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**Diet, diel activity and prey handling
during food provisioning in the
common barn owl (*Tyto alba*): a
comparative study using
continuous camera monitoring data
from three European countries**

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M-NF: Natural Resource Management

Acknowledgements

With this master's thesis I conclude my time as a student at the Norwegian University of Life Sciences and the Faculty of Environmental Sciences and Natural Resource Management. Working on this thesis has been both challenging and rewarding, and it has provided me with valuable insight and tools regarding scientific methods generally and behavioral studies specifically.

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Abstract

Even though various aspects of the barn owl's (*Tyto alba*) diet and breeding ecology have been extensively studied in the past, high-resolution data on diel activity and prey handling at the nest are still scarce. This study investigated food provisioning, prey handling and diel activity patterns at three barn owl nests in Spain, England, and Ireland respectively, using the method of continuous camera monitoring. I monitored one month of the nestling period from each nest using video recordings from the breeding season of 2022 and 2023, observing which prey types were delivered, prey condition, timing of delivery and how prey was handled at the nest. Of the 1500 prey deliveries observed, small mammals accounted for as much as 95% of the total, with rodents (Rodentia) comprising the largest portion (79 %) and shrews (Soricidae) the second largest portion (15%). Less than 0.7% of the total deliveries were non-mammalian prey. Observation of hunting times revealed a strictly nocturnal activity pattern. Variations in night length due to latitudinal differences enabled longer nights and subsequently more hunting hours for the barn owls at the Spanish nest compared to the English and Irish nests. Prey were delivered intact in 99 % of the instances where condition could be determined, and decapitation of prey occurred only eight times in total. The probability of prey being stored decreased with increasing nestling age for nearly all prey groups, and shrews had a lower probability of being stored than other prey groups for all ages. The probability of nestlings feeding with maternal assistance decreased with nestling age, with a 50% probability of independent feeding occurring at ages 22 days and 16 days for the English and Irish nest respectively. Delivery rates were correlated with nestling age, with the rate initially increasing before diminishing as the nestlings aged and prepared for fledging. Camera monitoring proved to be an efficient way to obtain high resolution data on the barn owl's food provisioning behavior. My results suggest that provisioning barn owls prefer to hunt small mammals, and while usually hunting opportunistically, might have the ability to select appropriately sized prey based on the nestlings' current swallowing capacity. Low decapitation rates further indicate that barn owl pellets are a reliable data source for diet and small mammal assessment studies and may contain less bias than pellets from other raptors. Furthermore, variations in night length across latitudes may influence hunting behavior, with southern barn owls potentially benefiting from longer hunting hours in summer. However, northern barn owls may compensate for shorter nights with higher hunting effort per hour. Future studies on barn owl foraging ecology should include latitudinal variations in night length to gain a better understanding of potential fitness implications.

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1. INTRODUCTION

Raptorial birds are top predators inhabiting nearly all terrestrial ecosystems, playing a key role in prey population regulation and structuring natural communities (Sarasola et al., 2018). Most raptors are altricial, indicating that their nestlings are entirely reliant on thermoregulation and parental food provisioning post-hatching to survive and grow (Starck & Ricklefs, 1998; Sarasola et al., 2018). Parental food provisioning involves the allocation of time and energy by the parents in procuring and delivering food to the nest (Taylor, 1994). Provisioning behavior is essential for nestling survival and growth, being a key determinant of the nestlings' development, fitness and future reproductive success (Ligon, 1999; Kölliker et al., 2012). Studying key behavioral parameters such as parental investment, prey choice and diel activity in raptors can provide crucial information on the raptor's survival, biology and breeding success (Otterbeck et al., 2015), in addition to knowledge on prey population fluctuations and predator-prey interactions (Korpimäki, 1988; Salamolard et al., 2000). Most of the studies on this topic are carried out during the breeding season, as bird activity is often concentrated around the nest area and dietary and behavioral data is easy to collect (Lewis et al., 2004).

Collecting data on different stages of the nestling rearing period, from egg laying to fledging, requires a close look into the nest. This is however not an unproblematic operation, as human presence may disturb the birds and affect the parameters being studied (Götmark, 1992). Long-term nest studies based on direct observations from hides requires a considerable amount of field work, and may not be possible in instances where nests are difficult to reach (e.g. nests on cliffs or in tall trees) (Reif & Tornberg, 2006). Prolonged human presence in the vicinity of nests may also alter the natural behavior of the study species, decrease nest attendance (Spaul & Heath, 2017), negatively affect nesting success (Brambilla et al., 2004; Arroyo & Razin, 2006; Garcia et al., 2006), or potentially cause abandonment of the nest site (Fyfe & Olendorff, 1976). Collecting data on diet alone has typically involved less disturbance, with analysis of prey remains in regurgitated pellets being a common method. This method has however shown to potentially give biased results as some prey items are more conserved in the pellets than others (Simmons et al., 1991; Tornberg & Reif, 2006; Zárbybnická et al., 2011).

Advancements in camera technology have introduced an alternative to observations from a hide and analyses of pellets when studying raptor diet and breeding behavior. Several studies in the past have used photography or video cameras to monitor diet and nesting behavior in raptors (e.g Häkkinen, 1977; Wille & Kampp, 1983; Reif & Tornberg, 2006; Dias et al., 2021) and the methods have proved to be less biased, less invasive, less time-consuming and less costly than direct observations from a hide (Cutler & Swann, 1999; García-Salgado et al., 2015). Continuous camera monitoring of nests can provide access to detailed observation of activities both inside and outside the nest cavity throughout the 24-hour-cycle and the entire nesting period, giving high resolution data on multiple variables related to diet and breeding behavior at once. Though there will always exist some uncertainty when visually identifying prey from video, camera monitoring presents as one of the most accurate methods for estimating raptor diet today (Lewis et al., 2004). The method is especially useful for studying species that can inhabit artificial nest boxes, as installing and operating camera equipment in these boxes is easier than for natural and often hard to reach nest sites (Surmacki & Podkowa, 2022).

The common barn owl (*Tyto alba*) regularly uses artificial nest boxes and is therefore an appropriate study species. Belonging to the oldest surviving taxonomic group of owls, Tytonidae, the barn owl has a wide distribution, with 10-28 subspecies inhabiting all continents apart from Antarctica (Bruce, 1999; Aliabadian et al., 2016). The species is flexible in terms of habitat, varying from forest, grasslands, and desert, in addition to urban and agricultural landscapes, but tend to hunt in open landscapes where prey is accessible and easy to detect (Roulin, 2020). Barn owls predominantly prey on small mammals, comprising an estimated 72-99% of the diet globally (Taylor, 1994; Roulin, 2020). The main mammalian prey groups across all continents are shrews (Soricidae) and small rodents (Rodentia), while non-mammalian prey consisting of amphibians, reptiles, birds and invertebrates comprise only a small portion of the diet (Taylor, 1994; Roulin, 2020). Voles (Microtinae) are particularly prominent, and is a basic food type for barn owls in nearly all countries and habitats (Lovari, 1974; Bunn et al., 1982). The barn owl show a numeric response to vole fluctuations, with annual breeding success, fecundity and both adult and juvenile mortality correlating with the abundance of voles (Taylor, 1994; Klok & de Roos, 2007; Pavlůvčık et al., 2015). Vole population dynamics is thus a major determinant of barn owl population persistence (Klok & de Roos, 2007).

Information on the barn owl's diet derives from numerous studies carried out throughout many years and in many different countries. Due to the species' cosmopolitan distribution, proximity to human settlement in agricultural habitats and ease of data collection, its diet has been extensively studied in the past, with more than 1600 diet studies existing today (Roulin, 2020). The majority of these studies have used the method of pellet analysis, and although being considered to provide an accurate indication of the diet (Taylor, 1994), it is susceptible to potential bias (Simmons et al., 1991; Yom-Tov & Wool, 1997; Meek et al., 2012). One source of bias in pellet analyses is that the providing bird decapitates prey prior to delivery at the nest, which could introduce a source of error as the analyses are often based on skull and jaw identification alone. Decapitation of prey prior to delivery at the nest is common in other raptors such as the Eurasian kestrel (*Falco tinnunculus*) (Steen et al., 2010) and the boreal owl (*Aegolius funereus*) (Zárybnická et al., 2011), but the extent, frequency and function of this behavior in the barn owl is still unknown (Taylor, 1994). Decapitation has been observed in a few studies on e.g. Czech and Swiss barn owls (Pikula et al., 1984; Roulin, 2020), while other studies show no accounts of this behavior (Taylor, 1994). Like many other raptors, barn owls bring one prey item at a time back to the nest, termed central place foraging and single-prey loading (Orians & Pearson, 1979). This facilitates easy identification of prey and observation of prey condition through camera monitoring, revealing the extent of decapitation prior to nest delivery.

Barn owls are prolific breeders and lay an average of 4-7 eggs per clutch, with the number varying depending on food availability and environmental conditions (Bunn et al., 1982; Taylor, 1994). Timing of reproduction is highly flexible, and laying dates are adjusted based on climatic conditions and abundance of small mammals (Chausson et al., 2014; Roulin, 2020). Under good conditions, barn owls can produce two broods per breeding season if the first clutch is laid early in the spring or if the abundance of prey is especially high (Bunn et al., 1982; Jackson & Cresswell, 2017). Unfavorable climatic conditions and low prey abundance can however impair reproduction and increase nestling mortality (Chausson et al., 2014). Barn owls exhibit separate parental roles, with the male responsible for hunting and the female responsible for feeding and distributing food among the nestlings during the first half of the nestling period (Bunn et al., 1982; Roulin, 2020). If the male cannot meet the increasing food demand as nestlings grow older, the female joins the male in hunting usually 14-17 days after the first egg hatched (Taylor, 1994; Roulin, 2020).

How food is handled at the nest is a good indication of nestling growth and development. During the initial phase of the rearing period, barn owl nestlings rely on maternal assistance for feeding, gradually transitioning to self-feeding as they mature (Bunn et al., 1982; Taylor, 1994). The onset of independent feeding among raptor nestlings is influenced by factors such as prey size (Sonerud et al., 2014a; Sonerud et al., 2014b) and nestling developmental stage, particularly the swallowing constraint of nestlings' gape size (Slagsvold & Wiebe, 2007; Steen et al., 2010) which is tightly linked to nestling age. Barn owls also often provide more food than what is demanded at the moment, leaving prey items in food stores at the nest for later consumption (Roulin, 2020). Camera monitoring offers a convenient means to observe various aspects of prey handling at the nest, including which prey items are preferentially eaten or stored, at what age the nestlings begin to feed independently and the factors influencing it.

How an animal distributes its activity throughout the 24-hour day is defined as its diel activity (Refinetti, 2008). The barn owl is largely considered to exhibit a nocturnal activity pattern, with key adaptations for hunting in the dark, including an acute sense of hearing supported by a large facial disc for amplifying sound, and large eyes adapted to low light conditions (Bruce, 1999; Roulin, 2020). The nocturnal activity pattern likely evolved in the barn owl as a mechanism to avoid predators and reduce foraging competition with other predatory birds (Roulin, 2020). However, barn owls have regularly been observed hunting during the day in places like Samoa, Tonga and parts of Great Britain (Bunn et al., 1982; Roulin, 2020). The extent and reasons for daytime hunting are still largely unknown, but may include food scarcity, unfavorable weather conditions, and that solely hunting at night is insufficient to meet the needs of the broods, particularly where the nights are short in summer (Bunn et al., 1982; Roulin, 2020). Studying the diel activity pattern is crucial for understanding barn owl breeding biology, as it dictates the timeframe available for providing food for the nestlings. Using continuous camera surveillance allows for detailed monitoring of daily provisioning activity, unveiling the extent of daytime hunting and providing high-resolution data on the overall activity pattern throughout the nestling period.

The barn owl is a well-studied raptor, and much is already known about its behavior and ecology. However, high-resolution data on diel activity and prey handling at the nest on the local scale are still scarce, even though it is considered an integral aspect of the overall foraging behavior. This study set out to investigate these parameters in detail by analyzing and comparing data collected from video monitoring of three barn owl nests from different

countries in Europe during the first part of the nestling period. Specifically, the study aimed to answer the following research questions: (1) Which prey groups are most often delivered by provisioning barn owl parents? I anticipated that the majority of prey items delivered would be small mammals, particularly rodents and shrews, as previous studies have consistently demonstrated these to be the most prevalent prey groups across various countries (Bunn et al., 1982; Taylor, 1994; Roulin, 2020). (2) What are the parents' diel activity pattern when provisioning for young? Due to the barn owl's nocturnal adaptations (Roulin, 2020), I expected most of the hunting activity to occur during the night. (3) How does nestling age influence prey handling and storing, and at what age does independent feeding occur? Nestling age is correlated with the ability to feed independently and food demand (Taylor, 1994; Roulin, 2020), so I expected a reduced amount of assisted feeding and storing as the nestlings age. (4) To what extent do barn owls decapitate their prey prior to nest delivery? Data on prey decapitation in barn owls are still inconclusive. However, other raptors frequently exhibit this behavior (Steen et al., 2010; Zárbynická et al., 2011) so I would expect to find some accounts of decapitation in barn owls as well.

2. METHODS

2.1 Study site

Using continuous camera monitoring as a source for data collection, three barn owl nests in Spain, England, and Ireland respectively, were studied for the first part of the nestling season. The monitored nests were located in Cabaneros National Park in central Spain (39.30°N, 4.25°W), the barony of Duhallow in the south of Ireland (52.35°N, 8.68°W), and in the Blackdown Hills, Somerset, UK (50.97°N, 3.22°W) (coordinates are estimated to the nearest town due to confidentiality of exact location). The nest locations will hereby be referred to as Cabaneros, Duhallow and Somerset respectively (Figure 1). A total of approximately 30 days per nest were monitored from the beginning of May to the beginning of June.

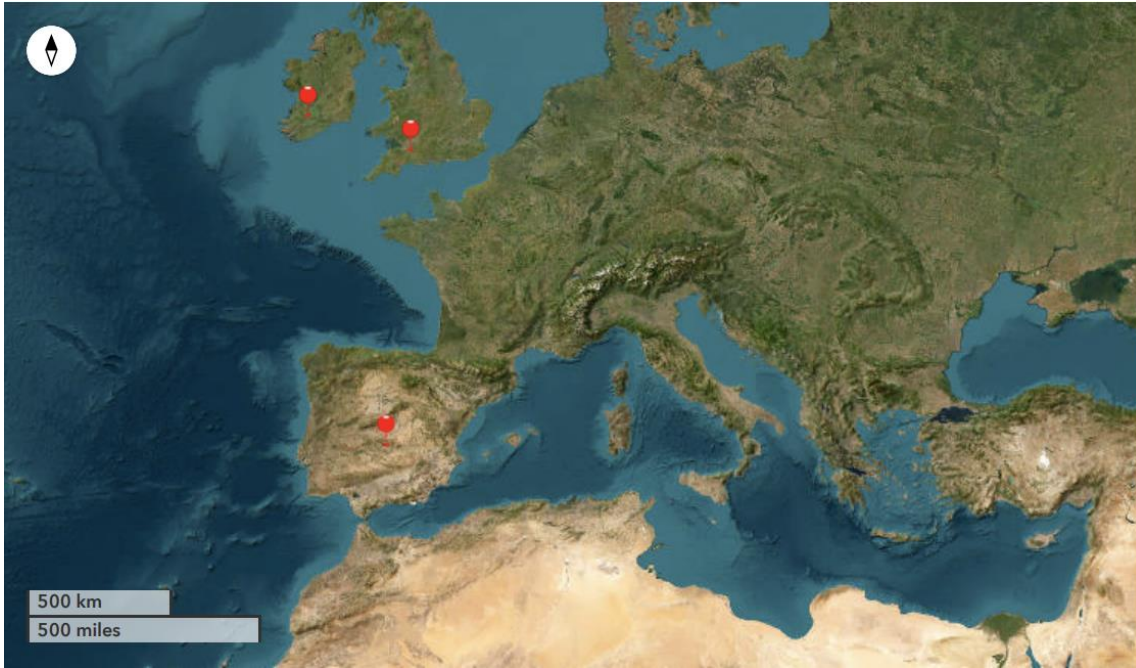


Figure 1: Map showing the locations of the three barn owl nests used in this study. The map was created using MapMaker 4.0 (National Geographic/ESRI, 2023)

Cabaneros

The nest in Spain was located at the Cabaneros National Park visitor center, close to the municipality Pueblonuevo del Bullaque in the province of Ciudad Real. The national park covers an area of 409 km² where the landscape and characteristic species of the Mediterranean forest are represented. The predominant habitat near the nest is known as “raña”, consisting of extensive plains covered with grasslands and specked with isolated large trees and shrubs adapted to water scarcity. The weather is typical of the Mediterranean climate, with high temperatures during the day and low precipitation levels (SEO/BirdLife, 2023). The barn owl pair nested in a nest box mounted beneath the rear porch of the national park’s visitor center “Casa Palillos”. The nest box has been utilized for nearly two decades, with barn owls breeding in it almost every year. Monitoring of this nest box commenced in 2018 and has continued every breeding season since then. However, as the owls are not ringed, it remains uncertain whether the same pair has been breeding in the nest box for consecutive years (SEO/BirdLife, 2023). The cameras were set up and run by staff at SEO BirdLife as a collaboration with the national park, and the footage was live streamed to SEO Birdlife’s YouTube channel during the breeding season of 2022. There were two camera setups showing both the outside entrance to the nest and the interior, providing a good view of

the delivered prey from different angles (Figure 2 and 3). During the breeding season of 2022, the barn owl pair reared six nestlings who all survived the entire study period.

With the permission from collaborators at SEO/Birdlife, recording from the live stream was initiated on May 10th, 2022, and ended on July 7th, 2022. A total of about 1300 hours of video footage was recorded and downloaded to an external hard drive for use in my project. From the available footage, data were collected from May 10th to June 10th.



Figure 2: Photo of the nest box and camera setup at the Cabaneros nest in 2023. The upper photo shows the nest box with the installation of the interior camera. The lower photo shows the exterior camera. Photo: SEO/BirdLife.

Somerset

Situated on the border of Somerset and Devon in the UK, the nest box was located on a private property in the Blackdown Hills. The nest box was installed in a barn surrounded by unimproved grassland fields, natural hedgerows, and banks with no major roads in the vicinity. Two web cameras were installed, one internal showing the inside of the nest box (Figure 4), and one external showing the opening and outer ledge. Staff at the Somerset Wildlife Trust were responsible for operating the cameras, which broadcast a continuous livestream of the nest box to their homepage year-round. Recording of the live stream commenced on May 5th, 2023 and ended on July 3rd, 2023. Approximately 1440 hours of

footage was recorded to be used in my project. From the available footage, data was collected from May 10th to June 11th. The female laid five eggs but only four hatched. The four nestlings survived the entire study period and all successfully fledged.

Duhallow

The nest in Ireland was located in the barony of Duhallow, County Cork, in the south of Ireland. The nest was situated in an old cottage with a straw-thatched roof, beneath a newer iron roof, positioned within a tunnel in the old thatch. Surrounding the nest site, the area forms a mosaic of rough grassland habitat and larger expanses of improved grassland, with some conifer forest plantations and smaller areas of deciduous woodland. Hedgerows in the area are mostly intensely managed and there is no arable farmland. Two cameras were set up, one internal showing the inside of the nest (Figure 5) and one external showing the entrance. The cameras were set up and run by Alan McCarthy and John Lusby of BirdWatch Ireland, with guidance and assistance from Jason Fathers of Wildlife Windows Ltd. The cameras used were standard CCTV cameras, and the video was live streamed to BirdWatch Ireland's YouTube channel. Recording of the live stream commenced on May 5th, 2023 and ended on June 7th, 2023. Approximately 790 hours of footage was recorded to be used in my project. From the available footage, data were collected from the time period of May 5th to June 6th. The female laid five eggs which all hatched and all nestlings survived throughout the study period. However, the female disappeared around June 2nd, leaving the male to care for the nestlings alone. On June 7th, Staff at BirdWatch Ireland took the two youngest nestlings into care due to lack of food. The youngest nestling died soon after, while the other was successfully rehabilitated and released back into the wild in the autumn. The male successfully raised the three remaining chicks to fledging (A. McCarthy, pers. comm).

2.2 Expected prey species

As previous barn owl diet studies have shown the majority of the diet to consist of small mammals (Taylor, 1994; Roulin, 2020), rodents of the families Muridae and Cricetidae, and mammalian insectivores of the family Soricidae were expected to comprise most of the delivered prey items in my study, with species composition depending on presence and distribution in the three countries. In Britain and Ireland, barn owls feed almost exclusively on

small mammals (Glue, 1974). The only representative from the Cricetidae family in Ireland is the introduced bank vole (*Myodes glareolus*), while England additionally has the field vole (*Microtus agrestis*) and the water vole (*Arvicola amphibius*). The water vole has however lately had sharp population declines (Couzens et al., 2021), and was not expected to be abundant in the diet. In the Muridae family, the wood mouse (*Apodemus sylvaticus*), the house mouse (*Mus musculus*), the brown rat (*Rattus norvegicus*) and the black rat (*Rattus rattus*) are found in both countries, while the yellow-necked mouse (*Apodemus flavicollis*) and harvest mouse (*Micromys minutus*) are exclusive to England (Couzens et al., 2021). From the Soricidae family, expected species in England include the common shrew (*Sorex araneus*), pygmy shrew (*Sorex minutus*) and Eurasian water shrew (*Neomys fodiens*) (Glue, 1974). In Ireland, only the pygmy shrew and the newly introduced greater-white toothed shrew (*Crocidura russula*) are present. The invasive greater white-toothed shrew, known for its rapid range expansion, has demonstrated a capacity to drive local populations of pygmy shrew to extinction (Tosh et al., 2008; McDevitt et al., 2014), and has been found in county Cork where the filmed barn owl nest was located. The common frog (*Rana temporaria*) and the common toad (*Bufo bufo*), has also been found in British barn owl pellets, although in much smaller quantities than mammalian prey (Glue, 1974).

