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Diet, diel pattern of prey deliveries and prey handling of nesting urban peregrines (*Falco peregrinus*) in UK, as revealed by continuous video monitoring

Jenny Standahl Pettersen

Natural Resource Management

Acknowledgements

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Jenny Standahl Pettersen

Abstract

The diet, prey handling behaviour and diel pattern of prey deliveries of an urban nesting pair of the peregrine falcon (*Falco peregrinus*) in Cromer, UK, was studied through continuous video recording at the nest. The study covered the recordings of the period from the first egg hatched in May until fledging in June. A total of 267 prey items, of which all of them birds, were recorded delivered at the nest during the period. Pigeons (Columbidae) were the most important prey type, both by number and gross prey body mass, comprising 39 % and 72 % respectively. Starlings were the second most common prey type, accounting for 16 % by number and 8 % of total gross prey body mass. The probability of a prey delivery was highest in the morning and in the evening and lowest around solar noon, although the delivery rate varied between the different prey categories. The female delivered the majority of prey items, which differs from earlier findings of that the male performs most of the hunting and providing of prey items for the family. However, this was most likely caused by an assumed food-transfer between the sexes prior to delivery. The probability that a prey item was delivered by the female was affected by nestling age and depended on prey group. The probability that a prey item was decapitated prior to delivery decreased with nestling age and was affected by prey category. Both parents handled prey items at the nest, though the female more than the male. The probability that the male fed the nestlings increased with nestling age and was higher for starling than for all other prey groups. The nestlings were first seen handling a prey unassisted 29 days after hatching. In future studies it could be useful to include additional camera angles and direct observations of the nest to get a wider perspective of the circumstances related to prey deliveries and feeding events.

Sammendrag

Dietten, døgnmønster for byttedyrleveranser og håndtering av byttedyr til et hekkende par av vandrefalk (*Falco peregrinus*) i Cromer, Storbritannia, ble studert gjennom kontinuerlig videoopptak ved reiret. Studien omfattet opptak av perioden fra det første egget klekket i mai til ungene ble flygedyktige i juni. Totalt ble det registrert 267 byttedyr, hvorav alle var fugler, levert på reiret i perioden. Duer (Columbidae) var den viktigste byttedyrtypen i både antall og brutto byttedyrkroppsmasse, og utgjorde henholdsvis 39 % og 72 %. Stær var den nest vanligste byttetyper, og sto for 16 % av det totale antallet og 8 % av total brutto kroppsmasse. Sannsynligheten for en byttedyrlevering var høyest om morgenen og om kvelden og lavest midt på dagen, men leveringsraten varierte mellom de ulike byttedyrkategoriene. Hunnen leverte de fleste byttedyrene, noe som skiller seg fra tidligere funn av at hannen utfører mesteparten av jakten og forsyner familien med bytter. Trolig var dette forårsaket av en antatt byttedyroverlevering mellom kjønnene før levering ved reiret. Sannsynligheten for at et bytte ble levert av hunnen var påvirket av ungenes alder og avhengig av byttegruppe. Sannsynligheten for at et bytte ble dekapitert før levering avtok med ungenes alder og ble påvirket av byttekategori. Begge foreldrene håndterte byttedyr ved reiret, men hunnen mer enn hannen. Sannsynligheten for at hannen matet ungene var positivt korrelert med ungenes alder og var høyere for stær enn for alle andre byttedyrgrupper. Ungene ble observert håndtere et bytte uten hjelp for første gang 29 dager etter klekking. I fremtidige studier kan det være nyttig å inkludere flere kameravinkler, samt direkte observasjoner ved reiret, for å få et bredere perspektiv på omstendighetene rundt byttedyrleveranser og fôringer.

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Introduction

The idea of coevolution caused by the dynamic relationship between predator and prey, is widely accepted. Changes in the density of a prey population may cause both functional and numerical responses in their predator (Solomon 1949, as cited in Andersson & Erlinge, 1977). The strength of the response depends mainly on the flexibility of the predator's diet, but also the availability of alternative prey, amount of surplus killing and litter size. Functional responses are characterized by the changes in a predator's diet, in which number of prey taken per unit of time increases with increasing prey density. Numerical responses define the changes in predator density; recruitment, mortality, immigration and emigration, as a function of changing prey density (Andersson & Erlinge, 1977).

The continuous urbanisation and deterioration of natural environments creates considerable pressure on species depending on their native habitat, and important interactions between species are being tested. Some species however, with a predominance of birds, have managed to adapt to urban environments. This novel environment may facilitate a spectre of new opportunities and food sources, thus, allowing some populations to increase (Maclean, 2010). The species in focus in this study forms a representative example of successful range expansions as a result of high adaptability to novel areas.

The traditional nesting habitat of peregrine falcon (*Falco peregrinus*), hereafter termed "peregrine", in the UK is rocky shores and steep, cliff walls. However, peregrines have shown a great flexibility and adaptability through their increasing use of urban sites, such as power stations, bridges, churches, and tall buildings (Banks et al., 2003). A national survey from early 2000' revealed that approximately 4 % of the UK's breeding peregrines had urban environments in their home range (Crick et al., 2003, as cited in Drewitt & Dixon, 2008).

The peregrine is a specialised predator, and almost the entire diet consists of birds (Ratcliffe, 2010). However, the great diversity of birds included in the diet, depending on what is locally available, reflects how this species have been able to adapt to a broad range of habitats all over the world (Ratcliffe, 2010). Urban sites are likely to hold great populations of the feral pigeon (*Columba livia*), thus facilitating high accessibility of a major prey for the peregrine (Banks et al., 2003). The diet of peregrines ranging by the sea cliffs in coastal areas does not differ markedly from the diet of the urban peregrines. However, the diet of the former individuals includes a greater number of waders, gulls, and terns in addition to domestic pigeons (Ratcliffe, 2010).

Contrary to smaller birds like e.g., terns (Sternidae) and herons (Ardeidae), that capture vertebrate prey by their bill, usually followed by swallowing the prey whole, raptors, like the peregrine, capture prey with their feet and use their bill to tear the prey apart prior to consuming (Slagsvold & Sonnerud, 2007). While the terns' and herons' choice of prey are constrained by swallowing capacity, the peregrine are therefore allowed to hunt large prey relative to their body size (Slagsvold & Sonnerud, 2007). The cost of hunting larger prey is longer preparation time (Slagsvold & Sonnerud, 2007). Even though food preparation is both time and energy consuming, modification of the prey item leads to increased nutrient concentration uptake, by removing undesirable prey parts (Kaspari, 1990).

As the case for most other raptors, the peregrine has reversed sexual size dimorphism (RSD). While the female peregrine weighs up to 1350 g, the male usually weighs up to only 800 g, which means that the female is capable of killing larger prey than the male (Ratcliffe, 2010). Many hypotheses have been proposed in the attempt to explain the mechanisms behind RSD in raptors. Slagsvold & Sonnerud (2007) stressed how variation in prey size and ingestion rate may affect sex roles in raptors. An expected negative relationship between ingestion rate and prey size, due to extended handling time of larger prey, may affect prey choice and thereby body size. To maximize feeding efficiency of nestlings, there should be a selection for separate sex roles. Whereas one parent performs most of the hunting, usually the male in the case of raptors, the other parent, usually the female, prepare the prey and feed the nestlings (Slagsvold & Sonnerud, 2007).

The degree of RSD in raptors have also been linked to the speed and agility of the main prey type they feed on (Newton, 1979). Raptors feeding on immobile preys like carcasses and snails show negligible or just slightly levels of reversed size dimorphism. Raptors feeding on insects, reptiles, mammals, and fish form a medium level of RSD, while those feeding on birds mainly, represents the highest degree of RSD. This pattern is consistent even among raptors within the same genus (Newton, 1979). Additionally, the relationship between the male and the female have been discussed as a cause of RSD, with the female being more dominant than the male. Although this may just as well be a result of RSD, rather than what is causing it.

The peregrine is probably most known for its exceptional hunting technique. When a target is chosen, the falcon performs the so called "stoop", by steering down towards the target in a sharp angle, with their wings fairly closed, hitting its target in a speed that often kills the prey

momentary (Ratcliffe, 2010). Due to this specialized hunting technique, the peregrine has a preference of open landscapes, and is usually absent in forested areas (Ratcliffe 2010).

The peregrine is known to be a daytime hunter. This is probably due to its specialized hunting technique, which requires a certain amount of light. Nevertheless, there are recent records of prey species, normally considered as nocturnal, being caught by the peregrine. This indicates its ability to hunt also at night-time taking advantage of artificial light, and how well it is adapting to urban environments by using the full, novel spectre of feeding opportunities (Drewitt & Dixon, 2008).

Video monitoring has become an increasingly used method when studying nesting peregrines. This relatively new approach gives a unique opportunity to gain insight into the behaviour and diet of peregrine nesting in urban areas (Dixon and Drewitt, 2018). Such information may contribute to a wider understanding of the breeding success, as well as survival, of the peregrine including urban habitats in its home range. Identifying factors affecting its choice of prey, diel activity patterns, and use of hunting area are important when trying to assess what external impacts may influence the peregrine population size. This information may contribute to improved management strategies and conservation of the species, especially considering peregrines ranging in urban areas.

Video recordings from Cromer Church tower, produced by the Cromer Peregrine Project, created an opportunity to observe a peregrine pair, as well as their nestlings, at a close hold, 24 hours a day, through the whole breeding season. Through processing video these recordings, facilitated by the Cromer Peregrine Project, the aim of my study was to observe and analyse the diet, behaviour, diel activity and prey delivery at the nest of the peregrine pair at the top of a church tower in the city centre of Cromer, UK. I wanted to gain a better understanding of the breeding pair's choice of prey, which parent who delivered, as well as handled the prey, and the number of prey delivered. I predicted that domestic doves would make up the highest proportion of prey delivered to the nest. However, with the short distance between the nesting location and the coastal line kept in mind, I assumed that also waders, gulls and terns would be included, but less dominant, in the diet.

Materials and methods

Study species

The peregrine is a medium sized bird, and a relatively large falcon. Their body length varies between 39-50 cm, and the wingspan is 95-110 cm (Cramp & Simmons, 1979). In the UK, breeding pairs are often found in the uplands of the north and west and by the steep, rocky shores at the seacoast (RSPB, 2021). Due to human-induced pesticides in the food chain, the population of peregrine suffered a great decline during the 1950s and 1960s (Ratcliffe, 2010). Through improved protection and management strategies, the population has been able to grow and recover, resulting in greater expansion into urban areas. Today, the number of breeding pairs in the UK are estimated to around 1500 (RSPB, 2021).

Study area and nest monitoring

My study examines the breeding season diet of a peregrine pair, ranging in urban environments, through continuous video recordings of an artificial nest located in Cromer, UK, May 2nd to June 9th, 2020, from hatching until the nestlings were 39 days old, and mostly absent from the nest.

