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Food provisioning in the Barn owls (*Tyto alba*): daily activity, prey handling and effect of rain.

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M-ECOL: Ecology

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With my deepest gratitude,
Rachel Ann Elder

Rachel Elder

ABSTRACT

Climate change has been an important phenomenon to research, especially as more studies come out detailing new effects of it. Most studies have been broad in scope, but it is important to gain a more detailed understanding of how climate change may affect populations and environments. This study set out to clarify the relationship between precipitation levels and the amount of prey delivered to the nest by barn owl (*Tyto alba*) parents during the nestling period, as well as analyze other factors in nest provisioning by barn owl parents. I observed cameras in two barn owl nests, one in Winterswijk, Netherlands and one in Somerset, UK, from May to the end of July 2021. I found that the parents at the Winterswijk nest only delivered prey during the night, but the parents at the Somerset nest made deliveries during both the night and the day. The probability of female delivery increased as the nestlings grew older at both nests. The probability of nestlings feeding with parental assistance decreased at both nests as nestlings grew older. The point at which it was equally probable for nestlings to feed with assistance as without assistance was 33 days at the Winterswijk nest and 23 days at the Somerset nest. Prey from the Soricidae family had an earlier decrease in the probability of assisted feeding than prey from Muridae or Cricetidae at the Winterswijk nest, perhaps because they are easier to swallow whole. They also had a lower probability of being stored than prey from Cricetidae at both nests and prey from Muridae at the nest in Winterswijk, possibly for the same reason. The probability of prey being stored decreased in both nests as nestlings grew older. Field voles (*Microtus agrestis*) were the most frequently delivered prey that could be identified at the species level (40%). Mice could not be identified at the species level, but all members of the Muridae family made up 10% of the prey delivered, and common shrews (*Sorex araneus*) made up 5%. Much of the 1,732 prey items recorded were unidentifiable (26%) or could only be identified as mammals (17%) and 74% of prey were identified as some form of small mammal. Rainfall was not shown to be a significant factor in the number of prey items delivered during the night in Winterswijk, but the amount of rain the day before had a significant negative effect on the number of prey delivered during the day in Somerset. Nestling age was the most important factor affecting the amount of prey delivered. This study only analyzed the effect of daily rainfall rather than hourly, so more comprehensive analyses are needed to yield more conclusive results going forward.

Keywords: *Tyto alba*, Barn Owl, precipitation, weather, climate change, nest provisioning, diel activity, prey selection

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INTRODUCTION AND BACKGROUND

Background

Scientists have been researching global climate change for decades and tracking its impact over time. Large-scale impacts such as extreme temperature events have become more common in the last century, and the climate has warmed by a considerable amount (Schär et al., 2004). The rate of this warming is exponential, and recent warming rates are greater now than in the past 1000 years (Walther et al., 2002). These are concerning findings as such changes may affect the population dynamics of species across the entire globe. Some dynamics are related to seasonality, such as species phenology, and some may change with altered landscapes, such as species range shifts and changes in the assemblages of species in ecological communities. All of these can, in turn, affect species interactions and have other unknown effects that are yet to be studied (Walther et al., 2002). Since these ecological effects are dependent on time and space, emphasis should be placed on conducting regionally specific studies to evaluate these effects on local ecosystems and species population dynamics.

In many species, individuals will alter their behavior in response to changing environmental conditions (Wong & Candolin, 2015). As such, behavioral plasticity is tantamount to adapting to climate change. Behavioral plasticity allows individuals to change the way they usually operate, a quality that may improve their fitness and likelihood of reproducing as the changing climate makes their previous behaviors less profitable, more dangerous, or impossible. One example of the importance of this quality in a changing world is how birds in urbanized landscapes have changed their vocal signals. This is meant to counteract noise pollution in the city so that their vocal signals might have a better chance of being heard. Another example is how some species have changed their foraging behavior in areas with more humans and traffic to avoid humans and vehicles (Wong & Candolin, 2015). On the other hand, behavioral plasticity may end up being to a detriment, such as when features in urbanized habitats (e.g., noise and light pollution) can impair sensory abilities, confuse habitat quality assessment abilities, or interfere with physiological processes (Wong & Candolin, 2015). When these behavioral changes extend to the factors affecting population growth or decline (birth, death, and migration) they have the potential to impact these species at the population level (Wong & Candolin, 2015). Therefore, when the changes are beneficial to native species, they can positively affect the population in areas such as urbanized habitats that have experienced human disturbance. However, if these changes are detrimental to native species, they could have an overall negative effect on the population in a disturbed area.

Behavioral plasticity can change species' interactions with each other as well as with their habitats. Species that disappear from a changed environment and adapt to a new one can become invasive to native populations if they are too successful and face little resistance (Wong & Candolin, 2015). This ability to change behaviors benefits the non-native species but harms the native species. Consumer-resource interactions, notably predator-prey interactions, can also be affected by climate change through altering traits such as search rate, detection distance, speed, and handling time (Wong & Candolin, 2015). Foraging behavior is yet another trait that can be affected by climate change. The aim of foraging strategies is to maximize energy gained over energy spent foraging (Ydenberg et al., 1994).

Aside from possibly affecting plasticity and foraging behavior, environmental changes might also affect prey availability. This can happen through phenological miscuing, as can be seen in some English counties, where researchers have observed trends toward earlier spring arrivals for many species (Crick, 2004). The phenomenon increases the chance of phenological mismatches between local species that normally interact. In the case of owls, this could be an issue if the time of hatching differs from seasonal fluctuations in the local rodent populations, thus influencing prey availability at a most crucial time in hatchling development. Another relevant example is how the influence of climate change on rodent population growth could lead to changes in foraging strategies for owls. This change in rodent population growth has already been observed during winter NAO (North Atlantic Oscillation) (Šipoš et al., 2017). If one year's winter NAO coincides with local inclement weather events, it could be the deciding factor in an owl family's breeding season being successful or not.

Other behaviors which are relevant to my study are diel activity, prey selection and prey handling (such as the sex of the provisioning parent, if nestlings feed assisted or unassisted, if prey is stored or eaten right away), as well as how nestling age affects these behaviors. While barn owls (*Tyto alba*) are primarily nocturnal where diel activity is concerned, there have been some cases of daytime activity within the species. Barn owls in Scotland, England and some Pacific islands are known to sometimes hunt during the day, and one of the nests I monitored was in England (Bruce, 1999). Prey selection gives some insight into the predator-prey dynamics at each location as it can be affected by prey availability, prey habitat selection, expected handling time, expected delivery rate, and the sex of the delivering parent, although barn owls show a strong bias in favor of small mammals in their diet (Bruce, 1999; Steen et al., 2012). The sex of the delivering parent can be affected by several factors as well. Females tend to brood rather than hunt in the earlier stages of the nestling period and will emerge to hunt around when the males decrease their rate of deliveries at the nest while also considering the minimum age that the nestlings can be left unattended (Durant et al., 2004). How the nestlings feed is also connected to many other elements I observe in this study. The age of the nestlings, as well as prey selection are all factors that can affect whether a nestling feeds with or without parental assistance (Sonerud et al., 2014a; Sonerud et al., 2014b). Whether nestlings feed assisted or unassisted, as well as prey selection and nestling age, in turn, may affect whether prey is stored as the female parent may select which prey to feed the nestlings, or the nestlings may decide to store prey when unattended based on food demand, handling time and whether they can swallow certain prey whole (Durant, 2004; Steen, 2012; Durant, 2013). Nestling age especially ties into all these factors as they are left unattended more often and can eat larger prey and eat with less assistance as they grow older (Durant et al., 2004; Sonerud et al., 2014a). Nestling age is also a major determining factor in food demand at the nest based on raptor nestling metabolism rates, which are affected by their stage of growth at a given point in their development (Steen et al., 2012). This rate often peaks around the time nestlings achieve their final body mass (Steen et al., 2012). My study examines all these dynamics in the two barn owl nests I monitored over the nestling period.

The common barn owl (*Tyto alba*) is a nocturnal bird of prey and a member of the owl family Tytonidae. Typical features of the barn owl are medium size, long legs, a heart-shaped white face and light brown plumage with juveniles and adult females tending to be slightly darker and more heavily spotted than adult males. It is one of the most widespread land bird species in the world (Figure 1) and can be found on every continent except for Antarctica (Bruce, 1999). Its preferred habitats include lowlands with scattered tree cover and hilly areas with a sufficient supply of small mammals (Bruce, 1999; Debruijn, 1994). Barn owls frequently occupy man-made landscapes that have non-intensive agricultural use, and the length of hedgerows, tree lines and woodland edges in such areas positively correlate with barn owl breeding density (Bruce, 1999; Debruijn, 1994). Decreases in foraging areas and food supply due to habitat loss and urbanization of countrysides are cited as large factors in the long-term decrease in barn owl populations (Bruce, 1999). Adverse climate conditions also seem to play a role in barn owl population decline (Bruce, 1999).

Changes to predator-prey relationships in an ecosystem are concerning as they may disrupt an ecosystem through top-down and bottom-up effects (Wong & Candolin, 2015). Most scientific understanding of the effects of climate change is in broad terms. Because of this, the study aims to narrow those terms down to a smaller, more specific scale and focus on determining the relationship between precipitation caused by climate change and western European barn owl nest provisioning. One climate-affected change that I will focus on in this study is increased precipitation, which has been observed in parts of the northern hemisphere (Walther et al., 2002). This is especially concerning as precipitation has the potential to influence foraging conditions for birds (Crick, 2004). For barn owls in western Europe, foraging is made less profitable as wind and rain increase, a pattern that is expected to become more frequent or extreme as the climate changes. This may make hunting less efficient for barn owls (McCafferty et al., 2001). Roosting can help barn owls conserve energy on wet days, but this strategy is not a panacea. If it becomes more frequently employed over time, the decision to favor energy saved by roosting over energy gained by hunting might eventually lead to declining fitness and population-level consequences (McCafferty et al., 2001).

This study is a follow-up to Arne Thomas Glåmseter's thesis on the same topic for the purposes of checking the conclusions of the previous study and possibly uncovering new findings (Glåmseter, 2021). My study focuses on the local scale and aims to analyze the relationship between changes in weather and barn owl foraging and to predict how specific variables such as prey availability and diet composition may change for the barn owl. These predator-prey interactions are especially relevant to the study as I examine the foraging behavior of barn owls. It is necessary to analyze not only the global effects of climate change, but also smaller, more local-scale effects such as changes to foraging behavior in barn owls so that the scientific community can paint a more comprehensive and detailed picture of what to expect in the coming years as our climate continues to change. This study will specifically analyze the relationship between the amount of prey delivered and rainfall, nestling age, diel activity, which parent delivered the prey, what kind of prey was delivered, if nestlings ate assisted or not and if prey are stored or not.

MATERIALS AND METHODS

Study area and study species

The project monitored 2 common barn owl (*Tyto alba*) mated pairs and their hatchlings in the Netherlands and United Kingdom, respectively. The nest in the Netherlands is in Winterswijk (51.93°N, 6.72°E) and the nest in the UK is in Somerset (51.04°N, -2.88°W) (coordinates are approximated to the nearest city since the organizations requested not to publish exact coordinates of the nests) (Figure 1).

The climates in the UK and the Netherlands are cloudy and temperate and have considerable precipitation. In the Köppen-Geiger climate classification system, these regions both fall under the classification of oceanic climate (Cfb) (Peel et al., 2007). It is becoming more evident that the occurrence of extreme climate events is becoming more frequent in Europe, and extreme precipitation is expected to occur more frequently in the UK and Netherlands (Schär, 2004; Daniels, 2016; Christidis, 2021).

Barn owls in such climates use a strategy called roosting to compensate for rough weather patterns and to conserve energy (McCafferty et al., 2001). In Europe, they typically will roost in farm buildings and tree holes. This strategy allows them to replenish some energy lost when foraging. The impending threat of weather patterns in the Netherlands and UK becoming wetter and windier has the potential to negate some of the mitigating effects of roosting, decreasing the energy profitability of roosting. If this does end up being the case, it may lead to declines in the overall fitness of barn owls.

The common barn owl has a widespread distribution, but my study focuses on barn owls in western Europe (Figure 1). Within the Netherlands, the distribution of mated pairs is mostly even across the country with a slightly higher concentration in the south and east (Sovon, 2018). In the UK, barn owl distribution is most concentrated in the southern portion of the country, especially along the east coast (The Barn Owl Trust, 2014). However, this data comes from volunteer sighting records, so it is also possible that the lack of records in the northern regions is due to lower volunteer activity in those areas since the terrain is more mountainous and human populations lower than in the south.

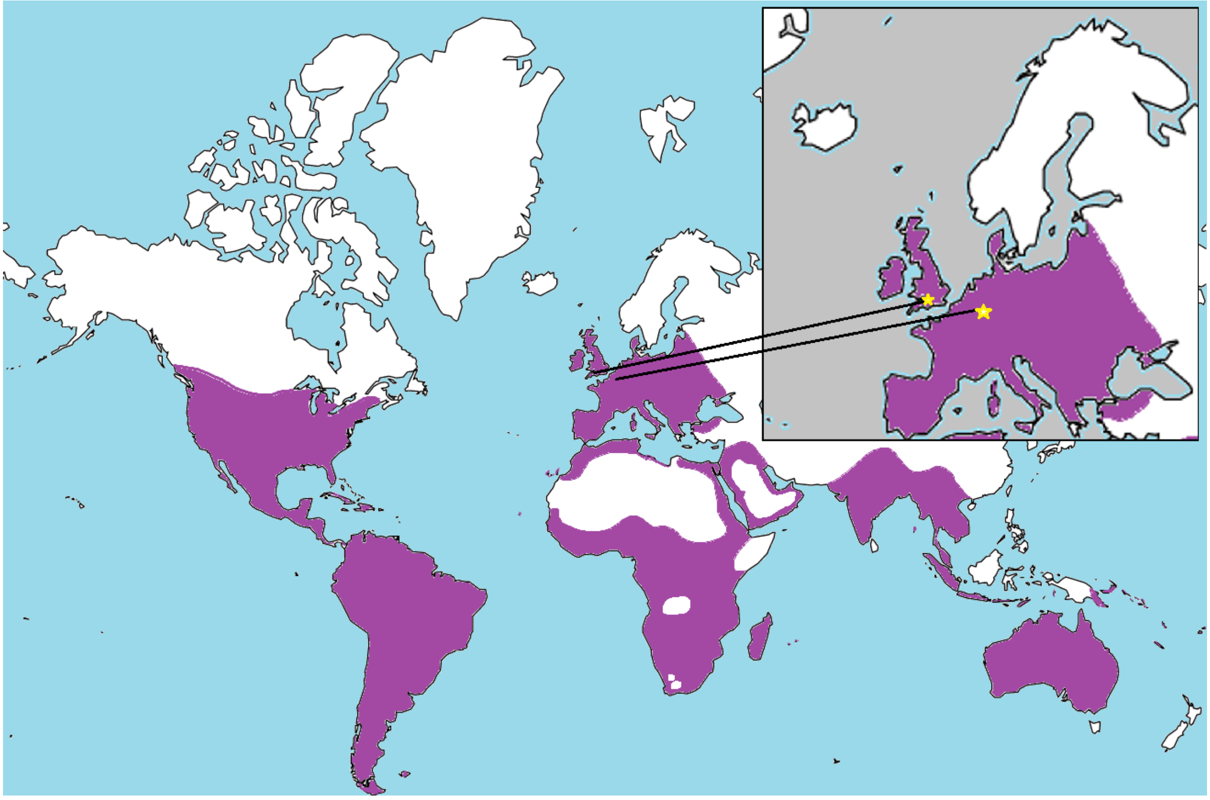


Figure 1. Worldwide distribution map of the common barn owl (*Tyto alba*), excluding Antarctica, as of 1999, with a special focus on Europe. The two locations, Winterswijk and Somerset, are depicted with yellow stars. This work 'Tyto alba world distribution', is a derivative of 'Creative commons vector clip art of political map of the world showing all the continents. Outline map of each continent in the world.' by OpenClipart used under Public Domain (2014). 'Tyto alba world distribution' was altered from the original work by Rachel Ann Elder after the map provided by Bruce (1999).

The nest in Winterswijk lies along the border with Germany. According to a correspondent at the Kerkuilen Werkgroep Nederland Foundation, it is in a reclaimed heathland landscape within a small-scale mosaic of intensive agricultural plots, small forest plots, wooded banks and various diverse scattered natural areas. Barn owl density in this area is high with 6-7 territories per atlas square ('atlasblok' in Dutch; a 5 by 5 km area used in national inventories in the Netherlands) on the Dutch side of the border (M. Mombarg, pers. comm.). The soil stays wet for a long time after rain in the spring due to an impermeable boulder clay layer present at a shallow depth throughout the area. The local mouse population breeds fairly late in the area due to early spring flooding, and 2021 was a rather cold spring (M. Mombarg, pers. comm.). The nest in Somerset is in the Levels near residential and agricultural areas. The owls at this nest are used to human presence and are even spotted during the daytime by the owner of the nest box. The Somerset Levels are managed wetlands with flat, wet meadows with ditches along the edges and low hills (The Royal Society for the Protection of Birds (RSPB), 2022). This area is especially significant to biodiversity and is one of Somerset's most protected landscapes (Somerset Wildlife Trust, 2022).

Western European barn owls typically lay eggs in March or April and incubate them right away. These clutches of eggs tend to consist of 4 to 6 eggs. In my study, both the Netherlands female and the UK female laid 6 eggs. In most cases, the eggs will hatch after about 30 days of incubation. The nestlings will stay in the nest for roughly 8 weeks until they eventually leave the nest (McCafferty et al., 2001). During this period parents will hunt for the offspring until they can hunt for themselves (around the beginning of August in western Europe). (Honer, 1963).

Barn owls are quite particular about their diet and have little flexibility in what they eat. Small mammals make up 74-100% of the common barn owl diet, with this typically being composed of only a few species, especially rats and mice (Muridae) worldwide, and voles (Cricetidae), gophers (Geomyidae) and shrews (Soricidae) in Europe (Bruce, 1999). Most of the rodents and shrews I expected to identify in this study include the short-tailed vole (*Microtus agrestis*), the common shrew (*Sorex araneus*), the wood mouse (*Apodemus sylvaticus*), the yellow-necked mouse (*Apodemus flavicollis*), the brown rat (*Rattus norvegicus*), the bank vole (*Clethrionomys glareolus*), the house mouse (*Mus musculus*), the pygmy shrew (*Sorex minutus*), the water shrew (*Neomys fodiens*), the water vole (*Arvicola amphibius*), the mole (*Talpa europaea*), the harvest mouse (*Micromys minutus*), and the rabbit (*Oryctolagus cuniculus*) (Glue, 1974). Barn owls in Europe will sometimes hunt other vertebrate and invertebrate prey, but it is less common. Rodent population cycles are even suspected to cause fluctuations in barn owl populations (Honer, 1963).

Data collection and data processing

I had access to cameras in 2 nests that I monitored and recorded data from, with permission from cooperating non-profit organizations that set up the cameras and streamed footage of the nests. The first nest located in Winterswijk, Netherlands was recorded by Vogelbescherming Nederland (Figure 2) (Vogelbeschirming Nederland, 2021), and the second in Somerset, England was recorded by Hawk and Owl Trust (Figure 3) (Hawk & Owl Trust, 2021). The types of cameras used varies between nests and organizations.