In Spain, previous barn owl pellet analyses in the study area have uncovered the most common prey species: the Mediterranean vole (*Microtus duodecimcostatus*) from the Cricetidae family, the house mouse, the Algerian mouse (*Mus spretus*), the wood mouse and the brown rat from the Muridae family, and the greater white-toothed shrew from the Soricidae family. The Iberian green frog (*Pelophylax perezi*) and Iberian spadefoot frog (*Pelobates cultripes*), as well as passerine birds (Passeriformes) were also found as prey in pellets (SEO/BirdLife, 2023).

2.3 Estimation of prey body mass

Prey body mass was estimated for each identified prey group (Table 1). Although each individual prey item will differ from conspecific prey items in terms of body mass, camera monitoring does not allow for distinguishing between individual differences in body mass. All individuals of the same prey group were therefore assigned the same estimated average body mass.

For the prey items identified to a higher level than species, I used the same method as Glåmseter (2019) to estimate body mass. For prey identified to order, family or as one of two potential species, I used the average body mass calculated from all individuals in the relevant group. For the prey that was unidentifiable I used a body mass average based on all identified prey. All body mass average estimates were made separately for each nest.

Table 1: Estimates for prey body mass. For the Eurasian house mouse and Eurasian harvest mouse, the estimates were based on body mass values found in Couzens et al. (2017). Estimates for the greater white-toothed shrew and the Algerian mouse were taken from Palomo et al. (2009) and Balloux et al. (1998). The rest of the prey body mass estimates were based on data from G.A. Sonerud (unpublished data).

Prey	Body mass (g)
Bank vole (<i>Myodes glareolus</i>)	20
Field vole (<i>Microtus agrestis</i>)	30
Water vole (<i>Arvicola amphibius</i>)	100
Wood mouse (<i>Apodemus sylvaticus</i>)	25
House mouse (<i>Mus domesticus</i>)	15
Harvest mouse (<i>Micromys minutus</i>)	10
Algerian mouse (<i>Mus spretus</i>)	16
Brown rat (<i>Rattus norvegicus</i>)	100
Common shrew (<i>Sorex araneus</i>)	10
Greater white-toothed shrew (<i>Crocidura russula</i>)	12
Eurasian water shrew (<i>Neomys fodiens</i>)	15
<i>Microtus</i> sp.	30
Bird (Passeriformes)	10
Common frog (<i>Rana temporaria</i>)	22
Insect	0.1

2.4 Data collection and data processing

The video material used in my study was recorded from their respective live streams and downloaded to three separate external hard drives by Ronny Steen with permission from the respective collaborators. To record the footage, the software OBS Studios (64-bit) version 29.0.2 (Bailey & OBS Studio Contributors, 2023) was used for the nest at Cabaneros, while a custom script that connected to the software FFmpeg (Tomar, 2006) was used for the other

two nest locations. From the downloaded video clips, data was collected using the software BORIS (Behavioral Observation Research Interactive Software) (Friard et al., 2016). From the nest in Cabaneros, both the external and the internal camera angles were used in the same picture frame (Figure 3). For the nests at Somerset and Duhallow, only the internal camera was used as BORIS operated too slow with both video files running in the program (Figures 4 and 5).



Figure 3: Inside and outside view of the nest box at Cabaneros (SEO/BirdLife, 2022).



Figure 4: Inside view of the nest box in Somerset (Somerset Wildlife Trust, 2023)



Figure 5: Inside view of the nest at Duhallow (BirdWatch Ireland, 2023)

For the nest at Cabaneros, the recordings were manually initiated and terminated in OBS Studios at approximately 24-hour intervals. This produced video clips with a duration of between 20 to 30 hours, which was manageable but not optimal for running in the data collection software BORIS, as the large files made the software run slow. Due to interruptions in internet connection, about 80 hours in total of the footage from the Cabaneros nest was lost during the study period. The video clips were saved as .flv files due to the compatibility of such files with both OBS Studios and BORIS. For the nests at Duhallow and Somerset, the recording process was enhanced by using a custom batch script which automatically initiated and terminated the recording sessions every six hours. This method reduced human error and ensured consistent data collection, producing clips with a duration of six hours each, which proved to be significantly easier to run in BORIS. The video clips were saved as .mp4 files, which proved easier to work with than .flv files due to the standard being more universally accepted. Only 10 hours at the Duhallow nest was lost due to internet failure, and no footage was lost at the Somerset nest.

When processing the video files in BORIS for data collection, an individual project file was made for each nest, where each video file was defined as an observation with its own ID. Over the course of approximately ten weeks, the video material was parsed through with a playback speed of about 10 times faster (sometimes up to 14 times faster) than the recording

speed, observing every prey delivery occurring at all times of day. Feeding behavior was recorded as an event when the parent delivered a prey item at the nest. During a feeding event, the video was paused and played back at low speed in order to visually determine the behavior. The following data points were collected for each event: the date and time of delivery (hour and minute), the type of prey (identified to the lowest taxonomic level possible), prey condition (intact, headless, plucked, eaten at), whether the nestlings fed independently or with parental assistance, whether the prey was swallowed whole or dismembered, and whether the prey was stored or ingested right away.

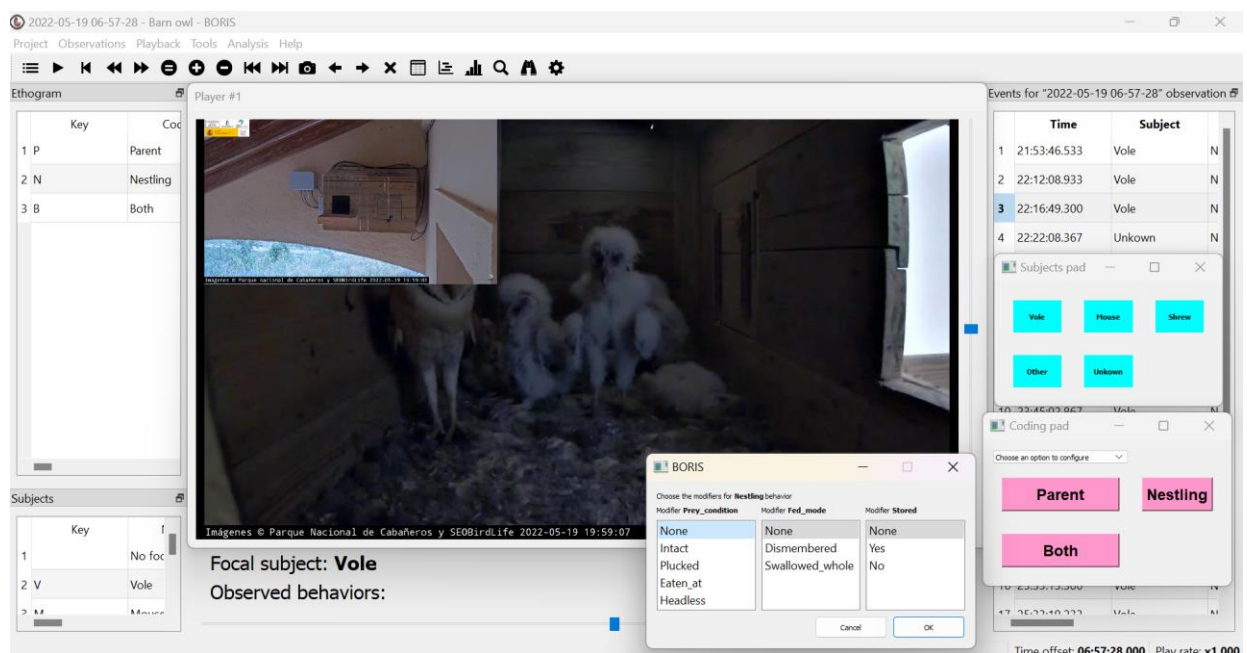


Figure 6: Setup in the data collection software BORIS ((Friard et al., 2016), with observation window displaying the video, coding and subjects pads for recording prey type and handling subject, and behavior modifiers to record condition, mode of feeding and storing.

When a delivery occurred, I first examined whether the prey was delivered intact or decapitated. Further, I examined whether the female would dismember the prey and feed the nestlings (assisted feeding), or if the nestlings would swallow the prey whole or dismember it independently of the female (unassisted feeding). If the prey item was handled right away either by the parent or the nestlings, it was categorized as “not stored”. If the prey item was left in the nest and neither the parent nor the nestling had shown interest in it for the following 15 minutes since delivery, it would be categorized as “stored”. The stored prey items were marked by number to keep track of how they were handled later, however this proved difficult in instances where prey was frequently moved out of sight. In these instances, handling was simply noted as “NA”. Using the time stamp on the video clips for reference, each clip was

given a time offset in BORIS where the time in hours and minutes at the beginning of the clip was added to each recorded event. This method ensured that the number of hours and minutes for each event corresponded with the time of day of the delivery and made the conversion to the correct time easier.

At the end of the data collection, the data points were exported from BORIS as an excel file for processing before being used in statistical analyses.

2.5 Prey identification

The prey was identified visually based on characteristics such as body size, the relative size of eyes and ears, color of the fur, relative tail length and overall appearance. All prey were initially classified into one of five categories: “Mouse” for the family Muridae, “Vole” for the family Cricetidae, “Shrew” for the family Soricidae, “Unknown” for unidentifiable mammalian prey and “Other” for non-mammalian prey (i.e birds and amphibians).

With the help of co-supervisor Geir A. Sonerud, the prey items were again examined after the initial data collection period and identified to the lowest taxonomical level possible, the aim being species level. Using his experience and expertise in identifying rodents and other small mammals, all delivered prey items were thoroughly assessed to obtain the most accurate identification. The identification process proved to be challenging due to variations both in video quality, camera angle and how visible the prey was to the camera. For prey items that were hard to discern, identification was limited to broad categorization, for instance “mammal” or “rodent”. Others could be identified to family level or as one of two species or groups. Particularly shrews and small bank voles turned out to be difficult to distinguish at times when the snout was not visible, as the tail is of approximately the same relative length. These were thus labeled as “shrew/bank vole”. Prey items of the Muridae family were easy to distinguish from the Soricidae and Cricetidae family due to the relative long tail and large ears and could often be excluded when there was uncertainty around a mammalian prey item with low visibility, thus being classified as “shrew/vole”. Within the Muridae family, distinguishing the wood mouse from the yellow-necked mouse was practically impossible, and these were grouped together in their genus *Apodemus*.

Prey identification was particularly challenging for the Cabaneros nest, as the IR-light on the internal camera malfunctioned nine days into the study period. In some instances,

identification was possible from the external camera alone, as prey was occasionally visible when the parents landed on the outer ledge of the nest with the prey held in the beak. Most of the time the parents flew directly into the nest box with the prey not visible from the external camera. A slight light emitted from the IR-light on the external camera reached inside the nest box making some internal identification possible, but most of the prey items could only be identified to levels higher than species. The darkness also made it difficult to see how the prey was handled within the nest. Data on handling and storing is therefore scarcer for the Cabaneros nest compared to the other two nests.

2.6 Nestling age determination

For all locations, nestling age was determined based on the first hatched nestling in the nest box. For the nest at Cabaneros, the cooperators at SEO/BirdLife documented the precise hatching dates of all 6 eggs, and determined the first hatching to occur on April 19th, 2022 and the last hatching to occur on May 2nd, 2022 (SEO/BirdLife, 2023). Using the first hatching as an age determinant, the age of the nestlings was then estimated to be 22 days at the start of the monitoring period on May 10th, 2022.

With the help from eager barn owl enthusiasts, I was able to retrieve the date for the first hatching from the nest in Somerset from the comment section log on the livestream and determine this to be May 1st, 2023. By my own observation, the last of the four eggs hatched on May 12th, 2023. The age of the nestlings was thus determined to be 10 days at the start of the video monitoring on May 10th, 2023.

With information given by cooperator Alan McCarthy from Birdwatch Ireland, the first and last nestling at the Duhallow nest site was determined to have hatched on May 3rd, 2022, and May 11th, 2022 respectively. Nestling age was thus determined to be 2 days at the start of the monitoring period on May 5th, 2023.

2.7 Statistical analysis

All statistical analyses were performed using the software R version 4.3.1 (R Core Team, 2023). Using the package “Activity” (Rowcliffe, 2023), diel activity curves were made for

each nest separately, both for total number of deliveries and separate for the most common prey families. The R package “suncalc” (Thieurmel & Elmarhraoui, 2022) was used to obtain an estimation of average sunset and sunrise times for the monitoring period for the different locations based on coordinates and time zones. The “plot”-function in base R was used for graphical presentation.

To investigate overlap in activity between the three locations, the package “Overlap” (Meredith et al., 2024) was used to create kernel density curves for pairwise comparison of activity between the nest locations. I used the coefficient of overlap (Δ_4), known as Dhat4 in R, to quantify the overlap (Ridout & Linkie, 2009) using the function “overlapEst”. Δ_4 ranges from 0 (no overlap) to 1 (complete overlap), with values > 0.75 indicating a high degree of overlap (Monterroso et al., 2014). The Watson-Wheeler test from the package “circular” (Agostinelli & Lund, 2023) was used to test for any significant differences in activity patterns between the nest locations.

To test whether the probability of hunting certain prey differed as the nestlings grew older, I used a multinomial log-linear model from the package “nnet” (Ripley & Venables, 2023). Prey family was set as the response variable, with the three most common prey families included (Muridae, Cricetida and Soricidae), and nestling age (days) was set as the explanatory variable.

Generalized linear effect models with binomial distributions (logistic regression) were used to explain the probability of prey being stored inside the nest cavity and the probability of assisted feeding. For both analyses, nestling age, prey family and the interaction term were set as explanatory variables. Both analyses were run for each nest location separately. For each analysis, four alternative models were tested for best fit with the explanatory variables; nestling age only, prey family only, nestling age and prey family, and the interaction between nestling age and prey family. To assess the statistical significance of nestling age on the probability of storing and independent feeding on prey from different families, and the difference between these families, I used the “relevel” function from base R to set each family as the intercept.

To test how prey delivery rates would change as the nestlings aged, I used a linear regression model with number of prey per day per nestling as response variable and nestling age and the quadratic term (nestling age)² as explanatory variables. The quadratic term was included to test for non-linearity as shown in Steen et al. (2010). Each nest was tested separately.

For analyses with alternative models containing different combinations of explanatory variables and interaction terms, I used the Akaike Information Criterion (AIC) (Akaike, 1978) for model comparison and selection with the R package “AICcmodavg” (Mazerolle, 2023). The model with the lowest AIC-score was selected as the best model.

2.8 Estimation of daytime and nighttime

Sunset and sunrise times were estimated as an average for the whole study period at each location using the package “suncalc” and the function “getSunlightTimes”. Average sunset and sunrise times were 21:30 and 06:58 for Cabaneros, 21:07 and 05:13 for Somerset, and 21:36 and 05:29 for Duhallow respectively. Using these estimates, nighttime and daytime were defined. For Cabaneros, nighttime was defined as 21:30 – 06:59 and daytime was defined as 07:00 to 21:29. For Somerset, nighttime was defined as 21:10 – 05:15 and daytime was defined as 05:16 - 21:09. For Duhallow, nighttime was defined as 21:35 – 05:30 and daytime was defined as 05:31 – 21:34.

2. RESULTS

3.1 Prey choice

A total of 1500 prey deliveries were observed across all three nest locations. Of all deliveries, 94.5% were identified as mammalian, of which 79.1% were rodents, 14.9% were shrews and 6.0% were unidentified mammals. A total of 73 prey items (4.9%) could not be identified at all due to poor video quality or high nest activity. Of non-mammalian prey groups, birds, amphibians and insects, constituted less than 0.7% of the total (Appendix 3).

In Cabaneros, mammalian prey accounted for 98.6% of the 660 prey items that could be identified, of which 86.5% were rodents of the families Muridae and Cricetidae, and 4.2% were shrews of the family Soricidae. The most common prey items were voles of the genus *Microtus* (44.7%), followed by the wood mouse (25.0%). Other rodents included the Algerian mouse (1.7%), the brown rat (0.1%), and rodent prey where species could not be conclusively

identified (7.3%). The greater white-toothed shrew was the only species of the Soricidae family delivered, constituting 3.9% of the total (Table 2).

For the nest in Somerset, all 361 delivered prey items were mammalian, with 97.0% being rodents of the families Muridae and Cricetidae, and 2.8% being shrews of the family Soricidae. The most common prey species delivered was the wood mouse (49.9%), followed by the field vole (40.7 %) (Table 3). From the Soricidae family, the common shrew was the only representative (2.8%). The rest of the identifiable prey items were bank voles (2.2%) and brown rats (0.6%).

At the Duhallow nest, 99.7% of the 405 delivered prey items that could be identified were mammalian, with rodents of the families Muridae and Cricetidae constituting 47.5%, and shrews of the family Soricidae constituting 40.7 % of the total deliveries. The most common prey item for the nest in Duhallow was the greater white-toothed shrew (40.7%), followed by the bank vole (25.5%) and the wood mouse (16.0%). Of the rarer deliveries were brown rats (3.7%) and one delivery of the common frog. 32 prey items (7.5%) could only be identified as mammalian, and 22 prey items (5.1%) could not be identified at all (Table 4).

At the Duhallow nest, there were six instances where prey was still alive when delivered and managed to escape before being eaten (five bank voles and one greater white-toothed shrew). In four instances, one of the parents were observed swallowing the prey inside the nest cavity. These were all omitted from the total count and further analyses.

Table 2: Prey deliveries at the Cabaneros nest location given as number of each prey type, percentage by number, estimated body mass, total body mass and percentage by body mass. All digits are rounded to one decimal place.

Prey item	Number	Percentage by number (%)	Estimated body mass (g)	Total body mass (g)	Percentage by mass (%)
Greater white-toothed shrew (<i>Crocidura russula</i>)	28	3.9	12.0	336.0	1.7
<i>Microtus</i> sp.	318	44.7	30.0	9540.0	47.8
Wood mouse (<i>Apodemus sylvaticus</i>)	178	25.0	25.0	4450.0	22.3
Algerian mouse (<i>Mus spretus</i>)	12	1.7	16.0	192.0	1.0
Wood mouse/Algerian mouse	4	0.6	24.4	97.6	0.5
Brown rat (<i>Rattus norvegicus</i>)	7	0.1	100.0	700.0	3.5
Muridae sp.	1	0.1	27.1	27.1	0.1
Unidentified rodent (Rodentia)	51	7.2	29.3	1494.3	7.5
Unidentified mammal (Mammalia)	52	7.3	28.5	1482.0	7.4
Bird (Passeriformes)	8	1.1	10.0	80.0	0.4
Insect	1	0.1	0.1	0.1	0.0005
Unidentified prey	52	7.3	30.0	1560.0	7.8
Total	712	100	-	19959.1	100

Table 3: Prey deliveries at the Somerset nest location given as number of each prey type, percentage by number, estimated body mass, total body mass and percentage by body mass. All digits are rounded to one decimal place.

Prey item	Number	Percentage by number (%)	Estimated body mass (g)	Total body mass (g)	Percentage by mass (%)
Common shrew (<i>Sorex araneus</i>)	10	2.8	10.0	100.0	1.0
Bank vole (<i>Myodes glareolus</i>)	8	2.2	20.0	160.0	1.6
Field vole (<i>Microtus agrestis</i>)	147	40.7	30.0	4410.0	45.1
Unidentified vole (Cricetidae)	7	1.9	29.5	206.5	2.1
Wood mouse (<i>Apodemus sylvaticus</i>)	180	49.9	25.0	4500.0	46.1
Brown rat (<i>Rattus norvegicus</i>)	2	0.6	100.0	200.0	2.0
Unidentified rodent (Rodentia)	6	1.7	27.5	165.0	1.7
Unidentified mammal (Mammalia)	1	0.3	27.0	27.0	0.3
Total	361	100	-	9768.5	100

Table 4: Prey deliveries at the Duhallow nest location given as number of each prey type, percentage by number, estimated body mass, total body mass and percentage by body mass. All digits are rounded to one decimal place.

