by varying the distance between the home cage and the feeder or by requiring the birds to fly back and forth between multiple feeders. In this manner, an experiment could test whether increased foraging effort (e.g. an increased energy-flux) leads to higher hoarding and/or consumption rates. Such an experimental setup would offer a way to explore the relationship between energy expenditure and hoarding behaviour.

11.8 Conclusion

In conclusion, this thesis sheds light on the mechanisms driving food-hoarding behaviour and winter fattening in Paridae, highlighting how these strategies help small birds navigate the energetic challenges of northern winters. Observational data on patterns of body mass fluctuations in titmice show that hoarding species rely less on fat reserves compared to non-hoarders, which aligns with optimal body mass theory. Findings from a citizen science study challenged the energy-flux hypothesis, showing an autumn peak in hoarding intensity, even when birds are food-supplemented. Finally, agent-based models demonstrate that simple decision rules, such as leftover-hoarding informed by physiological proxies, effectively replicate observed hoarding and retrieval patterns of short-term hoarding in winter. The models show that hoarding is especially beneficial when food is unpredictable and occasionally abundant. Furthermore, the hoarding strategies where "hoarding" and "foraging to eat" are controlled together seem a more plausible scenario than models where this is done separately.

Overall, this work underscores the importance of hoarding as an adaptive strategy and lays the foundation for future research to further explore the interplay between energy balance, environmental conditions, and behavioural decision-making.

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Supplementary materials

Contents

A. Chapter 2. Seasonal Fluctuations of Body Mass in UK Tit Species

A.1 Data Cleaning Process (BTO Data)

The bird data was collected by the British and Irish Ringing Scheme run by the British Trust for Ornithology (BTO). Before data cleaning, the records contained a total of 1,516,652 captures.

The following steps were taken to remove any erroneous data (outside plausible ranges) or data not relevant for the purposes of this project. See Table A.1 for a detailed overview of each cleaning step and the number of removed observations. Table A.2 and Table A.3 show the ranges for wing length and body mass that were used to select which observations are plausible.

Table A.1. Steps taken to clean the BTO data. Columns indicate the step name, a description of what happened and the number of removed and remaining observations after the step took place.

#	***Step name***	***N removed***	***N remaining***	***Description***
1	Raw data	-	1,516,666	The records as these were received from the BTO ringing scheme.
2	Marsh, willow and crested tit	20,623	1,496,043	Removed all records marked as Marsh, Willow and Crested tit as these will not be included in the analysis.
3	Species code or name unknown	0	1,496,043	Removed all records where the species name or species numeric identification code is unknown.
4	Species code incorrect	0	1,496,043	Any record for which the numeric identification code did not match with any of the species of interest, was removed (Euring Europe, 2023).
5.	Species code and name do not match	0	1,496,043	Records for which the numeric species code and the “English name” did not match were removed.
6.	Age NA	0	1,496,043	Records for which the age was not recorded, were removed.
7.	Juvenile birds	946,395	549,648	Records of juvenile birds were removed. EURING age codes were used, as corrected by the BTO ringing scheme. Records with classification 0 (age unknown), 1 (pullus), 1J (fledged, just out of nest), 2J (fully grown, year of hatching unknown, at least partly in juvenile plumage), 3 (hatched in current calendar year) and 3J (hatched in current calendar year and at least partly in juvenile plumage) were removed, only adult birds remain (du Feu et al., 2020).
8.	Weight unknown	17	549,631	Observations for which the bird weight was not recorded were removed.
9.	Unrealistic weights	7,584	542,047	Records where the weight of birds falls outside the reasonable range for the specific species, were removed. See Table 2 below.

10.	Wing length unknown	13,036	529,011	Observations for which the wing length was not recorded were removed.
11.	Unrealistic wing length	908	528,103	Records where the wing length of birds falls outside the reasonable range for the specific species, were removed. See Table 2 below.
12.	Locations outside UK	80	528,023	Locations outside the United Kingdom and Ireland were removed.
13.	Inaccurate days	0	528,023	Remove any records for which the day of observation is not quality assured. For this, the BTO “date accuracy” variable was used.
14.	Inaccurate times	0	528,023	Remove records for which the time of observation is not quality assured. For this, the BTO “date accuracy” variable was used. *
15.	Breeding & moulting	116,852	411,171	All data collected in the breeding and moulting season was removed. Only data collected between October 1st and March 31st remains.
16.	Outside of daylight	3,987	407,184	Remove records of which the time of capture is more than 1.5 hours outside the sunrise and sunset times for that day.
17.	Random selection per bird ID	78,728	328,456	From each individual bird ID, a single randomly selected sample was retained in the dataset. This was done to avoid the effects of repeated measures of the same bird.
18.	Remove without station <50km	372	828,084	Observations without a single weather station in within a 50-kilometre radius were removed.
18.	Weather match	31,006	297,078	Each observation was attempted to be matched with weather observations from the 3 days preceding the capture of the bird. The 3 weather stations closest to the capture location, but within a 50 km radius were selected. Starting from the closest station, the 3 dates ahead of capture were retrieved from each of the weather stations and used to calculate the 3-day average minimum. If fewer than 2 days across all 3 stations were available, the bird observation was removed.

Table A.2. The range of body mass for the included species. Data retrieved from the BTO page on bird biometrics were used. Numbers are in grams. Used ranges are taken as 25% of the range (min – max) below the observed minimum and above the observed maximum.

Species	***Range (g)***	***Minimal female (g)***	***Maximum male (g)***	***Range used (g)***
Blue tit	9.70-12.2	9.5	12.4	8.78 – 13.13
Coal tit	8.10–10.0	8.0	10.0	7.50- 10.50
Great tit	16.6 - 20.8	16.3	21.0	15.55-21.85

Table A.3. The range of wing length for the included species. Data retrieved from the BTO page on bird biometrics was used. numbers are in millimetres. Used ranges are taken as 25% of the range (min – max) below the observed minimum and above the observed maximum.

Species	***Range (mm)***	***Minimal female (mm)***	***Maximum male (mm)***	***Range used (mm)***
Blue tit	60.0-67.0	60.0	68.0	58.00-70.00
Coal tit	58.0-63.0	57.0	63.5	55.38-65.13
Great tit	71.0-79.0	71.0	79.0	69.00-81.00

A.2 Calculating Time and Day Variables (BTO Data)

To ensure accuracy of the time and date stamps used in our analysis, some additional data cleaning and manipulation took place

A.2.1 Time and Date Stamps

Using the *Lubridate* package in R, the timestamps for each record were converted into UTC, accounting for any differences between records observed under GMT and BST (Spinu et al., 2023). Separate variables for time, day in year, week in year, month in year and year were created.

A.1.1 Day Length and Proportion of Day

For the "time of day data", the sunrise and sunset times were added to each record, using the *StreamMetabolism* package in R (Sefick, 2023). Using these variables, all records made more than 1.5 hour before sunrise or after sunset were removed (see Table A.1 step 16).

For each observation timestamp, the number of hours passed since sunrise were calculated. Based on the sunrise and sunset times, a variable containing the 'proportion of day' was calculated as well:

$$proportionOfDay = \frac{hoursSinceSunrise}{dayLength}$$

A.3 Selecting a Proxy for Fat Reserves (BTO Data)

To investigate the fluctuations in fat reserves over time, a measure of bird body condition was selected. We decided to use the residual body mass over wing length as our proxy for fat reserves in each individual bird. Before reaching this decision, the following measures were considered:

A.3.1 Fat Scores

A common way of estimating fat reserves in alive birds is to use a visual fat scoring system such as the ESF (European Science Foundation) or BWG (Biometrics Working Group within the British and Irish ringing scheme) (British Trust for Ornithology, 2024; Kaiser, 1993). Fat scores are taken by visually inspecting the birds' fat deposits in the furcular and abdominal areas. A review of morphometric indices of body condition in birds has shown that fat scores are one of the better indices to measure body fat content for most species, including tits (Kaiser, 1993; Labocha & Hayes, 2012). The BTO data contains a field where the fat scores can be recorded. However, because over 83% of the cleaned data did not have information on the bird's fat scores, this is variable could not be used in my analysis.

A.3.2 Absolute Body Mass

Alternatively, Labocha and Hayes (2012) suggest that absolute body mass is a reasonable proxy for fat reserves in most bird species. To test if body mass and fat scores co-vary in our dataset, a Spearman's correlation was conducted to evaluate the relationship between fat score and body mass for each species. This was done on the subset of data for which fat scores and information on the fat scoring method were available, after translating fat scores taken with the BWG system into ESF scores. A weak significant positive relationship between fat score and body mass was found for all species in this subset (Table A.4). This suggests that the body mass of birds co-varies with the fat scores, which are known to reflect the bird's energy levels.

Table A.4. Spearman correlation results for the relationship between fat score and body mass for each species.

Species	***N***	***DF***	***r***	***Strength***	***p***	***Direction***
Blue Tit	48313	48311	0.24	weak	<.001	positive
Coal Tit	7234	7232	0.24	weak	<.001	positive
Great Tit	27200	27198	0.16	weak	<.001	positive

The absolute body mass is available across all records in our cleaned data. As it is correlated to fat-reserves, it would be a straightforward way of investigating changes in energy reserves over time. However, we first need to consider if there are other factors that affect variation in body mass over time.

A.3.3 Body Size

Another obvious candidate that affects body mass is the body size of the bird. Larger birds will automatically have a larger body mass. Even though body size is not expected to vary on a population level over time, we do not know if there are reasons why either larger or smaller birds are more likely to be caught during certain times of the year. For example, if there are differences in winter survival that would cause either larger or smaller bodied birds to survive, this would have an effect on the observed seasonal variation in body mass. The same argument can be made for female versus male birds. If the likelihood of catching male or female birds changes throughout the year, for example because of breeding behaviours, this can affect the observed patterns in body mass as male birds are generally larger. Therefore, the variation in body mass due to variation in body size should be accounted for (Krams et al., 2013).

To check if body mass and body size co-vary in our dataset, we used the wing length of the birds as a proxy for absolute body size. Wing length is the most frequently used proxy for body size in birds, and has been shown reliable in non-migratory species (Ashton, 2002). A Pearsons's correlation coefficient was conducted to evaluate the relationship between wing length and body mass. A moderate significant positive relationship between wing length and body mass was found for all species apart from the Crested Tit. The latter is likely due to the small sample size. This suggests that, indeed, wing length and body mass co-vary with each other and larger birds have larger body masses.

Table A.5. Results from the Pearsons correlations between wing length and body mass.

Species	***N***	***DF***	***r***	***Strength***	***p***	***Direction***
Blue Tit	295273	295271	0.45	moderate	<.001	positive
Coal Tit	55658	55655	0.33	moderate	<.001	positive
Great Tit	177092	177090	0.46	moderate	<.001	positive

A.3.4 Body Mass / Body Size Ratio

A common alternative way of estimating fat reserves, which takes the variation in absolute body size into account, is to take a ratio between the absolute body mass and the wing length of each individual bird (Green, 2001; Labocha & Hayes, 2012). These measurements are available throughout our dataset and allow us to calculate a bird Body Mass Index (BMI) according to the following formula (Krams et al., 2013):

$$BMI = \frac{bodyMass}{wingLength^3}$$

After calculating the BMI for each record, a Pearson correlation coefficient was conducted to evaluate the relationship between bird BMI and wing length. There was a strong significant negative relationship between wing length and BMI for all species (Table A.6).

Table A.6. Results from the Pearsons correlations between wing length and BMI

Species	***N***	***DF***	***r***	***Strength***	***p***	***Direction***
Blue Tit	295273	295271	-0.74	Strong	<.001	negative
Coal Tit	55658	55655	-0.74	strong	<.001	negative
Great Tit	177092	177090	-0.74	strong	<.001	negative

This index now correlates more strongly with wing length than the original body mass did. Therefore, the body mass/body size ratio was not used in our further analysis.

A.3.5 Residual Body Mass over Wing Length

Alternatively, several studies have used body mass regressed over wing length as a proxy for body condition (Labocha & Hayes, 2012; Schamber et al., 2009). Because the relationship between mass and wing length might not be linear, with different increases in mass for larger birds, we log-transformed the body mass and the wing length variables. Then, we regressed body mass on wing length, assuring that the residual body masses from the regression are no longer correlated with the body size of the bird. These residuals were used as the proxy for body condition. Note that the regressions are done on a species level, as species might have different relationships between body mass and body size. Figure A.1 shows the linear models for each of the species. The linear regression models are in Table A.7.

Table A.7. The linear regressions for the 3 species with log(body mass) ~ log (wing length).

Species	***Intercept***	***Slope***	***R-squared***	***p-value***
Blue tit	-1.67	0.98	0.23	<0.001
Coal tit	-0.82	0.74	0.12	<0.001
Great tit	-1.63	1.05	0.26	<0.001

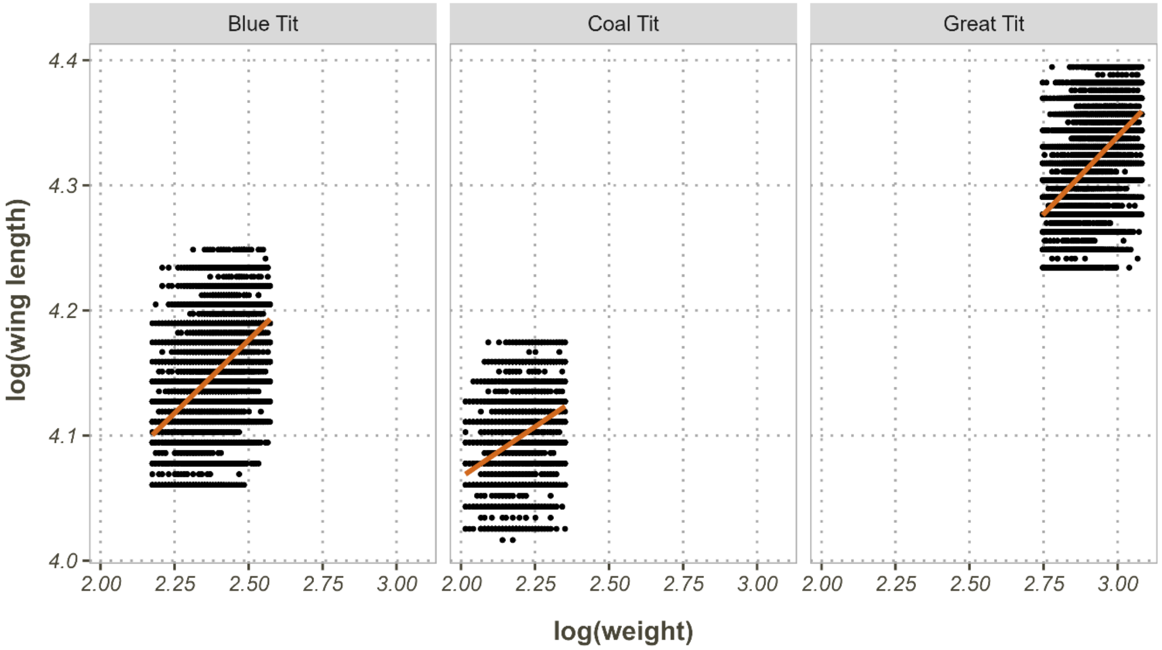


Figure A.1. The relationship between log(wing length) and log (weight), separated by species. The orange lines show the linear regression models (See Table A.1 for details).

After calculating the residual body mass for each record, a Pearson correlation coefficient was conducted to evaluate the relationship between residual body mass and wing length. There was no significant relationship between wing length and residual body mass for any of the species (Table A.8Table A.8).

Table A.8. Results from the Pearsons correlations between wing length and residual body mass

Species	*N*	*DF*	*r*	*Strength*	*p*	*Direction*
Blue Tit	295273	295271	0	-	0.961	-
Coal Tit	55658	55655	0	-	0.928	-
Great Tit	177092	177090	0	-	0.965	-

A Spearman's correlation was conducted to evaluate the relationship between fat score and residual body mass. This was done on the subset of data for which fat scores were available. There was a weak significant positive relationship between fat score and residual body mass for all species in this subset. This shows that our chosen proxy for variation in fat reserves, indeed co-varies with fat scores and does not co-vary with absolute body size (Table A.9).

Table A.9. Results from the Spearmans correlations between fat scores and residual body mass

Species	***N***	***DF***	***r***	***Strength***	***p***	***Direction***
Blue Tit	295273	295271	0.28	weak	<.001	positive
Coal Tit	55658	55655	0.25	weak	<.001	positive
Great Tit	177092	177090	0.21	weak	<.001	positive

For all species, there is a stronger correlation between fat scores and residual body mass than between fat scores and absolute body mass. Therefore, the residual body mass will be used as a proxy for bird body condition in our further analysis.

A.4 Correlations between Covariates

Before fitting the models, correlations between all variables were assessed to determine which could be included together. A cutoff value of Pearsons $r = 0.4$ (Table A.10). *Day length* and *day in season* covary. Therefore, these variables were not included in the models as covariates. *Day length* and *temperature* are not correlated throughout the full season, but if only looking at the first half (October – December), there is a strong correlation between the two, which is biologically expected. We therefore opt not to include these two variables in the models together.

Table A.10. Pearsons correlations between covariates in the models. N = 594,156 and DF = 594,154 for all correlations. Any correlation with a Pearsons r above 0.1 was considered problematic for variables to be included in models together.

Variables	***r***	***Strength***	***P***	***Direction***
Proportion of day ~ day in season	0.01	Weak	0.001	Positive
Proportion of day ~ temperature	-0.04	Weak	<0.001	Negative
Proportion of day ~ day length	-0.02	Weak	<0.001	Negative
Day in season ~ temperature	-0.32	Weak	<0.001	Negative
Day in season ~ day length	**0.57**	Moderate	<0.001	Positive
Day length ~ temperature	0.08	Weak	<0.001	Positive
Day length ~ temperature (1st half)	**0.54**	Moderate	<0.001	Positive

A.5 Data Cleaning Process (Weather Data)

Weather records were retrieved from the Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations data. The dataset used to match with the data from the BTO contains daily minimum and maximum temperatures of weather stations across the UK between 1990 and 2021 (Met Office, 2024).

Data was cleaned so that the temperature, timestamp and location information was reliable. Specific steps are shown in Table A.11 (daily MIDAS data).

Table A.11. MIDAS daily temperature dataset step-by-step cleaning process. Columns indicate the step name, a description of what happened and the number of removed and remaining observations after the step took place.

#	*Step name*	*N removed*	*N remaining*	*Description*
1	Raw data	-	6,755,089	The records as these were retrieved from the CEDA archives (Met Office, 2024).
2	Remove incorrect versions	278,996	6,476,093	Weather observations marked with “version 1” by the MET Office, are reliable. Any observations where the version number was not “1”, were removed (Sunter, 2021).
3	Remove missing source ID	0	6,476,093	Check if all observations have a “source ID”, which is the unique identifier for weather stations, linked to them.
4	Remove missing temperatures	111,448	6,364,645	Remove any observations where the minimum temperature is not available.
5	Remove erroneous observation lengths	130	6,364,515	Observations in this data set are either logged over the last 12 or 24 hours. Any duration other than those can be considered erroneous.
6	Remove stations with unknown / incorrect location	186,563	6,177,852	A list of all weather stations in the UK between 1990 and the present time was retrieved from the MIDAS Land and Marine Surface Stations dataset metadata. This list was subsetted for stations inside the British Isles (excluding overseas territories). The weather station list includes a “Source ID” (unique station identifier) for each station, as well as the coordinates of the station. Any observations in the daily weather data that came from a weather station not on the station list were removed.
7	Remove 21.00 observations	2,155,708	4,022,144	The weather data contains 3 types of observations: - 09.00 - 12 hours - 09.00 – 24 hours - 21.00 – 12 hours To assure that each bird observation is matched to a night-time minimum, any observations logged at 21.00 were removed.
8	Remove duplicates for 12 and 24 hours	630,109	3,392,035	In cases where there is both a 12 hour and a 24 hour observation is available for the same day and weather station, duplicates were removed after calculating the average daily minimum. See the “Calculating night-time minima” section below for more detail.
9	Remove data for stations not in BTO data	217,232	3,174,803	After creating a distance matrix between each observation point in the BTO data and each of the weather stations, only data from weather stations that were in the top 3 closest stations within 50km of a BTO observations were retained (see A.7).

