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The Effects of Precipitation on Parental Food Provisioning in the Barn Owls (*Tyto alba*) Breeding in Norfolk, UK

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M-NF: Management of Natural Resources

PREFACE

This master's thesis concludes my master's degree in Natural Resource Management from the Faculty of Environmental Sciences and Natural Resource Management at the Norwegian University of Life Sciences (NMBU).

This thesis would not have been possible without my main supervisor, Ronny Steen, and my co-supervisor, Geir A. Sonerud. Many thanks to Ronny Steen for his help regarding the statistics, prey identification, proofreading, and for providing me with valuable feedback and positive comments on my work. Many thanks to Geir A. Sonerud for his help regarding prey identification and proofreading, sharing his knowledge and providing me with valuable feedback.

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ABSTRACT

Even though scientists have extensively studied the barn owl (*Tyto alba*), there is limited information on how climatic conditions influence parental food provisioning in barn owls on a local scale. Worsened climatic conditions imposed by global climate change may affect the population dynamics in barn owls, and barn owls may experience long-term population declines. I studied how precipitation influences parental food provisioning by using weather data obtained from weather stations and camera surveillance at barn owl nests during the breeding season (May-August) in 2019 in Norfolk, UK. Camera surveillance enabled monitoring of prey delivery rate and owl diet on the scale of hours throughout the breeding season. I found small mammals accounting for as much as 98% of the prey deliveries. The field vole (*Microtus agrestis*) was the most abundant prey species both by number (38.5%) and mass (45.8%). Avian prey deliveries only occurred three times, whereas no deliveries of lizards, amphibians and invertebrates occurred. The probability of prey deliveries concerning the time of the day indicated a circadian activity rhythm and barn owls to be nocturnal hunters mainly. Prey deliveries peaked around midnight. The probability of prey deliveries from the families Arvicolidae, Muridae, and Soricidae, indicated a circadian rhythm and foraging primarily between sunset and sunrise. Prey was decapitated before delivery only on a few occasions, in five of 647 prey deliveries, with three of the five deliveries happening the same hunting night. As few studies have addressed the prevalence of decapitated prey before delivery, future studies may further explore this issue. Nestling feeding unassisted increased as the nestlings grew older. At the age of 18.6 days, it was 50% likely that the nestlings ingested prey without maternal help. As the nestlings grew older, prey deliveries by the female became more likely, while the probability of prey deliveries inside the nest cavity decreased. The number of prey deliveries ranged from no deliveries up to 20 deliveries a day. On average, seven to eight prey items were delivered to the two nestlings in each nest, indicating that each nestling consumed three to four prey items each day. The number of prey deliveries at night decreased with increasing daily rainfall, implying that barn owls may limit hunting when it rains. An increase in prey deliveries during the daytime was related to the two last days of rainfall. Two days with rainfall compelled the owls to hunt during the daytime to provide enough food for the nestlings. Few prey deliveries the previous night was still the best explanation for an increase in daytime deliveries. My results suggest that precipitation must be considered an important factor when evaluating how weather conditions affect parental food provisioning. Further research on how weather conditions influence parental food provisioning in barn owls should also include other factors such as wind and temperature. Future studies exploring this issue will enhance our understanding of how barn owl populations will respond to more frequent extreme weather events in the future.

Keywords: The barn owl, *Tyto alba*, climate change, precipitation, weather conditions, food provisioning, prey deliveries, prey selection, circadian

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1. INTRODUCTION

Global climate change is expected to affect all levels of the Earth's biodiversity (Bellard et al., 2012) and may exceed habitat loss as the main threat to biodiversity (Leadley et al., 2010; Bellard et al., 2012). Hence, to predict the response of biodiversity to climate change and its consequences for a species' population dynamics, it is necessary to take an in-depth approach, studying key parameters such as reproductive success and species' survival in relation to climatic conditions (Walther et al., 2002; Crick, 2004; Bellard et al., 2012; Beever et al., 2017).

Climatic conditions affect the population dynamics in birds (Crick, 2004). Recent climate change strongly influences birds (Crick, 2004; Carey, 2009; Jenouvrier, 2013), and unless birds can adapt to changing conditions, climate change may severely impact their migration and reproduction. When exposed to variations in precipitation or temperature, non-migratory birds may face food shortages and breeding mismatches (Crick, 2004; Carey, 2009).

Parental food provisioning in birds concerns energy and time spent by the parents in obtaining and delivering food to their nestlings (Taylor, 2004; Ydenberg et al., 2007). According to foraging theory, the ultimate purpose of foraging and prey selection is to maximise the net rate of energy gain while foraging (Derting & Cranford, 1989; Taylor, 2004; Stephens & Krebs, 2019). The energy gained and expended during foraging is generally measured as both a cost and a benefit, hence referred to as the net rate of energy gain (Stephens & Krebs, 2019). Because the parents must secure enough nutrients and energy for the nestlings, this might affect their survival and reproductive success (Houston, 1987; Ydenberg et al., 1994; Taylor, 2004). Foraging at minimal costs may enhance resilience to challenging conditions during the breeding season (Taylor, 2004).

Prey availability place constraints on food provisioning and reproductive success in birds, as foraging costs may increase in times with scarce food sources (Crick, 2004). Rodent populations fluctuate between season and years (Steen et al., 1990; Krebs, 2013). In the UK, the rodent population peak usually occurs late in the breeding season, from July to August (Bunn et al., 1982). Several species display interspecific temporal population synchrony (Bjørnstad et al., 1999), e.g., field vole populations in the northern UK exhibit three to four-year cycles (Lambin et al., 2000), in many parts similar to those described in Fennoscandia (Steen et al., 1996; Bjørnstad et al., 1999). Field vole populations may experience collapses with subsequent periods without recovery in numbers (Lambin et al., 2000). Multiannual

population cycles have fascinated scientists for a long time (Sonerud, 1988; Turchin, 2013), and several hypotheses have been promoted to explain these (Krebs & Myers, 1974; Hansson & Henttonen, 1985; Ims & Steen, 1990; Selås, 1997). In predators, such as raptors and owls, which hunt small mammals, survival and reproduction are closely linked with prey abundance (Newton, 1979; Sonerud, 1988; Steen, 2010).

The barn owl (*Tyto alba*) generally hunts small mammals in open lands, such as fields and grasslands. Crops, hedgerows, banks, and woodland edges are more valuable foraging habitat in anthropogenically modified landscapes (Glue, 1974; Bunn et al., 1982; Taylor, 2004; Bond et al., 2005). Food requirements in barn owls will fluctuate depending on factors such as the bird's activity, time of the year, and prevailing weather conditions (Taylor, 2004). Considering that small mammals, particularly rodents, make up most of the diet, barn owls are greatly exposed to any temporal change in prey abundance (Bunn et al., 1982; Love et al., 2000). In times of low prey availability, the owls must abandon their traditional hunting grounds searching for prey elsewhere (Bunn et al., 1982; Taylor, 2004). Food shortage may impair reproduction and nestling survival (Shawyer & Shawyer, 1995; Bond et al., 2005) and simultaneously increase adult mortality risk. Within dense populations, higher adult mortality can result in population declines (Roulin, 2020). In general, barn owls exhibit more significant population size variations annually than other similar-sized raptors, such as kestrels, which exploit similar foraging habitats. Especially after harsh winters and in years with low prey availability, barn owl populations may collapse (Roulin, 2020).

Several barn owl populations worldwide suffered long-term declines during the 20th century (Taylor, 2004; Roulin, 2020). Once regarded as the most abundant owl species in the UK, the UK population experienced substantial declines from 1850 to 1950, mainly due to habitat loss (Leech et al., 2009; Roulin, 2020). A study by Shawyer (1987) indicated a 66% population decline, from 240 (8.4 pairs per km²) (Blaker, 1933) to only 82 (2.9 pairs per km²) breeding pairs in northwest Norfolk (Johnson, 1994). However, more recent studies suggest the UK barn owl populations may have stabilised and that the last century population declines are halted (Toms, 1997; Toms et al., 2001; Leech et al., 2009). Nevertheless, the barn owl is included on the UK Birds of Conservation Concern Amber List under international criteria due to habitat loss and unfavourable conservation status in Europe (Ranner et al., 1994; Leech et al., 2009).

Weather conditions are especially critical for barn owls when incubating eggs and rearing nestlings (Shawyer & Banks, 1987; Taylor, 2004). Prevailing weather conditions may influence the owls' diurnal rhythm, activity level, and the timing of breeding according to the

seasons (Taylor, 2004; Bourgault et al., 2010; Chausson et al., 2014a). The timing of breeding activities should coincide with the most favourable weather conditions (Bourgault et al., 2010; Chausson et al., 2014a). Under appropriate conditions, barn owls can produce up to two broods annually (Bunn et al., 1982; Chausson et al., 2014b). Under unfavourable conditions, especially if heavy rain or windy weather, breeding performance could be impaired (McCafferty et al., 2001). Hence, alterations in weather conditions during breeding may inhibit reproduction and be critical for nestling survival (Chausson et al., 2014a).

Worsened weather conditions involve changes in precipitation, which is directly influenced by climate change in global warming (Trenberth, 2011). When global warming causes the water holding capacity in the air to rise, the water vapour in the atmosphere will increase as well. Thus, a greater risk of storm and tropical cyclones, including increased moisture, induces more intense precipitation events (Trenberth, 2011). Heavy rain will prevent the barn owls from hunting successfully (Bunn et al., 1982; Chausson et al., 2014a). The rain will hamper their hearing and vision, and their loose plumage saturates when capturing prey in wet grass (Bunn et al., 1982; Shawyer & Banks, 1987). In addition to adversely affecting flight- and hunting performance, heavy rain could affect prey availability, possibly reducing the amount of food for the nestlings (Crick, 2004).

Even though the impact of weather on bird populations has been studied broadly during recent decades, most studies are on a macro level (Crick, 2004). Furthermore, as barn owls are cosmopolitan and often live close to humans, the barn owl has been the subject of extensive studies over the last century. Still, there is limited information about how weather conditions affect parental food provisioning in barn owls on a local scale. Barn owls are particularly sensitive to environmental factors, and they are among the species to first suffer in worsened weather conditions (Roulin, 2020). If extreme weather events, such as more intense precipitation events and periods with strong wind (Pereira et al., 2010; Trenberth, 2011; Bellard et al., 2012), occur more regularly, barn owl populations may experience long-term declines (Roulin, 2020). Hence, in-depth studies are necessary to understand how weather conditions may affect barn owl ecosystems on a local scale (Wong & Candolin, 2015).

In this study, I aimed to analyse potential climatic effects on the foraging behaviour of barn owls during the critical breeding season by focusing on the amount of precipitation on a local scale. In particular, this study was designed to answer the following questions: (1) Which prey species are preferred (i.e., type of prey, biomass) by barn owls? (1) I would expect the diet to be mainly small mammals. Several studies have demonstrated that shrews

and rodents make up most of the barn owl diet in the UK (Glue, 1974; Bunn et al., 1982; Taylor, 2004). (2) How is the diel activity pattern regarding prey deliveries in barn owls? (2) Barn owls are well adapted to be nocturnal hunters (Roulin, 2020). I assumed the barn owls would mostly hunt at night, although barn owls regularly hunt during the daytime in the northern UK (Taylor, 2004). (3) What is the effect of precipitation on the barn owl's parental effort? (3) I predicted fewer prey deliveries with increased daily rainfall, as studies suggest that barn owls limit hunting during rain (Taylor, 2004; Roulin, 2020). However, after some days with rainfall, I would expect the barn owls had to leave the nest during the daytime to compensate for fewer prey deliveries (see Chausson et al., 2014a). Additionally, I predicted that the previous night's prey delivery numbers would influence daytime deliveries. The parents may already have provided sufficient food or need to compensate for few deliveries the night before.

2. METHODS

2.1 Study site

By using camera surveillance, prey deliveries at two barn owl nests were studied during the breeding season in 2019 over a period of 73 days (28th of May to 1st of August). The study was performed at two locations in Norfolk, in East Anglia County in the UK. One study site, hereafter referred to as Nar Valley, was situated inland in the Midwest. The other study site, hereafter referred to as Broads Authority, was located closer to the coast in the East. The two locations were based approximately 73 km apart (Figure 1).

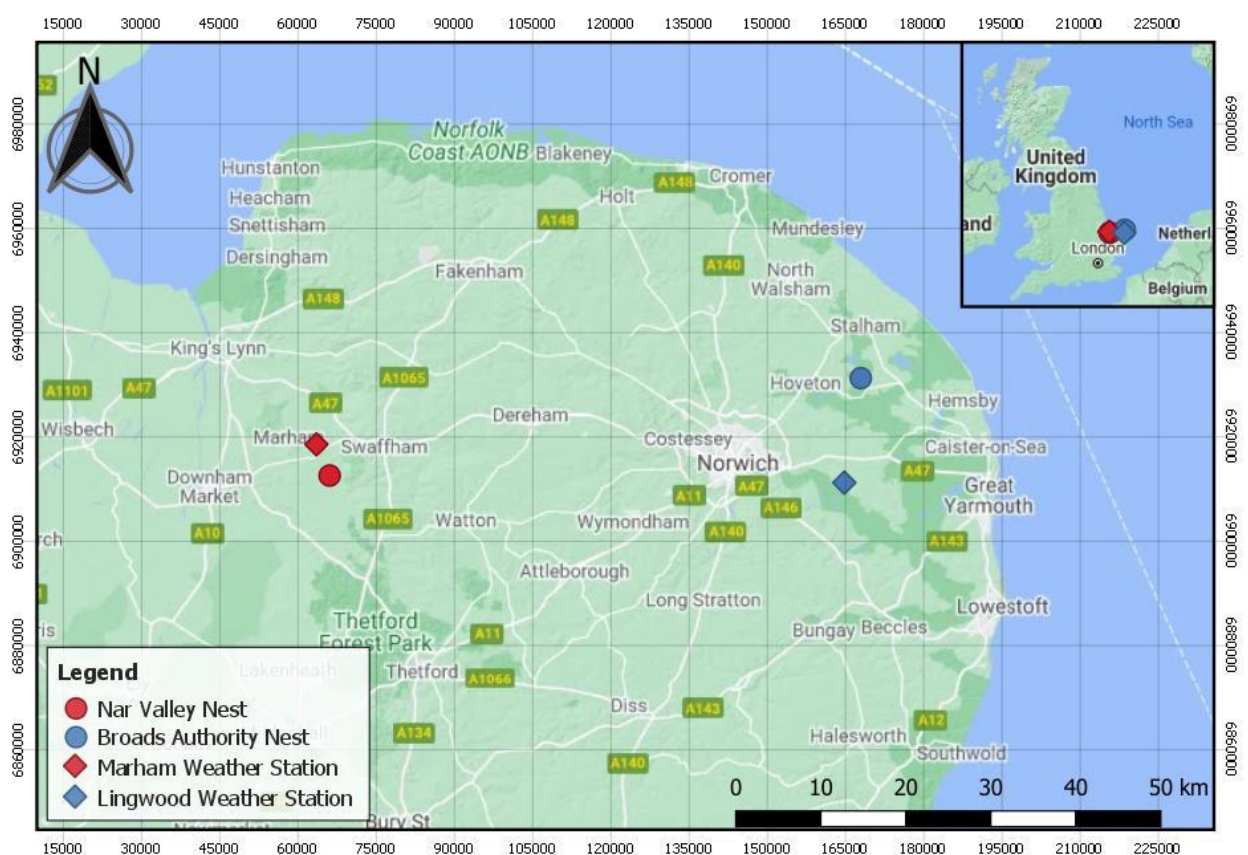


Figure 1. Map of the study area in Norfolk, UK, including the nest locations in Nar Valley (65981.54, 6912536.45) and Broads Authority (167919.27, 6931234.68), and the weather stations in Marham (63452.11, 6918517.99) and Lingwood (164752.85, 6911181.79). The map was created in QGIS (version 3.12.3-București) using the reference coordinate system WGS84 Geographic Coordinate System (EPSG:3857).

Nar Valley

The nest in Nar Valley (52°37'02.6" N 0°35'33.8" E) was located inland in the Midwest, close to the village Beachamwell, in Norfolk, UK. The nest box was situated in an old oak (*Quercus robur*) (Figure 2). Pastoral areas dominated the surrounding landscape with surrounding patches of woodlands. Camera surveillance in Nar Valley was initiated on the 28th of May 2019, with the first video recording starting at 18:00:57 hours. Camera

surveillance was terminated on the 8th of July, with the last video recording ending at 04:00:53 hours. A local ornithologist at the Nar Valley Ornithological Society (NarVOS) operated the nest box camera during the study period. Three barn owl nestlings hatched in the nest, but the smallest nestling died on the 28th of May. In combination with the camera mounting, the two surviving nestlings were ringed on the 28th of May, when the oldest nestling was 21 days old. Both barn owl parents were ringed before the camera surveillance was initiated. The female parent was ringed on the left foot, while the male parent was ringed on the right foot.

Broads Authority

The nest in Broads Authority (52°43'09.3" N 1°30'30.4" E) was located in the East, close to River Ant in the How Hill National Nature Reserve, near the village Ludham in Norfolk, UK. The nest box was situated in a tree close to a river system flowing from the River Ant (Figure 2). A mixture of rivers, farmland, and woodlands in the East formed the surrounding landscape. Camera surveillance in Broads Authority was initiated on the 28th of May 2019, with the first video recording starting at 13:10:32 hours. Camera surveillance was terminated on the 1st of August, with the last video recording ending at 08:04:27 hours. Staff at the Broads Authority operated the nest box camera during the study period. In the nest, two barn owl nestlings hatched, and both nestlings survived. Both nestlings were ringed on the 16th of July when the oldest nestling was 47 days old. The barn owl parents were not identified to be ringed in advance of the camera surveillance.



Figure 2. The picture on the left shows Ronny Steen mounting the nest box camera in an old oak in Nar Valley in February 2019. The picture on the right shows the mounted nest box and the surrounding landscape in Broads Authority in February 2019. Photo: Ronny Steen.

2.2 Study species

The barn owl

The barn owl belongs in the order Strigiformes and the family Tytonidae. The family Tytonidae consists of two subfamilies, where the subfamily Tytoninae includes barn owls and grass owls. The barn owl, one of few existing cosmopolitan animals, is the most widespread owl globally (Bunn et al., 1982; Roulin, 2020). The barn owl shows a fair degree of adaptability to several habitat variations, and it favours a dry climate and open plain in the lowland for hunting (Bunn et al., 1982).