Both nests were streamed and recorded continuously until the end of the data collection period. I had different methods for recording and storing streams depending on the stream service used by each organization. The data from Vogelbescherming Nederland was recorded using OBS Studio (Bailey & OBS Studio Contributors), where the URL of the stream was set as the source to screen-record, with permission from Vogelbescherming Nederland. The data from Hawk and Owl Trust was provided by the organization granting me access to their cloud drive where their own recording of the full stream was stored. This data was all downloaded to an external hard drive as well. The nest in Winterswijk could be viewed from 3 different cameras, one inside the nest and two outside the nest. The nest in Somerset only had one camera which was situated inside the nest.

Figure 2. Inside view of the nest in Winterswijk with a minimized view outside of the nest window on VSPlayer (Hangzhou Hikvision Digital Technology Co. Ltd., 2022; Vogelbeschirming Nederland, 2021).

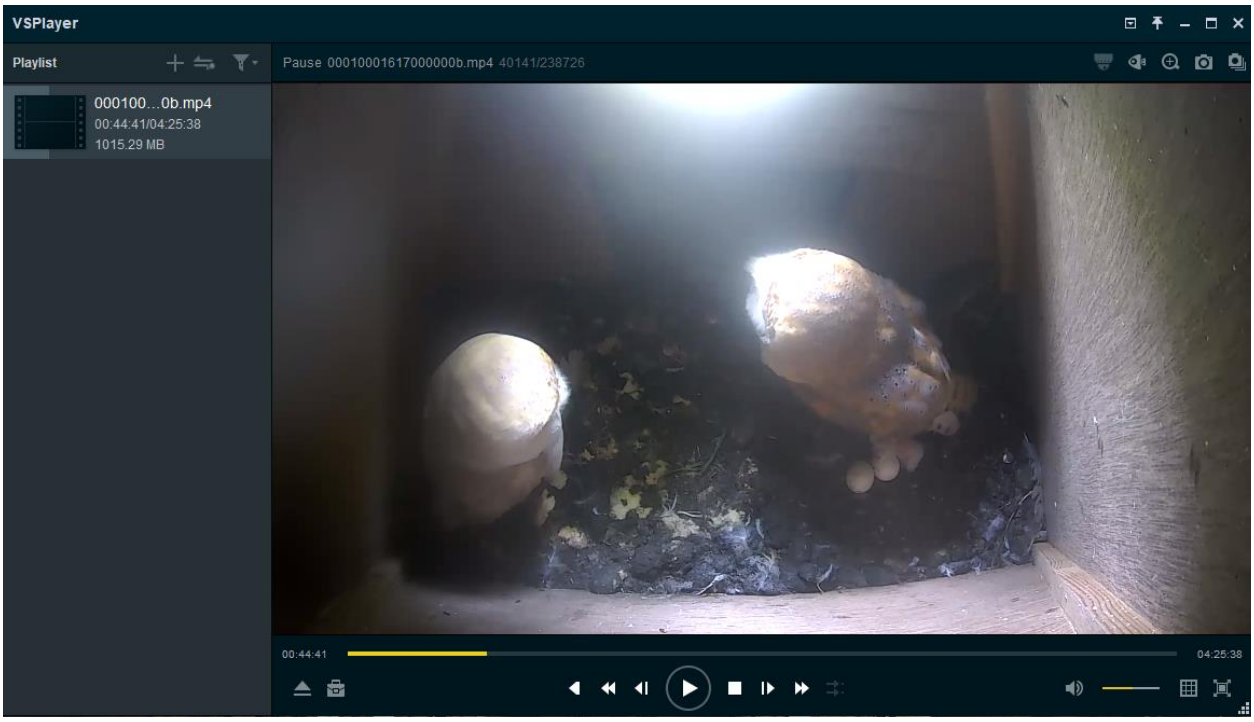
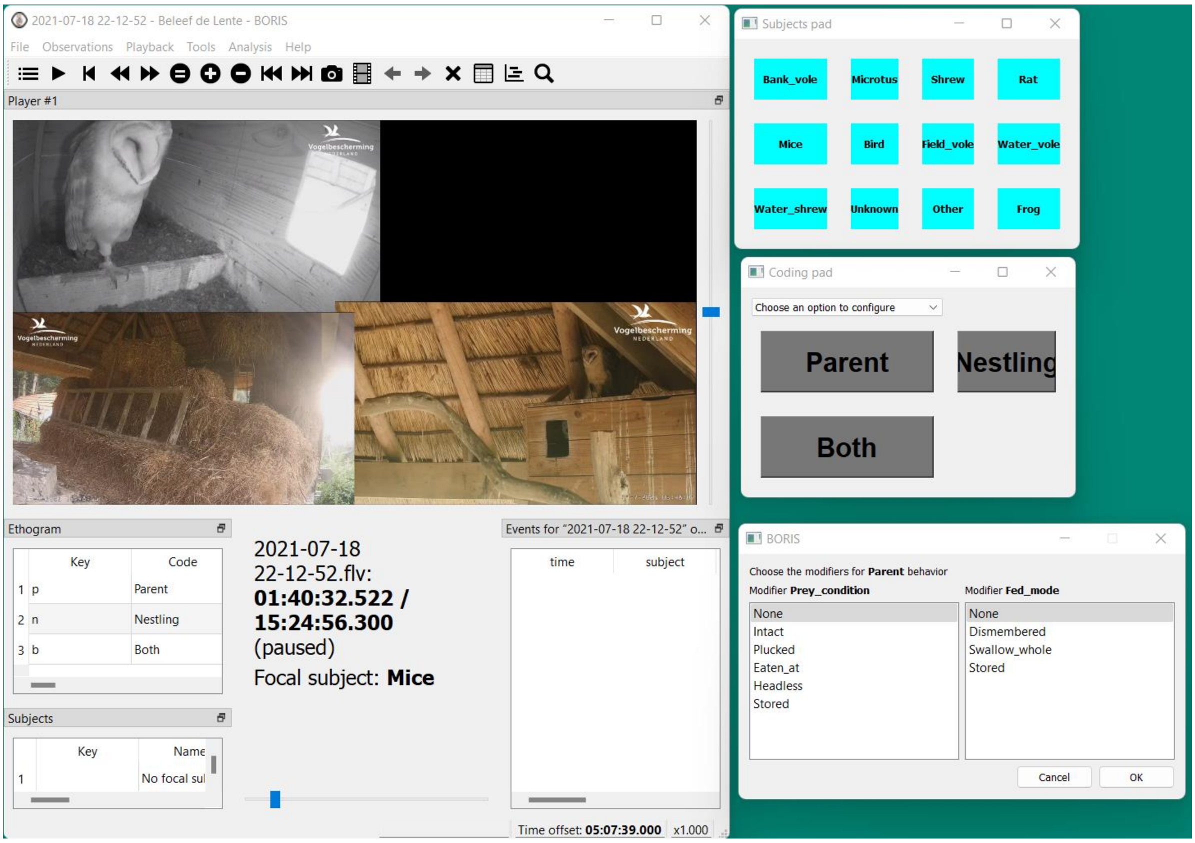


Figure 3. Inside view of the nest in Somerset on VSPlayer (Hangzhou Hikvision Digital Technology Co. Ltd., 2022; Hawk & Owl Trust, 2021).

Data collection for Vogelbescherming Nederland began May 21, 2021, 9 days after the first egg hatched (since that is how long it took to get the screen-recording running smoothly), and ended July 31, 2021, when the hatchlings were mostly independent. Data collection for Hawk and Owl Trust began May 10, 2021, the day the first egg hatched, and ended July 12, 2021, when the hatchlings were mostly independent and doing a large portion of their feeding outside of the range of the camera. The type of data collected was the kind of prey brought to the nest, the amount of prey brought to the nest, the age of the nestling at each event, which parent delivered the prey, the condition the prey was delivered in, how the prey was handled at the nest and the time and date prey was brought to the nest. I used Behavioral Observation Research Interactive Software (known as BORIS) (Friard & Gamba, 2016) to parse through the footage amassed and make observations when prey was brought to the nest to manually evaluate these variables which were used in the statistical analyses. I used BORIS to identify prey with co-supervisor Geir Andreas Sonerud. Over the course of several weeks we paused, replayed, and zoomed in on the footage for each observed prey delivery and determined prey ID using species description and Dr. Sonerud's prior experience identifying small mammals that feature in barn owl diets. The prey type categories are prey group, order, family and species, but how specific the categories are depends on how identifiable each prey item is from the footage. Less distinct species were grouped together in their genus or families when exact species could not be determined from the video quality (Steen, 2010). Behavior categories were determined in much the same way as prey species. While recording initial observations in BORIS, I observed which parent delivered the prey. In Winterswijk this was determined by brooding behavior early in the nestling period and by ring status after each parent's sex was established (the male had a ring on his leg and the female did not). In Somerset this was determined by brooding behavior early in the nestling period and by feather pattern after I became familiar with each parent's appearance (the female being darker and more heavily spotted, as is typical in barn owls) (Bruce, 1999). While recording prey deliveries in BORIS, I took note of whether prey was delivered with their head attached or decapitated, and after the delivery I watched for the first 10 minutes after delivery to see if prey was swallowed whole by the nestling (feeding unassisted), dismembered by the female and fed to the nestlings (feeding assisted), dismembered by the nestling and eaten (feeding unassisted) or stored by either the female or nestlings (Figure 4). The weather data was collected by taking the daily precipitation from Meteo Bredevoort in the Netherlands (Meteo Bredevoort, 2021) and the Met Office in the UK (Met Office, 2021).



	Key	Code
1	p	Parent
2	n	Nestling
3	b	Both

2021-07-18 22-12-52.flv: **01:40:32.522 / 15:24:56.300** (paused)

Focal subject: **Mice**

Subjects

	Key	Name
1		No focal sul

time	subject

Time offset: **05:07:39.000** x1.000

Choose the modifiers for **Parent** behavior

Modifier **Prey_condition**	Modifier **Fed_mode**
None	None
Intact	Dismembered
Plucked	Swallow_whole
Eaten_at	Stored
Headless	
Stored	

Figure 4. Data collection setup in BORIS (Friard & Gamba, 2016). At this stage in Nestling development, all 3 cameras were included in the observation window. To the right are the subjects and coding pads as well as behavior modifiers to record each observed delivery and prey handling.

When processing the data, I noticed irregularities in the timestamps for prey events in the Somerset nest. The owner of the camera provided documents for each set of recordings listing the start and end time and date for each file. Unlike the Winterswijk nest, the Somerset nest did not display the timestamp on the footage, and footage from this nest also needed to be re-encoded for it to be processed in BORIS (Friard & Gamba, 2016). This led the footage from Somerset to be compressed in some manner, and video files that had been re-encoded were often shorter in duration than the original file, and the time calculated in BORIS for each event was therefore inaccurate. Since time and date are important to the analysis for daily activity and daily rainfall, I looked for a solution to find the accurate time of each prey event. It was also important to ensure that prey events were not missed due to any frames being dropped from the re-encoded videos. The owner of the camera was contacted to find out which company it was from and which video player was most compatible with this format of video. It was determined that VSPlayer from Hikvision was the most compatible with the original video files and provided the most accurate timestamps when confirming the duration and start and end time of each clip with the documents provided to us (Hangzhou Hikvision Digital Technology Co. Ltd., 2022). I deemed it necessary to review any video file that had a time difference of 10 minutes or longer between the original file and re-encoded file. This criterion is most likely sufficient since time must be accurate to the hour, not minute, of a delivery. The original files that met this criteria were run in MotionMeerkat to detect prey events in each file (Weinstein, 2015). The settings used for this were background variation = 3, speed of target organism = 3 and minimum object size = 20%. I also cropped the area of motion detection to approximately the top 20% of the screen since prey were delivered from the top of the nest box. When a file was processed in MotionMeerkat I then compared the events detected with those found in BORIS to check if any events were cut in the re-encoded files as well as to find the accurate time of each event. Time and date were accurately displayed in VSPlayer as far as I was able to determine, so the time data was updated to fit what was displayed for each prey item from files I ran. There did not seem to be any prey events cut from the re-encoded footage, but cross-referencing data entries in MotionMeerkat and VSPlayer provided more accurate time data. After I was satisfied that the time for each prey event was represented as accurately as possible in the data I moved on to the analysis.

Statistical analysis

All statistical analyses were conducted in R (R Core Team, 2022). To estimate daily prey delivery patters with activity plots, I used the R package ‘Activity’ v. 1.3.1 (Rowcliffe, 2022) for each location separately. To compare these activity patterns between locations I used the R package ‘Overlap’ v. 0.3.4 (Meredith & Ridout, 2021). The estimator Δ_4 was used to calculate the overlap coefficient (Meredith & Ridout, 2021). The coefficient of overlap Δ_4, known as ‘Dhat4’ in R, is a nonparametric descriptive variable for temporal overlap between two different kernel density curves. Where $\Delta_4 =0$ there is no overlap, and when $\Delta_4 =1$ there is a complete temporal overlap between pairs of variables. I considered Δ_4 0.75 as high degree of temporal overlap between observations of the compared variables, as defined by Monterroso et al., (2014). Bootstrapping for the estimated 95% confidence intervals for Δ was done using the function ‘overlap’. The Mardia-Watson-Wheeler test (from the ‘circular’ package) was used to test if the activity patterns differed significantly between the two localities (Portugues, 2022).

For each nest, I tested for asymmetric parental roles in terms of providing food to the nestlings. The response variable for this was delivering parent (female vs. male). The explanatory variables were nestling age, prey group and the interaction term. In addition to nest provisioning, I also tested the probability of parents assisting the nestlings in feeding on the prey (feeding assisted vs. unassisted). This test had the same explanatory variables used in testing for nest provisioning. Next, I tested the probability of prey being stored (stored vs. not stored) with the same explanatory variables as the previous above. For these analyses, I used generalized linear effects models (glm), logistic regression with binomial distribution, from the ‘stats’ package. Each test was run separately for each location.

For each nest, I tested the probability of the 3 main prey families (i.e., voles (Cricetidae), mice (Muridae) and shrews (Soricidae)) delivered at the nest differing throughout the nestling period. I used multinomial log-linear model (function ‘Multinom’ from the ‘nnet’ package), with 3 main prey group as response variable and nestling age (days) as explanatory variables (Ripley, 2022).

For each nest, I tested if the number of prey deliveries during the night was affected by nestling age (days), rainfall (mm) and rainfall the day before (mm). Nestling age was also a control since prey delivered is partially governed by nestling food demand, which is affected by their age (Steen et al., 2012). The variable rainfall (mm) refers to current rainfall, which is rain that fell from 20:00 the day before to 20:00 on the current day. These times were chosen since most of the period occurs after midnight. The variable rainfall the day before (mm) refers to rain that fell from 20:00 two days before to 20:00 one day before. I used the quadratic term ‘nestling age^2’ to see if there was a non-linear relationship (Steen et al., 2012). Similarly, for Somerset only given that there were no prey deliveries during the day at Winterswijk, I tested if number of prey deliveries during the day was affected by nestling age (days), rainfall (mm) and rainfall the day before (mm). I used the quadratic term ‘nestling age^2’ to see if there was a non-linear relationship.

For all the models with several explanatory variables and interaction terms I tested which models were the best using the ‘AICcmodavg’ package (Mazerolle, 2020). The best models were chosen based on which had the lowest AICc or was the most parsimonious model (Burnham et al., 2011).

For graphical presentation I used ‘ggeffects’ to get predictions and ‘ggplot2’ for creating the graphs (Wickham, 2016; Lüdecke, 2018).

RESULTS

Daily activity

Periods for sunrise and sunset were determined in R (appendix 7). Night was defined as 21:00-5:00 (including the whole hour 5), while day was defined as 6:00-20:00 (including the whole hour 20). Curves displaying the distribution of activity throughout the day in both nests for the most common prey families identified show clear nocturnal patterns for the Winterswijk nest, with almost no activity taking place after sunrise and before sunset (Figure 5). The Somerset nest, on the other hand, had some activity peaks during daylight hours, especially for the prey families Cricetidae and Soricidae (Figure 5).

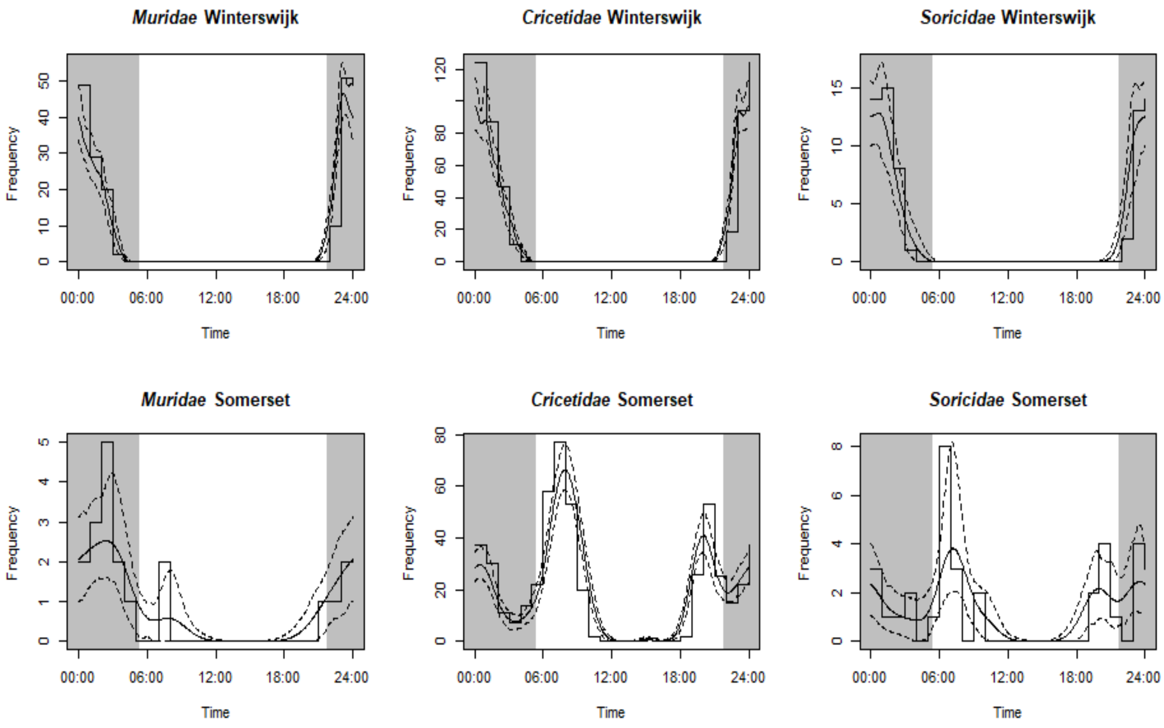


Figure 5. Diel activity curves of distribution of prey delivered from each prey family in each nest throughout the day. The shaded areas are what I considered nighttime for my study. The dotted lines above and below the curve are the 95% confidence intervals.

