Male prey delivery and female aggression in the Eurasian kestrel (Falco tinnunculus)

Hannens bytteleveringer og hunnens aggresjon hos tårnfalk (Falco tinnunculus)

Anette Nodeland

NORWEGIAN UNIVERSITY OF LIFE SCIENCES
Department of Ecology and Natural Resource Management
Master Thesis 60 credits 2013

Acknowledgements

This thesis came together with the help from my two supervisors, Professor Geir A. Sonerud and Ph.D. Ronny Steen. Ronny has been of help with both the technical and statistical part of this thesis, while Geir has helped identifying prey items, keeping my spirits high and guiding me throughout this thesis. An additional thank to Professor Vidar Selås who took the time to identify prey items together with Geir and I over several days. Thank to Stine Marie Engmark Espe for her company and our work together, both during our fieldwork, but also during the statistical analysis and the writing of this journey. A special thanks to Cathrine Sussane Torjussen for volunteering in helping Stine Espe and me with the fieldwork in Trysil, during our last week of collecting data. Of course I also want to thank Ole Petter Blestad for lending us his nest boxes, marking the nestlings and therefore providing us with data.

Financially I was supported by Viltfondet (DN) and Lånekassa during the fieldwork in summer of 2012. With their help I could easily focus on the fieldwork, not having to work that summer.

Last, I want to thank those that mean the most to me, my parents, my brother and my boyfriend for reviewing my drafts, comforting and supporting me. I also need to thank my two dogs for keeping me sane and giving me breaks and joy during our walks and cuddles.

Anette Nodeland Ås, December 2013

Abstract

I studied the foraging strategy in a generalist raptor, the Eurasian kestrel (*Falco tinnunculus*), in a year with low populations of *Microtus* voles and bank vole (*Myodes glareolus*). By video filming prey delivered at the nest, and simultaneously observing the prey allocation behavior outside the nest. The most common prey types delivered at the five nests studied were the common lizard (*Zootoca vivipara*), followed by birds, voles (*Microtus* and *Myodes*), and shrews (Soricidae). I found that the probability that the kestrel returned with items of the same prey type repeatedly differed between prey types, and also depended on weather conditions. The common lizard was more likely to be delivered repeatedly with higher ambient temperature, while shrews were more likely to be delivered repeatedly with lower temperature. For birds no weather variable had an effect, and almost all avian prey delivered repeatedly were nestlings or newly fledged young. This could indicate that a central place foraging kestrel adopts a win-stay strategy, concentrating on prey types with high availability at specific weather conditions. I found that the female was more likely to show aggression towards the male when he delivered the prey directly at the nest than when he delivered the prey to the female outside the nest.

Sammendrag

Jeg undersøkte hvordan fødesøket hos en generalist blandt rovfuglene, tårnfalken (*Falco tinnunculus*) var i et år med lav populasjon av *Microtus* og klatremus (*Myodes glareolus)*. Dette gjorde jeg ved å videofilme byttedyr levert på redet, samtidig som jeg observerte atferden når byttet ble overlevert fra hann til hunn. Det vanligste byttedyret levert på de fem studerte reirene var nordfirfisle (*Zootoca vivipara)*, fulgt av fugler, stumpmus (*Microtus* og *Myodes*) og spissmus (Soricidae). Jeg fant ut at sannsynligheten for at tårnfalken leverte samme type byttedyr etter hverandre var forskjellig mellom type byttedyr, og var avhengig av været. Det var mer sannsynlig at firfisle ble levert flere ganger etter hverandre hvis det var høy temperatur, og mer sannsynlig at flere spissmus ble levert etter hverandre ved lav temperatur. For fugler ga ikke værvariabler noen effekt, og fugler som ble levert flere ganger etter hverandre var som regel reirunger, eller unger som nylig hadde forlatt redet. Dette kan tyde på at en tårnfalk, som returnerer med byttet til et sentralt punkt slik som et reir, har tilpasset seg en vinn-vent strategi, og konsentrerer seg om byttedyr som er lette å få tak i, ved spesifikke værforhold. Jeg fant også ut at hunnens aggresjon var større når hannen leverte byttet direkte på reiret sammenlignet med når hannen leverte til hunnen utenfor reiret. Dette antyder at hunnen forsøker å forhindre hannen i å levere direkte til ungene, sannsynligvis for å kunne kontrollere allokeringen av hannens leveranser mellom seg selv og ungene.

Table of Contents

Introduction

In many species in many taxonomic groups, parents provide food and care for their offspring. While some care-giving parents provide only protection for their young, some also provide food (Klug & Bonsall 2010). Food provisioning means that the parents make resources which are initially unavailable to the young because of e.g. size, shape, feathers and coating, available to them. To offspring, there are many advantages from food provisioning; more energy may be invested in growth, and predation risk is lowered (Farmer 2000). A recent study indicated that parental provisioning is more likely to evolve, and is favored, if the provisioning is more efficient then self-feeding (Gardner & Smiseth 2011). Among birds there are species with self-feeding offspring (e.g. ducks Anatidae), and species where parents feed their dependent offspring (e.g. tits Paridae). One of the differences between these two groups is that self-feeding offspring most often have only one care-giving parent (the female), while offspring dependent on being fed receive bi-parental care. The latter hatch as undeveloped and dependent nestlings, needing help from the parents for allocation of prey (Klug & Bonsall 2010). Raptors (hawks Accipitriformes, falcons Falconiformes, and owls Strigiformes) are among the birds with bi-parental care, and in this group, female-biased sexual size dimorphism is common (Newton 1079).

Repeated deliveries

What raptors captures and where they find prey for its nestlings are affected by prey abundance and time and energy spent searching for prey. During my study period there was low abundance of voles (Cricetidae), severely affecting the kestrels food supply. Many raptors can use the win-stay hunting strategy, meaning that the raptor will return to the last successful hunting area (Sonerud 1985). This will therefore, in most cases, lead to repeated deliveries of the same type of prey (Sonerud 1985; Steen et al. 2011a; Steen et al. 2011b). Previously there have been some studies of raptors using the win-stay hunting strategy, based on data collected by observations from a hide (Sonerud 1985) and more recently by video monitoring (Steen et al. 2011b). Combining distant observations from a hide and close-up video surveillance of the nest during deliveries will provide data on the deliveries, which is an indicator on localization of the hunting area, and time between each delivery. Observing repeated deliveries of the same prey type at the nest is a necessary condition for documenting a win-stay strategy (Steen et al. 2011a), but not a sufficient condition, because the same prey type may be taken at different sites during the same environmental conditions. To document use of a win-stay strategy, radio telemetry would be needed to verify that the predator actually return to the same site. Because the activity level of different prey types would be affected by different short-term changes in the environment, repeated deliveries of one prey type would be affected by different environmental variables than repeated deliveries of another prey type. Thus, I predict that repeated deliveries of the endothermic prey like lizards would be more likely with higher ambient temperature (cf. Steen et al. 2011a).