Cromer is a coastal town located on the north coast of the English county of Norfolk (52°56'N, 1°18'E), 37 km north of Norwich and 186 km north-northeast of London. The town is characterized by its coastal cliffs, which stretches up to 70 m high in the eastern part (Visit North Norfolk, 2022)

The church tower of the Parish Church of St Peter & St Paul, hereafter termed as Cromer church, is with its 48.7 m high tower, the tallest church tower in Norfolk. The Church is located in the town centre on the north coast of the English county of Norfolk (Experience Norfolk, 2022), only 150 m from the sea and approximately 700 m from more open undeveloped land areas (Google, n.d.).

A male peregrine was first time seen in the Cromer Church tower in late 2018. Some months later (2019) he formed a pair with an arriving female peregrine, and the first mating attempt was observed in early March 2019. A basic CCTV system was installed next to the nest within a few days to enable observing the peregrines at a direct and close hold. After short

time, 3 eggs were laid and this created the foundation of the Cromer Peregrine Project (Cromer Peregrine Project 2022).

In 2019 an artificial nest platform was mounted on Cromer Church tower. The installation of a new, high-definition camera system in 2019, including functions as Pan, Tilt and zoom, has made it possible to get 360-degree views of the nest location at the top of the church tower (Cromer Peregrine Project, 2022). As in 2019, 3 eggs were laid in 2020, all hatched, and all 3 nestlings survived to fledging. The breeding pair of 2020 are assumed to be the same pair as in 2019, but the birds were not ringed (Smith, 2020b).

Video processing

To analyse the video recordings, I used the software “BORIS” (“Behavioral Observational Research Interactive Software”), version 7.12.2. BORIS is a free and open-source software that enables the user to easily log events when processing video/audio recordings and live observations (Friard & Gamba, 2016). In BORIS I set subject as “prey type”, e.g., “pigeon”, “wader” or “small passerine”. Ethogram was set to “feeder” (parent or nestling or both). Two modifiers were created, first “prey condition”; e.g., “intact”, “plucked”, decapitated or “eaten at” (i.e., breast or other parts of the body). The second modifier was set as “feed mode”, which included “dismembered or swallowed whole”. A new “observation” contained one single videoclip. Every observation got its unique observation ID equivalent to the name of the videoclip. By using this set up I was able to easily click in every new event (feeding bout), and quickly register all the variables. I was able to jump forward or backward, if something seemed unclear, and to speed up – up to 30 times faster.

For every prey item delivered at the nest, I coded the following variables: 1) The time of day of the event. 2) The sex of the delivering parent. I distinguished the two sexes based on morphological traits, such as colour, the shape of the head, and behaviour (the female was more dominant than the male). 3) The condition of the prey delivered (whether the prey item was intact, decapitated, plucked or eaten at prior to delivery). 4) Whether the feeder was the male or the female. Both parents delivered and fed the nestlings. When the male delivered prey items and the female was absent, the male would start to feed the nestlings, but was at a point replaced by the female who then completed the feeding event. This happened in almost every case in the beginning of the period, and more rarely as the nestlings grew older. In these cases, I registered both of the parents as feeders. Simultaneous feeding with two different prey

items happened on only a very few occasions, and this was registered as two different feeding events. On some occasions either the female, the male or the nestlings were observed picking up prey remains from the ground. These occasions were not incorporated as independent feeding events, but rather defined as part of an earlier feeding event. 5) Whether the nestlings were fed by the adults or fed of the prey item unassisted. 6) My assumption of which taxonomic family the prey item belonged to.

To avoid double counting in cases where two or more feeding events occurred within a short distance of time, I set the limit for a feeding event being unique, to minimum half an hour between the end of one feeding event to the start of another.

Further prey identification was done by an expert; Vidar Selås. All prey items were classified to the lowest taxonomic level possible. Identification of the prey's condition, and identification of the feeder (male or female) was done with assistance from Geir A. Sonerud.

Gross body mass (g), i.e., the estimated body mass of every prey item, was included in the analysis. Due to small intraspecific variations in bird body mass, I was able to obtain these data from mean values listed in Cramp & Simmons (1983), Cramp (1985, 1988), Cramp & Perrins (1994), Selås (2001) and G.A. Sonerud (personal comment). (see appendix 1).

Statistical analysis

Statistical analyses and construction of figures was performed with Microsoft Excel Spreadsheet Software and R Studio version 1.2.5033 (R studio team, 2022). The standard criterion of statistical significance was set to $\alpha = 0.05$, and all residuals were checked for normality. Estimates are presented as mean $\pm$ SE (standard error).

To analyse the diel activity (24-h) I used the cosinor-analysis in R (Pita et al., 2011). To find the best model based on the lowest AIC-value, I kept the model if the difference (ΔAIC) between AICc and AICcmin was larger than 2.0 (Anderson & Burnham, 2004). See appendix 2 for models tested (M1-M6) and parameter estimates.

I run the best model in R, using generalised linear models (GLM) with logistic regression and binomial distribution. The explanatory variable was set as time of day, and the response variable was set as probability of prey delivery within an hour block, whereas the binomial outcome was “0” (not delivered) and “1” (delivered). This is a conservative measure,

considering that more than one prey item may have been delivered within an hour block. Mean expected delivering rate was expressed as MESOR (midline estimating statistic of rhythm). The delivery rate was defined as significantly high or low when the confidence interval was higher or lower than MESOR, respectively.

Four additional tests were conducted to test the delivery rate of each of the main prey groups; pigeon, starling, thrush and wader, frequently delivered at the peregrine nest. The explanatory variable was set as time of day, and the response variable was set as probability of either a pigeon, starling, thrush or wader being delivered within an hour block. For AICc models and parameter estimates for all four tests, see appendix 5, 7, 9 and 11.

I used ANOVA to test the distribution of prey species delivered at the nest, in relation to nestling age. Explanatory variable for the distribution of prey species in relation to nestling age was prey group.

I performed logistic regression by likelihood ratio to test for effects on the following response variables: the probability that the delivering parent was female rather than male, whether a prey item was decapitated prior to delivery at the nest and whether the prey items were handled by the female, the male or the nestlings.

The explanatory variables for the probability that the delivering parent was the female rather than the male were nestling age and prey group. The explanatory variables for whether a prey item was decapitated prior to delivery were nestling age, prey group and prey body mass. The explanatory variables for whether the prey items were handled by the female, male or the nestlings, were nestling age and prey group.

Results

Prey delivered at the nest

A total of 267 prey items were delivered at the nest during the study period. All the prey items delivered were birds, including 104 identified to species level, 110 to genus level, 4 to family level, and 24 to order level. Twelve birds were not possible to identify either due to being hidden behind the delivering parent or having been plucked or eaten at prior to delivery. These were identified to class (Aves) only (table 1). Although the pigeons delivered at the nest most likely belonged to different species, the majority were either decapitated, plucked or

eaten at prior to delivery, resulting in limited possibility to distinguish the different species, thus all of them were generalized and termed “pigeons”. Thrush and starling were both common prey and were often difficult to distinguish due to similar size and colours, hence I added the term “thrush/starling” and 12 prey items were put into this category (table 1). Gross prey body mass was on average 178.2 ± 7.9 g ($n = 255$), with range 15 - 500 g, and median = 95 g.

Pigeon species contributed with 72.3 % and thus the highest proportion of the total gross body mass. Pigeon species were also the most common prey type by number, comprising 104 of 267 (39 %) of prey items recorded. Starling were the second most common prey species, accounting for 16.1 % of total prey items and 7.6 % of total gross body mass (table 1).

Table 1. Prey deliveries recorded by video monitoring at the peregrine nest, given as percentage by number, both when unidentified prey items are included and excluded in the total number of deliveries. Gross prey body mass is the estimated body mass of the prey at the moment of capture. Gross body mass for each species is listed in appendix 1.

Prey category	Prey number		Prey percentage (identified N=255)	Gross body mass	
	N	%		g	%
Water rail (<i>Rallus aquaticus</i>)	1	0.4	0.4	120	0.26
Red knot (<i>Calidris canutus</i>)	1	0.4	0.4	140	0.31
Ringed plover (<i>Charadrius hiaticula</i>)	5	1.9	2.0	300	0.66
Sanderling (<i>Calidris alba</i>)	1	0.4	0.4	60	0.13
Dunlin (<i>Calidris alpina</i>)	3	1.1	1.2	180	0.40
Temminck's stint (<i>Calidris temminckii</i>)	1	0.4	0.4	30	0.07
Little stint (<i>Calidris minuta</i>)	5	1.9	2.0	150	0.33
Common redshank (<i>Tringa tetanus</i>)	6	2.3	2.4	720	1.58
Spotted redshank (<i>Tringa erythropus</i>)	1	0.4	0.4	140	0.31
Common snipe (<i>Gallinago gallinago</i>)	1	0.4	0.4	100	0.22
Snipes/sandpiper (small) (Scolopacidae)	3	1.1	1.2	180	0.40
Pigeon (<i>Columba</i> spp.)	104	39.0	40.8	32864	72.34
Common swift (<i>Apus apus</i>)	9	3.4	3.5	360	0.79
Great spotted woodpecker (<i>Dendrocopos major</i>)	1	0.4	0.4	90	0.20
Mistle thrush (<i>Turdus viscivorus</i>)	1	0.4	0.4	130	0.29
Common blackbird (<i>Turdus merula</i>)	20	7.5	7.8	1900	4.18
Thrush (<i>Turdus</i> spp.)	3	1.1	1.2	240	0.53
Western jackdaw (<i>Corvus monedula</i>)	3	1.1	1.2	468	1.03
Crow (<i>Corvus</i> spp.)	3	1.1	1.2	1500	3.30
Starling (<i>Sturnus vulgaris</i>)	43	16.1	16.9	3440	7.57
House sparrow (<i>Passer domesticus</i>)	1	0.4	0.4	30	0.07
Sparrow (Passeridae)	1	0.4	0.4	30	0.07
European goldfinch (<i>Carduelis carduelis</i>)	1	0.4	0.4	15	0.03
Thrush/Starling indet.	13	4.9	5.1	1040	2.29
Medium-sized passerines indet.	13	4.9	5.1	1040	2.29
Small passerines indet.	11	4.1	4.3	165	0.36
Indet.	12	4.5	-	-	-
Total	267	100	100	45432	100

Prey deliveries in relation to time of the day

Based on the cosinor analysis, the probability of a prey being delivered at the nest as a function of time of the day was best explained by model 5, with the lowest AIC value. Model selection and parameter estimates of the best model are given in appendix 2.