Frequency (Overlap)

Overlap between activity in Winterswijk and Somerset was calculated for the most frequently delivered prey families (Figure 6). There was the most overlap for the family Muridae with a Dhat4 value of 0.59 and Watson-Wheeler test value of 8.4 (Appendix 8-9). There was very little overlap in activity between Winterswijk and Somerset for the Cricetidae family (Dhat4 = 0.26) and for the Soricidae family (Dhat4 = 0.34) (Appendix 8-9). The Somerset nest has far more diurnal activity than the Winterswijk nest (Figure 5).

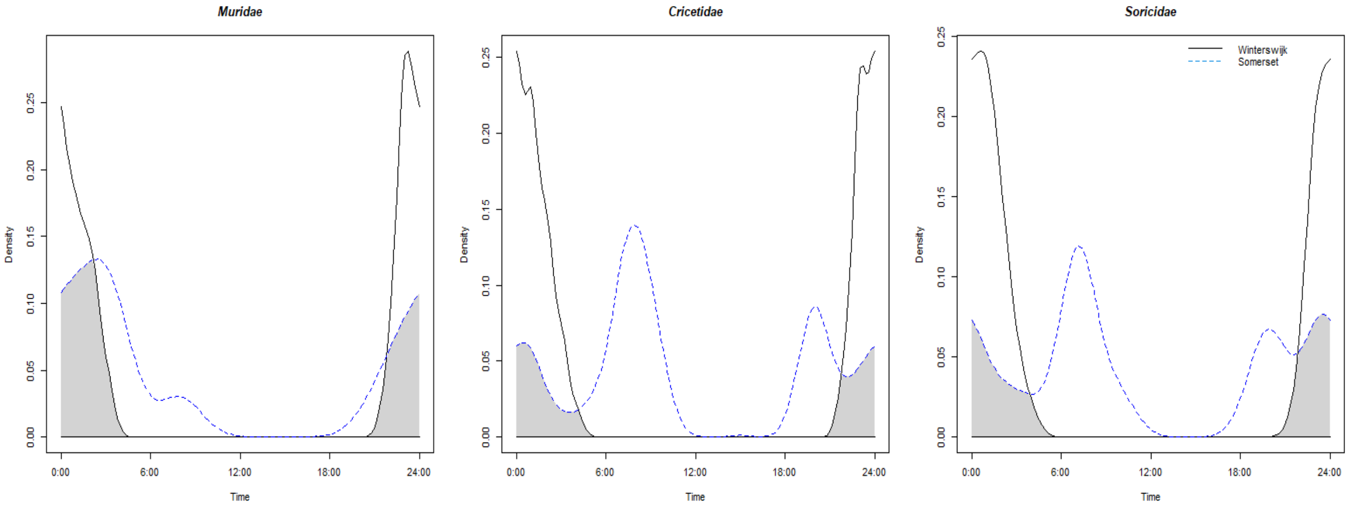


Figure 6. Kernel density curves of activity throughout the day across prey family at both nests and the overlap between them. The solid curve represents the nest in Winterswijk and the dotted curve represents the nest in Somerset. The shaded area represents where activity at the nests in Winterswijk and Somerset overlap in time and density.

Prey handling

Delivering parent

The Winterswijk subset of data where the delivering parent could be identified includes 577 data points. The model with nestling age (days) and prey family was the best model (Appendix 1). Other models which were tested and discarded due to lower fit include nestling age (days) only, prey family only, and the interaction between nestling age (days) and prey family (Appendix 1). All parameter estimates in the best-fitted model were significant (Table 1). The probability of the female parent delivering prey increased across all prey families as the nestlings grew older, especially for the family Soricidae (Figure 7).

The Somerset subset of data where the delivering parent could be identified includes 298 data points. The model with nestling age (in days) and prey family was the best model (Appendix 2). While it has a close AIC value to another model, this one was less complex. Other models which were tested and discarded due to lower fit include nestling age (days) only, prey family only, and the interaction between nestling age (days) and prey family (Appendix 2). All parameters in the best-fitted model were significant predictors except for the Muridae prey family (Table 2). The probability of the female parent delivering prey increased across all prey families as the nestlings grew older, especially for the family Soricidae (Figure 8).

Table 1. Parameter estimates of the best-fitted model for the effect of nestling age (days) and prey family on the probability of female delivery of prey in the Winterswijk nest by barn owls (n = 577), intercept = Cricetidae family.

Coefficients	Estimate	Standard error	z	P
(Intercept)	-3.99	0.41	-9.71	<0.001
Nestling age	0.08	0.01	7.25	<0.001
Muridae family	0.88	0.22	3.93	<0.001
Soricidae family	2.62	0.36	7.22	<0.001

Figure 7. Probability of female delivery by nestling age and prey family in Winterswijk. The solid lines are the probability curves for each prey family and the shaded areas are the confidence intervals.

Table 2. Parameter estimates of the best-fitted model for the effect of nestling age (days) and prey family on the probability of female delivery of prey in the Somerset nest by barn owls (n = 298), intercept = Cricetidae family.

Coefficients	Estimate	Standard error	z	P
(Intercept)	-5.63	0.67	-8.45	<0.001
Nestling age	0.19	0.02	7.72	<0.001
Muridae family	0.06	1.02	0.06	0.96
Soricidae family	2.22	0.81	2.74	<0.01

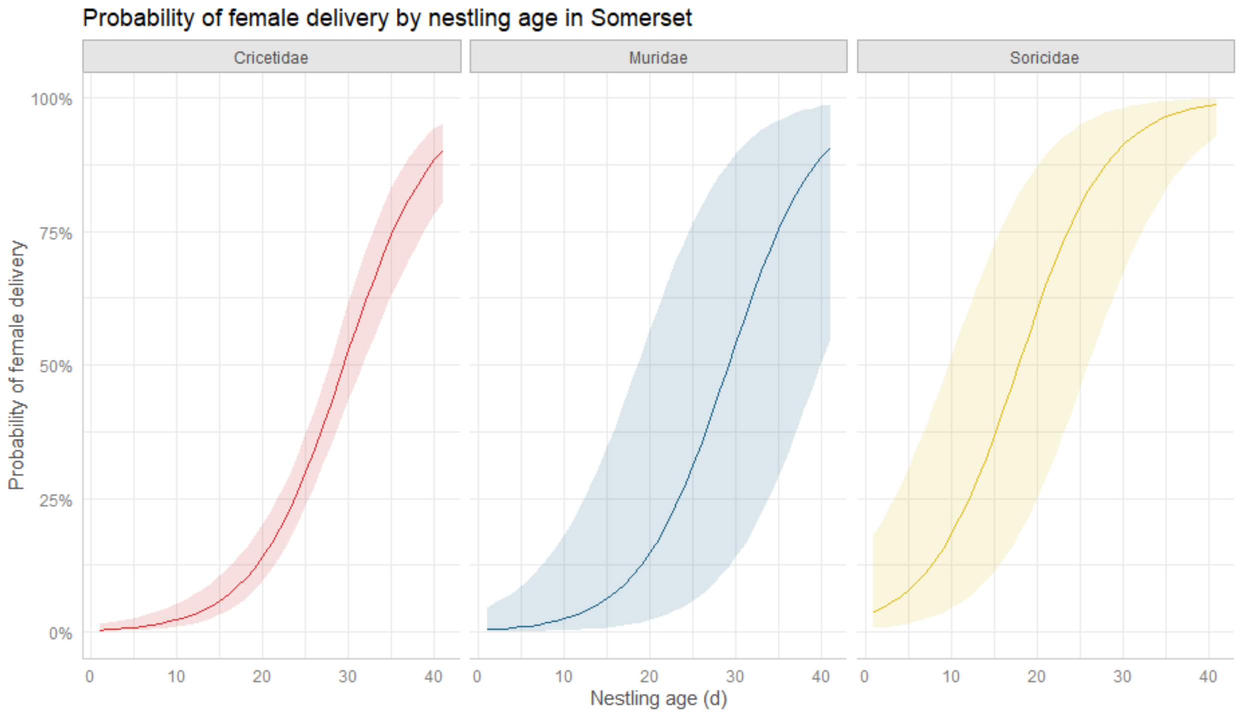


Figure 8. Probability of female delivery by nestling age and prey family in Somerset. The solid lines are the probability curves for each prey family and the shaded areas are the confidence intervals. Muridae and Soricidae had small sample sizes, hence the large confidence intervals.

Condition of prey upon delivery

Decapitated prey were too rare in my study to do an analysis, but there were still some cases of it occurring. There were 7 decapitated prey delivered to the nest in Winterswijk and 2 decapitated prey delivered to the nest in Somerset (Table 3, 4).

In Winterswijk, 6 of the decapitated prey were delivered by the male and 1 delivered by the female. Of the decapitated prey, 5 were field voles, 1 was a bank vole and 1 was a mouse. Almost all were stored by a parent, except for 1 which was dismembered by the female (Table 3).

In Somerset, 1 prey item was delivered by the male and 1 was delivered without being able to determine the sex of the parent. Of the decapitated prey, both were field voles. The parent stored 1 decapitated vole and a nestling swallowed the other one whole (Table 4).

Table 3. Demographics of prey that were delivered decapitated to the nest in Winterswijk, including prey identification, sex of the delivering parent and how the prey was eaten or stored.

Prey ID	Delivering parent	Feeding method
Field vole	Male	Dismembered by female
Field vole	Male	Stored by parent
Field vole	Male	Stored by parent
Bank vole	Male	Stored by parent
Field vole	Male	Stored by parent
Unidentified mouse	Female	Stored by parent
Field vole	Male	Stored by parent

Table 4. Demographics of prey that were delivered decapitated to the nest in Somerset, including prey identification, sex of the delivering parent and how the prey was eaten or stored.

Prey ID	Delivering parent	Feeding method
Field vole	Male	Stored by parent
Field vole	N/A	Swallowed whole by nestling

Feeding assisted or unassisted

The Winterswijk subset of data where feeder (parent or nestling) was identified includes 596 data points. The model with nestling age and prey family was the best model (Appendix 3). Other models which were tested and discarded due to lower fit include nestling age only, prey family only, and the interaction between nestling age and prey family (Appendix 3). All parameters in the best-fitting model were significant predictors except for the Muridae prey family (Table 5). The probability of the nestlings feeding assisted by a parent decreased across all prey families as the nestlings grew older and feeding unassisted occurred at a younger age for shrews than for rodents (mice and voles) (Figure 9).

The Somerset subset of data where feeder (parent or nestling) was identified includes 525 data points. The model with nestling age and prey family was the best model (Appendix 4). Other models which were tested and discarded due to lower fit include nestling age only, prey family only, and the interaction between nestling age and prey family (Appendix 4). All parameters in the best-fitted model were significant predictors except for the Muridae prey family (Table 6). The probability of the nestlings feeding assisted by a parent decreased across all prey families as the nestlings grew older and feeding unassisted occurred at a younger age for shrews than for rodents (Figure 10).

At the Winterswijk nest, the probability of a nestling feeding assisted was equal to the probability of a nestling feeding unassisted when the oldest nestling was 33 days old (Figure 11). At the Somerset nest, the probability of a nestling feeding assisted was equal to the probability of a nestling feeding unassisted when the oldest nestling was 23.3 days old (Figure 12).

Table 5. Parameter estimates of the best-fitted model for the effect of nestling age (days) and prey family on the probability of nestlings feeding with parental assistance in the Winterswijk nest by barn owls (n = 596), intercept = Cricetidae family.

Coefficients	Estimate	Standard error	z	P
(Intercept)	6.84	0.55	12.50	<0.001
Nestling age	-0.20	0.02	-12.42	<0.001
Muridae family	-0.48	0.25	-1.90	0.06
Soricidae family	-1.30	0.38	-3.46	<0.001

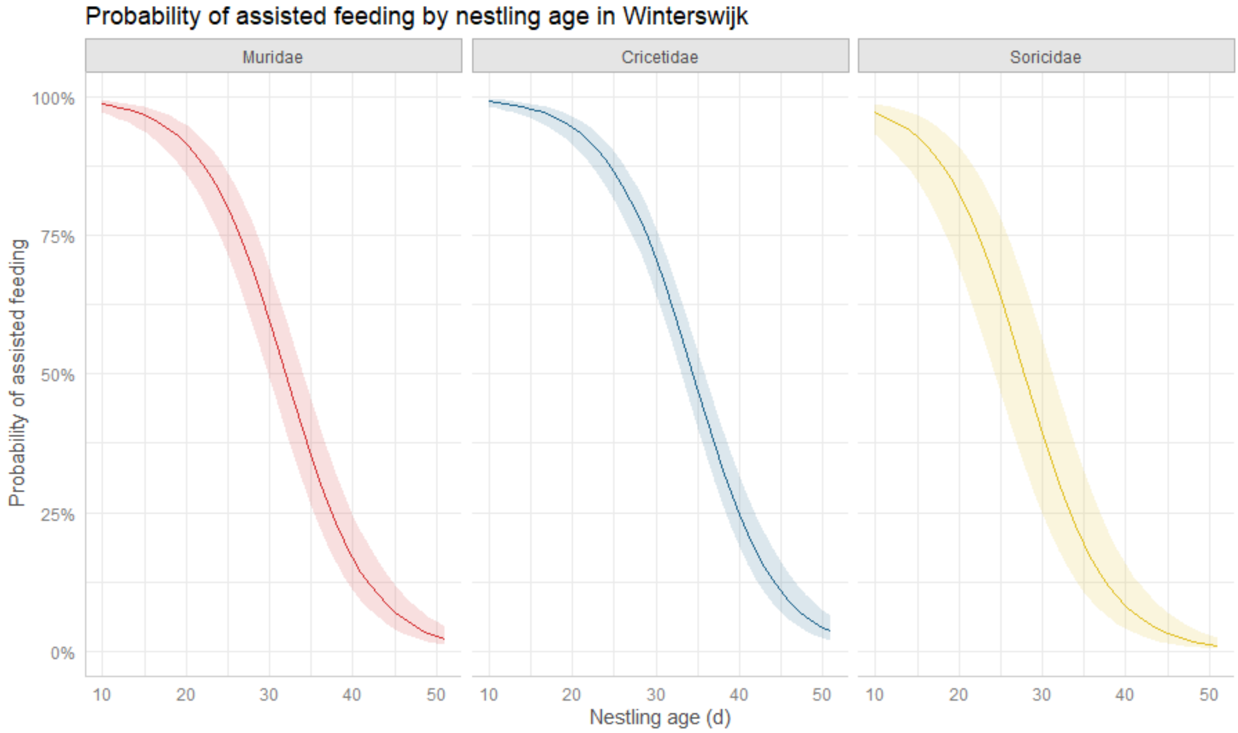


Figure 9. Probability of assisted feeding by nestling age and prey family in Winterswijk. The solid lines are the probability curves for each prey family and the shaded areas are the confidence intervals.

Table 6. Parameter estimates of the best-fitted model for the effect of nestling age (days) and prey family on the probability of nestlings feeding with parental assistance in the Somerset nest by barn owls (n = 526), intercept = Cricetidae family.

Coefficients	Estimate	Standard error	z	P
(Intercept)	12.61	1.58	7.96	<0.001
Nestling age	-0.53	0.07	-8.01	<0.001
Muridae family	-8.09	3.37	-2.40	0.02
Soricidae family	-4.27	1.60	-2.68	<0.01

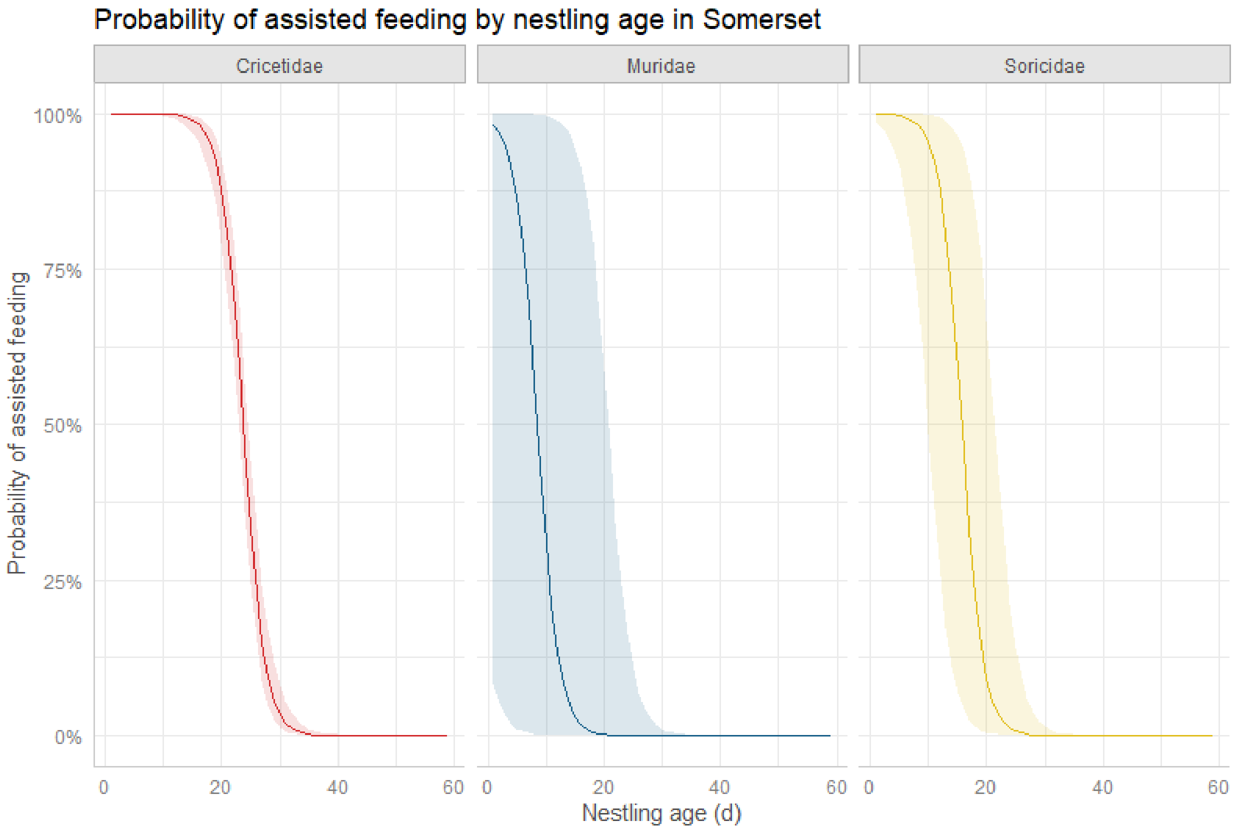


Figure 10. Probability of assisted feeding by nestling age and prey family in Somerset. The solid lines are the probability curves for each prey family and the shaded areas are the confidence intervals. The sample size for Muridae was small, so the curve has larger confidence intervals.