In the UK, the barn owl nests in temperate zones, usually between April-June (Bunn et al., 1982). The clutch size is highly variable, ranging from two to 18 eggs (Taylor, 2004), but five eggs' clutches are most common (Bunn et al., 1982). The nestlings remain in the nest for seven to ten weeks, and they are capable of flight at around 56 days. However, they will remain dependent on their parents for another three to five weeks (Bunn et al., 1982). The barn owl is usually monogamous, and the male provides all prey for the family, assisted by the female in the later part of the breeding season (Bunn et al., 1982). An individual barn owl typically consumes three to four prey items per day. Thus, a family with two or more nestlings devours 1200-3500 prey during the rearing period. Hence, they will need between 5000-7000 prey items in total each year (Roulin, 2020). The barn owl preys mostly on small mammals, mainly rodents and shrews (Glue, 1974; Taylor, 2004).

The potential prey species

Rodents belong in the order of Rodentia, which include voles (Arvicolidae) and mice (Muridae). Species of voles that exist in the study areas include the field vole (*Microtus agrestis*), the bank vole (*Myodes glareolus*), and the European water vole (*Arvicola amphibious*). The European water vole has experienced a sharp population decline in the UK and is almost completely limited to areas managed for wildlife (Couzens et al., 2017). In this case, the nest in Broads Authority was located inside the How Hill National Nature Reserve. Species of mice that exist in the study areas include the wood mouse (*Apodemus sylvaticus*), the yellow-necked wood mouse (*Apodemus flavicollis*), the brown rat (*Rattus norvegicus*), the Eurasian house mouse (*Mus musculus*), and the Eurasian harvest mouse (*Micromys minutus*). The Eurasian harvest mouse is uncommon in the UK (Couzens et al., 2017). However, according to Buckley (1977), data collection at a study site in East Norfolk during 1969-1973 suggest Eurasian harvest mice account for more of the barn owl diet in parts of Norfolk than elsewhere in the UK.

Shrews (Soricidae) belong in the order Eulipotyphla. Species of shrews that exist in the study areas include the common shrew (*Sorex araneus*), the Eurasian pygmy shrew (*Sorex minutus*), and the Eurasian water shrew (*Neomys fodiens*). The Eurasian water shrew populations in the UK are declining due to habitat loss and pollution (Couzens et al., 2017). Other prey species in the study areas include the European mole (*Talpa europaea*), and various birds, amphibians, lizards and invertebrates (Bunn et al., 1982; Taylor, 2004; Couzens et al., 2017).

2.3 Technical specifications

Nest camera monitoring setup and camera surveillance

Ronny Steen mounted nest box cameras in Nar Valley and Broads Authority in February 2019. Both locations experienced successful barn owl hatching in the nest boxes in 2019. Water-proof housing covered the nest cameras, and IR lights enabled monitoring at night. The nest cameras were mounted corresponding to Steen (2009), with the camera attached beneath the nest box cover facing the nest box entrance (Figure 3). The nest cameras were operated remotely by a 25 m cable connected to a mini digital recorder (mini-DVR) storing the video on SD cards (maximum 32 GB), enabling battery maintenance and data collecting without the need to approach the nest boxes. The mini-DVR enables video motion detection, with the detection area set to the nest box entrance. Event-based recordings reduce the number of excessive recordings. A marine lead battery (12 VDC 80 Ah) powered the whole system.



Figure 3. The picture shows how the nest box camera was mounted in February 2019. Photo: Ronny Steen.

Data collection and data processing

In this study, a total of 27 201 video files and approximately 152 hours of video (152:11:45) were collected from the nest box recordings between the 28th of May and the 1st of August. In Nar Valley, the nest box camera produced 17 912 video files (18.35GB) and approximately 102 hours of video (102:19:01) between the 28th of May and the 8th of July. In Broads Authority, the nest box camera produced 9 289 video files (12.5GB) and approximately 50 hours of video (49:52:44) between the 28th of May and the 1st of August.

The nest box cameras recorded video when there was movement at the nest box entrance. However, several video files were generated by insects flying around inside the nest box. The video files generated from the nest box camera in Nar Valley were stored on SD cards and delivered by post to Norway. Using an SD card reader, I transferred the files to my computer for storage. The video files generated from the Broads Authority nest box camera I obtained online through WeTransfer file sharing downloading them to my computer for storage. Next, I manually sorted the video files to eliminate unimportant files.

Weather data

I obtained the meteorological variables for each nest location with hourly measurements from Met Office, UK. The weather datasets included daily total rainfall (mm) and daily minimum, maximum, and mean temperature (°C). For Nar Valley, data were obtained from the weather station in Marham (52°39'00.0" N 0°34'12.0" E), 4.2 km from the nest. For Broads Authority, data were obtained from the weather station in Lingwood (52°36'36.0" N 1°28'48.0" E), Strumpshaw Hill, 12 km from the nest.

2.4 Video analysis

Data reviewing

I reviewed the video recordings from January 2020 to September 2020 using VLC Media Player (version 3.0.10). I documented the main events, including the date and time of the barn owl parents' arrival at the nest (with or without prey), the time of departure from the nest, and the feeding time in a Microsoft Word (version 2008) document. Also, when the nestlings went outside and back inside the nest cavity throughout the study period were documented. The data was later transferred manually to a Microsoft Excel (version 2008) document.

Prey identification

Ronny Steen, Geir A. Sonerud and I reviewed the video recordings concerning prey items from October 2020 to December 2020. We identified the avian prey items from their body size, size of the beak, amount and pattern of the feathers, size of the toes, and overall appearance. We identified mammalian prey items from their body size, tail length and type, skin colour and skin colour separation, ear shape and size, eye shape and size, snout shape and length, fur type, and overall appearance (Table 1, Figure 4-6).

Table 1. Characteristics used to distinguish the different mammalian prey items (Couzens et al., 2017).

Mammalian prey	Characteristics for identification
Field vole (<i>Microtus agrestis</i>)	Short tail (less than half the body length). Short ears, almost hidden in the fur. Brighter body sides.
Bank vole (<i>Myodes glareolus</i>)	Medium long tail (half to two-thirds of the body length). Prominent ears. Two-toned skin.
European water vole (<i>Arvicola amphibious</i>)	Large body size. Medium long furry tail. Furry body appearance.
Common shrew (<i>Sorex araneus</i>)	Pointed snout. Long hairy tail. Small ears. Less contrasting skin than the Eurasian water shrew.
Eurasian water shrew (<i>Neomys fodiens</i>)	More sharply contrasting skin, black above and white below, than the common shrew.
Wood mouse (<i>Apodemus sylvaticus</i>)	Long tail. Prominent ears. Large eyes. Two toned skin, white underneath.
Brown rat (<i>Rattus norvegicus</i>)	Large body size. Long tail. More pointed snout and larger ears than the European water vole.
Eurasian house mouse (<i>Mus musculus</i>)	Less prominent eyes and ears than the wood mouse.
Eurasian harvest mouse (<i>Micromys minutus</i>)	Very small. Smaller eyes than the wood mouse.



Figure 4. Photos from the nest-box cameras used to distinguish between the field vole and the bank vole. The field vole (left) shows the typical characteristics with a short tail and relatively small ears and eyes. The bank vole (right) displays a longer tail (half to two-thirds of the body length) than the field vole (less than half the body length) (Couzens et al., 2017).



Figure 5. Photos from the nest-box cameras used to distinguish between the common shrew and the Eurasian water shrew. The common shrew (left) shows the typical characteristics with a pointed snout, small ears, and a long tail. The Eurasian water shrew (right) shows the typical appearance of a shrew with dark colour skin separation specific to the Eurasian water shrew (Couzens et al., 2017).



Figure 6. Photos from the nest-box cameras used to distinguish between the wood mouse and the brown rat. The wood mouse (left) shows the typical characteristics with a long tail, large eyes, and prominent ears. The brown rat (right) displays a larger size, long and thicker tail, and more prominent legs than the wood mouse (Couzens et al., 2017).

Identifying prey by video observation turned out to be challenging. During the early nesting period in Broads Authority, the camera angle made it sometimes difficult to witness the prey delivery. Due to the pace of delivery, few video frames displaying the prey and the condition of prey items further complicated the identification process. As the nestlings grew older, high nestling activity and prey deliveries outside the nest cavity made identification impossible. A few prey items were not identifiable and marked as ‘unidentified prey’. Several mammalian prey items were challenging to identify closer than order or family. They were scored as either ‘unidentified vole’, ‘unidentified mice’, ‘unidentified small rodent’, or ‘unidentified small mammal’ by how easily we could identify them. We recognised some prey items as one of two species, thus marked as ‘field/bank vole’ and ‘common

shrew/Eurasian water shrew’. We could not identify the avian prey items closer than family, thus marked as ‘unidentified partridge’ and ‘unidentified sparrow’.

A few prey items could, in reality, be another species. It was not possible to distinguish between the Eurasian pygmy shrew, which is widely distributed in the UK (Couzens et al., 2017), and juvenile or smaller specimens of the common shrew. Distinguishing between the wood mouse and the yellow-necked wood mouse was neither doable. However, the yellow-necked wood mouse is far less common in the UK and has not been registered in the study area in Nar Valley since the period 1960-1992. On the other hand, the yellow-necked wood mouse was registered in parts of the study area in Broads Authority in the period 2000-2016 (Crawley et al., 2020) (Appendix 1).

2.5 Prey body mass estimation

I assigned an estimated body mass to all prey items. Individuals differed in size within each species. However, estimating individual body mass based on video observation would not be accurate. Hence, all individuals for the specific species were assigned the same body mass (Table 2).

Table 2. Prey body mass estimation for the mammalian and avian prey items. Prey body mass estimates for the species Eurasian house mouse and Eurasian harvest mouse were selected based on body mass values found in Couzens et al. (2017). Prey body mass estimates for the remaining prey types were set based on body mass data from G.A. Sonerud (unpublished data).

Prey type	Body mass estimation (g)
Field vole (<i>Microtus agrestis</i>)	30
Bank vole (<i>Myodes glareolus</i>)	20
European water vole (<i>Arvicola amphibious</i>)	100
Common shrew (<i>Sorex araneus</i>)	10
Eurasian water shrew (<i>Neomys fodiens</i>)	15
Wood mouse (<i>Apodemus sylvaticus</i>)	25
Brown rat (<i>Rattus norvegicus</i>)	100
Eurasian house mouse (<i>Mus musculus</i>)	15
Eurasian harvest mouse (<i>Micromys minutus</i>)	10
Partridge (Galliformes sp.)	30
Unidentified sparrow (Passeriformes sp.)	10

We identified some of the prey items as one of two species. When estimating the body mass for these specimens, I calculated a weighted average based on the number of individuals of each species delivered. For prey items identified to family, order, or prey group, I calculated a weighted average of all delivered prey in the specific group, order, or family. Correspondingly, I calculated the body mass of the unidentified prey items based on the

weighted averaged of all delivered prey items. All calculations were made for each nest separately.

2.6 Nestling age determination

For both nest locations, the nestling age was determined for the first hatched nestling. In an online meeting on the 24th of February 2021, Ronny Steen, Geir A. Sonerud and I defined the age of the oldest nestling in Broads Authority by using a guide for ageing young barn owls (Richards & Ramsden, 2012) combined with Ronny Steen's and Geir A. Sonerud's knowledge. In Nar Valley, we received information about the nestling age from Allan Hale at the Nar Valley Ornithological Society (NarVOS).

2.7 Statistical analysis

The statistical analyses were performed with the statistical software program R (version 3.6.2) using generalised linear mixed-effect regression models and the Laplace approximation technique for parameter estimation in the 'lme4' package. 'Nest ID', expressed as ϵ in the formula for the diel activity models, was included in all tests as a random effect. The reason for adding the random variable was to check for repeated measurements and variation between pairs (Pinheiro & Bates, 2006; Steen, 2010; Sonerud et al., 2013).

Analysing prey delivery in relation to the time of the day

The diel activity analyses of prey delivery as a function of the time of the day were performed using generalised linear mixed-effect models in the 'lme4' package (Pinheiro & Bates, 2006). First, a model concerning all prey deliveries involving both nests and a model for each separate nest was established. Next, models concerning the prey families Arvicolidae, Muridae and Soricidae, separately involving both nests, were established. For the latter, mammalian prey items not identified to species were excluded. Also, the avian prey items delivered were not included due to insufficient data (3 specimens).

In order to analyse prey delivery in relation to the time of the day, a model of the barn owl's circadian activity was established using the cosine-based mixed-effects regression model (cosinor method) (Steen, 2017). The periodic component of the time series was expressed by pairs of sine and cosine functions (Nelson et al., 1979), as demonstrated by Pita et al. (2011) and Steen (2017). The response variable was set as the probability of prey delivery per hour. The explanatory variable 'time of the day', expressed as x in the formula, was selected as the hours divided into hour blocks (i.e. 0-24 h), where each observed hour

block was the sample unit (Steen, 2017). The hour blocks with prey deliveries were scored as ‘1’, while the hour blocks without deliveries were scored as ‘0’.

Nine diel activity models were established (including the random model M_0), where one harmonic (parameter) was added for each model, i.e., model 0 included zero harmonics, while model 1 included one harmonic. By adding harmonics, a higher proportion of fluctuations are considered by the model. However, adding too many harmonics can complexify the model. Besides, for each added harmonic, one degree of freedom (df) is lost (James et al., 2013). The degrees of freedom (df) is defined as the sample size (n) minus the number of parameters (p) estimated from the data (Crawley, 2005). The formulas for the diel activity models were as following:

$$M_0: \log(f(x)) = a_0 + \varepsilon$$

$$M_1: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \varepsilon$$

$$M_2: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2x2\pi x}{24} + b_2 \sin \frac{2x2\pi x}{24} \right) + \varepsilon$$

$$M_3: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2x2\pi x}{24} + b_2 \sin \frac{2x2\pi x}{24} \right) + \left(a_3 \cos \frac{3x2\pi x}{24} + b_3 \sin \frac{3x2\pi x}{24} \right) + \varepsilon$$

$$M_4: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2x2\pi x}{24} + b_2 \sin \frac{2x2\pi x}{24} \right) + \left(a_3 \cos \frac{3x2\pi x}{24} + b_3 \sin \frac{3x2\pi x}{24} \right) + \left(a_4 \cos \frac{4x2\pi x}{24} + b_4 \sin \frac{4x2\pi x}{24} \right) + \varepsilon$$

$$M_5: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2x2\pi x}{24} + b_2 \sin \frac{2x2\pi x}{24} \right) + \left(a_3 \cos \frac{3x2\pi x}{24} + b_3 \sin \frac{3x2\pi x}{24} \right) + \left(a_4 \cos \frac{4x2\pi x}{24} + b_4 \sin \frac{4x2\pi x}{24} \right) + \left(a_5 \cos \frac{5x2\pi x}{24} + b_5 \sin \frac{5x2\pi x}{24} \right) + \varepsilon$$

$$M_6: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2x2\pi x}{24} + b_2 \sin \frac{2x2\pi x}{24} \right) + \left(a_3 \cos \frac{3x2\pi x}{24} + b_3 \sin \frac{3x2\pi x}{24} \right) + \left(a_4 \cos \frac{4x2\pi x}{24} + b_4 \sin \frac{4x2\pi x}{24} \right) + \left(a_5 \cos \frac{5x2\pi x}{24} + b_5 \sin \frac{5x2\pi x}{24} \right) + \left(a_6 \cos \frac{6x2\pi x}{24} + b_6 \sin \frac{6x2\pi x}{24} \right) + \varepsilon$$

$$M_7: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2x2\pi x}{24} + b_2 \sin \frac{2x2\pi x}{24} \right) + \left(a_3 \cos \frac{3x2\pi x}{24} + b_3 \sin \frac{3x2\pi x}{24} \right) + \left(a_4 \cos \frac{4x2\pi x}{24} + b_4 \sin \frac{4x2\pi x}{24} \right) + \left(a_5 \cos \frac{5x2\pi x}{24} + b_5 \sin \frac{5x2\pi x}{24} \right) + \left(a_6 \cos \frac{6x2\pi x}{24} + b_6 \sin \frac{6x2\pi x}{24} \right) + \left(a_7 \cos \frac{7x2\pi x}{24} + b_7 \sin \frac{7x2\pi x}{24} \right) + \varepsilon$$

$$M_8: \log(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}\right) + \left(a_2 \cos \frac{2x2\pi x}{24} + b_2 \sin \frac{2x2\pi x}{24}\right) + \left(a_3 \cos \frac{3x2\pi x}{24} + b_3 \sin \frac{3x2\pi x}{24}\right) + \left(a_4 \cos \frac{4x2\pi x}{24} + b_4 \sin \frac{4x2\pi x}{24}\right) + \left(a_5 \cos \frac{5x2\pi x}{24} + b_5 \sin \frac{5x2\pi x}{24}\right) + \left(a_6 \cos \frac{6x2\pi x}{24} + b_6 \sin \frac{6x2\pi x}{24}\right) + \left(a_7 \cos \frac{7x2\pi x}{24} + b_7 \sin \frac{7x2\pi x}{24}\right) + \left(a_8 \cos \frac{8x2\pi x}{24} + b_8 \sin \frac{8x2\pi x}{24}\right) + \varepsilon$$

Each model's (M₀-M₈) AICc value was calculated using the small-sample correction of Akaike's information criterion (AICc) (Akaike, 1978; Burnham & Anderson, 1998) as demonstrated by Steen (2017). Each model (M₁-M₈) was then compared with the random model (M₀) to find the best-fitted model. The models were then sorted according to their AICc values, where the best-fitted model would be the model with the lowest AICc value (Steen, 2017). Also, considerable support can be acknowledged for the models where the difference in AICc relative to AICc_{min} are < 2 (Burnham & Anderson, 1998), as specified by Steen (2017).

The graphical presentations are predictions from the best-fitted models. The straight dotted line in the graphical presentations represents the average cycle value (MESOR). The barn owl's main activity period was defined as the time of the day when the activity was above MESOR (Navarro et al., 2013; Steen & Barmoen, 2017). Next, the 95% confidence intervals were calculated by model-based parametric bootstrapping for mixed models with the 'bootMer' function in the 'lme4' package (Steen & Barmoen, 2017). One hundred simulations were bootstrapped, enabling scattering computation (James et al., 2013). Further, the data were examined by how it coincided with the period of day and night. The average time of sunrise and sunset in the study period were calculated by adding the specific coordinates for the nest sites in the 'maptools' function in R (version 3.6.2). Lastly, the results were assessed and interpreted to see if there was a significant correlation between the two parameter sets.