A.6 Calculating Night-time Minima (Weather Data)

For mu analysis, I am interested in the effects of season, temperature and species on the fat reserve of the birds. The weather data contains minimum and maximum temperatures across 12 or 24-hour periods. In total, there are 3 types of daily temperatures available in the weather dataset:

1. Minimum/maximum temperature across a 12-hour period from 21.00-09.00. These are logged under the 09.00 timestamp.
2. Minimum/maximum temperature across a 24-hour period from 09.00-09.00. These are logged under the 09.00 timestamp once the observation period has finished.
3. Minimum/maximum temperature across a 12-hour period from 09.00-21.00. These are logged under the 21.00 timestamp

I focussed on the daily minima, which occur during night-time, close to sunrise. This means that any minimum temperature recorded in the 12-hour observation period between 09.00-21.00 can be removed (Step 7 in Table A.11). In some cases, a weather station has both a 12 and a 24-hour record available for the same day, logged at 09.00. Upon further inspection, small differences (up to 1 degree) were seen between the 12 and 24-hour minimum air temperature observations, even though these should be the same. This is likely due to the type of measurement device that was used (Sunter, 2021). I used the mean minimum air temperature taken across the 12 and 24-hour observation if both were available. If only one of the two was available, the minimum air temperature of the single observation was used. Any duplicates were removed (Step 8 in Table A.11).

A.7 Matching the BTO Data with Weather Data

From the cleaned BTO data (after step 17 in Table A.1), I extracted a list with the longitude and latitude of each of the 5140 unique observation locations. The same was done from the cleaned weather data, resulting in a total of 827 weather station locations.

A distance matrix was generated with distances between each of the BTO locations and each of the weather station locations using the *geosphere* package (Hijmans et al., 2022). Using this matrix, each BTO observation was assigned a 1st, 2nd and 3rd closest weather station ID. BTO observations that did not have any weather stations within a 50 km radius were removed at this point.

Then, for each observation in the BTO data, the weather records from the 1st , 2nd and 3rd closest weather stations were pulled. Weather observations are logged at 09:00 in the morning, covering either a 12-hour or 24-hour period. As a result, the minimum temperature recorded at 09:00

typically occurs just before sunrise on the same day. To avoid differences in effect size based on how close in time the bird was captured to this minimum, the weather record for the day of capture was excluded from the analysis (Gosler, 2002). For example, if a bird was caught on Friday, it would be matched with the minimum temperatures from Monday night, Tuesday night, and Wednesday night. If data was not available for one or more of the days from the closest weather station, data from the 2nd closest weather station was used for the remaining days. If this was also not available, data from the 3rd closest weather station was used. This assures that the data used to calculate the 3-day average minimum was retrieved from the closest weather station possible. The records for the 3 days were checked to make sure no weather station further than 50km away was used, before calculating the 3-day average minimum. If more than 1 out of 3 data points was missing, the BTO observation for this location and time was removed. This process resulted in a final number of 297,078 observations, all including the average minimum temperature of the 3 nights ahead of the day the bird was caught.

A.8 Modelling Details

A.8.1 Model 1

Table A.12. Model 1 - GAM: residual body mass morning ~ s(day in season, k = 7), gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.02	0.00	-92.11	< 0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	5.96	6.00	180.35	< 0.001

A.1.1 Model 2

Table A.13. Model 2 - GAM: residual BM ~ s(day in season , k = 7), gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	0.05	0.00	106.45	< 0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	5.55	5.92	64.49	< 0.001

A.1.2 Model 3

Table A.14. Model 3 - GAM: residual BM ~ s(day in season, k = 7), gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.00	0.00	-0.00	1
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	5.98	6.00	1,190.57	< 0.001

A.1.3 Model 4

Table A.15. Model 4 – GAM: residual BM ~ s(day in season, k = 7) + s(proportion of day, k = 4), gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.00	0.00	-0.00	1
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	6.00	6.00	1,305.60	< 0.001
	s(proportion of day)	1.94	1.94	22,009.78	<0.001

A.1.4 Model 5

Table A.16. Model 5 – GAM: residual body mass– s(day in season, k = 7) + s(proportion of day, k = 4) + ti(day within year, proportion of day, k =(7,4)), gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.00	0.00	0.54	0.59
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	5.99	6.00	1,307.42	< 0.001
	s(proportion of day)	1.99	2.00	21,777.04	<0.001
	ti(proportion of day, day in season)	9.04	10.53	34.12	<0.001

A.1.5 Model 4

Table A.17. Model 4 linear – GAM: residual BM ~ s(day within year, k = 7) + proportion of day, gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.032	0.00	-179,21	<0.001
	Proportion of day	0.09	0.00	209.84	<0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	6.00	6.00	1,328.10	< 0.001

A.1.6 Model 5

Table A.18. Model 5 linear – GAM: residual body mass – s(day in season, k = 7) + proportion of day + ti(day in season, proportion of day, k =(7,5), bs = ("cr", "tp"), m = (2,1)), gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.032	0.00	-178.34	<0.001
	Proportion of day	0.09	0.00	208.89	<0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	5.97	6.00	1,335.51	< 0.001
	ti(day in season, proportion of day)	16.34	24.00	15.16	<0.001

A.1.7 Model 6

Table A.19. Model 6 – GAM: residual body mass – s(day in season, k = 7) + s(proportion of day, k = 4) + ti(day within year, proportion of day, k =(7,4))+ ti(day within year, by = species, k = 7) + ti (proportion of day, by = species, k = 4) + ti(proportion of day, day within season, by = species, k = (4,7)), gamma = 1.4

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.00	0.00	-2.36	0.018
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day in season)	5.79	5.82	8.97	< 0.001
	s(proportion of day)	1.93	1.96	8,652.75	<0.001
	ti(proportion of day, day in season)	4.64	6.04	13.69	<0.001
	ti(day in season):Blue tit	1.94	2.47	0.51	0.571
	ti(day in season):Coal tit	5.67	5.67	7.07	<0.001
	ti(day in season):Great tit	5.67	5.67	32.95	<0.001
	ti(proportion of day):Blue tit	0.67	0.67	453.04	<0.001
	ti(proportion of day):Coal tit	1.66	1.67	27.72	<0.001
	ti(proportion of day):Great tit	1.24	1.48	84.37	<0.001
	ti(proportion of day, day in season):Blue tit	9.08	10.43	6.41	<0.001
	ti(proportion of day, day in season):Coal tit	5.62	7.33	3.31	0.002
	ti(proportion of day, day in season):Great tit	0.75	0.75	0.02	0.906

A.1.8 Model 7

Table A.20. Residual body mass ~ s(temperature, k = 4) + s(proportion of day, k = 4) + ti(temperature, proportion of day, k = (4,4)) + ti(temperature, species, k = 4) + ti(proportion of day, species, k = 4) + ti(proportion of day, temperature, species, = (4,4))

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.00	0.00	-2.00	0.046
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(temperature)	1.78	1.89	465.19	< 0.001
	s(proportion of day)	1.88	1.96	8,613.04	<0.001
	ti(proportion of day, temperature)	2.36	2.84	10.465	<0.001
	ti(temperature):Blue tit	1.67	1.67	18.08	<0.001
	ti(temperature):Coal tit	0.77	0.80	10.30	0.004
	ti(temperature):Great tit	1.67	1.67	72.62	<0.001
	ti(proportion of day):Blue tit	0.67	0.67	449.97	<0.001
	ti(proportion of day):Coal tit	1.61	1.67	37.05	<0.001
	ti(proportion of day):Great tit	1.33	1.55	53.71	<0.001
	ti(proportion of day, day in season):Blue tit	1.04	1.20	4.51	0.018
	ti(proportion of day, day in season):Coal tit	1.45	1.65	3.70	0.025
	ti(proportion of day, day in season):Great tit	1.76	2.12	8.62	<0.001

A.1.9 Model 8

Table A.21. Residual body mass ~ s(day length, k = 4) + s(proportion of day, k = 4) + ti(day length, proportion of day, k = (4,4)) + ti(day length, species, k = 4) + ti(proportion of day, species, k =4) + ti(proportion of day, day length, species, k = (4,4)

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.00	0.00	-0.66	0.50
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day length)	1.87	1.93	2,580.41	<0.001
	s(proportion of day)	1.72	1.90	7,726.36	<0.001
	ti(proportion of day, day length)	3.50	3.70	3.46	0.005
	ti(day length):Blue tit	1.38	1.55	74.93	<0.001
	ti(day length):Coal tit	0.68	0.68	54.58	<0.001
	ti(day length):Great tit	1.55	1.64	10.73	0.009
	ti(proportion of day):Blue tit	0.67	0.67	496.41	<0.001
	ti(proportion of day):Coal tit	1.64	1.67	34.37	<0.001
	ti(proportion of day):Great tit	1.45	1.61	84.38	<0.001
	ti(proportion of day, temperature):Blue tit	2.09	2.46	5.08	0.006
	ti(proportion of day, temperature):Coal tit	1.67	1.74	4.68	0.008
	ti(proportion of day, temperature):Great tit	0.75	0.75	5.11	0.050

B. Chapter 3. Using Citizen Science to Understand The Drivers Of Hoarding Motivation in Titmice

B.1 Volunteer Protocol

The following pages (15 – 22) include the volunteer protocols as these were used in the data collection seasons 20022/2023 and 2023/2024. This guideline is made for volunteers in the UK. Guidelines for the USA and Canada include the same information but have different wording and other species. It starts on the next page.

VOLUNTEER GUIDELINES

Thank you for signing up to be a volunteer on our study about foraging behaviour in tits. We are excited to get your help, so let's get started!

This document will guide you through everything you need to know to help us out and observe foraging behaviour at the feeders in your garden. Make sure to check out the detailed instructions on how to record your observations in the step-by-step guide below.

All documents and online forms can also be found on our website. Please contact us if you have any questions at caching.birds@newcastle.ac.uk. We are happy to help!

The Research Project

Surviving the winter can be a big challenge for birds, especially ones that remain at northern latitudes during winter. A lot of birds, such as several tit species, make use of garden feeders. They either eat the food directly from the feeders or hide the food in the surroundings to save it for later. This is called 'food hoarding' or 'food caching'. You may have seen this first-hand, where some tits move items from a food source to cache it in some moss, a tree or even a flowerpot. If you'd like to see an example of a coal tit caching, check this video. At 02.10 minutes, the coal tit picks up a seed and hides it on the branch nearby.

We are part of a research group at Newcastle University investigating how these birds decide when to eat food from feeders or when to hoard it. We do this by developing mathematical models, which we then test against reality with observational data from wild birds. This is where you, as one of our volunteers, are of key importance! The information that you collect, can help us answer important questions about how these birds survive the winter.

What will you be doing?

What you will be observing:

As part of our volunteer team, you will be observing tit behaviour. We'd like to know what species visit the feeder(s) in your garden, if they eat the food they find, or look for places to hoard it, what food they are attracted by and when they perform these behaviours. A pair of binoculars might come in handy! You can easily submit your observations with the online data submission form or our mobile application (see below). Offline data sheets are available if you'd prefer to write down your observations on paper.

Which species to observe:

For this study, we are interested in tit species. These include hoarding species such as coal tits, marsh tits, willow tits and crested tits but also non-hoarding species such as blue tits and great tits. For now, we will not need observations on other species that might visit your feeder. For more information on which species to observe, please check 'Bird ID information' below.

How much time you will spend:

You can make as many observations as is comfortable for you. A minimum of 1 hour per week would be great (this does not have to be all at the same time), but all observations, whether it is once a month or every day, are welcome!

Step-by-step guide

Step 1: start of the session

At the start of your session, you watch your feeder and wait until a suitable bird turns up. If a bird picks up a seed from the feeder, your first observation can start!

Step 2: observation

Once the bird picks up a seed from the feeder, it is important to watch its behaviour closely and record what happens. We are interested whether the bird eats the food or searches for a hiding spot. If both happen, we would like to know the order in which they occur.

On the data form, you can select one of the following behaviours:

1. **Disappear:** If the bird picks up a seed and disappears out of sight or drops the food. For example, when a bird flies into a bush with the food it collected and you can no longer see it.
2. **Eat:** If the bird eats the food item it picked up from the feeder. The bird will have a food item under one or both feet, whilst it is sitting on a perch or other substrate. The bird will be pecking at the food. If you are looking at the bird from a distance and cannot see the food, this will look like the bird is pecking at its feet. To see what this behaviour looks like, check out this video.
3. **Search:** If the bird picks up the food item and searches for a place to hide it. The bird will be moving across branches and other substrates holding a seed in its beak. Even if the bird does not successfully hide the food (or at least you don't observe it), please record the behaviour as 'Search'. If the bird does succeed to hoard the food, you can still log this as 'Search', since this is part of the behaviour. Check out this video to see what this behaviour looks like. From 01:00-01.10 minutes you can see the bird searching for a place to hide the food. At 01.11 the food item is hoarded.
4. **Eat then search:** If the bird first eats some of the food item and then looks for a place to hide it, please select this option.
5. **Search then eat:** If the bird first looks for a place to hide the food and then starts to eat it, please select this option.

Step 3: end observation

An observation of a bird can end in 4 ways:

1. The bird moves out of sight
2. The bird stays in sight but starts doing something else, not related to the food
3. The bird returns to the feeder and picks up a new seed (this means you start a new observation)
4. The bird shows a third behaviour (for example: search-eat-search). We are not interested in the third behaviour and your observation can end here.

Once your observation has ended you can fill in the other details and move on to the next one or end your session and submit your data.

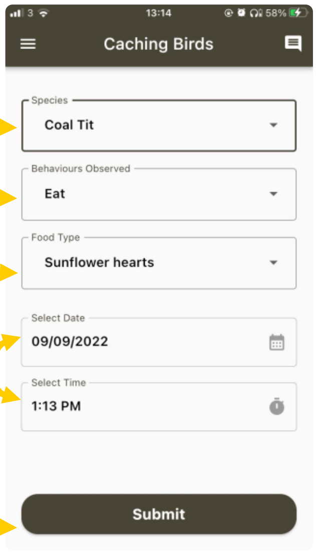
Step 4: fill in the details

Once the observation has ended, be sure to note down the time, the species you observed and (if you know it) what food the bird interacted with. There are 3 options to do this:

- **Data sheet**: On your printed data sheet, you can just circle the relevant options and write down the other details
- **Online form**: If you are submitting your data directly online, you'll notice drop-down boxes for the species/feed and dedicated fields to put in the time and date
- **Mobile app:** If you use our mobile application, you can record your observations as you go. The app is really easy to use and can be downloaded here (or search 'caching birds' in your App Store/Play Store):
    - For iOS
    - For Android

Once all the fields have been filled in, you are ready for your next observation (go back to step 2), or you can end your session. You are free to do as many sessions as you'd like per week. Here are examples of what our mobile App and the online form look like:

Mobile **Online form**



Species: Coal Tit

Behaviours Observed: Eat

Food Type: Sunflower hearts

Select Date: 09/09/2022

Select Time: 1:13 PM

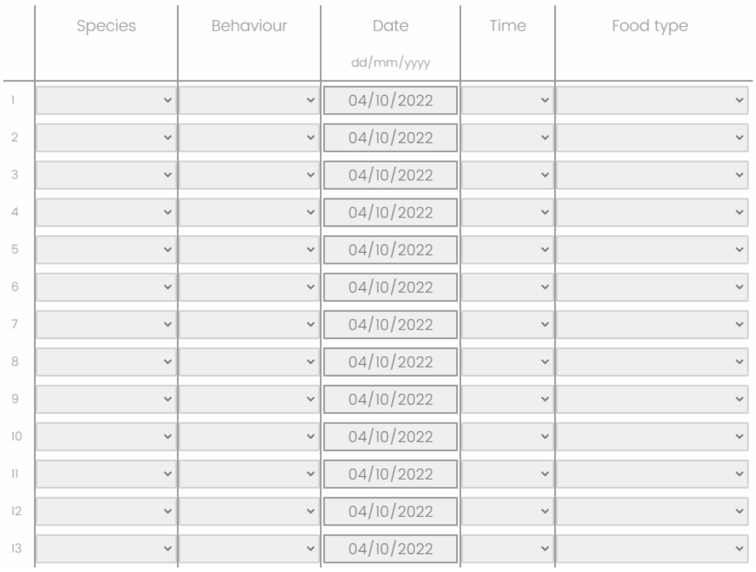
Select your species

Select the behaviour

And select your food

Date, time and location get recorded

Click 'submit' and you're done!



	Species	Behaviour	Date dd/mm/yyyy	Time	Food type
1			04/10/2022		
2			04/10/2022		
3			04/10/2022		
4			04/10/2022		
5			04/10/2022		
6			04/10/2022		
7			04/10/2022		
8			04/10/2022		
9			04/10/2022		
10			04/10/2022		
11			04/10/2022		
12			04/10/2022		
13			04/10/2022		

Step 5: submit your data

Once your session is finished and your data is collected, you can submit this to us. The online form also contains space for suggestions and feedback, so we can learn from your experience and hear about what did or didn't work.

If you have collected the data on the printed-out datasheets, you can go ahead and copy this into the online form. You can find the online form here. If you have any issues with the online form, you can contact us at: caching.birds@newcastle.ac.uk

If you collected your data with our mobile application, all is done. Your data will be submitted to us automatically!

Examples of observations

Example 1

Scenario: A Coal tit approaches your feeder that contains whole sunflower seeds and picks up a seed. The bird starts to move around on branches and looks for a place to hide its food. When it fails, it sits on a branch with the food between its feet and starts to eat it. After 10 seconds the bird flies away.

How to record this: You can record the behaviours by choosing an option from the drop-down list. In this case, the bird first searched for a place to hide the food and then proceeded to eat. You can choose the option 'Search then eat' from the menu. Species, date, time, and food type can all be chosen from dropdown lists

This will look like:

	Species	Behaviour	Date dd/mm/yyyy	Time	Food type
1	Coal tit	Search then eat	20/07/2022	01:30 PM	Whole sunflower seeds

Example 2

Scenario: A Marsh tit approaches your feeder that contains a mixture of seeds and picks up a seed. After moving to a branch, it gets startled and flies off into a bush. You lose sight of the bird.

How to record this: The observation started once the bird picked up the seed. However, the bird disappeared out of sight before another behaviour was seen. You can choose the option 'disappear' from the menu. Species, date, time, and food type can all be selected.

This will look like:

	Species	Behaviour	Date dd/mm/yyyy	Time	Food type
1	Marsh/Willow tit	Disappear	06/08/2022	7:30 AM	Mixed seeds

Example 3

Scenario: A Willow tit goes to your feeder that contains safflower seed and picks it up. After moving to a branch, it eats the seed. After it has done so, it returns to the feeder to pick up another seed. The bird then hoards the second seed and flies away.

How to record this: In this case, the bird ate the seed straight away, so you can choose ‘eat’. After this the bird returned to the feeder, which ends the observation. The second observation can also be logged, this would be a single ‘Search’. Note that this is a successful hoarding attempt and not just ‘searching’, but it does still get logged as ‘search’. Species, date, time, and food type can all be chosen from dropdown lists. ‘Safflower seed’ is not one of the options, you can select ‘other’.