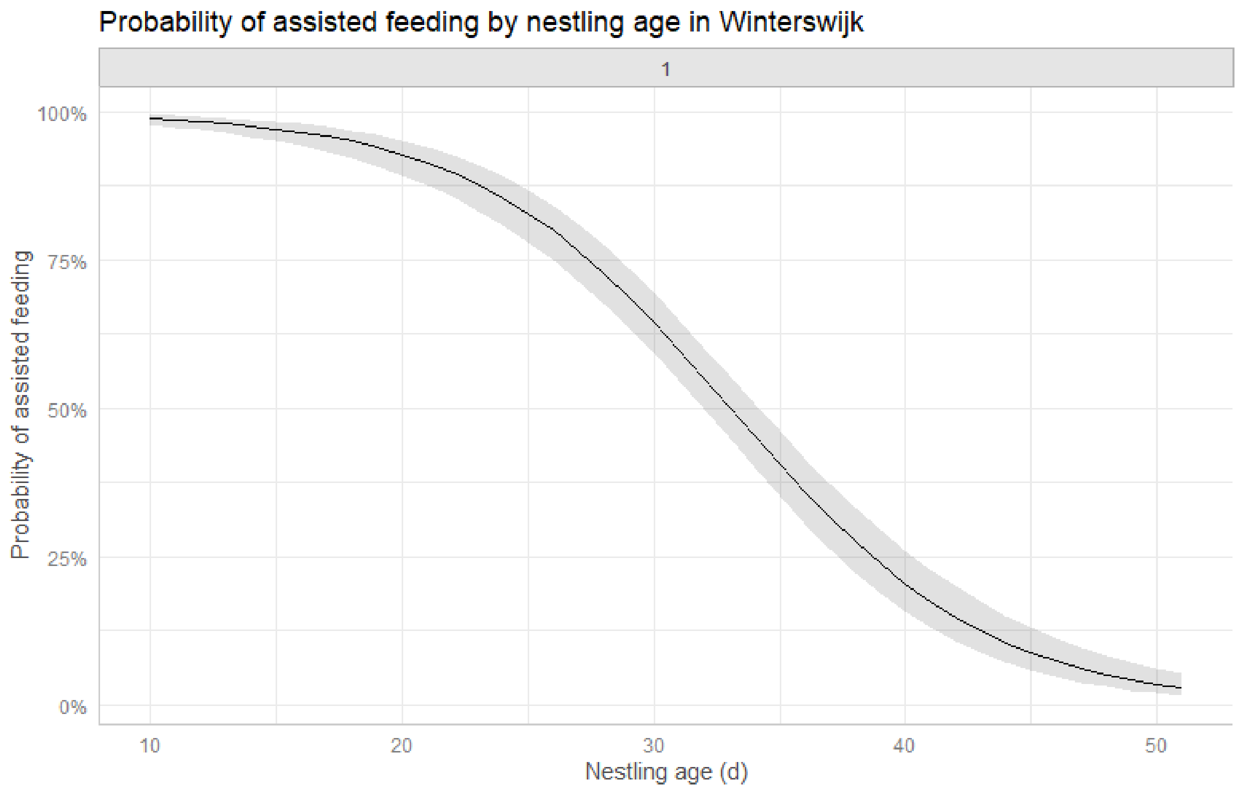


Figure 11. Probability of assisted feeding by nestling age in Winterswijk. The solid line is the probability curve and the shaded areas are the confidence intervals.

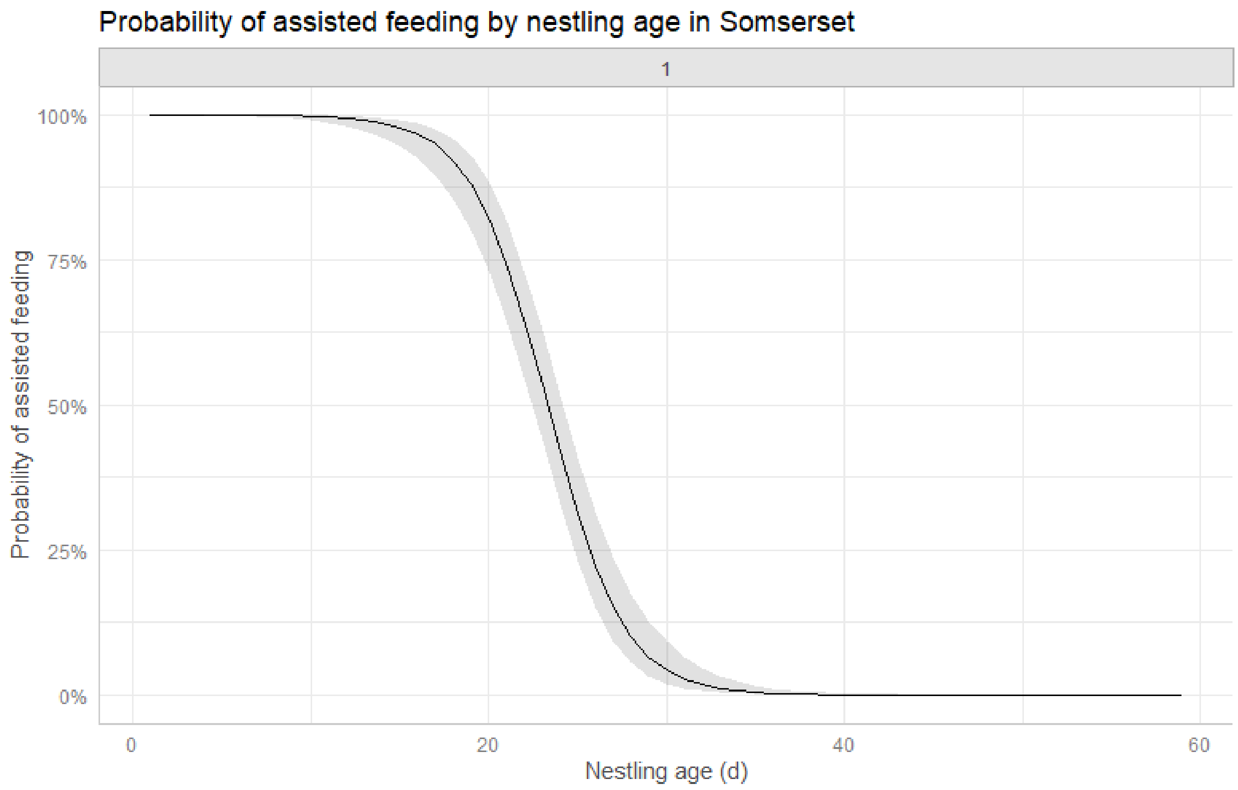


Figure 12. Probability of assisted feeding by nestling age in Somerset. The solid line is the probability curve and the shaded areas are the confidence intervals.

Stored or not

The Winterswijk subset of data where feeding method (stored, swallowed whole, or dismembered) was identified includes 552 data points. The model with nestling age and prey family was the best model (Appendix 5). Other models which were tested and discarded due to lower fit include nestling age only, prey family only and the interaction between nestling age and prey family (Appendix 5). All parameters in the best-fitted model were significant predictors except for the Muridae prey family (Table 7). The probability of the prey being stored decreased across all prey families as the nestlings grew older, especially for the family Soricidae (Figure 13).

The Somerset subset of data where feeding method (stored, swallowed whole, or dismembered) was identified includes 526 data points. The model with nestling age (in days) and prey family was the best model (Appendix 6). Other models which were tested and discarded due to lower fit include nestling age only, prey family only and the interaction between nestling age and prey family (Appendix 6). All parameters in the best-fitted model were significant predictors (Table 8). The probability of prey being stored decreased across all prey families as the nestlings grew older, especially for the families Muridae and Soricidae (Figure 14).

Table 7. Parameter estimates of the best-fitted model for the effect of nestling age (days) and prey family on the probability of storing prey in the Winterswijk nest by barn owls (n = 552), intercept = Cricetidae family.

Coefficients	Estimate	Standard error	z	P
(Intercept)	3.82	0.38	9.97	<0.001
Nestling age	-0.12	0.01	-9.72	<0.001
Muridae family	-0.18	0.22	-0.83	0.41
Soricidae family	-0.96	0.34	-2.82	<0.01

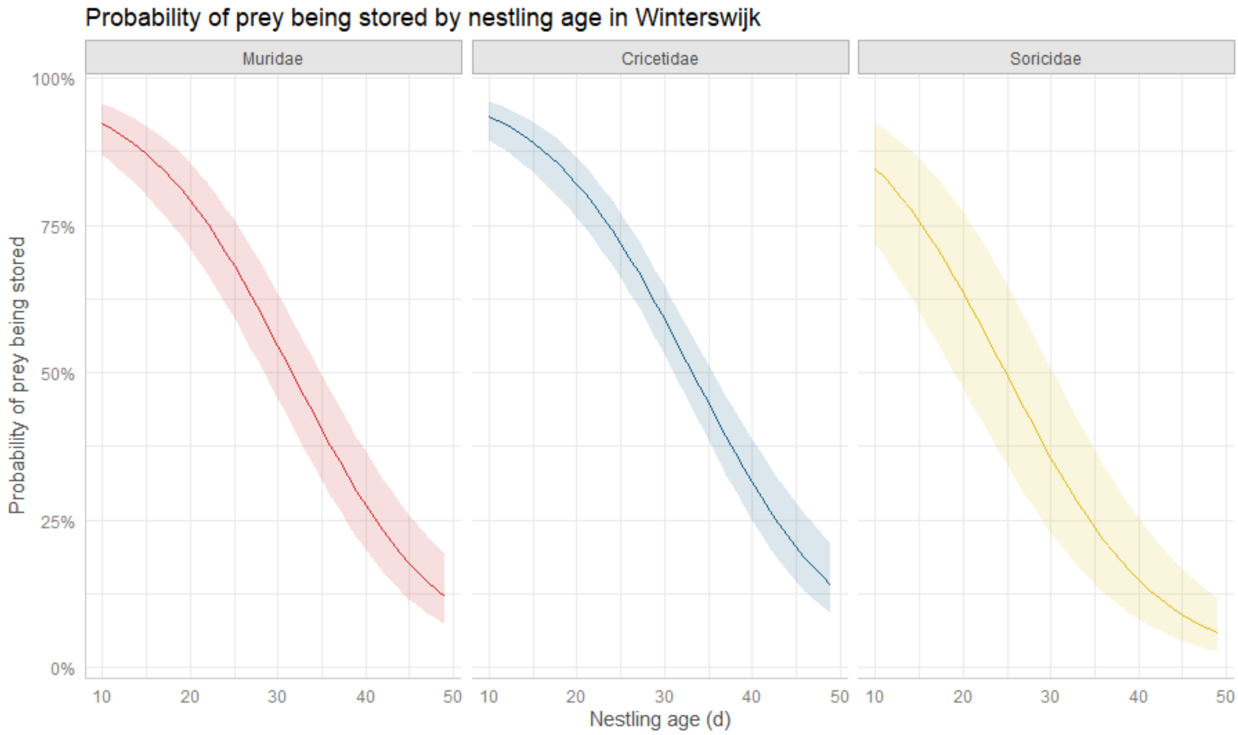


Figure 13. Probability of storing prey by nestling age and prey family in Winterswijk. The solid lines are the probability curves for each prey family and the shaded areas are the confidence intervals.

Table 8. Parameter estimates of the best-fitted model for the effect of nestling age (days) and prey family on the probability of storing prey in the Somerset nest by barn owls (n = 526), intercept = Cricetidae family.

Coefficients	**Estimate**	**Std. Error**	**z**	**P**
(Intercept)	2.02	0.26	7.85	<0.001
Nestling age	-0.08	0.01	-9.46	<0.001
Muridae family	-1.64	0.83	-1.98	<0.05
Soricidae family	-1.57	0.60	-2.61	<0.01

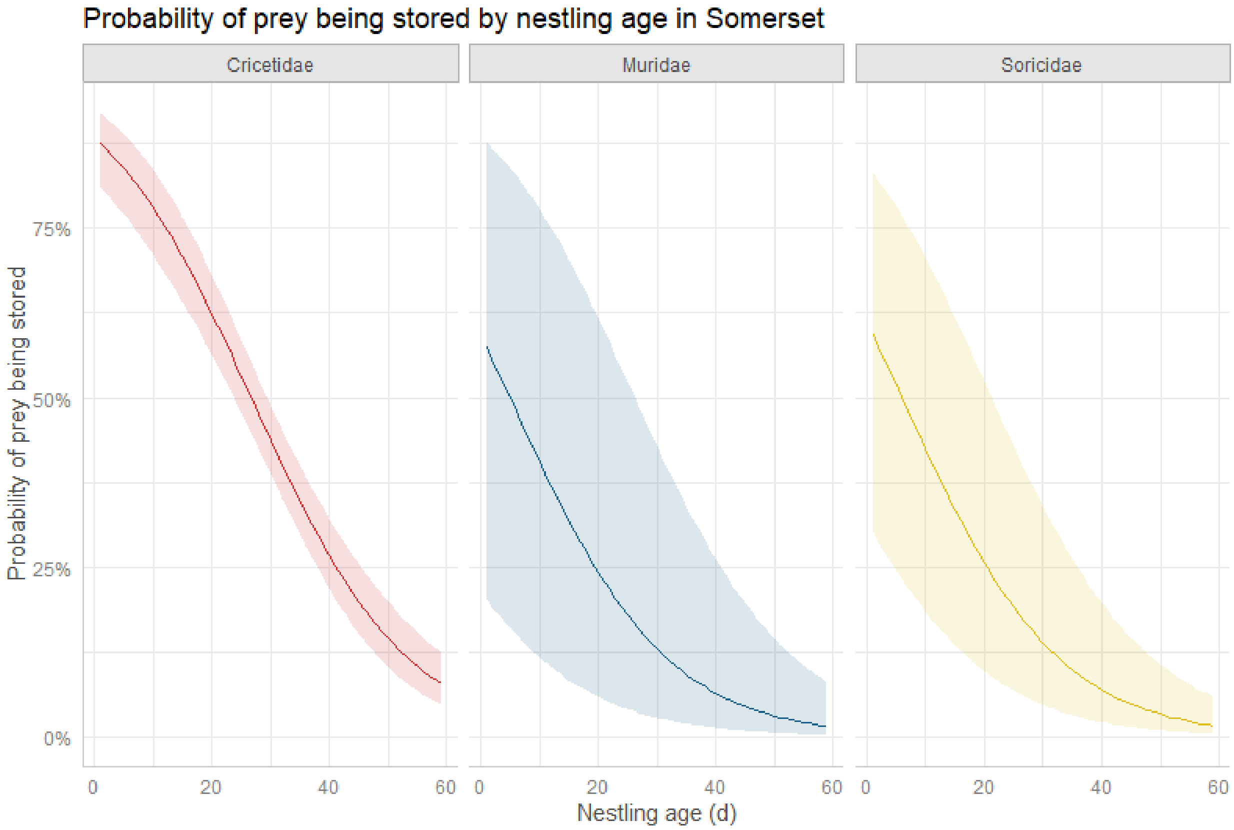


Figure 14. Probability of storing prey by nestling age and prey family in Somerset. The solid lines are the probability curves for each prey family and the shaded areas are the confidence intervals. Muridae and Soricidae had small sample sizes, hence the large confidence intervals.

Prey selection

Of the prey families that were identified, Cricetidae was the most frequently delivered at both nests (Table 9). The field vole (*Microtus agrestis*) was the most commonly delivered prey species that could be identified at the species level at both nests (Table 10). Muridae had the second most frequent grand total and was the second most frequently delivered at the Winterswijk nest. The prey from the family Muridae that were delivered were almost all mice, although one common rat (*Rattus norvegicus*) was delivered at the Winterswijk nest

(Table 10). Soricidae was the third most frequently delivered by grand total and the second most delivered at the Somerset nest. The prey from the family Soricidae were almost all common shrews (*Sorex araneus*), although one water shrew (*Neomys fodiens*) was delivered at the Somerset nest. There was only one member of the Talpidae family delivered, and it was delivered at the Somerset nest (Table 9).

In both nests, nestling age had a slight positive effect on predicted probability of prey delivery for Muridae and Soricidae, but a slight negative effect on Cricetidae (Figure 15). The effect of nestling age (days) on probability of prey delivery from certain prey families was not significant for Winterswijk (AIC = 1024.51) (P = 0.52), but was significant for Somerset (AIC = 397.18) (P = 0.001) (Tables 11, 12) (Appendix 13). The probability of Cricetidae delivery was higher in both nests than Muridae and Soricidae, especially in Somerset (Figure 15).

Table 9. Prey counts for each nest by prey family. N/A represents prey that were not conclusively identified at the family level.

Prey family	Winterswijk	Somerset	Grand total
Cricetidae	382	475	857
Muridae	161	19	180
Soricidae	53	32	85
Talpidae	0	1	1
N/A	400	209	609
Grand total	**996**	**736**	**1732**

Table 10. Prey counts for each nest by prey species (common name). N/A represents prey that were not conclusively identified at the species level.

Prey species	Winterswijk	Somerset	Grand total
Field vole (*Microtus agrestis*)	321	377	698
Bank vole (*Myodes glareolus*)	20	8	28
Water vole (*Arvicola amphibious*)	2	4	6
Unidentified mouse (Muridae sp.)	160	19	177
Common rat	1	0	1
European mole	0	1	1
Common shrew (*Sorex araneus*)	53	31	84
Water shrew	0	1	1
Unidentified mammal (Mammalia)	88	203	291
Unidentified prey	351	92	443
Grand total	**996**	**736**	**1732**

Table 11. Analysis of deviance (type II test) for effect of nestling age on probability of prey delivery from different prey families (Cricitedae, Muridae, Soricidae) at the nest in Winterswijk. Response = Prey family.

	LR Chisq	**Df**	**Pr(>Chisq)**
Nestling age	1.29	2	0.52

Table 12. Analysis of deviance (type II test) for effect of nestling age on probability of prey delivery from different prey families (Cricitedae, Muridae, Soricidae) at the nest in Somerset. Response = Prey family.

	LR Chisq	**Df**	**Pr(>Chisq)**
Nestling age	13.07	2	0.001 **

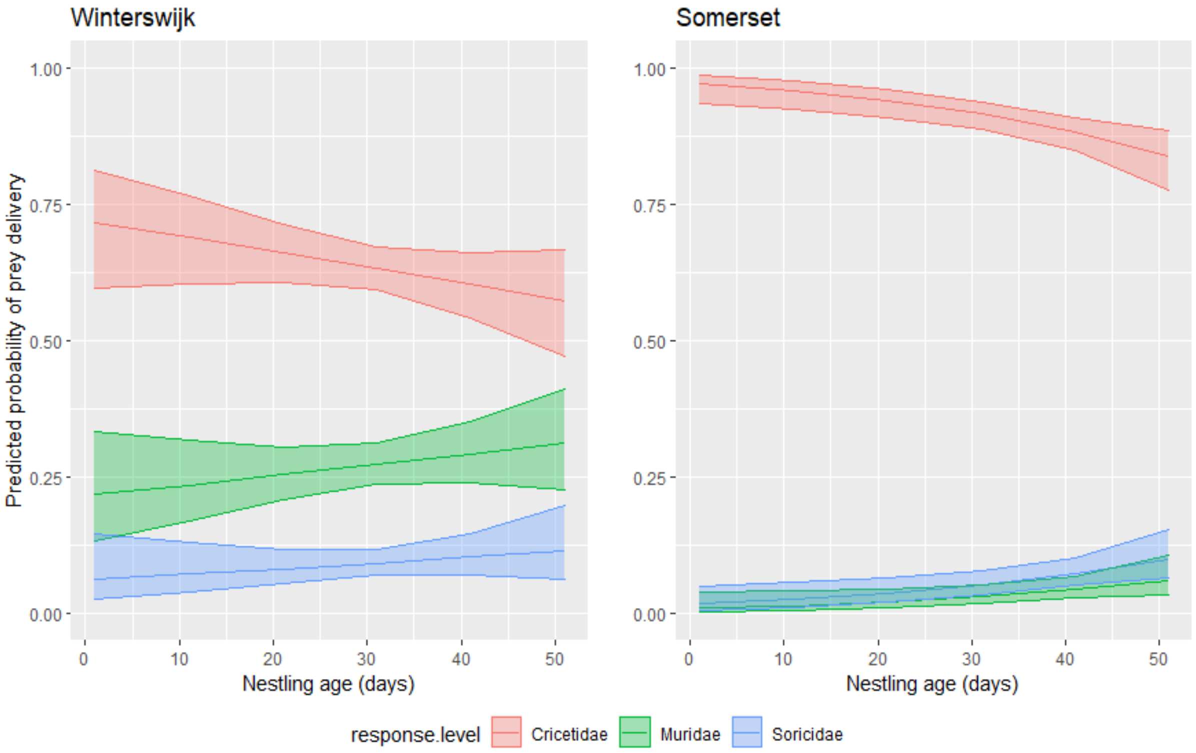


Figure 15. Multi-comparison graphs from each nest (Winterswijk and Somerset) of the probability of prey delivery as a function of nestling age from each of the most frequently identified prey families. The solid lines are the probability curves for each prey family and the shaded areas are the confidence intervals.