Analysing the probability of nestling feeding unassisted, the female delivering prey, and delivering prey inside the nest cavity

The analyses of the probability of nestling feeding unassisted, the female delivering prey, and delivering prey inside the nest cavity were performed using generalised linear mixed-effect models in the 'lme4' package (Pinheiro & Bates, 2006). In order to perform the analyses, models were established using mixed-effects regression models based on binomial distribution. The response variables were set as the 'probability of nestling feeding', the 'probability of female delivering prey', and the 'probability of delivering prey inside'. The explanatory variables were set as the 'nestling age (d)' and the 'prey body mass (g)'. The

best-fitted model, with the lowest AICc value (Steen, 2017), were calculated from the small-sample correction of Akaike's information criterion (AICc) (Akaike, 1978). No test was carried out for the probability of decapitated prey items at the delivery time, considering the low number of incidents.

For the first analysis, the 'nestling age (d)' and the 'prey body mass (g)' were set as the explanatory variables. 'Nestling age (d)' was defined as days that elapsed since the first nestling hatched in the nest. Nestling feeding was scored as '1', while indefinite nestling was scored as '0'. 'Nestling feeding' was defined as when the nestling received the prey in its beak. For the second analysis, the 'nestling age (d)' and the 'prey body mass (g)' were set as the explanatory variables. Prey deliveries by the female were scored as '1', while prey deliveries by the male were scored as '0'. 'Female delivering prey' was defined as when the female parent delivered the prey. For the third analysis, the 'nestling age (d)' was set as the explanatory variable. Prey delivery inside the nest was scored as '1', while prey delivery outside the nest was scored as '0'. 'Delivering prey inside' was defined as when the prey was delivered inside the nest cavity.

Analysing prey deliveries in relation to the amount of daily rainfall, amount of previous rainfall, and the number of prey delivered previous night

Weather data with hourly measurements enabled statistical analyses of correlations between weather parameters and prey delivery rate. The analyses of the number of prey deliveries in relation to the amount of daily rainfall, the amount of previous rainfall, and the number of prey the previous night were performed using generalised linear mixed-effect models in the 'lme4' package (Pinheiro & Bates, 2006).

For the analyses, a decision was made to use the main activity period rather than the time between sunset and sunrise in the study area since the barn owl's main activity period initiated before sunset. Thus, the number of prey deliveries at night was defined as deliveries in the barn owl's main activity period, defined as the time from 21:00 to 03:30 hours. From hereafter, prey deliveries in the main activity period are referred to as prey deliveries at night. In order to do the analyses, models were established using mixed-effects regression models based on Poisson distribution. The formula for the number of prey delivery models was as following:

$$\log\mu = \alpha + \beta x$$

The small-sample correction of Akaike's information criterion (AICc) (Akaike, 1978) was used to calculate each model's AICc value. The best-fitted model was the model with the lowest AICc value (Steen, 2017).

For the first analysis, the 'amount of daily rainfall (mm)' and the 'nestling age (d)' were set as explanatory variables and 'number of prey deliveries' as the response variable. The explanatory variable 'amount of daily rainfall (mm)' was selected as rainfall from 0 to 30 mm. Daily rainfall (mm) was defined as the total rainfall from 09:00 to 09:00 hours the following day.

For the second analysis, the 'amount of rainfall (mm) - the present day, the two last days, and three last days', were set as explanatory variables and 'number of daytime deliveries' as the response variable. The explanatory variable 'amount of rainfall (mm) the two last days' was selected as rainfall from 0 to 35 mm. The number of prey deliveries during the daytime was defined as deliveries from 03:30 to 21:00 hours. The amount of rainfall (mm) for the two last days was defined as the total rainfall from 09:00 hours the previous day until 09:00 hours the following day. To clarify, if today is the 10th of June, the two last days of rainfall would be rainfall from 09:00 hours the 9th of June until 09:00 hours the 11th of June.

For the third analysis, the 'number of prey previous night' was set as the explanatory variable and the 'number of daytime deliveries' as the response variable. The explanatory variable 'number of prey previous night' was selected as prey deliveries from 0 to 18. The number of prey deliveries during the daytime was defined as deliveries from 03:30-21:00 hours.

The days without complete camera surveillance were excluded from the tests. Accordingly, the days following the initiation of prey deliveries outside the nest were ruled out, considering the possibility of insufficient prey delivery numbers. Prey deliveries 'outside the nest' were defined as deliveries either on the edge of or outside the nest opening.

In Nar Valley, one of the nestlings first made it up to the edge of the nest opening on the 16th of June (Figure 7) at the age of 40 days. The nestlings started to step in and out of the nest from the 18th of June. From the 24th of June, the nestlings frequently stepped in and out of the nest. The frequency increased further between the 26th and 28th of June. The first prey delivery outside the nest happened on the 28th of June (Figure 7). From the 2nd of July and onwards, until camera surveillance was terminated on the 8th of July, all prey items were delivered outside the nest. Furthermore, the video files between the 30th of June and the 2nd of July were corrupted. Hence, days after the 28th of June in Nar Valley were ruled out from the tests (Appendix 2).



Figure 7. Photos of the first time one of the nestlings went outside the nest in Nar Valley (left) on the 16th of June, and the first prey delivery occurrence outside the nest in Nar Valley (right) on the 28th of June.

In Broads Authority, one of the nestlings first made it up to the edge of the nest opening on the 16th of July (Figure 8) at the age of 47 days. From the 17th of July 2019, the nestlings frequently stepped in and out of the nest. The first prey delivery outside the nest happened on the 17th of July (Figure 8). From the 17th of July and onwards, until the camera surveillance termination on the 1st of August, the vast majority of the prey items were delivered outside the nest. Hence, days after the 16th of July in Broads Authority were ruled out from the tests (Appendix 2).



Figure 8. Photos of the first time one of the nestlings went outside the nest in Broads Authority (left) on the 16th of July, and the first prey delivery occurrence outside the nest in Broads Authority (right) on the 17th of July.

3. RESULTS

3.1 Choice of prey

A total of 647 prey items were recorded delivered at the two barn owl nests (Table 3). In Nar Valley, 284 prey items were delivered at the nest, while 363 prey items were delivered at the nest in Broads Authority (Appendix 3). Mammalian prey accounted for 98% of all the prey items, with 634 prey items. Apart from the unidentified small mammals (4.5%), rodents and shrews made up all the mammalian prey. Rodents were the most common prey order delivered at both nests. The prey items delivered were by number, 98.0% mammalian, 0.5% avian (3 prey items), and 1.5% unidentified (10 prey items). The three avian prey specimens were identified as two partridges in the order Galliformes, and one unidentified sparrow in the order Passeriformes.

The field vole was the most numerous prey species delivered, with 249 prey items. Field voles made up 39.3% of all mammalian prey and 38.5% of all prey (Table 3). Besides, field voles were the most frequent prey delivered at both nests, accounting for 116 prey items (40.8%) in Nar Valley and 133 prey items (36.6%) in Broads Authority (Appendix 3). The common shrew was the second most numerous species delivered, with 127 prey items. Common shrews made up 20.0% of all mammalian prey and 19.6% of all prey (Table 3). Common shrews were the second most frequent prey delivered in Broads Authority, accounting for 100 prey items (27.5%). In Nar Valley, common shrews were the third most abundant species with 27 prey items (9.5%) (Appendix 3). The wood mouse was the third most numerous species delivered, with 109 prey items. Wood mice made up 17.2% of all mammalian prey and 16.8% of all prey (Table 3), accounting for 82 prey items (28.9%) in Nar Valley and 27 prey items (7.4%) in Broads Authority. In Nar Valley, wood mice were the second most abundant prey delivered (Appendix 3).

There were some noticeable differences in the prey deliveries between the nests. Firstly, shrews accounted for a larger proportion of the prey items in Broads Authority than in Nar Valley. Common shrews accounted for 27.5% of the prey deliveries in Broads Authority, while only 9.5% in Nar Valley. One specimen of the Eurasian water shrew was detected in Nar Valley, while two specimens were detected in Broads Authority. Furthermore, eight specimens were identified as either the Eurasian water shrew or the common shrew in Broads Authority. Secondly, the European water vole was delivered seven times in Broads Authority, while it was never detected in Nar Valley (Appendix 3).

In total, the biomass delivered at the two barn owl nests was 16295.9 g, of which mammalian prey items accounted for 98.1% (15983.1 g). Unidentified prey items made up 1.5% (242.8 g) of the total delivered biomass, while birds accounted for only 0.4% (70 g). Field voles contributed most to biomass, accounting for 45.8% (7470 g). Wood mice contributed the second-most, accounting for 16.7% (2725 g), while common shrews made the third-largest contribution, accounting for 7.8% (1270 g) (Table 3).

Table 3. Prey deliveries at the barn owl nests arranged by prey type, distributed by the number of prey items, percentage by number, average body mass, total body mass, and percentage by mass. All digits are rounded to one decimal place.

Prey type	Number of prey items	Percentage by number (%)	Average body mass (g)	Total body mass (g)	Percentage by mass (%)
Field vole (<i>Microtus agrestis</i>)	249	38.5	30	7470	45.8
Bank vole (<i>Myodes glareolus</i>)	30	4.6	20	600	3.7
Field/Bank vole	36	5.6	28.9	1041.6	6.4
European water vole (<i>Arvicola amphibious</i>)	7	1.1	100	700	4.3
Common shrew (<i>Sorex araneus</i>)	127	19.6	10	1270	7.8
Eurasian water shrew (<i>Neomys fodiens</i>)	3	0.5	15	45	0.3
Common shrew/Eurasian water shrew	8	1.2	10.1	80.8	0.5
Wood mouse (<i>Apodemus sylvaticus</i>)	109	16.8	25	2725	16.7
Brown rat (<i>Rattus norvegicus</i>)	4	0.6	100	400	2.5
Eurasian house mouse (<i>Mus musculus</i>)	1	0.2	15	15	0.1
Eurasian harvest mouse (<i>Micromys minutus</i>)	1	0.2	10	10	0.1
Unidentified vole (Arvicolidae sp.)	19	2.9	32.4	616.1	3.8
Unidentified mice (Muridae sp.)	5	0.8	25.6	128.1	0.8
Unidentified small rodent (Rodentia)	6	0.9	29.3	175.8	1.1
Unidentified small mammal (Mammalia)	29	4.5	24.3	705.7	4.3
Mammals in total	634	98	25.2	15983.1	98.1
Partridge (Galliformes sp.)	2	0.3	30	60	0.4
Unidentified sparrow (Passeriformes sp.)	1	0.2	10	10	0.1
Birds in total	3	0.5	23.3	70	0.5
Unidentified prey in total	10	1.5	24.3	242.8	1.5
All prey in total	647	100	25.2	16295.9	≈100

3.1.1 Prey delivery in relation to the time of the day

The probability of prey deliveries as a function of the time of the day indicated a circadian activity rhythm in the barn owls during the study period (Figure 9). The highest probability of a prey delivery at night occurred between hour blocks 23:00 and 02:00 and peaked between 23:30 and 00:30 hours with a probability of c. 0.7. During the study, sunrise occurred on average at approximately 04:45 hours and sunset at approximately 21:15 hours.

There was generally a low probability of prey delivery between sunrise and sunset. The probability of prey delivery was slightly higher in the morning than in the afternoon, with more deliveries between 09:00 and 11:00 hours. Prey deliveries were least likely between hour blocks 13:00 and 18:00. The probability of prey deliveries increased after hour block 18:00 and peaked between 23:30 and 00:30 hours (Figure 9). There was almost an identical pattern at the two localities, with minor differences in the probability of prey delivery

concerning the time of the day. In Broads Authority, the main activity period initiated earlier, and there was a marginally higher peak of prey deliveries (Appendix 4 and Appendix 6).

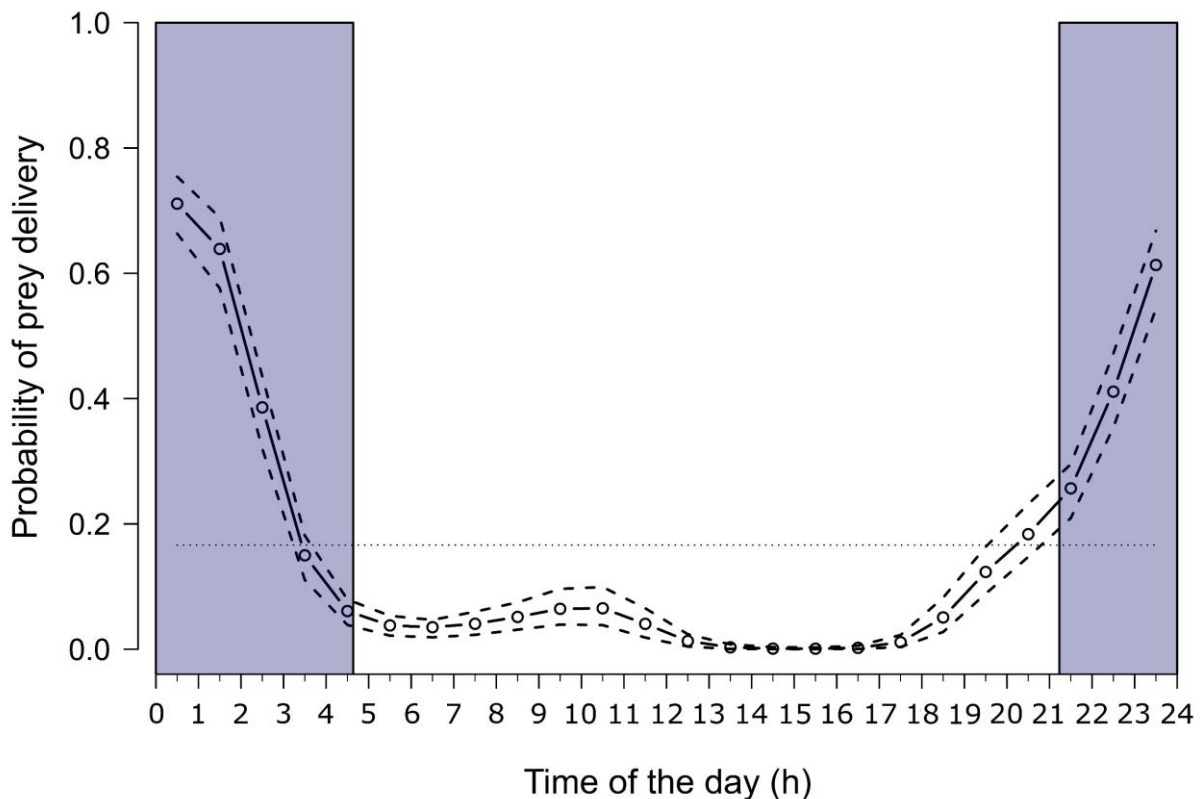


Figure 9. The probability of prey delivery within an hour block at a barn owl nest. The curve describes the best-fitted model of diel activity for all prey items calculated from the generalised linear mixed-effect models based on the cosinor method, corrected for the random effect of nest ID. The dotted curve displays the 95% confidence interval for all prey deliveries calculated by the model-based parametric bootstrapping for mixed models. The dark field displays the night (sunset-sunrise) of the study area in the relevant time period. The dotted horizontal line displays the average activity throughout the day (MESOR) ($n = 2178$, random effect = 2).

3.1.2 Mammalian prey delivery in relation to the time of the day

The probability of prey deliveries according to the time of the day for the prey families Arvicolidae, Muridae, and Soricidae, displayed a similar pattern corresponding to the circadian activity rhythm in barn owls for all prey deliveries (Figure 10). Most prey items were delivered between sunset and sunrise, and the highest probability of prey delivery at night occurred between hour blocks 23:30 and 01:30.

There was generally a low probability of prey delivery between sunrise and sunset for all the families. However, there was a slightly higher probability of deliveries of Arvicolidae prey in the daytime between 07:30 and 11:30 hours (Figure 10). The main activity period for deliveries of Arvicolidae prey initiated earlier and concluded later than deliveries of Muridae and Soricidae prey. Deliveries of Arvicolidae prey was most likely overall and peaked between hour blocks 00:00 and 01:30 with a probability of c. 0.3 (Figure 10). Deliveries of

Muridae prey peaked at a lower probability and initiated later in the evening than deliveries of Arvicolidae prey and peaked between hour blocks 00:00 and 01:00 with a probability of c. 0.2 (Figure 10). Deliveries of Soricidae prey displayed a similar pattern to the deliveries of Muridae prey but initiated earlier in the evening and peaked between hour blocks 23:00 and 00:00 with a probability of c. 0.2 (Figure 10). The statistical tests did not include the unidentified small rodents (6 specimens), the unidentified small mammals (29 specimens), the unidentified prey (10 specimens), and the avian prey (3 specimens).

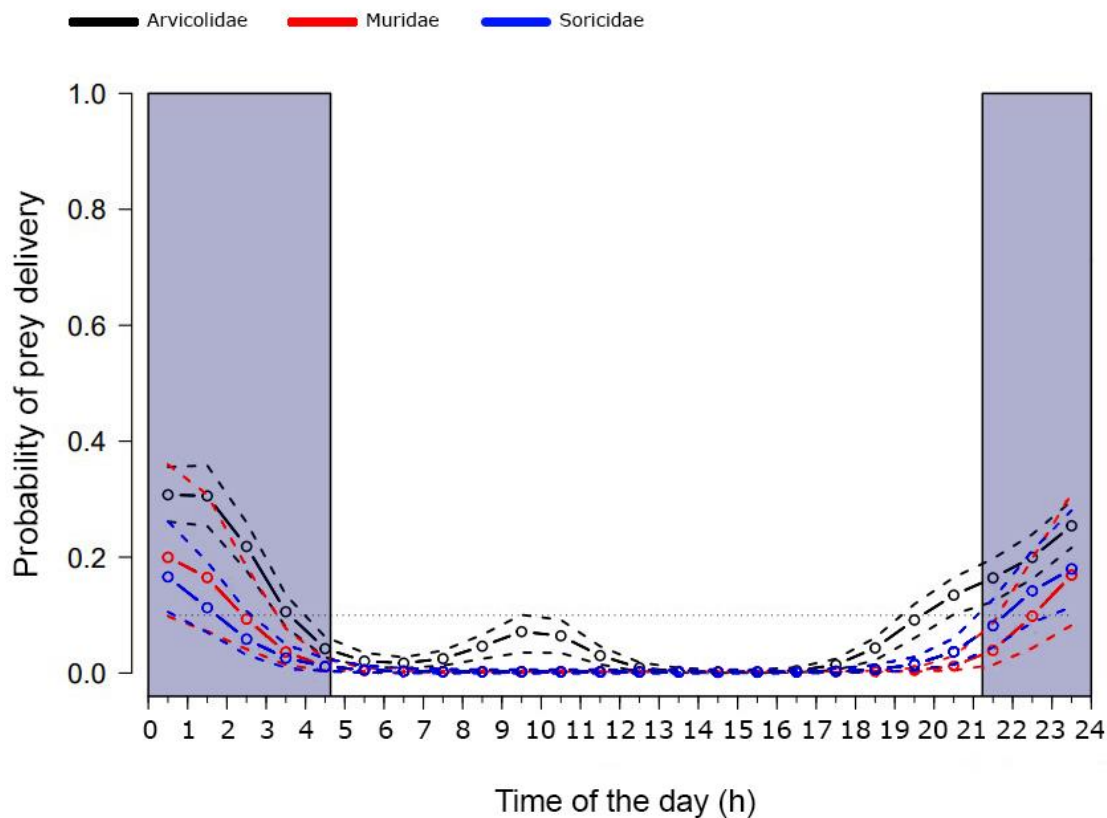


Figure 10. The probability of prey delivery within an hour block at a barn owl nest for the prey families Arvicolidae, Muridae, and Soricidae. The curves describe the best-fitted models of diel activity calculated from the generalised linear mixed-effect models based on the cosinor method, corrected for the random effect of nest ID. The black curve describes the model for the prey family Arvicolidae (the field vole, the bank vole, and the European water vole). The red curve describes the model for the prey family Muridae (the wood mouse, the Eurasian harvest mouse, the Eurasian house mouse, and the brown rat). The blue curve describes the model for the prey family Soricidae (the common shrew and the Eurasian water shrew), predicted from the best-fitted model of diel activity. The coloured dotted curves display the 95% confidence interval for the representative family calculated by the model-based parametric bootstrapping for mixed models. The dark field displays the night (sunset-sunrise) of the study area in the relevant time period. The dotted horizontal line displays the average activity throughout the day (MESOR) ($n = 2296$, random effect = 2).