Prey item	Number	Percentage by number(%)	Estimated body mass (g)	Total body mass (g)	Percentage by mass (%)
Greater white-toothed shrew (<i>Crocidura russula</i>)	174	40.7	12.0	2088.0	23.8
Bank vole (<i>Myodes glareolus</i>)	110	25.8	25.0	2200.0	25.1
Wood mouse (<i>Apodemus sylvaticus</i>)	71	16.6	25.0	1800.0	20.5
Brown rat (<i>Rattus norvegicus</i>)	16	3.7	100.0	1500.0	17.1
Wood mouse/Brown rat	1	0.2	38.8	38.8	0.4
Unidentified mammal (Mammalia)	32	7.5	20.7	662.4	7.5
Common frog (<i>Rana temporaria</i>)	1	0.2	22.0	22.0	0.6
Unidentified prey	22	5.2	20.7	455.4	5.2
Total	427	100	-	8766.6	100

3.1.1 Prey choice and nestling age

For the nests in Cabaneros and Somerset, nestling age had a positive effect on the predicted probabilities of prey delivery from the Cricetidae family, a marginally positive effect on prey delivery from the Soricidae family, and a negative effect on prey delivery from the Muridae family (Figure 7). However, the ANOVA type II test from the multinomial regression analysis showed that the effect of nestling age on the predicted probabilities of delivery of prey from the most common prey families (Cricetidae, Muridae and Soricidae) was not significant for Cabaneros (Appendix 5), and only almost significant for Somerset (Appendix 6). For the nest in Duhallow, the effect of nestling age had a strong positive effect on predicted probability of delivery of prey from the Muridae family, and a negative effect on the probability of delivery from the Cricetidae and Soricidae families (Figure 7). For Duhallow, the effect was significant (Appendix 7).

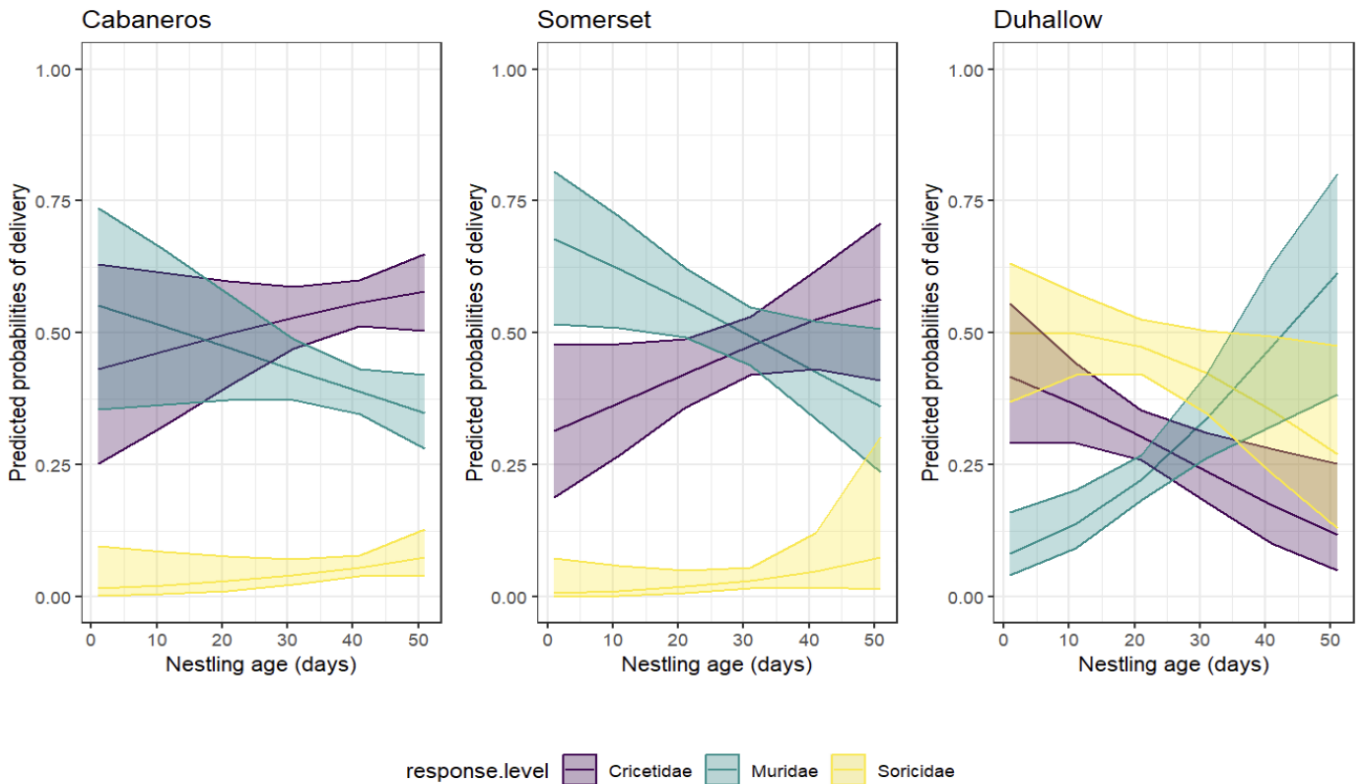


Figure 7: The predicted probabilities of delivery of prey from the families Cricetidae, Muridae and Soricidae at each location as a function of nestling age (days). The solid line represents the predicted probability for delivery of each family and the shaded area represents the confidence intervals.

3.2 Diel activity

Distribution curves for prey deliveries in relation to the time of day show a clear and strict nocturnal pattern for all three locations (Figure 8) and across all three of the most common prey families (Figure 9). There were no prey delivery activity during the daytime hours for any of the nests. At all nests, activity peaked between the hours of approximately 23:00 and 02:00. Prey deliveries commenced at sunset and ended at sunrise at all locations. At Somerset and Duhallow, prey delivery rate dropped to zero at around 05:00, while at Cabaneros there was a slightly longer activity period with some prey being delivered up until 07:00.

Deliveries of prey in the families Cricetidae, Muridae and Soricidae show the same nocturnal pattern individually as the total deliveries across all nests (Figure 9). For Somerset and Duhallow, there was a slight difference in the activity peaks for Muridae and Cricetidae, with Muridae deliveries peaking between the hours 23:00 and 24:00 and Cricetidae peaking

between the hours 01:00 and 02:00 in both locations. In Cabaneros, Cricetidae and Muridae both peaked between 23:00 and 01:00 (Figure 9).

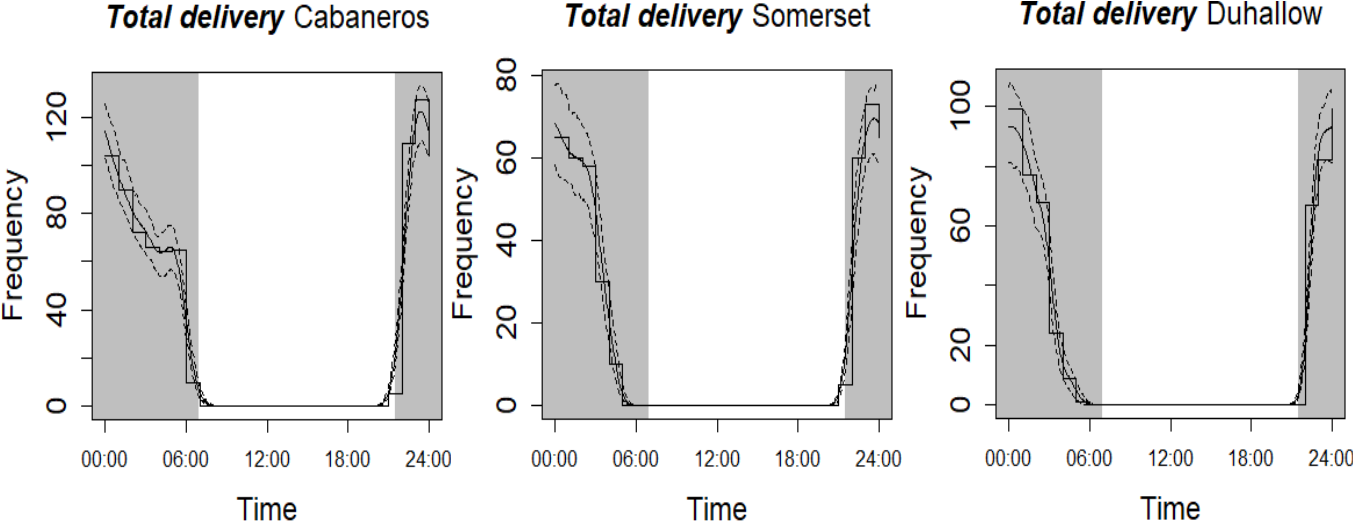


Figure 8: Curves showing the distribution of delivery for all prey items for each barn owl nest location during a 24-hour cycle. The shaded areas denote time blocks that are considered night time. The dotted lines represent the confidence intervals.

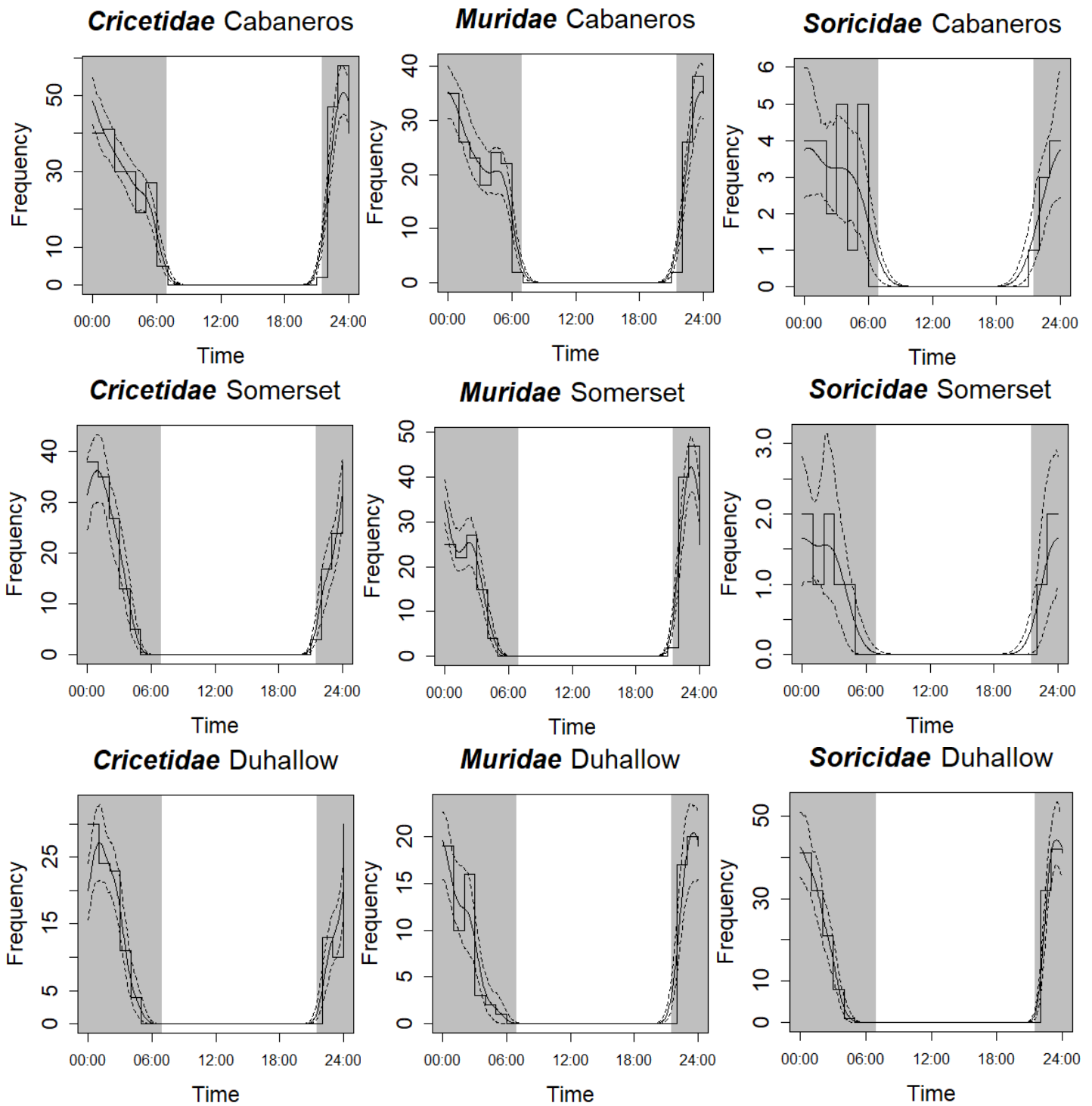


Figure 9: Curves showing the distribution of delivery for the most commonly delivered prey families for each barn owl nest location during a 24-hour cycle. The shaded areas denote time blocks that are considered night time. The dotted lines represent the confidence intervals.

3.2.1 Overlap

Overlap in diel activity was calculated for each pair of locations (Figure 10). All location pairs had a high degree of overlap, with Dhat4-values exceeding 0.75. Somerset and Duhallow showed the most overlap, while Cabaneros and Duhallow showed the least overlap (Table 5). The Watson-Wheeler test revealed that hunting activity patterns differed significantly between all location pairs, but with a smaller difference between Somerset and Duhallow than between the other location pairs (Table 6). While the main activity period started at approximately the same time, Cabaneros exhibited a lower hunting effort per hour, but a longer activity period, than the other two locations (Figure 10).

Table 5: Dhat4 overlap indexes for the pairwise comparison of diel activity between the nest locations.

Location pair	Dhat4
Cabaneros vs. Duhallow	0.78
Cabaneros vs. Somerset	0.82
Somerset vs. Duhallow	0.92

Table 6: Pairwise analysis of the difference in diel activity between the nest locations using Watson-Wheeler test for homogeneity.

Location pair	W	df	P
Cabaneros vs. Duhallow	60.83	2	<0.001
Cabaneros vs. Somerset	24.51	2	<0.001
Somerset vs. Duhallow	7.27	2	0.02

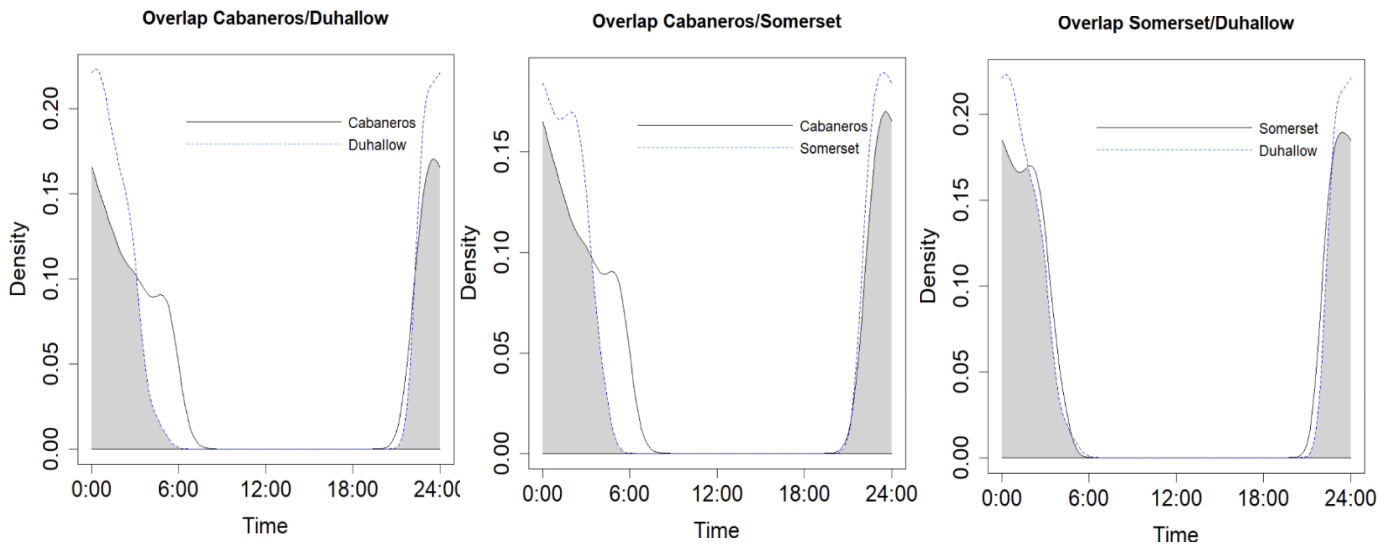


Figure 10: Overlap plots showing pairwise comparisons of kernel density curves for prey delivery at the three barn owl nest locations. The shaded area represents where prey delivery activity overlaps in time and density.

3.3 Prey handling

3.3.1 Prey condition

Of the 1455 prey items where condition could be determined, 99.0% were delivered intact. Only eight prey items in total were delivered decapitated. These included two birds in Cabaneros, one wood mouse, one field vole and one brown rat in Somerset, and three brown rats in Duhallow. Six prey items were delivered still alive. This included five bank voles and one greater white-toothed shrew, which were all delivered at the Duhallow nest. Condition could not be determined for 51 of the prey items (Table 8).

Table 8: Summary of prey condition for all delivered prey items where condition could be determined.

Prey condition	Number	Percentage (%)
Intact	1441	99.03
Decapitated	8	0.55
Alive	6	0.41
Total	1455	100.00

3.3.2 Probability of storing

For all nests, nestling age had an almost consistent negative effect on the predicted probability of prey being stored inside the nest cavity. For the nest in Cabaneros, the model with the interaction between nestling age and prey family was the best fit (see Appendix 9 for model comparison). As nestlings grew older, the probability of a delivered prey being stored decreased for prey items of the families Muridae and Soricidae, while the probability of a delivered prey of the Cricetidae family being stored increased slightly, as shown in the best fitted model (Figure 11). However, nestling age was only a significant predictor on the probability of storing prey of the Muridae family (Appendix 12) but was not a significant predictor on the probability of storing prey of the Soricidae family (Appendix 13) or of the Cricetidae family (Table 9). The overall probability of storing, regardless of nestling age, was significantly higher for prey of the Muridae family compared to prey of the Cricetidae family (Table 9), but there were no significant difference between the Soricidae and Muridae families, or between the Soricidae and Cricetidae families (Appendix 13). The results from Cabaneros are however likely to be biased, as the malfunctioning camera light made it challenging to observe how the prey items were handled by the nestlings, especially as they grew larger and started to block the camera. Therefore, most of the data on prey handling and storing from the late part of the study period was marked as missing values (“NA”) and it is likely that this has affected the results.

For the nest in Somerset, the model with nestling age and prey family as predictor variables was the best fitted model (see Appendix 10 for model comparison). As nestlings grew older the probability of a prey being stored decreased across all families (Figure 12), and nestling age had a significant negative effect on the probability of a prey item being stored for prey of all the most common families ($p < 0.0001$ for the families Cricetidae, Muridae and Soricidae). Comparisons on storing probability between the families showed no significant differences on the probability of storing between Soricidae and Muridae (Appendix 14 and 15) or Soricidae and Cricetidae (Table 10), but there was a significant difference between Muridae and Cricetidae (Table 10). The probability of storing prey from the Cricetidae family is slightly higher than for the Muridae family at any given nestling age (Figure 12).

For the nest in Duhallow, the model with nestling age and prey family as predictor variables was the best fitted model (see Appendix 11 for model comparison). As nestlings grew older the probability of a prey being stored decreased across all families (Figure 13), and nestling

age had a significant negative effect on the probability of a prey item being stored for prey of all the most common families ($p < 0.0001$ for the families Cricetidae, Muridae and Soricidae). Comparisons on storing probability between the families showed no significant difference on the probability of storing between prey of the families Cricetidae and Muridae (Table 11), but there was a significant difference between Soricidae and Cricetidae, and between Soricidae and Muridae (Appendix 17). The probability of storing prey from the Soricidae family is lower than for prey of both the Cricetidae and Muridae family at any given nestling age (Figure 13).

Table 9: Parameter estimates of the best fitted model for the effect of nestling age and prey family on the probability of a delivered prey being stored for the barn owl nest in Cabaneros ($n = 459$). Intercept = Cricetidae family.

	Estimate	Std. error	z	P-value
(Intercept)	-1.06	0.70	-1.52	0.126
Nestling age	0.01	0.02	0.48	0.629
Prey family Muridae	2.83	0.98	2.89	0.003
Prey family Soricidae	2.07	2.60	0.79	0.424
Nestling age:Prey family Muridae	-0.07	0.02	-3.05	0.002
Nestling age:Prey family Soricidae	-0.08	0.07	-1.16	0.243

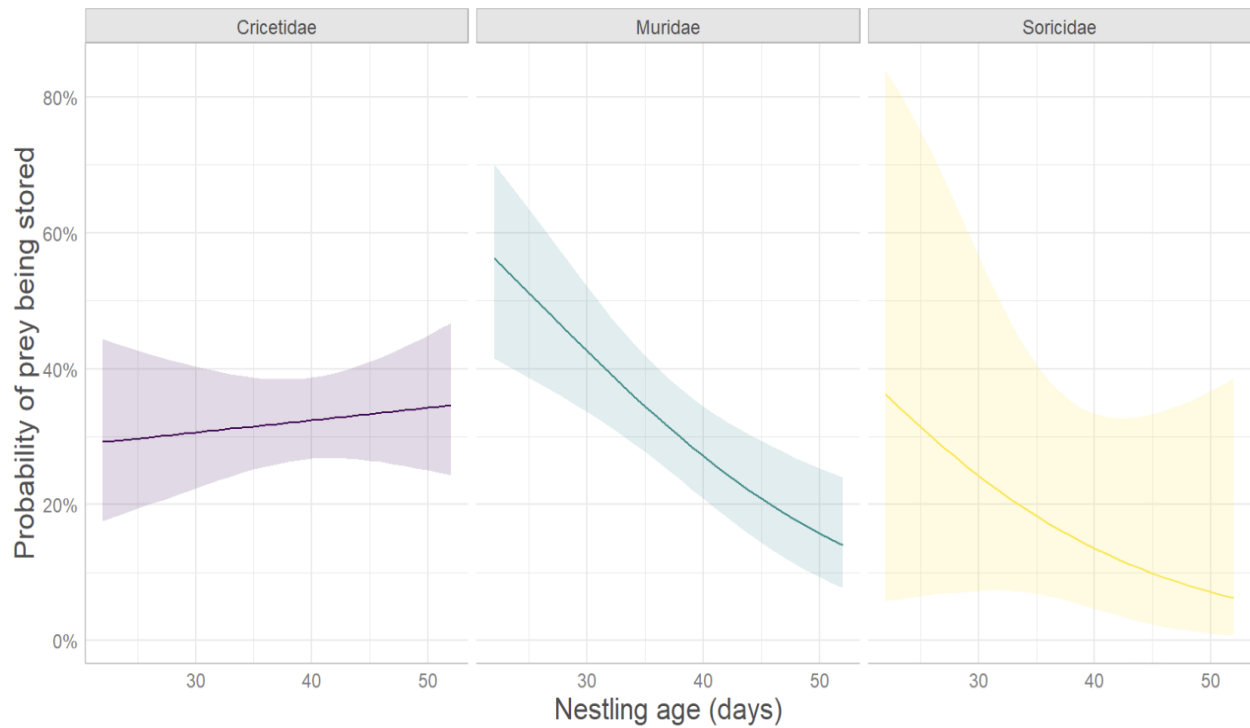


Figure 11: Predicted probability of a delivered prey being stored inside the barn owl nest cavity as an effect of prey family and nestling age in Cabaneros. The solid lines are the predicted probabilities, and the shaded areas are the 95% confidence intervals.