Weather

For Winterswijk, two models were selected based on the model selection table for predicting the number of prey during the night (Appendix 14). Model 1 (AIC = 446.85) was the best model and only included nestling age, and nestling age^2 as independent variables (Table 13) (Appendix 15). The best model did not include rainfall as a variable and nestling age had a significant effect on the number of prey delivered during the night (Table 13). The number of prey delivered per night increased as the nestlings aged until they reached around 39 days old, after which the number of prey delivered decreased (Figure 16). Only the number of prey delivered during the night was analyzed in Winterswijk and not the number of prey delivered during the day because activity at this nest was overwhelmingly nocturnal and there were not enough deliveries during the day to justify an analysis.

The alternative model tested for Winterswijk included rainfall (mm) as a parameter, along with nestling age (days) and nestling age^2 (day^2) (AIC = 448.08). Rainfall had a negative effect on number of prey delivered during the night, but the effect was not significant (Table 14) (Appendix 16). The confidence intervals for the lowest and highest ranges of rainfall (mm) also overlapped quite a lot (Figure 17).

Table 13. Model estimates for number of prey delivered at the nest during the night as a function of nestling age (days) and nestling age^2 (days2) in Winterswijk (Model 1).

Coefficients	Estimate	Std. Error	z	P
(Intercept)	-0.51	0.17	-2.99	<0.01
NestlingAge	0.07	0.01	8.04	<0.001
I(NestlingAge^2)	-0.00	0.00	-9.24	<0.001

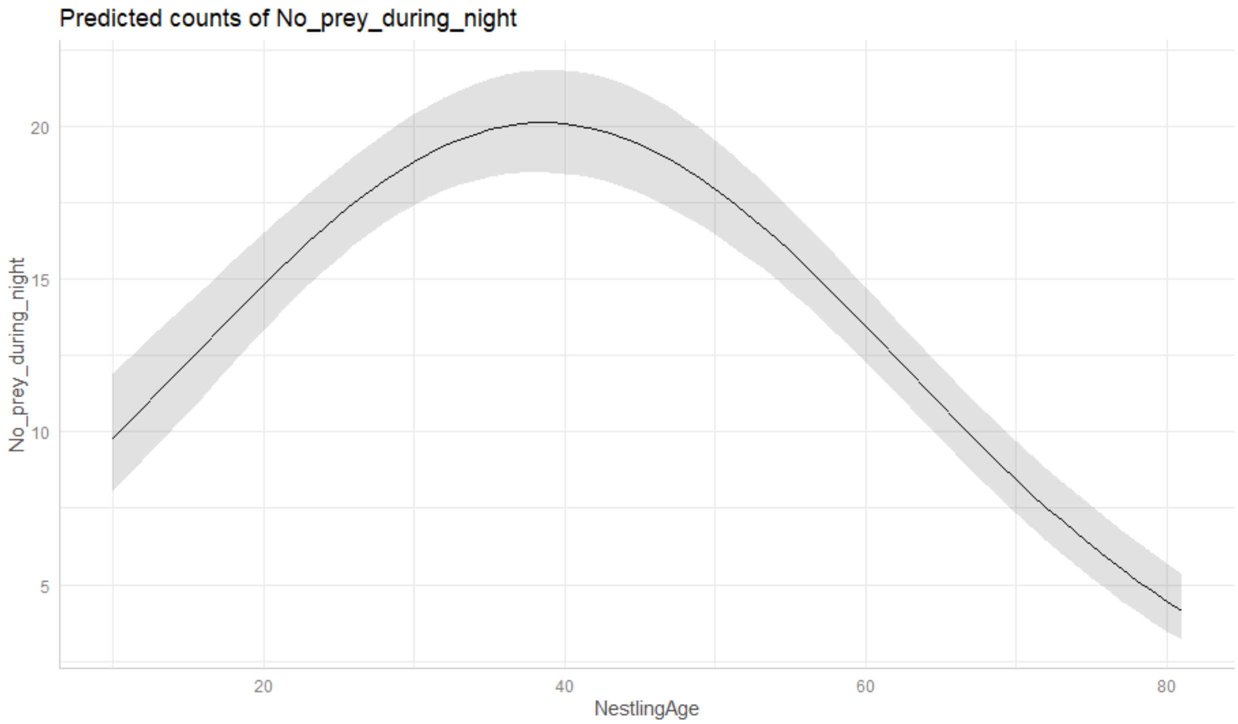


Figure 16. Model for predicted counts of number of prey delivered during the night as a function of nestling age in Winterswijk (Model 1). The solid line is the probability curve and the shaded areas are the 95% confidence intervals.

Table 14. Model estimates based on the alternative model for number of prey delivered to the nest during the night as a function of rainfall (mm), nestling age (days) and nestling age^2 (days2) in Winterswijk (Model 2).

Coefficients	Estimate	Std. Error	z	P
(Intercept)	<-0.001	<0.001	-2.99	<0.01
NestlingAge	<0.001	<0.001	8.06	<0.001
I(NestlingAge^2)	<-0.001	<0.001	-9.26	<0.001
Rainfall	<-0.001	<0.001	-0.87	0.39

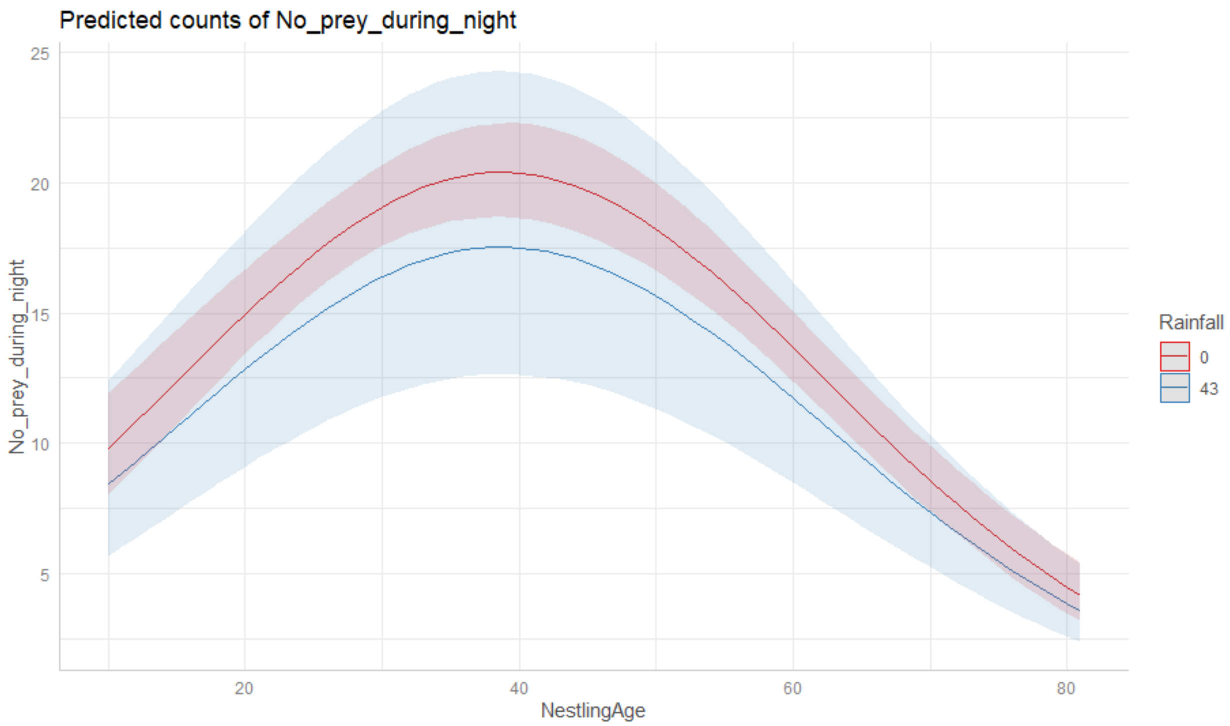


Figure 17. Predicted counts of number of prey delivered during the night as a function of nestling age (days) and rainfall (mm) in Winterswijk (Model 2). The solid lines are the probability curves for number of prey during the night at the highest (0 mm) and lowest (43 mm) amounts of rainfall and the shaded areas are the 95% confidence intervals.

For Somerset, a couple of models were considered since there were enough daytime deliveries to analyze number of prey delivered during the day. Model 1 (AIC = 279.77) included nestling age (days), nestling age^2 (days^2) and rainfall (mm) as parameters for prey delivered during the night (Appendix 19). Rainfall was found to not be significant (P = 0.06), but still had a higher effect than in Winterswijk (Table 15). Rainfall still appeared to have a negative effect on the number of prey delivered during the night (Figure 18).

There were also alternative plots based on Model 1 that show different configurations of the data. For the average amount of rainfall (2.8 mm), the amount of prey delivered during the night increased with nestling age (days) until the oldest nestling reached about 42 days old, at which point the number of prey decreased (Figure 19). For both the highest and lowest ranges of nestling age (days), the amount of prey delivered during the night decreased as rainfall (mm) increased (Figure 20). This effect was stronger when nestlings were younger than when they were older.

Out of the models tested for effects on the number of prey delivered during the day, Model 1 was selected as the best (AIC = 395.55) (Appendix 21). All variables in this model were significant, including rainfall the day before (mm) (P-value = 0.05) (Table 16). Regardless of the effect of rainfall the day before, the number of prey delivered during the night increased with nestling age until the oldest nestling was around 41 days old, at which time it started to decrease (Figure 21). Higher amounts of rainfall the day before (mm) did have a negative effect on the number of prey delivered during the day. Some alternative plots were also created for this model. For the average amount of rainfall the day before (2.6 mm), the amount of prey delivered during the night increased until the oldest nestling reached an age of around 41 days, and then began to decrease as the nestlings aged after that (Figure 22). For both the highest and lowest ranges of nestling age (days), the amount of prey delivered during the day decreased as rainfall the day before (mm) increased (Figure 23). This effect was stronger when nestlings were younger than when they were older.

Table 15. Model estimates for number of prey delivered to the nest during the night as a function of nestling age (days), nestling age^2 (days2) and rainfall (mm) in Somerset (Model 1).

Coefficients	**Estimate**	**Std. Error**	**z**	**P**
(Intercept)	-1.66	0.30	-5.59	<0.001
Nestling age	0.05	0.02	2.89	<0.01
I(NestlingAge^2)	<-0.001	<0.001	-2.34	<0.05
Rainfall	-0.04	0.02	-1.87	0.06

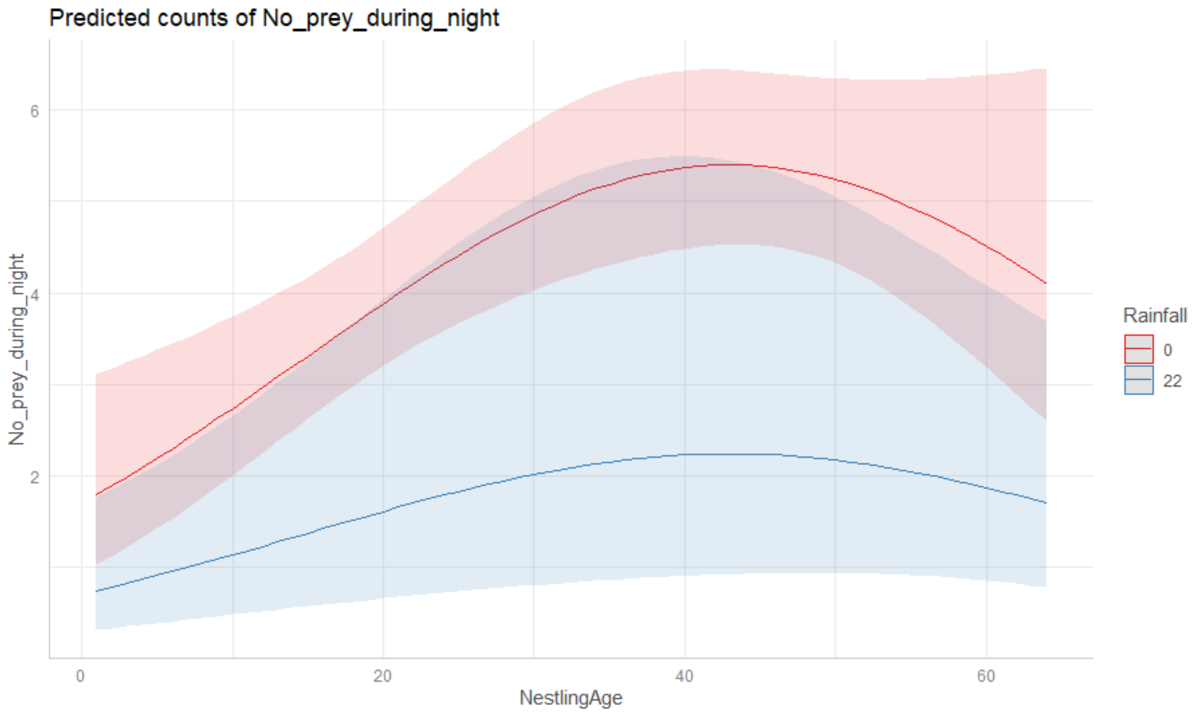


Figure 18. Model for predicted counts of number of prey delivered during the night as a function of nestling age (days), Nestling age^2 (days^2) and rainfall (mm) in Somerset (Model 1). The solid lines are the probability curves for number of prey during the night at the highest (0 mm) and lowest (22 mm) amounts of rainfall and the shaded areas are the 95% confidence intervals.

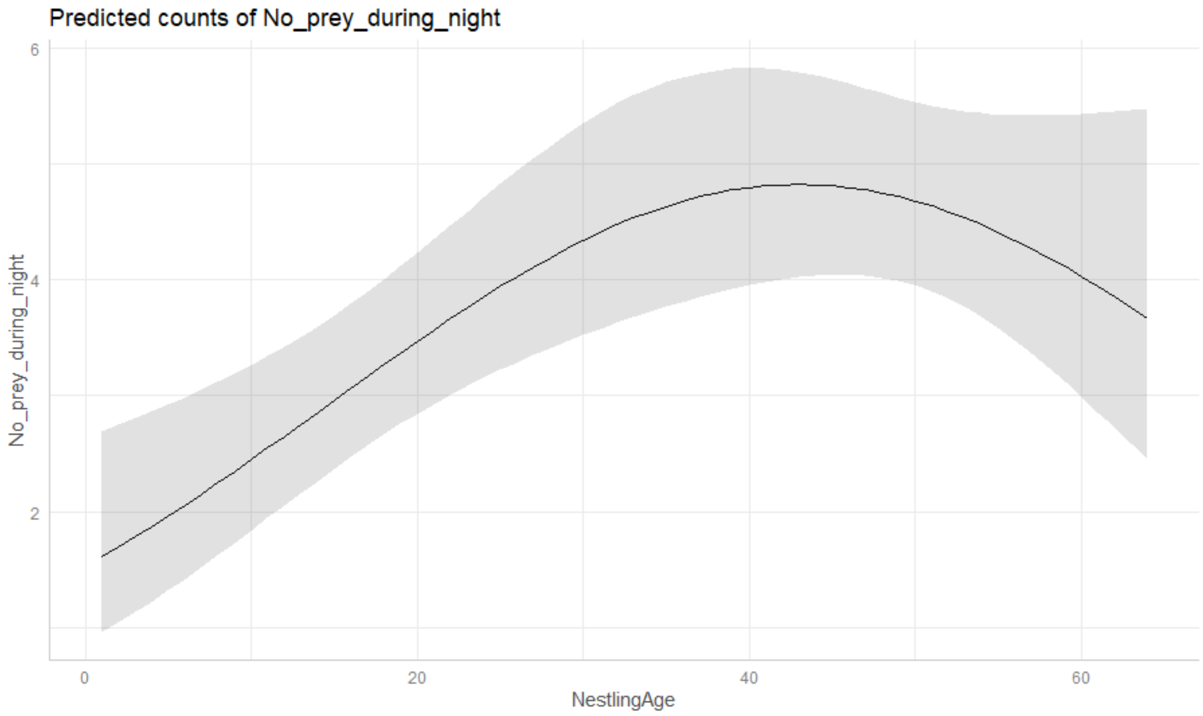


Figure 19. Predicted counts of number of prey delivered during the night in Somerset as a function of nestling age (days) for average rainfall (2.8 mm). The solid line is the probability curve and the shaded areas are the 95% confidence intervals.