This will look like:

	Species	Behaviour	Date dd/mm/yyyy	Time	Food type
1	Marsh/Willow tit	Eat	11/09/2022	10:00 AM	Other
2	Marsh/Willow tit	Search	11/09/2022	10:00 AM	Other

Example 4

Scenario: A Blue tit approaches your feeder that contains peanuts and picks up a food item. The bird sits on a branch with the food between its feet and starts to eat it. The bird then flies away.

How to record this: In this case, the bird ate the food straight away. You can choose the option ‘Eat’ from the menu. Species, date, time, and food type can all be chosen from dropdown lists.

This will look like:

	Species	Behaviour	Date dd/mm/yyyy	Time	Food type
1	Blue tit	Eat	11/09/2022	09:30 PM	Peanuts

Bird ID Information

These are the species that are included in our study. Some of them might visit the feeder in your yard. If you'd like to see some images and read some information about the different species, please click on the names next to the pictures below. To check which species occur in your area, you can use the Merlin bird app (download onto your phone or tablet here). Use the 'explore birds' function, fill in your location, and check which tit species are likely to occur in your area.

Coal tit

Marsh tit/
Willow tit

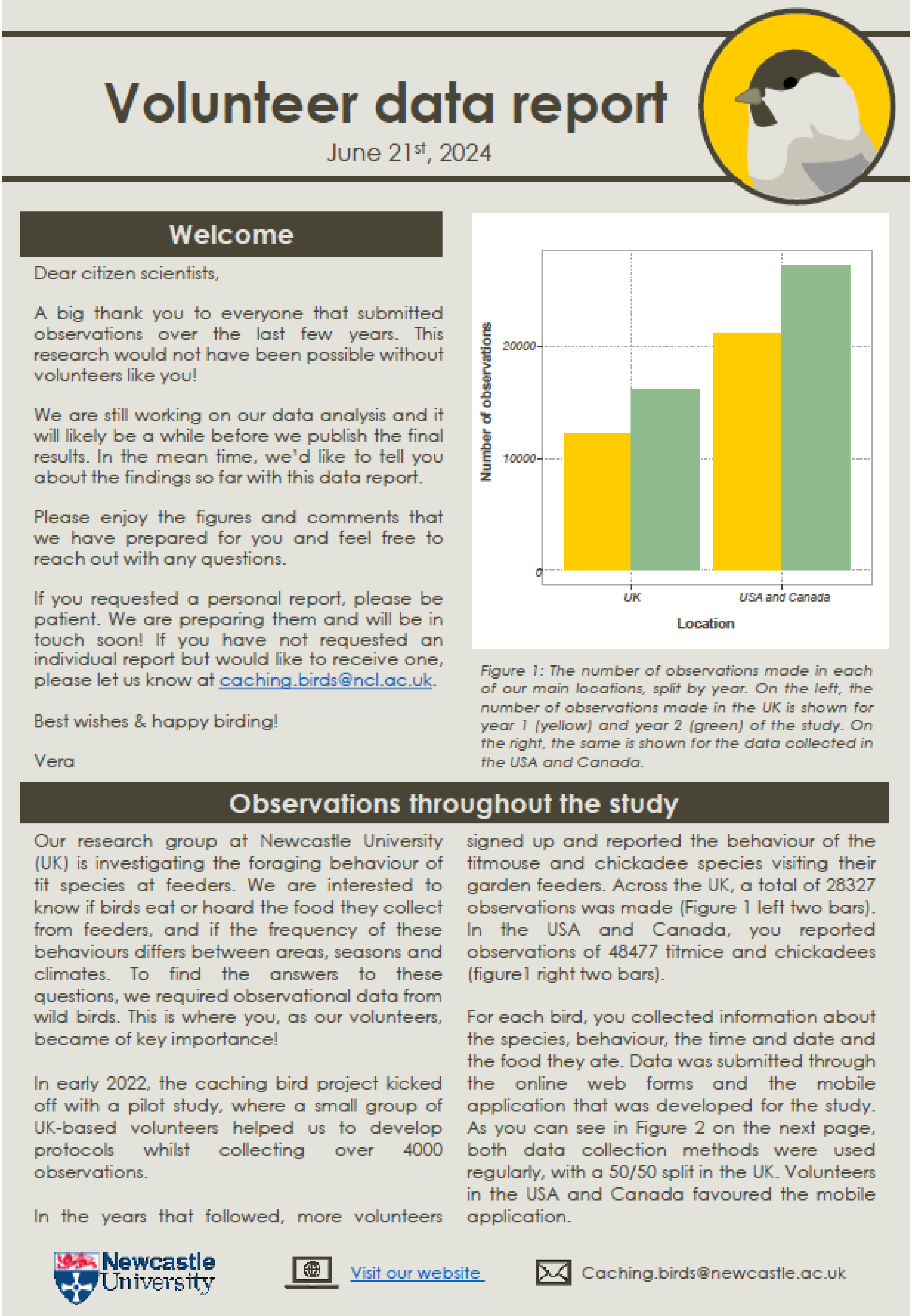
Great tit

Blue tit

Crested tit

B.2 Final Volunteer Data Report

The volunteer data report as distributed in June 2024, after the final data collection season had ended.



Volunteer data report

June 21st, 2024

Welcome

Dear citizen scientists,

A big thank you to everyone that submitted observations over the last few years. This research would not have been possible without volunteers like you!

We are still working on our data analysis and it will likely be a while before we publish the final results. In the mean time, we'd like to tell you about the findings so far with this data report.

Please enjoy the figures and comments that we have prepared for you and feel free to reach out with any questions.

If you requested a personal report, please be patient. We are preparing them and will be in touch soon! If you have not requested an individual report but would like to receive one, please let us know at caching.birds@ncl.ac.uk.

Best wishes & happy birding!

Vera

Figure 1: The number of observations made in each of our main locations, split by year. On the left, the number of observations made in the UK is shown for year 1 (yellow) and year 2 (green) of the study. On the right, the same is shown for the data collected in the USA and Canada.

Observations throughout the study

Our research group at Newcastle University (UK) is investigating the foraging behaviour of tit species at feeders. We are interested to know if birds eat or hoard the food they collect from feeders, and if the frequency of these behaviours differs between areas, seasons and climates. To find the answers to these questions, we required observational data from wild birds. This is where you, as our volunteers, became of key importance!

In early 2022, the caching bird project kicked off with a pilot study, where a small group of UK-based volunteers helped us to develop protocols whilst collecting over 4000 observations.

In the years that followed, more volunteers signed up and reported the behaviour of the titmouse and chickadee species visiting their garden feeders. Across the UK, a total of 28327 observations was made (Figure 1 left two bars). In the USA and Canada, you reported observations of 48477 titmice and chickadees (figure1 right two bars).

For each bird, you collected information about the species, behaviour, the time and date and the food they ate. Data was submitted through the online web forms and the mobile application that was developed for the study. As you can see in Figure 2 on the next page, both data collection methods were used regularly, with a 50/50 split in the UK. Volunteers in the USA and Canada favoured the mobile application.

Newcastle University

Visit our website

Caching.birds@newcastle.ac.uk

Species observed

In the UK, we studied the Blue tit, Coal tit, Crested tit, Great tit, Marsh tit and Willow tit. We grouped Marsh and Willow tits together for our analysis, because it is tricky to tell them apart from a distance (Figure 3). The Blue tit and Great tit are non-hoarding species, which means that we can use them as a control in our analysis (more about this later!).

In the USA and Canada, different species of titmice are present. The full list of chickadees and titmice included in the study is shown in Figure 4. Again, we grouped some of the species that live in the same area and look almost identical (Figure 4).

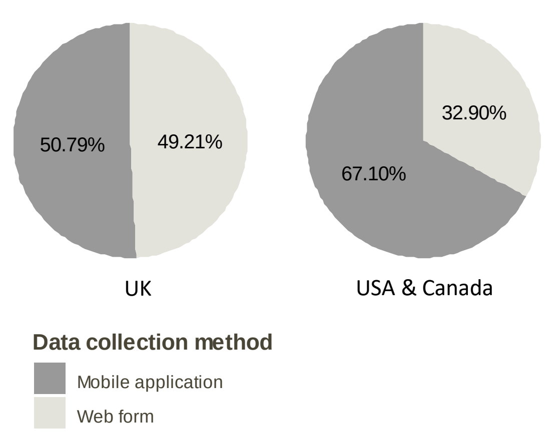
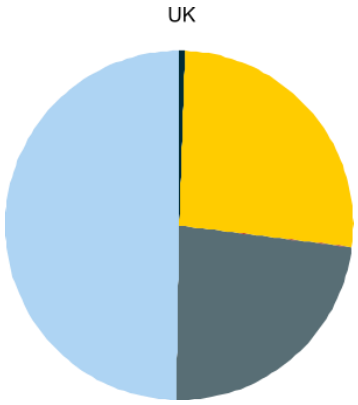
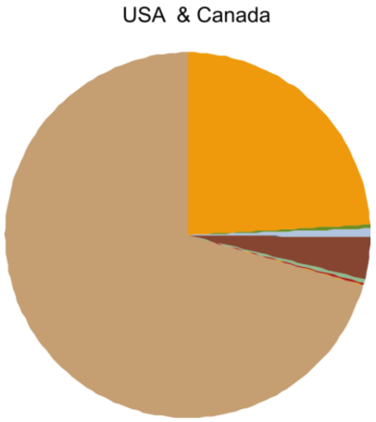


Figure 2: The percentage of observations logged with the mobile application and the online data submission form, split per location.



	Species	Frequency	%
■	Blue tit	14,092	49.75
■	Coal tit	6,593	23.27
■	Crested tit	7	0.02
■	Great tit	7,486	26.43
■	Marsh/Willow tit	149	0.53

Figure 3: The species included in our study for the United Kingdom. The pie chart includes the percentage of observations for each species, as indicated in the table on the right. Under "Frequency" the absolute number of observations for each species is listed.



	Species	Frequency	%
■	Black-capped/Carolina chickadee	34,186	70.52
■	Black-crested titmouse	30	0.06
■	Boreal Chickadee	89	0.18
■	Bridled Titmouse	171	0.35
■	Chestnut-backed chickadee	1,784	3.68
■	Grey-headed chickadee	9	0.02
■	Juniper/Oak titmouse	375	0.77
■	Mexican Chickadee	1	0.002
■	Mountain Chickadee	163	0.34
■	Tufted Titmouse	11,669	24.07

Figure 4: The species included in our study for the United States of America and Canada. The pie chart includes the percentage of observations for each species, as indicated in the table on the right. Under "Frequency" the absolute number of observations for each species is listed.

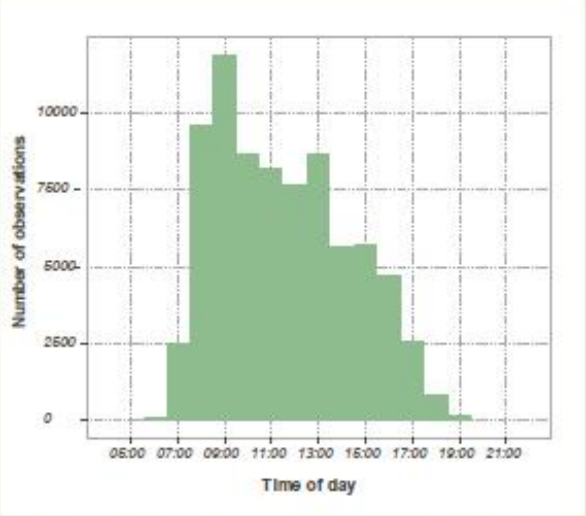


Figure 5: The number of observations at each time of the day, shown for the entire data set (UK, USA and Canada combined). Observations are grouped in 1-hour slots so that the bar for "09:00" includes observations between 09.00-10.00, the bar for "11:00" includes observations between 11.00-12.00, etc.

Behaviours reported

Figure 6 shows the behaviours that were reported for the non-hoarding and hoarding species in the UK, as well as all birds in the USA and Canada. Note that birds for the latter location have not been split up, because most of the species are known to hoard. For this pie chart, we left out Chestnut-backed chickadees as there are no known records of these birds hoarding in the wild preceding this study. All other species present in the USA and Canada are included.

Most non-hoarding birds were seen to eat seeds (or other foods) they retrieved from feeders (65%). For hoarding species in the UK, only 32% of birds were reported to eat the food they found, with a large majority of birds disappearing (58%). 11% of hoarding birds in the UK showed hoarding-related behaviour, were they were observed either searching for a hiding spot, or actively hoarding items (yellow shades in Figure 6). In the USA and Canada, hoarding birds were less likely to disappear (40%), but showed hoarding behaviours slightly more often (15%).

On the next page, we will further investigate if these patterns change throughout the year. Do hoarding birds increase their hoarding frequency in winter, even if they have access to feeders?

Time of observations

Volunteers watched the birds in their gardens at all times of day . Figure 5 shows at which times in the day volunteers reported birds visiting their garden feeders. As you can see, most observations were made in the morning, with a peak around 09:00. The number of observations per hour slowly decreases throughout the day, with most observations logged before 20.00. You can even see a small peak around lunch time!

A lovely shot of a black-capped chickadee in early spring, sent in by Shirley Rushforth Guinn.

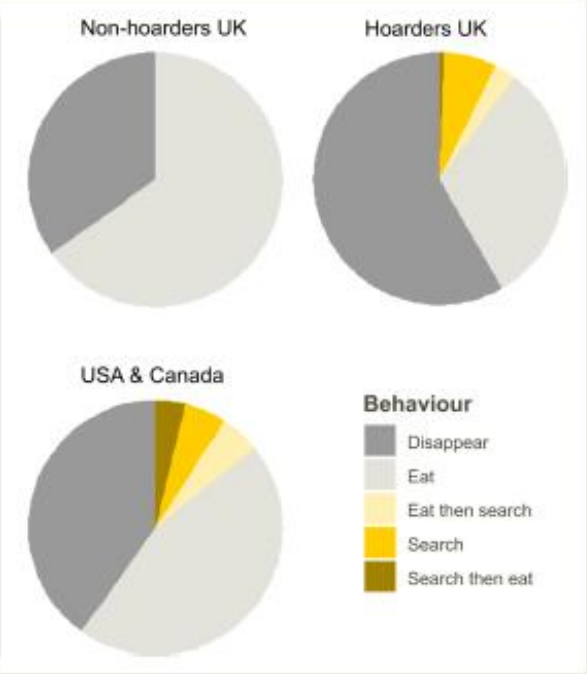


Figure 6: Behaviours observed in 3 groups of birds. Top left: non-hoarding birds in the UK. Top right: hoarding species in the UK. Bottom right: all chickadee and titmouse species in the USA and Canada, Chestnut-backed chickadees excluded.

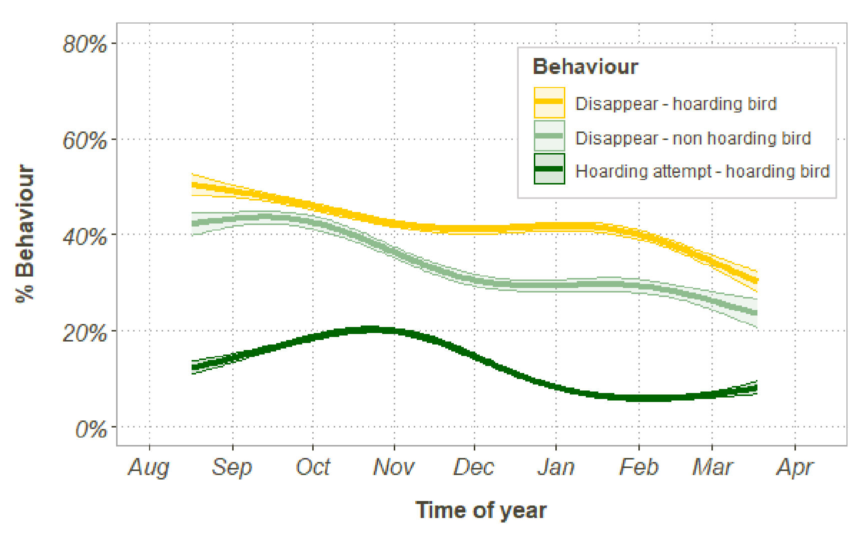


Figure 7: Percentage of observed behaviours throughout the year. Top line: the percentage of hoarding birds that disappear. Middle line: percentage of non-hoarding birds that disappear. Bottom line: percentage of hoarding birds that engage in hoarding behaviour. The opaque area around the lines marks the 95% Confidence Interval. This graph is for all of the data, including birds from the UK, the USA and Canada.

Hoarding over time

When we analyse the prevalence of hoarding-related behaviours throughout the year, a pattern emerges. Throughout September, October and November, the percentage of birds that performs hoarding related behaviours increases (bottom line Figure 7). This peaks at the start of November, with almost 20% of the observations in hoarding species displaying hoarding related ("search", "search then eat" and "eat then search" in the study). The percentage of birds hoarding declines gradually during winter, with a small increase in spring. These results are similar to field observations of titmice, where other researchers have shown a peak in hoarding behaviour during the autumn months.

But what about the disappearing birds? Hoarding birds are more likely to disappear after visiting a feeder than non-hoarding birds. This could be because they are subordinate to other species, such as the coal tits in the UK, that are subordinate to the larger great tits that visit the same feeders. Subordinate birds are more likely to fly away from the feeder before eating or hoarding their food. In addition, hoarding birds might disappear because they are looking for cache sites away from the feeder.

The top 2 lines in Figure 7 show that disappearing rates go down throughout winter for both the hoarding (yellow) and non-hoarding species (light green). One possible explanation for this, is that when the days get shorter and leaves start falling, birds become easier to observe. However, disappearance rates decline more quickly for non-hoarding birds than for hoarding birds. In the figure, you can see this as the top 2 lines moving away from each other in late November and December. This difference in disappearing rate between hoarders and non hoarders suggests that at least some of the disappearing birds are searching for cache sites, and that the percentage of birds hoarding might be larger than what was directly observed by our volunteers.

In conclusion, a peak in hoarding behaviour can be observed in autumn, even when the birds have reliable food sources available to them, such as feeders. The most likely reason for the drop of hoarding behaviour in winter would be the shortening of days. Birds need to eat more food to survive the long and cold winter nights and might just not have enough time to hoard.

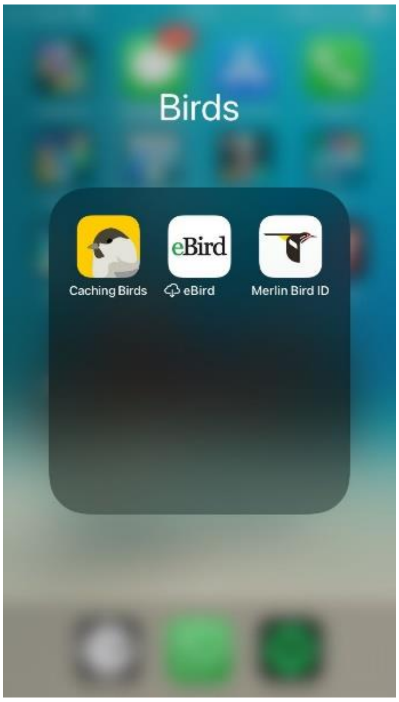
Thank you!

Finally, one last thank you to all of our volunteers! You have collected an amazing amount of data and we are looking forward to analysing the results further. If you have any questions, comments or concerns about the study, or would like your personal information to be removed, please get in touch at: caching.birds@newcastle.ac.uk

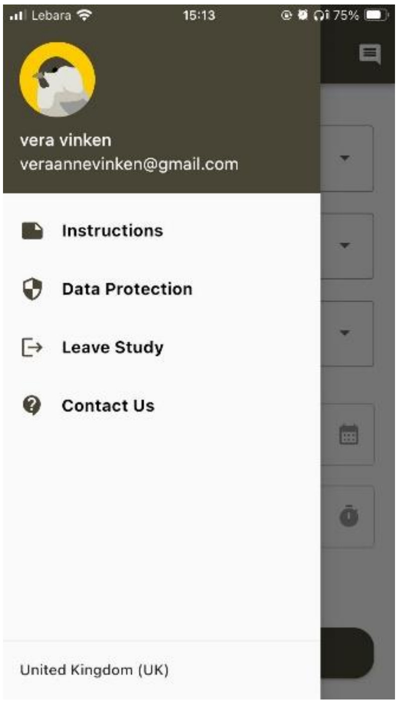
B.3 Mobile application details

Overview of the mobile application that was used by volunteers for data collection throughout 2022-2024: 1) Thumbnail, 2) App contents, 3) Instructions (1/2), 4) Instructions (2/2), 5) Data submission and 6) Feedback.