The earliest prey delivery was registered at 03:56 hours, and the latest delivery at 21:42 hours. In total, eight prey items were recorded before sunrise and three after sunrise. The probability of at least one prey delivery at the nest per hour-block was highest from 04 hours (sunrise) until 11 hours in the morning, and from 17 hours until 21 hours (sunset) in the evening. The highest peaks occurred within the 04:00-05:00 hour block and the 19:00-20:00 hour block. Thus, prey items were delivered at a higher frequency around sunrise and sunset, compared to the hour blocks around solar noon. The delivery rate was significantly higher than randomly expected from 4-5 hours until 7-8 hours and from 17-18 hours until 20 hours. The delivery rate was significantly lower than randomly expected from c. 20-21 hours until 03-04 hours (figure 1).

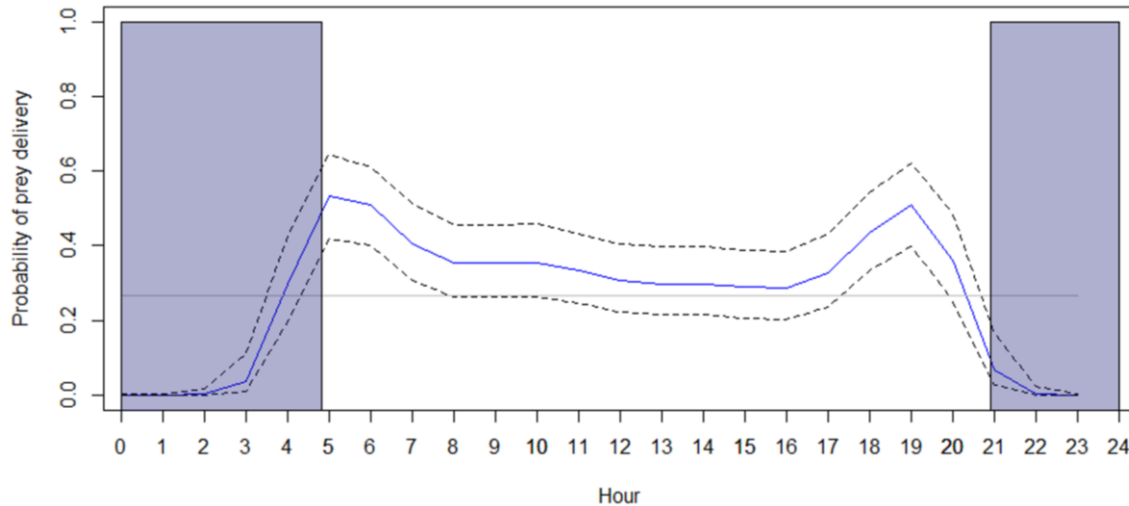


Figure 1. The probability of at that least one prey item was delivered within an hour-block at the peregrine nest as a function of time of the day, represented by the blue solid line. The upper and lower 95% confidence intervals are represented by the upper and lower dashed lines. The grey horizontal line represents MESOR. The grey area on each side represents nighttime. The average time of sunrise, solar noon, and sunset, based on the mean date of the study period (May 21st) was at 04:49 hours, 12:52 hours and 20:56 hours, respectively. Result from the best model (model 5).

Probability of delivery of separate prey groups in relation to time of the day

Based on the cosinor analysis, the probability of a pigeon being delivered at the nest as a function of time of the day was best explained by model 4, with the lowest AIC value. Model selection and parameter estimates of the best model are given in appendix 5.

The probability that at least one pigeon (n=96) was delivered at the nest was highest in the morning (06:00-07:00 hour block) and in the evening (18:00-19:00 hour block). The delivery rate was significantly higher than randomly expected from 05-06 hours until 08 hours and from 17 hours until 19-20 hours. The delivery rate was significantly lower than randomly expected between 21 hours and 04 hours (figure 2a).

Based on the cosinor analysis, the probability of a starling being delivered at the nest as a function of time of the day was best explained by model 4, with the lowest AIC value. Model selection and parameter estimates of the best model are given in appendix 7.

The delivery rate of starling (n=42) was highest in the morning and in the evening, peaking in the exact same hours as for pigeon (06:00-07:00 hour block and 18:00-19:00 hour block), although the peaks were lower for starling than for pigeon. The delivery rate was significantly higher than randomly expected from 05 hours until 06-07 hours and from 18 until 19 hours. The delivery rate was significantly lower than randomly expected between 21 hours and 03 hours (figure 2b).

Based on the cosinor analysis, the probability of a thrush being delivered at the nest as a function of time of the day was best explained by model 4, with the lowest AIC value. Model selection and parameter estimates of the best model are given in appendix 9.

The delivery rate of thrush (n=22) peaked in the morning (05 hours) and in the evening (18:00-19:00 hour block). Additionally, there was a tendency of a third peak during midday (11:00-12:00). The delivery rate was significantly higher than randomly expected around 05 hours and around 19 hours. The delivery rate was significantly lower than randomly expected between 23 hours and 02 hours (figure 2c).

Based on the cosinor analysis, the probability of a wader being delivered at the nest as a function of time of the day was best explained by model 2, with the second lowest AIC value, and lower degrees of freedom than model 3 that had the lowest AIC value. Model selection and parameter estimates of the best model are given in appendix 11.

The diel pattern of wader (n=26) differed from the other prey groups, with only one significant peak, around solar noon (12:00-13:00 hour block). The delivery rate was significantly higher than randomly expected from 10-11 hours until 14-15 hours. The delivery rate was significantly lower than randomly expected between 21 hours and 03 hours (figure 2d).

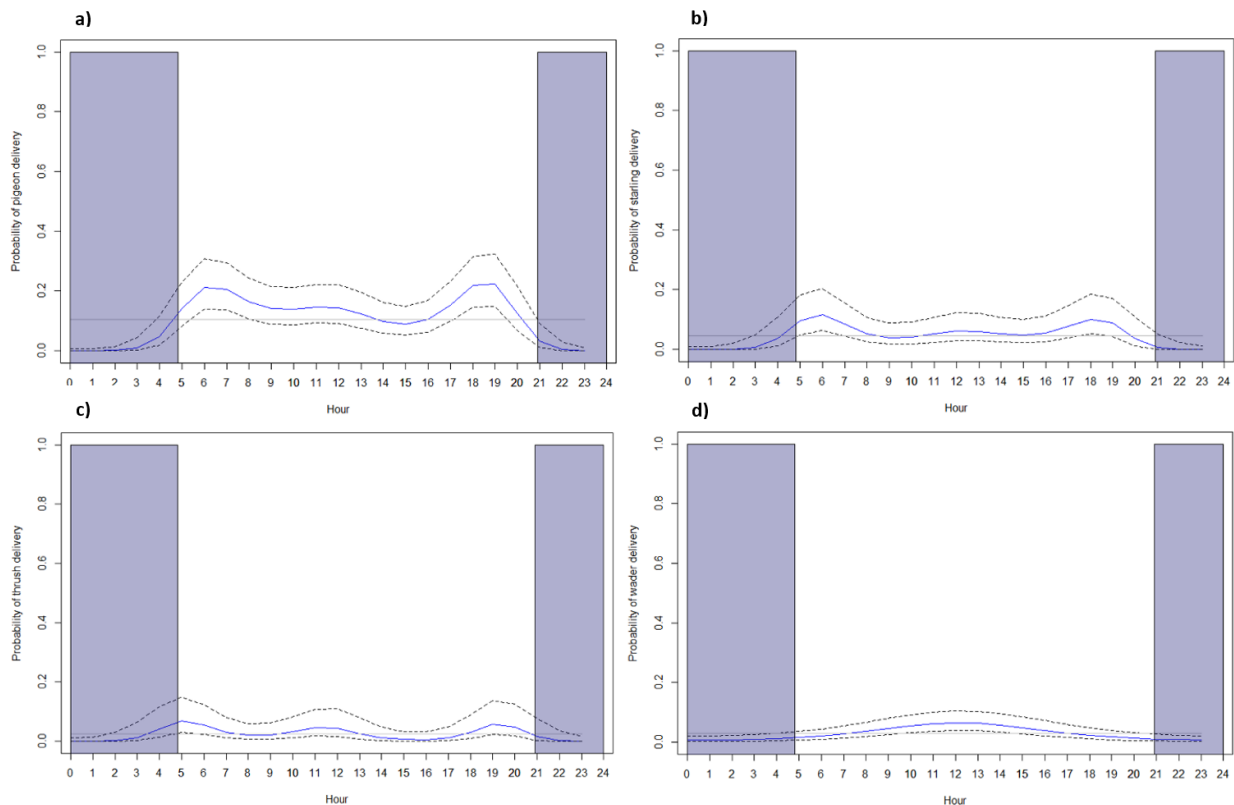


Figure 2. The probability of that at least one prey item of the separate prey groups was delivered within an hour-block at the peregrine nest as a function of time of the day, represented by the blue solid line. The delivery rate of each species is represented in their respective graph. The upper and lower 95% confidence intervals are represented by the upper and lower dashed lines. The grey horizontal line represents MESOR. The grey area on each side represents nighttime. The average time of sunrise, solar noon, and sunset, based on the mean date of the study period (May 21th) was at 04:49 hours, 12:52 hours and 20:56 hours, respectively.

The delivering parent

The delivering parent's sex was determined for 244 of 267 deliveries. The female accounted for 125 (51.2 %) of the deliveries, and the male for 119 (48.8 %). For 23 prey items no deliverer was registered. The probability that the female was the delivering parent was affected by nestling age and prey group. The probability that the female delivered a pigeon or crow was overall high but decreased slightly with increasing nestling age. The probability that the female delivered a wader or starling was high in the very beginning of the nesting period, but decreased sharply with increasing nestling age, and the probability for starling became zero after 12 days. The probability that the female delivered a small passerine was high in the beginning but decreased with increasing nestling age. Contrastingly, the probability of that the female delivered a medium passerine or a thrush was relatively low in the beginning and increased with increasing nestling age (table 2, figure 3).

When the male delivered a prey at the nest it was either handed over to the female, or the male started feeding the nestlings and was at a point replaced by the female who completed the feeding, or the male fed the nestlings without any interruption from the female. The two former were the most prominent in the beginning of the nesting period, while the latter was the most prominent in the last half of the nesting period.