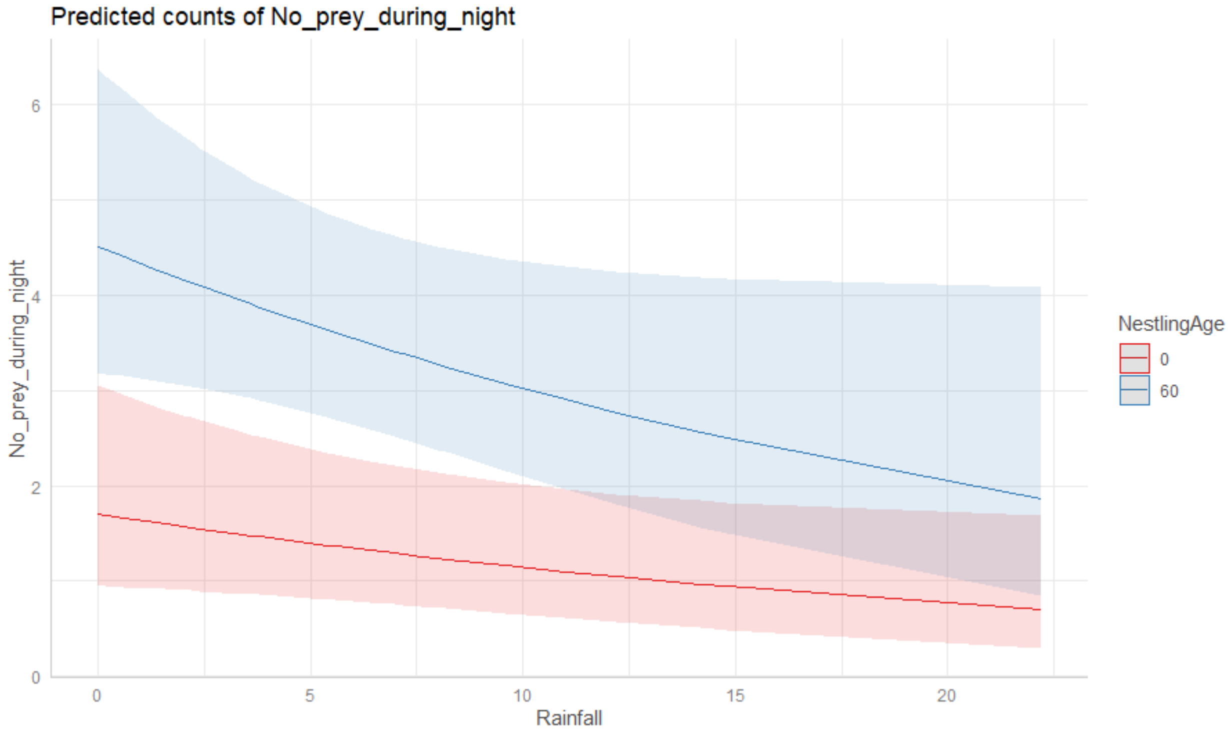


Figure 20. Predicted counts of number of prey delivered during the night in Somerset as a function of rainfall (mm) for the highest and lowest nestling ages. The solid lines are the probability curves for number of prey during the night at the highest (0 days) and lowest (60 days) age of the nestlings and the shaded areas are the 95% confidence intervals.

Table 16. Model estimates for number of prey delivered during the day as a function of nestling age (days), nestling age^2 (days2) and rainfall the day before (mm) in Somerset (Model 1).

Coefficients	**Estimate**	**Std. Error**	**z**	**P**
(Intercept)	-0.70	0.19	-3.72	<0.001
NestlingAge	0.04	0.01	3.59	<0.001
I(NestlingAge^2)	-0.00	0.00	-2.96	<0.001
RainfallDayBefore	-0.03	0.01	-1.93	0.05

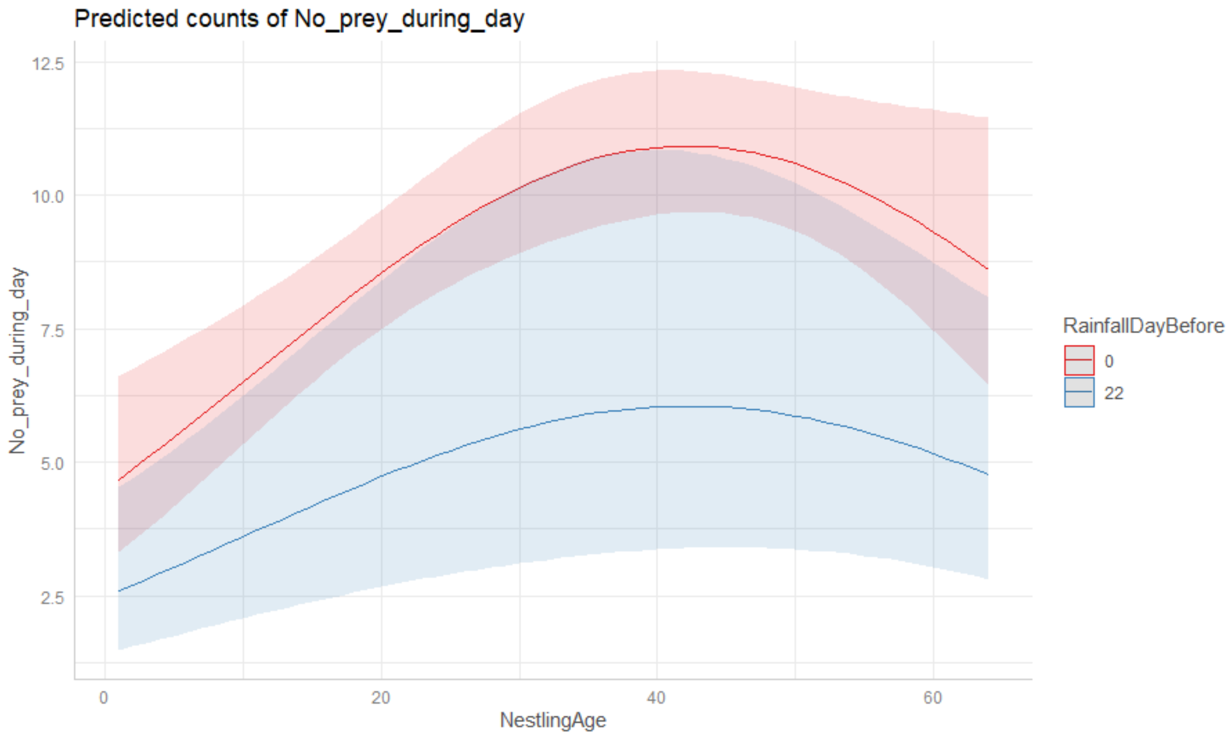


Figure 21. Predicted counts of number of prey delivered during the day as a function of nestling age (days), Nestling age^2 (days^2) and rainfall the day before (mm) in Somerset (Model 1). The solid lines are the probability curves for number of prey during the day at the highest (0 mm) and lowest (22 mm) amounts of rain the day before and the shaded areas are the 95% confidence intervals.

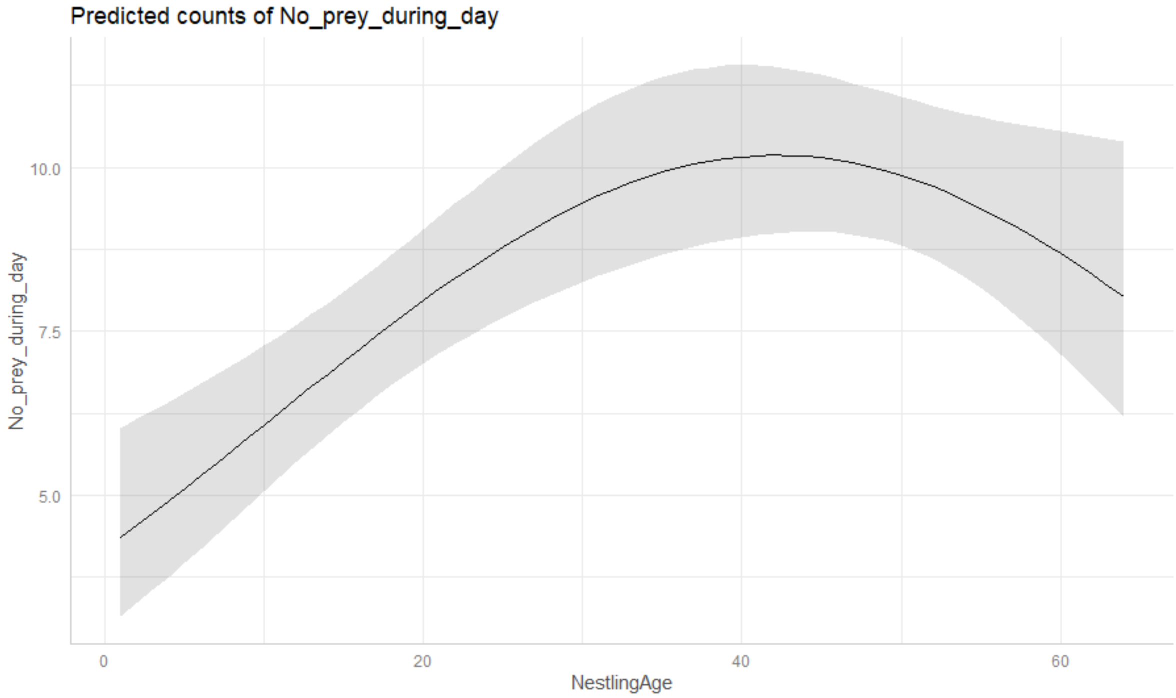


Figure 22. Predicted counts for the number of prey delivered during the day in Somerset as a function of nestling age (days) for average rainfall the day before (2.6 mm). The solid line is the probability curve and the shaded areas are the confidence intervals.

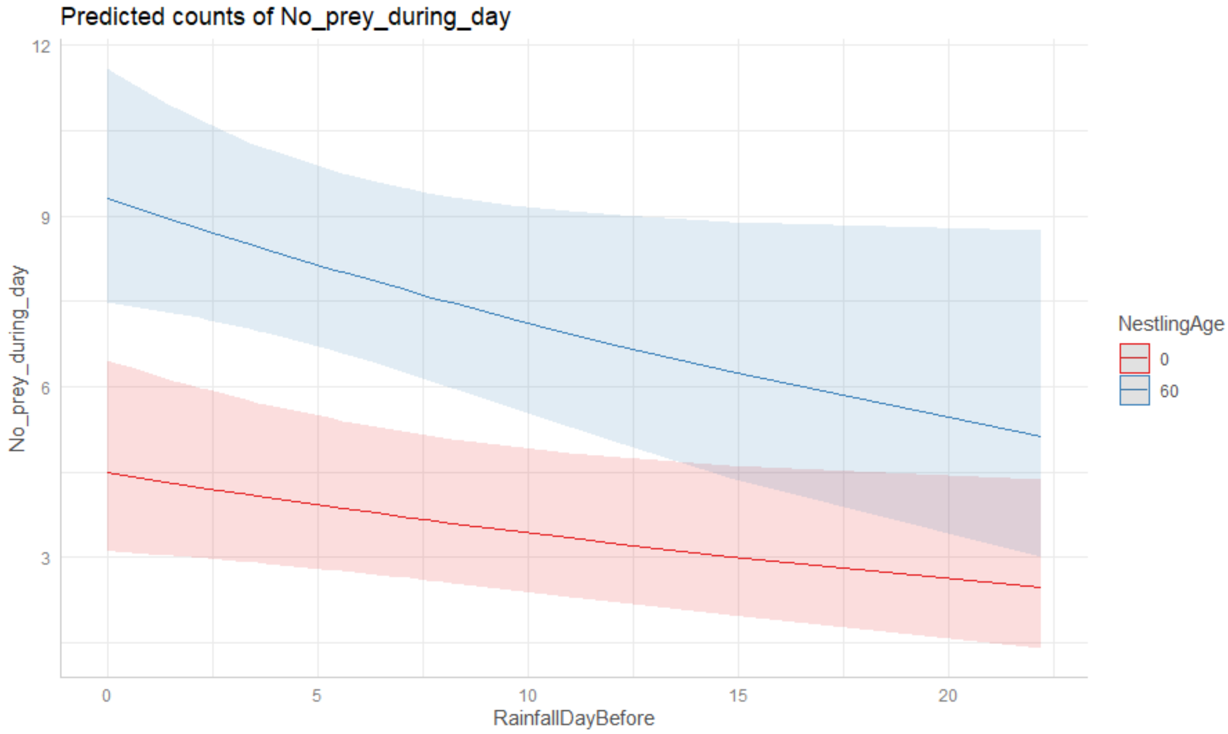


Figure 23. Predicted counts for the number of prey delivered during the day in Somerset as a function of rainfall the day before (mm) for the highest (60 days) and lowest (0 days) nestling ages. The solid lines are the probability curves and the shaded areas are the 95% confidence intervals for each nestling age.

DISCUSSION

Daily activity

Activity at the nest in Winterswijk was strictly nocturnal. Activity peaked around midnight regardless of prey family and there were no deliveries at the nest between 06:00 and 20:00. This was an expected behavioral pattern as barn owls are mostly nocturnal and their visual systems function well enough in darkness (Scriba et al., 2017) along with having a very acute sense of hearing and ability to locate prey through sound due to their specialized facial discs (Bruce, 1999). This nest is also in a mostly natural and agricultural area, and therefore less susceptible to human disturbance in daylight hours. There was some activity with the nestlings flapping and moving around in the nest during the day (pers. obs.), but this kind of behavior is normal for nestlings during the day (Scriba et al., 2017).

Activity at the nest in Somerset was more mixed, with peaks during both nighttime and daylight hours. Vole (Cricetidae) and shrew (Soricidae) deliveries in particular had peaks in the morning, with shorter peaks in the evening before and after sunset. Mice (Muridae) deliveries peaked during the nighttime after midnight, but the Muridae family also had the lowest sample size in my analysis at this nest. The diel activity observed at this nest differs from the nests in the previous master's study, which were primarily nocturnal with low daytime activity (Glåmseter, 2021). Hunting during the daytime is not unusual for barn owls in Scotland, England and various Pacific islands, so these findings aren't completely exceptional given the location of this nest (Bruce, 1999). The owner of the nest box has also reportedly seen the owls out of the nest during the daytime (M. Fuller, pers. comm.). Some possible explanations for this pattern are prey availability and activity and human disturbance. The Somerset nest is in closer proximity to human settlements and farms than the nest in Winterswijk, so it is possible that human land use and activity has an indirect or direct effect on the activity of the barn owls. Human activity and land use might change prey occurrence, making prey more available in the early morning or late afternoon (Caldwell et al., 2022). It may also negatively influence the barn owl parents' abilities to rest during the day, making them more vigilant and thus increasing their opportunities to spot prey nearby (Scriba, 2014; Almasi, 2015). Human proximity could also lessen the likelihood of barn owls being mobbed by other birds, therefore making it safer to hunt during the daytime than it would otherwise have been (Pavey & Smyth, 1998). There is also the possibility that this diel pattern from the parents in Somerset is influenced by individual personality variation, which is a phenomenon that has a strong theoretical literature base but which lacks sufficient direct testing at the moment (Dall & Griffith, 2014).

Frequency (Temporal overlap)

The two nests had a very low degree of temporal overlap between them in prey deliveries for the families Cricetidae and Soricidae. This could be due to having different environmental conditions. Although both locations are categorized as oceanic climates (Peel et al., 2007), they are at different latitudes and have slightly differing mosaics with Winterswijk having more natural areas, Somerset having more residential areas and both locations having some agricultural activity. There was more overlap for the Muridae family, but Muridae and Soricidae both have rather low sample sizes compared to Cricetidae and are unequally ranked between the two nests, with Muridae being second most frequently delivered at Winterswijk and third most frequent at Somerset. Therefore, the overlap for Cricetidae is more reliable for comparing activity at the nests. As far as diel activity of prey goes, some common prey such as field voles (*Microtus agrestis*) and common shrews (*Sorex araneus*) are active both day and night and have peaks at night (Erkinaro, 1961; Ivanter, 2002). Field voles are mostly nocturnal May through August with the largest peaks around 11 p.m. and 4 a.m. in May and June and around 00:00 and 01:00 in August (Erkinaro, 1961). Common shrews showed peak daytime activity around 06:00-08:00, 12:00-14:00 and 20:00-22:00 in June, around 06:00-08:00, 16:00-18:00 and 18:00-20:00 in July, and around 06:00-08:00, 10:00-14:00 and 18:00-20:00 in August (Ivanter & Makarov, 2002). Harvest mice (*Micromys minutus*) also display both nocturnal and diurnal activity (Darinot, 2016). Some locally common mouse species such as house mice (*Mus musculus*) and wood mice (*Apodemus sylvaticus*) are mostly nocturnal (Wolton, 1983; Robbers, 2015). The house mouse is highly nocturnal with some daytime activity from spring to autumn and activity peaks around 04:30, 13:00 and 00:00 (Cross, 1967; Robbers et al., 2015). The wood mouse was active from 21:00-04:00 from 20 May-2 June, while in 11-22 June it was active from around 07:00-16:00 and 19:00-03:30 with peaks around 23:30 and 01:30 (Wolton, 1983). The bank vole (*Myodes glareolus*), on the other hand, is mostly diurnal with peaks around 20:00 and 06:00 in the summer (Greenwood, 1978).

Prey handling

Delivering parent

At both nests, the probability of female prey delivery increased as the nestlings grew older. This result was expected because the female is able to leave the nest more frequently as the nestlings become more independent and able to eat the delivered prey without any assistance (Steen et al., 2012). The probability of female delivery when the oldest nestling was 40 days old was higher at the Somerset nest than the Winterswijk nest across all prey families. This is possibly because there was only one camera which was inside the nest at Somerset, so the male could have been delivering prey to the female outside the nest, but since I only saw the female bring prey into the nest and not what happens outside of the nest box, that delivery would be categorized as a female delivery. The Winterswijk nest had three cameras, two of which were outside the nest, so the risk of a discrepancy between the parent that hunted the prey and the parent that delivered the prey was lower (but not negligible) at this nest (Sonerud et al., 2013).

Similarly to other raptors, barn owls have asymmetrical parenting roles and barn owl females only begin hunting after brooding for some time (Durant et al., 2004). The female has to balance her own interests in future reproduction against her offsprings' interests in feeding and thermoregulation since nestlings are unable to maintain their own body temperature before 15-20 days old (Durant et al., 2004). Durant et al. (2004) found that the female leaves the nest to hunt for the first time after about 15 days from the hatching of the first egg. This pattern is ascribed to the male parent no longer delivering enough prey to meet the nest food requirements (Durant et al., 2004). It is suspected that environmental conditions and food availability contribute to the level of male investment.

Condition of prey upon delivery

Decapitated mammalian prey were rare in my study, and they seem to be rare in some of the few studies which include decapitation in their analysis, although some found higher amounts of decapitated prey among large rodents and avian prey and others were inconclusive on just how much decapitation features in barn owl diets (Glue, 1967; Hafidzi & Na Im, 2003; Taylor, 2003). Nearly all decapitated prey in my study were field voles, which may be due to their larger size since decapitating them could make them easier for nestlings to eat when they are young, or make them less heavy, reducing energetic costs of delivering to the nest (Glue, 1967; Steen, 2010; Durant, 2013). They could've also been decapitated because the parent was hungry and fed on part of the prey, killing two birds with one stone, so to speak, by making them easier for the nestlings to eat as well. This practice was rare in my study, so whatever reason the parents had for doing it was unlikely to be worth the time and effort it would take to decapitate their prey.

Feeding assisted or unassisted

Occurrences of nestlings feeding assisted decreased as nestlings grew older for both nests. This result was expected since the nestlings become more independent and the female parent ventures out of the nest to hunt more as the nestlings age (Durant et al., 2004). In raptors, prey partitioning is positively linked to prey size, with the time a female spent handling prey in the nest increasing with prey size (Sonerud et al., 2014b). This implies a link between prey size and probability of nestlings feeding with parental assistance. In Winterswijk, the probability of assisted feeding decreased sooner for the family Soricidae than for Muridae or Cricetidae. This could be due to the shape and size of shrews as they are quite small and have a cylindrical body shape which is easy for nestlings to swallow whole (Steen et al., 2010).

The sample size for Soricidae is lower than for Cricetidae or Muridae, but it was still a significant coefficient. I would have also expected a faster decrease for Muridae since the mice captured were smaller than the voles (Cricetidae), but perhaps the shape made them just as difficult to swallow whole as voles were. In Somerset, the probability of assisted feeding decreased sooner for the family Muridae than for Cricetidae or Soricidae, but Muridae family was not a significant coefficient in the analysis and the sample size for Muridae was the lowest of the three families. Therefore, there may be little merit to interpreting it as actually occurring sooner than the other families.

