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Abstract

The diet, diel pattern of prey deliveries, and prey handling behaviour of a nesting pair of the peregrine falcon (*Falco peregrinus*) in southeast Norway was studied with video recording equipment at the nest and direct observations of parental behaviour and interactions in the vicinity. The study was conducted from the single nestling was 10 days old until it fledged. A total of 88 prey items were recorded delivered, all of which were birds. The most important prey type were thrushes (*Turdus* sp.), by both numbers (47.7%) and net body mass delivered (57.1%). Small and larger passerines pooled was the next most important prey type by number (39.8%), but contributed little (9.8%) by net body mass. Woodpigeons (*Columba palumbus*) made up only 6.8% by numbers and was the next most important prey type by net body mass delivered (29.2%). The probability of delivering a prey item at the nest was highest during morning and evening, and lowest around midday. The probability of delivering a thrush rather than a small passerine was low in the morning and the evening, and high near midday. The female was recorded to deliver the majority of prey (95%) at the nest, whereas the male started to deliver prey items directly at the nest from when the nestling was 30 days old. Outside the nest, I observed the male was delivering some prey items to the female, whereas the female dismembered the prey and fed the nestling. The probability that a prey item had been plucked prior to delivery at the nest decreased with increasing prey body mass when the nestling fed unassisted, but not when the female fed the nestling. The probability that a prey item was decapitated before delivery was lower if the prey item was a thrush than when it was another kind of bird, and decreased with nestling age. The nestling required maternal assistance in feeding until it was 29 days old. Handling time increased with body mass of the prey, both when the female assisted in feeding the nestling and when the nestling fed unassisted. I was unable to decide whether some of the prey items delivered at the nest had been retrieved from caches, so the time of delivery was not necessarily shortly after capture for all prey. Future studies should include this aspect by the use of a thermal-imagery camera in addition to regular video camera.

Sammendrag

Dietten, døgnmønster for byttedyrleveringer, og behandling av byttedyr for et hekkende par av vandrefalk (*Falco peregrinus*) ble studert med videoopptak på reiret og direkteobservasjoner av atferden til og interaksjonene mellom foreldrene i nærheten av reirområdet. Studiet ble gjennomført i sørøst-Norge fra da den eneste ungen i reiret var 10 dager gammel til den ble flygedyktig. Totalt 88 byttedyr ble filmet levert, hvorav alle var fugler. Den viktigste byttetypen var troster (*Turdus* sp.), både i antall (47.7%) og i nettovekt levert (57.1%). Småfugl var den nest viktigste byttetypen i antall (39.8%), men bidro lite (9.8%) i nettovekt. Ringdue (*Columba palumbus*) utgjorde kun 6.8% i antall og var den nest viktigste byttetypen i nettovekt (29.2%). Sannsynligheten for å levere et byttedyr til reiret var høyest på morgenen og kvelden, og lavest midt på dagen. Sannsynligheten for å levere en trost i stedet for en småfugl var lav på morgenen og kvelden, og høy midt på dagen. Hunnen leverte, ut fra opptakene, flesteparten av byttedyrene (95%) til reiret, mens hannen begynte å levere byttedyr direkte til reiret fra da ungen var 30 dager gammel. Utenfor reiret observerte jeg at hannen allokerte byttedyr til hunnen, mens hunnen preparerte byttedyret og matet ungen. Sannsynligheten for at et byttedyr var ribbet før levering til reiret minket med økende byttevekt når ungen spiste selv, men ikke når hunnen matet ungen. Sannsynligheten for at et byttedyr ble dekapitert før levering var lavere for troster enn for andre typer fugl, og minket med ungens alder. Ungen behøvde å bli matet av hunnen frem til den var 29 dager gammel. Håndteringstid økte med byttevekt, både når hunnen matet ungen og når ungen spiste selv. Jeg kunne ikke finne ut om noen av de leverte byttedyrene hadde blitt hentet fra et lagringssted, og derfor var ikke leveringstidspunktet nødvendigvis alltid like etter at byttedyret ble fanget. Fremtidige studier burde inkludere dette aspektet ved å bruke et termisk kamera som supplement til videokamera.

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Introduction

Among birds that provision food to their young, raptors (hawks (Accipitriformes), falcons (Falconiformes), and owls (Strigiformes)) are unique in having asymmetric parental roles where the female performs most of the care at the nest including handling and feeding, and the male provides all of the food for the family (Newton 1979, Cramp & Simmons 1980). The evolution of asymmetric roles is a resolve of the conflict between collecting and processing food, which due to the prolonged time spent feeding would have otherwise led to one parent waiting for the other to finish feeding the young (Sonerud et al. 2014a). Raptors catch and hold prey with their feet, which frees their bill to be used as a specialised tool for tearing a prey into small pieces that are then ingested (Slagsvold & Sonerud 2007). Handling time of prey are for this reason extended, and is expected to be increased further while provisioning nidicolous young, when the morsels torn off the prey must be small enough for the nestlings to ingest. Efficient handling would therefore be important to reduce handling time (Steen et al. 2010). The female is confined to the nest for handling and feeding dependent nestlings until they have become physically capable of handling prey items without assistance, after which she assists the male in provisioning food (Newton 1979, Ratcliffe 2010). The time at which assisted feeding cease is related to the prey type delivered and size of prey (Sonerud et al. 2014a). Birds, with protruding appendages such as bill, wings and long tarsi, and bodies covered with feathers, need more careful handling and preparation prior to feeding and require the nestlings to be more physically developed to handle, than other prey types that can be swallowed whole (Steen et al. 2010, Sonerud et al. 2013, 2014a,b). In addition, the female may continue to feed the nestlings large prey items long after the nestlings are able to handle prey on their own (Sonerud et al. 2014a). The distinct parent roles has been thought to relate to the evolution of reversed sexual size dimorphism (RSD) in raptors, where the female is larger than the male (Newton 1979, Ratcliffe 2010). The degree of which RSD is expressed vary between raptors, and has been suggested to relate to the type of prey and size of prey caught, and the extent in time of which nestlings require assistance in being fed, i.e. how long the asymmetrical parental roles are upheld (Sonerud et al. 2014a). Detailed studies on the degree of preparation and handling in relation to the type of prey and the extent of parental care have, however, been conducted for only a handful of species of raptor (Sonerud et al. 2014a).

The peregrine falcon (*Falco peregrinus*), hereafter termed as peregrine, is widespread on all continents except Antarctica, and occur in many types of habitats, but avoid densely forested areas (del Hoyo et al. 1994, Ratcliffe 2010). It prefers tall cliffs surrounded by open landscapes for breeding, both for the inaccessibility for nest predators and as they provide optimal hunting conditions (Jenkins 2000a). Its diet has been reported to consist chiefly of birds, with rare occasions of mammals, reptiles and fish (Cramp & Simmons 1980, Bradley & Oliphant 1991, del Hoyo et al. 1994, Hetzler 2013). Barton & Houston (1994, 1996) found that raptors that hunt by actively chasing prey, such as the peregrine, had evolved a lighter and smaller digestive tract and larger pectoral muscles than raptors hunting slow-moving prey, for providing the agility and acceleration necessary to catch fast-moving, agile prey. The sizes of avian prey reported taken by the peregrines range from the smallest songbirds at 9 g to well over 1000 g (e.g. Mearns 1983), and lists of bird species known to have been taken as prey totals over 130 in Britain and 210 in Central Europe (Ratcliffe 2010). Despite the high diversity of prey recorded, the trend is that a few prey species make up the bulk of the diets and the majority of prey taken lie in the weight range of 50-500 g (Ratcliffe 2010). Prey species are taken according to their availability (Ratcliffe 2010), which can be defined as the number of a particular prey species that are present and can be found by the predator, i.e. appear conspicuously. A change in the behaviour of a prey, e.g. when a bird forage in open areas or flies in a straightforward path over open country, would then increase its availability. Despite extensive knowledge on the diverse avian diet of the peregrine in the breeding season, few if any studies have investigated how its selection of prey affects the degree of handling and feeding time of nestlings. The broad choice of prey species would make the peregrine an excellent raptor for studying how these factors change.

In this study, I investigated the prey composition of a peregrine pair in a lowland area by recording prey deliveries at a nest with one nestling. First, I wanted to analyse the diet during the breeding season, focusing on the importance of the species or genera that make up the majority of the diet (Ratcliffe 2010). Second, I wanted to analyse the time of day and the weather conditions when prey are delivered at the nest. The relative availability of prey may be related to the time of day, i.e. prey are more active and may thus be more easily spotted at certain times of the day. Unfavourable weather conditions like heavy rain do not favour active behaviour, and the raptors would more likely wait or prioritise brooding or shading the nestlings than provision food. Third, I wanted to analyse prey handling and parental behaviour of the peregrines at the nest. Handling of prey would vary with prey size, as well as with

nestling age, in terms of the female feeding dependent nestlings or the nestlings ingesting prey unassisted. Despite being a well-studied raptor across the world, the peregrine has never been studied in detail with a video camera in Norway before. This would be a unique opportunity to analyse the diet in detail, as well as observing family-related behaviour and handling of prey at the nest.

Methods

Study area, study species, and prey availability

The fieldwork was conducted from 8 June to 5 July in 2015 in Re municipality in Vestfold county (59º25' N; 10º17' E). The study area is a hill surrounded by a mosaic of standing forest, clearcut areas and cultivated land, and in close vicinity to several small lakes and streams. This area is situated within the boreonemoral zone (Moen 1998), and the vegetation is a species rich mixed-type forest in the lowland becoming more pine-dominated near the hilltop. Near the cliff are some settlements and a trafficked county road. A pathway leading to the top of the hill is regularly used for recreation, and the hillside is used for paragliding in the summer months, although this was not seen during my fieldwork period.

I video monitored prey deliveries at a nest of a breeding pair of the peregrine, and observed the behaviour of the falcon in the surrounding area. The peregrine is monogamous (Cramp & Simmons 1980) and known to defend a nesting territory (Hardey et al. 2006), so I assumed that the male or female arriving at the nest were the same two individuals throughout the filming period. The nest was located on a broad ledge in a steep hillside facing south. The video camera was fixed to a wooden plank, and then placed diagonally and steadily toward the cliff wall. The camera lens was adjusted to attain a near-horizontal overview. The installation of the camera and equipment took place when the nestling was approximately 10 days old. A peregrine nestling reaches thermal independence at this age and thus requires less brooding from the parents (Hardey et al. 2006), thus disturbance at the nest is less critical. The exact age of the nestling was determined by studying online pictures of the day-to-day development of peregrine chicks kept in captivity.

The TOV-E project monitors a network of census routes, representing the whole country, for registering and monitoring the common migratory birds in Norway (Kålås et al. 2014, Framstad 2015). Count survey data were collected annually between late May and early July, i.e. in the same season as my study, and may thus be a good indicator of prey composition in the breeding season. There was an overall increase in numbers of observed passerine birds at the monitored census points from 2013 to 2014 (Framstad 2015). Thrush (*Turdus* sp.) species such as redwing (*Turdus iliacus*), song thrush (*Turdus philomelos*) and fieldfare (*Turdus pilaris*), and the woodpigeon (*Columba palumbus*) occurred in a higher percentage of the routes, and more pairs were observed in 2014, compared to 2013 (Framstad 2014, 2015; Kålås

et al. 2014). Thrushes and woodpigeon were among the top observed species of bird in terms of number of census routes seen at, with redwing, song thrush and fieldfare observed in >50% of the 349 census routes in 2014 (Framstad 2015). Additionally, at two bird-monitoring stations that lie along important migration routes for bird populations in southern Norway, the number of migrating birds caught and ringed in 2014 was 40% higher than their own long-term average for the monitoring period of 1990-2013 (Heggøy et al. 2015). The numbers caught during the cold and wet spring of 2015 was lower than the long-term average, and especially low for the insect-eating warblers (Phylloscopidae) and thrushes (Røer 2015, García et al. 2016).

Direct observation, video monitoring & weather data

I observed the behaviour of the falcons outside the nest, such as transfer of prey from the male to the female. While hidden from sight 300-400 m away from the nest I used a Celestron 52250 Ultima Zoom spotting scope with 20-60x zoom and 80mm lens. In addition to the rare occurrence of prey transfers between the male and female, I also kept track of the movements of the adult female; whether she perched and waited at a cliff or flew off with the male to assist in the hunt.