Aggression

Most raptors have female-biased sexual size dimorphism, meaning that the females are larger than the males (Mueller, 1990; Andersson, 1994; Massemin et al., 2000; Krüger, 2005). One hypothesis for female-biased sexual size dimorphism is that different-sized sexes can exploit different feeding niches, which would reduce the food competition between male and female (Selander, 1966; Snyder & Wiley, 1976; Newton, 1979). One would thus expect larger females to have higher fitness than smaller ones when food is scarce, but Massemin et al. (2000) on the contrary showed that in the Eurasian kestrel (*Falco tinnunculus*), smaller females produced more nestlings in a year with few voles.

The reason for, and the maintenance of, female-biased sexual size dimorphism in raptors may be the different reproductive roles of the sexes (Slagsvold & Sonerud, 2007; Sonerud et al., 2013). In most other raptors, the male provides all prey during the first part of the nestling period. In many raptors with female-biased sexual size dimorphism, aggression from the female towards the male occurs when the male returns with a prey item (Cramp & Simmons, 1980; Cramp, 1985; Sonerud et al., 2013). The reason for this aggression is unknown. When feeding the young, the female will eat some, or all, of the prey delivered by the male (Kristiansen, 2003;

Brodin et al., 2003). The male should therefore give captured prey directly to his young to maximize his own fitness, instead of delivering prey to the female and risk feeding her at the expense of his offspring (Sonerud et al. 2013). At the same time the male should maximize his foraging time, and therefore deliver prey to the female and leave it to her to divide the prey and feed the young. Some females desert the nest and their young, after having fed on the prey items the male has delivered, either to ensure her own survival (Dawson & Bortolotti, 2002; Eldegard & Sonerud 2009; Eldegard & Sonerud, 2010; Sonerud et al., 2013) or to initiate a new brood with another male (Kelly & Kennedy, 1993; Eldegard & Sonerud 2009). The desertion by the female will not have severe effects on survival if the young are old enough to ingest prey by themselves (Kristiansen, 2003; Sonerud et al. 2013).

When the male provides the female and the dependent nestlings with food, the female may thus show aggression towards the male to increase her control over the allocation of prey delivered. Therefore, larger prey may provide more food for female self-feeding, and the female would be more eager to achieve control over such prey. Hence, I predict that a larger prey item will lead to more aggression. Furthermore, the female´s control over prey allocation is more at risk when the male attempts to deliver the prey directly to the nest than when the male delivers the prey to the female outside the nest. Hence, I predict that the female will show more aggression towards the male when he delivers the prey to the female directly on the nest.

I used the Eurasian kestrel, hereafter termed the kestrel, as study species because of its frequent use of artificial nest boxes, toleration towards humans and disturbance, its wide diet, and the fact that it is a single-prey loader (Cramp & Simmons, 1980; Village, 1990; Forsman, 1999), facilitating identification of prey delivered at the nest. With a body mass of males of ca. 210 g, the kestrel is a relatively small raptor, and the female is only a little larger than the male (Village, 1990). The kestrels breeding in Norway, and other Nordic countries, are migratory, but farther south in Europe they are resident, breeding even in cities (Village, 1990; Forsman, 1999). The kestrel is a generalist predator, with a diet consisting mostly of birds, lizards, rodents, shrews and insects (Village, 1990). Kestrels adapt their diet to what is available, and show a functional response to voles (Korpimäki, 1985; Village, 1990).

Methods

Study area

I collected data from five nests of the kestrel in Trysil municipality, Hedmark county, in south-eastern Norway (61° 12´ - 61° 15´ N; 12° 58´ - 12° 62´ E) during June and July in 2012. The five nest sites were all in the boreal zone, primary containing Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), but the corresponding habitats differed somewhat from each other. The habitat around two of the nest sites (terme 305 and OP20), where quite similar; large clear-cuts with scattered pine trees left as seed trees. A third nest site (termed 079) was in the middle of a clear-cut, with denser spruce forest around. The fourth nest site (termed 085) was on the edge of a pine forest towards a bog. The fifth nest site (termed 072) was in a pine plantation regrown after clear-cutting some years ago, near a small farm. All nest sites were in short distances (50-150 m) from small and secluded forest roads.

Data collecting and monitoring

I videotaped prey deliveries at the kestrel nests in order to identify prey items and record when they were delivered (Zarybnicka et al., 2010; Steen et al., 2011b). A small camera was attached inside the nest box, with the lens pointing towards the opening of the nest box. The camera was connected to a DVR digital video recorder placed on the ground at the base of the nest tree. The camera had a motion detector, and started recording at 10 s interval after being triggered. All data was collected and saved on a SD card, and the camera was powered by a 12VDC (18Ah) battery (for more information, see Steen 2009). Therefore, I was able to monitor all of the nests even when I was not present.

I also collected data on the aggression of the female towards the male when the male returned with prey, by sitting in a hide and monitoring each nest over several hours at a time, varying from early morning to early afternoon. During the same time, the prey deliveries at the nest were recorded on video. The kestrel started the hunting at around 05 hours, and continued hunting until around 21 hours. During a total daily observation period of 3-8 hours, my fellow student (Stine Espe) and I switched place after approximately four hours. I took note of every observed prey delivery at the nest, every handover from the male to the female, and every accompanying noise, in addition to observations of the weather. I put up the hide within 100 m from the nest, and limited the motion and noise around the nest to a minimum, in order to avoid scaring and disturbing the kestrels.

Data

When observing the nests I focused on registering if there was aggression during the delivery from the male to the female. If I was unsure if there was aggression or not, I scored it as unknown. If scored as aggression it was clearly aggression between the two parents, i.e. the female almost flew the male down, looking like an attack (Cramp & Simmons, 1980; Cramp, 1985; Sonerud et al., 2013). This means that the male came flying, and just before, or during, alert sounds, the female grabbed the prey from him. In addition to watching this from the hide, I registered some circumstances on tape where the male delivered the prey at the nest, and the female was either in the nest box or entering it. When this happened I was able to score it as either no aggression or aggression. I scored it as aggression if the female grabbed the prey from the male’s beak, made herself appearing bigger by raising her feathers, screamed or pushed him out. If the male delivered the prey directly to the nest without the female being involved I scored it as not applicable.

In eight cases I observed the female in the nest box before she flew out and came back within a time range from 20 s to 2 min 20 s. In these circumstances, I have interpreted it to be the male coming with a prey item, and the female flying out to collect it, before returning with it.

To estimate the small mammal prey abundance around each nest site, 30 snap traps were put out in each of the four cardinal directions (north, south, east and west), with an interval of 10 m. The traps were checked after one night and collected after two nights, making a total of 240 trap nights per nest. This method is not optimal, because different small mammal species are not equally trappable, but it can be a helpful tool to give an approximate index of population density for each species (Village, 1990). From this snap trappings it was confirmed that 2012 was a low year for wood lemming (*Myopus schisticolor*) and *Microtus* voles (for more information on trapping results, see Espe (2013)). Therefore, there were very few breeding attempts by the kestrel in the study area.