Stored or not

For both nests, the probability of prey being stored decreased as the nestlings aged. Nestling age governs food demand in kestrel nests as food demand initially increases as nestlings age until it begins to decline, either because of lower food demands or lower vole availability (Steen et al., 2012). Nestlings do not require as much at the beginning as they do when they are a few days older, so the higher initial probability of prey being stored likely has something to do with prey not being consumed at a rate comparable to prey being delivered. This is especially likely as barn owls typically deliver prey to their nestlings in the first part of the night (Durant et al., 2013). Storing prey to be consumed when the parents are not provisioning the nest would benefit the nestlings and allow them to feed more times throughout a 24-hour period, especially in the earlier stages when the nestlings require assisted feeding and consume prey more slowly. The decline of storing probability as nestlings age could be related to the earlier discussion on how male barn owls will no longer deliver enough prey to meet the nest food requirements after some time, and while the female begins to hunt too, she also has her own food requirements to attend to so she can maintain her own fitness and improve the success of future reproduction (Durant, 2004). As prey deliveries become less frequent, there is less of a need to store the prey since there is not as much excess. There is also less female control over food allocation as the female starts to leave the nest, so the unattended nestlings have more freedom to eat the food stores available in the nest. Older (and therefore larger) nestlings are also more adept at eating prey without assistance, possibly reducing the need to leave prey items uneaten until the female parent can assist in feeding.

Roulin (2004) presents three hypotheses for why barn owls store prey in the nest. The first hypothesis, the ‘insurance’ hypothesis, suggests that prey is stored as insurance against temporary food shortages. This could be beneficial to the hunting parents as it would allow them to conserve energy and mass by avoiding hunting when the costs of hunting are higher, such as when weather is an obstacle to hunting (Roulin, 2004). The second hypothesis, the ‘large prey’ hypothesis, cites the nestlings’ lack of effectiveness in feeding on large prey without assistance as a driving factor behind leaving uneaten prey items in the nest. Prioritizing consuming prey that are easier to eat without assistance until the female parent returns to dismember larger prey would give the nestlings an opportunity to feed more frequently as long as the prey selection allows for it. The third hypothesis, the ‘feeding time’ hypothesis, suggests that food is stored to give nestlings the freedom to feed whenever (Roulin, 2004). This would allow the parents to take care of their own food requirements after hunting for a shorter period to provide for the nestlings without sacrificing the body condition of the nestlings, creating a balance between the fitness of the parents for future reproduction and the fitness of the nestlings, which also serves to pass on the genes of the parents.

At the nest in Winterswijk, prey from the Soricidae family had a lower probability of being stored than prey from the Cricetidae or Muridae families. This could be due to the previously mentioned size and shape of shrews being easier to swallow whole, thus making them more viable for eating right after delivery rather than storing. At the nest in Somerset, prey from both the Muridae and Soricidae families had a lower probability of being stored than Cricetidae. This may be due to mice and shrews typically being smaller than voles, especially field voles which were the most common species at both nests. This supports the ‘large prey’ hypothesis. Voles were also delivered far more frequently than either mice or shrews, so there may have been less of a scarcity mindset when voles were delivered as opposed to mice and shrews.

Prey selection

At both nests, prey from the family Cricetidae and specifically the field vole (*Microtus agrestis*) were the most frequently delivered prey by far. The field vole is one of the most common mammals in the UK and is widespread across northern and central Europe (Mathias et al., 2017; The Wildlife Trusts). Voles in general are one of the main prey species for barn owls (Klok & de Roos, 2007). The next most identified prey families were Muridae and Soricidae. Unlike the previous master’s thesis on this topic, which identified 3 avian prey items, the nests I monitored did not deliver any prey that I identified as avian (Glåmseter, 2021).

For both nests there was a positive relationship between nestling age and probability of prey delivery for the Muridae and Soricidae families, and a negative relationship between nestling age and probability of Cricetidae deliveries. Since the parents spent less time at the nest as the nestlings got older, perhaps they prioritized delivering prey that the nestlings could eat without assistance (Steen et al., 2012).

Weather

Rainfall was not a significant variable affecting the number of prey delivered during the night at the nest in Winterswijk, in contrast to the previous master's study which had 'amount of daily rainfall (mm)' as its most significant explanatory variable (Glåmseter, 2021). The Winterswijk nest had more days of heavy rain than the Somerset nest, so perhaps a larger dataset would have yielded more significant results if the analysis included a wider range of daily precipitation values at each nest. Nestling age, on the other hand, had a very significant effect on the number of prey delivered to the nest during the night, likely for reasons which will be discussed below.

Rainfall was nearly significant in affecting the number of prey delivered during the night in Somerset, and with a larger dataset, the pattern might have become more clear. There was also not a lot of rain at this nest site for the duration of the observation period, so there were not many data points for the density response when rainfall is very high. The amount of rainfall the day before did have a significant effect on the amount of prey delivered at the nest during the day. This could be because the grass would have more water collected on it after a long rain rather than during. Barn owls often glide through fields while hunting, and more water collected on the blades would lead to more waterlogging of the barn owl's wings as the wings come into contact with the blades (Shawyer & Banks, 1987). This waterlogging could negatively affect their hunting abilities and make the energy cost of hunting higher (Shawyer, 1987; McCafferty, 2001). Like at the Winterswijk nest, nestling age also had a significant effect on prey delivered during the night to this nest.

Nestling age being a significant factor affecting prey delivered was not a surprising outcome since for raptors, nestling age and growth rate heavily influences demand for food at the nest, affecting parental hunting efforts in turn (Durant et al., 2004; Steen et al., 2012). Raptor studies have provided evidence for parents adjusting their daily prey deliveries to meet the nestlings' demands based on their growth rate which typically peaks when the nestlings are near their final body mass (Durant et al., 2004; Steen et al., 2012). In my study, the peak was around 37-40 days in Winterswijk and 40-43 days in Somerset. The eggs at these nests were not all laid and hatched at the same time per clutch, so regarding this study it is unsure of whether the peak was dependent on the oldest nestling's growth rate and demands in each nest or if it was dependent on all the nestlings in the nest. My study also did not include prey mass, but rather prey number only. The prey mass could also affect delivery rate since smaller prey would need to be more numerous to meet the same caloric value as larger prey. Studies on raptor nestling age and prey delivery rate often include prey mass, so perhaps analyzing that factor would give more detailed insight into how parental hunting efforts are affected by weather and nestling age in this study (Steen et al., 2011; Steen et al., 2012).

Other than a the few differences in results discussed above, the results in my study ended up being similar to those of the previous master's study, although I did not include prey body mass as a factor and the previous study did not include prey family in the analyses (Glåmseter, 2021). The fact that there were differences, however infrequent, underscores the importance of conducting similar studies on this topic over multiple years and at different locations to gain a more comprehensive understanding of the effects of different factors on barn owl nest provisioning, with an emphasis on the effects of weather.

CONCLUSION

At the beginning of this study, I set out to gain a better understanding of the effect of increased precipitation on nest provisioning abilities in barn owls, as well as analyze other factors in nest provisioning strategies. Many of the findings in this study aligned with those in previous literature, while others revealed a need for further investigation. Diel activity at the at the nest in the Netherlands was strictly nocturnal while the activity at the nest in the UK was more flexible and displayed hunting during both the daytime and nighttime. Prey delivery and handling at the nest showed a clear relationship to nestling age. The probability of female prey delivery increased for both nests as the nestlings grew older. The probability of nestlings feeding with parental assistance as well as the probability of prey being stored decreased as the nestlings grew older. Prey selection at both nests was heavily skewed in favor of field voles. Mice and shrews were the next most identified prey at both nests. All the prey identified in this study were mammalian, although that does not account for prey that could not successfully be identified at the class level. Still, the barn owls in this study displayed a substantial preference for mammalian prey. In my study, rainfall only had a significant effect on prey deliveries at the Somerset nest and the amount of rainfall the day before had a significant negative effect on the amount of prey delivered during the day in Somerset. Nestling age had the strongest effect on prey deliveries at both nests and was the most important factor in the amount of prey deliveries across the board. These results underline the importance of conducting more studies on this topic, as more extreme weather events, including heavy precipitation, are expected to increase with climate change.

REFERENCES

Almasi, B., Béziers, P., Roulin, A. & Jenni, L. (2015). Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. Oecologia, 179 (1): 89-101. doi: 10.1007/s00442-015-3318-2.

Akaike, H. (1978). On the Likelihood of a Time Series Model. *Journal of the Royal Statistical Society: Series D (The Statistician)*, 27 (3-4): 217-235. doi: https://doi.org/10.2307/2988185.

Bailey, H. & OBS Studio Contributors. *OBS Studio – Open Broadcaster Software*. Available at: https://obsproject.com/ (accessed: 2022).

Bruce, M. D. (1999). Family Tytonidae (Barn-owls). In del Hoyo, J., Elliott, A. & Sargatal, J. (eds) vol. 5. Barn-owls to Hummingbirds. *Handbook of the Birds of the World*, pp. 34-75. Barcelona: Lynx Edicions.

Burnham, K. P., Anderson, D. R. & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65 (1): 23-35. doi: 10.1007/s00265-010-1029-6.

Caldwell, M. R., Mario, J. & Klip, K. (2022). Patterns of wildlife activity and predator-prey dynamics in a highly touristed area. *The Southwestern naturalist*, 66 (1): 35-47. doi: 10.1894/0038-4909-66.1.35.

Christidis, N., McCarthy, M., Cotterill, D. & Stott, P. A. (2021). Record-breaking daily rainfall in the United Kingdom and the role of anthropogenic forcings. Atmospheric Science Letters: 9. doi: 10.1002/asl.1033.

Crick, H. Q. P. (2004). The impact of climate change on birds. *Ibis*, 146 (s1): 48-56. doi: https://doi.org/10.1111/j.1474-919X.2004.00327.x.

Cross, R. M. (1967). *Studies on the ecology, physiology and taxonomy of the Harvest mouse, Micromys minutus (Pallas)*: University of Southampton.

Dall, S. & Griffith, S. (2014). An empiricist guide to animal personality variation in ecology and evolution. *Frontiers in Ecology and Evolution*, 2. doi: 10.3389/fevo.2014.00003.

Daniels, E., Lenderink, G., Hutjes, R. & Holtslag, A. (2016). Relative impacts of land use and climate change on summer precipitation in the Netherlands. Hydrol. Earth Syst. Sci., 20 (10): 4129-4142. doi: 10.5194/hess-20-4129-2016.

Darinot, F. (2016). The harvest mouse (<i>Micromys minutus</i> Pallas, 1771) as prey: a literature review. *Folia Zoologica*, 65 (2): 117-137, 21.

Debruijn, O. (1994). Population ecology and conservation of the barn owl *Tyto alba* in farmland habitats in Liemers and Achterhoek (The Netherlands). *Ardea*, 82 (1): 1-109.

Durant, J. M., Gendner, J.-P. & Handrich, Y. (2004). Should I brood or should I hunt: a female barn owls dilemma. *Canadian Journal of Zoology*, 82 (7): 1011-1016. doi: 10.1139/z04-078.

Durant, J. M., Hjermann, D. Ø. & Handrich, Y. (2013). Diel feeding strategy during breeding in male Barn Owls (*Tyto alba*). *Journal of Ornithology*, 154 (3): 863-869. doi: 10.1007/s10336-013-0956-1.

Erkinaro, E. (1961). The Seasonal Change of the Activity of Microtus agrestis. *Oikos*, 12 (1): 157-163. doi: 10.2307/3565176.

Friard, O. & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7 (11): 1325-1330. doi: https://doi.org/10.1111/2041-210X.12584.

Fuller, M. (2022). *Barn owl nest access correspondence - Somerset.*

Glue, D. E. (1967). Prey taken by the Barn Owl in England and Wales. *Bird Study*, 14 (3): 169-183. doi: 10.1080/00063656709476160.

Glue, D. E. (1974). Food of the Barn Owl in Britain and Ireland. *Bird Study*, 21 (3): 200-210. doi: 10.1080/00063657409476419.

Glåmseter, A. T. (2021). *Climate effects on parental food provisioning in the barn owls (Tyto alba) breeding in Norfolk, UK, by the use of nest cameras.*: Norwegian University of Life Sciences. Unpublished manuscript.

Greenwood, P. J. (1978). Timing of Activity of the Bank Vole Clethrionomys Glareolus and the Wood Mouse Apodemus Sylvaticus in a Deciduous Woodland. *Oikos*, 31 (1): 123-127. doi: 10.2307/3543393.

Hafidzi, M. & Na Im, M. (2003). Prey selection by barn owls in rice fields in Malaysia. *ACIAR Monograph Series*, 96: 220-223.

Hangzhou Hikvision Digital Technology Co. Ltd. (2022). *HIKIN | Software | Hikvision*. Available at: https://www.hikvision.com/en/support/download/software/hikin/.

Hawk & Owl Trust. (2021). *Barn Owl Cam Live - Somerset*. Available at: https://hawkandowltrust.org/web-cam-live/barn-owl-cam-live-somerset (accessed: 2021).

Honer, M. (1963). Observations on the Barn Owl (*Tyto alba guttata*) in the Netherlands in relation to its ecology and population fluctuations. *Ardea*, 51: 158-195.

Ivanter, E. V. & Makarov, A. M. (2002). Daily Activity and Mobility of the Common Shrew (Sorex araneus L.). *Russian journal of ecology*, 33 (4): 280-285. doi: 10.1023/A:1016224522263.

Klok, C. & de Roos, A. M. (2007). Effects of vole fluctuations on the population dynamics of the barn owl *Tyto alba*. *Acta Biotheoretica*, 55 (3): 227-241. doi: 10.1007/s10441-007-9013-x.

Lüdecke, D. (2018). ggeffects: Create Tidy Data Frames of Marginal Effects for 'ggplot' from Model Outputs. Journal of Open Source Software, 3 (26): Compute marginal effects and adjusted predictions from statistical models and returns the result as tidy data frames. These data frames are ready to use with the 'ggplot2'-package. Effects and predictions can be calculated for many different models. Interaction terms, splines and polynomial terms are also supported. The main functions are ggpredict(), ggemmeans() and ggeffect(). There is a generic plot()-method to plot the results using 'ggplot2'. doi: 10.21105/joss.00772.

Mathias, M. d. L., Hart, E. B., Ramalhinho, M. d. G. & Jaarola, M. (2017). *Microtus agrestis* (Rodentia: Cricetidae). *Mammalian species*, 49 (944): 23-39. doi: 10.1093/mspecies/sex003.

Mazerolle, M. J. (2020). *Model Selection and Multimodel Inference Based on (Q)AIC(c)* (Version 2.3-1). Package.

McCafferty, D. J., Moncrieff, J. B. & Taylor, I. R. (2001). How much energy do barn owls (*Tyto alba*) save by roosting? *Journal of Thermal Biology*, 26 (3): 193-203. doi: https://doi.org/10.1016/S0306-4565(00)00042-5.

Meredith, M. & Ridout, M. (2021). *Estimates of Coefficient of Overlapping for Animal Activity Patterns* (Version 0.3.4). Package.

Met Office. (2021). *Meteorological data for Yeovilton from May 1, 2021 to August 31, 2021*. Archive, N. M. L. a. (ed.).

Meteo Bredevoort. (2021). *Archief Meteo Bredevoort*. Available at: http://www.meteo-bredevoort.nl/archief.html (accessed: March 24, 2022).

Mombarg, M. (2021). *Barn owl nest access correspondence - Winterswijk.*

Monterroso, P., Alves, P. C. & Ferreras, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence.

Behavioral Ecology and Sociobiology, 68 (9): 1403-1417. doi: 10.1007/s00265-014-1748-1.

OpenClipart. (2014). *Public Domain Outline political world map vector graphics*. Free SVG.

Pavey, C. R. & Smyth, A. K. (1998). Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Anim Behav*, 55 (2): 313-318. doi: 10.1006/anbe.1997.0633.

Peel, M. C., Finlayson, B. L. & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.*, 11 (5): 1633-1644. doi: 10.5194/hess-11-1633-2007.

Portugues, E. (2022). *Watson-Williams Test of Homogeneity of Means* (Version 0.4-95). Function. Available at: https://www.rdocumentation.org/packages/circular/versions/0.4-95/topics/watson.wheeler.test.

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/.

Ripley, B. (2022). *Fit Multinomial Log-linear Models* (Version 7.3-17). Function. Available at: https://rdocumentation.org/packages/nnet/versions/7.3-17.

Robbers, Y., Koster, E. A. S., Krijbolder, D. I., Ruijs, A., van Berloo, S. & Meijer, J. H. (2015). Temporal behaviour profiles of Mus musculus in nature are affected by population activity. *Physiology & Behavior*, 139: 351-360. doi: https://doi.org/10.1016/j.physbeh.2014.11.020.

Roulin, A. (2004). The function of food stores in bird nests: observations and experiments in the barn owl *Tyto alba*. *Ardea*, 92 (1): 69-78.

Rowcliffe, M. (2022). *Animal Activity Statistics* (Version 1.3.2). Package.

Schär, C., Vidale, P. L., Lüthi, D., Frei, C., Häberli, C., Liniger, M. A. & Appenzeller, C. (2004). The role of increasing temperature variability in European summer heatwaves. *Nature*, 427 (6972): 332-336. doi: 10.1038/nature02300.

Scriba, M. F., Rattenborg, N. C., Dreiss, A. N., Vyssotski, A. L. & Roulin, A. (2014). Sleep and vigilance linked to melanism in wild barn owls. J Evol Biol, 27 (10): 2057-2068. doi: 10.1111/jeb.12450.

Scriba, M. F., Dreiss, A. N., Henry, I., Béziers, P., Ruppli, C., Ifrid, E., Ducouret, P., Da Silva, A., Monstiers, B. d., Vyssotski, A. L., et al. (2017). Nocturnal, diurnal and bimodal patterns of locomotion, sibling interactions and sleep in nestling Barn Owls. *Journal of Ornithology*, 158 (4): 1001-1012. doi: 10.1007/s10336-017-1458-3.

Shawyer, C. & Banks, P. (1987). Barn Owls on the Brink. *New Scientist*, 116 (1591): 30-33.

Šipoš, J., Suchomel, J., Purchart, L. & Kindlmann, P. (2017). Main determinants of rodent population fluctuations in managed Central European temperate lowland forests. *Mammal Research*, 62 (3): 283-295. doi: 10.1007/s13364-017-0316-2.

Somerset Wildlife Trust. (2022). *Levels & Moors*. Available at: https://www.somersetwildlife.org/create-living-landscapes/levels-moors.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2013). Size-biased allocation of prey from male to offspring via female: family conflicts, prey selection, and evolution of sexual size dimorphism in raptors. *Oecologia*, 172 (1): 93-107. doi: 10.1007/s00442-012-2491-9.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2014a). Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian kestrel. *Animal behaviour*, 96: 31-38. doi: 10.1016/j.anbehav.2014.07.011.