Table 10: Parameter estimates of the best fitted model for the effect of nestling age and prey family on probability of storing for the barn owl nest in Somerset (n = 347). Intercept = Cricetidae family.

	Estimate	Std. error	z	P-value
(Intercept)	3.73	0.50	7.38	<0.001
Nestling age	-0.10	0.01	-6.86	<0.001
Prey family (Muridae)	-0.73	0.25	-2.91	<0.001
Prey family (Soricidae)	-1.46	0.78	-1.87	0.061

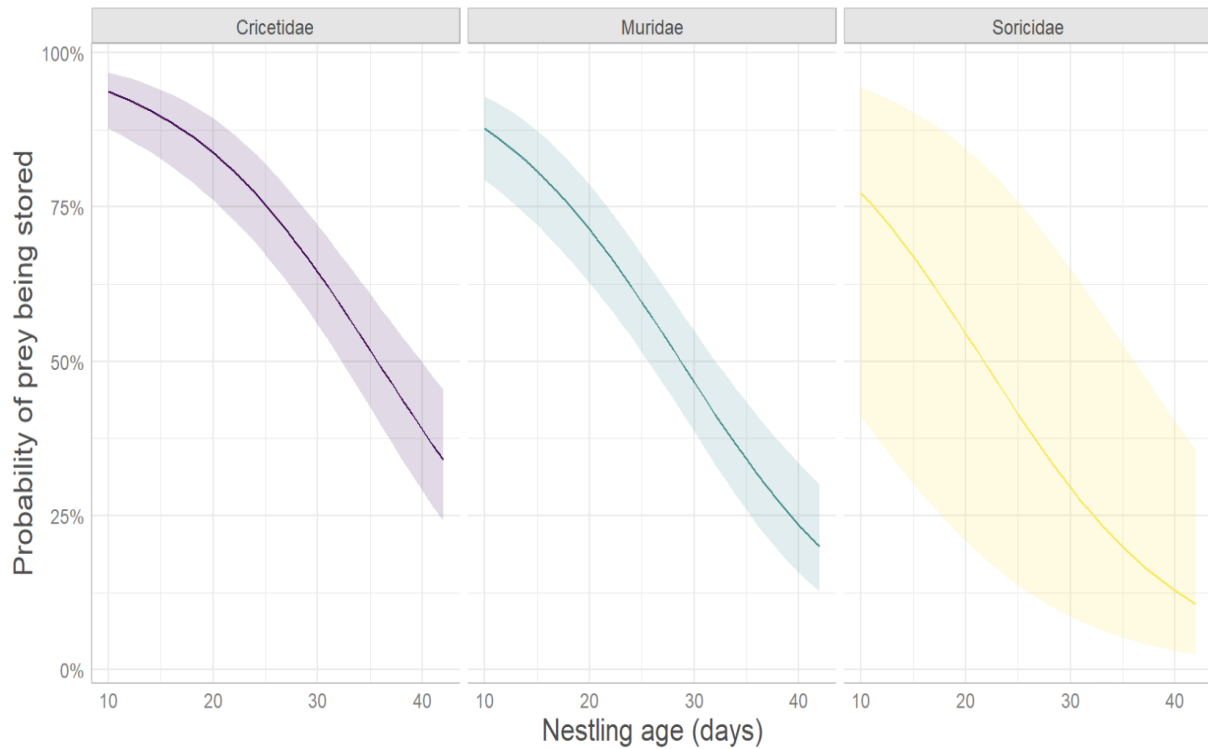


Figure 12: Predicted probability of a delivered prey being stored inside the nest cavity as an effect of prey family and nestling age for the barn owl nest in Somerset. The solid line is the predicted probabilities, and the shaded areas are the 95% confidence intervals.

Table 11: Parameter estimates of the bests fitted model for the effect of nestling age and prey family on the probability of a delivered prey being stored for the barn owl nest in Duhallow (n = 369). Intercept = Cricetidae family

	Estimate	Std. error	z	P-value
(Intercept)	3.27	0.45	7.18	<0.001
Nestling age	-0.17	0.02	-8.84	<0.001
Prey family (Muridae)	0.63	0.35	1.81	0.070
Prey family (Soricidae)	-0.91	0.31	-2.96	0.003

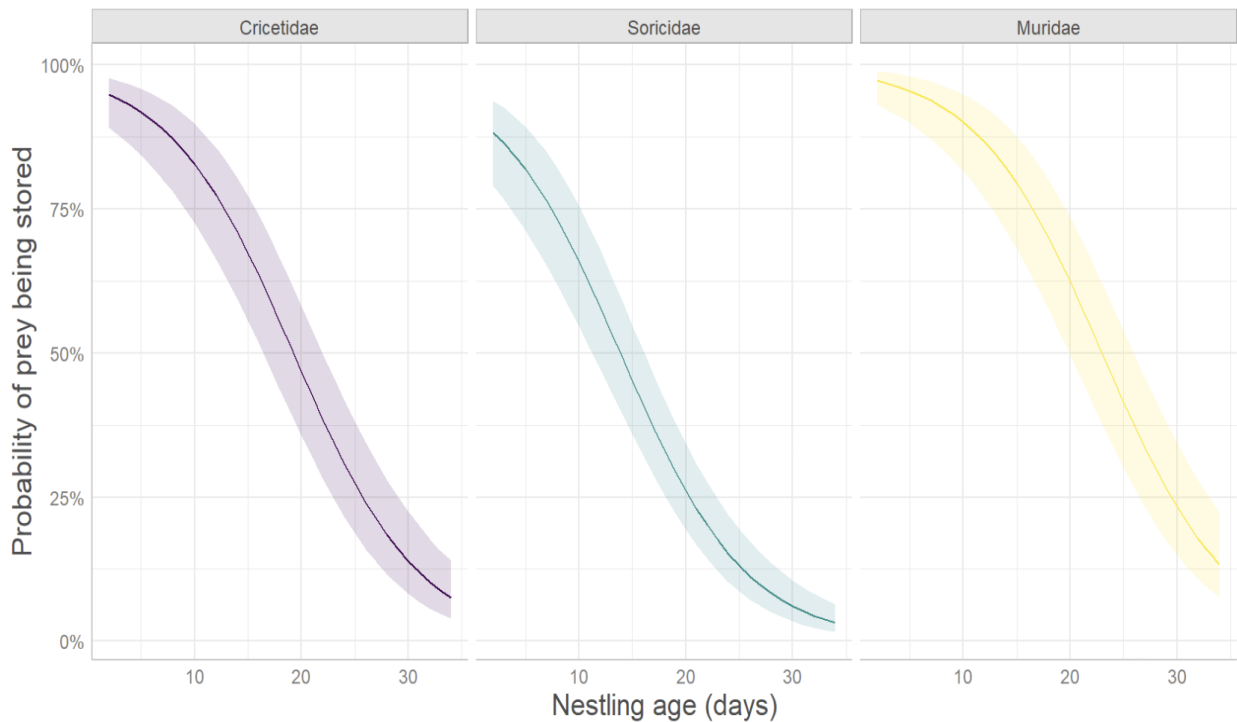


Figure 13: Predicted probability of a delivered prey being stored inside the nest cavity as an effect of prey family and nestling age for the barn owl nest in Duhallow. The solid line is the predicted probabilities, and the shaded areas are the 95% confidence intervals.

3.3.3 Independent feeding

For the nest in Cabaneros, filming started when the nestlings were 22 days old and too few events of assisted feeding were observed to run any statistical tests. Assisted feeding occurred a total of six times, each when the nestlings were 23 days old. From 23 days old and to the end of the study period, the nestlings fed independently.

For the two other nests, four models to explain the probability of assisted feeding were tested for best fit. With the response variable being assisted feeding, the predictor variables tested were nestling age and prey family, the interaction between nestling age and prey family, nestling age only and prey family only.

For the nest in Somerset, the model with nestling age only had the lowest AIC-score and was selected as the best model (see Appendix 18 for model comparison). Nestling age had a significant negative effect on the probability of assisted feeding (Table 12). The model with nestling age and prey family was selected as the second-best model and is also presented

below. Nestling age had a significant negative effect on the probability of assisted feeding for all prey families ($p < 0.0001$ for prey families Cricetidae, Muridae and Soricidae respectively), with no significant difference between the families (Appendix 20-22). The nestlings had a 50% probability of feeding unassisted at 22 days old and estimated complete independent feeding at 35 days old (Figure 14).

For the nest in Duhallow, the model with nestling age and prey family had the lowest AIC-score and was selected as the best model (see Appendix 19 for model comparison). Nestling age had a significant negative effect on the probability of assisted feeding for all prey families ($p < 0.0001$ for prey families Cricetidae, Muridae and Soricidae respectively). No significant difference on probability of independent feeding between prey families Muridae and Cricetidae was observed (Table 13), but there was a significant difference between Soricidae and Cricetidae, and between Soricidae and Muridae (Appendix 25). The probability of nestlings ingesting shrews of the family Soricidae assisted decreased faster as they aged than for the families Cricetidae and Muridae (Figure 16). The model with nestling age only is also presented below for comparison, although not being the best model. The nestlings had a 50% probability of feeding unassisted at 16 days old and estimated complete independent feeding at 25 days old (Figure 17).

Table 12: Parameter estimates of the best fitted model for the effect of nestling age on probability of assisted feeding for the barn owl nest in Somerset ($n = 312$).

	Estimate	Std. error	z	P-value
(Intercept)	7.95	1.04	7.65	< 0.001
Nestling age	-0.36	0.04	-8.26	< 0.001

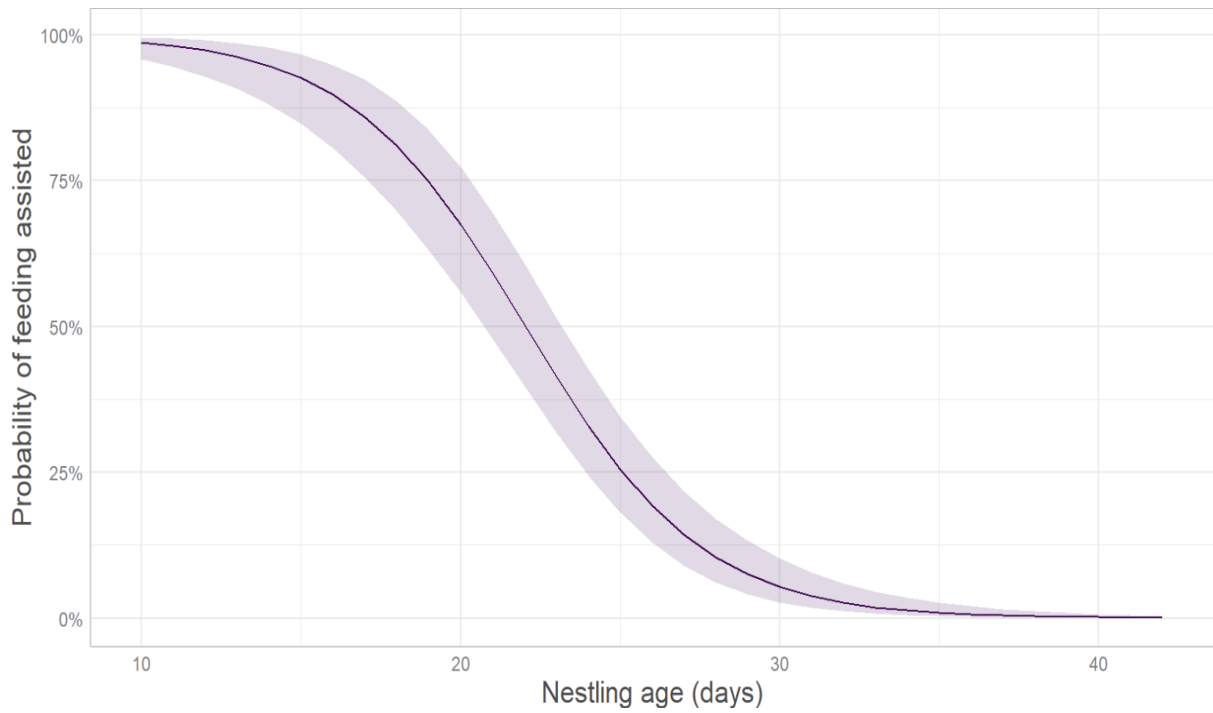


Figure 14: Predicted probability of a prey being fed to the nestlings assisted as an effect of nestling age at the barn owl nest in Somerset. The solid line is the predicted probabilities, and the shaded area is the 95% confidence interval.

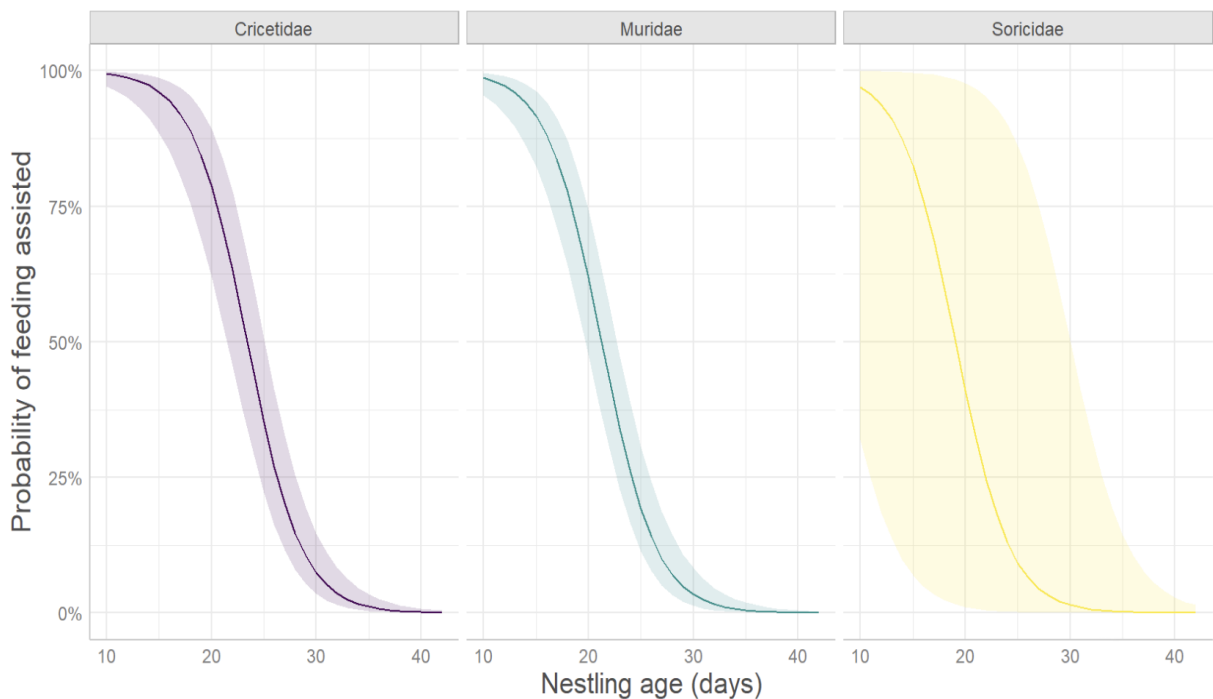


Figure 15: Predicted probability of a prey being fed to a nestling assisted as an effect of nestling age and prey family at the barn owl nest in Somerset. The solid lines are the predicted probabilities, and the shaded areas are the 95% confidence intervals.

Table 13: Parameter estimates of the best fitted model for the effect of nestling age and prey family on probability of assisted feeding at the barn owl nest in Duhallow (n = 370). Intercept = Cricetidae family.

	Estimate	Std. error	z	P-value
(Intercept)	9.67	1.34	7.22	<0.001
Nestling age	-0.55	0.07	-8.17	<0.001
Prey family (Muridae)	1.12	0.65	1.74	0.082
Prey family (Soricidae)	-1.76	0.60	-2.92	0.003

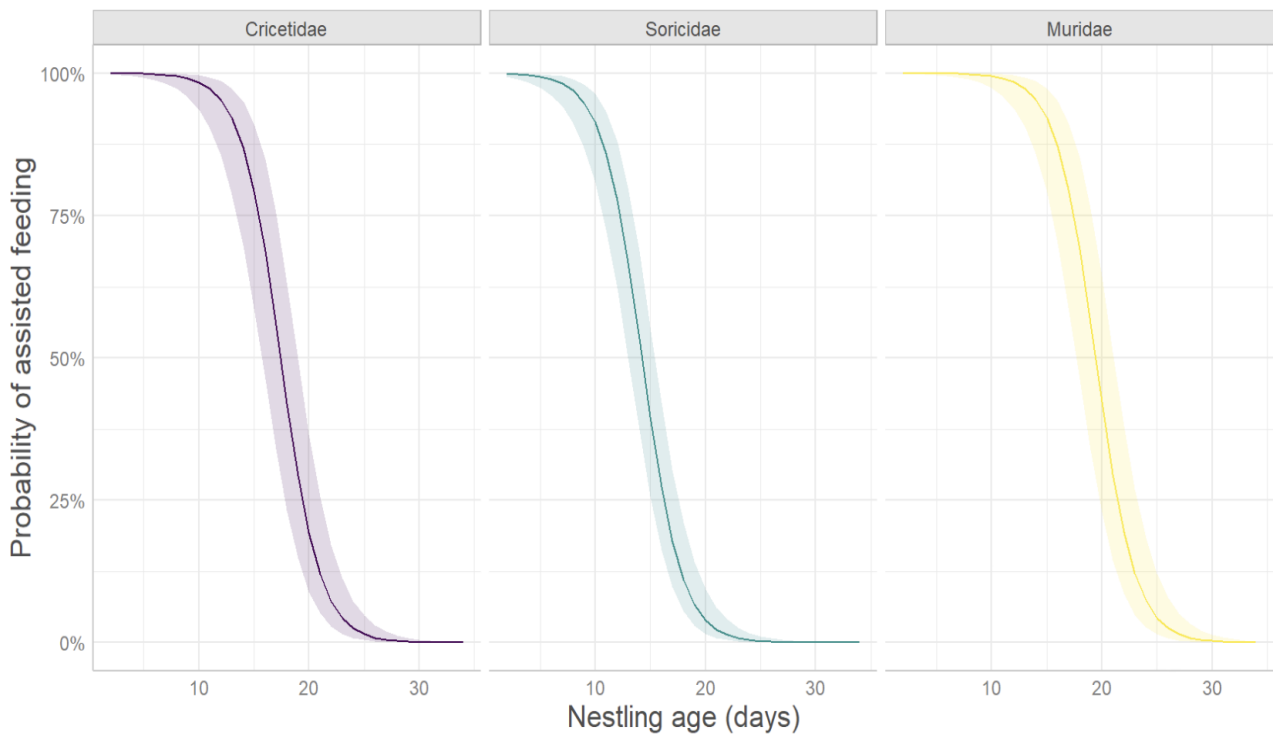


Figure 16: Predicted probability of a prey being fed to a nestling assisted as an effect of nestling age and prey family at the barn owl nest in Duhallow. The solid lines are the predicted probabilities, and the shaded areas are the 95% confidence intervals.