The body mass of each prey type except birds was taken as the mean body mass of prey items of that type delivered to kestrel nests in a previous year in the same area (Steen et al., 2011b). Because my data were collected in a year with few *Microtus* voles and bank voles, it is possible that the body mass of the prey items were a little lower than in the study of Steen et al. (2011b). The body mass of avian prey was estimated for each item separately from the size relative to the kestrels appearing on the video screen.

All data on the weather variables were downloaded from the Norwegian Meteorological Institute web portal (eKlima 2013). These data were collected by the official meteorological station “Trysil Vegstasjon”, situated central in my study area (61°29’N, 12°27’E). Wind speed (10 m above ground), temperature and rain fall were collected every hour. Each prey item delivered to the nest was linked with the weather conditions from “Trysil Vegstasjon” from the respective hour. Mean temperature at the time off prey delivery was 15.2°C ± 0.1°C with a minimum of 5.1°C and a maximum of 23.7°C. The mean wind speed at the time of prey delivery was 2.6 ± 0.1 ms^{-1}, with a minimum 0.2 ms^{-1} and a maximum of 6.5 ms^{-1}. Mean rainfall measured from an hour before delivery to the time of delivery was 0.08 ± 0.07 mm, with a minimum and maximum of respectively 0 mm and 4.0 mm.

Several unfortunate incidents caused my sample size to be reduced. Firstly, I caught on tape a pine marten (*Martes martes*) killing and removing all three nestlings in one of the nests that I studied (nest OP20). Secondly, ca. two weeks later I found the closest kestrel nest studied, only 1 km away (nest 305), to be empty. I suspect that the same marten individual visited that nest as well. Unfortunately the camera was not recording when predation happened in the second nest, and I can therefore not be sure if the marten was the predator or not. Thirdly, one female deserted her nest (nest 079) after having been marked with a radio transmitter. The male continued caring for the brood after his mate's desertion.

Statistical analysis

All analysis were run in the statistical software program R 2.15.2 (R Development Core Team 2013). The analysis on repeated prey deliveries from the male was run with nestling age and the nest ID as random effects (Pinheiro & Bates, 2000; Steen at al., 2012), to control for any differences between the broods and the breeding pairs.

The analysis on repeated prey deliveries were first run in order to find the best model, and thereafter testing this model with the three main prey types. I included all weather conditions and interactions between these as response variables, and then selected the model with the lowest AIC-value and fewest variables as the best model (Burnham & Anderson, 1998). Other models with an AIC-value ≤ 2.0 lower than the best model were competing models (Burnham, 2002), and further analyzed if necessary. The model numbers to which I refer in the text were automatically generated by the statistical software.

I was interested in testing if the kestrel hunted specific prey items at specific times, depending on time of day, and the weather variables ambient temperature, rainfall and wind speed. Before I ran the tests on repeated deliveries, I sorted the dataset and excluded deliveries of *Microtus* voles, bank vole (*Myodes glareolus*), unidentified mammals, and infrequent prey types (insects, slow worm (*Anguis fragilis*), common frog (*Rana temporaria*) and toad (*Bufo bufo*)). I also excluded prey delivered when the female was the hunter and when the sex of the hunter was unknown, two missing values on time of the delivery, missing values on temperature, and missing values on the response whether an item being of the same or different type as the last one. I first removed the deliveries when the female was the hunter because there were only three cases of this, and the deliveries when the sex of the hunter was unknown to ensure that I followed the same individual on the successive hunting trips. After having excluding these cases, the datasets on bank vole and *Microtus* voles were too small, and were therefore excluded. I was left with a total of 161 prey items, delivered segregated on 49 birds, 29 shrews, and 83 lizards.

For the aggression analysis I excluded deliveries of unidentified mammals, infrequent prey types (insects, slow worm, frog and toad), deliveries when the female was the hunter and all cases were it was unknown if there had been aggression or not. I remained with 15 cases of aggression, and 30 cases with no aggression.

Results

Prey delivered at the nest

A total of 443 prey items were delivered during video monitoring at the five nests. Of these, 141 lizards (*Zootoca vivipara*), 1 frog, 2 toads, 79 shrews (*Soricidae*), 46 *Microtus* voles, 45 bank voles, 108 birds and 2 slow-worms were identified, while 5 items were categorized as a mammal, 6 items as a vole, and the remaining 8 items were unknown. In 68 cases the delivery were also observed from the hide. Most prey items were taken by the males, and I only registered 3 prey items taken, for sure, by the females.

Repeated deliveries for the three main prey types pooled

I started the analysis with all the weather variables (rainfall, wind speed, ambient temperature), which sex that hunted and delivered the prey item, time of day, time since last delivery, what type of prey, body mass of prey, age of nestlings and preystatus (whole, decapitated, plucked). After the first analysis the three best models were 173, 198 and 246 (table 1).Model 173 included the variables prey type, ambient temperature, and the interaction between these two. Model 246 included the same variables, and also rainfall, while model 198 included windspeed instead of rainfall. I ran all three models, but model 246 had autocorrelation between rainfall and ambient temperature, and was therefore excluded from further analysis (Table 1).

Table 1. AIC table of the three best models for the probability that a prey item delivered at a kestrel nest was of the same type as the previous prey item delivered.

Model	Variables	AIC	Rank
173	3	205.37	1
246	4	204.89	2
198	4	205.00	2

In model 173 the probability that an item delivered was of the same type as the previous item delivered was significantly affected by prey type, ambient temperature, and the interaction between prey type and temperature. The effect of temperature differed significantly between lizard and shrew, significantly between lizard and birds, and marginally significantly between shrew and bird (Table 2).

Table 2. Parameter estimates from the best fitted generalized linear mixed-effect model with binominal distribution, corrected for the random effect of nest ID (n=5), for the probability that a prey item delivered was of the same type as the previous item delivered. Model 173.

	Estimate	SE	z	P
Prey type				
Lizard vs. shrew	10.86	3.33	3.26	0.001
Lizard vs. bird	6.20	2.73	2.28	0.02
Shrew vs. bird	-4.66	3.05	-1.53	0.13
Ambient temperature				
Lizard	0.46	0.13	3.45	0.0006
Shrew	-0.34	0.19	-1.81	0.07
Bird	-0.0073	0.10	-0.07	0.9
Prey type x ambient temperature				
Lizard vs. shrew	-0.80	0.23	-3.49	0.0005
Lizard vs. bird	-0.5	0.17	-2.79	0.005
Shrew vs. bird	0.33	0.21	1.56	0.1