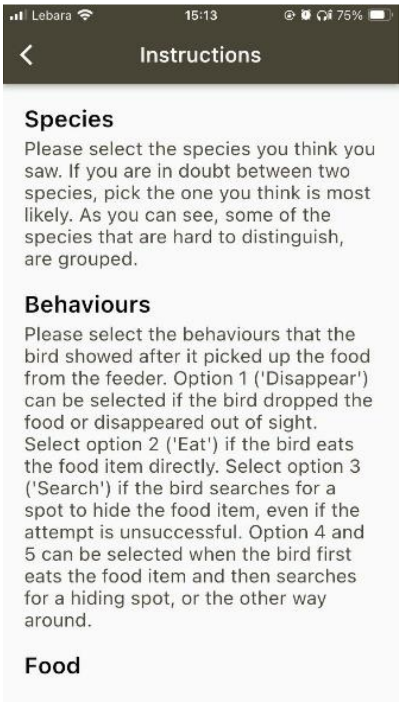
a)



b)



c)



Species

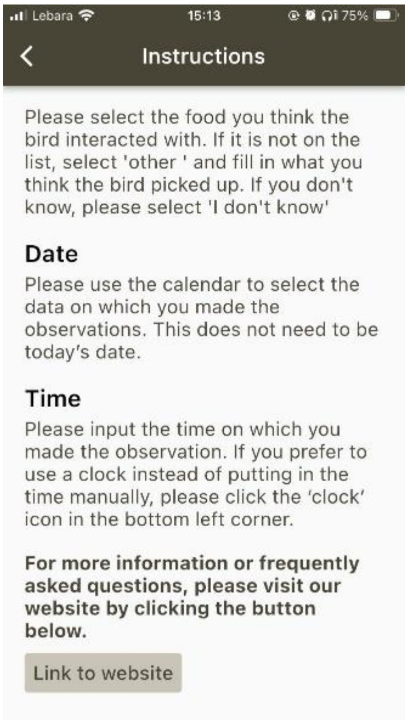
Please select the species you think you saw. If you are in doubt between two species, pick the one you think is most likely. As you can see, some of the species that are hard to distinguish, are grouped.

Behaviours

Please select the behaviours that the bird showed after it picked up the food from the feeder. Option 1 ('Disappear') can be selected if the bird dropped the food or disappeared out of sight. Select option 2 ('Eat') if the bird eats the food item directly. Select option 3 ('Search') if the bird searches for a spot to hide the food item, even if the attempt is unsuccessful. Option 4 and 5 can be selected when the bird first eats the food item and then searches for a hiding spot, or the other way around.

Food

d)



Please select the food you think the bird interacted with. If it is not on the list, select 'other ' and fill in what you think the bird picked up. If you don't know, please select 'I don't know'

Date

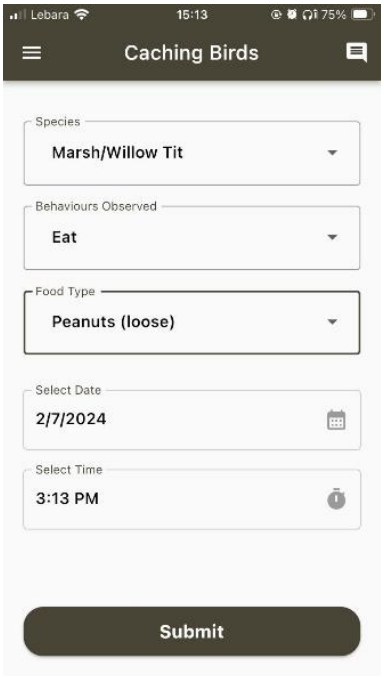
Please use the calendar to select the data on which you made the observations. This does not need to be today's date.

Time

Please input the time on which you made the observation. If you prefer to use a clock instead of putting in the time manually, please click the 'clock' icon in the bottom left corner.

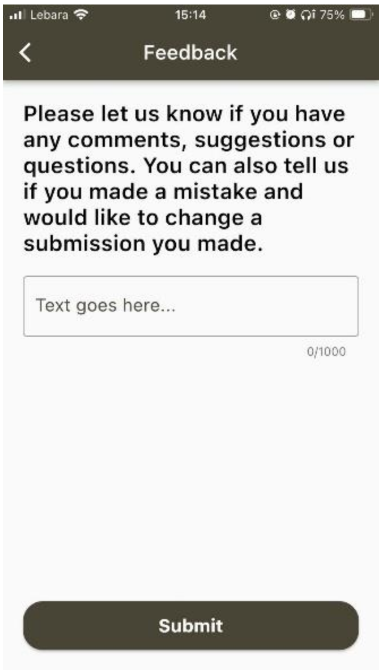
For more information or frequently asked questions, please visit our website by clicking the button below.

e)



Species: Marsh/Willow Tit
Behaviours Observed: Eat
Food Type: Peanuts (loose)
Select Date: 2/7/2024
Select Time: 3:13 PM

f)



Please let us know if you have any comments, suggestions or questions. You can also tell us if you made a mistake and would like to change a submission you made.

B.4 Data Cleaning and Manipulation

The data was collected across two periods between August 2022 – May 2023 and August 2023 and May 2024. A total of 616 volunteers signed up, of which 396 participated actively in the study. 88 volunteers participated from the UK and 308 volunteers from the United States of America and Canada.

A total of 47,927 observations were made before data cleaning. The table below shows the steps that were taken through the data cleaning and manipulation process.

Table B.1. Cleaning of the data collected from the mobile application

#	*Step name*	*N removed*	*N remaining*	*Description*
1	Raw data	0	47,927	Data as retrieved from the Firebase database, transformed from JSON to CSV format.
2	Remove emails not registered	7,031	40,896	Observations made by volunteers using an email address that is not on the registration list were removed.
3	Remove missing data	0	40,896	Observations where the behaviour, time of day, email address and/or species is missing, were removed.

Table B.2. Cleaning of the data collected with the web forms

#	Step name	N removed	N remaining	Description
1	Raw data	0	30,935	Data as retrieved from Qualtrics in csv format. Note that observations from empty rows in the data form, or with missing information are not included here.
2	Remove without location/registration	1	30,934	Remove observations that cannot be linked to a registered volunteer, and therefore do not have a location linked to them.
3	Remove faulty dates	0	30,934	Observations were checked to see if they were registered under the correct season. Observations that were logged exactly 1 year after they were submitted were corrected. Other instances were removed.

Table B.3. Cleaning of merged data from the web form and the mobile application

#	Step name	N removed	N remaining	Description
1	Merged data	0	71,830	Merged data from the mobile application and the online data form. See **Error! Reference source not found.** and Table B.2
2	Remove incorrect locations	0	71,830	Checked on the map if any locations appeared outside the UK, USA or Canada.
3	Remove outside collection season	3,402	68,428	Data collection seasons were set between August 15th and March 31st, in order to assure good data density across both years of data collection. Observations outside these timeframes were removed.
4	Remove volunteers with >1% data AND hoarding >30%	16,548	51,880	All volunteers who contributed to more than 1% of the data points were flagged and further inspected. This was done to make sure that volunteers with large numbers of observations were not affecting the dataset too much. Observations made by volunteers that observed more than 30% hoarding behaviours, which is three times the amount observed in the general data set (at the end of step 3), were removed.
5	Remove volunteers with incorrect hoarding species AND hoarding >30%	705	51,175	Volunteers that reported non-hoarding species (Great tit and Blue tit) to hoard, were flagged and further inspected. As in step 4, if volunteers observed more than 30% hoarding behaviours, their observations were removed.
6	Remove incorrect hoarding species	234	50,941	Observations made of non-hoarding species (Great tit and Blue tit) reported to hoard, were removed. These are made by volunteers who

				otherwise have a “normal” behaviour distribution (as tested under step 5).
7	Remove volunteers with “odd” food and hoarding >30%	38	50,897	Volunteers who reported “odd” food types in the column for “food type”, were flagged. These were items such as “water” or “pizza”. If a volunteer was flagged, their observations were further inspected. As in step 4, if volunteers observed more than 30% hoarding behaviours, their observations were removed.
8	Remove “odd” food observations	6	50,897	Remove observations of “odd” food types. These were items such as “water” or “pizza”. Observations from volunteers not flagged under step 7.
9	Remove species with n <3000	2,444	48,453	Removed any species with fewer than 3000 observations.

B.5 Descriptive Information

After data filtering, the final number of observations was 48,453. 15479 observations were made in the United Kingdom and 32,974 were made in the United States of America and Canada. Of the total, 17,549 observations were made using the web form and 30,904 using the mobile application. Table B.4 shows the number of birds observed for each species.

Table B.4. Number of birds observed of each species.

Species	***N***
Black-capped/Carolina chickadee	22,095
Blue tit	7,888
Coal tit	3,230
Great tit	4,461
Tufted titmouse	10,879

Figure B.1 shows the percentages of each of the behaviours observed across the different species. The numbers above the pie charts indicate the number of birds observed of each species. Note that in general, the hoarding species show between 8 – 11% hoarding-related behaviours. Non-hoarding species are most often seen to eat food items they find. The number of observations made per week is shown in **Error! Reference source not found.**. Locations of v olunteers that are included in the dataset are shown in Figure B.2.

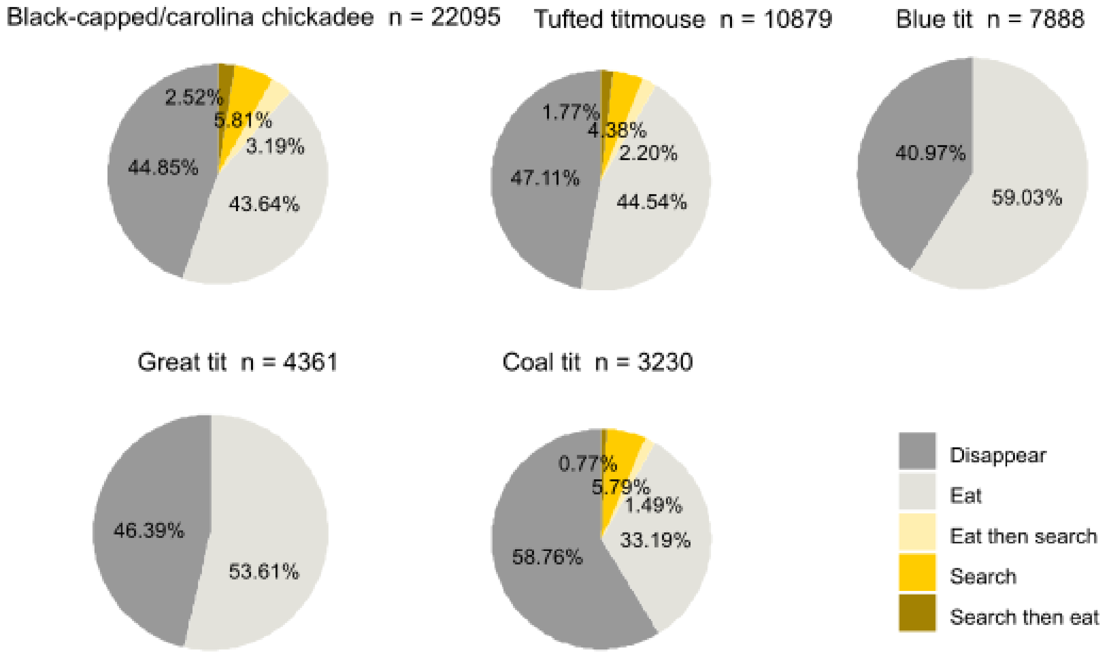
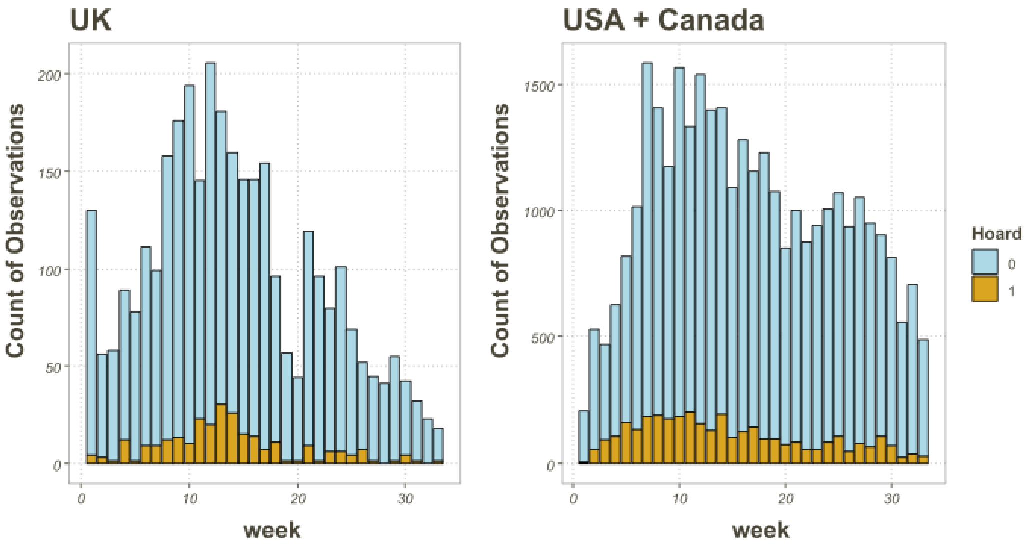


Figure B.1. Percentages of behaviours reported across species. Black-capped/Carolina chickadees and Tufted titmice from the USA and Canada. Blue tits, Great tits and Coal tits as observed in the United Kingdom.



***b** Number of observations made per week in the UK (left) and the USA and Canada (right). The yellow part of the bars indicates hoarding observations, all other behaviours (eat and disappear) are in blue.*

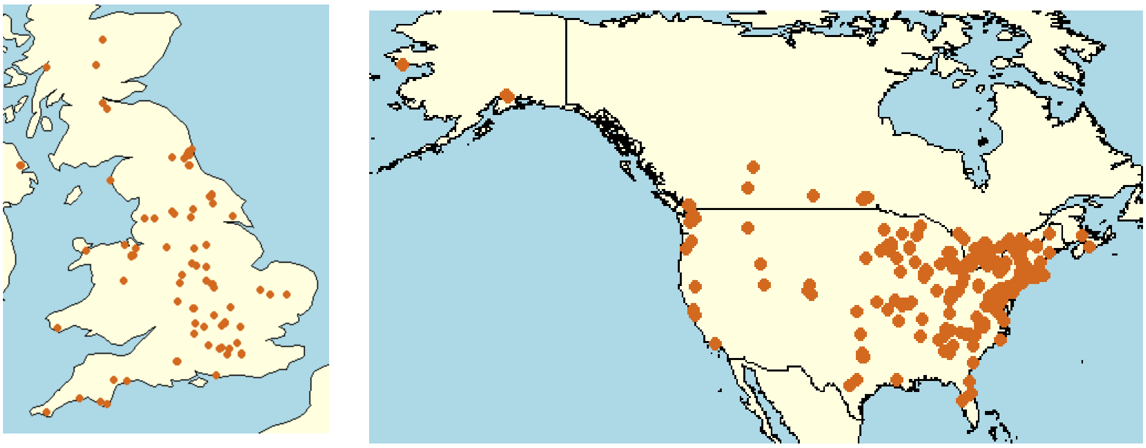


Figure B.2. Volunteer locations in the UK (left) and the USA and Canada (right).

Table B.5. Number of food items reported per food type. The "other" category contains items such as peanut butter, berries and millet.

Food type	***N***
Fat/suet	2,488
I don't know	1,008
Invertebrate	161
Other	1,096
Peanuts (loose)	7,392
Seed/nut (other)	9,460
Sunflower hearts	11,993
Whole sunflower seeds	14,855

Table B.5 reports the number of observations that were reported for each of the food items. Figure B.3 shows the number of observations made for each food category, split by items hoarded or eaten/disappeared with.

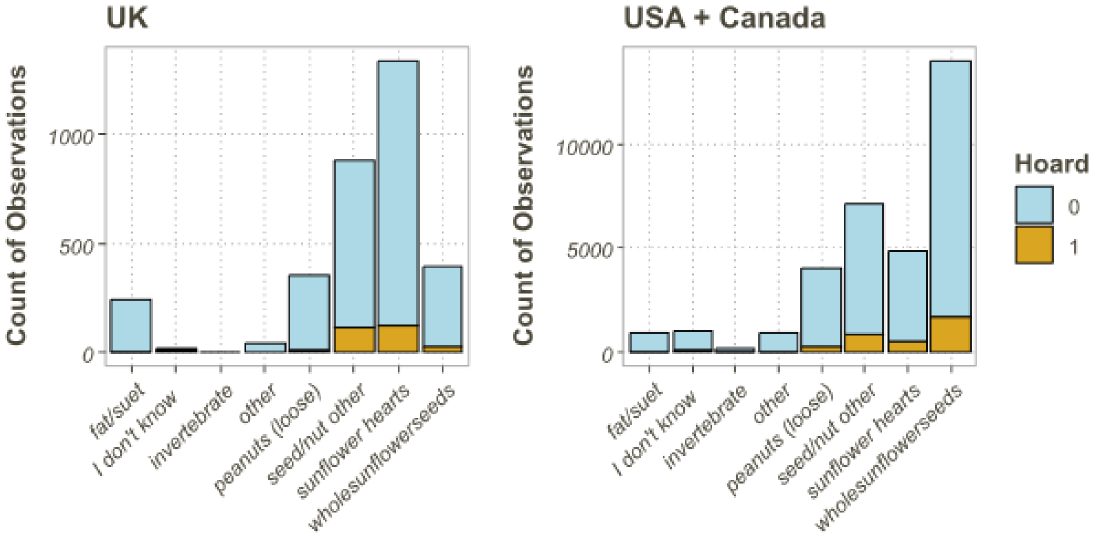


Figure B.3. Number of food items observed per country. The yellow part of the bars reflects hoarded items. The light blue (top) part of the bar reflects items that were eaten or that the bird disappeared with.

B.6 Testing Correlations

Before fitting the models, correlations between all variables were assessed to determine which could be included together. A cutoff value of Pearsons $r = 0.4$ (Table B.6).

Day length and *day* covary, as well as *day* and *temperature*. Therefore, these variables were not included in the models as covariates. Table B.6. Pearsons correlations between covariates in the models. Any correlation with a Pearsons r above 0.1 was considered problematic for variables to be included in models together. See Table B.7.

Table B.7. Results from the Spearmans correlations.

Variables	***r***	***Strength***	***P***	***Direction***
Day in season ~ day length (Hoarding UK data)	-0.441	Moderate	<0.001	Negative
Day in season ~ day length (Hoarding USA data)	-0.175	Weak	<0.001	Negative
Day in season ~ temperature (Hoarding UK data)	-0.641	Strong	<0.001	Negative

Factor variables were also investigated using ANOVA and eta-squared to determine the effect sizes. Whilst significant relationships were found, effect sizes were very small, so variables were included into the models together. See Table B.8.

Table B.8. Results from the ANOVAs end eta-squared tests.