Due to the nesting ledge being inaccessible, a professional climber assisted in setting up the equipment at the nest. The filming started on the day of setup (8 June), when the single nestling in the brood was 10 days old. The methods used for filming were the same as described by Steen (2009). The monitoring lasted for 27 days (until 5 July), of which 4 full days failed to be recorded and 8 additional days were only partly recorded due to the unpredictability of knowing when the memory of the SD-card was full. There were no prey deliveries occurring at the nest after 1 July due to the nestling having fledged. Thus, in total 11 days were completely recorded. I used a charge-coupled device (CCD) camera equipped with a wide-angle lens to cover most of the nesting ledge. Frame rate was 25 pictures per second, and resolution was set at 704 x 576 lines. The camera did not capture any recordings during the darkest hours, i.e. between midnight and 03:00 hours (local summer time). Of 649 total hours of monitoring 213 (32.8%) were lost due to technical failure, resulting in 436 effective hours of monitoring in total.

The camera was connected to a mini digital video recorder (mini-DVR) with a 100 m long video cable. The mini-DVR used was a Secumate H.264 Mini Portable DVR. A sealed 12 V DC lead battery supplied the mini DVR and the camera with power. A cable converter was added to reduce the voltage to the mini-DVR from 12 V to 5 V. The mini DVR stored data on SD-cards and was placed in a waterproof plastic container. The container and lead battery were placed under a tree approximately 90 m away from the nesting ledge. In this way, I minimised the chance of being seen by and thus disturbing the peregrines while checking and changing the equipment. The SD-cards used were of type SDHC Class 4 with 32 GB of storage, and were replaced every 3-6 days. The data were transferred to a laptop with an SD-card reader. Two SD-cards of 32 GB were kept in cycle to ensure continuous recording. A small monitor was brought along whenever the SD-cards were replaced, and connected to the mini DVR to do control checks and adjust the settings when necessary. I also checked that there was no peregrine activity ongoing in front of the camera at the time of replacement, in order to not disturb or cancel any active recording of a prey delivery.

The mini-DVR had a 'motion detection' setting, which allowed me setting it to record only when movement was detected in the camera view, such as an adult peregrine landing with a prey item. In order to have the setting only detecting movement in certain areas of the camera view, such as corners and edges, I set the detection area with a masking tool (see Steen (2009) for a practical example). With this set-up, the motion sensor would trigger a recording when one of the parents entered or left the nest. The sensitivity of detection was set at the highest level as default. This setting as well as the detection area was adjusted based on the results from watching the early video recordings. In this way, the number of recordings without prey deliveries or handling was reduced. When triggered, the DVR was set to record for 10 s as well as to include the action 5 s prior to the trigger. In this way, for clips with prey delivery, the behaviour of the nestling prior to the parent landing was also included. The DVR continued to record for as long as any motion kept triggering the sensor. The date and time of day was recorded for each video clip recorded. For further details of the video equipment, see Steen (2009).

I obtained data on temperature and precipitation during the period of filming from Ramnes weather station, situated 10.1 km from the nest, where temperature and precipitation was logged hourly by the Norwegian Meteorological Institute (eKlima 2015). This data was

presented in UTC time, whereas local summer time in Norway was UTC +2. For each prey delivery I then used the temperature value two hours earlier on the dataset from eKlima (2015), i.e. for a prey delivered at 13:00 hours I used the corresponding temperature for when the time in the meteorological dataset was 11. I interpolated temperatures from present time (t) to the next hour (t+1) to get an estimated air temperature for every 10 minutes, i.e. for a prey delivery at 13:26 hours I interpolated the temperature from 11 to 12 (UTC) in the dataset from eKlima (2015), which corresponded to 13:00-14:00 hours in UTC +2. For each prey delivery I then used the temperature at the nearest 10 minutes, i.e. for a prey delivered at 13:26 hours I used the temperature at 13:30 hours. In this way, I avoided getting exact similar temperatures for deliveries within the same hour.

Prey delivery, identification, and feeding behaviour

All delivered prey items recorded at the nest were identified to the lowest taxonomic level possible. When identifying the prey to species, each recorded prey delivery was displayed on a 42 inch screen. The video was, when needed, played frame by frame, and I took screenshots of frames that could provide an estimate of the size of the falcon relative to the prey. Whenever an estimate of the size of a prey item was uncertain, I drew silhouettes on transparency paper of the adult peregrine holding the prey. I zoomed in on screenshots in order to draw the silhouettes of the adult peregrine equally large, for reliable comparisons. Any prey item of uncertain size was then compared with silhouettes of identified prey to get a reliable estimate of size. To get an overview of the size of an unplucked prey relative to a plucked one, I drew silhouettes of two frozen specimens, one of a song thrush and one of a great tit (*Parus major*), when unplucked and when plucked. The specimens had been found dead from natural causes. The silhouettes were then compared to a stuffed specimen of the peregrine to get a reliable estimate of the difference in size between the falcon and its prey items.

The sex of the delivering parent was determined from morphological features and size, and was registered at each delivery. Time of arrival by the delivering parent was also recorded. To get the time that had elapsed since the previous delivery, I subtracted the time at delivery of the previous prey (n-1) from the time at delivery of the present prey (n). To get the time of delivery expressed as time from solar noon, I subtracted the time at prey delivery with the average time of solar noon during the recording period, which was at 13:21 hours, and then

used the absolute value to correct for any negative signs. To estimate the mean delivery rates (prey deliveries per hour) for the 11 days that were fully recorded, I first calculated the amount of hours the peregrine was active, for each day. I did this by subtracting the time at the first delivery of the day from the time at the last delivery of the day. Then, I found the number of prey deliveries recorded for that day. Lastly, I divided the latter with the former, to get delivery rates per hour for each of the 11 days. I used the mean of these 11 delivery rates as an estimate of delivery rate per hour at the nest.

I also recorded signs of preparation of the prey item prior to delivery at the nest, i.e. whether the prey item was decapitated, whether it was plucked, or whether it had already been eaten at before delivery. I also recorded whether the female assisted in feeding or the nestling fed unassisted for each prey item.

Bird body mass has a relatively small intraspecific variation; therefore a mean value for each prey species was obtained from data most pertinent to the breeding season in Fennoscandia (Cramp 1985, 1988, 1992; Cramp & Perrins 1994; Selås 2001). For passerines, juveniles were assigned the same body mass as adults. This data was used as gross prey body mass, which was defined as the estimated weight of the prey species at the moment of capture. See Appendix 1 for a list of the body masses used for each prey species or group in this study. Net prey body mass was defined as the estimated mean weight at delivery, corrected for decapitation, plucking and partial consumption prior to delivery. When estimating body mass of decapitated birds, I subtracted 12.9% from the gross prey body mass, based on data from feeding behaviour of raptors in captivity (T. Slagsvold & G.A. Sonerud, unpublished data). I used the same estimation for birds that had been plucked and decapitated, as feathers add little to weight (V. Selås, pers.comm.). When estimating body mass of partially consumed prey I subtracted the judged weight of missing appendages, such as head (see above), feet and wings, and calculated an estimate of the proportion of the prey item missing (V. Selås, pers.comm.).

I estimated the handling time for each prey item delivered at the nest (measured to the nearest s), both when the female assisted the nestling in feeding and when the nestling fed unassisted. I used the same definition of handling time as Steen (2010) used on his studies on the Eurasian kestrel (*Falco tinnunculus*). This definition was also used by Skouen (2012), and

was given as the time that elapsed from when the female or nestling bent its head down to tear off the first piece of the prey item, until the item had been completely consumed or abandoned. I also registered time spent plucking the prey item, whenever it occurred at the nest. I defined plucking time as time elapsed from the female or nestling first bent down its head to pluck feathers, until plucking of prey ended. Time spent plucking the prey item and time spent feeding were summarised to handling time. By definition, handling time in general also includes time spent capturing and preparing a prey item prior to delivery, but this was not accounted for due to difficulties in observing the peregrines preparing the prey outside the nest, and because the peregrines could not be observed when hunting. If the feeding or plucking session stopped for more than 5 s, I excluded this pause from the handling time. Cleaning after a feeding, i.e. when the female or nestling started to pick up spilled leftovers on the ground, was not included as handling time, as it was not possible to distinguish which prey item the leftovers originated from. Handling time was not obtained for 7 of the 88 prey items delivered at the nest, either due to recording error, or to the fact that the prey item was consumed outside camera range.

Due to miscalculations in the settings of the motion sensor, some of the recording sessions of feeding and plucking were incomplete. I therefore used the same method as used by Skouen (2012) to categorise the feeding and plucking sessions into four categories: 1) Complete recording. 2) Recording with exact start and stop time of handling of prey, but with one or several cuts in timeline in between. This could overestimate the time spent feeding or plucking, because some pauses longer than 5 s may not have been detected. 3) Recording where either start or stop time were missing. For these recordings, I calculated a minimum and maximum handling time, and then used the mean of the max and min time as the estimated handling time of the prey items in this category. Maximum time at the start of the session (start time) was set as the time at the last recording before a cut in timeline, where the next recording displayed the female or nestling feeding off or plucking the prey item. Maximum time at the end of the session (stop time) was set as the time at the next recording after the previous recording had displayed the female or nestling feeding off or plucking the prey item. Minimum time at the start of the session was set as the time at the recording where the female or nestling was first seen feeding off or plucking the prey item. Minimum time at the end of the session was set as the time at the last recording before a cut in timeline that showed the female or nestling feeding off or plucking the prey item, where the next recording displayed the female or nestling finished handling the prey. 4) Recording where only

maximum or minimum time could be set due to an extended cut in timeline. Due to this category consisting of insecure sets of data, handling time was not set for the few recordings assigned. Of 88 prey items recorded delivered, 40 were assigned to category 1, 20 to category 2, 21 to category 3, and 7 to category 4.

If the female or nestling had a pause longer than five minutes during a feeding or plucking session, the session was recorded as two different bouts. I added the handling time of all bouts belonging to the same prey item to get one total handling time for that prey item. The nestling had to feed unassisted in all bouts in order to be assigned for the handling of a prey item. Handling time would be assigned the female if she fed the nestling in one or more bouts. Each bout was categorised with the same methods as above (see also Skouen 2012). When summarising the bouts the handling time could therefore consist of different categories (1-4), and the bout with the highest category number determined the category of that prey item. Thus, for a prey item consumed over 3 bouts of which 2 of the bouts are complete (category 1) and one is incomplete, e.g. in category 2, the prey item would be categorised as 2. This method corrected for monitoring error.

Statistical analysis

I performed all statistical analyses, and constructed all figures, with the software JMP® version 10.0.0 (SAS 2015) and the software R, version 3.1.0 (R Development Core Team 2016). The standard criterion of statistical significance was $\alpha = 0.05$. All residuals were checked for normality. Estimates are presented as mean $\pm$ SE (standard error).

Contingency analysis was used to test for association between the probability of a prey item being decapitated and whether the prey item delivered was a thrush or not, between prey group and whether a prey item was plucked at the nest, and between prey group and feeder. I used logistic regression by likelihood ratio to test for effects of different variables on the following response variables: the probability that a thrush rather than a small passerine was delivered at the nest, the probability that the delivering sex was male or female, whether a prey item was plucked, decapitated or partly consumed prior to delivery at the nest, whether a prey item was plucked at the nest, and whether the female or the nestling handled the prey.

The explanatory variables on the probability that a thrush rather than a small passerine was delivered at the nest were nestling age, ambient air temperature (^{o}C) at the time of delivery, rain (mm per hour) at the time of delivery, time elapsed since the previous delivery, and time from solar noon. The explanatory variables for whether the delivering sex was male or female, were nestling age, gross prey body mass, air temperature at the time of delivery, and all interactions between the variables. The explanatory variables on whether a prey item was decapitated, partly consumed or plucked prior to delivery were nestling age, gross prey body mass, air temperature, and the interaction between nestling age and prey body mass. Whether the prey item was a thrush or not was also used as an explanatory variable for the probability of being decapitated. The explanatory variables on whether a prey item was plucked at the nest were nestling age, gross prey body mass, feeder, time between deliveries, time since solar noon, and all interactions between the variables. The explanatory variables on whether the female or nestling handled the prey were nestling age, gross prey body mass, and their interaction.