Table 2. Parameter estimates from the logistic regression model of the probability that the female peregrine delivered a prey item to the nest. N=244

Explanatory variable	Estimate	SE	z value	p
Intercept	-0.51	0.76	-0.67	0.51
Nestling age	0.02	0.03	0.66	0.51
Prey group (Pigeon and Crow)	1.95	0.90	2.17	0.03
Prey group (Small passerine)	1.41	1.18	1.19	0.23
Prey group (Starling)	3.36	1.51	2.22	0.03
Prey group (Thrush)	-0.75	2.99	-0.25	0.80
Prey group (Wader)	2.94	1.67	1.76	0.08
Nestling age*Prey group (Pigeon and Crow)	-0.05	0.04	-1.18	0.24
Nestling age*Prey group (Small passerine)	-0.08	0.06	-1.31	0.19
Nestling age*Prey group (Starling)	-0.73	0.34	-2.13	0.03
Nestling age*Prey group (Thrush)	-0.01	0.10	-0.11	0.91
Nestling age*Prey group (Wader)	-0.21	0.10	-2.17	0.03

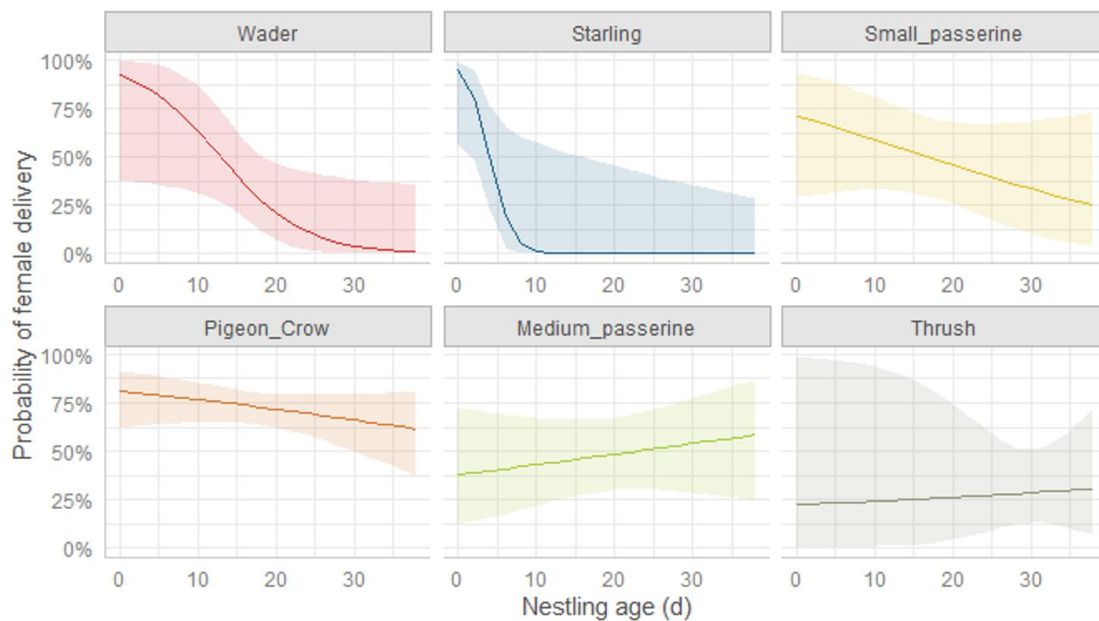


Figure 3. The predicted probability that a prey item was delivered at the peregrine nest by the female, as a function of nestling age and prey group (parameter estimates given in table 2).

The average nestling age at which a prey item of either of the prey groups was delivered at the nest, did not differ significantly between the prey groups, except for thrush, which was delivered later in the nesting period. The very first thrush was recorded delivered at the nest on May 13th (figure 4).

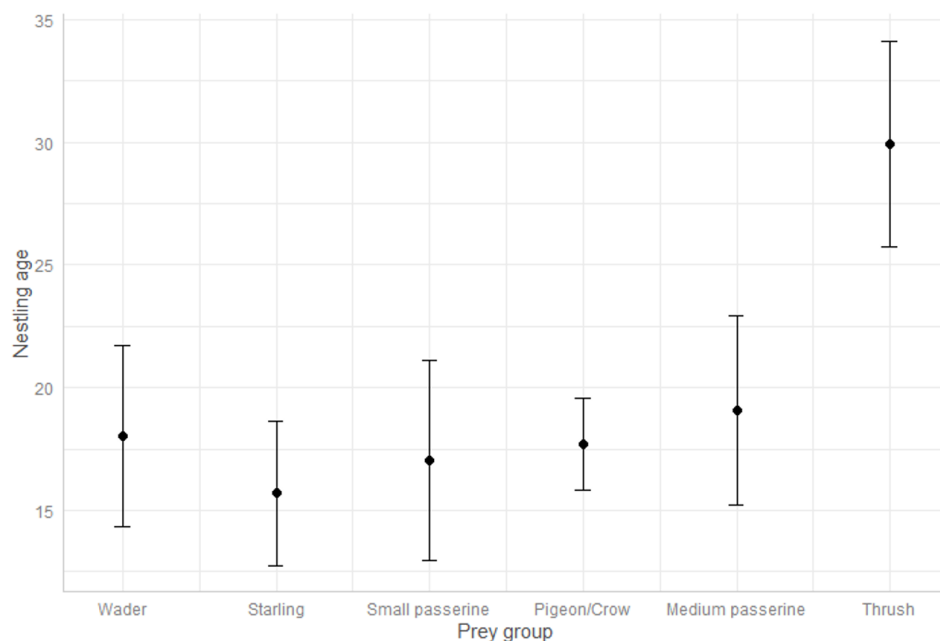


Figure 4. The predicted distribution of prey species delivered at the peregrine nest, in relation to nestling age (± 95 CI).

Preparing prey prior to delivery

The majority of prey items were prepared before being delivered at the nest. Of 222 determined prey items, 116 (52.3 %) were decapitated prior to delivery. The probability that a prey item was decapitated prior to delivery increased with nestling age and was affected by prey category (table 3 figure 5). The probability of being decapitated was overall higher for pigeons (and crows) and middle-sized passerines. The probability decreased for all prey groups with increasing nestling age (table 3, figure 5).

The probability of being decapitated was affected by prey body mass, and the probability was highest for prey items of high body mass and lowest for prey items of low body mass. The

probability decreased for all weight classes with increasing nestling age (table 4, figure 6). Prey category gave a better explanation than body mass (see AIC value appendix 15).

Table 3. Parameter estimates from a logistic regression model of the probability that a prey was decapitated prior to delivery, as a function of nestling age and prey group. N = 222

Explanatory variable	Estimate	SE	z value	p
Intercept	3.24	0.82	3.99	<0.0001
Nestling age	-0.07	0.02	-3.61	0.0003
Prey group (Pigeon and Crow)	1.001	0.79	1.27	0.20
Prey group (Small passerine)	-1.52	0.87	-1.74	0.08
Prey group (Starling)	-1.88	0.76	-2.47	0.01
Prey group (Thrush)	-2.10	0.85	-2.46	0.01
Prey group (Wader)	-1.59	0.80	-1.98	0.05

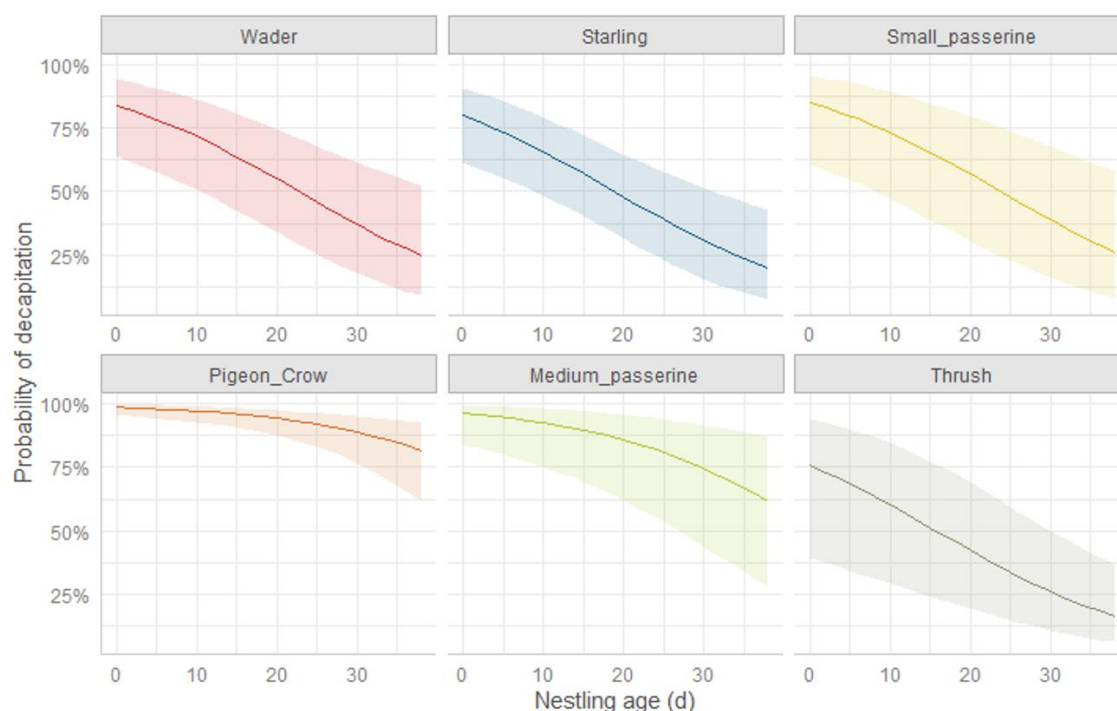


Figure 5. The predicted probability that a prey item was decapitated prior to delivery at the nest, as a function of nestling age and prey group (parameter estimates given in table 3).

Table 4. Parameter estimates from a logistic regression model of the probability that a prey item was decapitated prior to delivery, as a function of nestling age and prey body mass. N=222

Explanatory variable	Estimate	SE	z value	p
Intercept	1.01	0.43	2.31	0.02
Nestling age	-0.07	0.02	-4.21	<0.0001
Prey body mass	0.01	0.001	5.34	<0.0001