3.2 Prey handling

3.2.1 Probability of prey being decapitated before delivery

Prey was decapitated before delivery in only 5 of 647 (0.8%) prey deliveries. All prey deliveries involving decapitated prey items occurred in Nar Valley, which accounted for 1.8% of the prey deliveries in Nar Valley (Table 4). The decapitated prey items were three specimens of the field vole and two specimens of the brown rat. Three decapitated prey items were delivered at night on the 15th of June when the nestling age was 38-39 days. The other two decapitated prey items were delivered on the 30th of May and on the 21st of June when the nestling age was 23 and 45 days.

Table 4. Prey being decapitated before delivery at the barn owl nests. All digits are rounded to one decimal place.

Nest location	Number of prey items	Number of decapitated prey items	Percentage by number (%)
Nar Valley	284	5	1.8
Broads Authority	363	0	0
All nests in total	647	5	0.8

3.2.2 Probability of nestling feeding unassisted

The model with ‘nestling age (d)’ as the explanatory variable (AICc = 301.4) was the best model to explain the probability of nestling feeding unassisted. The models with nestling feeding unassisted explained by ‘prey body mass (g)’ (AICc = 646.6), ‘nestling age (d)’ and ‘prey body mass (g)’ (AICc = 303.0) and the interaction between the variables ‘nestling age (d)’ and ‘prey body mass (g)’ (AICc = 304.1) made no significant contribution to the model and were discarded (Appendix 20-23).

The probability of nestling feeding unassisted increased significantly (< 0.001) as the nestlings grew older (Figure 11, Table 5). At the age of 18.6 days, it was 50% likely that nestlings consumed prey without maternal help. When the nestlings reached an age of more than 40 days, they ingested almost all prey unassisted. Nestling feeding unassisted was most unlikely just after the nestlings hatched (Figure 11). Nestling feeding unassisted occurred 490 times (75.5%) (Appendix 24). The remaining 157 prey deliveries (24.3%) were registered as indefinite feeding (Appendix 24), as parental feeding was not registered during the study period. In Broads Authority, on the 9th of June, when the oldest nestling was ten days old, the first registration of nestling feeding unassisted occurred. From the 15th of June, the majority of the observations were registered as nestling feeding unassisted. In Nar Valley, the camera

surveillance did not initiate before the 28th of May, when the oldest nestling was already 21 days old. Nestling feeding unassisted occurred regularly from this date.

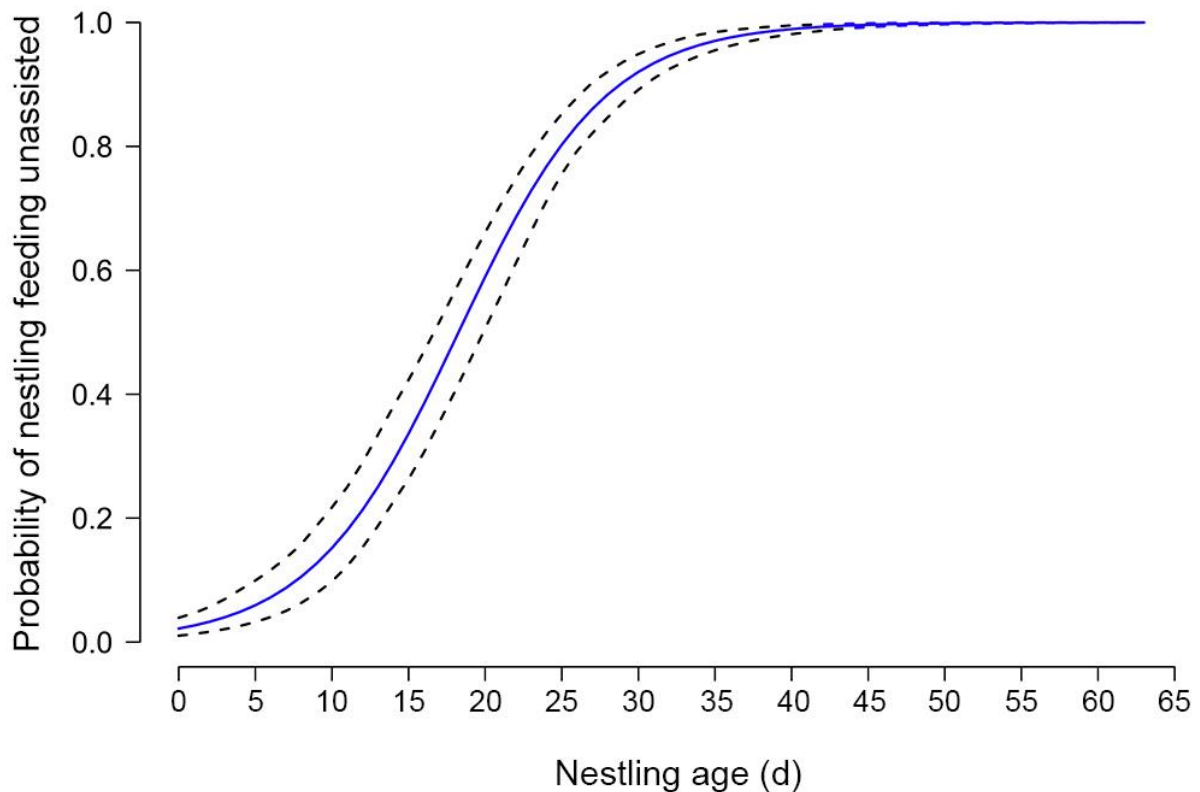


Figure 11. The probability of nestling feeding unassisted rather than indefinite feeding as a function of nestling age (d). The blue curve describes the regression model calculated from the generalised linear mixed-effect models based on binomial distribution, corrected for the random effect of nest ID. The dotted curves display the 95% confidence interval.

Table 5. Parameter estimates from the best-fitted generalised linear mixed-effect models based on binomial distribution for the model of the probability of nestling feeding unassisted rather than indefinite feeding as a function of nestling age (d), corrected for the random effect of nest ID (n = 647, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-3.80	0.65	-5.83	<0.001
Nestling age	0.21	0.27	7.65	<0.001

3.2.3 Probability of the female delivering prey

The model with ‘nestling age (d)’ as the explanatory variable (AICc = 300.5) was the best model to explain the probability of the female delivering prey. The models with prey deliveries by the female explained by ‘prey body mass (g)’ (AICc = 312.6), ‘nestling age (d)’ and ‘prey body mass (g)’ (AICc = 300.8) and the interaction between the variables ‘nestling age (d)’ and ‘prey body mass (g)’ (AICc = 302.1) made no significant contribution to the model and were discarded (Appendix 25-27).

The probability of the female delivering prey increased significantly (< 0.001) as the nestlings grew older (Figure 12, Table 6). When the nestlings reached an age of more than 50 days, the probability of the female delivering prey reached 0.4. Prey deliveries by the female was least likely just after the nestlings hatched (Figure 12). Prey deliveries by the female occurred 61 times (9.4%), while the male delivered prey 342 times (52.9%). The remaining 244 prey deliveries (37.7%) were registered as indefinite (Appendix 24).

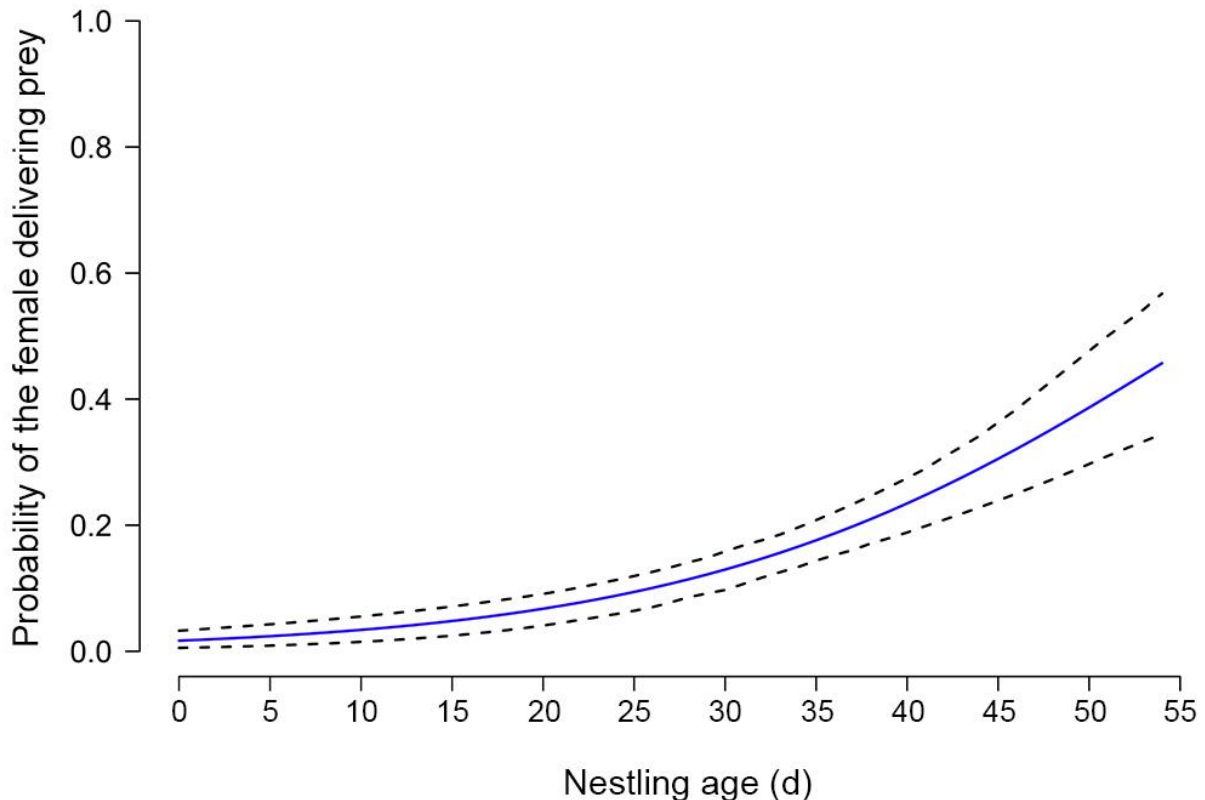


Figure 12. The probability of the female delivering prey as a function of nestling age (d). The blue curve describes the regression model calculated from the generalised linear mixed-effect models based on binomial distribution, corrected for the random effect of nest ID. The dotted curves display the 95% confidence interval.

Table 6. Parameter estimates from the best-fitted generalised linear mixed-effect models based on binomial distribution for the model of the probability of the female delivering prey as a function of nestling age (d), corrected for the random effect of nest ID ($n = 403$, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-4.07	0.48	-8.56	<0.001
Nestling age	0.07	0.01	5.95	<0.001

3.2.4 Probability of delivering prey inside the nest cavity

The model with ‘nestling age (d)’ as the explanatory variable was selected to explain the probability of delivering prey inside the nest cavity. The probability of prey delivery inside the nest cavity decreased significantly (< 0.001) as the nestlings grew older (Figure 13, Table

7). When the nestlings reached an age of more than 50 days, no prey deliveries occurred inside the nest cavity (Figure 13). Prey delivery inside the nest cavity was most likely just after the nestlings hatched. Prey deliveries inside the nest cavity occurred 225 times (34.8%), while deliveries outside the nest cavity occurred 422 times (65.2%) (Appendix 24).

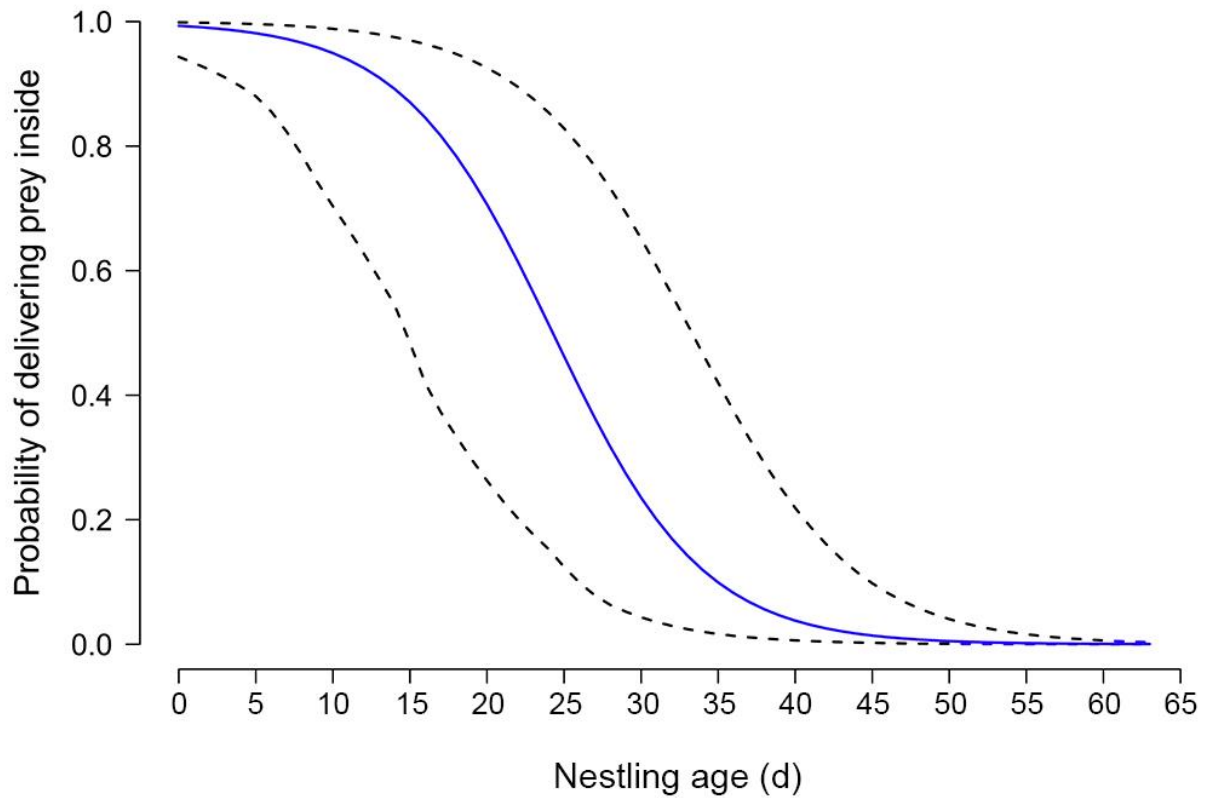


Figure 13. The probability of delivering prey inside the nest cavity as a function of nestling age (d). The blue curve describes the regression model calculated from the generalised linear mixed-effect models based on binomial distribution, corrected for the random effect of nest ID. The dotted curves display the 95% confidence interval.

Table 7. Parameter estimates from the best-fitted generalised linear mixed-effect models based on binomial distribution for the model of delivering prey inside the nest cavity as a function of nestling age (d), corrected for the random effect of nest ID (n = 647, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	4.99	1.18	4.22	<0.001
Nestling age	-0.21	0.02	-11.84	<0.001

3.3 Number of prey deliveries

In this study, 647 prey items were recorded delivered at the nests. In Broads Authority, the camera surveillance initiated before the nestlings hatched, while in Nar Valley, the oldest nestling was already 21 days old when camera surveillance was established. The daily delivery rate, defined as the number of prey deliveries between 00:00 and 23:59 hours, varied from 1 to 20 prey items during the study period. In Nar Valley, the highest number of prey items delivered were 20 prey items on the 14th of June, when the nestling age was 38 days. In Broads Authority, the highest number of prey items delivered were 18 prey items on the 20th of June, when the nestling age was 21 days (Appendix 2).

The delivery rate at night varied from 0 to 17 prey items during the study period. In Nar Valley, the highest number of prey items delivered were 17 prey items on the 16th of June when the nestling age was 40 days. In Broads Authority, the highest number of prey items delivered were 14 prey items. Such a high delivery number occurred on the 9th of June when the nestling age was ten days and on the 4th of July when the nestling age was 35 days. On average, daily prey deliveries were 8.2 prey items in Nar Valley and 7.2 prey items in Broads Authority. At night, the average number of prey deliveries were 7.1 prey items in Nar Valley and 5.6 prey items in Broads Authority (Appendix 2).

3.3.1 Prey deliveries at night in relation to the amount of daily rainfall

The model with prey deliveries at night explained by the ‘amount of daily rainfall (mm)’ (AICc = 354.0) surpassed the models with the ‘nestling age (d)’ and the ‘amount of daily rainfall (mm)’ as the explanatory variables (AICc = 354.4, AICc = 356.4) (Appendix 28). Thus, the models with the number of prey deliveries explained by the variables ‘nestling age (d)’ and the ‘amount of daily rainfall (mm)’ were discarded.