I used generalised linear models (GLM) with a normal distribution and identity link function to test for effects of selected explanatory variables on handling time when the female fed the nestling, on handling time (log_{10}-transformed) when the nestling fed unassisted, on the number of meals per prey item for the two feeder scenarios, and on the time between each prey delivery at the nest. Handling time was log_{10}-transformed for scenarios of nestling as feeder, in order to get normal-distributed residuals for the variable. The explanatory variables for handling time with female as feeder were net prey body mass (log_{10}-transformed), nestling age, interaction between the former, and recording category (1-4). For handling time with nestling as feeder (log_{10}-transformed), the explanatory variables used were net prey body mass, nestling age, the interaction between the former, and recording category. The explanatory variables for the number of bouts per prey item for both female and nestling as feeder were nestling age, net prey body mass, whether the prey was plucked before delivery, time between deliveries and time from solar noon. The explanatory variables for time between prey deliveries were nestling age, gross prey body mass, feeder and time from solar noon.

The analysis on prey deliveries as a function of the time of day were executed in R with the cosinor-analysis, used for modeling circadian activity rhythms, to find the best model based on the lowest AIC-value (see Pita et al. 2011 for more detail). See Appendix 2 for the raw

data used for this analysis. I kept the model if the difference in AIC (ΔAIC) between the best and the next best model was larger than 2.0 (Burnham & Anderson 1998). The best model was then run using generalised linear models with logistic regression and binomial distribution. The response in the test was 'not delivered' or 'delivered' with input values of 0 and 1, respectively. The explanatory variable used was time of the day, divided into one-hour blocks from 0 to 23.

Results

Prey delivered at the nest

In total 88 prey items were recorded as delivered at the peregrine nest during the video monitoring period. All prey items were birds, of which 23 were identified to species level and another 28 to genus and 2 to family. A total of 32 birds were not possible to identify to either species or genus, and were grouped according to size, i.e. small and larger passerines. Finally, 3 prey items were hidden behind the delivering falcon and thus identified to class (Aves) only. The average gross body mass of prey was 88.2 ± 12.9 g, whereas the average net body mass, i.e. when delivered at the nest, was 67.7 ± 8.6 g. Thrushes were the most common prey category by number, the second most contributing to total gross prey mass, and the most contributing to total net prey mass, comprising 31.8%, 29.9%, and 34.6% respectively (Table 1). Small passerines were common by numbers but low by body mass, comprising 21.6% of all recorded prey items delivered but only 3.8% and 4.3% of total gross and total net prey mass delivered, respectively. Woodpigeons comprised only 6.8% of all prey items delivered, but 39.6% of total gross prey mass and 29.2% of total net prey mass delivered (Table 1). Gross and net body mass for each prey species and prey category are given in Appendix 1.

All thrushes pooled made up 42 of 88 prey items, i.e. 47.7% of all recorded prey items delivered, 48.4% of total gross prey mass and 57.1% of total net prey mass delivered. Small and larger passerines (with a weight of 25 g and less) pooled comprised 35 of 88 prey items, i.e. 39.8% of all recorded prey items delivered, but contributed only 8.6% and 9.8% of total gross and net prey mass delivered, respectively. Out of 85 identifiable prey items, 83 could be classified as either thrush, pigeon or small passerine; only the swift (*Apus apus*) and the magpie (*Pica pica*) did not fall into one of the three categories. From here on out these classifications are mentioned as 'prey group'.

Table 1. Prey deliveries successfully recorded by video monitoring at the peregrine nest, given as percentage by number and percentage by the estimated prey body mass, given as gross and net body mass values, for each prey category. Gross prey body mass is the estimated weight of the prey species at the moment of capture, whereas net prey body mass is the estimated mean weight at delivery, corrected for decapitation, plucking and partial consumption prior to delivery.

| Prey category | Prey number | | Prey mass (g) | | | |
| | | | Gross | | Net | |
	N	%	g	%	g	%
Woodpigeon (*Columba palumbus*)	6	6.8	2970	39.6	1680	29.2
Common swift (*Apus apus*)	1	1.1	40	0.5	35	0.6
Blackbird (*Turdus merula*)	7	8.0	665	8.9	616	10.7
Fieldfare (*Turdus pilaris*)	5	5.7	525	7.0	500	8.7
Song thrush (*Turdus philomelos*)	1	1.1	74	1.0	74	1.3
Mistle thrush (*Turdus viscivorus*)	1	1.1	120	1.6	105	1.8
Thrush indet. (*Turdus* sp.)	28	31.8	2240	29.9	1988	34.6
Lesser whitethroat (*Sylvia curruca*)	1	1.1	12	0.2	12	0.2
Warbler (Phylloscopidae)	2	2.3	20	0.3	18	0.3
Eurasian magpie (*Pica pica*)	1	1.1	220	2.9	192	3.3
Small passerines indet.	19	21.6	285	3.8	247	4.3
Larger passerines indet.	13	14.8	325	4.3	286	5.0
Bird indet.	3	3.4	-	-	-	-
Total	88	99.9	7496	100.0	5753	100.0

Weather data and effects of time on prey deliveries

During the monitoring period, only 3 days had any notable registrations of rainfall, i.e. the overall amount of rainfall was negligible. The mean air temperature at the time of prey delivery was 15.5 ± 0.4 °C (range 6.0 - 24.4 °C). The weather condition at nearly all of the observation days in the field was clear (pers.obs.). Neither ambient temperature nor rainfall were significant in any of the tests performed.

In total 11 of 24 recording days were fully monitored, and in another 3 recording days at least 80% of the day was represented in the saved recordings. No recordings were made for 5 of the 24 days with the video equipment running. For the 11 days with representative recordings for the full day, the peregrines delivered 4-8 prey items to the nest per day, with an average of 5.8 ± 0.4 prey items per day (n = 11). The delivery rate was 0.45 ± 0.04 prey items per hour (range 0.35-0.74 deliveries per hour, n = 11). There was a significant relationship between the time elapsed between successive deliveries of prey at the nest and the time of day, set as the

number of hours from solar noon (Table 2). The time elapsed between successive deliveries to the nest decreased with increasing time from solar noon. The frequency of prey deliveries were thus higher in the morning and the evening, compared to near midday (Figure 1).

Table 2. Generalised linear model (GLM) of significant effects on the amount of time elapsed between successive prey deliveries at the peregrine nest. The current prey delivery (n) rather than the previous prey delivery (n-1) was scored for each data point. Whole model: $N = 68$, $\chi^2 = 7.21$, $df = 1$, $p = 0.0072$.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	3.772	0.461			
Time from solar noon	-0.268	0.097	1	7.21	0.0072

The earliest delivery was recorded at 04:03 hours, and the latest delivery at 22:44 hours. Thus the peregrine seemed to forage for up to 19 hours per day, approximately. A majority of the prey deliveries occurred during the morning and the evening, between 5:00 and 9:00 hours and between 17:00 and 21:00 hours. Noticeably fewer prey items were delivered around midday, between 10:00 and 16:00 hours. In the morning and the evening, the peregrines usually delivered a prey item within 3 hours since their previous delivery. During the midday, particularly between 11:00 and 15:00 hours, there was usually at least a 3-hour gap between the successive prey deliveries (Figure 1). Only deliveries made within each day were included; between-day deliveries (where the previous prey was delivered in the evening and the next prey the following morning) were not included in the analysis.
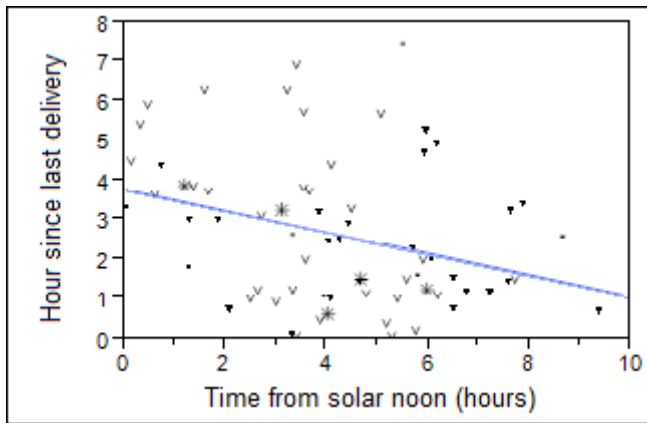
Figure 1. The time elapsed (hours) between successive prey deliveries at the peregrine nest as a function of time from solar noon for the recording period (13:21 hours). Each sample unit have a symbol designation that represents its prey group classification, i.e. thrushes denoted with a 'v', small and larger passerines with a triangle, pigeons with a star, and the other prey with a dot. Whole model: N = 68, χ^2 = 7.21, df = 1, p = 0.0072.

From 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 M3, with the lowest AIC value (Table 3). The parameter estimates of the best model is given in Appendix 3. The probability of a prey delivery at the nest was highest during the 07-08 hour block and the 19-20 hour block (Figure 2).

Table 3. Output from the cosinor analysis performed in R, of the three best models for the probability that a prey was delivered at the peregrine nest as a function of the time of the day. For raw material used for the dataset and parameter estimates of the best model, see Appendix 2 and 3.

Model	df	AIC	ΔAIC
M3	7	377.97	0.00
M2	5	380.54	2.57
M1	3	410.42	32.45

16
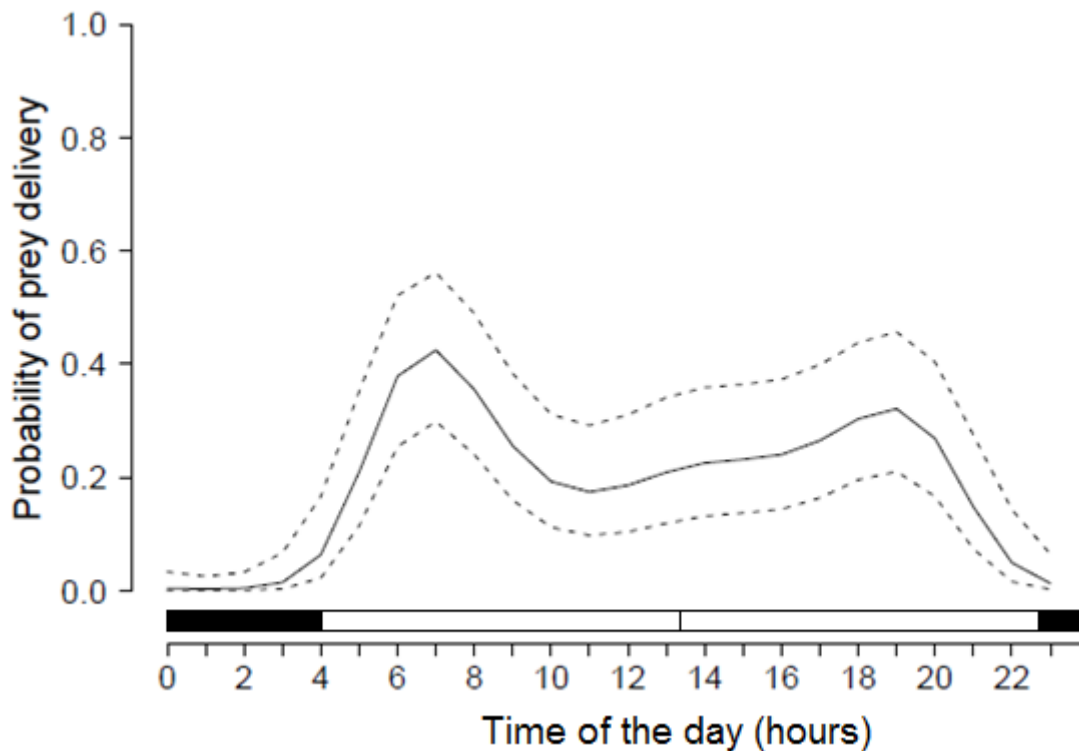
Figure 2. Result from the generalised linear model (GLM), performed in R, on the probability that a prey was delivered at the peregrine nest as a function of the time of the day. The bar at the bottom represent nighttime (black), daytime (white), and the time at solar noon. The average time of sunrise, solar noon, and sunset for the monitoring period was at 04:02, 13:21, and 22:42 hours, respectively, at the mean date of the filming (21 June). The figure was based on the best model (M3) derived from the cosinor analysis in R, see Table 3 and Appendix 2, 3 (n = 436).