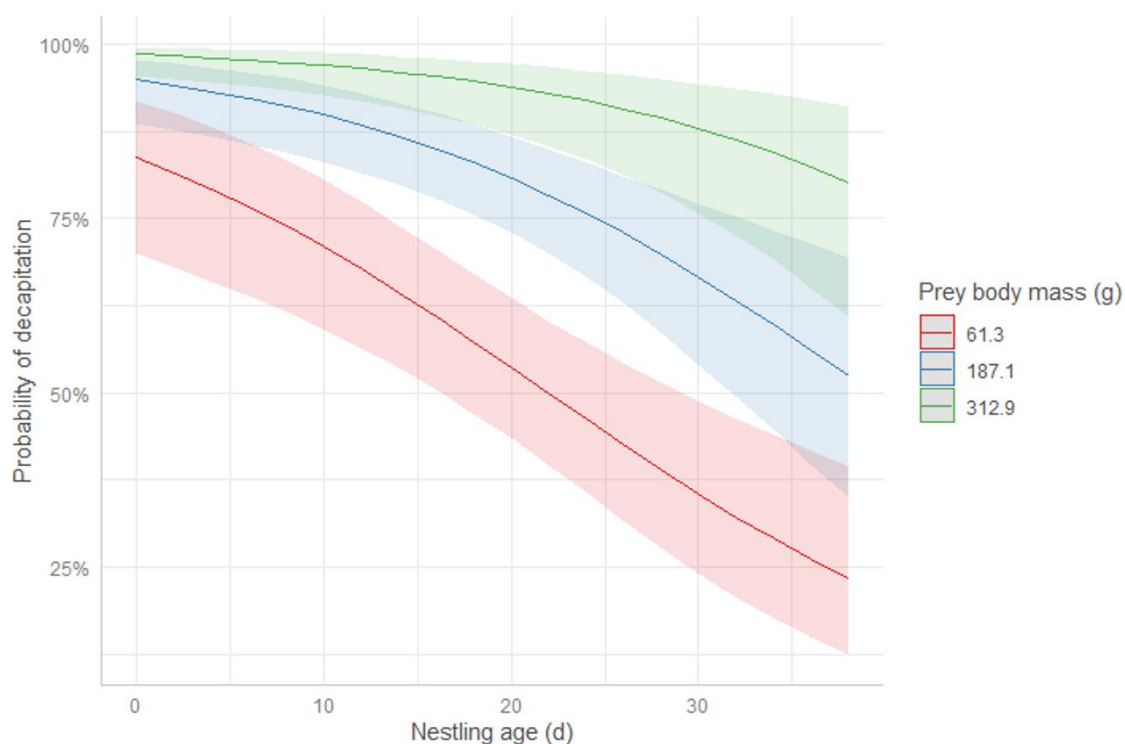


Figure 6. The predicted probability that a prey item was decapitated prior to delivery at the nest, as a function of nestling age and prey body mass (parameter estimates given in table 4).

Handling of prey items at the nest

Out of 267 prey items delivered at the peregrine nest, the feeder(s) was determined for 247. The female handled 163 (66 %) and the male handled 22 (9 %) while 27 (11 %) prey items were handled partly by the male and partly by the female. A nestling was observed feeding unassisted for the first time 28 days after hatching. The nestlings handled in total 35 of 247 prey items (14.2 %) during the nesting period.

The probability of that the parents fed the nestlings decreased with increasing nestling age. After 33 days, there was 50 % probability of that the nestlings fed unassisted. The nestlings handled prey items of lower body mass at an earlier point than prey items of higher body mass (table 5, figure 7). The male was recorded feeding the nestlings for the first time when the nestlings were 10 days old. The probability that the male was the feeder increased with increasing nestling age and was higher for starling (table 6, figure 8).

Table 5. Parameter estimates from a logistic regression model of the probability that the parents fed the nestlings rather than the nestlings fed unassisted. N=247

Explanatory variable	Estimate	SE	z value	p
Intercept	15.42	3.10	4.99	<0.0001
Nestling age	-0.54	0.11	-5.10	<0.0001
Prey body mass	0.01	0.003	3.60	0.0003

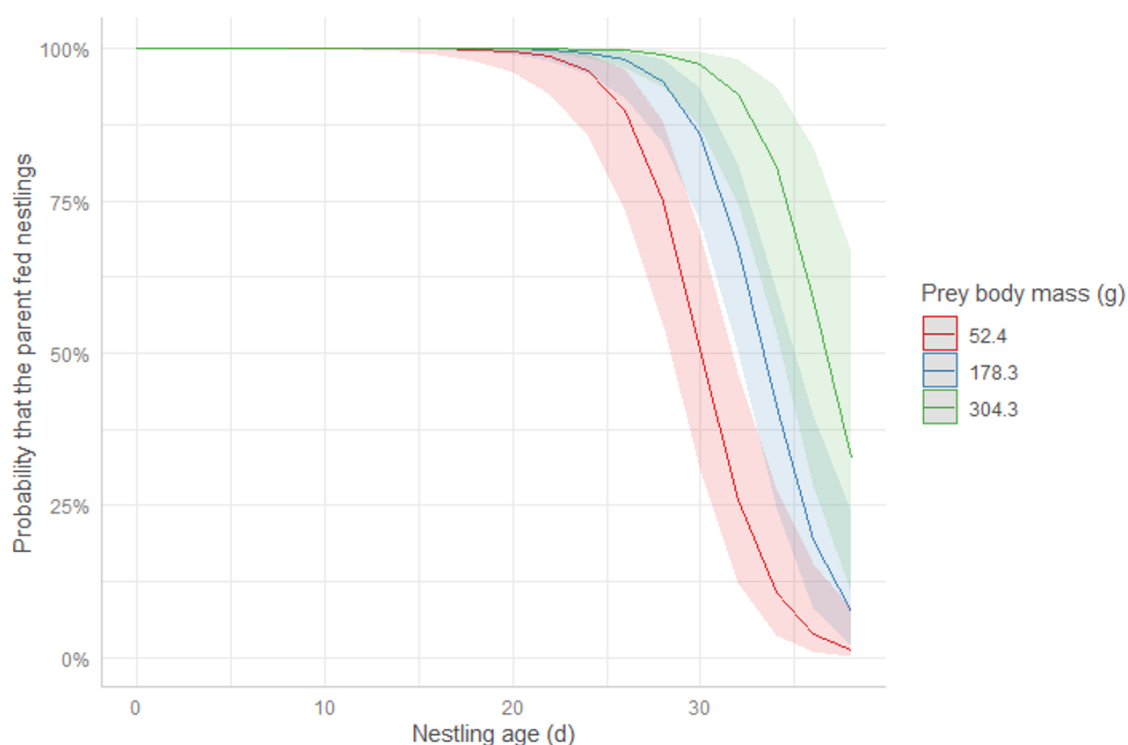


Figure 7. The predicted probability that the parents fed the nestlings rather than the nestlings fed unassisted, as a function of nestling age and prey body mass (parameter estimates given in table 5).

Table 6. Parameter estimates from a logistic regression model of the probability that the male peregrine fed the nestlings. N=185

Explanatory variable	Estimate	SE	z value	p
Intercept	-4.19	1.18	-3.54	0.0004
Nestling age	0.09	0.03	3.34	0.0008
Prey group (Pigeon and Crow)	0.26	1.13	0.23	0.82
Prey group (Small passerine)	-15.80	1481.70	-0.01	0.99
Prey group (Starling)	2.37	1.18	2.01	0.04
Prey group (Thrush)	-0.47	1.55	-0.30	0.76
Prey group (Wader)	0.28	1.31	0.21	0.83

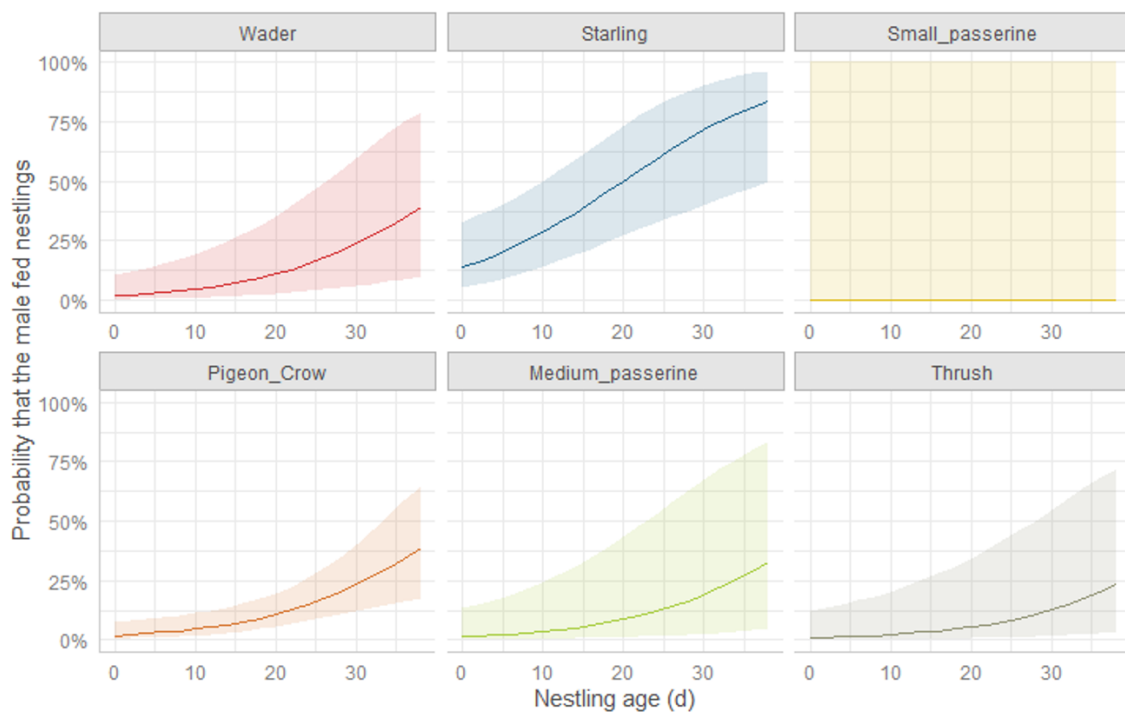


Figure 8. The predicted probability of that the male fed the nestlings, as a function of nestling age and prey group (parameter estimates given in table 6).

Discussion

Prey delivered at the nest

All the 267 prey items delivered at the peregrine nest were birds. This finding of a complete avian diet is in well agreement with previous studies of the peregrine (Cramp & Simmons 1980; Olsen et al., 2008; Ratcliffe 2010), although prey of other taxonomic groups, like rabbits, bats and snakes, have also been reported (Mearns, 1983; Lopez & Lopez, 2009; Ratcliffe, 2010; Dixon & Drewitt, 2018). Despite the fact that the peregrine is considered as a bird specialist (Ratcliffe, 2010), it appears to be quite a generalist in the composition of bird species included in its diet. A long-term study conducted by Dixon and Drewitt (2018) revealed a large breadth in the diet of urban Peregrines, in which remains of 102 bird species was found during a 20-year period. In Britain only, as much as 137 species are known to have been taken by the peregrine (Ratcliffe, 2010).

Nevertheless, the predominance of a few avian species, and other species forming a smaller part of the peregrines diet, is in line with several other studies (Mearns, 1983; Lopez & Lopez, 2009; Ratcliffe, 2010). This can be explained by the peregrines hunting what is locally available (Ratcliffe, 2010). Thus, the peregrine's diet might offer insight into the avifauna present in a particular region. Long-term studies have revealed shifts in the peregrine's diet caused by switches in the relative abundance of their prey species (Olsen et al., 2008). Such functional responses are to be expected for an opportunistic hunter like the peregrine. It has also been suggested that the peregrine tend to specialize in temperate climate, and rather generalize their diet when the climate gets more extreme (Jenkins, 2000; Lopez & Lopez, 2009).