Variables	***Df***	***Sum sq***	***Mean Sq***	***F-value***	***P***	***Effect size***
Day ~ species (UK data)	2	82251	41125	10.97	<0.001	1.42e-03 (small)
Day ~ species (North America data)	1	34530	34530	10.08	0.002	3.06e-04 (small)
Day ~ latitude (North America data)	1	474621	474621	139.1	<0.001	4.21e-03 (small)
Day ~ species (Hoarding North America)	1	3735	3725	1.058	0.304	5.90e-05 (small)
Day ~ latitude (Hoarding North America)	1	380537	380537	108.4	<0.001	6.01e-03 (small)

A Chi-square test was conducted to test for the correlation between species and latitude bin in the North American data and the Hoarding North America data. For the North America data, there was a significant relationship between the two ($\chi^2 = 503.78, df = 1, p<0.001$). However, the effect size, calculated as *Cramers V*, was 0.12, indicating a weak association. For the Hoarding North America data, there was a significant relationship as well ($\chi^2 = 192.94, df = 1, p <0.001$), with a *Cramers V* of 0.10, indicating a weak effect.

B.7 Modelling Details

B.7.1 Model 1

*Table B.9. GAM results: Disappearing index ~ s(day, k = 4)+ species + ti(day * species, k = 4) + s(+ s(1|Volunteer_ID) on the “UK” data.*

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-1.155	0.201	-5.732	< 0.001
	Coal Tit	1.243	0.054	22.910	<0.001
	Great Tit	0.24	0.042	5.585	<0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	ti(day * species): Blue Tit	2.811	2.970	35.357	< 0.001
	ti(day*species): Coal Tit	2.618	2.894	14.407	0.008
	ti(day*species): Great Tit	1.125	1.505	2.619	0.134
	s(day)	1.016	1.021	65.721	<0.001
	s(1|Volunteer_ID)	55.058	64.000	165.657	<0.001

B.7.2 Model 2

*Table B.10. GAM results. Disappearing index ~ s(day, k = 4)+ species + ti(day * species, k = 4) + s(1|Volunteer_ID) on the "North America" data.*

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.483	0.078	-6.213	< 0.001
	Tufted titmouse	-0.106	0.031	-3.393	<0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	ti(day * species): Black-capped/Carolina Chickadee	2.440	2.784	241.426	<0.001
	ti(day*species): Tufted Titmouse	1.001	1.002	113.021	<0.001
	s(day)	0.002	0.003	0.00 0	0.983
	s(1|Volunteer_ID)	172.133	227.00	5,239.199	<0.001

B.7.3 Model 3

*Table B.11. GAM results: Disappearing index ~ s(day, k = 4)+ species + latitude + ti(day * species, k = 4) + ti(day*species, k = 4) + (species * latitude) + s(1|Volunteer_ID) on the "North America" data.*

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-0.584	0.096	-6.119	<0.001
	Latitude:South	0.294	0.162	1.817	0.069
	Species:Tufted titmouse	-0.102	0.049	-2.072	0.038
	South * Tufted titmouse	0.010	0.065	0.162	0.871
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	ti(day * Black-capped Chickadee * North)	1.444	1.743	183.232	<0.001
	ti(day * Tufted Titmouse * North)	2.676	2.923	127.193	<0.001
	ti(day * Black-capped Chickadee * South)	1.000	1.000	34.137	<0.001
	ti(day * Tufted Titmouse * South)	1.00	0.001	4.473	0.035
	ti(day * Black-capped Chickadee)	0.001	0.001	0.001	0.980
	ti(day * Tufted Titmouse)	0.000	0.001	0.000	0.996
	ti(day * North)	0.001	0.002	0.001	0.970
	ti(day * South)	1.573	1.868	18.563	0.002
	s(day)	0.005	0.008	0.003	0.958
	s(1|Volunteer ID)	170.763	227.000	5,017.552	<0.001

B.7.4 Model 4

Table B.12. GAM results: Hoarding index ~ s(day, k = 4) + s(1|Volunteer_ID) on the "Hoarding UK "data.

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-1.662	0.258	-6.429	<0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day)	2.783	2.961	37.885	<0.001
	s(1|Volunteer ID)	30.815	47.000	147.110	<0.001

B.7.5 Model 5

*GAM result: Hoarding index ~ s(day, k = 4)+ species + ti(day * species, k = 4) + s(1|Volunteer_ID) on the "Hoarding North America" data.*

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-1.480	0.101	-14.613	<0.001
	Tufted titmouse	-0.150	0.057	-2.618	0.009
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	ti(day * species): Black-capped/Carolina Chickadee	2.833	2.977	209.194	<0.001
	ti(day*species): Tufted Titmouse	1.001	1.001	45.574	<0.001
	s(day)	0.000	0.001	0.000	0.992
	s(1|Volunteer_ID)	154.417	218.000	2,481.597	<0.001

B.7.6 Model 6

*Table B.13. GAM Result: Hoarding index ~ s(day, k = 4)+ species + latitude + ti(day * species, k = 4) + ti(day*species, k = 4) + (species * latitude) + s(1|Volunteer_ID) on the "Hoarding North America" data.*

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-1.341	0.125	-10.753	<0.001
	Latitude:South	-0.473	0.215	-2.196	0.028
	Species:Tufted titmouse	-0.265	0.079	-3.342	<0.001
	South * Tufted titmouse	0.257	0.118	2.186	0.029
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	ti(day * Black-capped Chickadee * North)	1.001	1.001	29.274	<0.001
	ti(day * Tufted Titmouse * North)	1.000	1.000	10.835	0.001
	ti(day * Black-capped Chickadee * South)	1.000	1.001	36.508	<0.001
	ti(day * Tufted Titmouse * South)	1.001	1.002	15.175	<0.001
	ti(day * Black-capped Chickadee)	1.687	1.919	13.552	0.003
	ti(day * Tufted Titmouse)	0.000	0.000	0.000	0.9988
	ti(day * North)	0.000	0.000	0.000	0.998
	ti(day * South)	1.682	1.914	17.480	0.002
	s(day)	0.000	0.000	0.000	0.998
	s(1|Volunteer ID)	153.577	217.000	2,413.687	0.000

B.7.7 Model 7

Table B.14. GAM results: Hoarding index ~ s(day length, k = 4) + s(1|Volunteer_ID) on the "Hoarding UK "data.

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-1.555	0.224	-6.934	<0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(day)	1.424	1.660	3.511	0.078
	s(1|Volunteer ID)	28.217	47.000	160.214	<0.001

B.7.8 Model 8

*Table B.15. GAM result: Hoarding index ~ s(day length, k = 4)+ species + ti(day length * species, k = 4) + s(1|Volunteer_ID) on the "Hoarding North America" data.*

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-1.348	0.104	-12.959	<0.001
	Species:Tufted titmouse	-0.146	0.062	-2.366	0.018
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	ti(day length * species): Black-capped/Carolina Chickadee	1.795	1.949	5.647	0.039
	ti(day length *species): Tufted Titmouse	1.000	1.000	0.873	0.350
	s(day length)	0.000	0.000	0.000	0.999
	s(1|Volunteer_ID)	154.191	217.000	2,464.825	<0.001

B.7.9 Model 9

Table B.16. GAM results: Hoarding index ~ s(temperature, k = 4) + s(1|Volunteer_ID) on the "Hoarding UK "data.

Component	***Term***	***Estimate***	***Std Error***	***t-value***	***p-value***
A. Parametric coefficients	(intercept)	-1.594	0.226	-7.040	<0.001
Component	***Term***	***Edf***	***Ref. df***	***F-value***	***p-value***
B. Smooth terms	s(temperature)	1.000	1.000	1.224	0.269
	s(1|Volunteer ID)	28.688	46.000	154.336	<0.001

C. Chapter 5. Agent-based Models of Small Birds in Winter: Decisions Based on Stomach Content

C.1 Energy Variable Plot for Direct-hoarding Models (H_{top} and R_{top})

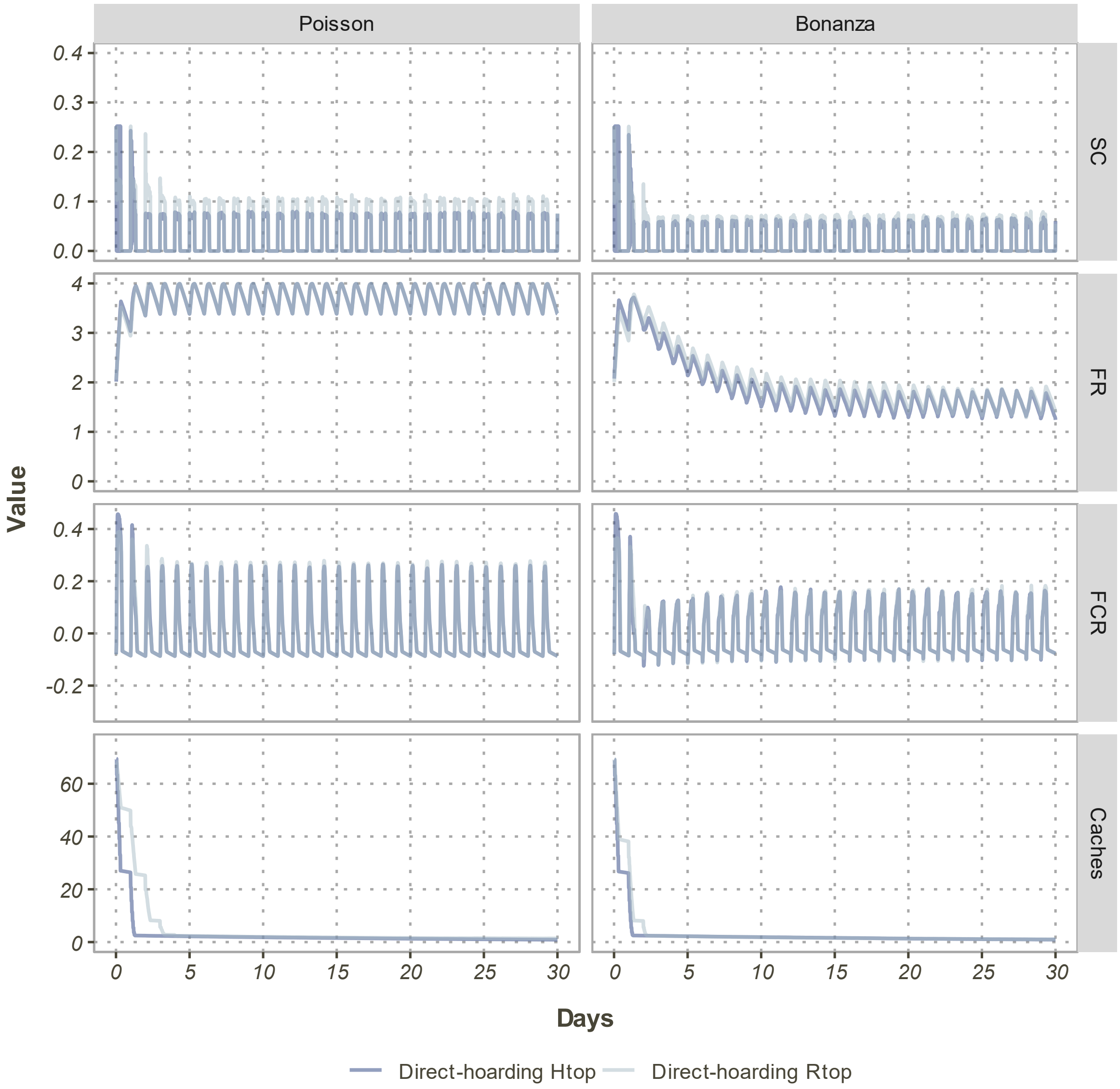


Figure C.1. Fluctuations in Stomach content, Fat reserve, Fat change rate, and the number of caches for models 1.3 and 1.4 in the two default environments. The x-axes show the number of days in the simulation that have passed. Y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours, and the number of caches.

C.2 Energy Variable Plot (Aggregated) for Direct-hoarding Models (H_{top} and R_{top})

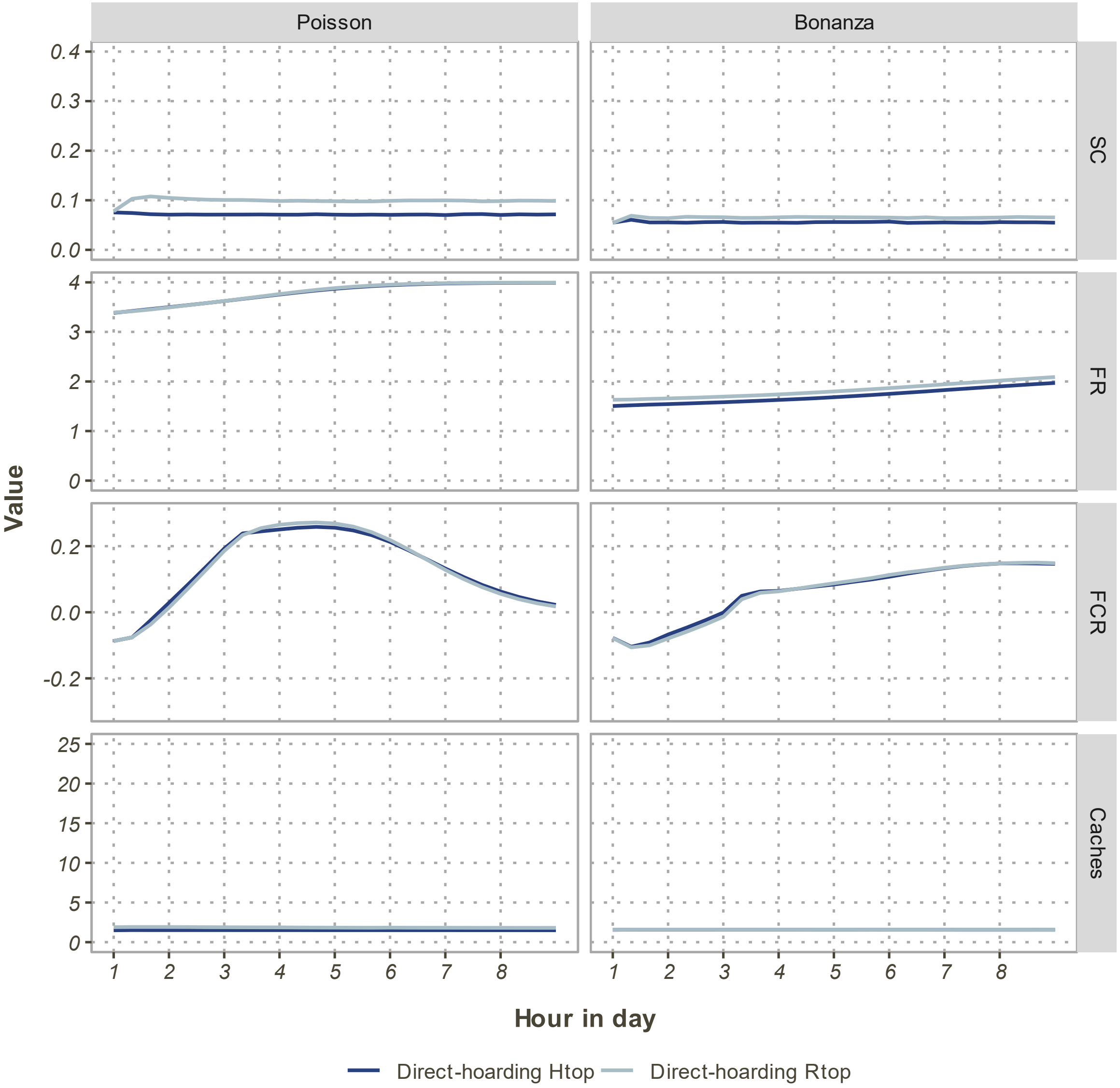


Figure C.2. Fluctuations in Stomach content, Fat reserve, Fat change rate and number of caches for models 1.3 and 1.4 in the two default environments aggregated across days 4-30 in the simulation. The x-axes show the hours within the daylight period that have passed. Numbers indicate the start of the hour. Y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours, and the number of caches.

C.3 Behaviour Plot for Direct-hoarding Models (H_{top} and R_{top})

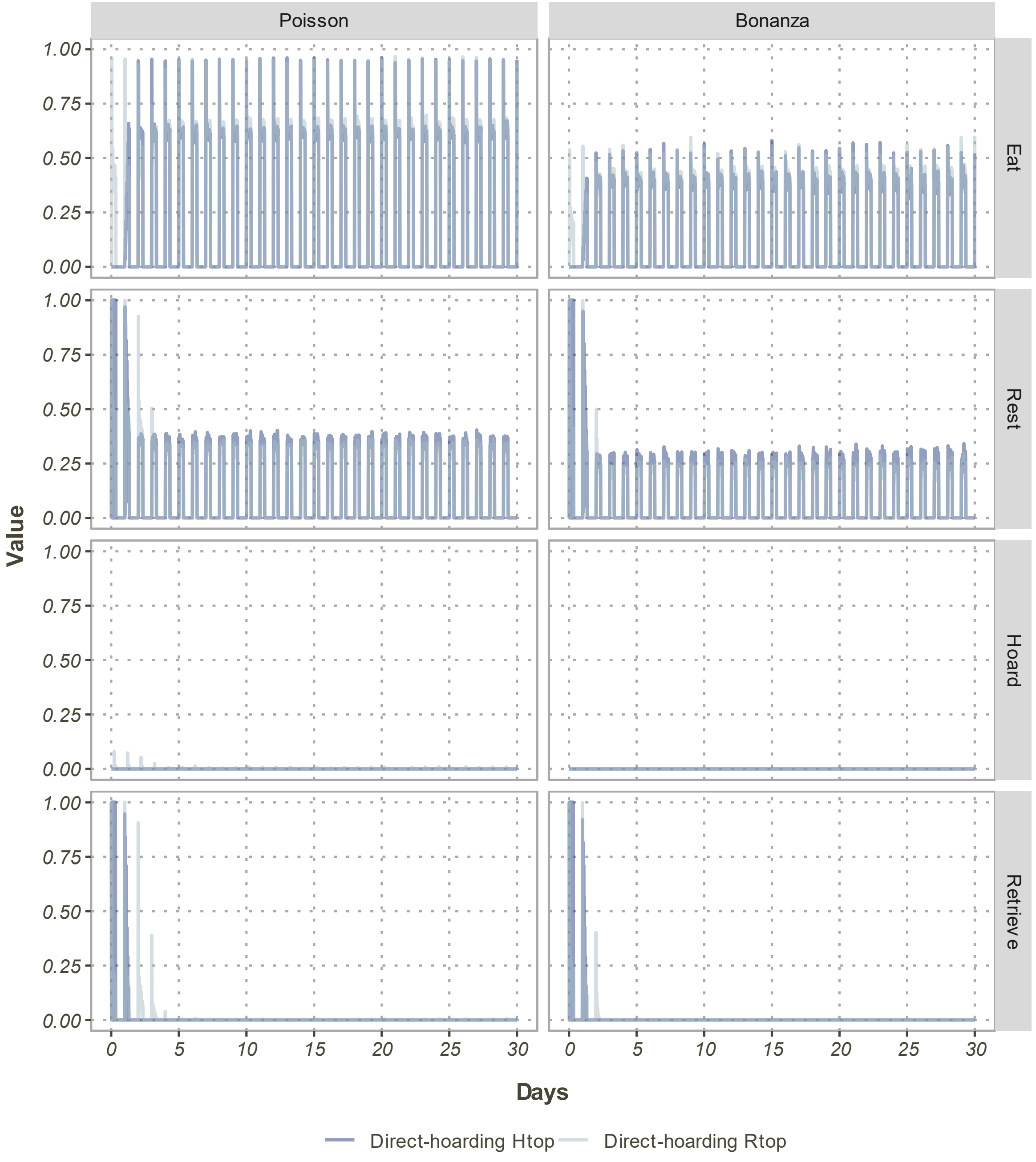


Figure C.3. Fluctuations in Eating, Resting, Direct-hoarding, and Retrieving behaviour throughout the simulation for models 1.3 and 1.4 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Note that the "Hoard" behaviour indicates the "direct-hoarding" behaviour.