The number of prey deliveries at night decreased significantly (< 0.001) with an increasing amount of daily rainfall (Figure 14, Table 8). Approximately 7 prey items were delivered in days without rainfall, within a 95% confidence interval range from > 6 to > 8 . The number of prey deliveries decreased to approximately 2 prey deliveries at 30 mm daily rainfall, within a 95% confidence interval range from > 1 to < 4 (Figure 14).

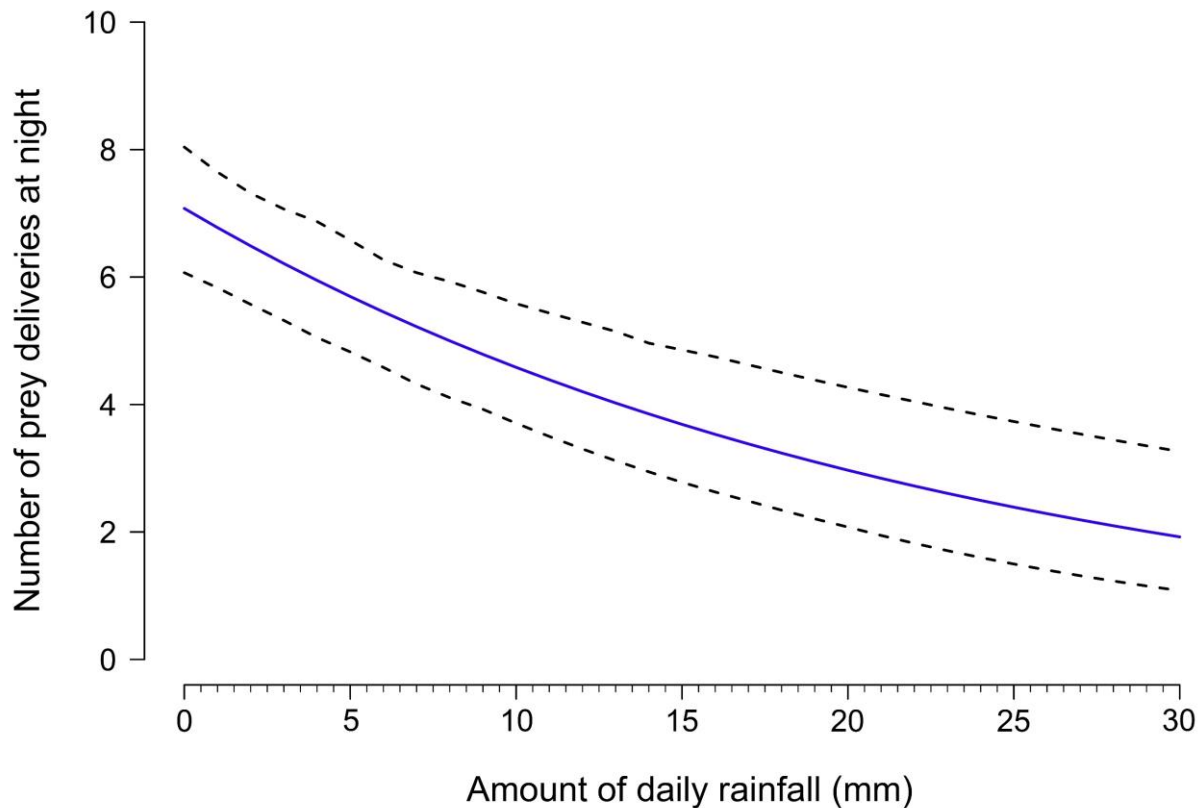


Figure 14. The number of prey deliveries at night in relation to the amount of daily rainfall (mm). The blue curve describes the regression model calculated from the generalised linear mixed-effect models based on Poisson distribution, corrected for the random effect of nest ID. The dotted curves display the 95% confidence interval.

Table 8. Parameter estimates from the best-fitted generalised linear mixed-effect models based on Poisson distribution for the model of the number of prey deliveries at night in relation to the amount of daily rainfall (mm), corrected for the random effect of nest ID ($n = 65$, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	1.96	0.10	19.11	<0.001
Rain	-0.04	0.01	-3.57	<0.001

3.3.2 Prey deliveries during daytime in relation to the amount of previous rainfall

The model with the ‘amount of rainfall (mm) the two last days’ as the explanatory variable ($AICc = 287.9$) exceeded the model with the ‘amount of rainfall (mm) the present day’ ($AICc = 290.3$), and the model with the ‘amount of rainfall (mm) the three last days’ ($AICc = 291.2$) as the explanatory variables (Appendix 29). Thus, the models with the number of prey deliveries explained by the variables ‘amount of rainfall (mm) the present day’ and the ‘amount of rainfall (mm) the three last days’ were discarded.

The number of daytime deliveries increased significantly (< 0.05) with an increasing amount of rainfall in the two last days (Figure 15, Table 9). The number of daytime deliveries was > 1 prey item without rainfall, within a 95% confidence interval range from < 1 to c. 2.

The number of prey deliveries increased to > 2 prey deliveries at 35 mm of rainfall, within a 95% confidence interval range from > 1 to < 5 (Figure 15).

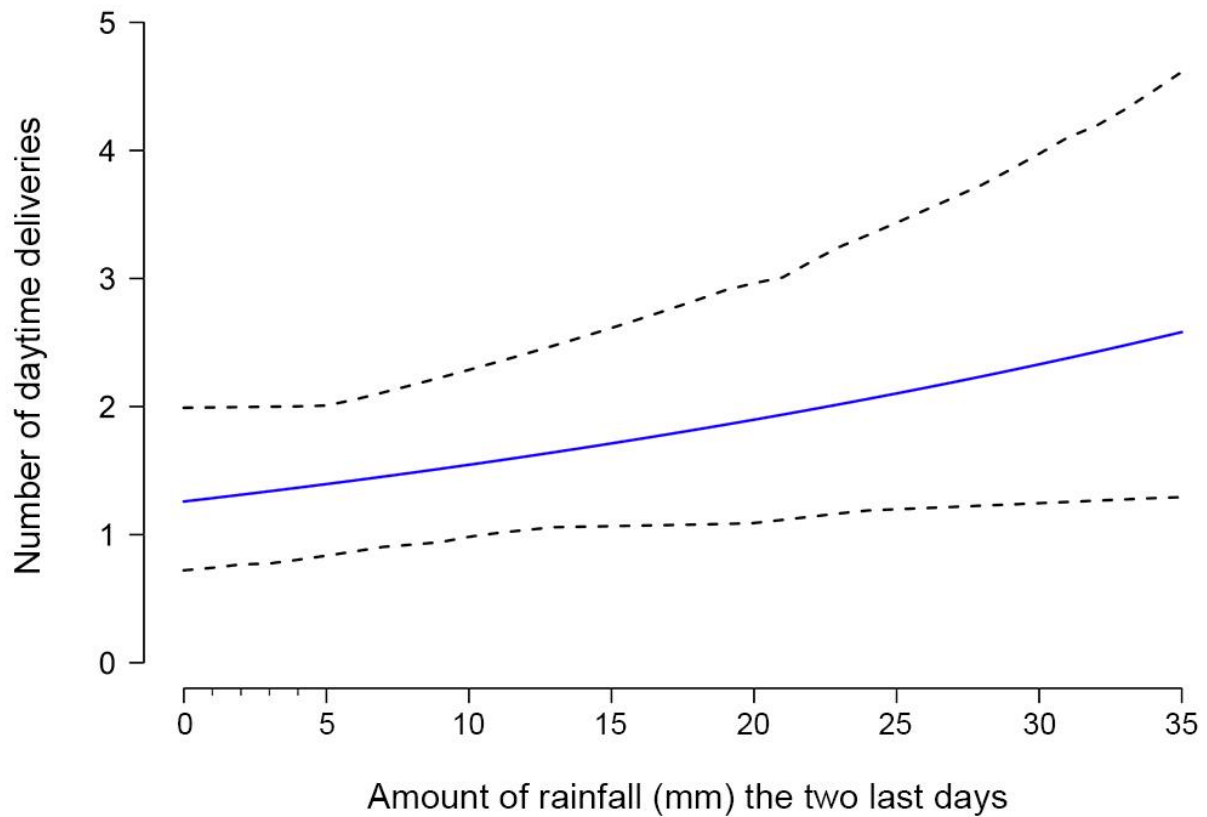


Figure 15. The number of prey deliveries during the daytime in relation to the amount of rainfall (mm) the two last days. The blue curve describes the regression model calculated from the generalised linear mixed-effect models based on Poisson distribution, corrected for the random effect of nest ID. The dotted curves display the 95% confidence interval.

Table 9. Parameter estimates from the best-fitted generalised linear mixed-effect models based on Poisson distribution for the model of the number of prey deliveries during the daytime in relation to the amount of rainfall (mm) the two last days, corrected for the random effect of nest ID (n = 65, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	0.23	0.32	0.71	0.48
Rain, the two last days	0.02	0.01	2.06	<0.05

3.3.3 Prey deliveries during daytime in relation to the number of prey delivered previous night

The model with prey deliveries during daytime explained by the ‘number of prey previous night’ (AICc = 280.5) surpassed the three models explained by the amount of the present and the two- and three last day’s rainfall (mm) (AICc = 290.3, 287.9 and 291.2) (Appendix 29).

The number of daytime deliveries decreased significantly (< 0.01) with an increasing number of prey deliveries the previous night (Figure 16, Table 10). With no prey deliveries the previous night, the number of prey deliveries was < 3 prey items, within a 95% confidence

interval range from < 2 to > 4 . The number of daytime deliveries decreased to ≤ 1 prey delivery when 10 and more prey items were delivered the night before, within a 95% confidence interval range from < 1 to > 1 (Figure 16).

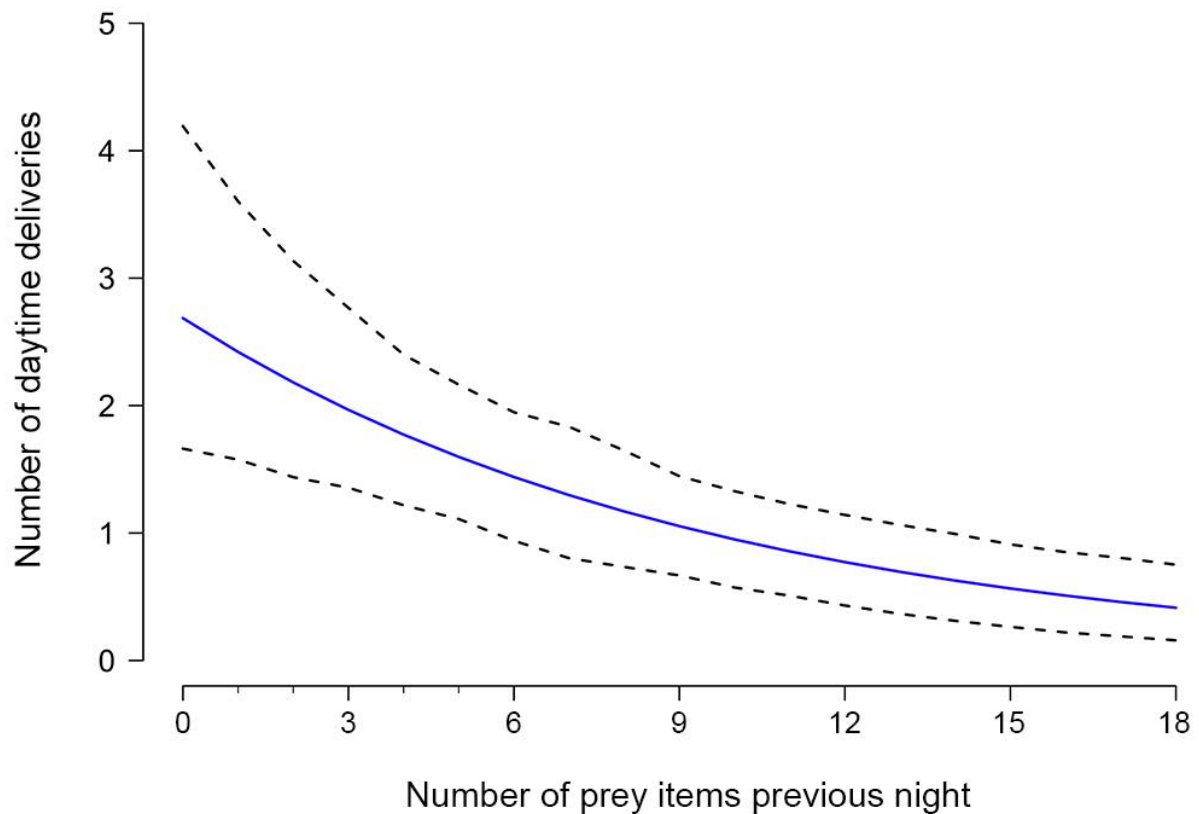


Figure 16. The number of prey deliveries during the daytime in relation to the number of prey items delivered the previous night. The blue curve describes the regression model calculated from the generalised linear mixed-effect models based on Poisson distribution, corrected for the random effect of nest ID. The dotted curves display the 95% confidence interval.

Table 10. Parameter estimates from the best-fitted generalised linear mixed-effect models based on Poisson distribution for the model of the number of prey deliveries during the daytime in relation to the number of prey items delivered the previous night, corrected for the random effect of nest ID ($n = 65$, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	0.99	0.30	3.28	<0.01
Number of prey previous night	-0.10	0.03	-3.21	<0.01

4. DISCUSSION

4.1 Choice of prey

The barn owls preferred mammalian prey, accounting for 98% of all the prey items. Except for the unidentified small mammals, rodents and shrews accounted for all the mammalian prey. The field vole was the most numerous prey species delivered at both nests. These findings are similar to a previous study based on analysis of barn owls' pellets in the UK, where rodents and shrews made up 90% of the diet, and field voles were the most common prey (Glue, 1974). Furthermore, an analysis of barn owl diet studies by Taylor (2004) demonstrated that rodents were the essential mammalian prey order in 47 of 52 diet surveys.

The common shrew was the second most frequent prey species. This corresponds to that common shrews are usually significant secondary prey species in Europe (Taylor, 2004). However, in Nar Valley, wood mice appeared more frequently than common shrews. This may be explained by increased availability of wood mice, low availability of shrews, or a combination of both factors. The number of wood mice included in the barn owl diet has increased, particularly in the eastern UK (Love et al., 2000). Furthermore, Roulin (2016) found in an analysis of 815 barn owl diet studies that the consumption of insectivorous mammals, which include shrews, has been declining in Europe since 1860.

Eleven different prey species, including nine mammalian species, were delivered at the nests. Similarly, in other studies from the UK, the number of prey species varied from five to eleven (Taylor, 2004). These findings indicate that barn owls are food generalists, not specialising in a single prey type. Barn owls are considered opportunistic predators (Hawbecker, 1945; Hamilton & Neill, 1981) but may decide which prey to capture if given a choice. Thus, flexibility in their diet simultaneously entails resilience to differences in prey abundance (Roulin, 2020). However, Taylor (2004) points out that barn owls could be recognised as specialists because they depend on small mammals primarily and are less flexible than most other small mammal predators. Nevertheless, Taylor (2004) elaborates that barn owls usually are specialists in productive areas with high prey availability, while in less productive habitats such as drier areas, they tend to be generalists.

Alternative prey represented by avian prey was delivered only three times, whereas no deliveries of lizards, amphibians and invertebrates occurred. Birds are usually captured more frequently when the abundance of mammalian prey items becomes scarce. In Ireland and the Isle of Man, where the field vole and the common shrew are absent, birds account for a significant proportion of the diet (Bunn et al., 1982). However, Love et al. (2000) claim that

the decline of birds in the barn owl diet is almost certainly due to the loss of suitable habitat for the birds. According to Taylor (2004), few deliveries of alternative prey may indicate that the preferred species are also the most profitable. However, changes in climatic conditions can influence the amount of alternative prey in the barn owl diet. Dramatic seasonal changes in dietary habits occurred in response to precipitation variations in barn owls breeding in Sicily, Italy, where a population of barn owls which were mainly dependent upon small mammals, changed their diet to insects accounting for 70-80% of the diet (Taylor, 2004).

The field vole was the most important prey species by biomass, accounting for 45.8% of the total delivered biomass. This finding corresponds to previous studies based on analysis of barn owls' pellets in the UK, where the field vole was the most important prey species by biomass in the UK, Scotland, and Wales (Glue, 1974; Brown, 1981; Taylor, 2004). In these studies, the field vole accounted for 63.3%, 64.9%, and 51.6% of the total biomass in the respective countries. In a study from Ireland, however, wood mice were the most important prey both by biomass and by number (Smal, 1987), which is likely related to the absence of the field vole and the common shrew in Ireland (Couzens et al., 2017). Studies have suggested that field vole populations in the UK declined due to the loss of rough grassland in the 20th century (Harris et al., 1995; Love et al., 2000). Even though the barn owl diet typically reflect the relative abundance of prey species, Love et al. (2000) found no significant change in the proportion of field voles in the barn owl diet between 1974 and 1997.

Considering that field voles make up a significant part of the barn owl diet, the owls are exposed to vole populations fluctuating between seasons and years (Bunn et al., 1982; Krebs, 2013). Population fluctuations can be separated by short-term (seasonal) and long-term (annual) fluctuations (Bunn et al., 1982; Taylor, 2004). In the UK and Scotland, the importance of field voles in the barn owl diet corresponds to seasonal abundance, decreasing through spring to a low in May and increasing through summer to reach a peak in late autumn and early winter (Webster, 1973; Tapper, 1979; Bunn et al., 1982; Richards, 1985; Love et al., 2000; Taylor, 2004). Usually, the number of barn owls in the spring correlates with the seasonal fluctuations in field vole populations (Taylor, 2004).

Long-term fluctuations are more complex. Field vole populations in the northern UK exhibit larger density differences in three to four-year cycles than within years (Lambin et al., 2000; Taylor, 2004). In the southern UK, a study indicated six-year cyclicity of field voles (Tapper, 1979). Still, additional data are needed to determine whether these were seasonal cycles and whether there is a north and south gradient of field vole population cycles within the UK (Lambin et al., 2000). Field vole populations experiencing collapses with subsequent

periods without recovery in numbers may impose food shortage for barn owls. This may significantly impact barn owl reproduction and population size (Shawyer & Shawyer, 1995; Lambin et al., 2000; Bond et al., 2005).