Sonerud, G. A., Steen, R., Selås, V., Aanonsen, O. M., Aasen, G.-H., Fagerland, K. L., Fosså, A., Kristiansen, L., Løw, L. M., Rønning, M. E., et al. (2014b). Evolution of parental roles in provisioning birds: diet determines role asymmetry in raptors. *Behavioral Ecology*, 25 (4): 762-772. doi: 10.1093/beheco/aru053.

Sovon. (2018). *Bird Atlas of the Netherlands*.

Steen, R. (2010). *Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (Falco tinnunculus)*. Ås, Norway: Norwegian University of Life Sciences.

Steen, R., Løw, L. M., Sonerud, G. A., Selås, V. & Slagsvold, T. (2010). The feeding constraint hypothesis: prey preparation as a function of nestling age and prey mass in the Eurasian kestrel. *Animal Behaviour*, 80 (1): 147-153. doi: 10.1016/j.anbehav.2010.04.015.

Steen, R., Løw, L. M., Sonerud, G. A., Selås, V. & Slagsvold, T. (2011). Prey delivery rates as estimates of prey consumption by Eurasian kestrel *Falco tinnunculus* nestlings. *Ardea*, 99 (1): 1-8, 8.

Steen, R., Sonerud, G. A. & Slagsvold, T. (2012). Parents adjust feeding effort in relation to nestling age in the Eurasian kestrel (*Falco tinnunculus*). *Journal of Ornithology*, 153 (4): 1087-1099. doi: 10.1007/s10336-012-0838-y.

Taylor, I. (2003). *Barn owls: predator-prey relationships and conservation*: Cambridge University Press.

The Barn Owl Trust. (2014). *UK Barn Owl Distribution May 2013 to October 2014*.

The Royal Society for the Protection of Birds (RSPB). (2022). *Somerset Levels and Moors Landscape Scale Conservation*. Available at: https://www.rspb.org.uk/our-work/conservation/landscape-scale-conservation/sites/somerset-levels-and-moors/ (accessed: 2022).

The Wildlife Trusts. *Field Vole*. Available at: https://www.wildlifetrusts.org/wildlife-explorer/mammals/field-vole (accessed: 2022).

Vogelbeschirming Nederland. (2021). *Kerkuil*. Available at: https://www.vogelbescherming.nl/beleefdelente/kerkuil (accessed: 2021).

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416 (6879): 389-395. doi: 10.1038/416389a.

Weinstein, B. G. (2015). MotionMeerkat: integrating motion video detection and ecological monitoring. *Methods in Ecology and Evolution*, 6.3: 357-362.

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis: Springer-Verlag New York.

Wolton, R. J. (1983). The Activity of Free-Ranging Wood Mice Apodemus sylvaticus. *Journal of Animal Ecology*, 52 (3): 781-794. doi: 10.2307/4453.

Wong, B. B. M. & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral ecology*, 26 (3): 665-673. doi: 10.1093/beheco/aru183.

Ydenberg, R., Welham, C., Schmid-Hempel, R., Schmid-Hempel, P. & Beauchamp, G. (1994). Time and energy constraints and the relationships between currencies in foraging theory. *Behavioral Ecology*, 5 (1): 28-34.

APPENDIX

Appendix 1. Model selection based on AICc (Akaike, 1978) of the generalized linear effects models for the probability of female delivery of prey as a function of nestling age (days), prey family, nestling age and prey family, and the interaction between nestling age and prey family in the Winterswijk nest location.

Models	**Parameters**	**df**	**AICc**
(mod2)	Nestling age + Prey family	4	589.48
(mod1)	Nestling age*Prey family	6	591.83
(mod3)	Prey family	3	648.29
(mod4)	Nestling age	2	653.39

Appendix 2. Model selection based on AICc (Akaike, 1978) of the generalized linear mixed effects models for the probability of female delivery of prey as a function of nestling age (days), prey family, nestling age and prey family, and the interaction between nestling age and prey family in the Somerset nest location

Models	**Parameters**	**df**	**AICc**
(mod1)	Nestling age*Prey family	6	261.79
(mod2)	Nestling age + Prey family	4	261.98
(mod4)	Nestling age	2	265.51
(mod3)	Prey family	3	360.10

Appendix 3. Model selection based on AICc (Akaike, 1978) of the generalized linear mixed effects models for the probability of assisted feeding as a function of nestling age (days), prey family, nestling age and prey family, and the interaction between nestling age and prey family in the Winterswijk nest location.

Models	**Parameters**	**df**	**AICc**
(mod2)	Nestling age + Prey family	4	525.07
(mod1)	Nestling age*Prey family	6	528.75
(mod4)	Nestling age	2	535.23
(mod3)	Prey family	3	807.30

Appendix 4. Model selection based on AICc (Akaike, 1978) of the generalized linear mixed effects models for the probability of assisted feeding as a function of nestling age (days), prey family, nestling age and prey family, and the interaction between nestling age and prey family in the Somerset nest location.

Models	**Parameters**	**df**	**AICc**
(mod2)	Nestling age + Prey family	4	154.95
(mod1)	Nestling age*Prey family	6	157.65
(mod4)	Nestling age	2	173.09
(mod3)	Prey family	3	647.59

Appendix 5. Model selection based on AICc (Akaike, 1978) of the generalized linear mixed effects models for the probability of storing prey as a function of nestling age (days), prey family, nestling age and prey family, and the interaction between nestling age and prey family in the Winterswijk nest location.

Models	Parameters	df	AICc
(mod2)	Nestling age + Prey family	4	633.65
(mod1)	Nestling age*Prey family	6	636.48
(mod4)	Nestling age	2	638.07
(mod3)	Prey family	3	754.26

Appendix 6. Model selection based on AICc (Akaike, 1978) of the generalized linear mixed effects models for the probability of storing prey as a function of nestling age (days), prey family, nestling age and prey family, and the interaction between nestling age and prey family in the Somerset nest location.

Models	Parameters	df	AICc
(mod2)	Nestling age + Prey family	4	578.84
(mod1)	Nestling age*Prey family	6	579.82
(mod4)	Nestling age	2	588.17
(mod3)	Prey family	3	692.47

Appendix 7. Calculated sunrise and sunset hours in the middle of the observation period (mid-summer 2021) in Winterswijk and Somerset.

```
> RiseWinterswijk
[1] 5.407516
> RiseSomerset
[1] 5.144453
> SetWinterswijk
[1] 21.75419
> SetSomerset
[1] 21.25705
```

Appendix 8. Dhat4 overlap indexes calculated using the overlap package (Meredith & Ridout, 2021) in R.

Prey family	Dhat4
Muridae	0.59
Cricetidae	0.26
Soricidae	0.34

Appendix 9. Difference between Winterswijk and Somerset nests using Watson-Wheeler test for homogeneity (Portugues, 2022) for the most frequently delivered prey families.

Prey family	W	df	P
Muridae	8.4	2	0.02
Cricetidae	384.15	2	<0.001
Soricidae	28.26	2	<0.001

Appendix 10. Coefficients of multinomial log-linear models (Ripley, 2022) fitted for prey families as a function of nestling age (days) in Winterswijk and Somerset.

	Winterswijk		Somerset	
Prey family	**(Intercept)**	**Nestling age (days)**	**(Intercept)**	**Nestling age (days)**
Muridae	-1.18	0.01	-4.60	0.04
Soricidae	-2.59	0.02	-4.00	0.04

Appendix 11. Standard errors of multinomial log-linear models (Ripley, 2022) fitted for prey families as a function of nestling age (days) in Winterswijk and Somerset.

	Winterswijk		Somerset	
Prey family	**(Intercept)**	**Nestling age (days)**	**(Intercept)**	**Nestling age (days)**
Muridae	0.32	0.01	0.71	0.02
Soricidae	0.51	0.02	0.55	0.01

Appendix 12. Prey counts for each nest by prey order. N/A represents prey that were not conclusively identified at the order level.

Prey order	Winterswijk	Somerset	Grand Total
Rodentia	568	523	1091
N/A	375	180	555
Eulipotyphla	53	33	86
Grand total	**996**	**736**	**1732**

Appendix 13. Residual deviance and AICc (Akaike, 1978) of multinomial log-linear models fitted for Prey families as a function of nestling age (days) in Winterswijk and Somerset.

	Winterswijk	Somerset
Residual deviance	1016.51	389.18
AICc	1024.51	397.18

Appendix 14. Global model AICc (Akaike, 1978) ranking for Winterswijk number of prey during the night as a function of nestling age (days), nestling age^2 (day^2), rainfall (mm) and rainfall the day before (mm).

```
Global model call: glm(formula = No_prey_during_night ~ NestlingAge + I(NestlingAge^2) +
    Rainfall + RainfallDayBefore + offset(log(No_hours_night)),
    family = poisson(link = "log"), data = mG)
---
Model selection table
     (Int)     NsA      NsA^2       Rnf       RDB off(log(No_hrs_ngh)) df   logLik  AICc delta weight
20 -0.5074 0.06795 -0.0008801                                       +  3 -220.426 447.2  0.00  0.493
24 -0.5089 0.06849 -0.0008842 -0.003526                             +  4 -220.039 448.7  1.47  0.236
28 -0.5083 0.06827 -0.0008823           -0.002140                   +  4 -220.281 449.2  1.95  0.186
32 -0.5100 0.06879 -0.0008863 -0.003461 -0.002028                   +  5 -219.908 450.7  3.52  0.085
Models ranked by AICc(x)
```

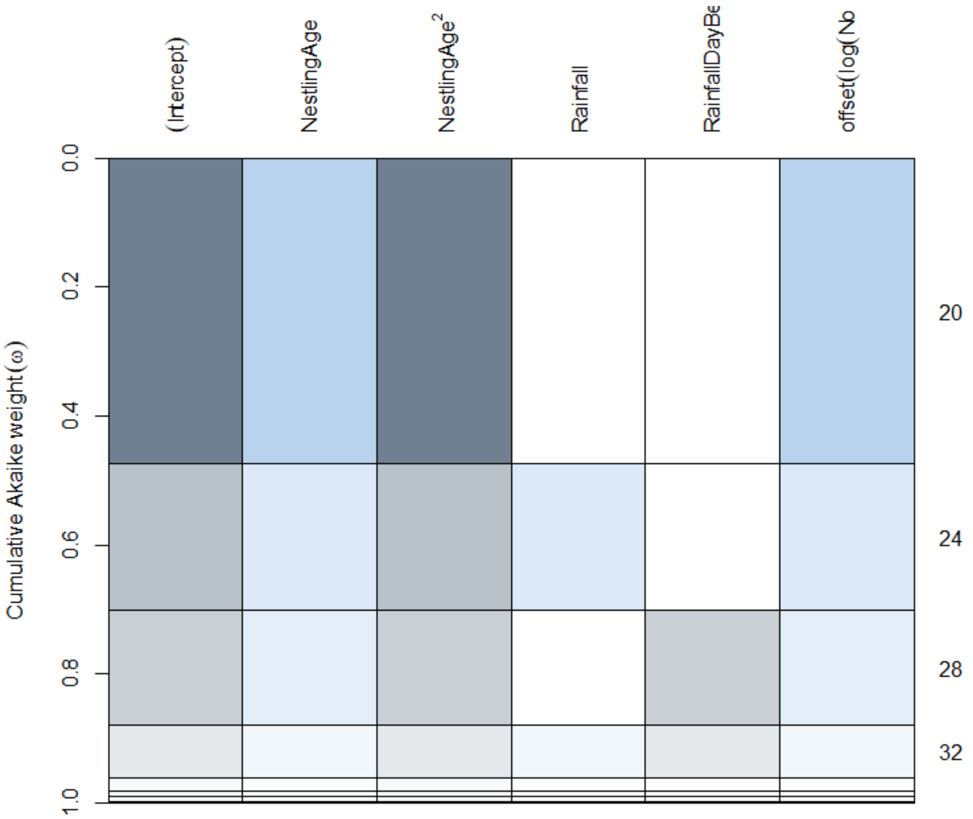
Appendix 15. Model estimates based on Model 1 for Winterswijk number of prey during the night as a function of nestling age (days) and nestling age^2 (day^2).

```
> M1<-glm(No_prey_during_night~NestlingAge+I(NestlingAge^2)
+         +offset(log(No_hours_night)),family = poisson(link = "log"), data= mG)
> summary(M1)

Call:
glm(formula = No_prey_during_night ~ NestlingAge + I(NestlingAge^2) +
    offset(log(No_hours_night)), family = poisson(link = "log"),
    data = mG)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.6898  -0.9558  -0.0002   0.7824   4.0839

Coefficients:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)      -0.5073913  0.1698265  -2.988  0.00281 **
NestlingAge       0.0679538  0.0084566   8.036 9.31e-16 ***
I(NestlingAge^2) -0.0008801  0.0000953  -9.235  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 258.61  on 71  degrees of freedom
Residual deviance: 130.10  on 69  degrees of freedom
AIC: 446.85

Number of Fisher Scoring iterations: 4
```

Appendix 16. Model estimates based on the alternative model for number of prey caught during the night as a function of rainfall (mm), nestling age (days) and nestling age^2 (days2) in Winterswijk.

```
> M2<-glm(No_prey_during_night~NestlingAge+I(NestlingAge^2)+Rainfall
+         +offset(log(No_hours_night)),family = poisson(link = "log"), data= mG)
> summary(M2) # Alternative model, rainfall not significant

Call:
glm(formula = No_prey_during_night ~ NestlingAge + I(NestlingAge^2) +
    Rainfall + offset(log(No_hours_night)), family = poisson(link = "log"),
    data = mG)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.6635  -0.9482   0.0762   0.7503   4.0153

Coefficients:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)      -5.089e-01  1.704e-01  -2.987  0.00282 **
NestlingAge       6.849e-02  8.496e-03   8.061 7.56e-16 ***
I(NestlingAge^2) -8.842e-04  9.552e-05  -9.256  < 2e-16 ***
Rainfall         -3.526e-03  4.070e-03  -0.866  0.38632
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 258.61  on 71  degrees of freedom
Residual deviance: 129.33  on 68  degrees of freedom
AIC: 448.08

Number of Fisher Scoring iterations: 4
```

Appendix 17. Model selection table based on the global model and including all variables being tested against number of prey caught during the night. These variables include nestling age (days), nestling age^2 (days^2), rainfall (mm) and rainfall the day before (mm).



Appendix 18. Global model AICc (Akaike, 1978) ranking for Somerset number of prey during the night as a function of nestling age (days), nestling age^2 (days^2), rainfall (mm) and rainfall the day before (mm).

```
Global model call: glm(formula = No_prey_during_night ~ NestlingAge + I(NestlingAge^2) +
    Rainfall + RainfallDayBefore + offset(log(No_hours_night)),
    family = poisson(link = "log"), data = mS)
---
Model selection table
    (Int)     NsA      NsA^2      Rnf      RDB off(log(No_hrs_ngh)) df   logLik  AICc delta weight
24 -1.664 0.05362 -0.0006233 -0.03997                             +  4 -135.884 280.4  0.00  0.362
32 -1.544 0.04730 -0.0005288 -0.03858 -0.02091                    +  5 -135.317 281.7  1.22  0.196
20 -1.915 0.06809 -0.0008512                                      +  3 -137.784 282.0  1.52  0.169
28 -1.771 0.06046 -0.0007355          -0.02412                    +  4 -137.075 282.8  2.38  0.110
30 -1.043 0.01158            -0.05407 -0.03222                    +  4 -137.192 283.1  2.62  0.098
22 -1.099 0.01156            -0.06098                             +  3 -138.752 283.9  3.46  0.064
Models ranked by AICc(x)
```

Appendix 19. Model estimates based on Model 1 for Somerset number of prey during the night as a function of nestling age (days), nestling age^2 (day^2) and rainfall (mm).

```
> M1<-glm(No_prey_during_night~NestlingAge++I(NestlingAge^2)+Rainfall
+         +offset(log(No_hours_night)),family = poisson(link = "log"), data= mS)
> summary(M1)

Call:
glm(formula = No_prey_during_night ~ NestlingAge + +I(NestlingAge^2) + 
    Rainfall + offset(log(No_hours_night)), family = poisson(link = "log"), 
    data = mS)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-3.2429  -0.9972  -0.3304   0.6411   2.9024  

Coefficients:
                   Estimate Std. Error z value Pr(>|z|)    
(Intercept)      -1.6640460  0.2977649  -5.588 2.29e-08 ***
NestlingAge       0.0536196  0.0185477   2.891  0.00384 ** 
I(NestlingAge^2) -0.0006233  0.0002669  -2.335  0.01953 *  
Rainfall         -0.0399659  0.0213492  -1.872  0.06121 .  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 124.637  on 63  degrees of freedom
Residual deviance:  99.814  on 60  degrees of freedom
AIC: 279.77

Number of Fisher Scoring iterations: 5
```

Appendix 20. Global model AICc (Akaike, 1978) ranking for Somerset number of prey during the day as a function of nestling age (days), nestling age^2 (days^2), rainfall (mm) and rainfall the day before (mm).

```
Global model call: glm(formula = No_prey_during_day ~ NestlingAge + I(NestlingAge^2) +
    Rainfall + RainfallDayBefore + offset(log(No_hours_day)),
    family = poisson(link = "log"), data = mS)
---
Model selection table
     (Int)     NsA      NsA^2      Rnf      RDB off(log(No_hrs_day)) df   logLik  AICc delta weight
28 -1.2420 0.03616 -0.0003786          -0.02769                    +  4 -184.302 377.3  0.00  0.415
32 -1.3260 0.04099 -0.0004525 0.011310 -0.02884                    +  5 -183.870 378.8  1.49  0.197
20 -1.4200 0.04563 -0.0005195                                      +  3 -186.424 379.2  1.97  0.155
26 -0.8982 0.01045                     -0.03990                    +  3 -186.911 380.2  2.94  0.096
24 -1.4970 0.05004 -0.0005871 0.009681                             +  4 -186.103 380.9  3.60  0.069
12  1.4780 0.03377 -0.0003415          -0.02825                       4 -186.108 380.9  3.61  0.068
Models ranked by AICc(x)
```

Appendix 21. Model estimates based on Model 1 for Somerset number of prey delivered during the day as a function of nestling age (days), nestling age^2 (days^2) and rainfall the day before (mm).

```
> M1<-glm(No_prey_during_day~NestlingAge+I(NestlingAge^2)+RainfallDayBefore
+         +offset(log(No_hours_night)),family = poisson(link = "log"), data= mS)
> summary(M1)

Call:
glm(formula = No_prey_during_day ~ NestlingAge + I(NestlingAge^2) +
    RainfallDayBefore + offset(log(No_hours_night)), family = poisson(link = "log"),
    data = mS)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-4.6187  -0.7883  -0.0090   0.6505   4.0715

Coefficients:
                    Estimate Std. Error z value Pr(>|z|)
(Intercept)       -0.6960768  0.1869402  -3.724 0.000196 ***
NestlingAge        0.0421940  0.0117504   3.591 0.000330 ***
I(NestlingAge^2)  -0.0005004  0.0001692  -2.958 0.003099 **
RainfallDayBefore -0.0268159  0.0138892  -1.931 0.053520 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 184.32  on 63  degrees of freedom
Residual deviance: 152.51  on 60  degrees of freedom
AIC: 395.55

Number of Fisher Scoring iterations: 5
```

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