C.4 Behaviour Plot (Aggregated) for Direct-hoarding Models (H_{top} and R_{top})

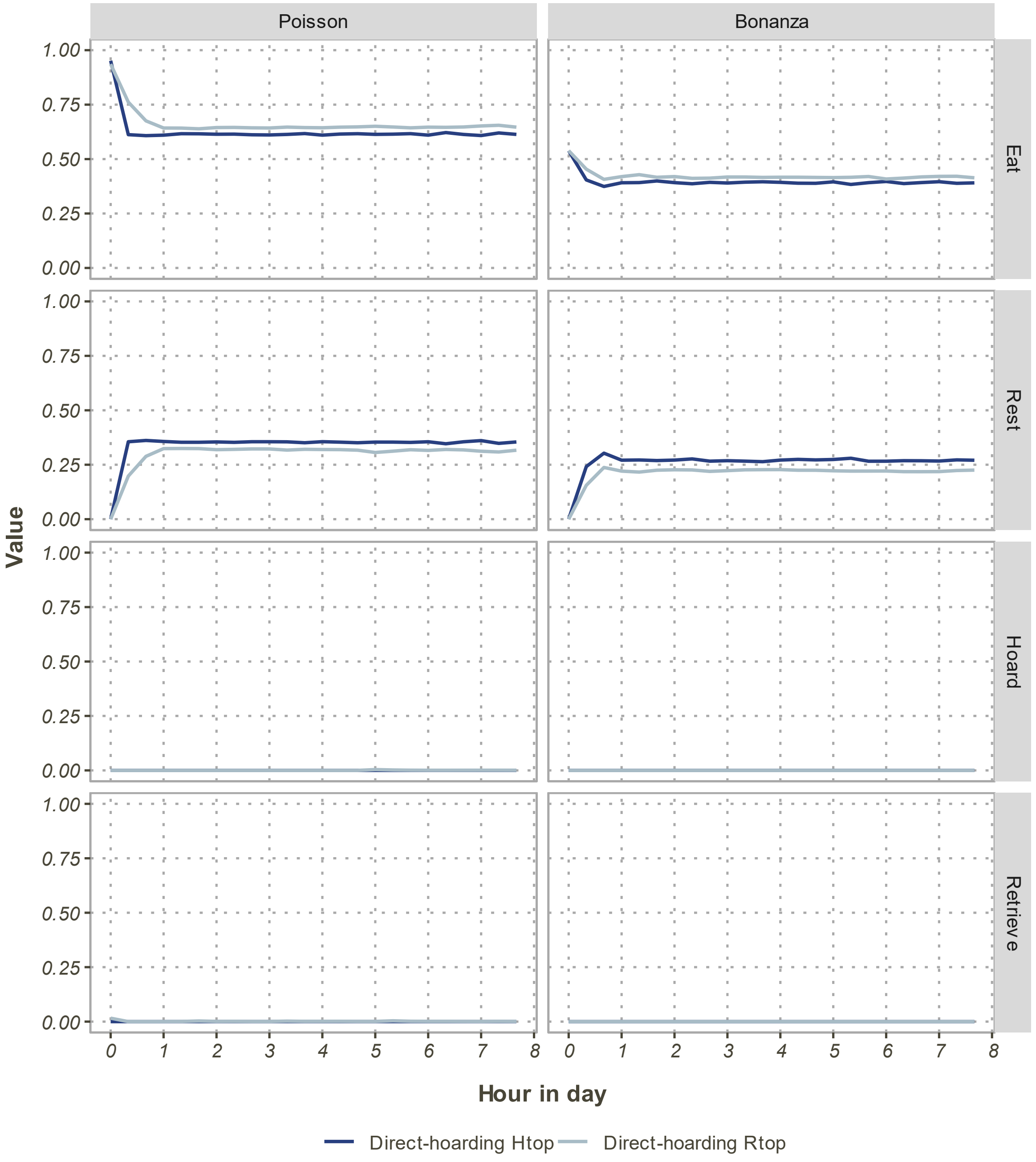


Figure C.4. Fluctuations in Eating, Resting, Direct-hoarding, and Retrieving behaviour days for models 1.3 and 1.4 in the two default environments aggregated across days 4-30 in the simulation. The x-axes reflect the number of hours after sunrise in the day. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Note that the "Hoard" behaviour indicates the "direct-hoard" behaviour. In the Hoarding and Retrieval graphs, the direct-hoarders (H_{top}) are underneath the line for direct-hoarders (R_{top}).

D. Chapter 6. Agent-based Models of Small Birds in Winter: Decisions Based on Fat Metabolism

D.1 Energy Variable Plot for Direct-hoarding Models (H_{top})

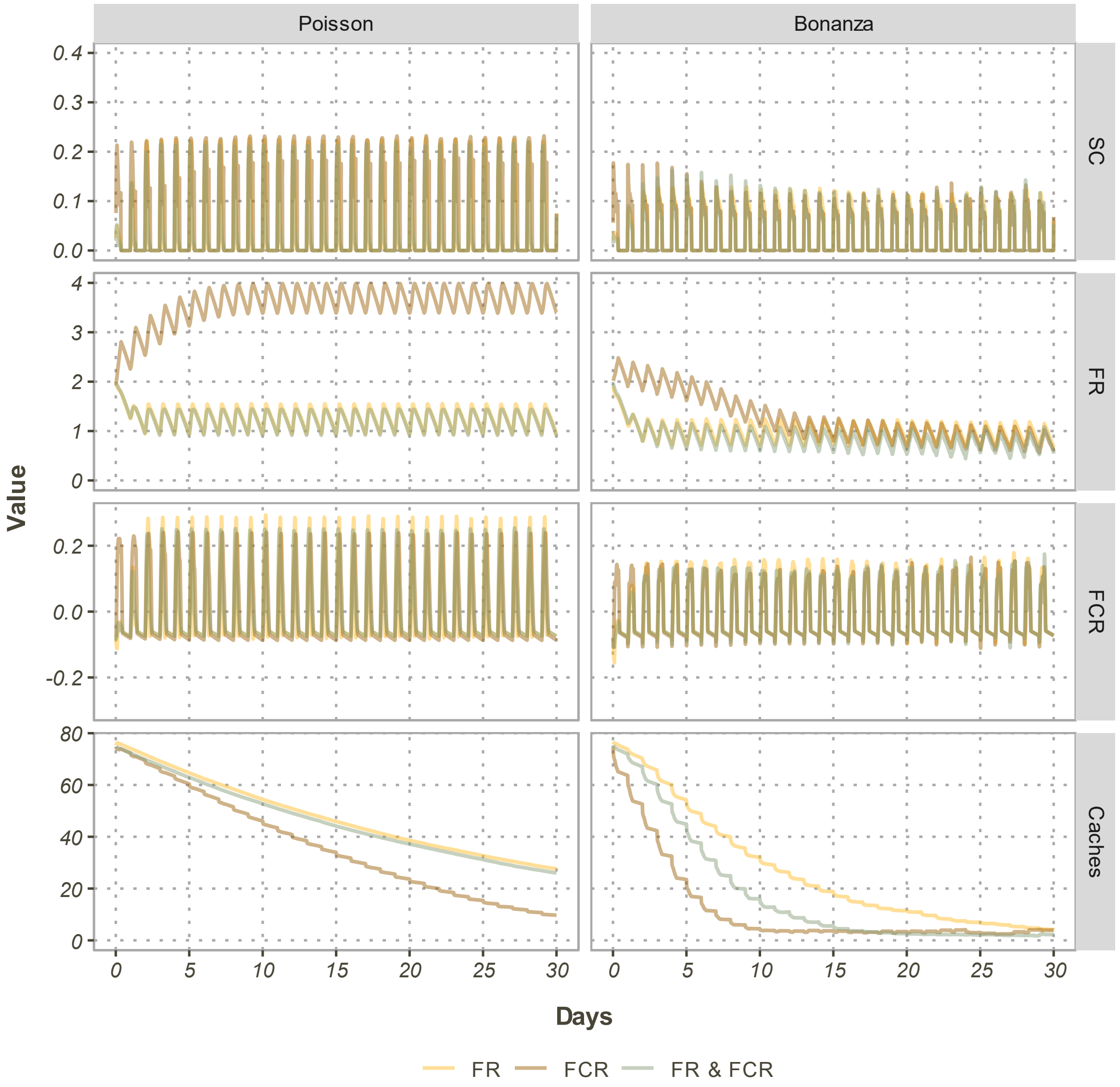


Figure D.1. Fluctuations in Stomach content, Fat reserve and Fat change rate for models 2.3, 3.3 and 4.3 in the two default environments. The x-axes show the number of days in the simulation that have passed. Y-axes show the Stomach content in grams, the Fat reserves in grams. the Fat change rate in grams/2 hours and the number of caches. Values are averages across all birds that are alive at each timestep.

D.2 Energy Variable Plot for Direct-hoarding Models (R_{top})

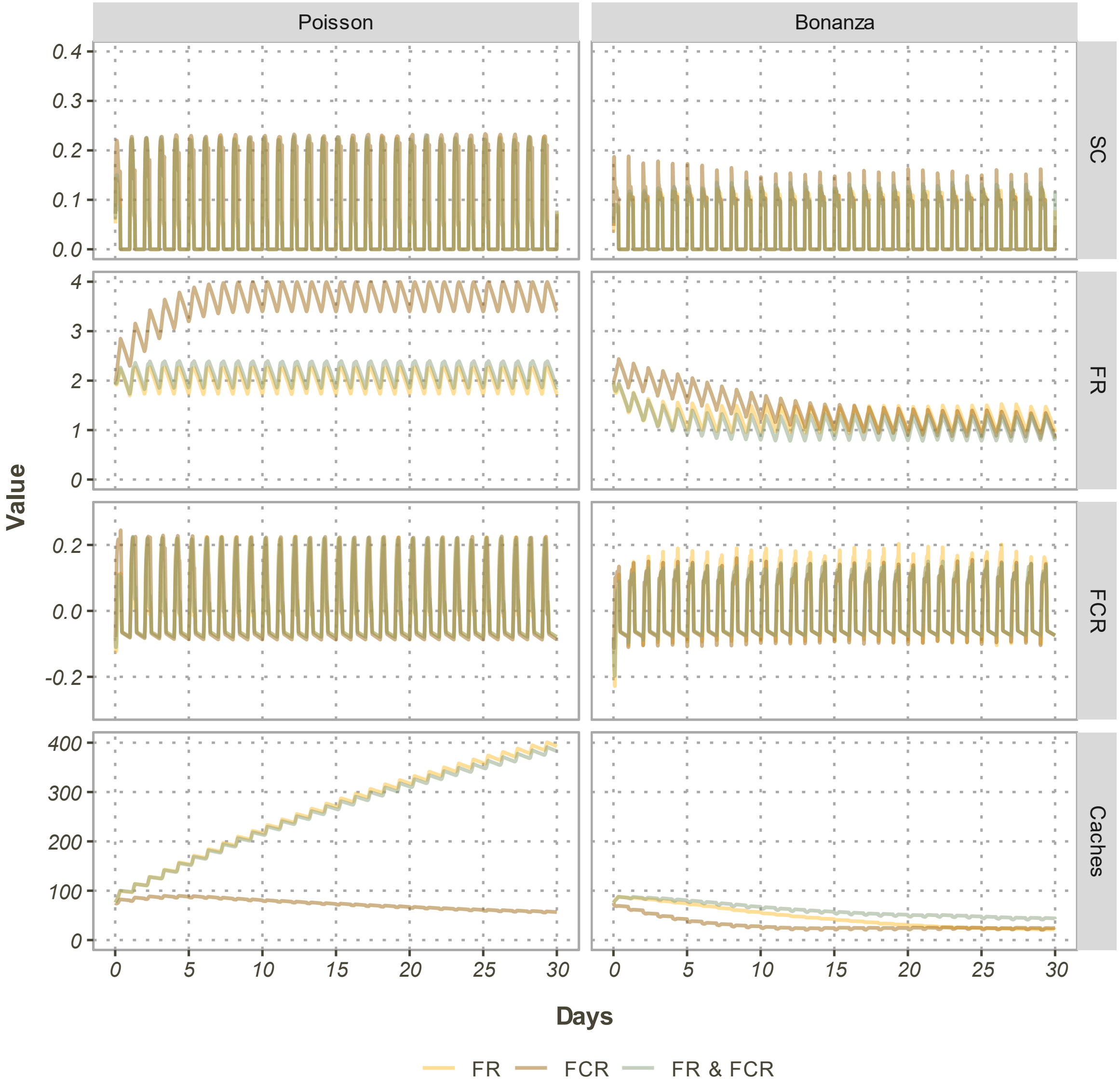


Figure D.2. Fluctuations in Stomach content, Fat reserve and Fat change rate for models 2.4, 3.4 and 4.4 in the two default environments. The x-axes show the number of days in the simulation that have passed. Y-axes show the Stomach content in grams, the Fat reserves in grams. the Fat change rate in grams/2 hours and the number of caches. Values are averages across all birds that are alive at each timestep.

D.3 Energy Variable Plot (Aggregated) for Direct-hoarding Models (H_{top})

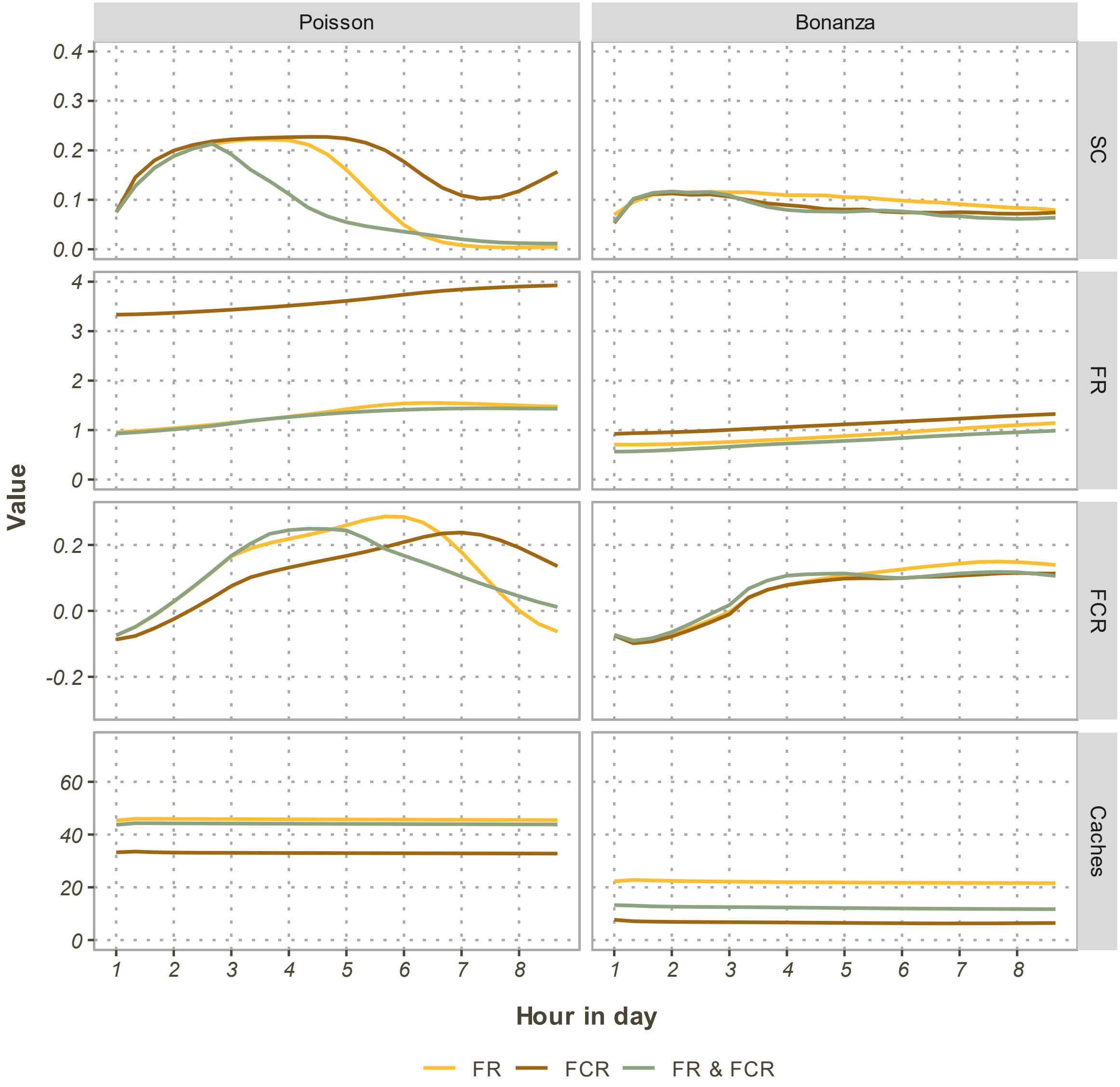


Figure D.3. Fluctuations in Stomach content, Fat reserve, Fat change rate and cache number for models 2.3, 3.3 and 4.3 in the two default environments aggregated across days 4-30 in the simulation. The x-axis shows the hours within the daylight period that have passed. Numbers indicate the start of the hour. Y-axes show the Stomach content in grams, the fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches.

D.4 Energy variable (Aggregated) Plot for Direct-hoarding Models (R_{top})

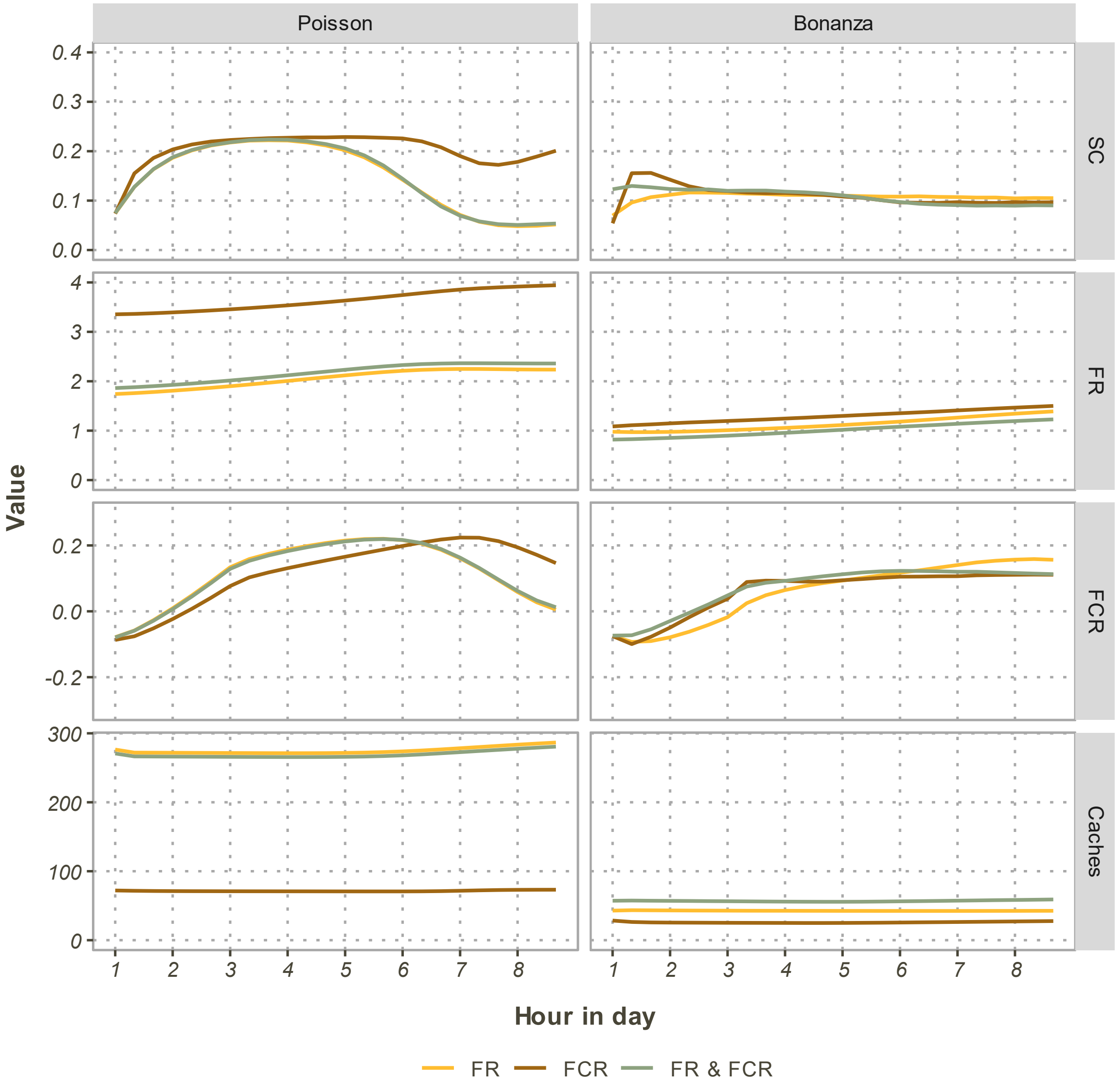


Figure D.4. Fluctuations in Stomach content, Fat reserve, Fat change rate and cache number for models 2.4, 3.4 and 4.4 in the two default environments aggregated across days 4-30 in the simulation. The x-axes show the hours within the daylight period that have passed. Numbers indicate the start of the hour. Y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches. Values are averaged across alive birds at each timestep.