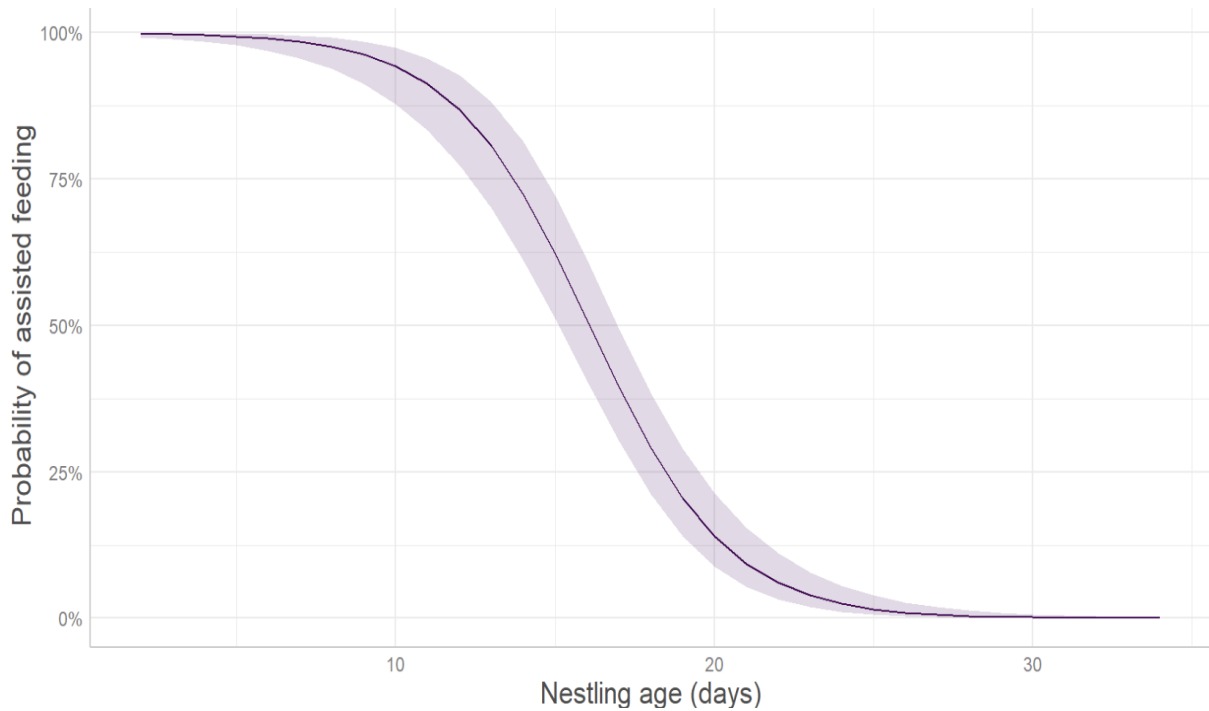


Figure 17: Predicted probability of a prey being fed to a nestling assisted as an effect of nestling age at the barn owl nest in Duhallow. The solid line is the predicted probabilities, and the shaded area is the 95% confidence interval.

3.4 Prey delivery rates

Daily delivery rates were defined as number of prey items delivered per 24-hour cycle, between the hours 00:00 and 23:59. In total, the daily delivery rates varied from two to 37 prey items. In Cabaneros, the highest number of prey delivered in one day was 37, and occurred when the nestlings were 43 days old. In Somerset, the highest number of prey delivered was 16 and occurred when the nestlings were 33 days old. In Duhallow, the highest number of prey delivered was 21 and occurred when the nestlings were 29 days old (Appendix 26). Mean daily delivery rates were 27.18 for Cabaneros, 11.09 for Somerset and 13.46 for Duhallow (Appendix 26). The nest at Cabaneros had the highest mean number of prey items per nestling per day, with 4.53, followed by Somerset with 2.77 and Duhallow with 2.69 (Appendix 26).

The linear regression model revealed a non-linear relationship between number of prey items delivered per day per nestling and nestling age. Both nestling age and the quadratic term (nestling age)² had a significant effect on predicted prey deliveries for the nest at Somerset (Table 14) and Duhallow (Table 15), indicating that as the nestlings aged there was an initial

rise in prey deliveries, but this rate of increase gradually declined over time. None of the predictors were significant for the nest at Cabaneros (Table 13). Delivery rates start to plateau at about 45, 35 and 30 days for Cabaneros, Somerset and Duhallow respectively. (Figure 18, 19 and 20).

Table 13: Parameter estimates of the linear model for the effect of nestling age on daily prey delivery rates at the barn owl nest in Cabaneros

	Estimate	Std. error	t	P-value
(Intercept)	-1.85	5.55	-0.33	0.743
Nestling age	0.27	0.29	0.94	0.362
(Nestling age) ²	-0.00	0.00	-0.73	0.475

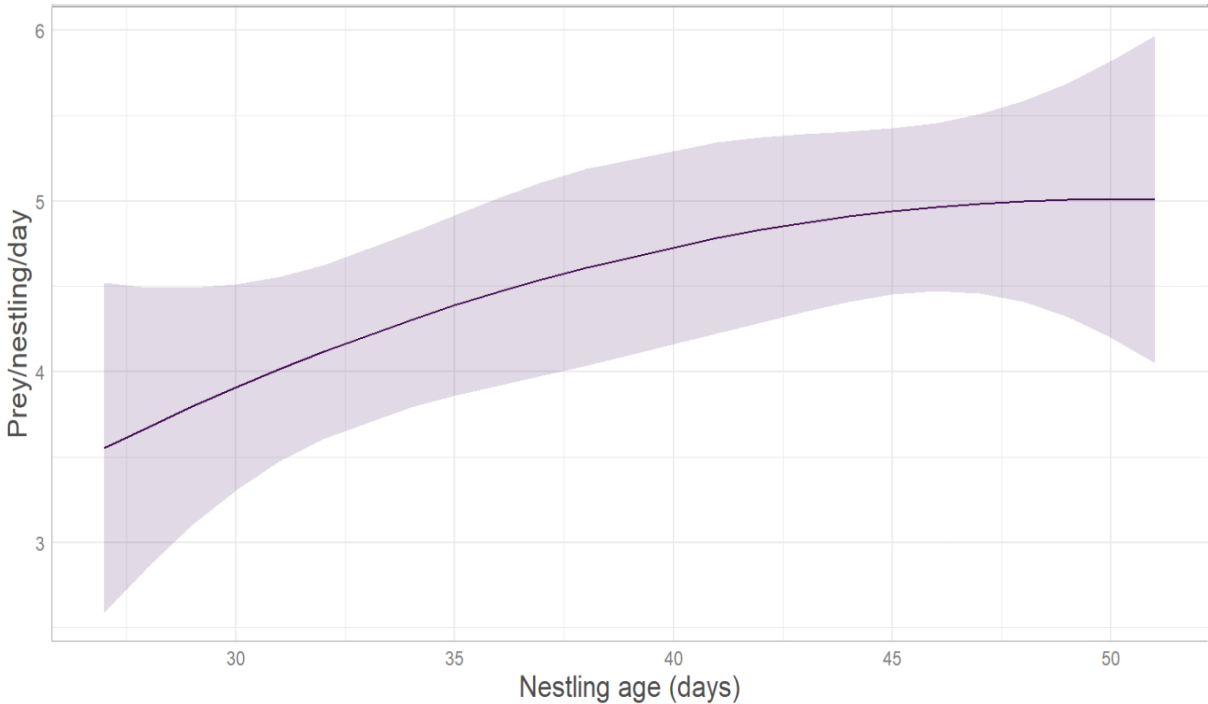


Figure 18: Predicted prey delivery rate per nestling per day as a function of nestling age for the barn owl nest in Cabaneros. The solid line represents the predicted delivery rate, and the shaded area represents the 95% confidence interval.

Table 14: Parameter estimates of the linear model for the effect of nestling age and the quadratic term nestling age² on daily prey delivery rates at the barn owl nest in Somerset.

	Estimate	Std. error	t	P-value
(Intercept)	-0.58	0.72	-0.80	0.427
Nestling age	0.22	0.06	3.56	0.001
(Nestling age) ²	-0.00	0.00	-2.51	0.018

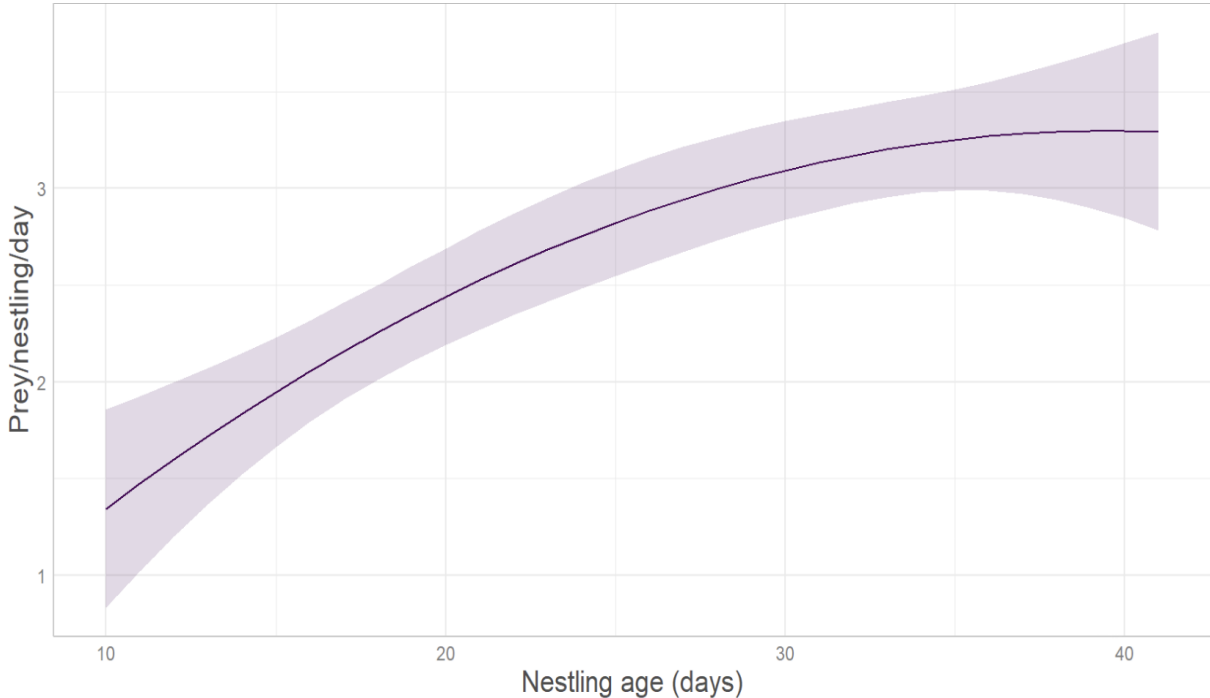


Figure 19: Predicted prey delivery rate per nestling per day as a function of nestling age for the barn owl nest in Somerset. The solid line represents the predicted delivery rate, and the shaded area represents the 95% confidence interval.

Table 15: Parameter estimates of the linear model for the effect of nestling age and the quadratic term nestling age² on daily prey delivery rates at the barn owl nest in Duhallow.

	Estimate	Std. error	t	P-value
(Intercept)	-0.00	0.45	-0.01	0.995
Nestling age	0.23	0.06	4.07	0.0003
(Nestling age) ²	-0.00	0.00	-2.38	0.025

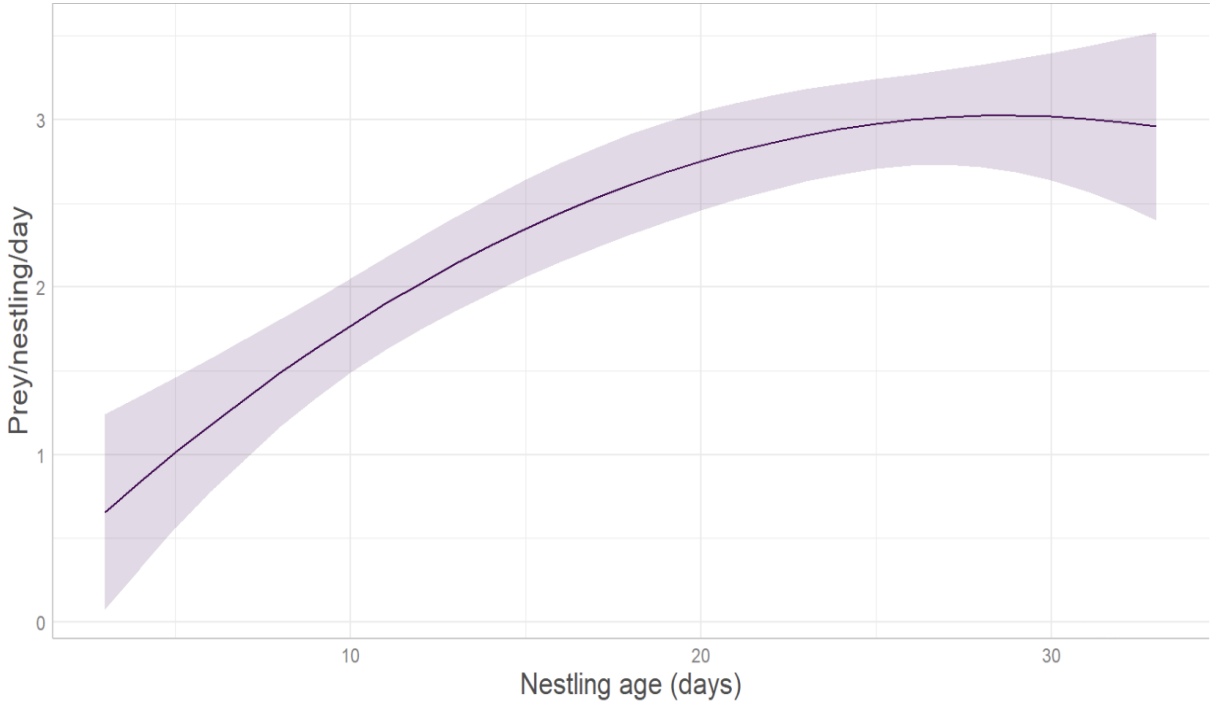


Figure 20: Predicted prey delivery rate per nestling per day as a function of nestling age for the barn owl nest in Duhallow. The solid line represents the predicted delivery rate, and the shaded area represents the 95% confidence interval.

4. DISCUSSION

4.1 Prey choice

In total, 95% of the delivered prey items across the three nests were identified as mammalian, with 79% being rodents. These findings resemble those from previous diet studies where it was estimated that 72 – 99% of the barn owl diet consists of mammals, with rodents constituting the biggest proportion of 77% on average in Europe (Roulin, 2020). This adds to the consensus that the barn owl is a specialist predator on small mammals (Glue, 1974; Bunn et al., 1982; Taylor, 1994; Pezzo & Morimando, 1995), although the small inclusion of non-mammalian prey items (eight birds, one frog and one insect) in my study proves the potential for diet flexibility. Even though the owls at all nests almost exclusively delivered small mammals, there were some noticeable differences in species composition between the nests.

In Somerset, the wood mouse was the most important prey item, constituting nearly 50% of the total number, and marginally outnumbering the field vole (41%). In Cabaneros and Duhallow, the wood mouse was considerably less important, constituting only 25% and 17% respectively. The field vole has previously been found to be the most common prey type for barn owls in the UK, and the wood mouse has been considered a secondary prey group, constituting only around 10% (Webster, 1973; Glue, 1974). In general, voles of the sub-family Microtinae are thought to be the most common and basic food type for barn owls in most countries (Lovari, 1974). However, numerous studies have concluded that barn owls have no real food preferences apart from a disinterest in invertebrates, and simply hunt animals small enough to be captured and killed by their method of hunting (Bunn et al., 1982). Many studies have found an inverse relationship between proportions of secondary prey species and Microtinae species captured (Bunn et al., 1982). This includes an increase in Muridae species (such as the wood mouse) when Microtinae species is low in abundance, thought to be attributed to the available habitats, with a higher abundance of Muridae species in wooded areas and a higher abundance of Microtinae species in more open cropland (Contoli, 1975; Lovari et al., 1976). Field vole populations fluctuate with cycles of 3-4 years (Lambin et al., 2000), meaning the abundance can be low in some years. In addition, a long term study revealed that the number of wood mice in barn owl pellets increased in the UK between 1974 and 1997 (Love et al., 2001). The high number of wood mice at the Somerset nest could therefore be explained by the combination of opportunistic hunting behavior and

either a relative low field vole population, a high wood mouse population or both, possibly also related to the availability of open crop lands and woodlands in the area.

While the proportion of shrews in Somerset and Cabaneros only constituted about 3% and 4%, respectively, it made up a staggering 41% in Duhallow. Typically, shrews are the second most caught prey type after rodents, constituting an average of 28% of the barn owl diet in Europe (Roulin, 2020). In Ireland however, shrews have historically not been an important part of the barn owl diet, constituting less than 15% (Glue, 1974; Smal, 1987), and the consumption of these insectivores have been declining in Europe over the past century (Roulin, 2016). The reason for the high percentage of shrews at the Duhallow nest site is likely due to the introduction of the greater white-toothed shrew to the country. Until recently, the only shrew species present in Ireland was the pygmy shrew, and although a regular prey item, it is mostly taken in small numbers (Glue, 1974). Ireland is an island with a limited native small mammal fauna, and the aggressive greater white-toothed shrew has shown a large invasive potential here. The species was first discovered in pellets from barn owls and kestrels in 2007 (Tosh et al., 2008). Since then, the species has expanded its territory by an average of 5.5 km/year, and outcompeted the pygmy shrew to the extent where it is completely absent in areas the greater white-toothed shrew has invaded (McDevitt et al., 2014; Browett et al., 2023). In my study, all shrews delivered at the Duhallow nest site were the greater white-toothed shrew. Combined with the findings of Smiddy (2018), who found that this species constitutes 68% of the remains found in barn owl pellets in the same county as my nest site (County Cork), it is likely that the greater white-toothed shrew is in high abundance and has invaded this area.

Although constituting 41% of the total number of deliveries in Duhallow, the greater white-toothed shrew constituted only 24% of the total estimated biomass, and the species is much smaller than the other available prey species (bank vole, wood mouse and brown rat). According to optimal foraging theory, the energetic cost of flying, encountering a prey, attacking and handling should always be reduced to maximize the net energetic gain (Trivers, 1972; Krebs et al., 2012). For owls, small prey items are more profitable than large prey items as they require proportionally less time for handling and ingestion, and thus provide a higher energy content per handling time (Slagsvold & Sonnerud, 2007; Slagsvold et al., 2010). The greater white-toothed shrew would be easy to detect if it is in high abundance, and demands less energy for handling, transportation, and preparation than larger prey such as the bank vole and the wood mouse. However, it would not provide as much food as larger prey. The same

inverse relationship between favorable Microtinae prey and secondary Muridae prey has been found between Microtinae and Soricidae as well (Webster, 1973), meaning a functional response exists where more shrews could be taken if the availability of voles is low. This is consistent with the prediction that less profitable species should be included in greater proportions as prey abundance declines (Taylor, 1994; Tores et al., 2005). Sonerud (1992) also highlights that in single-prey loaders, the profitability of a prey is determined by its weight and distance to the central place (the nest), and certain prey items will not be worth the transportation cost if their energy values are below a certain threshold. However, they could still be included in the diet by being consumed at the capture site by the forager (parent). Thus, if only prey observed delivered at the nest are considered, the significance of smaller prey items in the overall diet could be underestimated (Sonerud, 1992). In this case however, the high delivery rate of small shrews to the nest could indicate a functional response due to scarcity of larger prey that otherwise would be prioritized for transportation to the nest. The high delivery rate of shrews in Duhallow compared to the other two nest sites could therefore be explained by high relative abundance of the greater white-toothed shrew close to the nest and lower abundance of larger bank voles and wood mice. With no information on the local assemblage of small mammals it is however not possible to conclude.

The number of non-mammalian alternative prey delivered was low to non-existent across the barn owl nests. The nest at Cabaneros had the highest number, with eight birds and one insect delivered, while the nest at Somerset had one delivery of the common frog. The nest in Duhallow had no non-mammalian prey deliveries. Although the few occurrences show the barn owls' potential for diet flexibility, the low numbers suggest these prey items to be less favorable than mammals. Observations from several countries have shown that barn owls living in less productive areas (typically desert) with a low density of small mammals are more generalist and catch a wider diversity of prey, while in more productive areas with a greater availability of vole habitat, the diet is more specialized and the barn owls can often take just one or a few species of voles (Marti, 1988). Prey selection may therefore be dynamic, with a more specialized diet occurring when food conditions are good, and a more generalist diet when conditions are poor. This flexibility allows barn owls to survive both in more marginal habitats and in times of food scarcity (Taylor, 1994). In this context, my results suggest that the abundance of small mammals in all locations was likely high enough for the owls to specialize in more profitable prey and the need to hunt non-mammalian prey was therefore low.