In my study pigeons were the most important prey group, forming the highest proportion of delivered prey items (39 %), and of total gross prey body mass (72 %). This corresponds well with several other studies on the peregrines diet composition (Mearns, 1983; Rejt, 2001; Drewitt & Dixon, 2008; Lopez & Lopez, 2009; Ratcliffe, 2010; Dixon & Drewitt, 2018). Starling was another important prey group in my study, contributing to 16 % of total prey number and approximately 8 % of total prey gross body mass. Starlings are in Britain known to comprise a considerable part of peregrine's diet, especially during the breeding season (Drewitt & Dixon, 2008). In a study of the most important prey species for peregrines, conducted over five years (1975-1980), starling was found to be the second most important prey species by number and third most important by weight (Mearns, 1983). Starlings appear

to make up a considerable part of the peregrine's diet on other continents as well, such as in Australia (Olsen et al., 2008).

In the UK, there exists a well-known conflict between racing-dove enthusiasts and peregrine conservationists, due to the high losses of racing-doves to the peregrine (Humphreys et al., 2007; Ratcliffe 2010). The availability of racing doves varies temporally, both between the racing-season and the off-season, and within the racing-season due to races normally taking place on weekends. The location of racing and training routes determines the spatial variation in the abundance of racing pigeons (Dixon et al., 2018). Dixon et al (2018) found a steep increase in the occurrence of common pigeons in the peregrine's diet in April, a peak in June, and a decrease in September, thus in close connection with the pigeon racing season in Britain (April to September) (Humphreys et al., 2007). Such patterns are consistent with the peregrine falcon appearing to be an opportunistic generalist avian predator (Dixon et al., 2018).

Not surprisingly, considering the short distance between the nest and the coast, as much as ten species of waders were recorded in my study. However, when pooled, waders accounted for 10 % of total prey by number and approximately 5 % of total gross body mass, only. Though, this was slightly more than found in an inland study of urban nesting peregrines conducted in Norwich, UK, by Smith (2020a), who recorded 2 species of waders, which constituted less than 3 % of total prey by number and less than 4 % of total gross prey body mass. Contrary, in the same study, pigeons made up 60 % of total prey delivered at the nest and 86.1 % of total gross prey body mass, thus constituted an even higher proportion of the diet than in my study. Thrushes appeared to be the second most common prey category in the study conducted by Smith (2020a), and the most common prey category in an inland study conducted in Norway by Bech (2016). Starlings, which were the second most important prey group in my study, seemed to be of less importance in Smith's (2020a) study and absent in Bech's (2016) study. Starlings are of the species more frequently recorded in coastal compared to inland eyries (Mearns, 1983). However, lack of recorded starlings in Bech's study are possibly caused by the timing of seasonal migration. In a comparison of the diet of peregrines dwelling in various habitats, Mearns (1983) found no greater differences in prey items recorded among peregrines ranging in coastal versus inland habitats, than the differences between several inland habitats. This could be explained by a large proportion of other bird species, e.g., pigeons, doves and starlings, widespread in all different habitats, with the local prey availability representing a narrower proportion of the diet.

Factors determining the peregrine's choice of prey are many and complex. Availability, palatability, prey size, as well as individual variations in preferences and hunting ability might play important roles in prey selection, though these complexities are not yet fully understood (Ratcliffe, 2010).

Prey deliveries in relation to time of the day

During breeding, feeding activity peaked twice a day; in the morning hours (04:00-05:00) and in the evening hours (18:00-20:00). The feeding frequency was lower than randomly expected in the evening and through the night (21:00-03:00). This pattern is similar to those reported by Rejt (2001), who found the highest feeding activity in the morning between 04:00 and 06:00, and in the evening between 16:00 and 20:00. This is in well agreement with the peregrine being considered a daytime hunter. The peregrine hunts by sight and is somehow dependent on the light. However, food deliveries at night, as well as the occurrence of nocturnal immigrants in the peregrines diet, have been reported (Rejt, 2001; Drewitt & Dixon, 2008). In my study, eight prey items were delivered in the hours between sunset and sunrise. Notably, the studies of Rejt (2001) and Drewitt & Dixon (2008), as well as my own, were conducted in urban areas, thus artificial light from streets and buildings might be an important factor. However, it is also possible that the deliveries were derived from food caches. By capturing and storing temporally available food, a predator may increase its foraging efficiency as well as dampening the effect of critical hours when prey availability is scarce, such as through the night (Collopy, 1977).

Delivery of separate prey groups in relation to time of the day

For all prey groups tested, except waders, there was a higher delivery rate in the hours around sunrise and sunset. The delivery rates of pigeon, starling and thrush peaked in the exact same hours in the evening (18:00-19:00) and in the morning (06:00-07:00), except the delivery rate of thrush, which peaked even earlier in the morning (04 hours). Additionally, the delivery rate of thrush tended to peak during midday (11:00-12:00). Still, the general pattern for pigeon and starling, as well as all prey groups pooled, was a higher delivery rate in the morning and evening, with a calmer period in between, and a significantly low delivery rate between sunset and sunrise. Thereby, the peregrines could utilize the critical period before and after a long

and dark night, which is unfavourable time of day for a daytime hunter. Waders differed strikingly from the general pattern of delivery. The delivery rate of waders peaked only once, during solar noon (12:00-13:00). This could be explained by the foraging pattern of coastal shorebirds, which is temporally and spatially determined by the tidal cycle (van den Hout, 2010).

When trying to explain the patterns of delivery rate, it is necessary to consider both what drives the activity pattern of the different prey groups, as well as other factors that might determine the peregrine's choice of prey. To minimize predation risk, birds need to weigh forage activities against predation risk, a so called "starvation-predation trade-off" (Bonter et al., 2013). Therefore, foraging activities would be expected to be less efficient when feeding takes place in a high-risk area or during a time of the day when the risk of starvation is low. Conversely, time spent foraging is expected to be higher in low-risk areas, as well as in time of day when risk of starvation is higher, e.g., in the morning hours when most individuals are hungry (Quinn, 2012). Bird species living in different locations due to unique niches, would be expected to experience different patterns of predation. If the daily predation risk peaks in the morning and in the evening, bird should locate their foraging activities to middle of the day. Contrary, birds experiencing high predation risk during midday should tend to forage most intensely in the morning and in the evening (Pravosudov, 2001). However, such predictions are not always transferable to what is the cause in real life. Bonter et al (2013) found that the feeding activity of the bird population investigated continuously increased throughout the day until sunset, and then declined sharply.

Like other raptors, peregrines are single prey loaders, which means they are only capable of carrying one prey item at a time. The peregrine should consider the distance to a hunting area to optimize their hunting strategy. When the hunting area is in short distance to the nest, both large and small prey may be favoured, while only larger prey would be profitable when hunting in greater distance to the nest. When prey size is smaller, the feeding rate would be expected to be higher (Newton, 1979; Slagsvold & Sonnerud, 2007).

Nest provisioner

Of the recorded deliveries where the delivering sex was identified, the female delivered 51 % of the prey items. This is somewhat in contrast with results from studies of the asymmetric

parental roles of peregrines, stating that the female usually stays at the nest brooding and feeding the nestlings, while the male performs most of the hunting (Newton, 1979; Cramp and Simmons, 1980; Ratcliffe, 2010). Particularly in the beginning of the nesting period, the male performs all the hunting activity, followed by a food-transfer between the male and the female at the nest or in vicinity to the nest (Newton, 1979). This food-transfer did not necessarily occur in reach of the camera view in my study. Thus, there is reason to believe that the male in reality captured more prey than the female.

Whether the female was the delivering parent varied between prey groups and was affected by nestling age. The probability that the female was the delivering parent was high for all prey groups in the very beginning of the nesting period, except for medium passerines and thrushes, the latter might be explained by the fact that thrushes did not become a common prey until a later point in the nesting period. Shortly after hatching the delivery rate of wader and starling decreased drastically with increasing nestling age, of which the latter decreased to zero after twelve days. This is about the time where the female usually allows the male to feed the nestlings (Ratcliffe, 2010). As the nestlings get older and slightly less dependent on continuous brooding and shading, the female is able to contribute to hunting activities. At the same time as the female becomes more absent from the nest, the male usually increases his participation in feeding the nestlings (Rejt, 2001). In my study the male was observed delivering a prey item directly to the nestlings for the first time after ten days. From this point, direct delivery of prey items and feeding by the male occurred increasingly frequent. This was also seen in studies of other species, like the Eurasian Kestrel (*Falco tinnunculus*), where the male was more likely to deliver a prey item directly at the nest as the nestlings grew older (Sonerud et al., 2013). Individual variation in hunting and feeding patterns may occur. If food is less abundant, or if the male's hunting efforts is insufficient to satisfy the nestlings, the female may participate more in hunting activities, despite an increased risk of predators at the unguarded nest (Newton, 1979).

The probability that the female delivered a pigeon or crow to nest was overall high through the nesting period and decreased only slightly as the nestlings grew older. As much as 71 % of the pigeon deliveries and all the crow deliveries was performed by the female.

Contrastingly, 77 % of the starling deliveries was performed by the male. It is tempting to draw a conclusion of that the female in general had captured prey of higher body mass than the male. Partitioning within the food spectrum between the larger and the smaller sex is one

of many hypotheses proposed to explain the reversed sexual size dimorphism among raptors (Newton, 1979). This theory lack evidence and does not account for the food-transfer between the male and the female, which are known frequently to occur prior to delivery (Sonerud et al., 2013). Sonerud et al (2013) found no difference in prey selection between male and female kestrels, another raptor species with known high degree of RSD. The observed difference in size of prey delivered at the nest was rather caused by the allocation of larger prey items between the male and the female prior to delivery, meanwhile smaller prey items were delivered directly to the nestlings by the male. Thus, looking exclusively at prey deliveries at the nest would cause a bias when investigating the inter-sexual differences in prey selection by raptors (Sonerud et al., 2013).

Preparing prey prior to delivery

Of the prey items 52 % were decapitated prior to delivery. Additionally, most of the prey items were plucked or eaten at prior to delivery, although this was not included in my analysis. The probability of a prey being decapitated was affected by prey category, of which the probability of decapitation was highest for pigeons and middle-sized passerines. Whether a prey item was decapitated or not was also affected by prey body mass, with increasing probability of decapitation with heavier prey items. The probability of decapitation decreased for all prey categories, as well as for all weight classes, with increasing nestling age. This is in accordance with the feeding constraint hypothesis, which state that the degree of prey preparation increases with prey size and decreases with nestling age (Slagsvold & Wiebe, 2007; Steen et al., 2010). Removing the head of a prey is a way of modifying it to the swallowing capacity of the nestlings (Steen et al., 2010), and is usually taking place at the capture site, or in vicinity of the nest (Newton, 1979), or at the nest as seen regularly in my study.