D.5 Behaviour Plot for Direct-hoarding Models (H_{top})

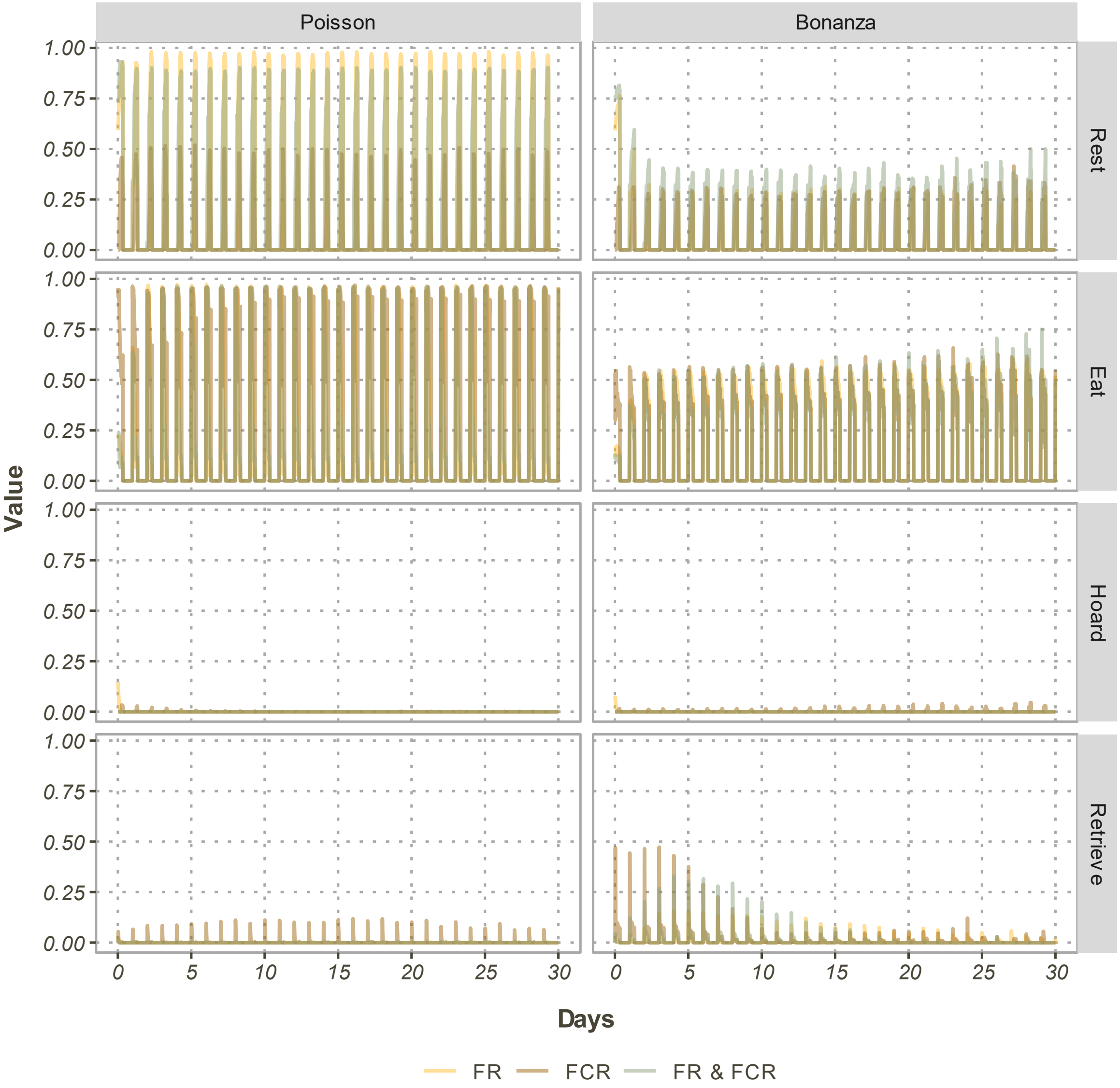


Figure D.5. Fluctuations in Eating, Resting, Direct-hoarding, and Retrieving behaviour throughout the simulation for direct -hoarding models 2.3, 3.3 and 4.3 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Values are the proportion of alive birds exhibiting the behaviour at each timestep of the simulation.

D.6 Behaviour Plot for direct-hoarding Models (R_{top})

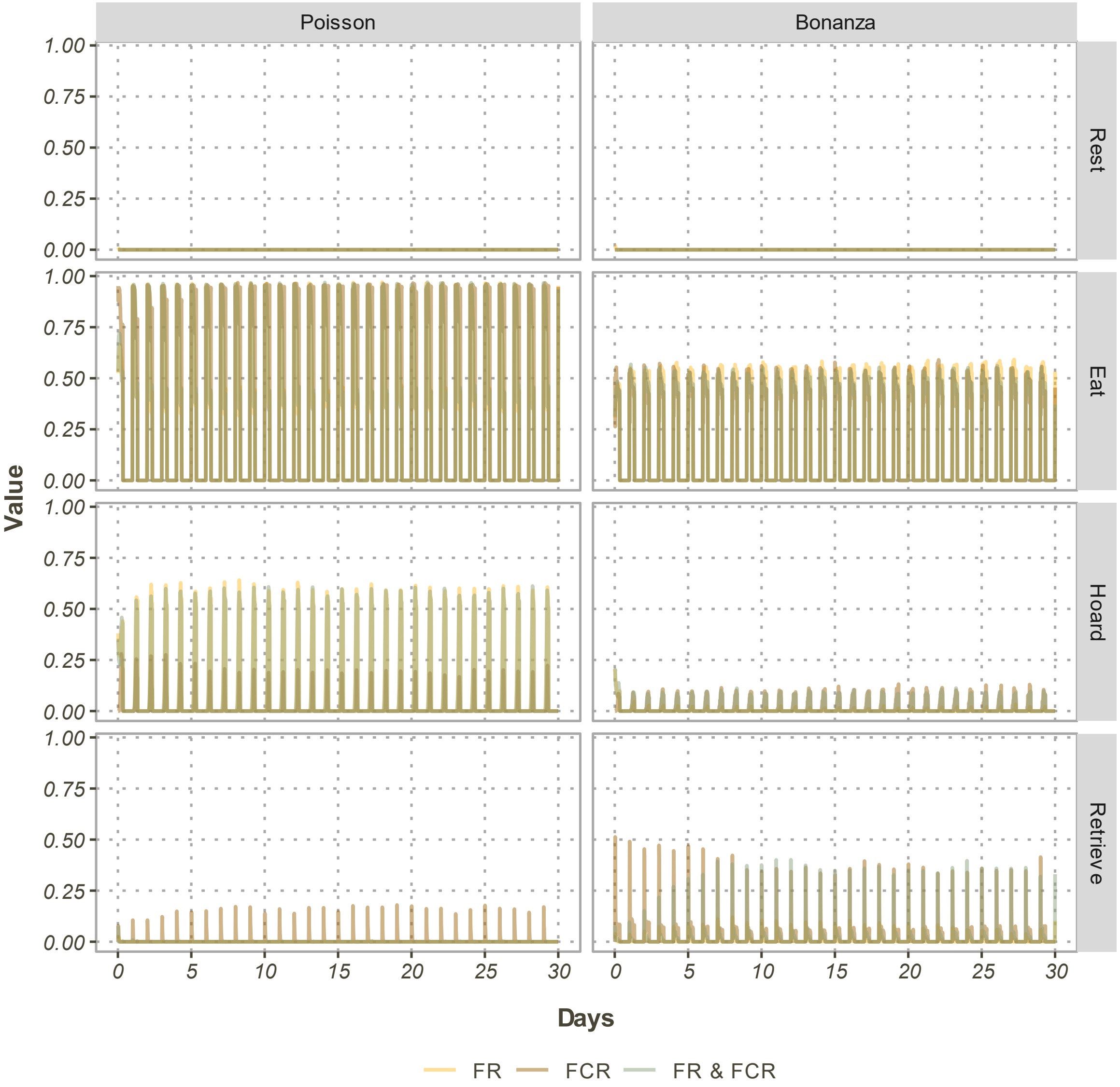


Figure D.6. Fluctuations in Eating, Resting, Direct-hoarding, and Retrieving behaviour throughout the simulation for direct -hoarding models 2.4, 3.4 and 4.4 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Values are the proportion of alive birds exhibiting the behaviour at each timestep of the simulation.

D.7 Behaviour Plot (Aggregated) for Direct-hoarding Models (H_{top})

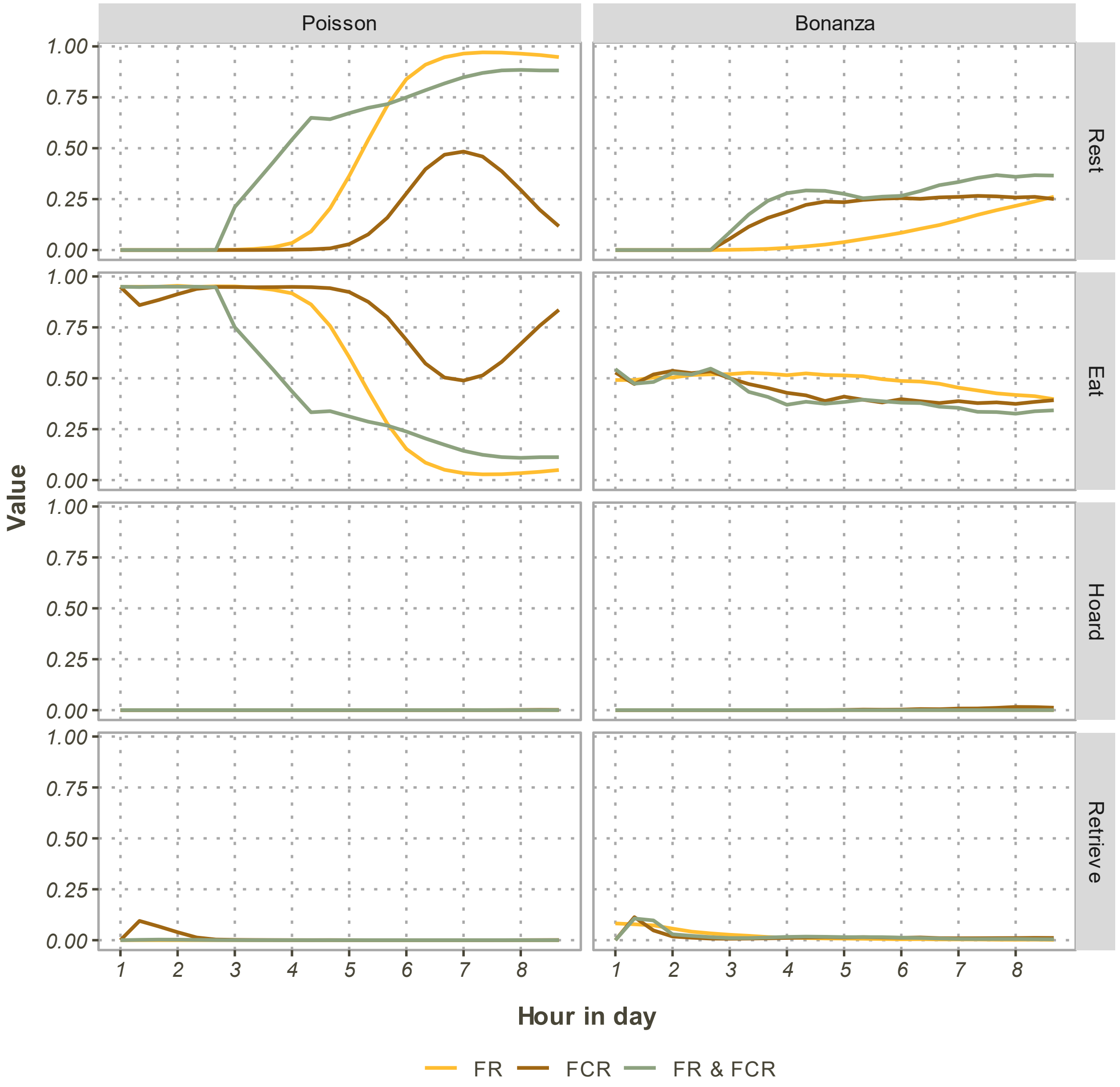


Figure D.7. Fluctuations in Eating, Resting, Direct-hoarding, and Retrieving behaviour for direct-hoarding models 2.3, 3.3 and 4.3 in the two default environments aggregated across days 4-30 in the simulation. The x-axes reflect the number of hours after sunrise in the day. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep.

D.8 Behaviour Plot (Aggregated) for Direct-hoarding models (R_{top})

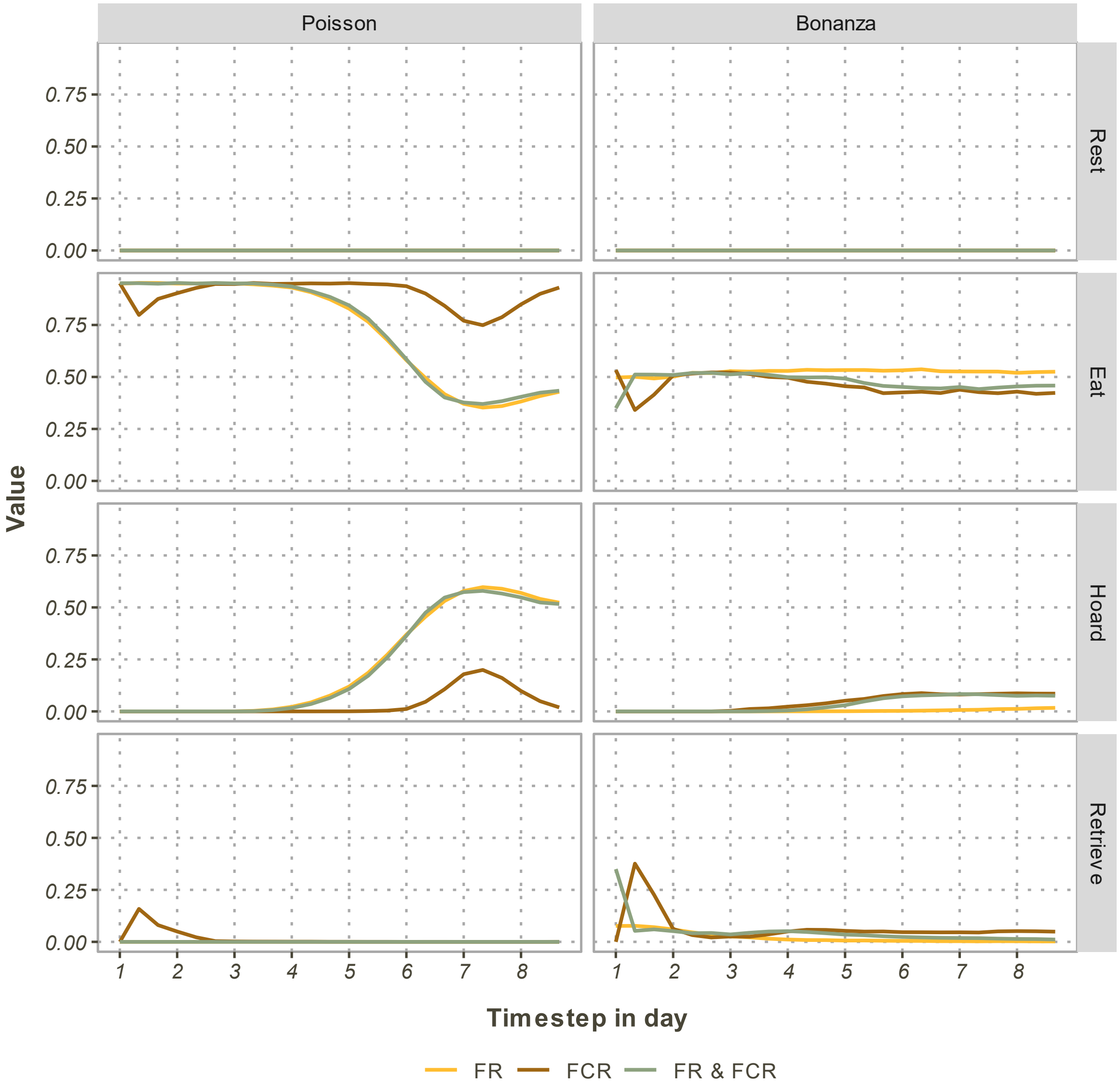


Figure D.8. Fluctuations in Eating, Resting, Direct-hoarding, and Retrieving behaviour for direct-hoarding models 2.4, 3.4 and 4.4 in the two default environments aggregated across days 4-30 in the simulation. The x-axes reflect the number of hours after sunrise in the day. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep.