4.1.1 Prey choice and nestling age

As the barn owl nestlings aged, there were changes in the composition of which prey items were most likely to be delivered at all nests. As raptor nestlings grow older, they are increasingly capable of handling and eating prey independently from the female's assistance due to larger gape size (Steen et al., 2010). At the Duhallow nest, predicted delivery of Soricidae and Cricetidae prey decreased while Muridae prey increased as nestlings aged. The decrease in Soricidae could be explained by increased food demand and increasing ability to ingest prey independently. With an average of about 12 g, the greater white-toothed shrew provides less than half the amount of meat as that of the wood mouse or bank vole. The decrease in deliveries of Soricidae started when the nestlings were about 20 days old, at which point they were able to ingest prey more or less independently. While it would be beneficial for the parent barn owls to hunt small prey items like shrews while the nestlings were young and incapable of handling larger prey items themselves, the cost of flying, capturing and transporting enough shrews to sustain older nestlings could be bigger than the cost of capturing fewer but bigger prey items such as the wood mouse. If this is the case, it indicates that the barn owl might not be a complete opportunist predator, but has the ability to select smaller prey appropriate for young nestlings and then relax prey selection as the nestlings grow larger and the food demand and need for hunting efficiency increases (Roulin, 2020). This partially selective behavior in the barn owl is supported by several other studies (e.g. Muñoz-Pedreros & Murua, 1990; Tores et al., 2005). Steen et al. (2012) found a similar pattern in reverse for the kestrel, where the parents adjust prey selection towards smaller prey items as nestlings grow older and become more adept at handling prey, relieving the parents from the task of dismembering prey to feed the nestlings. Another possible explanation could be differential prey deliveries between the sexes. Previous studies have shown that male barn owls tend to hunt smaller prey items than females, which may be attributed to the smaller body size of the male compared to the female (Pande & Dahanukar, 2012). Female barn owls usually join the male in hunting around 14-17 days after the first hatching (Roulin, 2020). In my study, this coincided with the simultaneous decrease in small Soricidae prey and increase in larger Muridae prey at the Duhallow nest. However, this hypothesis would not explain the decrease in delivery of Cricetidae prey with nestling age at this nest, as bank voles (the only available vole in Ireland) would be about the same size as the wood mouse (which was delivered at an increased rate in the same time period). It is not possible to conclusively explain the decrease of the delivery of bank voles without data on the local small mammal

assemblage, but a possible explanation could simply be that the abundance of wood mice increased throughout the study period and the barn owl parents, being opportunistic, caught a larger proportion of these at the expense of voles.

For both the nest in Somerset and that in Cabaneros, the number of deliveries of Soricidae prey was too low to show any significant changes in delivery rate. However, the analysis showed that the probability of deliveries of Muridae prey decreased while the probability of deliveries of Cricetidae prey increased as nestlings aged. The effect of nestling age was however not a significant predictor for prey delivery either locations, and opportunistic behavior and prey availability is likely the explanation for the observed results.

4.2 Diel activity

Distribution curves of prey deliveries in relation to time of day revealed a strict nocturnal activity pattern for the barn owls at all three nest locations, where hunting was initiated at sunset and ended at sunrise. These results add to the evidence from previous studies stating that the barn owl is mainly a nocturnal hunter (Marti, 1974; Taylor, 1994; Roulin, 2020). Unlike the findings of Glåmseter (2021), my results showed no activity during the hours from 18:00 to sunset when daylight persisted. There were no instances of daytime hunting observed, which differs from the findings of Elder (2022), who found some daytime hunting to occur in barn owls in Somerset. Activity at all three nest locations commenced between the hours 22:00 and 23:00, with only a few deliveries occurring between 21:00 and 22:00 at Somerset and Cabaneros, indicating that none of the barn owls started their hunting period before sunset. Due to differences in latitudes, the sun in Cabaneros sets earlier and rises later than in Somerset and Duhallow during the study period, providing approximately one and a half more hours of darkness. The barn owls at Cabaneros had a prolonged hunting period compared to the other two locations, extending 1-2 hours, likely due to these differences in sunset and sunrise times. This could indicate that the barn owls tend to take full advantage of the nighttime hours, and that barn owls at southern latitudes have more hours available to hunt in the darkness than those of more northern latitudes during the breeding season of spring and early summer in the northern hemisphere.

For many diurnal taxa, increased daylight availability, for instance achieved through migration to higher latitudes, has been shown to increase fecundity (Bryant, 1997; Schekkerman et al.,

2003; Anderson-Teixeira & Jetz, 2005). The daylight availability hypothesis states that for diurnal birds, daylight is a resource, and migrating to higher latitudes with longer daylight hours in summer provides fitness benefits (Sockman & Hurlbert, 2020). Diurnal birds can thus capitalise on increases in day length, as longer days enable birds to prolong their activity (Pokrovsky et al., 2021). For instance, Sanz et al. (2000) found a tendency of higher parental investment in higher latitude populations of Great tits (*Parus major*) compared to lower latitude populations due to longer daylight hours for foraging. Conversely, Zarybnicka et al (2012) found the same pattern in reverse for nocturnal boreal owls (*Aegolius funereus*), with owls of higher latitudes being constrained by the short nights during summer compared to lower latitudes, which could limit the number of nestlings they can raise. There are at the moment no studies on the impact of night length across latitudes for barn owls. In my study, the parents at Cabaneros successfully raised six fledglings, compared to four for Somerset and Duhallow (one nestling died before fledging at Duhallow). Additionally, the number of prey items delivered per day per nestling was significantly higher for Cabaneros compared to the other locations. This could however be due to the nestlings being older and having a higher food demand when filming took place in Cabaneros than in Somerset and Duhallow. Although the sample size is far too small to draw any conclusions, my results show that hunting for nestlings tend to initiate at sunset and end at sunrise, and that the length of the hunting period is determined by the time available between sunset and sunrise. Whether there exist variations in parental provisioning and brood size due to time constraints in barn owls at different latitudes is however beyond the scope of my study.

The overlap plots of kernel densities showed a high degree of temporal overlap between all nests, with Somerset and Duhallow being the most similar in terms of hunting times and effort. This similarity is likely due to the geographic closeness of the locations, with sunset and sunrise times being only slightly offset. The temporal difference was higher when comparing these two to Cabaneros. The overlap plots showed a higher and narrower activity peak for Somerset and Duhallow over the course of the available nighttime hours, with a high hunting effort maintained throughout the whole night. Although Cabaneros exhibited a longer activity period due to longer nights, the collective hunting effort per hour was lower and distributed more evenly throughout the night here than at the other locations. This might indicate that although the parents at Cabaneros had more hours of nighttime to hunt, they did not maintain the same efficiency in hunting throughout the night as the more northern barn owls. A study on boreal owls found higher prey delivery rates in northern populations

compared to more southern populations during nestling rearing, and suggesting this to be a compensation for shorter nights (Zárybnická et al., 2012). Although more comparative research is needed to draw conclusions, my results show a higher hunting effort per hour for the owls with shorter nights at higher latitudes, suggesting the compensatory behaviour found for boreal owls could occur in the barn owl as well.

The strictly nocturnal activity pattern shown in my results was not surprising, given the barn owl's adaptations to hunt in darkness. However, barn owls in England (but not Ireland) have regularly been observed hunting in the daylight (Taylor, 1994; Roulin, 2020). The reasons for daylight hunting are yet unknown, and there is not enough quantitative data to draw conclusions on this. Some proposed hypotheses include food scarcity, that the nights are too short or that solely hunting during the night is insufficient to meet the needs of the brood (Roulin, 2020). Additionally, barn owls rarely hunt during heavy rain and precipitation has been shown to impair hunting success (Chausson et al., 2014; Roulin, 2020; Glåmseter, 2021). Therefore, hunting is generally avoided during heavy rainfall and male barn owls tend to rest during more than 90% of rainy nights (Roulin, 2020). This could force them to hunt during the daytime if an insufficient amount of prey was caught during a rainy night. In fact, Glåmseter (2021) found that daytime hunting increased with increasing precipitation the previous two days. The barn owls in Somerset (the only location in England) had a brood of only four nestlings and managed to deliver an average of 2.8 prey items per nestling per day throughout the study period. This might indicate that there was no shortage of food available in the area, and that hunting during the daytime was not needed to sustain the nestlings. Rainfall during my study period was also very low, with only two days of rain. This indicates that the parents were likely not constrained by rainfall and were able to hunt efficiently every night. Although daytime hunting in the barn owl has been observed regularly in England, my results show a complete nocturnal pattern for all locations, suggesting that daytime hunting is not favourable under good conditions.

4.2.1 Delivery times for different prey families

My results showed only small differences in timing of deliveries between the prey families Cricetidae, Muridae and Soricidae. For the nests at Somerset and Duhallow, delivery of Muridae prey peaked slightly earlier than that of Cricetidae prey, with a Muridae peak between 23:00-00:00 and a Cricetidae peak between 00:00 – 02:00. This might indicate that

Muridae are more available than Cricetidae early in the night at the two locations. These findings contrast with the results of Glåmseter (2021), who found Muridae to be delivered more frequently later in the night. While mice of the Muridae family are mostly nocturnal (Crawley et al., 2020), voles of the Cricetidae are active both during the day and night (Gliwicz & Dabrowski, 2008; Crawley et al., 2020), and the vole availability may fluctuate throughout the 24-hour cycle (Daan & Slopeema, 1978; Taylor, 1994). The reasons for the different peaks in delivery of mice and voles could be the barn owl's tendency to hunt opportunistically. Voles are generally the preferred prey species of most barn owls (Bunn et al., 1982), and their proportion of the diet is positively correlated with their abundance (Bernard et al., 2010; Roulin, 2020). The nocturnal activity pattern of rodents is influenced by many factors including moonlight, predators and population density (Lehmann & Sommersberg, 1980; Gliwicz & Dabrowski, 2008). Given the barn owl's opportunistic tendency, my results could indicate that the barn owl settled for wood mice early in the night before switching to voles later in the night when they are more active and more available. This pattern was not observed in Cabaneros, where Cricetidae and Muridae deliveries both peaked at the same time around 22:00 – 02:00.

4.3 Prey handling

4.3.1 Prey condition

The majority (96%) of the prey delivered were delivered intact. Only eight prey items in total across all nests were delivered decapitated (0.5%), indicating that preparation of prey before delivery at the nest was not common for the barn owls in my study. Decapitation has been found to be common in other birds of prey such as the Eurasian kestrel (Steen et al., 2010) and boreal owl (Zárybnická et al., 2011), but the occurrence of this behaviour in the barn owl is less conclusive. A study from the Czech Republic found a 33% decapitation rate (Pikula et al., 1984), while another study from Scotland found no counts of decapitation (Taylor, 1994; Roulin, 2020). One possible explanation for the occurrence of decapitation in birds of prey caring for altricial young is proposed by the feeding constraint hypothesis. According to this hypothesis, young nestlings lack the ability to consume larger prey items that are part of the adult diet, leading to increased preparation of prey with larger prey sizes and reduced preparation as nestlings age and their gape size increases (Slagsvold & Wiebe, 2007; Steen et

al., 2010). Other possible explanations proposed by Roulin (2020) include removing the head for lighter transportation load, and the parent consuming the head themselves as brain tissue is high in nutrients. However, none of these hypotheses have been thoroughly tested for the barn owl.

Raptor pellets are frequently used to assess both the diet and the relative abundance of local small mammal populations from skull and jaw identification (Meek et al., 2012; Viteri et al., 2022). A study comparing remains in pellets of the boreal owl and prey identified by camera monitoring, found a bias where the amount of voles and mice were underestimated in pellets, likely due to the high frequency of decapitation as observed by camera monitoring (Zárybnická et al., 2011). Similar bias due to decapitation has also been found in pellets from the Common Buzzard (*Buteo buteo*) (Tornberg & Reif, 2006). My results resemble the findings of Glåmseter (2021) and Elder (2022), and contribute to the evidence that decapitation prior to nest delivery is rare in the barn owl (Glue, 1967). Additionally, Dodson and Wexlar (1979) found that cranial bones were only broken 30% of the time in barn owls compared to 80% in the screech owl (*Otus asio*), and barn owls returned 80% of skulls intact in their pellets. With a low frequency of prey decapitation and a high frequency of skull conservation, it is likely that using barn owl pellets for diet and small mammal population assessment is more suitable and has less bias than pellets from other raptors where decapitation is more common.

4.3.2 Probability of storing

For all nests, the probability of storing prey decreased as the nestlings aged for all the most common prey families, with the exception of Cricetidae prey for the Cabaneros nest where nestling age was not a significant predictor. These results are in accordance with previous studies (Roulin, 2004; Elder, 2022), and is likely related to the nestlings' food demand and their dependence on the female to prepare the food for them. Food demand is lower in younger than older nestlings, but studies have shown that the male's hunting effort tends to be somewhat fixed, often delivering more prey than the nestlings' current food requirements (Roulin, 2020). Provisioning barn owls reduce flying cost by postponing their own meals to the end of the night, minimizing their own body weight while hunting (Durant & Handrich, 2013). Therefore, parents tend to deliver most of the prey during the first few hours of the night, and have to estimate how much food the nestlings will consume over 24 hours (Roulin,

2020). In addition, the feeding constraint hypothesis states that the gape size limits the swallowing capacity to small pieces (Slagsvold & Wiebe, 2007; Steen et al., 2010), making young nestlings dependent on the female to prepare the prey for them. Low food demand, disproportionate high hunting effort early in the night and time-consuming maternal feeding is therefore likely the reason for the high probability of prey storing when nestlings are young. With increasing age, storing becomes less frequent as nestlings can ingest more on their own and are not constrained by waiting for the female to assist them.

Three hypotheses have been proposed to explain why owls store food during the nestling period. The insurance hypothesis explains food storing as a means to prepare for temporary food shortage due to bad weather conditions, thereby increasing foraging effort for a limited period when conditions are good (Korpimäki, 1987). This allows for a subsequently reduced foraging effort when the cost of hunting increases, as previously shown in shrikes (Carlson, 1985; Hernández, 1995). If this is the case, delivery rates should be lower the following night after a night of high storing activity (Roulin, 2004). If the parents store prey in anticipation of a possible food shortage, it is also to be expected that some prey may rot and be wasted due to the nestlings' inability to consume the food before it perishes (Roulin, 2004). The second hypothesis, named the large prey hypothesis (Korpimäki, 1987), explains storing as a result of the inability of nestlings to consume large prey on their own, as explained by the feeding constraint hypothesis (Slagsvold & Wiebe, 2007; Steen et al., 2010), or that they preferentially consume smaller and easier to handle prey first and take larger prey only when the energetic benefit outweighs the cost of handling and processing (Roulin, 2004). If large prey items are too big for the nestlings' appetite or their ability to handle them, the hypothesis predicts that smaller prey are eaten first and large prey are over-represented in food stores (Roulin, 2004). This would explain why food stores in owls have previously been found to contain the largest prey items in the diet (Korpimäki, 1987). The third hypothesis, proposed by Roulin (2004), is called the feeding time hypothesis. This hypothesis takes into consideration the constraints of nocturnal hunting and the digestive constraints of the nestlings, and explains storing as a means for the nestlings to eat throughout the 24-hour cycle and not only at night when hunting takes place. As the minimum time for digestion and pellet egestion is 2.25 hours (Guerin, 1928, cited in Roulin, 2004) and 6.5 hours respectively (Smith & Richmond, 1972), the parents bring more food at night than what is manageable at the time, which predicts that the nestlings are willing to eat the stored prey later at night or during the day when hunting is terminated (Roulin, 2004; Roulin, 2020). Observations of the female

feeding young nestlings up to every hour throughout the day supports this hypothesis (Bunn et al., 1982). Contrary to the insurance hypothesis, this hypothesis predicts the surplus prey to be consumed before the following sunset, instead of rotting away.

In my study, the probability of storing prey from the Soricidae family was lower than for prey of the Muridae and Cricetidae families for all nestling ages at all nests. The number of shrews delivered at the Cabaneros nest was too small for the effect of nestling age to be significant and results from prey identification at this location are likely biased due to high numbers of missing values. However, the effect was significant for both the Somerset and Duhallow nest site. The low probability of storing shrews was especially prominent at the Duhallow nest, where shrews comprised 41% of all delivered prey, and had a significant lower storing probability than the other prey families. As shrews are much smaller than mice and voles and thus easier to consume without maternal assistance (Steen, 2010), this finding supports the large-prey hypothesis and the prediction that small prey items are preferentially eaten first. Additionally, all stored prey were eventually consumed by the nestlings (and occasionally the parents) during the night and following day, with none going to waste due to rotting (pers.obs). Also, prey delivery rates were not lower on nights following high storing activity. This would contradict the predictions of the insurance hypothesis, but support the predictions of the feeding time hypothesis stating that the nestlings distribute food throughout the 24-hour cycle due to digestive constraints.

In accordance with other studies, my results show that storing prey in the nest is common for the barn owl during the nestling period, storing activity decreases as the nestlings age, and that the reasons for storing can be explained both by the large-prey hypothesis and the feeding time hypothesis.

4.3.3 Independent feeding

The probability of assisted feeding decreased as the nestlings aged for the Somerset and Duhallow nest, with estimated complete independence at around 35 and 25 days respectively. These results were not surprising as barn owl nestlings has been shown to progressively gain feeding independence with age (Bunn et al., 1982; Taylor, 1994). My results resemble those from previous studies on assisted feeding in other raptors (Steen et al., 2010; Sonerud et al., 2014b) and in barn owls (Glåmseter, 2021; Elder, 2022). For Cabaneros, too few instances of

assisted feeding were observed to run an analysis since the nestlings were already 22 days at the start of the monitoring period, but no observations of assisted feeding were observed after 23 days of age at this location.

Barn owls exhibit biparental care, with the male being the main food provider and the female being responsible for allocating and preparing the prey for the nestlings at the nest during the first two weeks after hatching of the first egg (Taylor, 1994; Roulin, 2020). As nestlings grow older, their gape size increases and they become able to swallow larger pieces on their own without maternal assistance (Steen et al., 2010), eventually being able to swallow whole prey items by themselves at two-three weeks old (Taylor, 1994; Dreiss et al., 2017). This frees up time for the female to join the male in hunting when her assistance is no longer needed at the nest (Sonerud et al., 2014b). The female barn owl typically begins to participate in hunting when the older nestlings can ingest prey somewhat independently, usually around 14-17 days old, if the male alone cannot meet the increasing food demand of the growing nestlings (Roulin, 2020). In my results, the estimated age when assisted feeding was as likely as unassisted feeding was 22 days for Somerset and 16 days for Duhallow, coinciding with the typical time interval the female leaves the nest to resume hunting.

The nestlings at Duhallow reached the 50% independence mark about six days sooner than the nestlings at Somerset. This difference in age could be explained by the greater number of shrews delivered at the Duhallow nest compared to the Somerset nest. Shrews are small prey items with a cylindrical body shape, making them easier to swallow than voles and mice (Steen, 2010). This is likely the reason for assisted feeding decreasing faster with age for the Soricidae family than the Cricetidae family and the Muridae family at the Duhallow nest. Young nestlings are less likely to consume large prey items unassisted due to swallowing constraints (Slagsvold & Wiebe, 2007), and the time spent by the female preparing larger prey is longer than for smaller prey (Sonerud et al., 2014b). The abundance of small shrews in Duhallow may therefore have allowed the nestlings to start feeding independently earlier and the female to resume hunting earlier.

4.5 Delivery rates

For all the nest locations there was a non-linear relationship in prey delivery rate, with the rate initially increasing before diminishing as the nestlings aged. The age at which the delivery

rate started to diminish was 45, 35 and 30 days old for Cabaneros, Somerset and Duhallow respectively, after which the rate started to plateau. These findings are in accordance with previous studies which found the delivery rates to increase in the early stages of development and diminish as the nestlings prepared for fledging (Bunn et al., 1982; Taylor, 1994; St. George & Johnson, 2021), with the food intake rates showing a bell shaped curve (Durant & Handrich, 1998). Barn owl nestlings reach the highest food demand when about 30-40 days old (Taylor, 1994; Roulin, 2020). At this age their food intake is at its highest with their body mass exceeding that of the parents (Roulin, 2020). This excess body mass is thought to be an insurance against periods of food scarcity (Durant & Handrich, 1998). From about 40 to 60 days old, the nestlings must shed excess body mass before fledging by reducing food intake (Bunn et al., 1982), which is likely why the delivery rates start to decline at this point.

Although Somerset and Duhallow show a similar shaped prey delivery curve, Duhallow has a higher mean daily prey delivery rate of 13.5 compared to 11.1 for Somerset. This is likely explained by Duhallow having one more nestling than Somerset and therefore having a higher food demand, as the mean daily delivery rate divided by brood size was very similar (2.77 for Somerset and 2.69 for Duhallow). Another explanation could be the high amount of small prey items in the diet at the Duhallow nest, in this case shrews, which are found to be positively correlated with higher delivery rates (Pande & Dahanukar, 2012; St. George & Johnson, 2021).

With a mean daily delivery rate of 27.2, Cabaneros stood out from the other locations in terms of hunting effort. Even though there were six nestlings in the brood, and they were older than the nestlings at the other locations when filming took place, the mean number of prey items per nestling per day was 4.5, which is nearly 70% higher than at the other locations. The parents at the Cabaneros nest did not seem to decrease delivery rates when the nestlings in theory should be shedding body mass, with the highest amount of prey deliveries occurring at 43 days of age. The high delivery rate could be an indication of high-quality habitats with good availability of prey. A study from Switzerland found that parents with large broods were more capable of feeding each nestling than parents with smaller broods, implying good access to quality habitats and enough resources to rear many high-quality offspring (Roulin, 2020). High female hunting effort could also be a factor. The degree of female barn owl hunting activity following the independence of nestlings can vary significantly, ranging from no contribution at all to nearly equalling that of the male (Bunn et al., 1982; Roulin, 2020).