Type of prey delivered

Thrushes and small passerines accounted for 77 of the 88 prey items recorded delivered at the nest. The time from solar noon had a significant effect on the probability that the prey item delivered at the nest was a thrush rather than a small passerine (Table 4). The probability that the prey item delivered at the nest was a thrush rather than a small passerine decreased with time from solar noon (Figure 3).

Table 4. Results from a likelihood ratio test in a logistic regression model of the probability of whether a thrush or a small passerine was delivered at the peregrine nest. Whole model: N = 77, χ^2 = 4.94, df = 1, p = 0.026.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	1.280	0.572			
Time from solar noon	-0.222	0.104	1	4.94	0.026

The probability was equal for either of the two prey types at 6 hours from solar noon, which was at 07:21 and 19:21 hours. Before the former and after the latter the probability of a small passerine being delivered was higher than that of a thrush (Figure 3). Neither air temperature, rain (mm per hour) at the time of delivery, time since previous prey delivery, or nestling age had any significant effect on which type of prey was delivered at the nest.
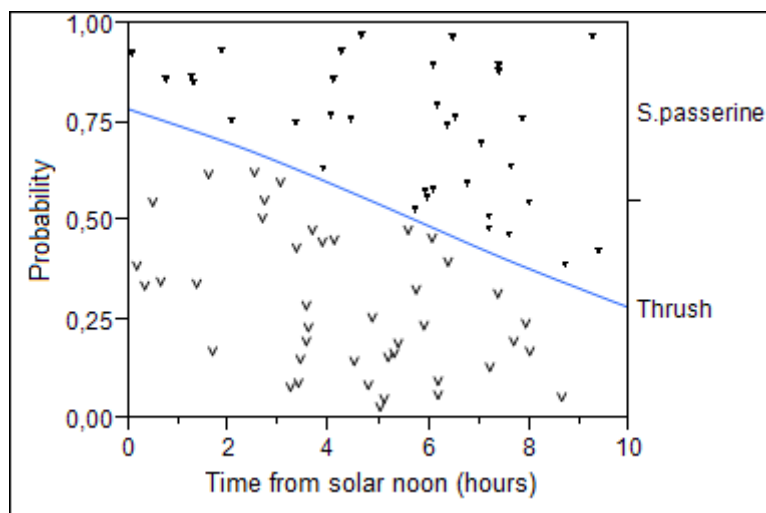
Figure 3. The probability that a prey item delivered at the peregrine nest was a thrush rather than a small passerine as a function of time from solar noon (13:21 hours). See fig. 1 for explanation of symbols. Whole model N = 77, χ^2 = 4.94, df = 1, p = 0.026.

The delivering sex

The sex of the delivering parent was determined for 80 of the 88 prey items delivered at the nest. The female delivered close to all of the prey items recorded (95%); the 4 prey items delivered by the male came during the last two days of the video recording period (Figure 4). There was a significant effect of nestling age on the probability that a prey item was delivered at the nest by the male (Table 5, Figure 4). Neither prey body mass, air temperature at the time of delivery, nor any relevant interaction had a significant effect on the probability that an item was delivered by the male.

Table 5. Results from a likelihood ratio test in a logistic regression model of the probability that the male peregrine delivered a prey item directly to the nest. Whole model: N = 80, χ^2 = 10.91, df = 1, p = 0.0010.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	-15.147	8.283			
Nestling age	0.437	0.266	1	10.91	0.0010
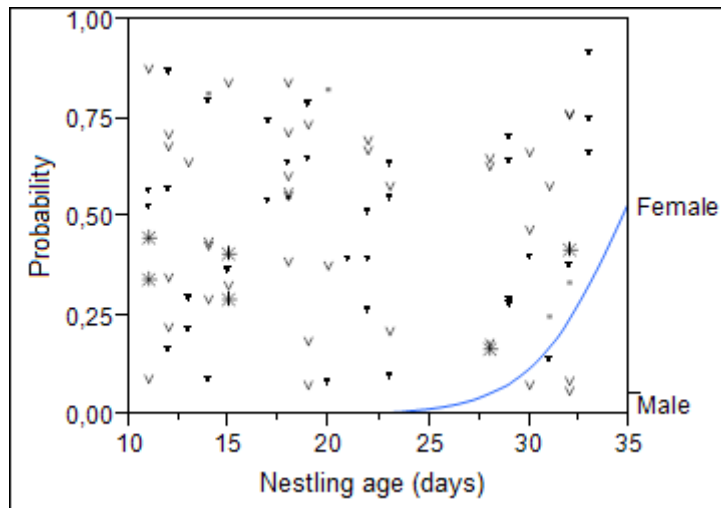
Figure 4. The probability that the male rather than the female delivered a prey at the peregrine nest as a function of nestling age. See fig. 1 for explanation of symbols. Whole model: N = 80, χ^2 = 10.91, df = 1, p = 0.0010.

Preparing before delivery

A high number of the prey items were prepared before being delivered at the nest; 75 of 85 (88.2%) were plucked and 72 of 85 (84.7%) were decapitated. Of the 10 unplucked prey items, 7 were identified as a thrush, 2 as a small passerine and 1 as a swift. Of the 13 prey items not decapitated before delivery, 12 were identified as a thrush, and 1 as a small passerine. The probability that the prey item was plucked prior to delivery at the nest was marginally non-significantly affected by gross prey body mass, and significantly affected by the interaction between feeder and gross prey body mass (Table 6). The probability decreased with increasing gross prey body mass when the nestling fed unassisted (Figure 5a), but not when the female fed the nestling (Figure 5b). Neither nestling age, time between delivery, time from solar noon nor other relevant interactions had any significant effect on whether a prey item was plucked at the nest.

Table 6. Results from a likelihood ratio test in a logistic regression of the probability that a prey item was plucked prior to delivery at the peregrine nest. Whole model: N = 83, χ^2 = 4.44, df = 3, p = 0.22.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	4.637	2.739			
Feeder	-0.389	0.462	1	0.65	0.42
Gross prey body mass	-0.033	0.031	1	3.06	0.080
Feeder*Gross prey body mass	-0.037	0.031	1	4.11	0.043

a)   b)
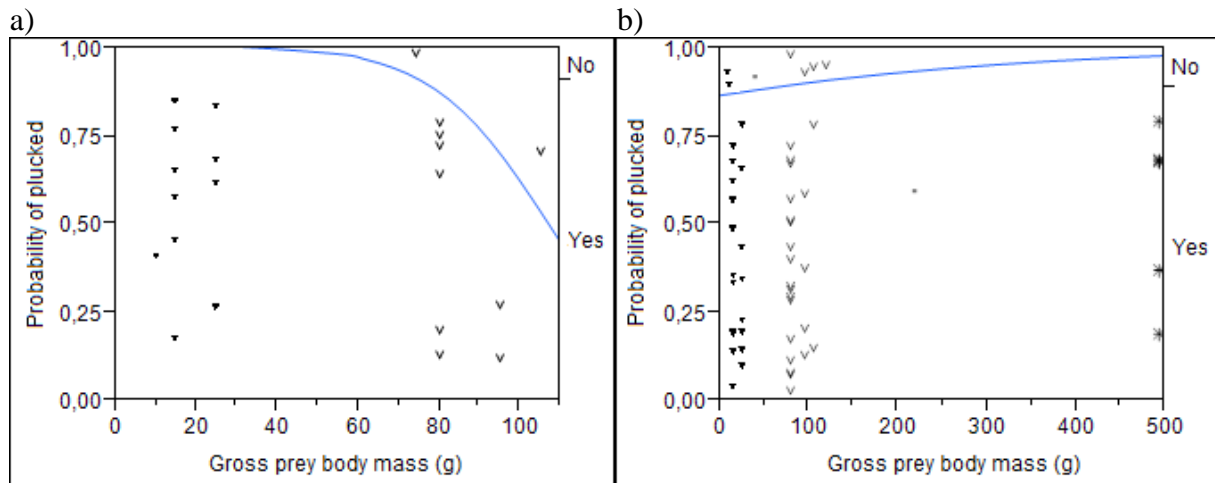
Figure 5. The probability that a prey item was plucked prior to delivery at the peregrine nest, as a function of gross prey body mass. a) Nestling as feeder only (N = 21, χ^2 = 3.70, df = 1, p = 0.055). b) Female as feeder only (N = 62, χ^2 = 0.69, df = 1, p = 0.41). See fig. 1 for explanation of symbols.

The probability of being decapitated was significantly affected by whether the prey item was a thrush rather than any other bird species, and marginally non-significantly affected by nestling age (Table 7). None of the other relevant explanatory variables had a significant effect on the probability of a prey item being decapitated before delivery.

Table 7. Results from a likelihood ratio test in a logistic regression model of the probability that a prey item was decapitated before being delivered at the peregrine nest. Whole model: N = 85, χ^2 = 16.42, df = 2, p = 0.0003.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	4.237	1.257			
Thrush or not	-1.439	0.540	1	13.04	0.0003
Nestling age	-0.082	0.046	1	3.45	0.063

The probability of decapitation decreased non-significantly with the age of the nestling, and was significantly lower if the prey item was a thrush than if it was another bird (Figure 6). Neither gross prey body mass, air temperature at delivery, nor the interaction between nestling age and gross prey body mass had any significant effect on the probability that a prey item was decapitated before delivery.
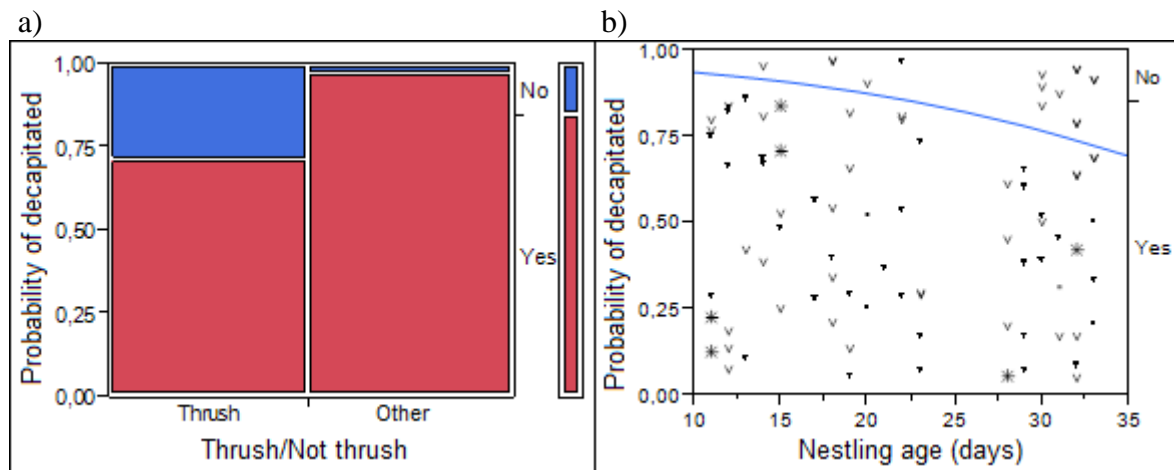
Figure 6. a) The probability that a thrush and another type of prey was decapitated prior to delivery at the peregrine nest. (N = 85, χ^2 = 12.97, df = 1, p = 0.0003.) b) The probability of a prey item delivered as decapitated at the nest, as a function of nestling age. See fig. 1 for explanation of symbols. Whole model: N = 85, χ^2 = 3.39, df = 1, p = 0.066.

Among the 85 prey items, 15 (18%) had been partly consumed by at least one of the adult peregrines before being delivered at the nest. All 6 pigeons had been partly consumed, and had also been decapitated, before being delivered at the nest. The probability that a prey item had been partly consumed before delivery increased significantly with gross prey body mass (Table 8, Figure 7). Air temperature, nestling age, and the interaction between it and prey body mass did not have a significant effect in the model.

Table 8. Results from a likelihood ratio test in a logistic regression model of the probability that a prey had been partly consumed before delivery at the peregrine nest. Whole model N = 85, χ^2 = 20.16, df = 1, p < 0.0001.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	-2.681	0.465			
Gross prey body mass	0.011	0.004	1	20.16	< 0.0001
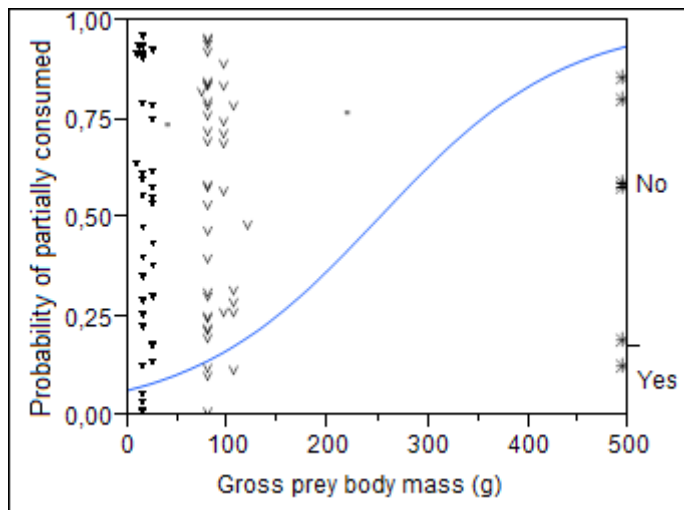
Figure 7. The probability that the adult peregrines had partially consumed a prey item before delivery at the peregrine nest as a function of gross prey body mass. See fig. 1 for explanation of symbols. Whole model: N = 85, χ^2 = 20.16, df = 1, p < 0.0001.

Preparing, handling and feeding at the nest

All 10 of the prey items that were recorded being plucked at the nest were thrushes. Out of ten prey items that were not plucked before delivery, five were recorded being plucked at the nest. The other five was plucked in two sessions, i.e. before delivered at the nest and also at the nest. Prey body mass and the interaction between feeder and prey body mass significantly affected the probability that a prey item was plucked at the nest (Table 9). The probability that an item was plucked at the nest increased with prey body mass when the nestling fed unassisted (Figure 8a), but not when the female fed the nestling (Figure 8b). Neither nestling age, time between delivery, time from solar noon nor other relevant interactions had any significant effect on whether a prey item was plucked at the nest.

Table 9. Results from a likelihood ratio test in a logistic regression model of the probability that a prey item was plucked at the peregrine nest. Whole model: N = 83, χ^2 = 4.92, df = 3, p = 0.18.

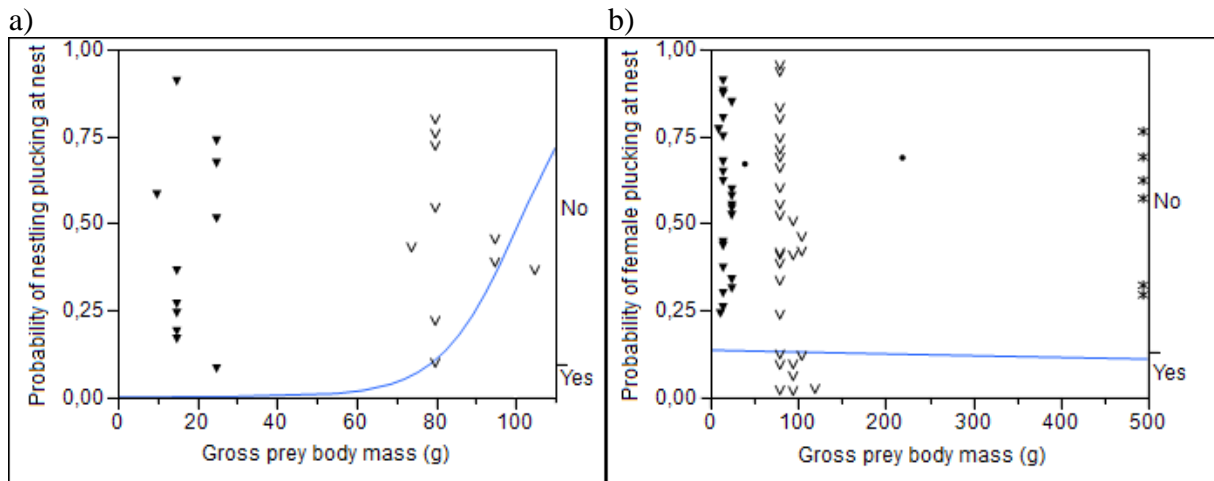| Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	-6.059	3.684			
Feeder	0.295	0.477	1	0.35	0.55
Gross prey body mass	0.051	0.041	1	4.56	0.033
Feeder*Gross prey body mass	0.051	0.041	1	4.73	0.030

Figure 8. The probability that a prey item was plucked at the peregrine nest, as a function of gross prey body mass. a) Nestling as feeder only (N = 21, χ^2 = 4.71, df = 1, p = 0.03). b) Female as feeder only (N = 62, χ^2 = 0.03, df = 1, p = 0.87). See fig. 1 for explanation of symbols.

For 86 prey items the feeder was scored. For 65 prey items the female dismembered the item and fed the nestling, of which 7 prey items were delivered unplucked. The nestling handled 21 prey items, of which 2 were delivered unplucked. Thus, the probability that a prey was plucked before delivery did not depend on whether the female fed the nestling or the nestling fed unassisted (χ^2 = 0.052, df = 1, p = 0.82). The female flew away again with one unplucked prey item, rather than feeding the nestling with it. The female handled more prey of various size, including all of the pigeons delivered, whereas the nestling handled a higher proportion of small passerines, with 11 of 21 prey handled being a small passerine.

Gross prey body mass and nestling age did significantly affect the probability that the female fed the nestling, rather than the nestling feeding unassisted (Table 10). The probability that the female assisted the nestling in feeding decreased with nestling age (Figure 9a), while it increased with gross prey body mass (Figure 9b). It was more likely that that the nestling fed on the prey item rather than the female, from when the nestling reached 29 days of age (Figure 9a). Neither ambient air temperature nor the interaction between nestling age and gross prey body mass significantly affected the probability.

Table 10. Results from a likelihood ratio test in a logistic regression model of the probability that the peregrine female fed the nestling, rather than the nestling ingested the prey unassisted. Whole model: N = 83, χ^2 = 54.34, df = 2, p < 0.0001.

Explanatory values	Estimate	SE	df	χ^2	p
Interaction	11.224	2.930			
Nestling age	-0.438	0.109	1	50.08	< 0.0001
Gross prey body mass	0.020	0.011	1	8.65	0.0033
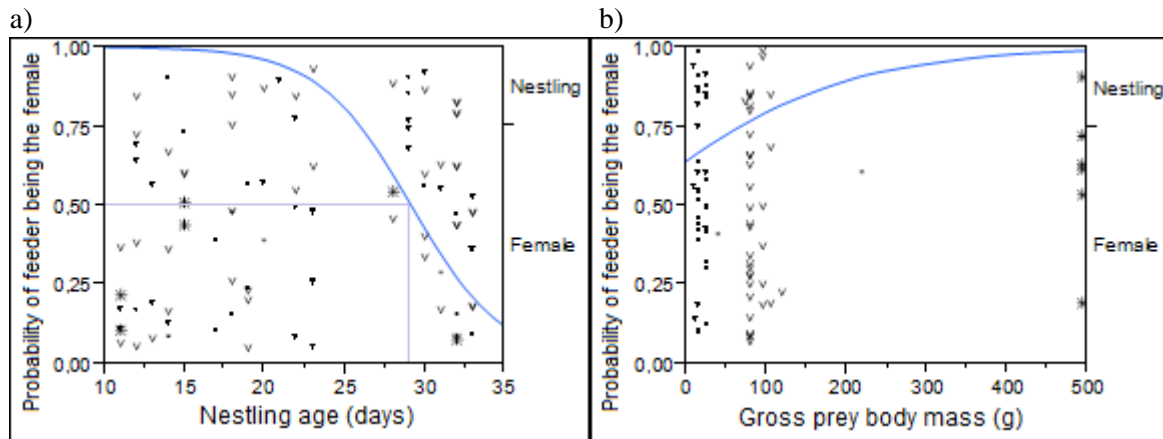
Figure 9. The probability that the peregrine female fed the nestling rather than the nestling fed unassisted, as a function of a) age of the nestling (whole model N = 86, χ^2 = 44.65, df = 1, p < 0.0001), and b) gross prey body mass (whole model N = 83, χ^2 = 4.26, df = 1, p = 0.039). See fig. 1 for explanation of symbols.

Number of meals

Only 5 out of 82 prey items handled had more than one recorded meal per prey item. Four of these were recorded for the nestling feeding unassisted. For prey items handled by the female, number of meals per prey item was significantly affected by nestling age (Table 11). Number of meals per prey item increased with nestling age. It must be emphasised that only one of the prey items that the female handled was registered with more than one meal, and that the nestling fed on the prey item unassisted during one of these meal periods, at the age of 33 days.

Table 11. Generalised linear model (GLM) of significant effects on number of meals per prey when the peregrine female fed the nestling. Whole model N = 65, χ^2 = 4.92, df = 1, p = 0.027.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	0.920	0.045			
Nestling age	0.005	0.002	1	4.92	0.027

For prey items handled by the nestling unassisted, nestling age and whether the prey item was plucked or not before delivery had a significant effect on the number of meals per prey item (Table 12). Number of meals decreased with increasing age of the nestling, and was higher if the prey item was not plucked before delivery (Figure 10). Neither net body mass, time elapsed since the previous delivery, nor time since solar noon had any significant effect on the number of meals needed to consume a prey item.

Table 12. Generalised linear model (GLM) of significant effects on number of meals per prey when the peregrine nestling fed unassisted. Whole model N = 17, χ^2 = 11.57, df = 2, p = 0.0031.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	6.818	1.706			
Nestling age	-0.155	0.056	1	6.33	0.012
Plucked or not	0.829	0.283	1	6.95	0.0084
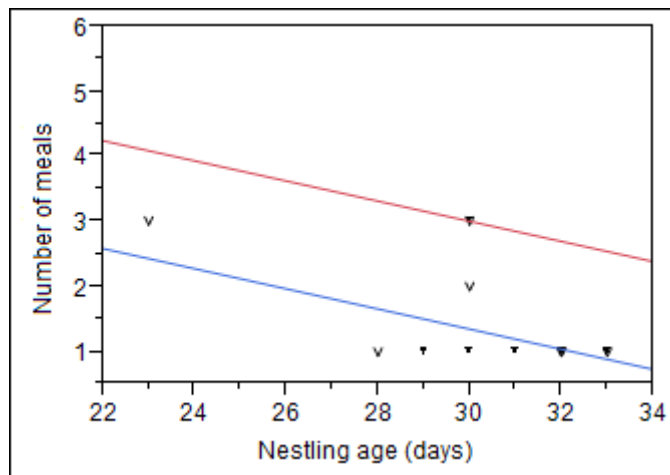
Figure 10. Number of meals per prey delivered as a function of nestling age, for prey items on which the peregrine nestling fed unassisted (blue line: plucked, red line: not plucked). See fig. 1 for explanation of symbols. Whole model N = 17, χ^2 = 11.57, df = 2, p = 0.0031.

Handling time

For prey items handled by the female, net prey body mass (log_{10}-transformed) significantly affected handling time (Table 13). Handling time increased with increasing net body mass (Figure 11). Recording category (1-4) was included in the model as an offset to correct for monitoring error. Handling time was not scored for any of the recordings in category 4. Net

prey body mass was log_{10}-transformed in order to obtain an explanatory variable with normal-distributed residuals.

Table 13. Generalised linear model of significant effects on handling time for prey items delivered at the peregrine nest when the female fed the nestling. Whole model N = 61, χ^2 = 10.01, df = 3, p = 0.019.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	135.328	106.763			
Net prey body mass (log_{10})	161.069	61.920	1	6.42	0.011
Recording category			2	4.89	0.087
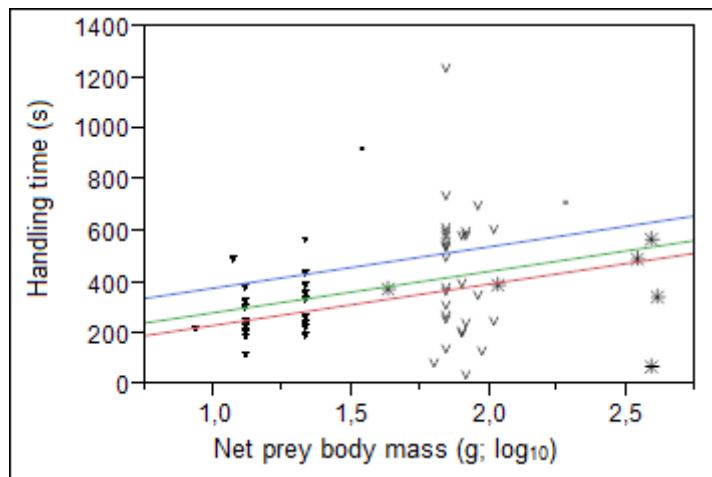
Figure 11. Handling time as a function of net body mass (log_{10}-transformed), when the peregrine female fed the nestling. The regression lines represent the trend for recordings of prey classified to corresponding recording category: red line: 1, green line: 2, blue line: 3. See fig. 1 for explanation of symbols. Whole model N = 61, χ^2 = 10.01, df = 3, p = 0.019.

For prey items handled by the nestling unassisted, the handling time (log_{10}-transformed) was significantly affected by net body mass of prey and by nestling age (Table 14). Handling time decreased with nestling age (Figure 12a), and increased with net body mass of prey (Figure 12b). Recording category (1-4) was included in the model as an offset to correct for monitoring error. Handling time was not scored for any of the recordings in category 4. Handling time was log_{10}-transformed in order to obtain a response variable with normal-distributed residuals.

Table 14. Generalised linear model of significant effects on handling time (s; $\log_{10}$-transformed) for prey items delivered at the peregrine nest when the nestling fed unassisted. Whole model N = 17, χ^2 = 20.34, df = 4, p = 0.0004.

Explanatory values	Estimate	SE	df	χ^2	p
Intercept	4.588	0.711			
Net prey body mass	0.008	0.002	1	12.20	0.0005
Nestling age	-0.076	0.023	1	8.44	0.0037
Recording category			2	3.27	0.20

a)

b)

Figure 12. Handling time (s; $\log_{10}$-transformed) as a function of a) nestling age (whole model N = 17, χ^2 = 3.98, df =1, p = 0.046), and as a function of b) net body mass (whole model N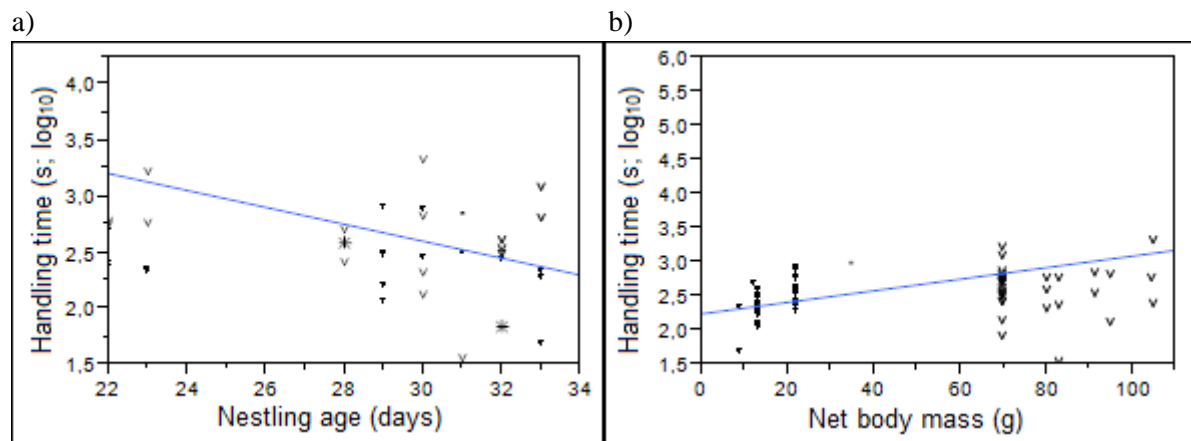 = 17, χ^2 = 11.23, df = 1, p = 0.0008), when the peregrine nestling fed unassisted rather than the female fed the nestling. See fig. 1 for explanation of symbols.

Discussion

Diet

All of the 88 prey items recorded as delivered at the peregrine nest were birds, of which thrushes pooled, small passerines pooled and woodpigeons constituted approximately 48%, 40% and 7% by number, respectively. The complete avian diet corresponds well to other studies as well as to literature on the peregrine (e.g. Cramp & Simmons 1980, del Hoyo et al. 1994). Studies on the diet composition of the peregrine shows a variety of results, i.e. some diet studies found that pigeons made up the highest proportions by frequency and mass (Jenkins 2000b, López-López et al. 2009, Ratcliffe 2010), while others found thrushes making up the highest proportion by frequency (Rizzolli et al. 2005). The common trend is that a few avian species comprise the majority of the total mass and numbers of prey items in the diet, despite that over 200 species of birds have been reported identified from peregrine diet analyses in Europe alone (del Hoyo et al. 1994, Ratcliffe 2010). Mearns (1983) found that for a collection of 3579 prey items, 15 out of 74 species accounted for over 90% by number and 95% by weight. This pattern has also been evident in other diet studies (e.g. Rosenfield et al. 1995; Olsen et al. 2004, 2008; Ratcliffe 2010), as well as in my study where thrushes and woodpigeons pooled comprised 55% by number and 86% by mass. In addition, some avian species appear to occur more often than other species in diet studies of peregrines, such as the woodpigeon, and thrush species such as the fieldfare, the song thrush and the blackbird (*Turdus merula*) (Ratcliffe 2010), as seen in my study.

The main difference between my results and the several other studies that report high proportions of pigeons, is the absence of the domestic pigeon and its feral version (*Columba livia domestica*) in my study area. The popularity of pigeon fancying and racing activities throughout the world have led to many local communities of domestic pigeons (Jerolmack 2007). Their vulnerable mode of flight during race events make them an easily accessible prey for peregrines (Humphreys et al. 2007, López-López et al. 2009, Ratcliffe 2010), especially as the pigeon racing season coincide with the breeding season of the peregrines (Humphreys et al. 2007). The effect of this may be seen in diet studies where domestic pigeons dominate, while the wild local bird fauna more narrowly represents diet proportions by number and mass. The diet analysis from my study area likely represents the local bird fauna in composition and availability. This contrasting difference in diet between habitats shows the opportunistic nature of the peregrine (Lindberg 2011).

Prey availability

The area of Solhomfjell was the area closest to and most representative of my study site to have accessible long-term monitoring data, being located approximately 80 km towards southwest. The number of passerines observed at the point count survey there in 2014 was above the average observed from 1993-2013, and above the numbers in 2013 (Framstad 2014, 2015). The population trends for the woodpigeon and most of the thrush species were reported as stable for the period 1996-2013. The fieldfare had a moderate decline whereas the song thrush had a moderate increase (Kålås et al. 2014). Three thrush species (fieldfare, song thrush, redwing) have been reported to occur in at least 56% of the point surveys, the blackbird in 46%, and the woodpigeon in 31% (Framstad 2015), showing that these species may commonly be available in the local bird fauna the peregrine inhabits. However, the spring of 2015 was wet and cold, which resulted in poor reproduction for small passerines, especially the species with insects as the main component of their diet (Røer 2015, García et al. 2016). The reduced availability of juvenile prey may in that regard have led to the peregrines investing more time to hunting, as the proportion of juvenile prey in the diet of peregrines has been shown to be considerable (Rosenfield et al. 1995). Olsen et al. (2008) found that the occurrence of prey species in the diet of peregrines corresponded broadly to their relative abundance data from local surveys, this held in particular for common species with high populations (but see Rosenfield et al. 1995). The diet composition in my study showed a similar correspondence to regional and national surveys, although it must be emphasised that my data represents only one nest from one season.

Effects of time on prey deliveries

The probability that a prey was delivered at the nest was highest in the early morning hour blocks (06:00-08:00) and in the evening hour blocks (18:00-20:00), and was at the lowest during midday hour blocks (10:00-12:00). The results are in accordance with those of Rejt (2001), whose study from an urban area reported the highest frequencies of parent feeding activities between 04:00-06:00 and 16:00-20:00 hours, and lowest between 9:00 and 10:00 hours. The earlier peak of frequencies in the morning compared to my results could be due to the availability of artificial light sources in urban areas, which enables hunting earlier in the morning. Also, Jenkins (2000b) found provisioning peaks in the early morning and late afternoon, but did not provide detail down to hours. For the goshawk (*Accipiter gentilis*), a raptor with a similar high proportion of its diet consisting of birds (see Tornberg & Reif 2007,

Sonerud et al. 2014a), Reif & Tornberg (2006) found delivery frequency peaks and lows at similar hours (i.e. peaks at 05:00-08:00 and 17:00-20:00 hours, low at 08:00-11:00 hours). Jenkins (2000a) found that the hunting frequency of the peregrine was the highest in the early morning and in the evening, and the lowest around midday. This may indicate that the availability of avian prey varies, based on the time of the day. During midday, when the temperature and sun intensity peaks, passerines and other birds may shift focus away from foraging to finding a source of shade for themselves or their chicks, thus avoiding the open habitats where the peregrine hunts. While raptors with a broader diet range may change to a more available prey type throughout the day (Steen et al. 2011a, Nodeland 2013), the peregrine is almost exclusively a bird feeder and a change of prey type may not be as profitable due to its less efficient digestive capacity (Barton & Houston 1993, Slagsvold & Sonerud 2007, Slagsvold et al. 2010). The peregrine is thus reliant on the relative availability of avian prey, which may be reflected from the distribution of deliveries over the course of the day.

On average, the peregrine delivered one prey item every 158 minutes. The delivery intervals (time since last delivery) over the course of the day varied from 5 minutes up to more than 7 hours, and became longer towards solar noon. The length of intervals corresponded well with the distribution of prey deliveries on the time of day. Temeles (1985) found that the attack success of the peregrine may vary considerably between and within habitats, ranging from 8% to 84%. Jenkins (2000a) found a correspondence between the frequency of deliveries and the frequency of hunting attempts per hour. The peregrine is a sit-and-wait predator, and rely on detecting moving prey to initiate a hunt (Dekker 2009). The delivery intervals may therefore rely on the availability of avian prey in the vicinity and the attack success, i.e. the delivery intervals would shorten with increasing availability of prey. The availability of prey may increase as the prey becomes increasingly vulnerable to detection by a predator, i.e. when foraging on open ground. The variation in delivery intervals could also be explained by the difficulty of catching avian prey as well as the low density of avian prey relative to non-avian prey (Temeles 1985). In addition, a prey item from a food cache may have been used as a food reserve while prey was less available, or when there was a long break in the provisioning of food (del Hoyo et al. 1994, Drewitt & Dixon 2008, Ratcliffe 2010). As caches are a source of quick access to food, it may explain some of the short intervals of food deliveries, especially if the male delivers a fresh prey item while the female has flown out to retrieve an item from a cache. Lastly, some of the short delivery intervals may be explained by the

delivery of prey species that may temporarily show a clumped distribution (Sonerud 1985), such as the fieldfare that nests in colonies (Svensson et al. 2004). Skouen (2012) suggested that golden eagles (*Aquila chrysaetos*) used a win-stay strategy when thrushes were delivered to the nest in rapid succession over a short period of time. This strategy suggests that a predator returns quickly to the capture site, which is favourable when hunting prey species with a clumped distribution (Sonerud 1985).

Type of prey delivered

Thrushes were the most important group of prey delivered at the peregrine nest, both by numbers and by mass. Similarly, thrushes were also the principal part of the breeding season diet, by numbers of prey, of peregrines elsewhere in Europe (33%, Rizzolli et al. 2005; 22%, Khlopotova 2013), and are often occurring in diet studies as an important component of the peregrine diet, even in urban areas (Rejt 2001, Drewitt & Dixon 2008, Ratcliffe 2010). In Australia the European starling (*Sturnus vulgaris*), being approximately the size of a thrush (Svensson et al. 2004), made up 23-36% of the diet by numbers in different sample years (Olsen et al. 2004, 2008). Overall, thrushes or thrush-sized birds seem to be an ideal, medium-sized prey item for peregrines. This trend may be due to thrushes being widespread and abundant over a range of habitats (Framstad 2015), their mode of foraging on the ground in open habitats, which leaves them vulnerable to detection, or a combination. In addition, the fieldfare nests in colonies (Svensson et al. 2004). The peregrine female was seen covered with dirt marks on her feathers during some prey deliveries (between 11 June and 13 June) (pers.obs.). This may suggest that she attacked at or near a colony of fieldfares, which are known to defend their nests from predators by defecating (Cramp 1988).

In my study, small-sized passerines constituted a high proportion of the diet, at 40% by number. Small-sized prey items have been reported to constitute an important part of the diet of the peregrine elsewhere, e.g. in some areas of the UK where medium- to small-sized passerines were the second most important group in the diet, by numbers (Ratcliffe 2010). Rosenfield et al. (1995) and Palmer et al. (2004) reported frequencies of small passerines of 86% and 54%, respectively, in their peregrine diet studies. The high proportion of small passerines could be explained by a higher ingestion rate for small than for large prey, which would reduce handling time and hasten the return to foraging for the male (Slagsvold & Sonerud 2007). However, some diet studies have found a trend where parents with small

broods delivered smaller items than those with large broods (Mearns 1983, Olsen et al. 1998, Jenkins 2000b, Palmer et al. 2004), and Olsen & Tucker (2003) came to the same result from a brood-size manipulation experiment with peregrines. The average gross prey mass delivered at the nest in my study, with one nestling, was 88 g. This is much lower than the averages from several other peregrine diet studies; 132 g (my estimate) in Palmer et al. (2004), 178 g in Rizzolli et al. (2005) and 205 g in López-López et al. (2009) (but see Rosenfield et al. 1995), but the nests in these studies often had more than one nestling. Therefore, the high proportion of small prey items in my study could also be due to a small brood size, which decreases the food demands at the nest. Due to small brood size, bringing small prey items would most likely be sufficient to satiate the food demands of the only nestling (Mearns 1983, Olsen et al. 1998, Jenkins 2000b, Olsen & Tucker 2003, Palmer et al. 2004). In addition, delivering small prey items to the nest would maximise ingestion rate, thus minimising handling time per prey item (Slagsvold et al. 2010).

The proportion of woodpigeons in the diet accounted for 7% by number of prey items delivered. Studies in Europe have found proportions of woodpigeons in the diet of breeding peregrines ranging from 1% to 20% (Rizzolli et al. 2005, López-López et al. 2009, Ratcliffe 2010). The low proportion of woodpigeons by numbers in general may suggest that its frequency and availability in the wild may not be sufficient to compose a major numeral part of the diet of breeding peregrines. However, the proportion by numbers do not accurately reflect the actual contribution to the total diet, as the woodpigeons do contribute a major proportion by mass, in my study 40%. The delivery of a woodpigeon, with an average mass of 495 g, would be sufficient food for more than one meal, which would lessen the need to hunt again for a period of time. Peregrines have been well documented to cache prey items (del Hoyo et al. 1994, Drewitt & Dixon 2008, Ratcliffe 2010). A large prey item such as a woodpigeon would therefore serve as a food provision for several feeding sessions and may lessen the amount of prey items needed per day to satiate the hunger of the nestlings.

The delivering sex

The female was recorded to have delivered all but four prey items at the nest, which were delivered directly by the male when the nestling was 30-32 days old. The asymmetric parental roles of raptors suggest that the male provide prey for the family and the female perform most of the parental care at the nest (Newton 1979, Cramp & Simmons 1980, Hardey et al. 2006,

Ratcliffe 2010). I observed transfer of prey from the male to the female outside the nest for some deliveries, and the female performed all of the feeding of the nestling as well as brooding at the nest, as expected. Thus, the male captured the majority of the prey items, which were allocated to the female prior to delivery at the nest (cf. Cramp & Simmons 1980, Sonerud et al. 2013). The distinct parental roles during the breeding season is well documented for nearly all species of raptors, and is linked to the evolution of reversed sexual size dimorphism (RSD), which is expressed in various degree among nearly all species of raptors (Newton 1979). The peregrine is a raptor with a high degree of size dimorphism, the female being 40-50% heavier and 15-20% larger, by linear measures, than the male (Cramp & Simmons 1980, del Hoyo et al. 1994, Hardey et al. 2006). Extreme degrees of RSD has been regarded as an adaptation for capturing agile avian prey, on top of the advantages of size dimorphism to monogamous species in widening the feeding niche during the breeding season (Newton 1979, Ratcliffe 2010).

Sonerud et al. (2014a) found that the extent of RSD, calculated as the ratio between female and male wing length, was related to female confinement to the nest and to the proportion of birds in the diet. In my study, female confinement to the nest, defined as the age above which the nestling fed unassisted on >50% of the prey items, was estimated to 29 days, which is also consistent with observations by Ratcliffe (2010). From this, and given that the diet of the peregrine was entirely comprised of birds, one would expect that the data from the peregrine would be comparable to data of other raptors with high degree of dimorphism. In my study, data on the female confinement to the nest, the proportion of avian prey in the diet, and extent of RSD, was similar to that of the goshawk and the Eurasian sparrowhawk (*Accipiter nisus*), two raptors with a high degree of size dimorphism (see Appendix 4). Female confinement to the nest was larger in the peregrine than in raptors with a smaller proportion of birds in their diet, such as the Eurasian kestrel (Steen et al. 2011b, Sonerud et al. 2014a). However, it was actually shorter than for the golden eagle, which may be explained by the high age at independence and the high body mass of prey in the golden eagle, prolonging confinement to the nest (Skouen 2012, Sonerud et al. 2014a).

According to Cramp & Simmons (1980), the male peregrine usually avoid the vicinity of the nesting ledge until the offspring reaches 30 days of age. In my study, however, for a few occasions when the nestling was at 14-18 days of age, the male landed at the nest without a

prey item, within minutes after female take-off from the nest ledge, and stayed there for a few minutes (pers.obs.). This behaviour could be the male guarding the young while the female was away. Carlier & Gallo (1995) suggested that the female will attempt to keep her dominance over the parental activities of the brood and keep the male away from the nest cliff, and that, if absent when the male lands at the nest with food, she would return to chase him off. The behaviour seen in my study, which did not involve deliveries of food, suggests that the female does not always chase off the male, and that the male may not avoid the vicinity of the nest ledge completely while the chicks are young. This is in accordance with Palmer et al. (2001) who found that peregrine male attendance at the nest was low, but not entirely absent until near fledging (see also Jenkins 2000b), suggesting that the male contribute a small part to parental care while the female is away. Overall, these observations may suggest that the female shows aggressive behaviour towards the male only selectively, e.g. during parental activities such as feeding and brooding, in order to prevent the male from feeding directly and to control the allocation of food between the nestling and herself (cf. Sonerud et al. 2013). Also, the extent of aggressive behaviour may vary intraspecifically.

Preparing prior to delivery at the nest

In my study, the peregrine plucked and decapitated the majority (88% and 85%, respectively) of the prey items prior to delivery at the nest. This was also noticed by Ratcliffe (2010) and Jenkins (2000b). However, Rosenfield et al. (1995) found that only 31% (my estimate) of the small prey items were delivered decapitated and plucked at the nest, whereas the majority (80%) of the larger prey items had been decapitated, thoroughly plucked and partially dismembered before delivery. A possible explanation for the high probability of delivering a decapitated prey could be that the male falcon may often eat the brains of prey items for himself while delivering the rest of the prey item to his mate or nestling (Ratcliffe 2010). In this way, the proportion of indigestible parts transported to the nest is reduced while effectively putting to use any nutritiously or energetically rich parts of an avian prey. The thorough plucking of prey items prior to delivery may also be a way to feed effectively on the energetically favourable parts of the prey (Kaspari 1990, 1991). Also, the peregrine may not have the gape size and thus, swallowing capacity to ingest prey items whole (Slagsvold & Sonerud 2007, Slagsvold et al. 2010; see also Kaspari 1990), unlike e.g. the Eurasian kestrel and the golden eagle (see Steen et al. 2010, Skouen 2012). This would opt for preparation of prey prior to ingestion or feeding. More importantly though, peregrines have small intestines,

and thus less efficient absorption of nutrients, which would give a need to selectively ingest parts of the prey item with high nutrient content (Barton & Houston 1993). The meat was ingested in small pieces, which would increase the surface area per unit weight of meat and allowing nutrients to be taken up more effectively when passing through the intestines (cf. Salmila 2011).

The adult peregrines had partly consumed 18% of the prey items prior to delivering them at the nest. The likelihood that an adult had eaten parts of the prey item prior to delivery at the nest increased with body mass of the prey. The probability that a small passerine or a thrush had been partly consumed before delivery was very low, and based on the video recordings in these cases, only a small proportion of the prey had been consumed (pers.obs.). In contrast, all of the pigeons delivered has been noticeably eaten at, and the proportion of the prey item that had been consumed was usually large. An explanation could be that pigeons are large enough to be used for more than one meal, thus the male may have consumed parts of the large prey item at the capture site to satiate himself, and then delivered it to the female to satiate the family at the nest. The female was also seen to carry the remains after a finished meal out of the nest for all six pigeons, suggesting that consuming part of the large prey items before delivery was not a hindrance for satiating the nestling and the female. Due to the small brood size in my study, the food demands were lower than would be for a larger brood size (e.g. Olsen & Tucker 2003). Therefore, the male may have consumed parts of large prey items to reduce his time needed for self-foraging without it being at the expense of satiating the brood.

Preparing, handling and feeding at the nest

Thrushes made up 7 out of the 10 prey items delivered whole, and made up all the prey items that were recorded to be plucked at the nest by either the female or nestling. The video recording was however unsuccessful in completely recording 5 of the 10 prey items that were delivered whole. Also, some of the prey items that were recorded being plucked at the nest, had previously been partly plucked before delivery, and the plucking for these lasted for only a few seconds. Some prey items may not have been plucked if the male prioritised returning quickly to the hunting area, e.g. due to a temporary high availability or clumped distribution of prey (Sonerud 1985). In this case, assuming that the male usually handles the prey before delivering to the female, the male would minimise his handling time by delivering the intact prey item to the female immediately after capture, thus allowing him to resume hunting.

The probability that the female handled a prey item and fed the nestling rather than the nestling handled unassisted, decreased with nestling age and increased with body mass of the prey item. Regardless of a large gap in video recordings (approximately 4 days), which started the day after the first observation of unassisted feeding by the nestling, the analysis did show a clear difference in the proportion of unassisted feeding between recordings prior to the gap and recordings after the gap. Avian prey items would be difficult to handle due to protruding parts such as bill, wings, feathers and tarsi, and therefore require thorough handling and partitioning to get to the profitable parts. Feeding time has been shown to be longer for avian prey than other prey types of the same body mass (Slagsvold & Sonerud 2007), and is thought to constrain the female to the nest for partitioning and distribution of food to the young for a considerable time (Sonerud et al. 2013, 2014a). As a nestling grows older, it gradually develops physically until it is able to grip and hold a prey item, and use its bill proficiently to handle and tear chunks of meat off it (Ratcliffe 2010). The nestling in my study handled its first prey item at 23 days of age, which fits with Ratcliffe's (2010) finding that peregrine nestlings begin assertively to grab at prey items at 24 days of age. The probability of the female feeding the nestling increased with prey body mass, which could be explained by the fact that the female handled all large prey items, i.e. the magpie and the woodpigeons. This is in accordance with studies of handling time in various raptors (Slagsvold & Sonerud 2007, Sonerud et al. 2014a). Another explanation may be that the female kept control of the large prey items in order to satiate herself as well as the nestling, by distributing the food between them (Sonerud et al. 2013).

Number of meals

When the female peregrine fed the nestling, number of meals per prey item increased with nestling age. However, the only prey item with more than one meal of which the female was registered as feeder, had a registration of the nestling feeding unassisted for the first bout. The result was likely due to the nestling being satiated before completely consuming the prey item. The later arriving adult female picked up the unused prey item and took full control of the distribution of the remainder between herself and the nestling, in accordance with the suggestion by Sonerud et al. (2013). The woodpigeons delivered at the nest were each consumed in one meal at the nest. However, considering their condition at delivery they had most likely been utilised for one or more meals outside the nest prior to delivery. This is corresponding with the observation above, that all of the pigeons delivered at the nest had

been partly consumed prior to delivery at the nest. Also, the remains were carried out of the nest by the female after the meal at the nest was finished (pers.obs.), likely for caching the item to utilise it for one or more meals later (Ratcliffe 2010, del Hoyo et al. 1994). According to Ratcliffe (2010), the peregrine takes two or even more meals from larger items. The number of meals for the large prey items delivered were therefore most likely underestimated, and the handling time of these prey items were also likely underestimated.

When the peregrine nestling fed unassisted, number of meals per prey item decreased with nestling age. The capability and efficiency of handling a prey item improves with age and the nestling becomes more proficient in general at tearing up prey as it ages. The nestling did not handle larger prey items as it aged, and never fed unassisted on avian prey larger than 120 g. Therefore, the decrease with age of the nestling may be explained by the nestling being able to eat more of the prey item per meal as it developed physically, e.g. the size of its digestive tract and gizzard increased, which allowed it to ingest more meat before reaching satiation (cf. Slagsvold & Sonerud 2007, Slagsvold et al. 2010).

Handling time

For the prey items which the peregrine female fed to the nestling, handling time increased with increasing net body mass of the prey item. This is in accordance with findings in other studies of handling time in raptors (Slagsvold & Sonerud 2007, Sonerud et al. 2014a). The likely explanation is that larger prey items have larger bones and stronger ligaments, which require more handling and effort to tear up pieces of meat (Slagsvold & Sonerud 2007). Still, when handling larger prey items, in particular large avian prey, strictly bird feeders such as the peregrine are considered more effective than raptors feeding on small mammals as well as birds (Slagsvold & Sonerud 2007). Bird feeders have evolved a long and narrow bill more specialised to pluck and tear up a prey, which could explain the effectiveness at handling large avian prey. Therefore one would expect handling time to increase with net body mass of prey more slowly for a bird feeder than a raptor with less proportion of birds in the diet (Slagsvold & Sonerud 2007).

Also for prey items handled by the peregrine nestling unassisted, handling time increased with net body mass of prey, as was the case for Eurasian kestrel nestlings (Steen 2004),

sparrowhawk nestlings (Aasen 2004), and golden eagle nestlings (Skouen 2012). Handling time of prey items handled by the peregrine nestling unassisted also decreased with nestling age. The nestling was observed to take many breaks, change position several times, and being seemingly confused while handling an unplucked prey item for the first time (pers.obs.). Ratcliffe (2010) mentioned that peregrine nestlings can rip up prey items proficiently at 31 days of age, which would be 8 days after the observation of the first prey item being handled unassisted in my study. Then, as the nestling became more physically capable of ingesting larger pieces and more experienced at handling prey items, it fed more efficiently and took fewer breaks, which reduced handling time.

Methodological challenges

In total 58% of the prey items in my study were identified to species or genus level. The high proportion of identification to this level is likely due to the high number of distinguishable thrushes identified to genus, as only a few of the small passerines were identified to species. A recurring flaw concerning video monitoring is the difficulty of taxonomically identifying prey to genus or species level, as most prey have been plucked of clues for identification prior to delivery at the nest (Jenkins 2000b, Redpath et al. 2001, Reif & Tornberg 2006, Zárybnická et al. 2011). In my study, identification by video recordings proved challenging due to the raptor plucking and removing identifiable feathers and appendages from the prey prior to delivery at the nest. In addition, the view was limited to the angle and position of the camera, with the possibility of the prey item being held away from or brought outside of camera view. The identification of prey item was therefore often based primarily on its size proportional to the female, which may be a subjective evaluation and source of bias (see also Tornberg & Reif 2007).

The use of indirect methods, i.e. analyses of pellets and prey remains, to estimate diet composition in raptors is biased in terms of the proportion of each prey and the total number of prey in the diet (Mearns 1983, Oro & Tella 1995, Lewis et al. 2004, Tornberg & Reif 2007, but see Rosenfield et al. 1995). The extent of this bias would also vary among raptor species (Slagsvold et al. 2010). Pellets overestimate small prey in the diet whereas remains overestimate large prey, thus each may bias the proportion that a prey constitute in the diet (Mearns 1983, Oro & Tella 1995, Redpath et al. 2001, Rutz 2003, Lewis et al. 2004). In addition, even the combined use of both may underrepresent the full complement of prey

items in the diet, as remains may be preserved unequally, and the conspicousness or undetectability of some species may bias the result (Mearns 1983, Rutz 2003, Lewis et al. 2004). Although shorter interval between the collecting of remains would reduce the bias (Tornberg & Reif 2007), prey items may also be carried away from the nest, as was observed for several prey items in my study. This would make accurate estimates of diet difficult to quantify by indirect methods (Drewitt & Dixon 2008, Slagsvold et al. 2010).

In comparison, the use of direct methods provides a more complete diet record by numbers, and a more accurate description of the full diet composition of raptors, although with less detail of prey to species level (e.g. Lewis et al. 2004, Redpath et al. 2001, García-Salgado et al. 2015). Video monitoring is able to provide information on aspects outside the range of what indirect methods could provide, such as handling time of prey and aspects of nest activity and parent-nestling interactions of raptors (Lewis et al. 2004, Jenkins 2000b, Steen et al. 2010, 2011b, Sonerud et al. 2013, 2014a,b). However, the use of either method involves disturbing the studied birds significantly, and using direct methods may not always be possible due to the inaccessibility of nests or disturbance-intolerant species (Reif & Tornberg 2006). Also, direct methods such as video recording is time-consuming, requires maintenance and can suffer from technical errors, and the costs of the equipment may make this method less suitable for collecting data over many nest sites compared to indirect methods (Reif & Tornberg 2006, Tornberg & Reif 2007, Skouen 2012, García-Salgado et al. 2015, but see López-López & Urios 2010). Several studies have suggested that a combination of both methods would give a more accurate assessment of diet, and reduce time spent monitoring (Rosenfield et al. 1995, Jenkins 2000b, Lewis et al. 2004, Zárybnická et al. 2011, García-Salgado et al. 2015).

Future considerations

In an ongoing study in Nottingham, UK, an urban peregrine nest is being video monitored with a thermal-imagery camera, which reveals whether prey items brought to the nest are fresh (i.e. warm) or have been taken from a cache (E. Kettel, pers.comm.), so far with promising results. This method may be an appropriate way to distinguish fresh from cached prey items at delivery also in non-urban areas. Determining when fresh prey and cached prey were brought to the nest would enable analyses of the conditions that may affect the

probability that a cached prey item rather than a fresh one will be delivered, factors such as e.g. delivery intervals, time of day, and weather conditions.

Time-lapse cameras has been used to record parental behaviour and provisioning of food at falcon nests (Jenkins 2000b), as well as a supplement to direct observations to record falcon behaviour, activity outside the nest, and attendance of adult falcons at the vicinity of the nest (R. Steen, pers.comm.). In my study, the time set aside for performing direct observations of the falcons outside the nest was reduced due to the maintenance issues regarding the video equipment. In addition, I was unable to correlate the observations outside the nest with recordings at the nest, as video was often missing for the days and hours when the direct observations were conducted. As a suggestion for future studies, the use of one or more time-lapse cameras stationed at areas adjacent to the nest could be a supplement to direct observations and would improve the likelihood of getting corresponding records of activities outside and at the nest.

The weather was consistently clear for nearly the whole duration of the monitoring period, and the stable weather was most likely the reason that the analysis did not show any effects of weather variables in my study. However, prey deliveries may be affected by unstable weather, although varying between raptors (Olsen & Olsen 1992). In addition, Jenkins (2000b) found that strong wind tended to positively affect food provisioning, although the number of observation days with strong wind were few. Also, the quantity of small passerine prey would be affected negatively by unstable or severe weather conditions (Røer 2015). Considering that climate change will have a negative effect on the stability of the weather into the future, I would suggest the gathering of meteorological information when studying raptors to investigate the effects of various weather conditions on their ecology.

Conclusion

The diet of the peregrines consisted entirely of birds, where thrushes were the dominating group by number and mass, and the woodpigeon the dominating species by mass. Small-sized passerines were also an important group of prey by numbers. This may suggest a higher importance of small prey during the breeding season than has been previously reported in literature. The male peregrine caught the highest amount of prey, which were transferred to

the female prior to delivery at the nest. This supports the theory of RSD in raptors, where the male is smaller than the female in order to catch more agile prey during the nestling period (Newton 1979, Ratcliffe 2010). Avian prey require more thorough handling and preparation before being ingested than other types of prey, and requires the nestling to be older before it can feed unassisted (Slagsvold & Sonerud 2007, Sonerud et al. 2013, 2014a). This suggests that the female is constrained to the nest for a longer period of time than raptors with a smaller proportion of birds in their diet (Sonerud et al. 2014a). The use of direct video-based monitoring supplied with observation from outside the nest provided broad information on the ecology of the peregrines during breeding, including the transfers of prey prior to delivery, time of day and frequency of deliveries, and handling of prey at the nest. Video monitoring also provided detailed information on the diet of the peregrines during the breeding season. There is still a need to assess the diet, and the degree of preparation and relative handling of different prey in relation to the selection of prey of the peregrine during the breeding season. The use of video recording as a tool to observe behaviour at the nest and to track performance to the time it was performed, is recommended for getting valuable information on the ecology of the peregrine, as well as for other raptors. In addition, the use of thermal-imagery camera is recommended to further improve the detail of information on the foraging performance and foraging behaviour of raptors.

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Appendix

Appendix 1. Mean gross prey body mass is the estimated weight of the prey species at the moment of capture, as gathered from literature (Cramp 1985, 1988, 1992; Cramp and Perrins 1994; Selås 2001). Mean net prey body mass is the estimated mean weight at delivery, corrected for decapitation, plucking and partial consumption prior to delivery.

Prey category	Mean gross body mass (g)	Mean net body mass (g)
Woodpigeon (*Columba palumbus*)	495	280
Common swift (*Apus apus*)	40	35
Blackbird (*Turdus merula*)	95	88
Fieldfare (*Turdus pilaris*)	105	100
Song thrush (*Turdus philomelos*)	74	74
Mistle thrush (*Turdus viscivorus*)	120	105
Thrush indet. (*Turdus sp.*)	80	71
Lesser whitethroat (*Sylvia curruca*)	12	12
Warbler (Phylloscopidae)	10	9
Eurasian magpie (*Pica pica*)	220	192
Small passerines indet.	15	13
Larger passerine indet.	25	22

Appendix 2. Raw material used for the cosinor analysis in Table 3 and Figure 2.

Hour-block	Number of deliveries	Number of hours monitored
00-01	0	19
01-02	0	19
02-03	0	19
03-04	0	19
04-05	1	19
05-06	5	19
06-07	9	19
07-08	7	19
08-09	4	19
09-10	7	19
10-11	5	18
11-12	2	16
12-13	2	16
13-14	3	15
14-15	6	16
15-16	1	16
16-17	6	16
17-18	7	16
18-19	5	18
19-20	8	20
20-21	3	21
21-22	4	20
22-23	3	19
23-24	0	19
Total	88	436

Appendix 3. Parameter estimates of the best model for Table 3, Figure 2.

Explanatory values	Estimate	SE	Z	p
Intercept	-2.059	0.246	-8.39	<0.0001
I(cos(2 * π * Hour/24))	-1.644	0.419	-3.93	<0.0001
I(sin(2 * π * Hour/24))	-0.329	0.203	-1.62	0.11
I(cos(2 * 2 * π * Hour/24))	-1.396	0.308	-4.53	<0.0001
I(sin(2 * 2 * π * Hour/24))	-0.649	0.244	-2.66	0.0077
I(cos(3 * 2 * π * Hour/24))	-0.335	0.237	-1.42	0.16
I(sin(3 * 2 * π * Hour/24))	-0.497	0.234	-2.13	0.033

Appendix 4. Data used to compare interspecies differences in the relationship between parental role asymmetry, diet and SSD.

Species	FCN	OIA	PAP	PBM	MBM	MWL	FWL
Peregrine falcon	29.0	98[1]	1.000	88.2	666[1]	309[1]	356[1]
Golden eagle[2]	40.3	140	0.691	483.8	3572	591	661
Goshawk[2]	29.0	77	0.953	167.6	865	327	367
Sparrowhawk[2]	29.4	57	1.000	27.0	144	203	240

FCN is female confinement to the nest, taken as the age (days) above which offspring ingested >50% of the prey unassisted. OIA is offspring age (days) at independence. PAP is the probability that a prey item recorded delivered in the study was a bird. PBM is gross body mass (g) of prey items recorded delivered in the study. MBM is adult male raptor body mass (g). MWL is adult male raptor wing length (mm). FWL is adult female raptor wing length (mm). Ratio SSD (FWL/MWL) was 1.15, 1.12, 1.12 and 1.18 for peregrine, golden eagle, goshawk, and sparrowhawk, respectively.
[1] from Cramp and Simmons (1980).
[2] data from Table 3 in Sonerud et al. (2014a).