E. Chapter 7. Agent-based Models of Small Birds in Winter: Decisions Based on Stomach Content and Fat Metabolism

E.1 Survival of Direct-hoarding Models across the 12 Parameterisation Environments

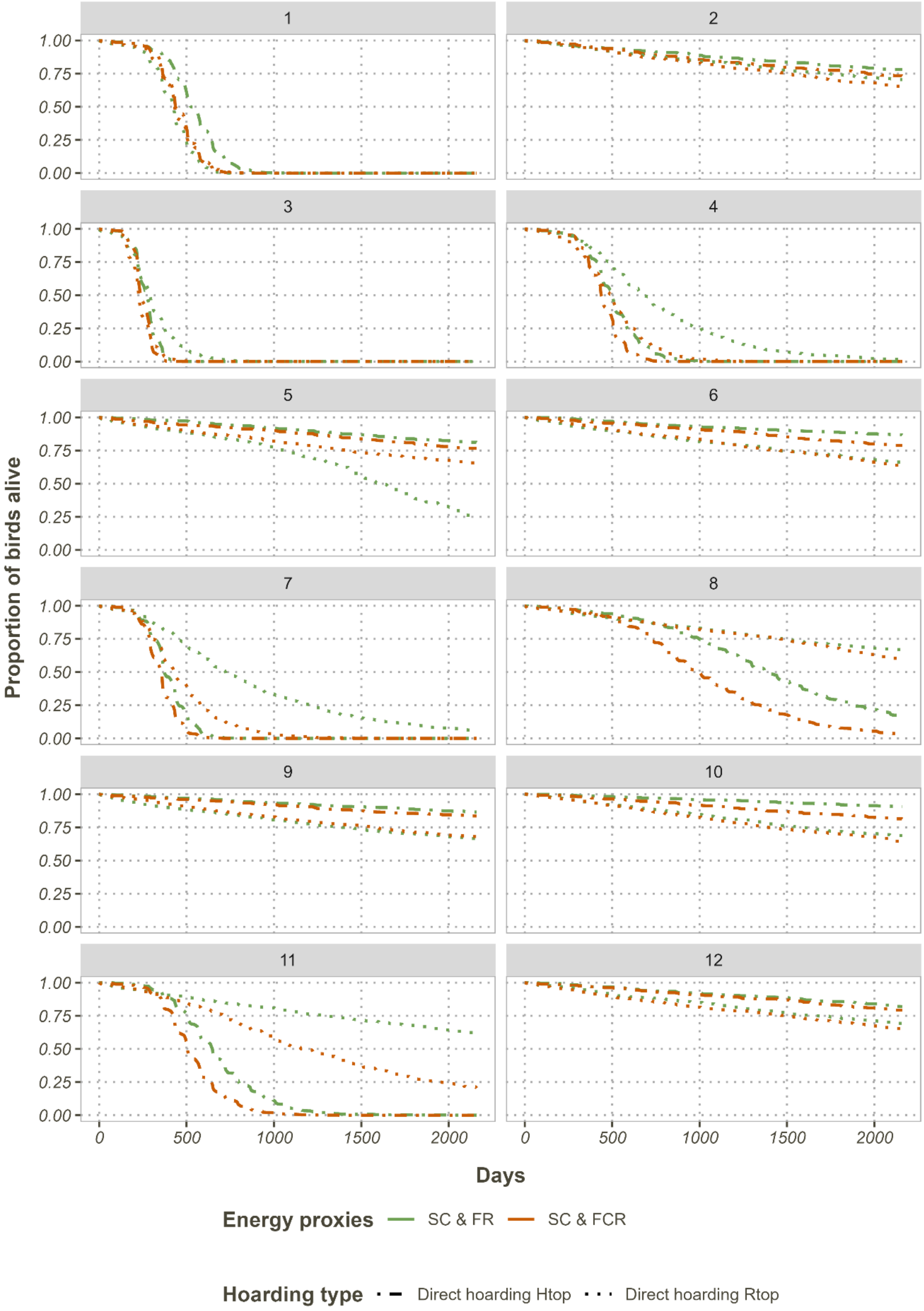


Figure E.1. Survival for models 5.3, 5.4, 6.3 and 6.4 across the 12 parametrisation environments (see Chapter 4). X-axes show the number of days in the simulation that have passed. The y-axes show the proportion of birds that are alive.

E.2 Energy Variable Plot for Direct-hoarding Models (H_{top})

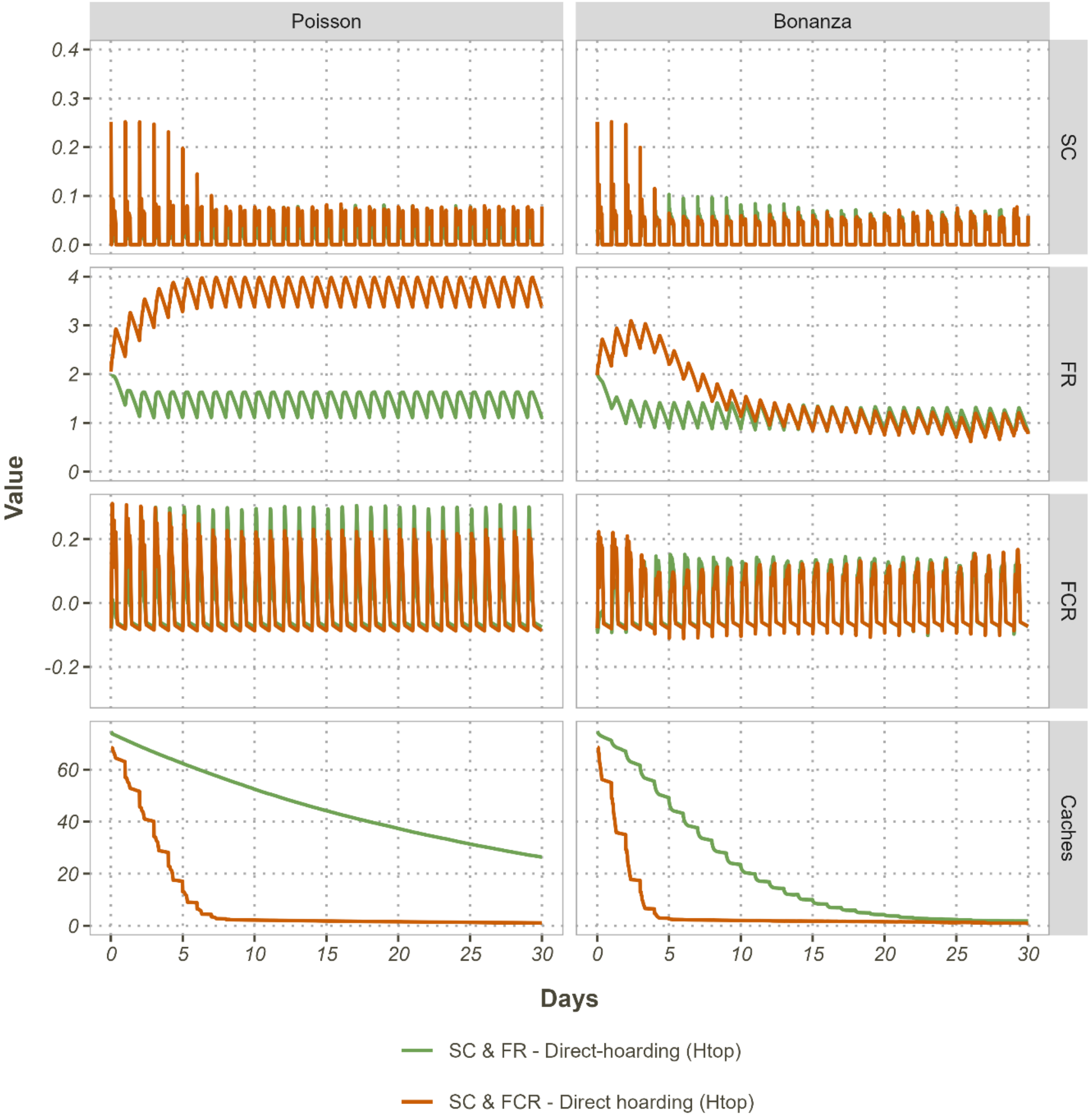


Figure E.2. Fluctuations in Stomach content, Fat reserve and Fat change rate for models 5.3 and 6.3 in the two default environments. The x-axes show the number of days in the simulation that have passed. Y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches. Values are averages across all birds that are alive at each timestep.

E.3 Energy Variable Plot (Aggregated) for Direct-hoarding Models (H_{top})

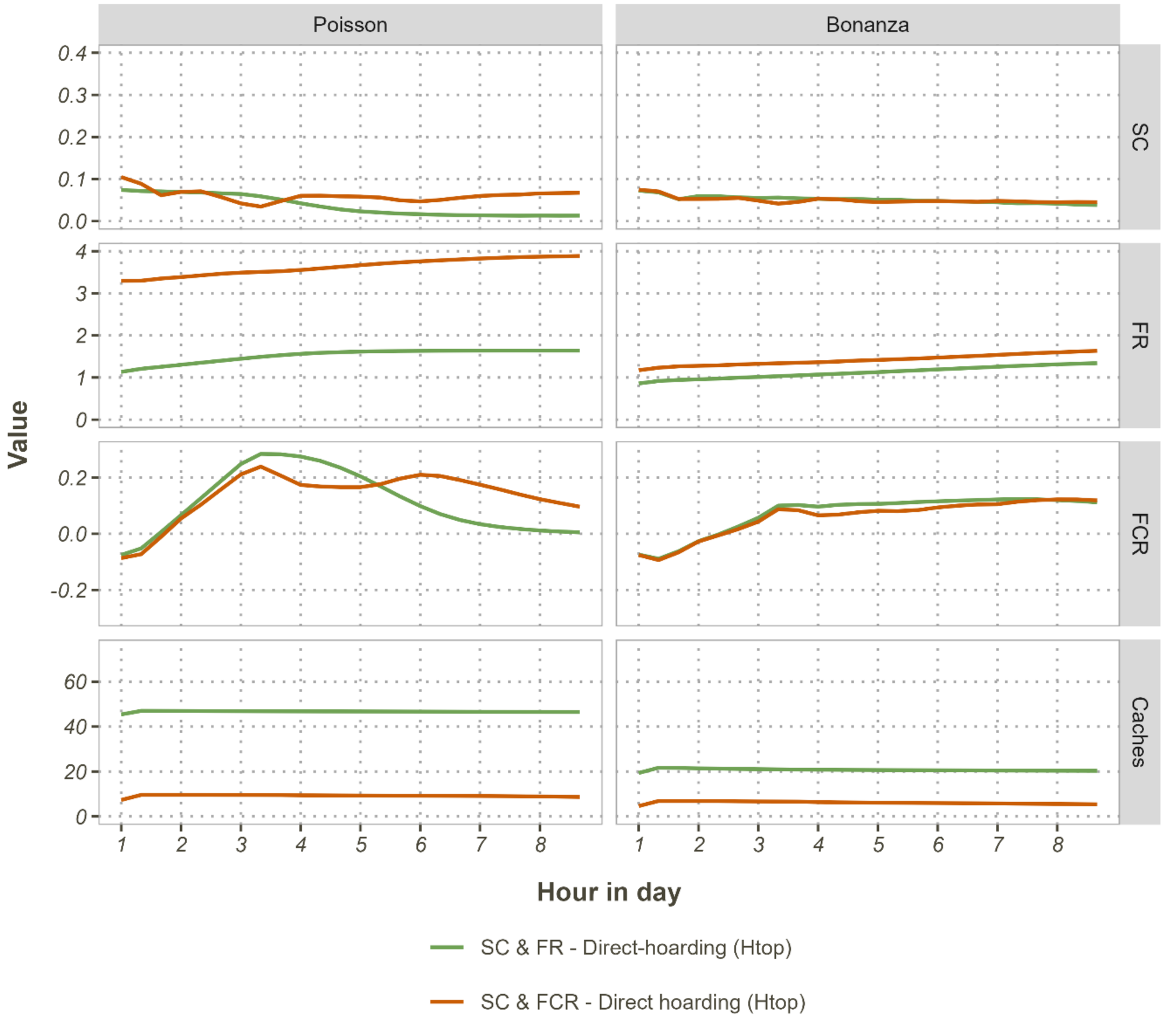


Figure E.3. Fluctuations in stomach content, Fat reserve, Fat change rate and cache number for models 5.3 and 6.3 in the two default environments. The x-axes show the hours within the daylight period that have passed. Numbers indicate the start of the hour. Y-axes show the Stomach content in grams, the Fat reserves in grams, the Fat change rate in grams/2 hours and the number of caches. Values are averaged across alive birds at each timestep within the day across days 4-30 in the simulation.

E.4 Behaviour Plot for Direct-hoarding Models (H_{top})

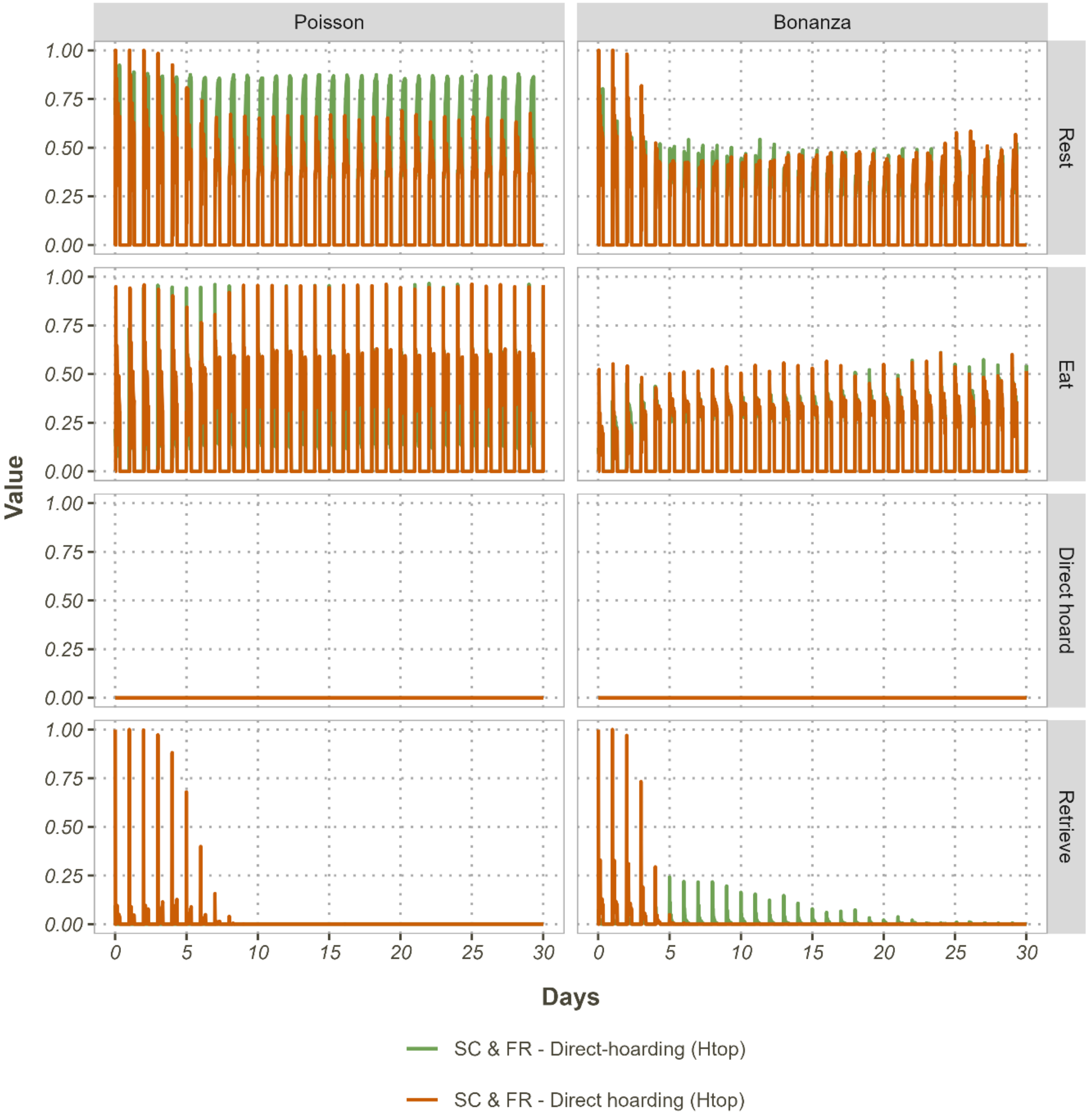


Figure E.4. Fluctuations in Eating, Resting, Direct-hoarding, and Retrieving behaviour throughout the simulation for direct -hoarding models 5.3 and 6.3 in the two default environments. The x-axes reflect the number of days in the simulation. The y-axes reflect the proportion of birds exhibiting the behaviour in each timestep. Values are the proportion of alive birds exhibiting the behaviour at each timestep of the simulation.

E.5 Behaviour Plot (Aggregated) for Direct-hoarding Models (H_{top})

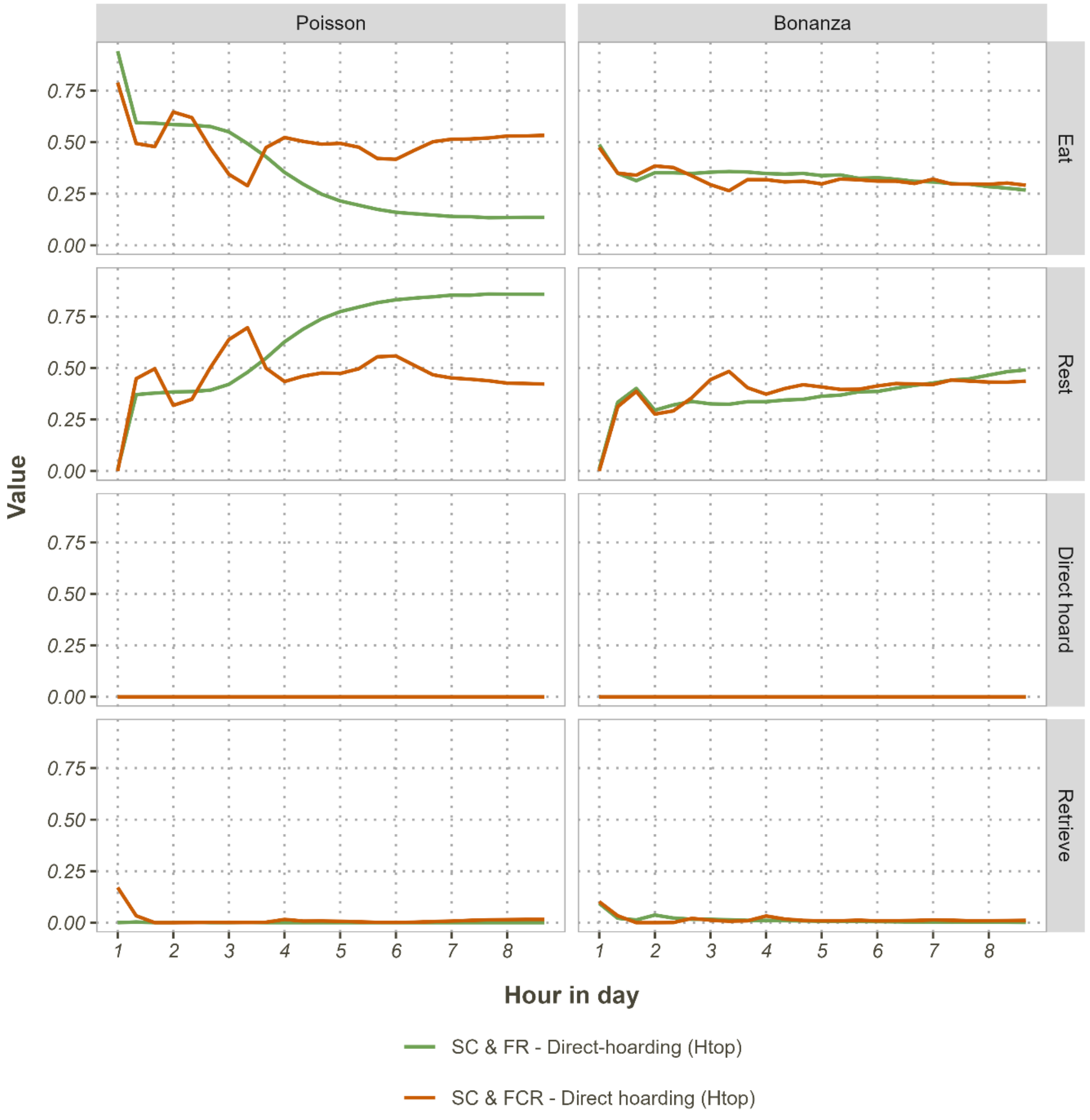


Figure E.5. Fluctuations in eating, resting, hoarding, and retrieving behaviour for direct-hoarding models 5.3 and 6.3 in the two default environments aggregated across days 4-30 in the simulation. The x-axis reflects the number of hours after sunrise in the day. The y-axis reflects the proportion of birds exhibiting the behaviour in each timestep. Values are proportions across alive birds at each timestep within the day across days 4-30 in the simulation.

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