5. CONCLUSION

By using continuous camera monitoring, details about the barn owl's food provisioning habits during nestling rearing were revealed in high resolution. Many of the findings resembled those reported in the literature, while some raised a need for further research. The delivered prey items consisted almost entirely of small mammals, with Microtinae voles and wood mice comprising a majority of the diet. Interestingly, the newly introduced greater white-toothed shrew comprised the largest portion of the diet at the Irish nest, highlighting the barn owl's opportunistic tendency to capture prey in accordance with their availability. Non-mammalian prey was captured only a total of ten times, emphasizing the barn owl's preference for mammalian prey when available. Hunting activity was strictly nocturnal for all locations. Variations in night length due to latitudinal differences allowed for a prolonged hunting duration at the Spanish nest location, while the shorter nights at the other two nests at higher latitudes seemed to be compensated for by increased hunting effort per hour. Decapitation of prey prior to delivery at the nest was observed in only eight out of 1449 instances where condition could be determined, adding to the evidence that such decapitation is rare in the barn owl. Prey handling at the nest was closely correlated to nestling age, with the probability of both storing and assisted feeding decreasing as the nestlings grew older. Prey delivery rates were also influenced by nestling age, with the delivery rate initially increasing before diminishing as the nestlings aged. This is in accordance with the consensus that nestlings must decrease food intake before fledging.

Monitoring nests by use of continuous camera surveillance has proven to be an efficient way of obtaining high-resolution data on the barn owl's behaviour related to food provisioning on the local scale. Still, more similar studies should be conducted in different areas of the world to obtain a clearer picture of the regional differences of the species, especially considering decapitation rates, diel activity patterns across latitudes and diet composition during the nestling period. These efforts will contribute to a more comprehensive understanding of the barn owl's breeding behavior and ecology on a global scale.

6. REFERENCES

- Agostinelli, C. & Lund, U. (2023). *Circular Statistics* (Version 0.5-0). Package. Available at: <https://CRAN.R-project.org/package=circular>.
- Akaike, H. (1978). On the Likelihood of a Time Series Model. *Journal of the Royal Statistical Society. Series D (The Statistician)*, 27 (3/4): 217-235. doi: 10.2307/2988185.
- Aliabadian, M., Alaei-Kakhki, N., Mirshamsi, O., Nijman, V. & Roulin, A. (2016). Phylogeny, biogeography, and diversification of barn owls (Aves: Strigiformes). *Biological Journal of the Linnean Society*, 119 (4): 904-918. doi: 10.1111/bij.12824.
- Anderson-Teixeira, K. & Jetz, W. (2005). The broad scale ecology of energy expenditure of endotherms. *Ecology Letters*, 8: 310-318. doi: 10.1111/j.1461-0248.2005.00723.x.
- Arroyo, B. & Razin, M. (2006). Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees. *Biological Conservation*, 128 (2): 276-284. doi: 10.1016/j.biocon.2005.09.035.
- Bailey, H. & OBS Studio Contributors. (2023). *OBS - Open Broadcaster Software* (Version 30.1). [Computer program]. Available at: <https://obsproject.com/>.
- Balloux, F., Goudet, J. & Perrin, N. (1998). Breeding System and Genetic Variance in the Monogamous, Semi-Social Shrew, *Crocidura russula*. *Evolution; international journal of organic evolution*, 52 (4): 1230-1235. doi: 10.1111/j.1558-5646.1998.tb01851.x.
- Bernard, N., Michelat, D., Raoul, F., Quéré, J.-P., Delattre, P. & Giraudoux, P. (2010). Dietary response of Barn Owls (*Tyto alba*) to large variations in populations of common voles (*Microtus arvalis*) and European water voles (*Arvicola terrestris*). *Canadian Journal of Zoology*, 88 (4): 416-426. doi: 10.1139/z10-011.
- Brambilla, M., Rubolini, D. & Guidali, F. (2004). Rock climbing and Raven *Corvus corax* occurrence depress breeding success of cliff-nesting Peregrines *Falco peregrinus*. *Ardeola: revista ibérica de ornitología*, 51 (2): 425-430.
- Browett, S. S., Synnott, R., O'Meara, D. B., Antwis, R. E., Browett, S. S., Bown, K. J., Wangenstein, O. S., Dawson, D. A., Searle, J. B., Yearsley, J. M., et al. (2023). Resource competition drives an invasion-replacement event among shrew species on an island. *J Anim Ecol*, 92 (3): 698-709. doi: 10.1111/1365-2656.13855.
- Bruce, M. D. (1999). Family Tytonidae (Barn-owls). In del Hoyo, J., Elliott, A. & Sargatal (ed.) vol. 5. Barn-owls to Hummingbirds. *Handbook of the Birds of the World*, pp. 34-75. Barcelona: Lynx Edicions.
- Bryant, D. M. (1997). Energy expenditure in wild birds. *Proceedings of the Nutrition Society*, 56 (3): 1025-1039. doi: 10.1079/PNS19970107.
- Bunn, D. S., Warburton, A. & Wilson, R. D. (1982). *The Barn Owl*. Calton, Staffordshire: T. & A.D. Poyser Ltd.
- Carlson, A. (1985). Central Place Food Caching: A Field Experiment with Red-Backed Shrikes (*Lanius collurio* L.). *Behavioral Ecology and Sociobiology*, 16 (4): 317-322. doi: 10.1007/BF00295544.
- Chausson, A., Henry, I., Almasi, B. & Roulin, A. (2014). Barn Owl (*Tyto alba*) breeding biology in relation to breeding season climate. *Journal of Ornithology*, 155 (1): 273-281. doi: 10.1007/s10336-013-1012-x.
- Contoli, L. (1975). Micro-Mammals and Environment in Central Italy: Data from *Tyto Alba* (Scop.) Pellets. *Italian Journal of Zoology*, 42: 223-229. doi: 10.1080/11250007509431434.
- Couzens, D., Swash, A., Still, R. & Dunn, J. (2021). *Britain's Mammals A Field Guide to the Mammals of Great Britain and Ireland*: Princeton University Press.

- Crawley, D., Coomber, F., Kubasiewicz, L., Harrower, C., Evans, P., Waggitt, J., Smith, B. & Mathews, F. (2020). *Atlas of the mammals of Great Britain and Northern Ireland*: Pelagic Publishing.
- Cutler, T. L. & Swann, D. E. (1999). Using Remote Photography in Wildlife Ecology: A Review. *Wildlife Society Bulletin (1973-2006)*, 27 (3): 571-581.
- Dias, H., Almeida, A., Maia-Júnior, J., Ribeiro, R., Torres, K., Godinho, A. & Silveira, L. S. D. (2021). Monitoring the feeding and parental care behavior of a pair of free-living owls (*Tyto furcata*) in the nest during the reproductive period in Rio de Janeiro, Brazil. *Brazilian journal of biology = Revista brasleira de biologia*, 84: e249169. doi: 10.1590/1519-6984.249169.
- Dodson, P. & Wexlar, D. (1979). Taphonomic investigations of owl pellets. *Paleobiology*, 5 (3): 275-284. doi: 10.1017/S0094837300006564.
- Dreiss, A. N., Ruppli, C. A., Delarbre, A., Faller, C. & Roulin, A. (2017). Responsiveness to siblings' need increases with age in vocally negotiating barn owl nestlings. *Behavioral Ecology and Sociobiology*, 71 (8): 1-12. doi: 10.1007/s00265-017-2342-0.
- Durant, J. & Handrich, Y. (1998). Growth and food requirement flexibility in captive chicks of the European barn owl (*Tyto alba*). *Journal of Zoology*, 245: 137-145. doi: 10.1111/j.1469-7998.1998.tb00083.x.
- Durant, J. & Handrich, Y. (2013). Diel feeding strategy during breeding in male Barn Owls (*Tyto alba*). *Journal of Ornithology*, 154. doi: 10.1007/s10336-013-0956-1.
- Daan, S. & Slopsema, S. (1978). Short-term rhythms in foraging behaviour of the common vole, *Microtus arvalis*. *Journal of comparative physiology*, 127 (3): 215-227. doi: 10.1007/BF01350112.
- Elder, R. A. (2022). *Food provisioning in the Barn owls (Tyto alba): daily activity, prey handling and effect of rain*. Masters thesis. Ås, Norway: Norwegian University of Life Sciences.
- Friard, O., Gamba, M. & Fitzjohn, R. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in ecology and evolution*, 7 (11): 1325-1330. doi: 10.1111/2041-210X.12584.
- Fyfe, R. W. & Olendorff, R. R. (1976). Minimizing the Dangers of Nesting Studies to Raptors and Other Sensitive Species. *Canadian Wildlife Service*: 17.
- García-Salgado, G., Rebollo, S., Pérez-Camacho, L., Martínez-Hestekamp, S., Navarro, A. & Fernández-Pereira, J.-M. (2015). Evaluation of Trail-Cameras for Analyzing the Diet of Nesting Raptors Using the Northern Goshawk as a Model. *PLoS one*, 10 (5). doi: 10.1371/journal.pone.0127585.
- Garcia, L., Arroyo, B., Margalida, A., Sánchez Mateos, R. & Oria, J. (2006). Effect of Human Activities on the Behaviour of Breeding Spanish Imperial Eagles (*Aquila adalberti*): Management Implications for the Conservation of a Threatened Species. *Animal Conservation*, 9 (1): 85-93. doi: 10.1111/j.1469-1795.2005.00016.x.
- Gliwicz, J. & Dabrowski, M. (2008). Ecological Factors Affecting the Diel Activity of Voles in a Multi-Species Community. *Annales Zoologici Fennici*, 45 (4): 242-247. doi: 10.5735/086.045.0401.
- Glue, D. E. (1967). Prey taken by the Barn Owl in England and Wales. *Bird Study*, 14 (3): 169-183. doi: 10.1080/00063656709476160.
- Glue, D. E. (1974). Food of the Barn Owl in Britain and Ireland. *Bird Study*, 21 (3): 200-210.
- Glåmseter, A. T. (2021). *Climate effects on parental food provisioning in the barn owls (Tyto alba) breeding in Norfolk, UK, by the use of nest cameras*. Masters thesis. Ås: Norwegian University of Life Sciences.
- Götmark, F. (1992). The Effects of Investigator Disturbance on Nesting Birds. In Power, D. M. (ed.) vol. 9 *Current Ornithology*, pp. 63-104. Boston: Springer.

- Hernández, Á. (1995). Temporal-Spatial Patterns of Food Caching in Two Sympatric Shrike Species. *The Condor*, 97 (4): 1002-1010. doi: 10.2307/1369539.
- Häkkinen, I. (1977). Food catch of the Osprey *Pandion haliaetus* during the breeding season. *Ornis Fennica*, 54 (4): 166–169.
- Jackson, P. & Cresswell, W. (2017). Factors determining the frequency and productivity of double brooding of Barn Owls *Tyto alba*. *Bird Study*, 64 (3): 353-361. doi: 10.1080/00063657.2017.1363716.
- Klok, C. & de Roos, A. M. (2007). Effects of vole fluctuations on the population dynamics of the barn owl *Tyto alba*. *Acta Biotheoretica*, 55 (3): 227-241. doi: 10.1007/s10441-007-9013-x.
- Korpimäki, E. (1987). Prey caching of breeding Tengmalm's Owls *Aegolius funereus* as a buffer against temporary food shortage. *Ibis*, 129: 499-510. doi: 10.1111/j.1474-919X.1987.tb08237.x.
- Korpimäki, E. (1988). Diet of breeding Tengmalm's Owls *Aegolius funereus*: Long-term changes and year-to-year variation under cyclic food conditions. *Ornis Fennica*, 65: 21-30.
- Krebs, J. R., Davies, N. B. & West, S. A. (2012). *An introduction to behavioural ecology*. 4 ed. Cambridge, MA, US: Wiley-Blackwell.
- Kölliker, M., Royle, N. & Smiseth, P. T. (2012). *The Evolution of Parental Care*: Oxford University Press.
- Lambin, X., Petty, S. & Mackinnon, J. (2000). Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, 69: 106-119. doi: 10.1046/j.1365-2656.2000.00380.x.
- Lehmann, U. & Sommersberg, C. W. (1980). Activity patterns of the common vole, *Microtus arvalis* — Automatic recording of behaviour in an enclosure. *Oecologia*, 47 (1): 61-75. doi: 10.1007/BF00541777.
- Lewis, S. B., Fuller, M. R. & Titus, K. (2004). A Comparison of 3 Methods for Assessing Raptor Diet during the Breeding Season. *Wildlife Society Bulletin (1973-2006)*, 32 (2): 373-385. doi: 10.2307/3784978.
- Ligon, J. D. (1999). *The Evolution of Avian Breeding Systems*: Oxford University Press.
- Lovari, S. (1974). The feeding habits of four raptors in central Italy. *Journal of Raptor Research*, 8 (3): 45 - 57.
- Lovari, S., Renzoni, A. & Fondi, R. (1976). The Predatory Habits of the Barn Owl (*Tyto Alba Scopoli*) in Relation to the Vegetation Cover. *Bollettino di zoologia*, 43 (1-2): 173-191. doi: 10.1080/11250007609434894.
- Love, R., Webon, C., Glue, D. & Harris, S. (2001). Changes in the food of British Barn Owls (*Tyto alba*) between 1974 and 1997. *Mammal Review*, 30 (2): 107-129. doi: 10.1046/j.1365-2907.2000.00060.x.
- Marti, C. D. (1974). Feeding Ecology of Four Sympatric Owls. *The Condor*, 76 (1): 45-61. doi: 10.2307/1365983.
- Marti, C. D. (1988). A long-term study of food-niche dynamics in the Common Barn-Owl: comparisons within and between populations. *Canadian Journal of Zoology*, 66 (8): 1803-1812. doi: 10.1139/z88-261.
- Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)* (Version 2.3.3). Package. Available at: <https://cran.r-project.org/package=AICcmodavg>.
- McDevitt, A. D., Montgomery, W. I., Tosh, D. G., Lusby, J., Reid, N., White, T. A., McDevitt, C. D., O'Halloran, J., Searle, J. B. & Yearsley, J. M. (2014). Invading and expanding: range dynamics and ecological consequences of the greater white-toothed shrew

- (*Crocidura russula*) invasion in Ireland. *PLoS One*, 9 (6): e100403. doi: 10.1371/journal.pone.0100403.
- Meek, W. R., Burman, P. J., Sparks, T. H., Nowakowski, M. & Burman, N. J. (2012). The use of Barn Owl *Tyto alba* pellets to assess population change in small mammals. *Bird Study*, 59 (2): 166-174. doi: 10.1080/00063657.2012.656076.
- Meredith, M., Ridout, M. & Campbell, L. A. D. (2024). *Estimates of Coefficient of Overlapping for Animal Activity Patterns* (Version 0.3.9). Package. Available at: <https://cran.r-project.org/web/packages/overlap/index.html>.
- Monterroso, P., Alves, P. C. & Ferreras, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. *Behavioral Ecology and Sociobiology*, 68 (9): 1403-1417. doi: 10.1007/s00265-014-1748-1.
- Muñoz-Pedreros, A. & Murua, R. (1990). Control of small Mammals in a Pine Plantation (Central- Chile) by Modification of the habitat on predators (*Tyto alba* Strigiforme and *Pseudalopex* spp Canidae). *Acta Oecologica*, 11 (2): 251-261.
- Orians, G. & Pearson, N. (1979). On the theory of central place foraging. Analysis of Ecological Systems. In Horn, D. J., Mitchell, R. D. & Sta, G. R. (eds) *Analysis of Ecological Systems*, pp. 155-177. Columbus: Ohio State University Press.
- Otterbeck, A., Lindén, A. & Roulét, E. (2015). Advantage of specialism: reproductive output is related to prey choice in a small raptor. *Oecologia*, 179. doi: 10.1007/s00442-015-3320-8.
- Palomo, L. J., Justo, E. R. & Vargas, J. M. (2009). *Mus spretus* (Rodentia: Muridae). *Mammalian Species* (840): 1-10. doi: 10.1644/840.1.
- Pande, S. & Dahanukar, N. (2012). Reversed Sexual Dimorphism and Differential Prey Delivery in Barn Owls (*Tyto alba*). *Journal of Raptor Research*, 46 (2): 184-189. doi: 10.3356/JRR-10-09.1.
- Pavluvčík, P., Poprach, K., Machar, I., Losík, J., Gouveia, A. & Tkadlec, E. (2015). Barn Owl Productivity Response to Variability of Vole Populations. *PloS one*, 10: e0145851. doi: 10.1371/journal.pone.0145851.
- Pezzo, F. & Morimando, F. (1995). Food habits of the barn owl, *Tyto alba*, in a Mediterranean rural area: Comparison with the diet of two sympatric carnivores. *Bollettino di zoologia*, 62 (4): 369-373. doi: 10.1080/11250009509356091.
- Pikula, J., Beklová, M. & Kubík, V. (1984). *The Breeding Bionomy of Tyto Alba*. 1 ed. Prague: Academia.
- Pokrovsky, I., Kölzsch, A., Sherub, S., Fiedler, W., Glazov, P., Kulikova, O., Wikelski, M. & Flack, A. (2021). Longer days enable higher diurnal activity for migratory birds. *Journal of Animal Ecology*, 90 (9): 2161-2171. doi: 10.1111/1365-2656.13484.
- R Core Team. (2023). *R: A language and environment for statistical computing*. Available at: https://www.r-project.org/?fbclid=IwAR33oeV7WgebG_YcZL9MWZq1kA7MTcDllyBvSYTpUjjUuw0vrVApsMYQ_aem_AUGXZbjPTGZEGnIQsZSQD-bey0j_2XgwwRzkd7yICgjLCd0ZAyq4h4aZpzoJ0A7ngK-EUfoLgr5XEIz7NkJMuMHC.
- Refinetti, R. (2008). The diversity of temporal niches in mammals. *Biological Rhythm Research*, 39: 173-192. doi: 10.1080/09291010701682690.
- Reif, V. & Tornberg, R. (2006). Using time-lapse digital video recording for a nesting study of birds of prey. *European Journal of Wildlife Research*, 52 (4): 251-258. doi: 10.1007/s10344-006-0039-1.
- Ridout, M. S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14 (3): 322-337. doi: 10.1198/jabes.2009.08038.

- Ripley, B. & Venables, W. (2023). *Feed-Forward Neural Networks and Multinomial Log-Linear Models* (Version 7.3-19). Package. Available at: <https://cran.r-project.org/web/packages/nnet/index.html>.
- Roulin, A. (2004). The function of food stores in bird nests: Observations and experiments in the Barn Owl *Tyto alba*. *Ardea*, 92 (1): 69-78.
- Roulin, A. (2016). Shrews and moles are less often captured by European Barn Owls *Tyto alba* nowadays than 150 years ago. *Bird Study*, 63 (4): 559-563. doi: 10.1080/00063657.2016.1240149.
- Roulin, A. (2020). *Barn owls : evolution and ecology with grass owls, masked owls and sooty owls*. Cambridge: Cambridge University Press.
- Rowcliffe, M. (2023). *Animal Activity Statistics* (Version 1.3.4). Package. Available at: <https://CRAN.R-project.org/package=activity>.
- Salamolard, M., Butet, A., Alain, L. & Bretagnolle, V. (2000). Responses of an Avian Predator to Variations in Prey Density at a Temperate Latitude. *Ecology*, 81. doi: 10.2307/177465.
- Sanz, J. J., Tinbergen, J. M., Moreno, J., Orell, M. & Verhulst, S. (2000). Latitudinal variation in parental energy expenditure during brood rearing in the great tit. *Oecologia*, 122 (2): 149-154. doi: 10.1007/PL00008842.
- Sarasola, J., Grande, J. M. & Negro, J. (2018). *Birds of Prey: Biology and conservation in the XXI century*. Cham, Switzerland: Springer International Publishing.
- Schekkerman, H., Tulp, I., Piersma, T. & Visser, G. H. (2003). Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. *Oecologia*, 134 (3): 332-342. doi: 10.1007/s00442-002-1124-0.
- SEO/BirdLife. (2023). *Estudio y seguimiento de rapaces en el Parque Nacional de Cabañeros año 2023*. Madrid: BirdLife International.
- Simmons, R., Avery, D. M. & Avery, G. (1991). Biases in diets determined from pellets and remains: Correction factors for a mammal and bird-eating raptor. *Journal of Raptor Research*, 25: 63-67.
- Slagsvold, T. & Sonerud, G. (2007). Prey size and ingestion rate in raptors: Importance for sex roles and reversed sexual size dimorphism. *Journal of Avian Biology*, 38 (6): 650-661. doi: 10.1111/j.2007.0908-8857.04022.x.
- Slagsvold, T. & Wiebe, K. L. (2007). Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. *Animal Behaviour*, 73 (4): 691-700. doi: 10.1016/j.anbehav.2006.05.021.
- Slagsvold, T., Sonerud, G., Grønlien, H. & Stige, L. (2010). Prey handling in raptors in relation to their morphology and feeding niches. *Journal of Avian Biology*, 41 (4): 488-497. doi: 10.1111/j.1600-048X.2010.05081.x.
- Smal, C. M. (1987). The diet of the Barn Owl *Tyto alba* in southern Ireland, with reference to a recently introduced prey species— the Bank Vole *Clethrionomys glareolus*. *Bird Study*, 34 (2): 113-125. doi: 10.1080/00063658709476946.
- Smith, C. R. & Richmond, M. E. (1972). Factors influencing pellet egestion and gastric Ph in the barn owl. *The Wilson Bulletin*, 84 (2): 179-186.
- Sockman, K. & Hurlbert, A. (2020). How the effects of latitude on daylight availability may have influenced the evolution of migration and photoperiodism. *Functional Ecology*, 34. doi: 10.1111/1365-2435.13578.
- Sonerud, G. A. (1992). Functional Responses of Birds of Prey: Biases Due to the Load-Size Effect in Central Place Foragers. *Oikos*, 63 (2): 223-232. doi: 10.2307/3545382.
- Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2014a). Evolution of parental roles in raptors: prey type determines role asymmetry

- in the Eurasian kestrel. *Animal Behaviour*, 96: 31-38. doi: 10.1016/j.anbehav.2014.07.011.
- Sonerud, G. A., Steen, R., Selås, V., Aanonsen, O. M., Aasen, G.-H., Fagerland, K. L., Fosså, A., Kristiansen, L., Løw, L. M., Rønning, M. E., et al. (2014b). Evolution of parental roles in provisioning birds: diet determines role asymmetry in raptors. *Behavioral Ecology*, 25 (4): 762-772. doi: 10.1093/beheco/aru053.
- Spaul, R. & Heath, J. (2017). Flushing Responses of Golden Eagles (*Aquila chrysaetos*) In Response To Recreation. *The Wilson Journal of Ornithology*, 129: 834-845. doi: 10.1676/16-165.1.
- St. George, D. A. & Johnson, M. D. (2021). Effects of habitat on prey delivery rate and prey species composition of breeding barn owls in winegrape vineyards. *Agriculture, Ecosystems & Environment*, 312: 107322. doi: 10.1016/j.agee.2021.107322.
- Starck, J. M. & Ricklefs, R. E. (1998). Variation, Constraint, and Phylogeny: Comparative Analysis of Variation in Growth. In Starck, J. M. & Ricklefs, R. E. (eds) *Avian Growth and Development*, p. 0: Oxford University Press.
- Steen, R. (2010). *Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (Falco tinnunculus)*. Phd thesis. Ås: Norwegian University of Life Sciences.
- Steen, R., Løw, L., Sonerud, G., Selås, V. & Slagsvold, T. (2010). The feeding constraint hypothesis: Prey preparation as a function of nestling age and prey mass in the Eurasian kestrel. *Animal Behaviour*, 80 (1): 147-153. doi: 10.1016/j.anbehav.2010.04.015.
- Steen, R., Sonerud, G. A. & Slagsvold, T. (2012). Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). *Journal of Ornithology*, 153 (4): 1087-1099. doi: 10.1007/s10336-012-0838-y.
- Surmacki, A. & Podkowa, P. (2022). The use of trail cameras to monitor species inhabiting artificial nest boxes. *Ecology and Evolution*, 12. doi: 10.1002/ece3.8550.
- Taylor, I. (1994). *Barn owls: Predator-Prey Relationships and Conservation*: Cambridge University Press.
- Thieurmel, B. & Elmarhraoui, A. (2022). *Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase* (Version 0.5.1). Package. Available at: <https://CRAN.R-project.org/package=suncalc>.
- Tomar, S. (2006). Converting video formats with FFmpeg. *Linux Journal*.
- Tores, M., Motro, Y., Motro, U. & Yom-Tova, Y. (2005). The barn owl- a selective opportunist predator. *Israel Journal of Zoology*, 51 (4): 349-360. doi: 10.1560/7862-9E5G-RQJJ-15BE.
- Tornberg, R. & Reif, V. (2006). Assessing the diet of birds of prey: A comparison of prey items found in nests and images. *Ornis Fennica*, 84.
- Tosh, D. G., Lusby, J., Montgomery, W. I. & O'Halloran, J. (2008). First record of greater white-toothed shrew *Crocidura russula* in Ireland. *Mammal review*, 38 (4): 321-326. doi: 10.1111/j.1365-2907.2008.00130.x.
- Trivers, R. (1972). Parental Investment and Sexual Selection. In Campbell, B. (ed.) *Sexual selection and the descent of man*, pp. 136-179. Chicago: Aldine.
- Viteri, M. C., Stegner, M. A. & Hadly, E. A. (2022). Assessing the reliability of raptor pellets in recording local small mammal diversity. *Quaternary Research*, 106: 1-10. doi: 10.1017/qua.2021.59.
- Webster, J. A. (1973). Seasonal Variation in Mammal Contents of Barn Owl Castings. *Bird Study*, 20 (3): 185-196. doi: 10.1080/00063657309476380.
- Wille, F. & Kampp, K. (1983). Food of the White-Tailed Eagle *Haliaeetus albicilla* in Greenland. *Holarctic Ecology*, 6 (1): 81-88.

- Yom-Tov, Y. & Wool, D. (1997). Do the Contents of Barn Owl Pellets Accurately Represent the Proportion of Prey Species in the Field? *The Condor*, 99 (4): 972-976. doi: 10.2307/1370149.
- Zárybnická, M., Riegert, J. & Šťastný, K. (2011). Diet composition in the Tengmalm's Owl *Aegolius funereus*: A comparison of camera surveillance and pellet analysis. *Ornis Fennica*, 88: 147–153. doi: 10.51812/of.133777.
- Zárybnická, M., Korpimäki, E. & Griesser, M. (2012). Dark or Short Nights: Differential Latitudinal Constraints in Nestling Provisioning Patterns of a Nocturnally Hunting Bird Species. *PloS one*, 7 (5). doi: 10.1371/journal.pone.0036932.

7. APPENDIX

Appendix 1: Total prey deliveries from all three nest locations distributed by number, percentage by number, estimated body mass, total body mass and percentage by body mass.

Prey item	Number delivered	Percentage by number (%)	Estimated body mass (g)	Total body mass (g)	Percentage by mass (%)
Common shrew (<i>Sorex araneus</i>)	10	0.7	10.0	100	0.29
Greater white-toothed shrew (<i>Crocidura russula</i>)	202	13.5	12.0	2424	6.28
Bank vole (<i>Myodes glareolus</i>)	118	7.9	20.0	2360	6.11
Field vole (<i>Microtus agrestis</i>)	147	9.8	30.0	4410	11.43
<i>Microtus sp.</i>	318	21.2	30.0	9540	24.73
Unidentified vole (Cricetidae)	7	0.5	29.5	206.5	0.53
Wood mouse (<i>Apodemus sylvaticus</i>)	429	28.6	25.0	10725	27.80
Algerian mouse (<i>Mus spretus</i>)	12	0.8	16.0	192	0.49
Wood mouse/Algerian mouse	4	0.3	24.4	97.6	0.25
Muridae sp.	1	0.1	27.1	27.1	0.07
Brown rat (<i>Rattus norvegicus</i>)	25	1.7	100.0	2500	6.48
Wood mouse/Brown rat	1	0.1	38.8	38.8	0.10
Unidentified rodent	57	3.8	29.1	1659.3	4.30
Unidentified mammal	85	5.7	25.5	2171.4	5.62
Bird (Passeriformes)	8	0.5	10.0	80	0.21
Common frog (<i>Rana temporaria</i>)	1	0.1	22.0	22	0.05
Insect	1	0.1	0.1	0.1	0.001
Unidentified prey	74	4.9	27.2	2015.4	5.22
Total	1500	100	-	38569.2	100

Appendix 2 : Prey deliveries from the three barn owl nest locations distributed by number and percentage for each location and total number for all nests. All digits are rounded to one decimal place.

Prey item	Cabaneros		Somerset		Duhallow		Total Number
	Number	Percentage (%)	Number	Percentage (%)	Number	Percentage (%)	
Common shrew (<i>Sorex araneus</i>)	-	-	10	2.8	-	-	10
Greater white-toothed shrew (<i>Crocidura russula</i>)	28	3.9	-	-	174	40.7	202
Bank vole (<i>Myodes glareolus</i>)	-	-	8	2.2	110	25.8	118
Field vole (<i>Microtus agrestis</i>)	-	-	147	40.7	-	-	147
Microtus sp.	318	44.6	-	-	-	-	318
Unidentified vole (Cricetidae)	-	-	7	2.0	-	-	7
Wood mouse (<i>Apodemus sylvaticus</i>)	178	25.0	180	49.9	71	16.6	429
Algerian mouse (<i>Mus spretus</i>)	12	1.7	-	-	-	-	12
Wood mouse/Algerian mouse	4	0.6	-	-	-	-	4
Muridae sp.	1	0.1	-	-	-	-	1
Brown rat (<i>Rattus norvegicus</i>)	7	1.0	2	0.6	16	3.7	25
Wood mouse/Brown rat	-	-	-	-	1	0.2	1
Unidentified rodent (Rodentia)	51	7.2	6	1.7	-	-	57
Unidentified mammal (Mammalia)	52	7.3	1	0.3	32	7.5	85
Bird (Passeriformes)	8	1.1	-	-	-	-	8
Common frog (<i>Rana temporaria</i>)	-	-	-	-	1	0.2	1
Insect	1	0.1	-	-	-	-	1
Unidentified prey	52	7.3	-	-	22	5.2	74
Total	712	100	361	100	427	100	1500

Appendix 3: Prey deliveries across all nests arranged by prey group, distributed by number and percentage.

Prey group	Number	Percentage (%)
Mammal	1417	94.46
Amphibian	1	0.07
Avian	8	0.53
Insect	1	0.07
Unknown	73	4.86
Total	1500	100

Appendix 4: Percentage of each prey family delivered at the three nests Cabaneros, Somerset and Duhallow.

Prey Family	Cabaneros (n = 712)	Somerset = (361)	Duhallow (n = 427)
Cricetidae	42.0	44.8	27.0
Muridae	30.3	50.4	20.6
Soricidae	4.1	2.8	41.4
Other	1.3	-	0.2
Unknown	22.3	2.0	10.8
Total	100	100	100

Appendix 5: The effect of nestling age on the predicted probabilities of delivery of prey from the most common prey families Cricetidae, Muridae and Soricidae for the nest in Cabaneros. ANOVA type II test (deviance) results from the multinomial regression (n = 544).

	LR Chisq	Df	Pr(>Chisq)
Nestling age	3.74	2	0.15

Appendix 6 The effect of nestling age on the predicted probabilities of delivery of prey from the most common prey families Cricetidae, Muridae and Soricidae for the nest in Somerset. ANOVA type II test (deviance) from the multinomial regression (n = 354).

	LR Chisq	Df	Pr(>Chisq)
Nestling age	5.51	2	0.06

Appendix 7: The effect of nestling age on the predicted probabilities of delivery of prey from the most common prey families Cricetidae, Muridae and Soricidae for the nest in Duhallow. ANOVA type II test (deviance) from the multinomial regression (n = 380).

	LR Chisq	Df	Pr(>Chisq)
Nestling age	14.32	2	0.0008

Appendix 8: Calculated sunrise and sunset times for the three locations based on an average for the whole period.

Location	Sunset	Sunrise
Cabaneros	21:32	06:59
Somerset	21:08	05:14
Duhallow	21:36	05:30

Appendix 9: AIC-based model selection (Akaike, 1978) of the generalized linear effects models for the probability of storing as a function of nestling age, prey family, nestling age and prey family and the interaction between nestling age and prey family for the nest in Cabaneros.

Models	Parameters	df	AIC	Δ AIC
Mod1	Nestling age:prey family	6	558.07	0.00
Mod4	Nestling age	2	563.24	5.17
Mod2	Nestling age + prey family	4	563.32	5.25
Mod3	Prey family	3	568.29	10.22

Appendix 10: AIC-based model selection (Akaike, 1978) of the generalized linear effects models for the probability of storing as a function of nestling age, prey family, nestling age and prey family and the interaction between nestling age and prey family for the nest in Somerset.

Models	Parameters	df	AIC	Δ AIC
Mod2	Nestling age + prey family	4	375.08	0.00
Mod1	Nestling age:prey family	6	378.55	3.47
Mod4	Nestling age	2	379.70	4.62
Mod3	Prey family	3	421.12	46.04

Appendix 11: AIC-based model selection (Akaike, 1978) of the generalized linear effects models for the probability of storing as a function of nestling age, prey family, nestling age and prey family and the interaction between nestling age and prey family for the nest in Duhallow.

Models	Parameters	df	AIC	Δ AIC
Mod2	Nestling age + prey family	4	364.71	0.00
Mod1	Nestling age:prey family	6	365.36	0.65
Mod3	Prey family	3	474.46	9.75
Mod4	Nestling age	2	383.62	18.91

Appendix 12: Parameter estimates of the best fitted model for the effect of nestling age and prey family on the probability of a delivered prey being stored for the barn owl nest in Cabaneros (n = 459). Intercept = Muridae family.

	Estimate	Std. error	z	P-value
(Intercept)	1.77	0.68	2.58	0.009
Nestling age	-0.07	0.02	-3.72	<0.001
Prey family Cricetidae	-2.84	0.98	-2.90	0.004
Prey family Soricidae	-0.76	2.59	-0.29	0.768
Nestling age:Prey family Cridetidae	0.08	0.02	3.05	0.002
Nestling age:Prey family Soricidae	-0.00	0.07	-0.04	0.970

Appendix 13: Parameter estimates of the best fitted model for the effect of nestling age and prey family on the probability of a delivered prey being stored for the barn owl nest in Cabaneros (n = 459). Intercept = Soricidae family.

	Estimate	Std. error	z	P-value
(Intercept)	1.00	2.50	0.40	0.688
Nestling age	-0.07	0.06	-1.08	0.280
Prey family Muridae	0.76	2.59	0.29	0.768
Prey family Cricetidae	-2.07	2.60	-0.80	0.425
Nestling age:Prey family Muridae	0.00	0.07	0.04	0.970
Nestling age:Prey family Cridetidae	0.08	0.07	1.16	0.243

Appendix 14: Parameter estimates of the best fitted model for the effect of nestling age and prey family on probability of storing for the barn owl nest in Somerset (n = 347). Intercept = Muridae family.

	Estimate	Std. error	z	P-value
(Intercept)	3.01	0.45	6.70	<0.001
Nestling age	-0.10	0.01	-6.87	<0.001
Prey family (Soricidae)	0.73	0.25	2.91	0.003
Prey family (Cricetidae)	-0.73	0.78	-0.95	0.344

Appendix 15: Parameter estimates of the best fitted model for the effect of nestling age and prey family on probability of storing for the barn owl nest in Somerset (n = 347). Intercept = Soricidae family.

	Estimate	Std. error	z	P-value
(Intercept)	2.27	0.87	2.59	<0.001
Nestling age	-0.10	0.01	-6.86	<0.001
Prey family (Muridae)	0.73	0.77	0.94	0.344
Prey family (Cricetidae)	1.46	0.78	1.87	0.061

Appendix 16: Parameter estimates of the best fitted model for the effect of nestling age and prey family on the probability of a delivered prey being stored for the barn owl nest in Duhallow (n = 369). Intercept = Muridae family

	Estimate	Std. error	z	P-value
(Intercept)	3.90	0.52	7.46	<0.001
Nestling age	-0.17	0.02	-8.84	<0.001
Prey family (Cricetidae)	-0.63	0.35	-1.81	0.070
Prey family (Soricidae)	-1.55	0.34	-4.55	<0.001

Appendix 17: Parameter estimates of the best fitted model for the effect of nestling age and prey family on the probability of a delivered prey being stored for the barn owl nest in Duhallow (n = 369). Intercept = Soricidae family

	Estimate	Std. error	z	P-value
(Intercept)	2.35	0.39	6.08	<0.001
Nestling age	-0.17	0.02	-8.84	<0.001
Prey family (Muridae)	1.55	0.34	4.56	<0.001
Prey family (Cricetidae)	0.91	0.31	2.97	0.003

Appendix 18: AIC-based model selection (Akaike, 1978) of the generalized linear effects models for the probability of assisted feeding as a function of nestling age, prey family, nestling age and prey family and the interaction between nestling age and prey family for the nest in Somerset.

Models	Parameters	df	AIC	ΔAIC
Mod4	Nestling age	2	154.36	0.00
Mod2	Nestling age + prey family	4	154.69	0.33
Mod1	Nestling age:prey family	6	158.05	3.69
Mod3	Prey family	3	365.71	211.35

Appendix 19: AIC-based model selection (Akaike, 1978) of the generalized linear effects models for the probability of assisted feeding as a function of nestling age, prey family, nestling age and prey family and the interaction between nestling age and prey family for the nest in Duhallow.

Models	Parameters	df	AIC	ΔAIC
Mod2	Nestling age + prey family	4	137.02	0.00
Mod1	Nestling age:prey family	6	138.33	1.31
Mod4	Nestling age	2	158.64	21.62
Mod3	Prey family	3	446.79	309.77

Appendix 20: Parameter estimates of the model for the effect of nestling age and prey family on probability of assisted feeding for the nest in Somerset (n =312). Intercept = Cricetidae family.

	Estimate	Std. error	z	P-value
(Intercept)	8.96	1.26	7.08	<0.001
Nestling age	-0.38	0.05	-1.78	<0.001
Prey family Muridae	-0.82	0.46	-1.78	0.075
Prey family Soricidae	-1.67	2.13	-0.78	0.433

Appendix 21: Parameter estimates of the model for the effect of nestling age and prey family on probability of assisted feeding for the nest in Somerset (n =312). Intercept = Muridae family.

	Estimate	Std. error	z	P-value
(Intercept)	8.13	1.10	7.43	<0.001
Nestling age	-0.38	0.05	-7.95	<0.001
Prey family Cricetidae	0.82	0.46	1.78	0.075
Prey family Soricidae	-0.85	2.11	-0.40	0.687

Appendix 22: Parameter estimates of the model for the effect of nestling age and prey family on probability of assisted feeding for the nest in Somerset (n =312). Intercept = Soricidae family.

	Estimate	Std. error	z	P-value
(Intercept)	7.29	2.31	3.15	<0.001
Nestling age	-0.38	0.05	-7.95	<0.001
Prey family Muridae	0.85	2.11	0.40	0.687
Prey family Cricetidae	1.67	2.13	0.78	0.433

Appendix 23: Parameter estimates of the model for the effect of nestling age on probability of assisted feeding for the nest in Duhallow (n = 370).

	Estimate	Std. error	z	P-value
(Intercept)	7.44	0.92	8.07	<0.001
Nestling age	-0.46	0.053	-8.75	<0.001

Appendix 24: Parameter estimates of the best fitted model for the effect of nestling age and prey family on probability of assisted feeding at the barn owl nest in Duhallow (n = 370). Intercept = Muridae family.

	Estimate	Std. error	z	P-value
(Intercept)	10.80	1.44	7.48	<0.001
Nestling age	-0.55	0.07	-8.18	<0.001
Prey family (Cricetidae)	-1.12	0.65	-1.74	0.082
Prey family (Soricidae)	-2.88	-4.33	-4.33	<0.001

Appendix 25: Parameter estimates of the best fitted model for the effect of nestling age and prey family on probability of assisted feeding at the barn owl nest in Duhallow (n = 370). Intercept = Soricidae family.

	Estimate	Std. error	z	P-value
(Intercept)	7.91	1.06	7.43	<0.001
Nestling age	-0.55	0.07	-8.17	<0.001
Prey family (Muridae)	2.89	0.67	4.32	<0.001
Prey family (Cricetidae)	1.76	0.60	2.91	0.003

Appendix 26: Prey delivery rates given as number of prey delivered between the hours 00:00 and 23:59 and number of prey per nestling (divided by brood size) distributed by nestling age (days). All days with incomplete video monitoring are omitted. Number of nestlings per nest were 6 for Cabaneros, 5 for Duhallow and 4 for Somerset, with no mortality during the monitoring period.

Cabaneros			Somerset			Duhallow		
Nestling age	Number of prey delivered	Number of prey per nestling	Nestling age	Number of prey delivered	Number of prey per nestling	Nestling age	Number of prey delivered	Number of prey per nestling
27	18	3.00	10	3	0.75	3	5	1.00
28	24	4.00	11	7	1.75	4	7	1.40
29	20	3.33	12	6	1.50	5	5	1.00
30	31	5.16	13	9	2.25	6	6	1.20
31	26	4.33	14	5	1.25	8	9	1.80
32	19	3.16	15	7	1.75	9	6	1.20
34	33	5.50	16	12	3.00	10	8	1.60
35	20	3.33	17	11	2.75	11	10	2.00
36	25	4.16	18	7	1.75	12	11	2.20
37	32	5.33	19	12	3.00	13	11	2.20
38	21	3.50	20	9	2.25	14	10	2.00
41	28	4.66	21	8	2.00	15	11	2.20
42	31	5.16	22	10	2.50	16	10	2.00
43	37	6.16	23	13	3.25	17	13	2.60
44	21	3.50	24	13	3.25	18	14	2.80
45	33	5.50	25	12	3.00	19	20	4.00
46	30	5.00	26	13	3.25	20	17	3.40
47	33	5.50	27	16	4.00	21	12	2.40
48	27	4.50	28	13	3.25	22	22	4.40
49	27	4.50	29	11	2.75	23	17	3.40
50	30	5.00	30	14	3.50	24	19	3.80
51	32	5.33	31	9	2.25	25	20	4.00
			32	13	3.25	26	22	4.40
			33	16	4.00	27	19	3.80
			34	14	3.50	28	17	3.40
			35	11	2.75	29	21	4.20
			36	12	3.00	30	11	2.20
			37	12	3.00	31	13	2.60
			38	14	3.50	32	19	3.80
			39	14	3.50	33	19	3.80
			40	13	3.25			
			41	16	4.00			
Mean delivery rate (per day/per nestling)	27.18	4.53		11.09	2.77		13.46	2.69



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