In my study pigeon, which is a relatively large bird, comprised 39 % of prey items delivered at the nest. A prey at this size requires more preparation than a smaller prey, considering the high mass of undesirable and low profitable parts, like the skull, which would exceed the gape of a young nestling. Smaller birds (e.g., starling and small passerines) tend to have softer skulls and may be easier to ingest by the nestlings at an earlier stage (Steen et al., 2010). The greater requirement of preparation of larger compared to smaller prey was in my study reflected by a higher rate of decapitation of the former. This may explain why the male

allocate a greater proportion of prey of high body mass to the female, so that she can spend time preparing the prey and feed the nestlings. When the female is in charge of brooding and feeding, the male can maximize his hunting efficiency by delivering prey completely or partly unprepared, spending as little time as possible at the nest, thus minimizing time between revisiting hunting areas with temporary high availability of prey (Slagsvold & Sonerud, 2007; Sonerud et al., 2013).

Handling of prey items at the nest

In 85 % of the feeding events, the feeder was one (or both) of the parents. The probability that the parents fed the nestlings decreased as the nestlings grew older. During the early part of the nesting period, the nestlings are fed with only small and soft lumps of meat (Newton, 1979). When the nestlings are satisfied the female will finish off the rest of the prey herself (Newton, 1979). As the nestlings grow older, less preparation is needed, and the nestlings are served with other parts of the prey (Newton, 1979). This goes on until a point where the nestlings are capable of feeding unassisted and the prey items are often simply dumped at the nest by the parents (Newton, 1979). The nestlings were observed feeding unassisted 29 days after hatching, corresponding well with the findings of Cramp & Simmons (1980) and Ratcliffe (2010), that peregrine nestlings are able to handle a prey by themselves after 30 and 31 days respectively, after which it happened increasingly frequent. However, signs of self-feeding are, as in my study, seen in earlier stages (Ratcliffe, 2010). Whether a prey item was handled unassisted was affected by prey body mass, of which prey of high body mass was handled at a later point than prey of low body mass. Raptors usually capture relatively large prey compared to most other birds. Furthermore, the handling time of avian prey is longer than for mammalian and invertebrate prey, due to the high amount of protruding and uneatable prey parts (Slagsvold & Sonerud, 2007). This may explain the long period of which the nestlings are incapable of handling a prey item unassisted, and thus the extended time of parental assistance. Even when the nestlings are capable of feeding unassisted, the female may continue to feed the nestlings to ensure fair allocation of food between them, as well as to herself (Newton, 1979).

The long handling time seen in raptors feeding on avian prey may favour separate sex roles, in which one of the parents perform most of the hunting while the other specialise on prey preparation and feeding the nestlings (Slagsvold & Sonerud, 2007). Thus, type and size of

prey comprising the diet, has been suggested to explain RSD in raptors (Slagsvold & Sonerud, 2007). As Newton (1979) noted; the more agile and larger the prey is compared to the body size of the raptor that hunts it, the higher degree of RSD.

In the beginning of the nesting period the feeder was exclusively the female. Among peregrines and raptors in general, the female is known to be very protective over her young (Newton, 1979; López-López et al., 2008; Sonerud et al., 2013; Sonerud et al., 2014b), and the male are even seen chased away by the female if he approaches the nest. However, the degree to which the female shows aggression against the male varies interspecifically (Cramp & Simmons, 1980) and may also vary intraspecifically. The female in my study did not show any particular aggression against the male, and rather accepted his presence even when the nestlings were relatively young. The very first time the male was recorded feeding the nestlings was 10 days after hatching, and after this point the male fed the nestlings regularly. Male participation in feeding the nestlings is not unusual for peregrines, but it happens rarely among other species of raptors (Ratcliffe, 2010). The probability that the male was the feeder was higher for starling than for all other prey groups. The male never fed the nestlings with small passerines, they were either handled unassisted by the nestlings, or they were likewise to larger prey items handed over to the female. Thus, starling seemed to be the optimal size of prey for the male to handle at the nest. Considering the hypotheses of that the male are less capable than the female of feeding the nestlings (Newton, 1979) it is conceivable that the male specialized on handling this type of prey, while the rest of the prey types were allocated to the female.

In my study the abundance of prey seemed to be relatively high, thus access to food was not a limiting factor. This could be the reason of the female's low degree of protective behaviour and aggression towards the male, observed at the nest. Thus, the male was allowed to participate in nestling care through the whole period. Furthermore, with high access to prey at short distance from the nest, the female was free to contribute to hunting activities without having to expose the young to danger. For further studies it would be interesting to investigate whether high prey accessibility only applies as observed to the Cromer peregrines, or if this is the cause for urban dwelling peregrines in general. If the latter is the case, we might expect improved breeding success and nestling survival of urban peregrines compared to rural ones.

Limitations

The peregrine's handling of prey appeared to be quite rough, often "destroying" the prey item completely prior to delivery. This resulted in challenging work when I tried to identify the prey species. In several cases only smaller body parts like bones and lumps of meat were delivered at the nest. Without characteristic parts like feathers, feet, beak, colour of the plumage, as well as body size, identification of prey species was difficult. Thus, a large proportion of prey items was identified to genus, family, or order level only. Quite often, the feeder would turn its back to the camera, almost as she or he was aware of being watched, which further complicated identification of prey.

The activity at the peregrine nest was recorded through two different camera angles. The first angle presented a view from the outside looking in, though close to and at the same level as the birds at the nest. The first weeks mostly this camera angle was used. The second angle had a view from the inside looking out, also in immediate vicinity to the nest but furthermore showing more of the roof outside the nesting box, and with the camera placed a little higher than the first one. This angle was mostly used the last weeks of the nesting period. The image from the second camera angle was noticeably less sharp than the image from the first angle. Thus, identification of prey items in the recordings from the second angle were a lot more challenging, and sometimes impossible. However, the second camera angle captured more of what happened outside the nest, thus, this view provided more information of any food-transfer between the sexes prior to delivery. For further studies my recommendation is to cover more of the nesting period through the first camera angle, as this in several would support the highest recording quality. Alternatively, my proposal would be to include both camera angles in the recordings, at least in the second half of the nesting period. In this way the observer would be given the opportunity to identify more of the prey delivered at the nest, especially in cases where the feeder turns its back to one of the cameras.

Conclusion

The diet of the Cromer peregrines included a wide variation of prey species associated with both urban and non-urban areas. All prey captured were birds, of which pigeon species proved to be the most common, suggesting that pigeons are an important prey group for the peregrines in the breeding season. Food availability was not a limiting factor and rather

appeared to be relatively high. The female delivered more prey items than the male, and this differed from the general pattern associated with RSD in raptors. However, this was probably caused by prey items being transferred to the female outside the nesting box. Both parents fed the nestlings, though the female more than the male, and the female seemed to show a low degree of aggression towards the male. The nestlings were able to feed unassisted as of 29 days after hatching, although occasional parental assistance continued until fledging. Due to the high mass of indigestible parts of avian compared to other types of prey, more preparation was needed prior to ingestion. This may explain the extended need of parental care seen in raptors with a complete avian diet (Sonerud et al., 2014a,b). Continuous video monitoring has offered a unique opportunity to gain close and detailed insight into the life and functions of breeding peregrines. In future studies it would be useful to modify this method, e.g., strive to include data on food-transfer between the sexes simultaneously with recordings of the nest, and thereby gain a better understanding of the mechanisms behind this phenomenon.

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Appendix

Appendix 1. Gross prey body mass, defined as the estimated weight of the prey item when captured, based on Cramp & Simmons (1983), Cramp (1985, 1988), Cramp & Perrins (1994), Selås (2001) and G.A. Sonerud (pers. comm.)

Prey species	Gross body mass (g)
Water rail (<i>Rallus aquaticus</i>)	120
Red knot (<i>Calidris canutus</i>)	140
Ringed plover (<i>Charadrius hiaticula</i>)	60
Sanderling (<i>Calidris alba</i>)	60
Dunlin (<i>Calidris alpina</i>)	60
Temminck's stint (<i>Calidris temminckii</i>)	30
Little stint (<i>Calidris minuta</i>)	30
Common redshank (<i>Tringa tetanus</i>)	120
Spotted redshank (<i>Tringa erythropus</i>)	140
Common snipe (<i>Gallinago gallinago</i>)	100
Sandpiper (small) (Scolopacidae)	60
Pigeon (<i>Columba</i> spp.)	316
Common swift (<i>Apus apus</i>)	40
Great spotted woodpecker (<i>Dendrocopos major</i>)	90
Mistle thrush (<i>Turdus viscivorus</i>)	130
Common blackbird (<i>Turdus merula</i>)	95
Thrush (<i>Turdus</i> spp.)	80
Western jackdaw (<i>Corvus monedula</i>)	156
Crow (<i>Corvus</i> spp.)	500
Starling (<i>Sturnus vulgaris</i>)	80
House sparrow (<i>Passer domesticus</i>)	30
Sparrow (Passeridae)	30
European goldfinch (<i>Carduelis carduelis</i>)	15
Thrush/Starling indet.	80
Medium-sized passerines indet.	80
Small passerines indet.	15

Appendix 2. Candidate models for the cosinor analysis of daily activity. The response variable “Prey” was whether there was a prey delivery within an hour-block during the 24-h monitoring period. The explanatory variable was time of the day. Model ‘M’1 is the null-model (intercept only) without any effect of the time of the day. Models “M2-6” with up to five harmonics (24, 12, 8, 6, and 4.8 h, respectively) to modulate the signal.

M1: `glm(Prey~1,data=visits,family=binomial)`

M2: `glm(Prey~I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24)),data=visits,family=binomial)`

M3: `glm(Prey~I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+
I(cos(2*2*pi*Hour/24))+I(sin(2*2*pi*Hour/24)),data=visits,family=binomial)`

M4: `glm(Prey~I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+
I(cos(2*2*pi*Hour/24))+I(sin(2*2*pi*Hour/24))+
I(cos(3*2*pi*Hour/24))+I(sin(3*2*pi*Hour/24)),data=visits,family=binomial)`

M5: `glm(Prey~I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+
I(cos(2*2*pi*Hour/24))+I(sin(2*2*pi*Hour/24))+
I(cos(3*2*pi*Hour/24))+I(sin(3*2*pi*Hour/24))+
I(cos(4*2*pi*Hour/24))+I(sin(4*2*pi*Hour/24)),data=visits,family=binomial)`

M6: `glm(Prey~I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+
I(cos(2*2*pi*Hour/24))+I(sin(2*2*pi*Hour/24))+
I(cos(3*2*pi*Hour/24))+I(sin(3*2*pi*Hour/24))+
I(cos(4*2*pi*Hour/24))+I(sin(4*2*pi*Hour/24))+
I(cos(5*2*pi*Hour/24))+I(sin(5*2*pi*Hour/24)),data=visits,family=binomial)`

Appendix 3. Model selection based on AICc, for all prey deliveries as a function of time of the day. Best model in bold.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
5	9	874.58	0.00	0.62	0.62	-428.19
6	11	876.85	2.27	0.20	0.81	-427.28
4	7	876.98	2.40	0.19	1.00	-431.43
3	5	914.97	40.38	0.00	1.00	-452.45
2	3	996.10	121.52	0.00	1.00	-495.04
1	1	1044.44	169.86	0.00	1.00	-521.22

Appendix 4. Parameter estimates from the selected model (Model 5), for all prey deliveries as a function of time of the day.