The barn owl diet may reflect habitat variations influencing small mammal communities compositions, as studies have shown a relationship between habitat and diet (Bunn et al., 1982; Taylor, 2004). In my study, the prey deliveries in Broads Authority and Nar Valley indicated differences in prey composition between the two localities. In Broads Authority, common shrews, Eurasian water shrews, and European water voles accounted for a more significant proportion of the prey deliveries. Considering the habitat in Broads Authority, it was more likely to be inhabited by species living near rivers and in dense vegetation. The European water vole rarely wanders far away from water sources and is commonly found along slow-flowing rivers (Couzens et al., 2017). Considering the closeness to the river and the dense vegetation, Eurasian water shrews and common shrews were also more likely to be found in Broads Authority.

An earlier study of the barn owl diet in Norfolk (see Buckley & Goldsmith, 1975) demonstrated the complexity of local variation between habitats. Field voles and common shrews were the only significant prey in pastoral areas, while in similar areas mixed with hedges and woodlands, other species such as the wood mouse, the brown rat and the bank vole accounted for a larger part of the diet (Taylor, 2004). However, a recent study from California, USA, found habitat to be a relatively weak predictor of variation in prey composition in barn owls breeding in winegrape vineyards. Nevertheless, in some nesting periods, a larger proportion of oak savannah, grassland, and uncultivated habitat proved to be important predictors of the barn owl diet (George & Johnson, 2021).

4.1.1 Prey delivery in relation to time of day

Using the cosinor method to analyse the diel activity rhythms demonstrated that the barn owls delivered prey mainly between sunset and sunrise, with an activity peak around midnight. Similar to other studies, the owls were nocturnal hunters primarily. The barn owl is well adapted to a nocturnal life with exceptional hearing capacity combined with visual ability in the dark (Taylor, 2004; Roulin, 2020). However, radiotelemetry is required to obtain details about foraging behaviour in nocturnal hunters (Taylor, 2004).

Most deliveries occurred between sunset and sunrise, but the diel activity rhythm indicated that hunting commenced in the early evening before it got dark. Hunting took place from around 18:00 hours, which gives about three to four hours foraging in daylight, as it

remains reasonably light after sunset for approximately 40 minutes (Bunn et al., 1982). These findings are similar to other studies where most hunting activity usually happened between early evening and sunrise (Bunn et al., 1982; Taylor, 2004).

During the daytime, the prey delivery numbers were generally low. However, the barn owls sometimes delivered prey during the morning and in the afternoon. Several forest barn owls regularly hunt during the day throughout the year (Bunn, 1972; Bunn et al., 1982), and barn owls in Scotland and the northern UK regularly hunt in daylight (Taylor, 2004).

Roulin (2020) highlights some hypotheses that may explain this behaviour, elaborating that these ideas cannot be evaluated due to the lack of quantitative data. Theories for barn owls hunting more frequently in daylight include food shortage, especially during winter, or that foraging only at night is insufficient to meet the nestling's food demand. In the UK, barn owls prey mainly upon the field vole. In contrast, the common vole (*Microtus arvalis*) is most preyed upon in mainland Europe, indicating that field voles may be more active than the common vole during the daytime. Another reason for daytime hunting could be that nights are too short due to the absence of total darkness in midsummer in the northern UK (Roulin, 2020). However, several other factors can explain daytime hunting, including weather conditions, e.g., rainfall which I will discuss later. Future studies may further explore whether barn owls in the north of the UK are more likely to hunt during the daytime than barn owls in the southern UK.

4.1.2 Mammalian prey delivery in relation to time of day

Prey deliveries from the mammalian families Arvicolidae, Muridae, and Soricidae, exhibited a strictly nocturnal activity rhythm and peaked around midnight. Arvicolidae prey items were the most likely prey delivered both at night and during the daytime, corresponding to field voles being the most frequent prey species in both nests. Deliveries of Arvicolidae prey items peaked between 00:00 and 01:30 hours, which partly coincides with the activity levels of voles being highest in the early part of the night before midnight (Taylor, 2004; Crawley et al., 2020). However, the common vole, and most likely other voles, tends to have periods of continuous activity in local populations. Hence, vole availability may fluctuate throughout the day and at night (Daan & Slopsema, 1978; Taylor, 2004).

Prey deliveries during the daytime were mainly made up of Arvicolidae prey, corresponding to that field voles, bank voles, and European water voles are active both day and night all year (Crawley et al., 2020). In contrast, wood mice and brown rats are primarily nocturnal. Shrews, on the other hand, are active at any time of day and night (Taylor, 2004;

Crawley et al., 2020). Prey from the family Arvicolidae had a slightly higher probability of being delivered in the morning and earlier in the evening than prey deliveries from the families Muridae and Soricidae. This may support Roulin (2020) suggestions of more frequent daytime hunting because field voles are active during the daytime. However, the voles' activity levels are related to temperature, and daytime activity is usually higher in winter than in summer (Taylor, 2004).

Prey deliveries from the family Muridae began later in the evening than Arvicolidae and Soricidae prey deliveries. This corresponds to that wood mice and brown rats are strictly nocturnal mammals. However, brown rats are often active during the daytime if food is abundant or the population density is high. In contrast, wood mice, which accounted for a more significant proportion of the barn owl diet, are entirely nocturnal (Crawley et al., 2020).

4.2 Prey handling

4.2.1 Probability of prey being decapitated before delivery

Prey was decapitated prior to delivery in only 5 of 647 (0.8%) prey deliveries. How frequent or widespread deliveries of decapitated prey items occur in barn owl prey deliveries is unknown (Taylor, 2004), and considerable differences are observed between studies. In a study from the Czech Republic, 33% of the prey items involved decapitation (Roulin, 2020). Differently, in a study from Scotland, none of the 614 prey items was decapitated before delivery (Taylor, 2004).

In my study, the decapitated prey were three specimens of the field vole and two specimens of the brown rat. The brown rat is large with an estimated prey body mass of 100 g. Also, the three decapitated field voles were relatively large compared to their average size observed. The feeding constraint hypothesis (see Steen et al., 2010) may explain why prey items were decapitated before delivery. As the nestlings' gape size limit and swallowing capacity increase with age (Steen et al., 2010), prey items being decapitated before delivery may facilitate the consumption of larger prey items in the early nestling stage.

Another explanation could be that the owls remove the body part with the least amount of flesh to reduce transportation load (Roulin, 2020). According to Roulin (2020), the largest prey items may in some cases be half the size of a breeding owl. For instance, rats are often decapitated before ingestion (Morton et al., 1977; Bontzorlos et al., 2005). However, Roulin (2020) argues that the owls would also dismember other large body parts and suggests decapitation may occur because the parents prefer to consume the head for themselves since the brain tissues are rich in nutrients.

Few occurrences of decapitated prey items may indicate that barn owls caught most prey items nearby or that most prey items were medium-sized. However, other studies in the UK have shown correspondingly low decapitation numbers (Taylor, 2004; Roulin, 2020), while higher numbers have been observed in other parts of Europe (Roulin, 2020). Thus, prey abundance and prey selection in different locations and habitats may affect the number of decapitated prey items. Interestingly, three of five decapitated prey items were delivered within a time interval of six hours the same hunting night. Due to few incidents of decapitation in total, it should be considered that 60% of the incidents occurred on the same night. Future studies could further explore this topic as the prevalence of decapitated prey before delivery in barn owls is not well documented (Taylor, 2004).

4.2.2 Probability of nestling feeding unassisted

The nestlings were more likely to ingest prey items without maternal help as they grew older and consumed approximately all prey unassisted when they reached 40 days of age. These findings correspond with the nestlings becoming more independent with age, forming an independent owl in less than 14 weeks (Bunn et al., 1982). When the nestlings are 40-45 days of age, they usually have reached a body mass greater than the parents (Roulin, 2020).

Similarly, Sonerud et al. (2014) found that nestling feeding unassisted rather than being fed by the female increased with nestling age for eight species of raptors. However, in my study, the statistical test involved nestling feeding unassisted rather than indefinite feeding, as nestlings being fed by the female was never observed. Methodological factors could explain the absence of parental feeding observations in Broads Authority. In contrast, parental feeding in Nar Valley was not observed because the nestlings were already more than 20 days old when camera surveillance was initiated.

In Broads Authority, the first observation of nestling feeding unassisted occurred when the oldest nestling was ten days old. Regarding the nestlings in both nests, it was 50% likely that nestlings at the age of 18.6 days ingested prey without maternal help. These findings coincide with the nestlings becoming thermally independent, the ability to maintain a high and constant body temperature (Dreiss et al., 2016), and consuming prey items by themselves when they turn two to three weeks old (Taylor, 2004; Dreiss et al., 2017). Roulin et al. (2012) elaborate that the nestlings at this time can swallow entire items and tear apart flesh.

4.2.3 Probability of the female delivering prey

Prey deliveries by the female became more likely as the barn owl nestlings grew older. When the nestlings reached an age of more than 50 days, the probability of prey delivery by the female reached 40%. These findings correspond to parental food provisioning in raptors (Eldegard & Sonerud, 2010). During the first half of the rearing period, the male barn owl is mainly responsible for hunting, while the female distributes the prey items among the nestlings (Bunn et al., 1982; Crick, 2004; Roulin, 2020). However, in situations where the male cannot meet the food demands, the female will contribute to the hunting in the earlier stages of the nestlings life (Roulin, 2020).

Usually, until all the nestlings are thermally independent, the female does not leave the nestlings alone in the nest (Taylor, 2004). In my study, the female in Broads Authority left the nest before the nestlings could regulate their body temperature, but mainly for shorter periods. However, how far away the female resided is unknown. The female leaving the nest was not a topical issue in Nar Valley because the nestlings were most likely already thermally independent when camera surveillance was initiated.

In my study, the female delivered only 9.4% of the prey items. However, 37.7% of the prey deliveries were registered as indefinite. Thus, it should be considered that the proportion may have been higher. The female usually delivers roughly a quarter of the prey items (Roulin, 2020). Nevertheless, males also contribute substantially more than females in the later nestling stage, both in barn owls (Roulin et al., 1999; Roulin & Bersier, 2007) and in other owls (Eldegard & Sonerud, 2012). In some studies, the female never contributed to food provisioning (Eldegard & Sonerud, 2009; Roulin, 2020).

4.2.4 Probability of delivering prey inside the nest cavity

Prey delivery inside the nest cavity was most likely just after the nestlings hatched. Prey deliveries outside the nest cavity occurred more frequently as the nestlings grew older. When the nestlings reached more than 50 days of age, almost all prey deliveries occurred outside the nest cavity. The first prey delivery outside the nest cavity happened at a nestling age of 48 days in Broads Authority and 52 days in Nar Valley. Similarly, the nestlings leave their nest for the first time at approximately 55 days in Europe (Roulin, 2020). Nevertheless, individual nestlings differ in their eagerness to explore the outside world. In a study from Switzerland, where nestlings were radio-tracked and explored areas up to 4 km from their nests, the nestlings made excursions outside the nest for the first time between 54 and 105 days, 74 days on average (Roulin, 2020).

In my study, it should be considered that nestling excursions may have involved no further exploration other than residing outside the nest cavity. According to Bunn et al. (1982), the first excursions outside the nest are only brief. In Nar Valley, one nestling first made it up to the edge of the nest opening at the age of 40 days. However, frequent excursions outside the nest cavity did not occur before 48-52 days of age. In Broads Authority, one nestling first made it up to the edge of the nest opening at the age of 47 days, and excursions outside the nest cavity frequently occurred from the following day. After the first nestling made it up to the edge of the nest opening, presumably the oldest, the other nestling tried to imitate their sibling in both nests. According to Bunn et al. (1982), the oldest nestling is almost always the first to leave the nest, and the other nestlings are usually quick to follow.

4.3 Number of prey deliveries

On average, the barn owl parents delivered approximately seven to eight prey items daily at each nest. Considering it was two nestlings in both nests, three to four prey items were assumed eaten by each nestling each day, corresponding to an individual barn owl typically consuming three to four prey items per day (Roulin, 2020). At night, the parents brought approximately five to seven prey items on average, which corresponds to most prey deliveries happening after sunset. The number of prey deliveries varied from no deliveries up to 20 prey items delivered a day. Twenty prey deliveries in one day are not surprising, as foraging success sometimes is exceptionally high. In the UK, a male barn owl delivered eleven prey items within an hour (Roulin, 2020).

Prey delivery rate will depend on several factors, such as fluctuations in prey abundance, the timing of prey activity, habitat quality, brood size, parental quality, and prey size. Weather conditions will also have significant importance as the males mainly rest on rainy nights (Roulin, 2020). Furthermore, barn owls are more likely to increase foraging costs when the nestling's food requirement is at its highest. Typically, this occurs later in the breeding season (i.e., July-August), which coincides with the rodents population peak in the UK (Bunn et al., 1982). In my study, prey deliveries often occurred outside the nest at the end of the breeding season, which complicated the measurement of prey delivery rate. For future studies, camera surveillance outside the nest cavity could be advantageous to estimate prey delivery rates throughout the breeding season.

4.3.1 Prey deliveries at night in relation to the amount of daily rainfall

Increasing daily rainfall negatively affected the prey delivery numbers at night. The probability for prey deliveries decreased to only two prey items a day when daily rainfall measured 30mm. These findings are consistent with the prediction that barn owls hunt less when it rains, as rain hampers hunting success and the prey delivery rate (Bunn et al., 1982; Michelat & Giraudoux, 1992; Chausson et al., 2014a). Usually, males rest for over 90% of rainy nights (Roulin, 2020), and the most experienced individuals refrain from hunting until the rain subsides (Bunn et al., 1982).

There may be several reasons why the barn owls mostly avoided hunting during rain. First and foremost, heavy rainfall is noisy and will hamper the owl's hearing capacity and vision, reducing their ability to detect prey. Also, hunting during heavy rainfall will cause their loose plumage to saturate when capturing prey in wet grass, making their feathers becoming too heavy to fly (Bunn et al., 1982; Shawyer & Banks, 1987; Roulin, 2020). They will also lose heat more rapidly, especially during rain combined with strong winds (Taylor, 2004). Their insulation capacity has been quantified to be reduced by 30% when their plumage becomes wet (McCafferty et al., 1998; Taylor, 2004). Usually, barn owls invest more energy into hunting at the end of the breeding season (i.e., July and August). During this period, the nestlings are most demanding in their food requirements (Bunn et al., 1982). This overlaps with the increase in the rodent population during late summer (Bunn et al., 1982; Love et al., 2000).

Some prey deliveries occurred on days with rainfall, possibly explained by shorter periods without rain throughout the day. The purpose of foraging is, according to foraging theory, to maximise the net rate of energy gain while foraging (Derting & Cranford, 1989; Stephens & Krebs, 2019). Hence, the barn owls must consider whether it is worthwhile foraging during rainy days or not. Since the barn owls decided to hunt during rainy days, they were most likely to use the sit-and-wait method. Waiting for prey to pass by is cost-effective, even though catching the prey can be time-consuming (Roulin, 2020). By returning to their roost site between hunts, the owls will save energy. Thermoregulation costs are highest when hunting during adverse weather conditions such as rainfall (McCafferty et al., 2001).

Some prey deliveries also occurred during nights with the heaviest rain. As both nestlings and the parents require food to survive, it is unlikely that the parents totally abandon foraging even though it rains for several days in a row. Compared to other owl species, barn owls have lower fat reserves, which may affect their resistance to starvation (Piechocki, 1961; Bunn et al., 1982). In a study by Johnson (1974), using standard metabolic rate estimates,

barn owls could not survive without food for more than eight days at a temperature of 20°C and probably less during the winter (Johnson, 1974; Taylor, 2004). However, in a study by Thouzeau et al. (1999), barn owls in captivity managed to survive without food between three and 15 days, nine days on average, when the temperature was as low as 5°C (Roulin, 2020). Still, lack of food is even more critical for young nestlings, which are not strong enough to survive even a few days without nutrients (Roulin, 2020). As studies have demonstrated that barn owls parents, in some incidents, have totally abandoned foraging under extremely wet conditions (Ritter & Gerner, 1977; Taylor, 2004), precipitation is a decisive determinant of reproductive success.

4.3.2 Prey deliveries during daytime in relation to the amount of previous rainfall

Daytime deliveries were affected by whether it rained or not the two last days. One day with rainfall was not sufficient to induce hunting during the daytime. Thus, it seemed that two days with rain compelled the owls to hunt during the daytime to provide enough food for the nestlings. These findings are in line with the prediction that barn owls need to compensate for fewer prey deliveries in days with rainfall by hunting in the daytime. However, they will most likely never fully compensate for the loss of prey the previous days. Interestingly, prey deliveries during the daytime were not related to rainfall in the three last days. Two days with rain was the threshold for providing food for the nestlings.

Few studies have explored this issue. However, a study by Chausson et al. (2014a) examining the relationship between prey body mass and previous rainfall indicated that short periods of rain did not have a long-term effect on the nestlings body condition. The study demonstrated that barn owls could offset the adverse effects of a rainy night. Only the amount of rain that fell the previous night negatively affected the nestlings body mass (Chausson et al., 2014a; Roulin, 2020). According to Chausson et al. (2014a), parents may increase the prey delivery rate after short periods of adverse hunting conditions or hunting conditions may improve after a period with heavy rain.

Interestingly, some studies (e.g., Hosking et al., 1945) have suggested that barn owls may foresee unfavourable weather conditions and increase hunting in the daytime before it starts raining (Bunn et al., 1982). However, Bunn (1972) found increased daytime hunting to not correlate to adverse or changing weather conditions, which did not support this theory. Also, barn owls do not usually store food supplies in case the weather gets worse. Even though most raptors and owls store food for later use, barn owls typically store food when foraging conditions are favourable and not necessarily when it might be helpful, such as

before rainy days. Instead, prey accumulates in the nests because the nestlings delay their meals (Roulin, 2004; Roulin, 2020).

In my study, the amount of rainfall proved to both affect daytime deliveries and deliveries at night. Thus, precipitation needs to be considered when evaluating how weather conditions affect food provisioning in barn owls. However, further data is required to assess to what extent precipitation influences parental effort. The duration of the rainfall and whether it rains when the nestlings are most vulnerable can be of great importance. Prolonged periods of rain may severely impact the nestlings body condition. The nestlings may be weak from an early age and remain weak, which later leads to poorer survivability (Chausson et al., 2014a).

4.3.3 Prey deliveries during daytime in relation to the number of prey delivered previous night

The number of prey delivered the night before affected the daytime deliveries. These findings are consistent with the prediction that the previous night's catch influence daytime deliveries. The parents may need to compensate for last night's poor catch or have already provided enough food for the nestlings. Prey deliveries the night before was a better explanation for the increase in daytime deliveries than previous rainfall. However, these factors are interrelated, as an increasing amount of daily rainfall negatively affected prey delivery numbers at night.

As barn owls are very sensitive to adverse weather conditions (Honer, 1963), other factors, such as wind and temperature, must also be considered when evaluating factors affecting the number of prey deliveries during nights. During windy nights, the barn owls exceptional hearing capacity may be impaired. However, barn owls can also be highly efficient predators in heavy wind, often capturing prey within five or ten minutes (Bunn et al., 1982). Barn owls are especially vulnerable to severe winter weather, mainly due to their high energy requirements for thermoregulation (Marti & Wagner, 1985; McCafferty et al., 2001). They lose considerable amounts of heat mainly due to sparse feathering (Kelso & Kelso, 1936; McCafferty et al., 2001). Compared to other owl species adapted to a colder climate, barn owls have fewer body feathers and are one of the few without feather on their legs (Roulin, 2020).

According to Shawyer and Banks (1987), field vole cycles in the UK are mainly caused by weather, particularly snow cover duration. In harsh winters, snow cover that remains for a long time will impair prey availability (Jenouvrier, 2013). Also, in studies from Fennoscandia, snow cover reduces the prey availability more for birds hunting voles in open grassland, e.g., barn owls, than for those who can hunt in forests (Sonerud, 1986).

Rainfall may also affect prey availability. In the long run, vole populations may increase due to vegetation growth after rain (Roulin, 2020). In contrast, vole activity may be reduced by rainfall, especially during heavy rain in combination with low temperatures, when voles will remain under dense cover by feeding on stored food (Lehmann & Sommersberg, 1980; Bunn et al., 1982; Taylor, 2004). Nevertheless, short breaks in the rainfall instantly cause periods of sustained vole activity, making them more vulnerable to predation (Lehmann & Sommersberg, 1980; Roulin, 2020). Even though Shawyer and Banks (1987) conclusions about vole cycles being caused by weather are open to criticism (Taylor, 2004), prey availability should be considered an essential factor of prey deliveries, whether due to snow cover, annual- or seasonal populations fluctuations or precipitation.

Several other factors may affect the number of prey deliveries at night, such as inexperience in hunting, threats from enemies, diseases, or impacts from human activities, e.g., habitat loss and climate change. Harsh weather conditions, especially in winter, can lead to evolutionary changes in barn owl biology (Roulin, 2020). There are already examples of barn owls maturing earlier (Taylor, 2004), and barn owls may reproduce at a higher rate by producing two to three annual broods with several offspring. Also, increased capacity to disperse long distances to use short-term resources could be beneficial (Roulin, 2020). According to Taylor (2004), much of the available evidence shows that barn owls have evolved a life history pattern involving more investment into reproduction than other similar-sized owls and raptors. By adapting to worsened weather conditions, the barn owls may mitigate the effects of climate change.

5. CONCLUSION

Similar to other studies, the barn owls preferred mammalian prey, particularly field voles. The barn owls delivered nine different mammalian species at the nests, while alternative prey represented by avian prey was delivered only three times. Thus, barn owls can be recognised as food generalists, not specialising in a single type of prey. However, they may also be regarded as specialists because they mainly depend on small mammals. The barn owls were mainly nocturnal hunters, and prey deliveries peaked around midnight. Future studies are required whether barn owls are more likely to hunt during the daytime in the northern UK than in the southern UK.

The amount of daily rainfall proved to negatively impact the number of prey deliveries at night, which corresponded to the prediction that the barn owl limits hunting when it rains. An increase in prey deliveries during the daytime was related to the two last days of rainfall. Two days with rainfall compelled the owls to hunt during the daytime to provide sufficient food. Poor catch the previous night was still the best factor to explain an increase in daytime deliveries. However, these factors are interrelated, and several other factors are likely to affect the number of prey deliveries.

My results suggest that precipitation must be considered an important factor when evaluating how climate affects food provisioning in barn owls. Still, more data is necessary to assess to what extent precipitation affects parental food provisioning. Therefore, future studies should continue to record the prey delivery rate before, during and after rainy days or nights (Roulin, 2020). This will provide valuable information about how the barn owl parents can compensate for the adverse effects of prey delivery decline following increased precipitation. Considering other factors such as wind and temperature will stimulate further research. Studying the factors influencing parental food provisioning and the possible linkages between climate change and population dynamics may give insight into how barn owl populations will respond to predicted climate change scenarios in the future.

6. REFERENCES

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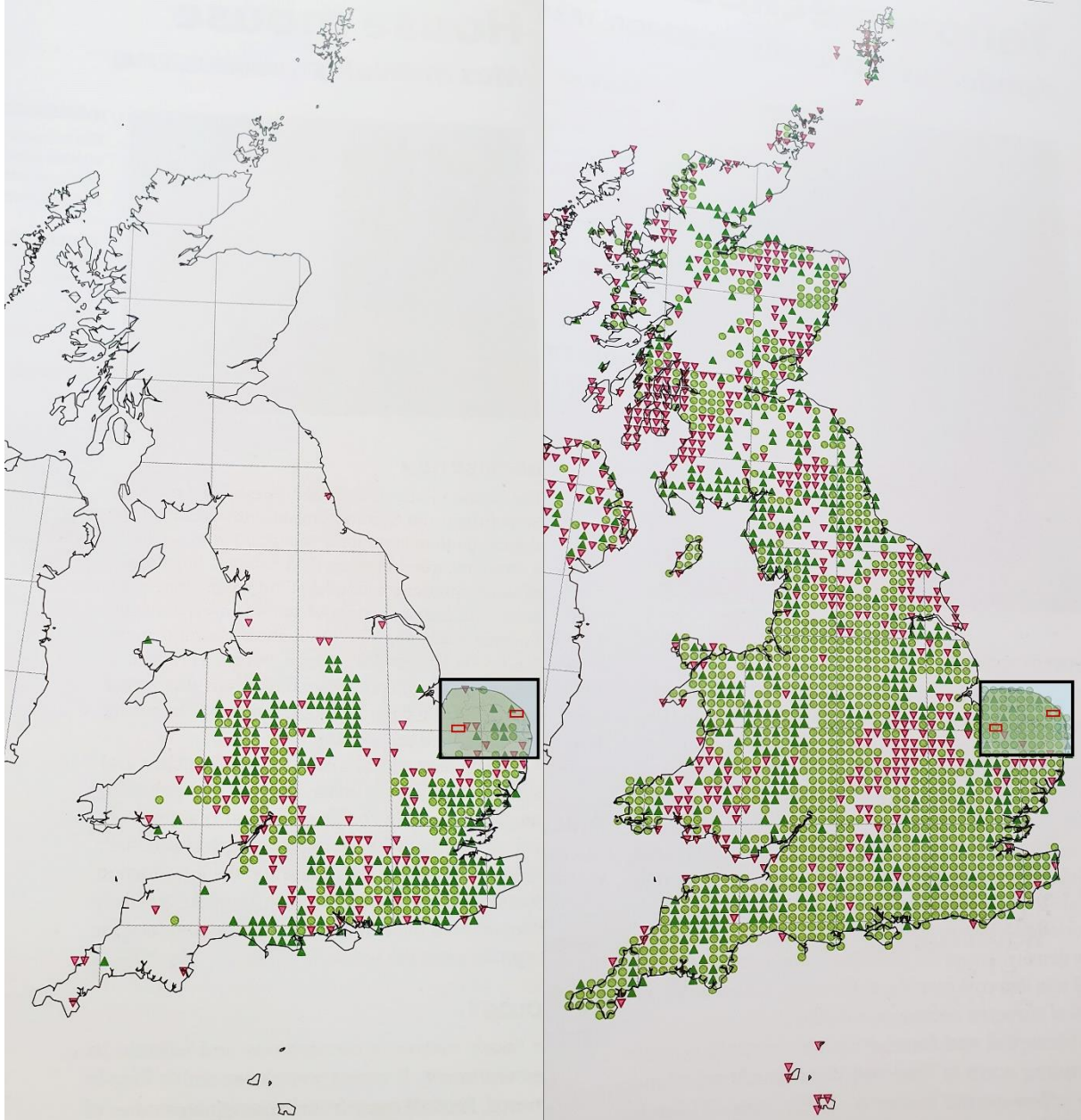
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A. APPENDIX

Appendix 1. Distribution of Yellow-necked wood mouse (left) and Wood mouse (right) in the UK. The red squares inside the black square indicate the study areas. The red downward triangle symbol represents the time period 1960-1992. The green circle symbol represents the time period 1960-1992 & 2000-2016. The dark green triangle symbol represents the time period 2000-2016. The distribution maps are edited from the maps of the distribution of Yellow-necked wood mouse (left) and Wood mouse (right) in the UK in Crawley et al. (2020).



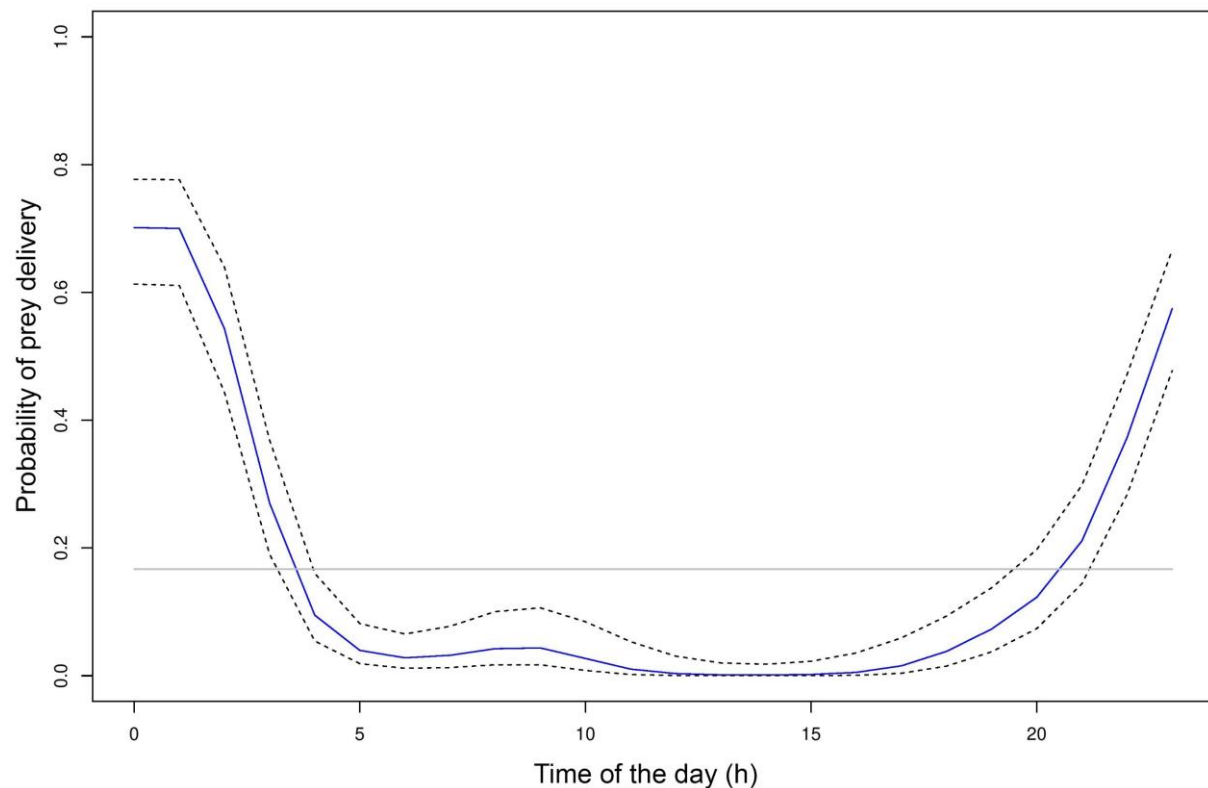
Appendix 2. The number of prey deliveries at the barn owl nests arranged by date, distributed by the nestling age and the number of prey items delivered during the daytime and at night in Nar Valley and Broads Authority. Daily delivery is defined as deliveries from 00:00 to 23:59 hours. Night delivery is defined as deliveries in the main activity period from 21:00 to 03:30 hours. The days following the introduction of prey delivery outside the nest and the days without complete camera surveillance, expressed by the symbol -, are excluded from the results.

Date	Nar Valley			Broads Authority		
	Number of prey items, daily	Number of prey items, night	Nestling age	Number of prey items, daily	Number of prey items, night	Nestling age
28.05.2019	-	3	21	-	4	0
29.05.2019	4	6	22	6	7	0
30.05.2019	10	15	23	6	7	0
31.05.2019	13	7	24	10	5	1
01.06.2019	6	5	25	5	3	2
02.06.2019	7	11	26	5	4	3
03.06.2019	11	9	27	5	7	4
04.06.2019	7	0	28	9	4	5
05.06.2019	12	5	29	5	7	6
06.06.2019	6	6	30	11	3	7
07.06.2019	9	5	31	8	5	8
08.06.2019	7	8	32	10	12	9
09.06.2019	7	11	33	15	14	10
10.06.2019	-	4	34	8	0	11
11.06.2019	2	2	35	1	4	12
12.06.2019	6	5	36	5	6	13
13.06.2019	3	4	37	5	5	14
14.06.2019	20	15	38	8	5	15
15.06.2019	12	8	39	6	6	16
16.06.2019	7	17	40	7	10	17
17.06.2019	14	5	41	8	3	18
18.06.2019	6	4	42	7	0	19
19.06.2019	7	4	43	4	5	20
20.06.2019	9	11	44	18	5	21
21.06.2019	8	8	45	8	3	22
22.06.2019	10	9	46	3	-	23
23.06.2019	7	8	47	-	-	-
24.06.2019	10	6	48	-	-	-
25.06.2019	6	8	49	-	-	-
26.06.2019	7	7	50	-	-	-
27.06.2019	5	5	51	-	-	-
28.06.2019	-	-	-	-	1	29
29.06.2019	-	-	-	4	7	30
30.06.2019	-	-	-	6	4	31
01.07.2019	-	-	-	7	6	32
02.07.2019	-	-	-	8	5	33
03.07.2019	-	-	-	6	4	34
04.07.2019	-	-	-	8	14	35
12.07.2019	-	-	-	-	9	43
13.07.2019	-	-	-	7	8	44
14.07.2019	-	-	-	11	10	45
15.07.2019	-	-	-	7	2	46
16.07.2019	-	-	-	6	4	47
Average number of prey items (daily/night)	8,2	7,1		7,2	5,6	

Appendix 3. Prey deliveries at the barn owl nests arranged by prey type, distributed by the number of prey items, percentage by number, average body mass, and total body mass sorted by nests. All digits are rounded to one decimal place.

Prey type	Nar Valley				Broads Authority			
	Number of prey items	Percentage by number (%)	Average body mass (g)	Total body mass (g)	Number of prey items	Percentage by number (%)	Average body mass (g)	Total body mass (g)
Field vole (<i>Microtus agrestis</i>)	116	40.8	30	3480	133	36.6	30	3990
Bank vole (<i>Myodes glareolus</i>)	25	8.8	20	500	5	1.4	20	100
Field/Bank vole	18	6.3	28.2	508.1	18	5	29.6	533.5
European water vole (<i>Arvicola amphibious</i>)	0	0	0	0	7	1.9	100	700
Common shrew (<i>Sorex araneus</i>)	27	9.5	10	270	100	27.5	10	1000
Eurasian water shrew (<i>Neomys fodiens</i>)	1	0.4	15	15	2	0.6	15	30
Common shrew/Eurasian water shrew	0	0	0	0	8	2.2	10.1	80.8
Wood mouse (<i>Apodemus sylvaticus</i>)	82	28.9	25	2050	27	7.4	25	675
Brown rat (<i>Rattus norvegicus</i>)	4	1.4	100	400	0	0	0	0
Eurasian house mouse (<i>Mus musculus</i>)	1	0.4	15	15	0	0	0	0
Eurasian harvest mouse (<i>Micromys minutus</i>)	1	0.4	10	10	0	0	0	0
Unidentified vole (Arvicolidae sp.)	1	0.4	28.2	28.2	18	5	32.7	587.9
Unidentified mice (Muridae sp.)	1	0.4	28.1	28.1	4	1.1	25	100
Unidentified small rodent (Rodentia)	4	1.4	28.2	112.8	2	0.6	31.5	63.1
Unidentified small mammal (Mammalia)	1	0.4	26.4	26.4	28	7.7	24.3	679.3
Mammals in total	282	99.3	26.4	7443.6	352	97	24.3	8539.5
Partridge (Galliformes sp.)	1	0.4	30	30	1	0.3	30	30
Unidentified sparrow (Passeriformes sp.)	1	0.4	10	10	0	0	0	0
Birds in total	2	0.7	20	40	1	0.3	30	30
Unidentified prey in total	0	0	0	0	10	2.8	24.3	242.8
All prey in total	284	100	26.4	7483.6	363	≈100	24.3	8812.2

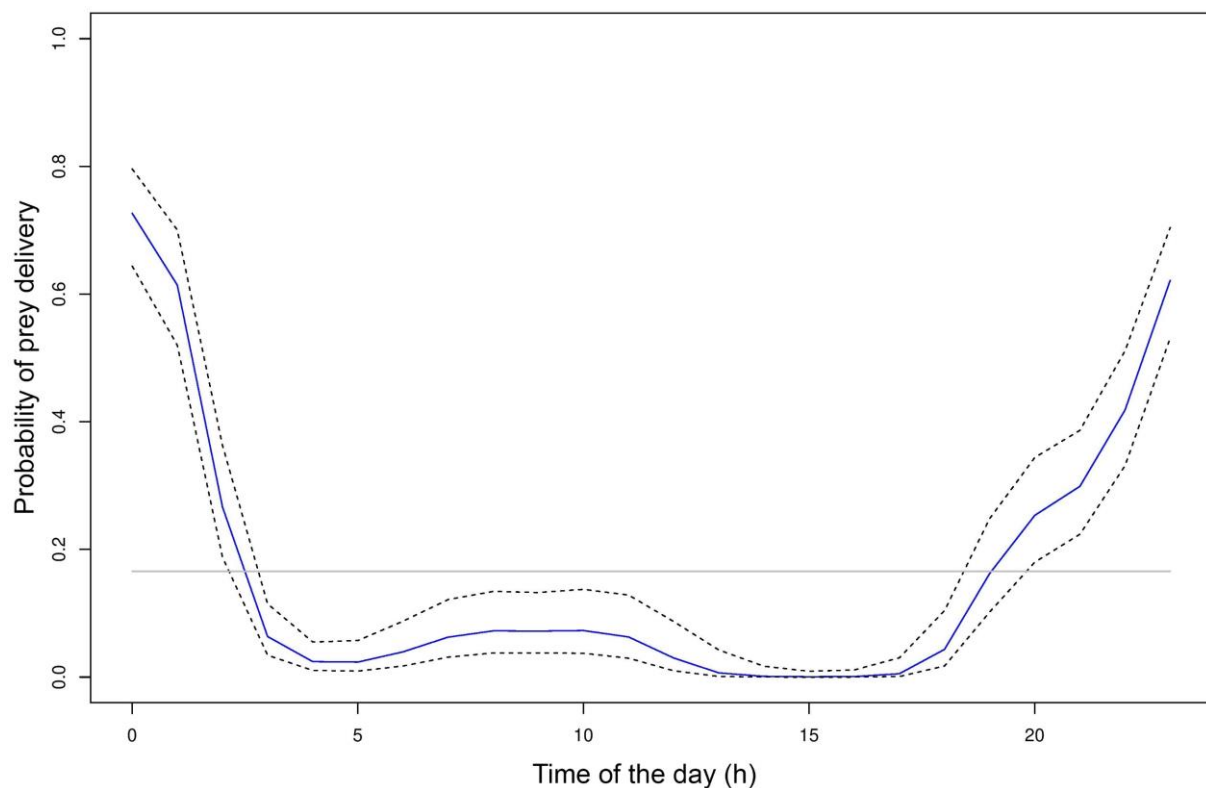
Appendix 4. The probability of prey delivery within an hour block at the barn owl nest in Nar Valley. The blue curve describes the best-fitted model of diel activity for all prey items in Nar Valley calculated from the generalised linear mixed-effect models based on the cosinor method, corrected for the random effect of nest ID. The dotted curve displays the 95% confidence interval for all prey deliveries in Nar Valley calculated by the model-based parametric bootstrapping for mixed models. The dark field displays the night (sunset-sunrise) of the study area in the relevant time period. The horizontal line displays the average activity throughout the day (MESOR).



Appendix 5. Parameter estimates from the best-fitted generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey delivery within an hour block at the barn owl nest in Nar Valley, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	1.61	0.09	-18.22	<0.001

Appendix 6. The probability of prey delivery within an hour block at the barn owl nest in Broads Authority. The blue curve describes the best-fitted model of diel activity for all prey items in Broads Authority calculated from the generalised linear mixed-effect models based on the cosinor method, corrected for the random effect of nest ID. The dotted curve displays the 95% confidence interval for all prey deliveries in Broads Authority calculated by the model-based parametric bootstrapping for mixed models. The dark field displays the night (sunset-sunrise) of the study area in the relevant time period. The horizontal line displays the average activity throughout the day (MESOR) (random effect = 2).



Appendix 7. Parameter estimates from the best-fitted generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey delivery within an hour block at the barn owl nest in Broads Authority, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-1.62	0.08	-21.29	<0.001

Appendix 8. Parameter estimates from the generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey delivery within an hour block at a barn owl nest, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-2.78	0.20	-13.49	<0.001
I(cos(2 * pi * Hour/24))	2.54	0.30	8.33	<0.001
I(sin(2 * pi * Hour/24))	0.57	0.26	2.19	<0.05
I(cos(2 * 2 * pi * Hour/24))	0.70	0.18	3.85	<0.001
I(sin(2 * 2 * pi * Hour/24))	-1.28	0.29	-4.31	<0.001
I(cos(3 * 2 * pi * Hour/24))	0.06	0.19	0.33	0.74
I(sin(3 * 2 * pi * Hour/24))	0.76	0.22	3.37	<0.001
I(cos(4 * 2 * pi * Hour/24))	0.36	0.15	2.36	<0.05
I(sin(4 * 2 * pi * Hour/24))	0.00	0.14	0.04	0.96

Appendix 9. Parameter estimates from the generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey delivery within an hour block at the barn owl nest in Nar Valley, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-2.89	0.30	-9.49	<0.001
I(cos(2 * pi * Hour/24))	2.86	0.47	6.00	<0.001
I(sin(2 * pi * Hour/24))	0.52	0.32	1.60	0.11
I(cos(2 * 2 * pi * Hour/24))	0.48	0.34	1.39	0.16
I(sin(2 * 2 * pi * Hour/24))	-0.69	0.37	-1.84	0.064
I(cos(3 * 2 * pi * Hour/24))	0.39	0.23	1.69	0.090
I(sin(3 * 2 * pi * Hour/24))	0.68	0.26	2.60	<0.01

Appendix 10. Parameter estimates from the generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey within an hour block at the barn owl nest in Broads Authority, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-2.81	0.26	-10.68	<0.001
I(cos(2 * pi * Hour/24))	2.29	0.36	6.32	<0.001
I(sin(2 * pi * Hour/24))	0.55	0.37	1.47	0.14
I(cos(2 * 2 * pi * Hour/24))	0.94	0.21	4.43	<0.001
I(sin(2 * 2 * pi * Hour/24))	-1.73	0.39	-4.35	<0.001
I(cos(3 * 2 * pi * Hour/24))	-0.06	0.26	-0.25	0.80
I(sin(3 * 2 * pi * Hour/24))	0.60	0.25	2.34	<0.05
I(cos(4 * 2 * pi * Hour/24))	0.62	0.21	2.90	<0.01
I(sin(4 * 2 * pi * Hour/24))	0.32	0.18	1.72	0.085

Appendix 11. Parameter estimates from the generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey delivery within an hour block at a barn owl nest for the prey family Arvicolidae, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-3.16	0.17	-17.81	<0.001
I(cos(2 * pi * Hour/24))	1.87	0.24	7.64	<0.001
I(sin(2 * pi * Hour/24))	0.33	0.20	1.63	0.10
I(cos(2 * 2 * pi * Hour/24))	0.40	0.18	2.26	<0.05
I(sin(2 * 2 * pi * Hour/24))	-1.06	0.22	-4.64	<0.001
I(cos(3 * 2 * pi * Hour/24))	0.06	0.14	0.45	0.65
I(sin(3 * 2 * pi * Hour/24))	0.81	0.17	4.73	<0.001

Appendix 12. Parameter estimates from the generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey delivery within an hour block at a barn owl nest for the prey family Muridae, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-7.89	0.98	-8.00	<0.001
I(cos(2 * pi * Hour/24))	6.49	0.90	7.17	<0.001
I(sin(2 * pi * Hour/24))	-0.06	0.28	-0.20	0.83

Appendix 13. Parameter estimates from the generalised linear mixed-effect models based on the cosinor method for the model of the probability of prey delivery within an hour block at a barn owl nest for the prey family Muridae, corrected for the random effect of nest ID (random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-4.66	0.47	-9.92	<0.001
I(cos(2 * pi * Hour/24))	2.32	0.45	5.09	<0.001
I(sin(2 * pi * Hour/24))	-0.30	0.42	-0.71	0.47
I(cos(2 * 2 * pi * Hour/24))	0.72	0.28	2.58	<0.01
I(sin(2 * 2 * pi * Hour/24))	-0.38	0.30	-1.26	0.21

Appendix 14. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of prey delivery within an hour block at a barn owl nest.

Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
M ₆ (mod7)	14	1306.14	0.00	0.41	0.41	-638.98
M ₇ (mod8)	16	1307.37	1.23	0.22	0.63	-637.56
M ₄ (mod5)	10	1307.87	1.73	0.17	0.80	-643.89
M ₅ (mod6)	12	1309.05	2.91	0.10	0.90	-642.45
M ₃ (mod4)	8	1309.91	3.76	0.06	0.96	-646.92
M ₈ (mod9)	18	1310.82	4.68	0.04	1.00	-637.25
M ₂ (mod3)	6	1336.39	30.24	0.00	1.00	-662.17
M ₁ (mod2)	4	1414.86	108.71	0.00	1.00	-703.42
M ₀ (mod1)	2	1963.43	657.28	0.00	1.00	-979.71

K = Number of parameters

AICc = Akaike's Information Criterion

Delta_AICc = Δ AICc = Difference in AICc from the best-fitted model

AICcWt = Model weight according to Δ AICc

Cum.Wt = Cumulative model weights

LL = Log-likelihood

Appendix 15. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of prey delivery within an hour block at the barn owl nest in Nar Valley.

Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
M ₄ (mod5)	9	526.79	0.00	0.44	0.44	-254.30
M ₃ (mod4)	7	527.28	0.48	0.34	0.78	-256.58
M ₅ (mod6)	11	529.90	3.10	0.09	0.87	-253.80
M ₆ (mod7)	13	530.50	3.71	0.07	0.94	-252.05
M ₇ (mod8)	15	532.02	5.23	0.03	0.97	-250.75
M ₈ (mod9)	17	533.62	6.82	0.01	0.99	-249.47
M ₂ (mod3)	5	534.24	7.44	0.01	1.00	-262.09
M ₁ (mod2)	3	549.20	22.41	0.00	1.00	-271.59
M ₀ (mod1)	1	834.28	307.48	0.00	1.00	-416.14

K = Number of parameters

AICc = Akaike's Information Criterion

Delta_AICc = Δ AICc = Difference in AICc from the best-fitted model

AICcWt = Model weight according to Δ AICc

Cum.Wt = Cumulative model weights

LL = Log-likelihood

Appendix 16. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of prey delivery within an hour block at the barn owl nest in Broads Authority.

Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
M ₇ (mod8)	15	760.55	0.00	0.45	0.45	-365.08
M ₄ (mod5)	9	761.93	1.38	0.23	0.68	-371.89
M ₅ (mod6)	11	762.74	2.19	0.15	0.83	-370.26
M ₈ (mod9)	17	763.90	3.35	0.08	0.92	-364.70
M ₆ (mod7)	13	763.96	3.41	0.08	1.00	-368.83
M ₃ (mod4)	7	771.29	10.73	0.00	1.00	-378.60
M ₂ (mod3)	5	787.36	26.81	0.00	1.00	-388.66
M ₁ (mod2)	3	854.35	93.80	0.00	1.00	-424.17
M ₀ (mod1)	1	1129.15	368.60	0.00	1.00	-563.57

K = Number of parameters

AICc = Akaike's Information Criterion

Delta_AICc = Δ AICc = Difference in AICc from the best-fitted model

AICcWt = Model weight according to Δ AICc

Cum.Wt = Cumulative model weights

LL = Log-likelihood

Appendix 17. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of prey delivery within an hour block at a barn owl nest for the prey family Arvicolidae.

Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
M ₄ (mod5)	10	1239.26	0.00	0.39	0.39	-609.58
M ₃ (mod4)	8	1239.35	0.09	0.37	0.76	-611.64
M ₅ (mod6)	12	1242.03	2.77	0.10	0.85	-608.95
M ₆ (mod7)	14	1242.53	3.27	0.08	0.93	-607.17
M ₇ (mod8)	16	1243.15	3.89	0.06	0.98	-605.46
M ₈ (mod9)	18	1245.76	6.49	0.02	1.00	-604.73
M ₂ (mod3)	6	1263.40	24.14	0.00	1.00	-625.68
M ₁ (mod2)	4	1286.93	47.67	0.00	1.00	-639.46
M ₀ (mod1)	2	1494.15	254.89	0.00	1.00	-745.07

K = Number of parameters

AICc = Akaike's Information Criterion

Delta_AICc = Δ AICc = Difference in AICc from the best-fitted model

AICcWt = Model weight according to Δ AICc

Cum.Wt = Cumulative model weights

LL = Log-likelihood

Appendix 18. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of prey delivery within an hour block at a barn owl nest for the prey family Muridae.

Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
M ₁ (mod2)	4	549.11	0.00	0.48	0.48	-270.55
M ₂ (mod3)	6	549.91	0.80	0.32	0.80	-268.94
M ₃ (mod4)	8	551.44	2.33	0.15	0.95	-267.69
M ₄ (mod5)	10	553.86	4.75	0.04	0.99	-266.88
M ₅ (mod6)	12	557.90	8.79	0.01	1.00	-266.88
M ₆ (mod7)	14	561.94	12.84	0.00	1.00	-266.88
M ₇ (mod8)	16	566.00	16.89	0.00	1.00	-266.88
M ₈ (mod9)	18	570.06	20.95	0.00	1.00	-266.88
M ₀ (mod1)	2	787.05	237.94	0.00	1.00	-391.52

K = Number of parameters

AICc = Akaike's Information Criterion

Delta_AICc = Δ AICc = Difference in AICc from the best-fitted model

AICcWt = Model weight according to Δ AICc

Cum.Wt = Cumulative model weights

LL = Log-likelihood

Appendix 19. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of prey delivery within an hour block at a barn owl nest for the prey family Soricidae.

Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
M ₃ (mod4)	8	668.25	0.00	0.41	0.41	-326.09
M ₂ (mod3)	6	669.44	1.19	0.22	0.63	-328.70
M ₄ (mod5)	10	670.56	2.31	0.13	0.76	-325.23
M ₅ (mod6)	12	670.91	2.66	0.11	0.86	-323.39
M ₆ (mod7)	14	671.78	3.54	0.07	0.93	-321.80
M ₁ (mod2)	4	672.56	4.32	0.05	0.98	-332.27
M ₇ (mod8)	16	674.51	6.27	0.02	1.00	-321.14
M ₈ (mod9)	18	678.57	10.33	0.00	1.00	-321.14
M ₀ (mod1)	2	864.47	196.23	0.00	1.00	-430.23

K = Number of parameters

AICc = Akaike's Information Criterion

Delta_AICc = Δ AICc = Difference in AICc from the best-fitted model

AICcWt = Model weight according to Δ AICc

Cum.Wt = Cumulative model weights

LL = Log-likelihood

Appendix 20. Parameter estimates from the generalised linear mixed-effect models based on binomial distribution for the model of the probability of nestling feeding unassisted rather than indefinite feeding as a function of prey body mass (g), corrected for the random effect of nest ID (n = 647, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	0.94	0.70	1.35	0.18
Prey body mass	0.02	0.01	2.35	<0.05

Appendix 21. Parameter estimates from the generalised linear mixed-effect models based on binomial distribution for the model of the probability of nestling feeding unassisted rather than indefinite feeding as a function of nestling age (d), and prey body mass (g), corrected for the random effect of nest ID (n = 647, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-3.71	0.67	-5.57	<0.001
Nestling age	0.21	0.03	7.64	<0.001
Prey body mass	-0.01	0.01	-0.61	0.54

Appendix 22. Parameter estimates from the generalised linear mixed-effect models based on binomial distribution for the model of the probability of nestling feeding unassisted rather than indefinite feeding as a function of nestling age (d), prey body mass (g), and the interaction between nestling age (d) and prey body mass (g), corrected for the random effect of nest ID (n = 647, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-4.20	0.84	-4.97	<0.001
Nestling age	0.24	0.04	6.23	<0.001
Prey body mass	0.02	0.02	0.67	0.50
Nestling age:Prey body mass	-0.00	0.00	-1.06	0.29

Appendix 23. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of nestling feeding unassisted rather than indefinite feeding as a function of nestling age (d), prey body mass (g), nestling age (d) and prey body mass (g), and the interaction between nestling age (d) and prey body mass (g).

Models	Parameters	df	AICc
M ₁ (mod4)	Nestling age	3	301.4
M ₂ (mod1)	Nestling age + Prey body mass	4	303.0
M ₃ (mod3)	Nestling age:Prey body mass	5	304.1
M ₄ (mod2)	Prey body mass	3	646.6

Appendix 24. Number of prey handling occurrences arranged by behaviour type, distributed by nest locations, all nests total, and percentage by number. All digits are rounded to one decimal place.

Type of behaviour	Nar Valley	Broads Authority	All nests in total	Percentage by number (%)
Nestling feeding unassisted	261	229	490	75.7
Indefinite feeding	23	134	157	24.3
Female delivering prey	58	3	61	9.4
Male delivering prey	191	151	342	52.9
Indefinite delivery	35	209	244	37.7
Delivering prey inside the nest cavity	93	132	225	34.8
Delivering prey outside the nest cavity	191	231	422	65.2

Appendix 25. Parameter estimates from the generalised linear mixed-effect models based on binomial distribution for the model of the probability of the female delivering prey as a function of nestling age (d), and prey body mass (g), corrected for the random effect of nest ID (n = 403, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-4.45	0.57	-7.82	<0.001
Nestling age	0.07	0.01	5.87	<0.001
Prey body mass	-0.01	0.01	1.39	0.16

Appendix 26. Parameter estimates from the generalised linear mixed-effect models based on binomial distribution for the model of the probability of the female delivering prey feeding as a function of nestling age (d), prey body mass (g), and the interaction between nestling age (d) and prey body mass (g), corrected for the random effect of nest ID (n = 403, random effect = 2).

Parameters	Estimates	Standard error	z-value	P-value
(Intercept)	-4.98	0.83	-5.98	<0.001
Nestling age	0.09	0.02	3.82	<0.001
Prey body mass	0.03	0.02	1.43	0.15
Nestling age:Prey body mass	-0.00	0.00	-0.88	0.38

Appendix 27. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the probability of the female delivering prey feeding as a function of nestling age (d), prey body mass (g), nestling age (d) and prey body mass (g), and the interaction between nestling age (d) and prey body mass (g), corrected for the random effect of nest ID.

Models	Parameters	df	AICc
M ₁ (mod4)	Nestling age	3	300.5
M ₂ (mod2)	Nestling age + Prey body mass	4	300.8
M ₃ (mod1)	Nestling age:Prey body mass	5	302.1
M ₄ (mod3)	Prey body mass	3	312.6

Appendix 28. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of the number of prey deliveries at night in relation to the amount of daily rainfall (mm), nestling age (d), and the amount of daily rainfall (mm) and nestling age (d).

Models	Parameters	df	AICc
M ₁ (mod2)	Daily rainfall	3	354.0
M ₂ (mod3)	Daily rainfall + Nestling age	3	354.4
M ₃ (mod4)	Daily rainfall + Nestling age	4	356.4

Appendix 29. Model selection from the generalised linear mixed-effect models based on Akaike's information criterion (AICc) (Akaike, 1978) for the model of prey deliveries during the daytime in relation to the amount of rainfall (mm) the present day, amount of rainfall (mm) the two last days, amount of rainfall (mm) the three last days, and the number of prey items delivered the previous night.

Models	Parameters	df	AICc
M ₁ (mod1)	Number of prey items the previous night	3	280.6
M ₂ (mod3)	Rainfall, the two last days	3	287.9
M ₃ (mod2)	Rainfall, the present day	3	290.3
M ₄ (mod4)	Rainfall, the three last days	3	291.2



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