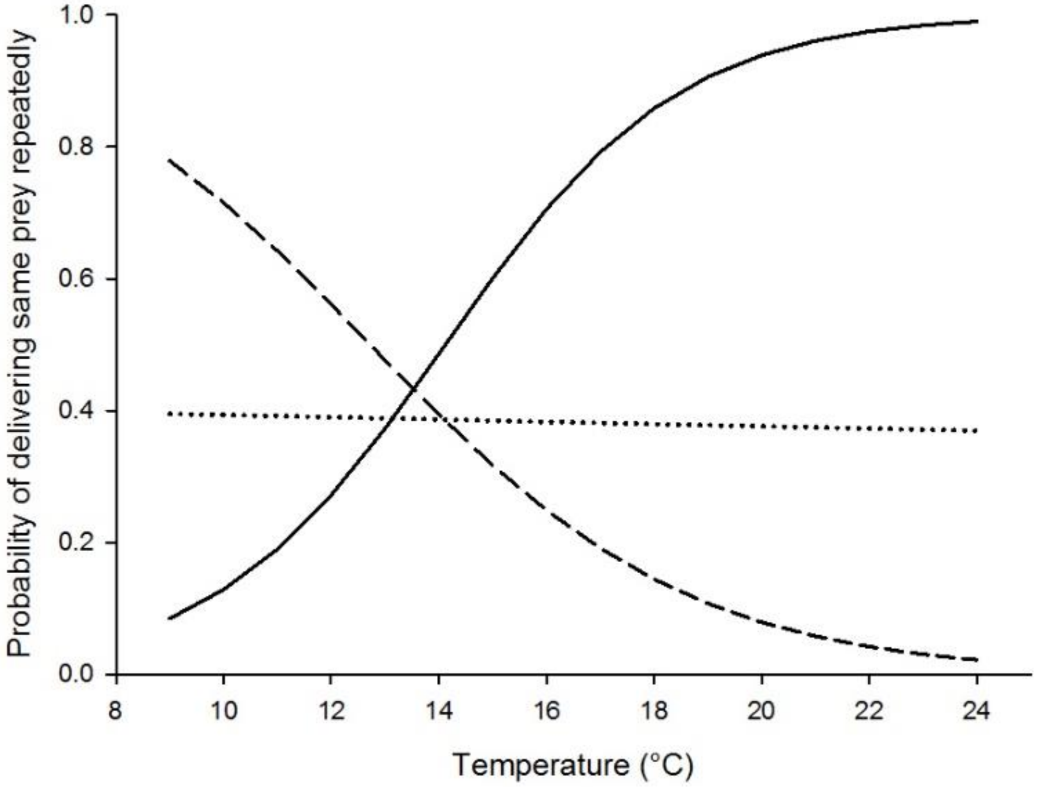
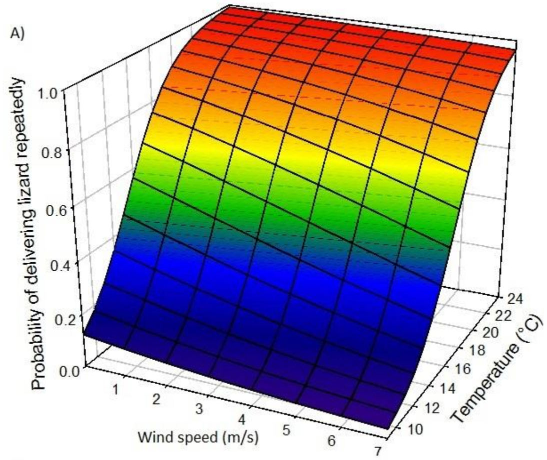


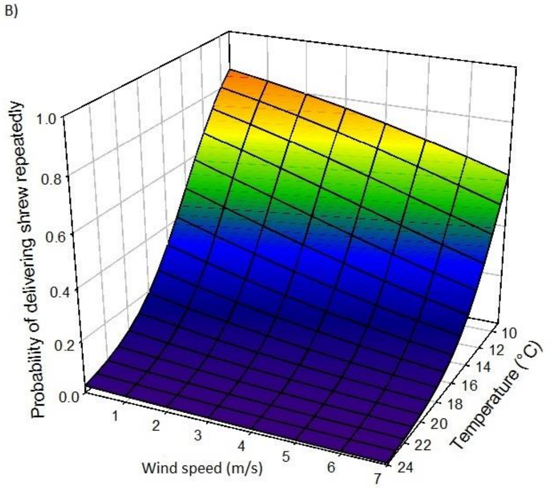
Figure 1. The probability of items of the same prey type being delivered repeatedly to the nest as a function of ambient temperature, for lizard (whole line), shrew (dashed line), and bird (dotted line). Results from model 173.

In model 198 the probability that an item delivered was of the same type as the previous item delivered was significantly affected by prey types, ambient temperature, wind speed and the interaction between prey type and temperature. The effect of temperature differed significantly between lizard and shrew, significantly between lizard and birds, and marginally significantly between shrew and bird (Table 3).

Table 3. Parameter estimates from the best fitted generalized linear mixed-effect model with binominal distribution, corrected for the random effect of nests (N=5), for the probability that a prey item delivered was of the same type as the previous item delivered. Model 198.

	Estimate	SE	Z	P
Prey type				
Lizard vs. shrew	10.93	3.28	3.34	0.0009
Lizard vs. bird	5.80	2.71	2.14	0.03
Shrew vs. bird	-5.13	3.02	-1.70	0.09
Ambient temperature				
Lizard	0.45	0.13	3.34	0.0008
Shrew	-0.36	0.18	-1.95	0.05
Bird	0.002	0.10	0.03	0.98
Wind speed				
Lizard	-0.19	0.12	-1.59	0.1
Shrew	-0,19	0.12	-1,59	0.1
Bird	-0,19	0.12	-1.59	0.1
Prey type x ambient temperature				
Lizard vs. shrew	-0.80	0.23	-3.55	0.0004
Lizard vs. bird	-0.44	0.17	-2.64	0.008
Shrew vs. bird	0.36	0.21	1.71	0.09





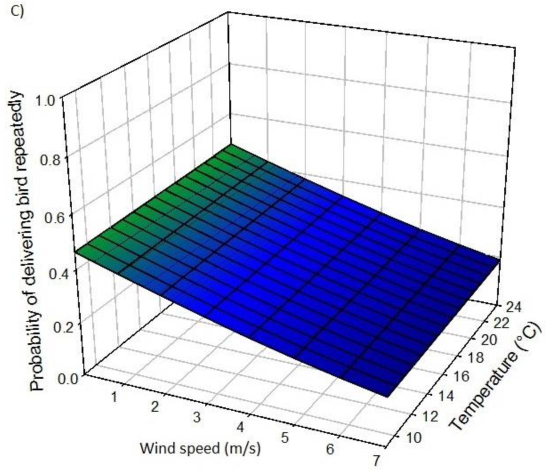


Figure 2.The probability that prey items of the same prey type were delivered repeatedly to the nest as a function of temperature and wind speed for lizard (a), shrew (b) and bird (c). The scale on both wind speed and ambient temperature equals the actual interval from when the data was gathered. Note that the temperature scale is opposite the others on figure 2b. Results from model 198

Repeated deliveries for the three main prey types separately

In order to check how the weather variables affected the probability of repeated delivery of each prey type, I tested the three main prey types separately. In these tests I used only data where the male delivered prey directly to the nestlings, or data where delivery from the male to the female had been observed. I thus used only data where the male was the hunter, to ensure that the same kestrel was followed, and to see if it captured the same prey type repeatedly.

Lizard

Model 17 included the variables ambient temperature and day of delivery (the latter meaning that the prey was either delivered on the same day as the previous prey item, or on the next day of filming, most often the next day). Model 18 included the variables unknown sex of previous hunter (meaning that the sex of the kestrel delivering the previous prey was unknown) and ambient temperature. Model 19 included the same variables as model 18, and in addition the variable day of delivery, which was also the second variable in Model 17. Model 19 had the lowest AIC, but was far from being significant, and is therefore not treated further in this thesis.

Table 4. AIC table for the three best models, for the probability of a prey item delivered was a lizard when the previous prey item was a lizard. N = 83

Model	Variables	AIC	Rank
19	3	93.90	1
17	2	96.62	2
18	2	96.70	3

In model 18, all variables and especially ambient temperature, were significant. This supports the results I found in the analysis where all prey items were included. I considered model 18 to be the best one to study further (table 5).

Table 5. Model 18, the probability of a prey item delivered was a lizard when the previous prey item was a lizard. N = 83

Explanatory variables	Estimate	SE	z	P
Intercept	-6.23	2.18	-2.86	0.004
Ambient temperature	0.46	0.14	3.33	0.0009
Hunter of previous prey	-1.14	0.53	-2.17	0.03

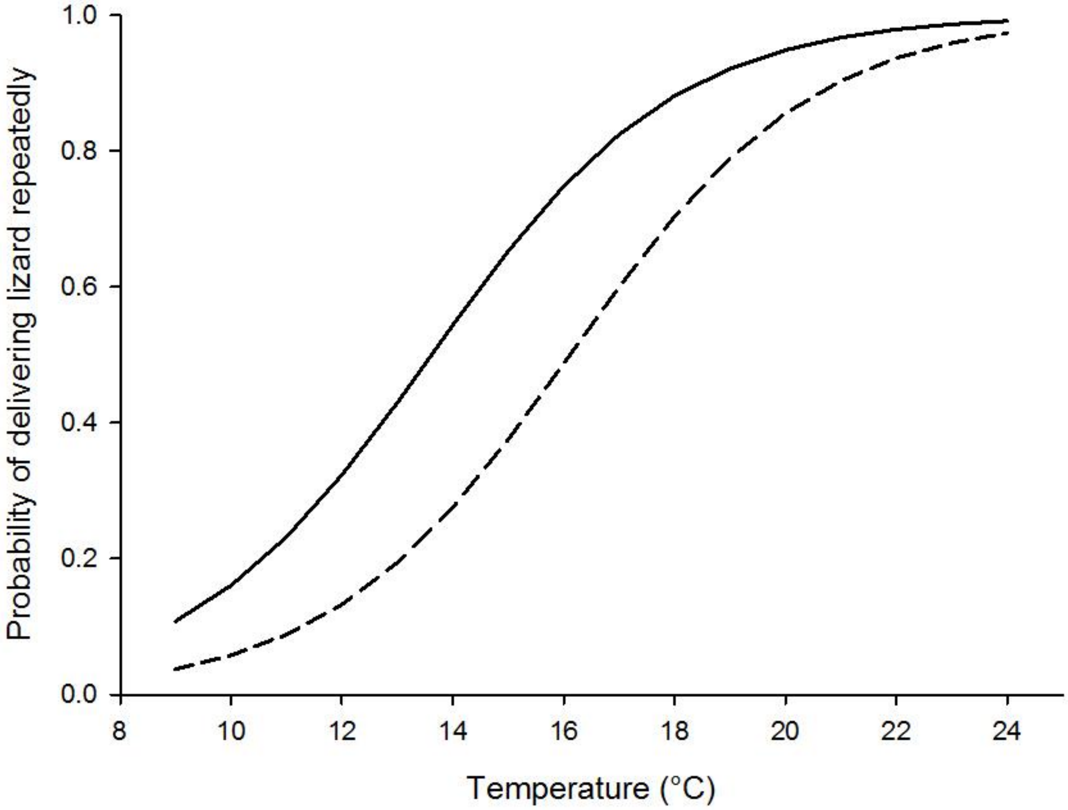


Figure 3. The probability of lizards being delivered repeatedly as a function of ambient temperature, where known previous hunter is represented with the whole line, and unknown previous hunter as dashed line. The temperature scale represents the temperatures when lizards were delivered at the nests.

Shrew

Both models include the variables ambient temperature and rainfall, but model 25 also included the variable day of delivery (Table 6). Since I found autocorrelation in a previous test, I investigated if it occurred here as well. However there was no autocorrelation between ambient temperature and wind speed in this case. Model 24 was not significant for any of the variables and was therefore not further investigated.

Table 6. AIC table for the two best models, for the probability of a prey item delivered was a shrew when the previous prey item was a shrew. N = 29

Model	Variables	AIC	Rank
24	2	33.59	1
25	3	35.19	2

Ambient temperature was the only significant variable in model 25. This supports the results I found earlier in the analysis with all three main prey types included. Rainfall showed only a trend (Table 7).

Table 7. Test results from model 25, for the probability of a prey item delivered was a shrew when the previous prey item was a shrew. N = 29

Explanatory variables	Estimate	SE	Z	P
Intercept	7.27	3.83	1.90	0.06
Ambient temperature	-0.61	0.29	-2.13	0.03
Rainfall	27.88	17.90	1.56	0.1

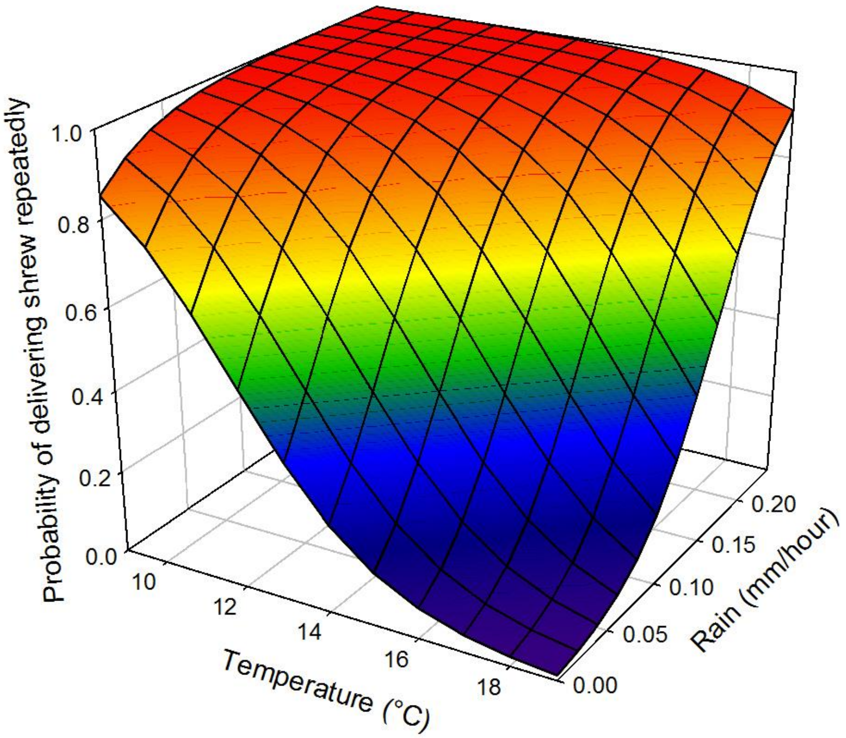


Figure 4. The probability of shrew being delivered repeatedly at kestrel nests as a function of ambient temperature and rainfall. Both variables are in the actual interval when shrews were delivered.

Bird

Table 8. AIC table for the two best models, for the probability of a prey item delivered was a bird when the previous prey item was a bird. N = 49

Model	Variables	AIC	Rank
4	1	66.45	1
3	1	67.19	2

The two best models included only one variable. Model 4 contained wind speed, and Model 8 rainfall. None of the models (4 and 3) were significant for any of the weather variables, but both showed a trend for wind speed (Tables 9 and 10).

Table 9. Test results from model 4, for the probability of a prey item delivered was a bird when the previous prey item was a bird. N = 49

Explanatory variables	Estimate	SE	Z	P
Intercept	0.55	0.79	0.70	0.5
Wind	-0.46	0.30	-1.57	0.1

Table 10. Test results from model 8, for the probability of a prey item delivered was a bird when the previous prey item was a bird. N = 49

Explanatory variables	Estimate	SE	Z	P
Intercept	-0.80	0.33	-2.42	0.02
Rain	3.14	2.84	1.11	0.3

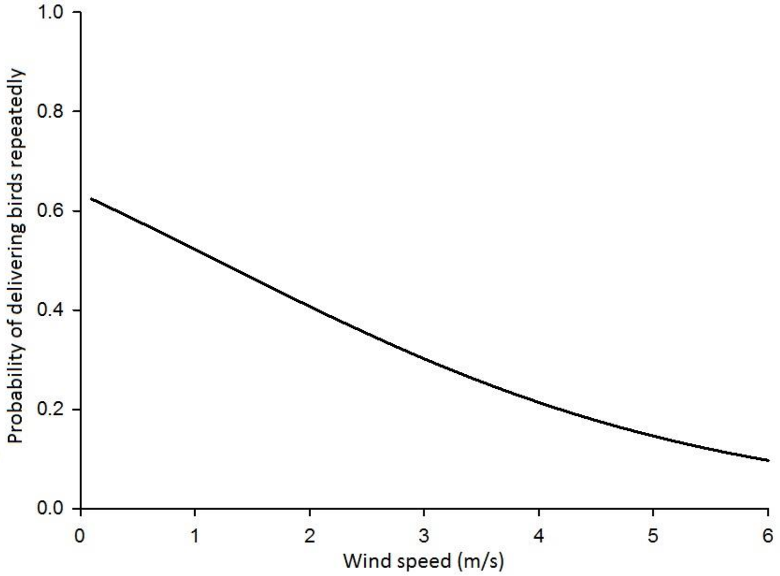


Figure 5. The probability of delivering birds repeatedly as a function of wind speed. The wind interval represents the actual interval when birds were delivered.

Aggression

The best model for explaining the probability of aggression from the female towards the male during prey delivery was model 4 (table 11). The female aggression as a function of either prey being delivered to the female outside the nest or directly at the was significant (table 12). The probability of aggression from the female was greater if the male delivered an item directly at the nest box (figure 6). The second best model (8) included prey type, but it was far from significant. The third best model (1) included the interaction between prey body mass and whether the prey item was delivered to the female or directly at the nest, but neither this was significant.

Table 11. AIC table for the best model, for the probability of aggression between the male and female. N = 45

Model	Variables	AIC	Rank
4	1	32.31	1
8	2	30.75	2
1	3	31.52	3

Table 12. Parameter estimates from a GLMM model with binominal distribution, corrected for the random effect of nest ID (n=5), with prey delivery from male to female outside the nest as intercept, for the probability of female aggression towards the male at prey delivery as an effect of whether the male delivered the prey to the female outside the nest or delivered the prey directly at the nest, and prey body mass (n=45).

Explanatory variables	Estimate	SE	Z	P
Intercept	2.67	0.73	3.66	<0.0001
Sex delivering at the nest	-4.47	1.06	-4.22	<0.0001

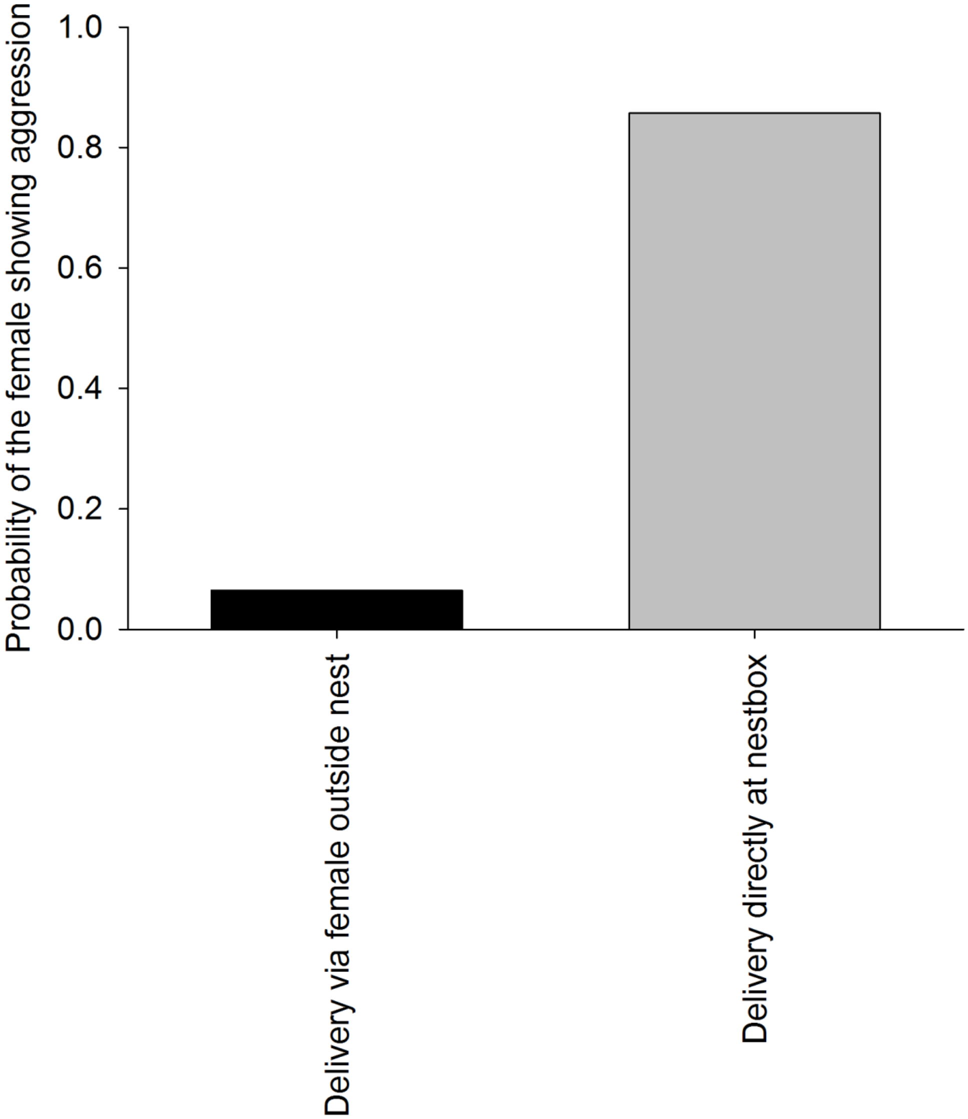


Figure 6. The predicted probability of female aggression towards the male at prey delivery as a function of whether the male delivered prey to the female outside the nest or delivered prey directly at the nest, corrected for the random effect of nest ID ($y = 1/1 + e^{-(2.67-4.47x)}$) ($z = -4.22$, $P < 0.001$, $n=45$, random effect = 5)

Discussion

Repeated deliveries

I found that the probability of repeated deliveries of lizards increased, with increasing ambient temperature. Higher temperature led to more lizards being delivered at kestrel nests in general (Yalden & Warburton, 1979; Løw, 2006; Steen et al., 2011a; Espe, 2013). At higher ambient temperature the lizards become more active and look for food, and are therefore easier targets for the kestrel (Craig, 1978). If lizards have a clumped spatial distribution, it will pay the kestrel to remember where to go to capture more lizards (Sonerud, 1985).

The probability of repeated deliveries of shrews increased with decreasing ambient temperature. When the ambient temperature is low, lizards are less available, leading to other prey types becoming relatively more available to the kestrels. Next to lizards, shrews are the vertebrate prey type most easy to handle for the kestrel nestlings (Sonerud et al. 2013). Thus, when lizards become less available, the kestrels may switch to shrews as prey. Alternatively, the shrews may become more active during colder periods, and thus easier to capture. Anyway, my findings supports the hypothesis that the kestrel is indeed hunting different prey types at different temperatures.

The probability of repeated deliveries of avian prey tended to decrease with increased wind speed. Strong wind may make precision flight, which is needed to capture birds, difficult for the kestrel. Avian prey items delivered repeatedly were often vulnerable young, either from a nest, or fledged young. This is supported by other studies, indicating that a kestrel rob a nest, or take several young fledged from the same nest (Sonerud, 1985; Sullivan, 1988; Village, 1990; Steen, 2004).

If the spatial distribution of prey is clumped, it would be more efficient to return to a previously successful site, than to hunt randomly (Sonerud et al. 2013). My results suggest that the kestrel hunt the same type of prey during same weather conditions. However, my study can not confirm that the kestrel adopted a win-stay strategy (see Tinbergen, 1981; Sonerud, 1985). The fault in my study is that I do not know where the kestrel captured its prey. Even if prey items of the same type are delivered repeatedly the kestrel has not necessarily returned repeatedly to the same hunting area. With the help of a radio transmitter on the kestrel, it would have been possible to follow the bird and see where it hunted (Village 1990; Eldegard & Sonerud 2011; Larsen 2012). Only if the kestrel returns to the last successful hunting area and delivers the same prey type, it can be confirmed that it has hunted with a win-stay strategy.

Unfortunately the only kestrel that was captured and equipped with a radio transmitter in my study, deserted her nest and flew out of reach from the receiver. Therefore, I was unable to verify whether repeated deliveries of items of the same prey type was really due to a return by the kestrel to the previous capture site.

Aggression

My analysis showed that the only variable that significantly explained the probability of aggression, from the female kestrel towards the male was whether the male delivered the prey directly to the nest with the female being present or to the female outside the nest. The female, most often, receive the prey item from the male, and allocates it between herself and the young. During the allocation she does not only dissemble the prey item, but she also have full control over the distribution; she can eat some, or all, of the prey item delivered to the nest by the male (Sonerud et al 2013). If the male delivers directly the item to the nestlings, the larger female (female-biased sexual size dimorphism), is cheated for food, and may therefore show aggression towards the male. Since the female broods, allocates and feeds the nestlings she is dependent on the male in order to get food (cf. Brodin et al. 2003; Eldegard & Sonerud 2010). Aggression may therefore be a result of hunger or desperation, as well as the need to allocate and control the feeding.

Neither prey mass nor prey type explained the probability of aggression. I would think that a smaller prey would lead to less aggression, since the gain for the female is small, and again that larger prey would increase the level of aggression. A small prey item, for instance a lizard, may already have been swallowed by one of the nestlings before the female arrives to the nest, and display of aggression may therefore be a waste of energy. The fact that the male often delivered large prey items that needed to be allocated by the female in order to feed the nestlings (Sonerud et al. 2013), may be a reason for why the females did not display aggression.

The female that most frequently displayed aggression in my study was also the largest of the females I monitored, and her partner was also the smallest of the males relative to their female companion, as far as I could judge from observations in the field and on video. She took advantage of this on several occasions, and had full control over the allocation of prey between herself and her offspring.

Unfortunately my observation and videotape data on aggression were quite limited, with only 15 cases of aggression from the female towards the male. On the other hand, I had 30 cases where I knew for sure that the female kestrels showed no aggression towards the male at prey transfer. This means that a third of my observations involved aggression. Again, the fact that my data were collected in a year with a low vole population, and in a summer with cold and rainy weather, restricted the number of observations and thus influenced the statistical tests on this thesis. Personal observations are given in Appendix 1.

Conclusion

Due to failure of radio marking the kestrels, I was unaware of the spatial whereabouts of the kestrels that I video filmed, and therefore unable to ensure that the kestrels had returned to the previous capture site when they delivered prey items of the same type repeatedly. I only knew what the kestrel returned with, and from these observations determined the probability for hunting the same prey repeatedly. The most prominent findings was that ambient temperature determined repeated deliveries of lizards and shrews.

There was a higher probability of aggression from the female towards the male when he delivered prey directly at the nest than when prey transfer occurred outside the nest. There were few breeding attempts during my study season due to low prey abundance, and the few females that bred were probably withholding their contribution to the nestlings to ensure their own survival. It would therefore be interesting to study the female kestrels' aggression behavior in a year with high prey abundance.

References

Andersson, M. (1994) Sexual selection. Princeton University Press, Princeton

Brodin, A., Jönsson, K. L. & Holmgren, N. (2003) Optimal energy allocation and behavior in female raptorial birds during the nestling period. Ecoscience 10:140-150

Burnham, K. P. (2002) Model selection and multimodel inference: practical information: theoretic approach. Springer, New York

Burnham, K. P. & Anderson, D.R (1998) Model selecting and inference: a practical information: theoretical approach. Springer, New York

Craig, R. B. (1978) An analysis of the predatory behavior of the loggerhead shrike. Auk 95:221-234

Cramp, S. (1985). The birds of the Western Palearctic, Vol IV, Oxford University Press, Oxford

Cramp, S. & Simmons, K. E. L. (1980) The birds of the Western Palearctic, Vol II, Oxford University press

Dawson, R. D. & Bortolotti, G. R. (2002) Experimental evidence for food limitation and sex-specific strategies of American kestrels (*Falco sparverius*) provisioning offspring. Behavioral Ecology and Sociobiology 52:43-52

Eadie, J. M. & Gauthier, G. (1985) Prospecting for nest sites by cavity-nesting duck of the genus *Bucephala*. Condor, 87:528-534

Eldegard, K. & Sonerud, G. A. (2009*)* Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. Proceedings of the Royal Society: Biological Sciences 276:1713-1721

Eldegard, K. & Sonerud, G. A. (2010) Experimental increase in food supply influences the outcome of within-family conflicts in Tengmalm's owl. Behavvioral Ecology and Sociobiology 64:815-826

Eldegard, K & Sonerud, G. A. (2012) Sex roles during post-fledging care in birds: female Tengmalm's owls contribute little to food provisioning. Journal of Ornithology 153:385-398

Espe, S. (2013) Functional response of the Eurasian kestrel (*Falco tinnuculus*) in a season with low vole abundance. Master thesis, Norwegian University of Life Sciences.

Farmer. C. G. (2000) Parental care: the key to understanding endothermy and other convergent features in birds and mammals. The American Naturalist 155: 326-334

Forsman, D. (1999) The raptors of Europe and the Middle East: handbook of field identification*.* T & A D Poyser, Berkhamsted, UK

Gardner, A. & Smiseth, P. T. (2011) Evolution of parental care driven by mutual reinforcement of parental food provisioning and sibling competition. Proceedings of the Royal Society B. 278: 196-203

Geng, R., Zhang, W.j., Ou, W., Sun, H.M., Lei, E.M., Gao, W. & Wang, H.T. (2009) Diet and prey consumption of breeding common kestrel (*Falco tinnunculuc*) in Northeast China. Progress in Natural Sciences 19: 1501-1507

Kelly, E. J. & Kennedy, P. L. (1993) A dynamic state variable model of mate desertion in Cooper's hawk. Ecology 74:351-366

Klug, H. & Bonsall, M. B. (2010) Life history and the evolution of parental care. Evolution 64: 823-835

Korpimäki, A. (1985) Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. Annales Zoologici Fennici 22:91-104

Kristiansen, L. (2003) Prey preparation time by Tengmalm's owl (*Aegolius funereus*) feeding nestlings. Cand scient thesis, Agricultural University of Norway

Krüger, O. (2005) The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. Evolutionary Ecology 19:467-486

Larsen, C. S. T. (2012) Habitat use and habitat-specific behavior of breeding female Eurasian kestrels (*Falco tinnunculus*) in a peak vole year in the boreal forest. Master thesis, Norwegian University of Life Sciences

Løw, L. M. (2006*)* Prey preparation and ingestion rate in breeding Eurasian kestrels, *Falco tinnunculus.* Master thesis, Norwegian University of life science.

Masman, D., Dijkstra, C. Daan, S. & Bult, A. (1989) Energetic limitation of an avian parental effort: field experiments in the kestrel (*Falco tinnunculus*). Journal of Evolutionary Biology 2: 243-455

Massemin, S., Korpimäki, E. & Wiehn, J. (2000) Reversed sexual size dimorphism in raptors: evaluation of the hypothesis in kestrels breeding in a temporally changing environment. Oecologica 124:26-32

Mueller, H. C. (1990) The evolution of reversed sexual dimorphism in size in monogamous species of bird. Biological Reviews 65:553-585

Newton, I. (1979) Population ecology of raptors. Poyser, Berkhamsted, UK

Pärt, T. & Doligez, B. (2003) Gathering public information for habitat selection: prospecting birds cue on parental activity. Proceedings of the Royal Society: Biological Sciences 270:1809-1813

Pinheiro, J. C. & Bates, D. M. (2000) Mixed effects models in S and S-PLUS. Springer, New York

R Develompent Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3.900051-07-0, URL. http://www.R-project.org/

Selander, R. K. (1966) Sexual dimorphism and differential niche utilization in birds. Condor 68:113-151

Slagsvold, T. & Sonerud, G. A (2007) Prey size and ingestion rate in raptors: importance for sex roles and reversed sexual dimorphism. Journal of Avian Biology 38:650-661

Snyder, N. F. R., & Wiley, J. W. (1976) Sexual size dimorphism in hawks and owls of North America. Ornithol Monographs 20

Sonerud, G. A. (1985) Brood movements in grouse and waders as defense against win-stay search in their predator. Oikos 44:287-300

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Selås, V. & Slagsvold, T. (2013*)* Size-biased allocation of prey from male to offspring via female: family conflicts, prey selection, and evolution of sexual size dimorphism in raptors. Oecologica 172:93-107

Steen, R. (2004) Food provisioning in the Eurasian kestrel (*Falco tinnunculus*): handling efficiency of prey delivered to the nest. Cand. Scient. Thesis, Agricultural University of Norway

Steen, R. (2009) A portable digital video surveillance system to monitor prey deliveries at raptor nests. Journal of Raptor Research 43:69-74

Steen, R., Løw, L. M. & Sonerud, G. A. (2011a) Delivery of Common Lizards (*Zootoca (Lacerta*) *vivipara*) to nests of Eurasian Kestrels (*Falco tinnunculus*) determined by solar height and ambient temperature. Canadian Journal of Zoology 89:199-205

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

Steen, R. & Sonerud, G. A. (2012) A bank vole *(Myodes glareolus)* with complete leucism captured by a Eurasian kestrel (*Falco tinnunculus*) in Norway. Annales Zoologici Fennici 49:306-308

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

Sullivan, K.A. (1988) Ontogeny of time-budgets in yellow-eyed juncos: adaptations to ecological constraints. Ecology 69:118-124

Tinbergen, J. M. (1981) Foraging decisions in startlings (*Sturnus vulgaris*). Ardea 69:1-67

Village, A. (1990) The kestrel. T & A D Poyser, Berkhamsted, UK

Yalden, D. W. & Warburton, A. B. (1979) The diet of the kestrel in the Lake District. Bird Study 26:163-170

Zarybnicka, M., Riegert, J. & Stastny, K (2010) Diet composition in the Tengmalm's owl, *Aegolius funereus*: a comparison of camera surveillance and pellet analysis. Ornis Fennica 88:147-158

Zicus, M. & Hennes, S. K. (1989) Nest prospecting by common goldeneyes. Condor, 91:807-812

Appendix 1: Personal observations

Based on visual inspection from the field and the video, the female at nest 072 was the largest of all kestrels studied, and her mate was young and very small compared to her (personal observation). On several occasions she blocked a part of the entrance to the nest with her body, like some cavity nesting birds do, controlling the male's whereabouts when arriving with a prey item (cf. Sonerud et al., 2013). This female had full control over the items that the male arrived with, determining what to eat for herself, and what to feed the young. On some occasions she even took the prey for herself, flying out of the nest with the entire prey item (cf. Brodin et al., 2003; Kristiansen, 2003)

This female in fact returned to the nest with what I believe was the remains of another kestrel.

On four occasions other kestrels were observed visiting the nests, and they may have been doing this as a nest prospecting for breeding the next year (cf. Eadie & Gauthier, 1985; Zicus & Hennes, 1989; Pärt & Doligez, 2003). Aggression was also seen between the kestrels that I studied, and these nest-prospecting kestrels.