Explanatory values	Estimates	SE	z-value	p-value
(Intercept)	-2.37	0.35	-6.71	<0.0001
I(cos(2 * pi * Hour/24))	-3.20	0.65	-4.93	<0.0001
I(sin(2 * pi * Hour/24))	0.01	0.14	0.07	0.94
I(cos(2 * 2 * pi * Hour/24))	-2.76	0.52	-5.32	<0.0001
I(sin(2 * 2 * pi * Hour/24))	-0.24	0.19	-1.27	0.20
I(cos(3 * 2 * pi * Hour/24))	-1.62	0.35	-4.58	0.00
I(sin(3 * 2 * pi * Hour/24))	-0.14	0.19	-0.72	0.47
I(cos(4 * 2 * pi * Hour/24))	-0.51	0.21	-2.37	0.02
I(sin(4 * 2 * pi * Hour/24))	-0.06	0.16	-0.39	0.70

Appendix 5. Model selection based on AICc, for pigeons delivered at the nest, as a function of time of the day. Best model in bold.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
4	7	557.76	0.00	0.65	0.65	-271.82
5	9	559.40	1.64	0.29	0.93	-270.60
6	11	562.60	4.84	0.06	0.99	-270.15
3	5	566.76	8.99	0.01	1.00	-278.35
2	3	598.23	40.47	0.00	1.00	-296.10
1	1	614.88	57.12	0.00	1.00	-306.44

Appendix 6. Parameter estimates from the selected model (Model 4), for pigeons delivered at the nest, as a function of time of the day.

Explanatory values	Estimates	SE	z-value	p-value
(Intercept)	-3.07	0.31	-9.76	<0.0001
I(cos(2 * pi * Hour/24))	-2.24	0.54	-4.11	<0.0001
I(sin(2 * pi * Hour/24))	-0.15	0.18	-0.84	0.40
I(cos(2 * 2 * pi * Hour/24))	-1.77	0.39	-4.51	<0.0001
I(sin(2 * 2 * pi * Hour/24))	-0.46	0.23	-2.03	0.04
I(cos(3 * 2 * pi * Hour/24))	-0.82	0.26	-3.19	0.001
I(sin(3 * 2 * pi * Hour/24))	-0.13	0.21	-0.63	0.53

Appendix 7. Model selection based on AICc, for starlings delivered at the nest, as a function of time of the day. Best model in bold.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
4	7	323.18	0.00	0.68	0.68	-154.53
5	9	325.96	2.78	0.17	0.84	-153.88
3	5	326.70	3.52	0.12	0.96	-158.32
6	11	328.90	5.72	0.04	1.00	-153.30
2	3	338.88	15.70	0.00	1.00	-166.43
1	1	341.74	18.55	0.00	1.00	-169.87

Appendix 8. Parameter estimates from the selected model (Model 4), for starlings delivered, as a function of time of the day.

Explanatory values	Estimates	SE	z-value	p-value
(Intercept)	-4.01	0.48	-8.37	<0.0001
I(cos(2 * pi * Hour/24))	-2.25	0.83	-2.70	0.01
I(sin(2 * pi * Hour/24))	-0.02	0.25	-0.10	0.92
I(cos(2 * 2 * pi * Hour/24))	-1.91	0.60	-3.17	0.001
I(sin(2 * 2 * pi * Hour/24))	0.01	0.31	0.02	0.98
I(cos(3 * 2 * pi * Hour/24))	-0.93	0.39	-2.38	0.02
I(sin(3 * 2 * pi * Hour/24))	-0.10	0.30	-0.34	0.73

Appendix 9. Model selection based on AICc, for thrushes delivered at the nest, as a function of time of the day. Best model in bold.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
4	7	203.97	0.00	0.66	0.66	-94.92
6	11	207.00	3.04	0.14	0.80	-92.35
5	9	207.58	3.62	0.11	0.91	-94.69
1	1	208.96	4.99	0.05	0.96	-103.48
2	3	210.88	6.92	0.02	0.98	-102.43
3	5	211.10	7.13	0.02	1.00	-100.51

Appendix 10. Parameter estimates from the selected model (Model 4), for thrushes delivered at the nest, as a function of time of the day.

Explanatory values	Estimates	SE	z-value	p-value
(Intercept)	-4.41	0.45	-9.73	<0.0001
I(cos(2 * pi * Hour/24))	-1.23	0.69	-1.78	0.08
I(sin(2 * pi * Hour/24))	0.33	0.32	1.01	0.31
I(cos(2 * 2 * pi * Hour/24))	-1.24	0.56	-2.21	0.03
I(sin(2 * 2 * pi * Hour/24))	-0.41	0.39	-1.05	0.29
I(cos(3 * 2 * pi * Hour/24))	-1.34	0.48	-2.81	0.004
I(sin(3 * 2 * pi * Hour/24))	0.003	0.37	0.01	0.99

Appendix 11. Model selection based on AICc, for waders delivered at the nest, as a function of time of the day. Best model in bold.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
3	5	227.42	0.00	0.44	0.44	-108.68
2	3	228.68	1.26	0.24	0.68	-111.33
6	11	229.23	1.81	0.18	0.85	-103.47
4	7	230.23	2.81	0.11	0.96	-108.05
5	9	232.45	5.03	0.04	1.00	-107.13
1	1	237.73	10.30	0.00	1.00	-117.86

Appendix 12. Parameter estimates from the selected model (Model 2), for waders delivered at the nest, as a function of time of the day.

Explanatory values	Estimates	SE	z-value	p-value
(Intercept)	-3.81	0.26	-14.68	<0.0001
I(cos(2 * pi * Hour/24))	-1.13	0.35	-3.25	0.001
I(sin(2 * pi * Hour/24))	-0.06	0.30	-0.21	0.83

Appendix 13. Candidate models used in the statistical analysis of the predicted probability that a prey item was delivered at the nest by the female:

- M1: `glm(Delivering_parent~Nestling_age*Weight,data=Delivery,family=binomial)`
M2: `glm(Delivering_parent~Nestling_age+Weight,data=Delivery,family=binomial)`
M3: `glm(Delivering_parent~Weight,data=Delivery,family=binomial)`
M4: `glm(Delivering_parent~Nestling_age,data=Delivery,family=binomial)`
M5: `glm(Delivering_parent~Nestling_age*Prey_group,data=Delivery,family=binomial)`
M6: `glm(Delivering_parent~Nestling_age+Prey_group,data=Delivery,family=binomial)`
M7: `glm(Delivering_parent~Prey_group,data=Delivery,family=binomial)`

Model selection based on AICc among seven types of candidate models. Of the probability that a prey item was delivered at the peregrine nest by the female. Best model in bold.

Model	Df	AIC
1	4	299.74
2	3	298.66
3	2	305.54
4	2	331.37
5	12	281.37
6	7	298.79
7	6	307.66

Appendix 14. Analysis of variance table (ANOVA). Distribution of prey species delivered at the peregrine nest, in relation to nestling age. N=244

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Prey group	5	3222.4	644.49	6.72	<0.0001

Appendix 15. Candidate models used in the statistical analysis of the predicted probability that a prey item was decapitated prior to delivery:

M1: `glm(Decap~Nestling_age*Prey_group,data=Delivery,family=binomial)`

M2: `glm(Decap~Nestling_age+Prey_group,data=Delivery,family=binomial)`

M3: `glm(Decap~Prey_group,data=Delivery,family=binomial)`

M4: `glm(Decap~Nestling_age,data=Delivery,family=binomial)`

M5: `glm(Decap~Nestling_age*Weight,data=Delivery,family=binomial)`

M6: `glm(Decap~Nestling_age+Weight,data=Delivery,family=binomial)`

M7: `glm(Decap~Weight,data=Delivery,family=binomial)`

Model selection based on AICc among seven types of candidate models. Of the probability that a prey item was decapitated prior to delivery at the nest, as a function of nestling age, prey group and weight. Best model(s) in bold.

Model	Df	AIC
1	12	193.39
2	7	192.40
3	6	204.75
4	2	234.25
5	4	195.93
6	3	194.61
7	2	212.56

Appendix 16. Candidate models used in the statistical analysis of the predicted probability that the parents fed the nestlings rather than the nestlings fed unassisted:

- M1: `glm(ParentFeeder~Nestling_age*Weight,data=Delivery,family=binomial)`
M2: `glm(ParentFeeder~Nestling_age+Weight,data=Delivery,family=binomial)`
M3: `glm(ParentFeeder~Weight,data=Delivery,family=binomial)`
M4: `glm(ParentFeeder~Nestling_age,data=Delivery,family=binomial)`
M5: `glm(ParentFeeder~Nestling_age*Prey_group,data=Delivery,family=binomial)`
M6: `glm(ParentFeeder~Nestling_age+Prey_group,data=Delivery,family=binomial)`
M7: `glm(ParentFeeder~Prey_group,data=Delivery,family=binomial)`

Model selection based on AICc among four types of candidate models. Of the probability that the parents fed the nestlings rather than the nestlings fed unassisted, as a function of nestling age and prey group. Best model in bold.

Model	Df	AIC
1	4	67.20
2	3	67.47
3	2	187.81
4	2	85.31
5	12	74.67
6	7	75.95
7	6	184.46

Appendix 17. Candidate models used in the statistical analysis of the predicted probability that the male fed the nestlings:

M1: `glm(MaleFeeder~Nestling_age*Weight,data=Delivery,family=binomial)`

M2: `glm(MaleFeeder~Nestling_age+Weight,data=Delivery,family=binomial)`

M3: `glm(MaleFeeder~Weight,data=Delivery,family=binomial)`

M4: `glm(MaleFeeder~Nestling_age,data=Delivery,family=binomial)`

M5: `glm(MaleFeeder~Nestling_age*Prey_group,data=Delivery,family=binomial)`

M6: `glm(MaleFeeder~Nestling_age+Prey_group,data=Delivery,family=binomial)`

M7: `glm(MaleFeeder~Prey_group,data=Delivery,family=binomial)`

Model selection based on AICc among four types of candidate models. Of the probability that the male fed the nestlings, as a function of nestling age. Best model in bold.

Model	Df	AIC
1	4	134.43
2	3	133.55
3	2	138.67
4	2	132.18
5	12	123.80
6	7	125.00
7	6	134.87



Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway