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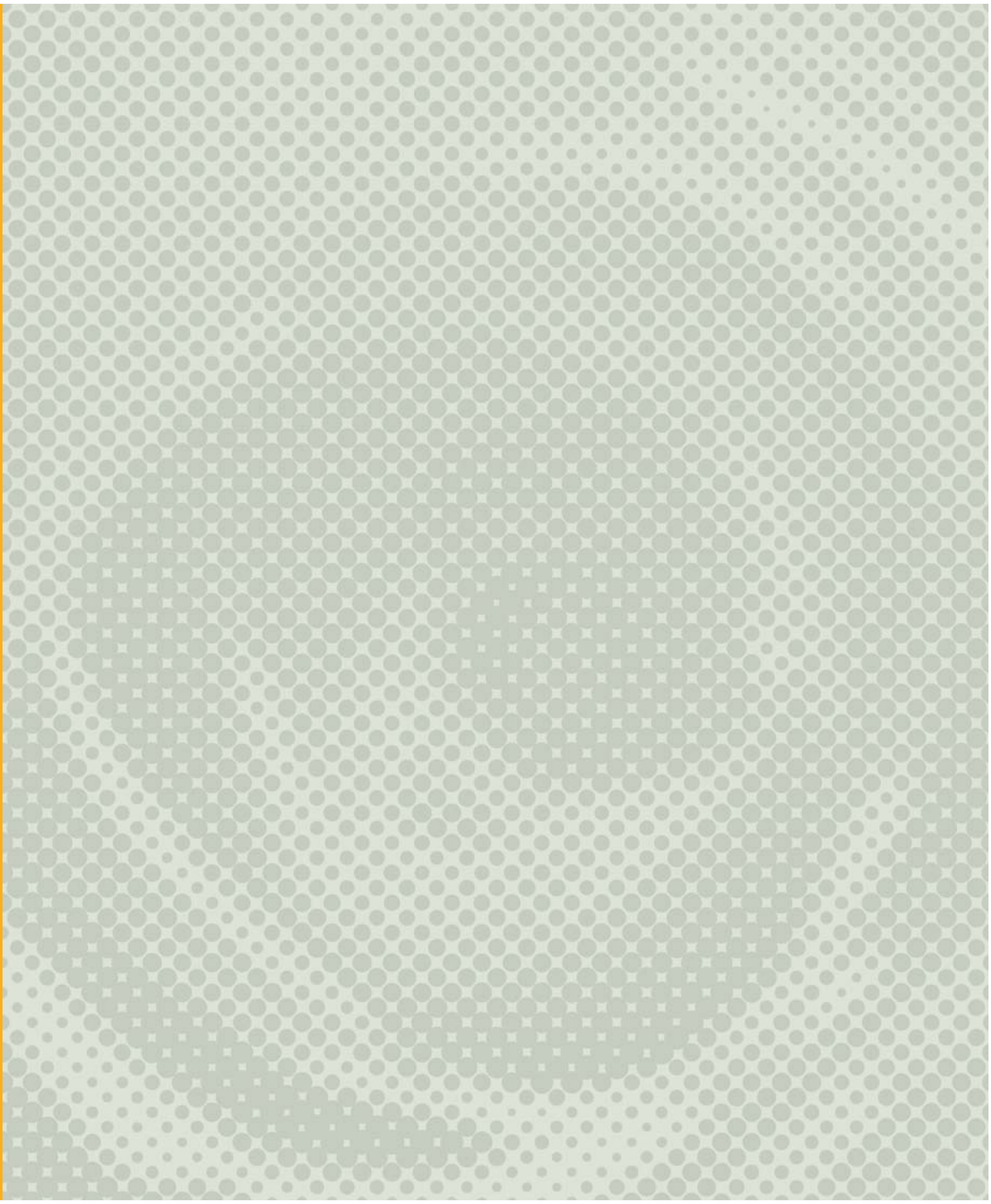
HANS STØVERN



Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management, INA
Master Thesis 60 credits 2012

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Ås, 2012

Preface

Nature and wild life have always been a great interest and source of appreciation for me, and working with this thesis, both during the field work and the time after, has given me valuable experience and knowledge about scientific work. I would like to thank Bjørn E. Foyn and Ole Petter Blestad for letting me use video surveillance at six of their nest boxes, and my supervisors Geir A. Sonerud and Ronny Steen for helpful supervising during the whole period and for all help with video analysis and statistical support. I would also like to thank Sari Cunningham, Cathrine S. Torjussen Larsen and Mikkel E. Christensen for great cooperation and help during the field work, and for making both the field work and the time after a social and interesting experience.

I would like to thank the Norwegian Directorate for Nature Management which financially supported my thesis, and Vidar Selås for help with identifying avian prey delivered at the kestrel nests. I also want to thank Leif Einar Støvern for proofreading the thesis, and my family and friends for all support and motivation during the whole Master period. Finally I would like to thank Jan-Kåre Arntzen for letting me use his car during the field work in Trysil, and for all help and support during the whole Master period.

Norwegian University of Life Sciences, 2012.

Hans Støvern

Abstract

I used video monitoring to study diet and prey delivery rate of six breeding pairs of the Eurasian kestrel (*Falco tinnunculus*) in Trysil, south eastern Norway, during the breeding season 2011.
A total of 284 prey items of 9 species were recorded delivered at the kestrel nests. The abundance of small mammals was estimated in each kestrel territory. Voles were the most abundant prey delivered at the nests. The kestrels showed a functional response to *Microtus* voles (Field vole (*Microtus agrestis*) and Root vole (*Microtus oeconomus*) pooled), but not to bank vole or wood lemming. This suggests that *Microtus* voles were preferred prey for the kestrels. Wood lemming was an alternative prey to *Microtus* voles, while bank vole had a negative, but insignificant trend. Birds or common lizard was not alternative prey to *Microtus* voles. Studies on predation on wood lemming by kestrels are rare, and I suggest that wood lemmings are caught only when the abundance of wood lemming is high and the abundance of *Microtus* voles is low. Common lizard were more frequently delivered between 9 am and 1 pm, and the probability of a bird being delivered at kestrel nests increased with solar height. The probability that a prey delivered at the nest was a wood lemming increased throughout the day, and was twice as high in the evening than in the morning. This may suggest that the wood lemming is more active in the evening and therefore more vulnerable to hunting kestrels, or may be mistaken for a *Microtus* vole as the daylight fades away.

Sammendrag

Jeg brukte video-overvåkning for å studere diett og leveringsrate av byttedyr på reir hos seks tårnfalkpar (*Falco tinnunculus*) i Trysil, Sørøst-Norge, i hekkesesongen 2011. Totalt ble 284 byttedyr registrert, levert fordelt over 9 arter. Tettheten av småpattedyr ble estimert med fellefangst for å få en indikasjon på hvor mye byttedyr det var i hvert enkelt tårnfalkterritorium. Smågnagere var den gruppen med flest leverte byttedyr, og tårnfalken hadde en funksjonell respons på *Microtus* gruppen (markmus (*Microtus agrestis*) og fjellrotte (*Microtus oeconomus*). Tårnfalken viste ikke funksjonell respons til tetteheten av klatremus eller skoglemen. Dette indikerer at *Microtus* gruppen er det prefererte byttedyret for tårnfaken. Skoglemmen var et alternativt byttedyr til *Microtus* for tårnfalken, mens det var en negativ, men ikke signifikant trend hos klatremus. Firfisle og fugl var ikke alternativt byttedyr for *Microtus*. Studier på fangstrater av skoglemmen hos tårnfalk er sjeldne, jeg resultater argumenterer for at skoglemmen blir tatt kun når tettheten av skoglemmen er høy og tettheten av *Microtus* er lav. Firfisle ble mest levert på tårnfalkreirene mellom klokka 9 og klokka 13, og sannsynligheten for at en fugl ble levert økte med økende solhøyde. Sannsynligheten for at et levert byttedyr var en skoglemmen økte med tid på dagen, og var dobbelt så høy på ettermiddagen som på formiddagen. Dette kan skyldes at skoglemen er mere aktiv på ettermiddagen og dermed mere sårbar for predetering av jaktende tårnfalk, eller den kan bli feilaktig fanget som en *Microtus* eller en klatremus når sollyset forsvinner.

Contents

Introduction

Raptors have attained a lot of interest and fascination, and studying their behavior, ecology and home range have increased our knowledge about these birds. Collection and delivery of food to the offspring is a form of provisioning (Ydenberg 2007). Such provisioning is well studied in birds (Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2010; 2011b), and the rate of food delivery highly influence the probability of offspring survival. This may result in a functional response to available prey in the nesting area (Korpimäki & Norrdahl 1991a; Sonerud & Steen 2010; Steen et al. 2011a). Understanding a predator's functional response is vital for understanding the effects that predation has on prey populations (Korpimäki & Norrdahl 1991a; Jaksić et al. 1992; Dale et al. 1994; Schenk & Bacher 2002; Millon et al. 2009; Nilsen et al. 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011b, and references therein). The methodological challenges and the complexity of a predator's exploitation of several prey populations have made such investigations difficult to conduct on wild animals.

The Eurasian kestrel (*Falco tinnunculus*), hereafter called kestrel, is an abundant diurnal bird of prey in Northern Europe (Cramp & Simmons 1980; Village 1990), that uses a wide range of different habitats ranging from boreal forests to large cities (Cramp & Simmons 1980; Village 1990; Riegert et al. 2010). The kestrel hunts in open areas, either from perches or from the air (Cramp & Simmons 1980; Korpimäki 1986; Sonerud 1986; Village 1990), and flight hunting includes both wind hovering and directional flight (Cramp & Simmons 1980; Masman & Klaassen 1987; Village 1990). Although kestrels mainly feed on small mammals such as voles (Cricetidae) (Cramp & Simmons 1980; Village 1990; Korpimäki & Norrdahl 1991a; Korpimäki & Wiehn 1998; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b), they will also include small birds, insects and lizards in their diet when given the chance to do so (Cramp & Simmons 1980; Village 1990; Korpimäki & Norrdahl 1991a; Korpimäki & Wiehn 1998; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b). Prey availability highly influence the amount of food delivered at the nest as well as the prey type distribution (Korpimäki & Norrdahl 1991a; Korpimäki & Wiehn 1998; Ydenberg 2007; Sonerud & Steen 2010; Steen et al. 2011a; 2011b; 2012), and prey availability may differ from year to year as voles in particular have large inter-annual population fluctuations (Sonerud 1986; Bondrup-Nielsen & Ims 1988; Korpimäki & Norrdahl 1991a; 1991b; Soneud 1992; Boonstra et al. 1998; Klemola et al. 1998; Korpimäki & Wiehn 1998; Eskelinen et al. 2004, and references therein). The amount of prey other than voles taken depend on the abundance of voles in the home range (Korpimäki & Norrdahl 1991a; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b), suggesting that shrews, birds, insects and lizards are alternative prey (Korpimäki & Norrdahl 1991a; Sonerud 1992; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2010; 2011a).

The male and female kestrel differ in their parental care and behavior (Cramp & Simmons 1980; Village 1990; Korpimäki & Wiehn 1998; Fargallo et al. 2003; Steen et al. 2010; 2012), with the male being the main provider of food and the female focusing on parental care such as incubation of the eggs and feeding the nestlings. Beyond the age of two weeks the nestlings are able to feed on their own, which results in both parents hunting and delivering prey at the nest (Cramp & Simmons 1980; Village 1990; Korpimäki & Wiehn 1998; Fargallo et al. 2003; Steen et al. 2012). Sonerud & Steen (2010) states that prey delivery and selection between male and female may be different, due to the different sex roles during the breeding season. The nestling's food acquirement varies during the breeding season (Ydenberg 2007; Steen et al. 2011b; 2012), and the parents may therefore optimize their provisioning during the breeding season by altering the selection of prey type and size to deliver at the nest.

To investigate prey selection and predation of a raptor, unbiased estimates of the diet are needed, and several possible approaches have been made (Redpath et al. 2001). According to several studies there are few estimates of prey delivery rates in the kestrel (Sonerud & Steen 2010; Steen et al. 2011b; 2012), and most have been based on direct observations from a hide in combination with analysis of prey remnants and regurgitated pellets found in or around the nests (Korpimäki & Norrdahl 1991a; Jaksić et al. 1992; Redpath & Thirsgood 1999; Salamolard et al. 2000; Redpath et al. 2001; Millon et al. 2009). More accurate prey delivery rates are to be expected from close-up video monitoring than from observations from a hide or analysis of pellets (Lewis et al. 2004; Steen 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b; 2012).

Several factors make the kestrel well suited as a study species on diet and prey delivery rate. i) The kestrel has a broad diet including small rodents, shrews, birds, lizards and insects (Cramp & Simmons 1980; Village 1990; Korpimäki & Norrdahl 1991a; Korpimäki & Wiehn 1998; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b; 2012), with prey that are relatively easy to identify (Sonerud & Steen 2010; Steen 2011a; 2012) and have a large variation in profitability due to variation in body size and handling time (Sonerud & Steen 2010; Steen 2011a; 2011b; 2012). ii) The kestrel is common and tolerant towards human disturbance (Cramp & Simmons 1980; Village 1990; Carillo & Aparicio 2001; Sonerud & Steen 2010; Steen et al. 2011a). iii) The kestrel frequently nests in artificial nest-boxes (Cramp & Simmons 1980; Village 1990; Korpimäki & Wiehn 1998; Riegert et al. 2010; Steen et al. 2010; 2011a; 2011b; 2012), which makes it easier to monitor prey deliveries at the nest via video recordings. iv) Video monitoring can be used for prey identification (Steen 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b). v) The kestrel hunts in open habitat (Cramp & Simmons 1980; Korpimäki 1986; Sonerud 1986; Village 1990), and is therefore relatively easy to observe. According to Carillo & Aparicio (2001) kestrels will not increase the intensity of their defensive behavior of the nest due to frequent human visits, and the kestrels should not become increasingly stressed and aggressive during my study.

Data collected by video recordings in kestrel nests through six breeding seasons in a boreal forest area in Hedmark suggest that the number of voles delivered at the nest increased with the abundance of voles in the nesting area, i. e. functional response (Sonerud & Steen 2010), while the number of birds delivered at the nest decreased with increasing abundance of voles. The number of lizards increased with increasing temperature (Steen et al. 2011a), independently of the vole density. If these three prey types are hunted in different habitats, then the variation in diet between years (depending on vole abundance and temperature) implies a variation in habitat use. The project aimed to test this by video record the prey delivery rate at the kestrel nests and measure the small mammal abundance in the area by snap-trapping in different habitats. Snap-trapping of small mammals in the kestrel territory will provide information on the abundance of prey in the kestrel territory, which is expected to influence prey selection and prey delivery rate. By using video to record all prey deliveries I aimed to minimize the problems inherent in previously conducted studies on functional response.

The aims of my thesis were as follows: 1) To compare the diet and prey delivery rate of six breeding kestrel pairs during the breeding season 2011 by video recording in the nest boxes and personal observations. 2) To test if the kestrel in boreal forest expresses functional response to voles and to reveal which prey is the alternative one in years with high vole density. This will give us an indication on whether kestrels have specific prey preferences during the breeding period.

Methods

Study area

The study area was in Trysil municipality in Hedmark county, located in south eastern Norway (61° 07´ - 61° 28´ N; 12° 06´ - 12° 43´ E). The home ranges of the kestrels were at altitudes of 600- 800 m, and the field work was conducted in June- July 2011. The project had access to > 300 nest-boxes, of which 150-300 are annually used by breeding kestrels. The six selected nests were in boxes with open front, situated 5 to 10 m above ground in clear-cuts or bogs. The study area was situated in the mid and north coniferous and birch forest zones (Moen 1998; Rekdal 2010), and the dominant habitat in the study area is coniferous forest dominated by Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*) of different age classes (Løken 2009; Rekdal 2010; Sonerud & Steen 2010). Swamp forest and bogs are also common, while farmland covers only a negligible part of the study area. The coniferous forest in the area is intensively managed with modern forestry techniques such as un-selective clear-cutting, regeneration by planting and selective cutting (thinning) (Rekdal 2010; Sonerud & Steen 2010). The six breeding females in my study did not have overlapping territories (Sari Cunningham, unpublished data), suggesting that they did not directly compete for resources or hunt in the same areas. As no male kestrels were captured and radio tagged I cannot say whether they had larger home ranges than the females, and thus may have had overlapping home ranges. For home range size of male kestrels in the study area see Løken (2009).

Video monitoring and analysis

To be able to test if the kestrel in boreal forest express functional response to vole population density, and to investigate which prey type is the alternative prey in years with low vole density, prey deliveries have been video recorded at the nest of 55 kestrel breeding pairs in this population over six years (Sonerud & Steen 2010; Steen et al. 2011a). Six nests was video recorded during the field season of 2011. Event triggered video recording was used in my study, and this will provide more accurate measurement of the diet and prey delivery rate than more traditional analysis (pellet samples, direct observation) (Lewis et al. 2004; Steen 2009; Sonerud & Steen 2010; Steen et al. 2011a; 2011b; 2012). A small camera was placed in the back corner underneath the nest-box roof, pointed towards the entrance, and mounted with a wide angle lens to cover a broad view inside the nest-box. The camera was connected to a digital video recorder (mini DVR), via a video cable, and the data collected was stored on SD cards. For more details see Steen (2009). When the camera was triggered by an entering bird, the camera recorded a 10 s long video clip that was used for prey identification.

The video clips were analyzed in the lab by the use of a projector, and each prey item delivered was identified to genus, or species if possible. Different species of shrews (*Sorex* spp.) were pooled as one prey type due to the difficulties in identifying the species on video. Due to the similarities in appearance and size field voles (*Microtus agrestis*) and root voles (*Microtus oeconomus*) are difficult to identify to species on video, and were therefore pooled as *Microtus* in the statistical analyzes. Although grey-sided voles (*Myodes rufocanus*) are rare in the study area (Sonerud & Steen 2010), and made up only 3 of the 448 small mammals caught in the traps during my study, there is a possibility that some prey identified as *Microtus* voles may actually be a grey-sided vole as they are difficult to unambiguously separate from *Microtus* voles in the video analysis. According to Hörnfeldt et al. (1990) grey-sided voles are as vulnerable to avian predation as *Microtus* voles and previous trappings in the same study area (Sonerud & Steen 2010) indicate similar use of clear-cuts by grey-sided voles as the *Microtus* voles, which make it possible that a few grey-sided voles were included in the *Microtus* prey group. Birds delivered at the nest were identified to species if possible, but pooled in the statistical analysis. No insects or frogs were delivered at the nest during the filming. This resulted in the following prey types in the analysis: *Microtus* voles (field vole and root vole, and possibly grey-sided vole), bank vole (*Myodes glareolus*), wood lemming (*Myopus schisticolor*), shrews (*Sorex* spp.), common lizard (*Zootoca* *vivipara*) and birds.

A total of 284 prey items were delivered at the nests during the filming for my dietary analysis. Additional prey delivered at the nests during the later filming combined with radio tracking of the females are not included in my analysis, except for one day (28 June) of radio tracking at the Husfliden nest. This day was included in my study because the nestlings were still very young (11 days old), and prey identification by video analysis was still possible as the nestlings did not cover the view of the prey by their size and movements.

The delivery rate was calculated for each prey type (see below), and taken as the number of prey items delivered per hour of kestrel foraging. Sunrise and sunset in the study area are at summer solstice approximately at 03:31am and 10:55pm, respectively, given as local summer time (GMT + 2 hours).The daily period of kestrel foraging can according to Sonerud & Steen (2010) be set to 20.5 hours, based on the average of two estimates from their study (Sonerud & Steen 2010). My study aimed at filming for a minimum of two days, which lead to a standard foraging period of minimum 41 hours. All nests were filmed for a foraging period of more than 41 hours, and one nest for a foraging period of more than 62 hours, and the number of hours filmed depended on logistic constraints such as amount of space on the SD cards, age of the nestlings and amount of triggered video per day. The average period during filming was 52.0± 0.3 (44.9-62.7) hours, in total 312 hours for the six nests.

Some of the prey items delivered at the nest were not possible to identify to species, and a few prey not even to genus or family, because they were either too much handled by the parent kestrel (i.e decapitated and skinned, or missing tail) for identification, the parent kestrel only delivered small pieces of a larger prey, the prey item was hidden under the parent kestrel on delivery, or hidden by begging nestlings during the parent's entry of the nest-boxes. To obtain the most accurate estimate of the delivery rate of each prey type, mammalian prey items that were not identified to species were distributed on the mammalian prey types (mentioned above) in proportion to the distribution of identified mammalian prey items from each nest. This means that if for instance a prey had been identified as either a bank vole or a *Microtus* vole, and with high certainty was not a shrew or a wood lemming, it was counted as p bank voles and 1-p *Microtus* voles, where p is the proportion of items identified as bank vole among prey items from the actual nest identified as bank vole or *Microtus* vole. A different scenario would be if a prey is identified as a vole, and with certainty not a shrew. Such prey would be counted as p bank voles, q *Microtus* voles and 1-p -q wood lemmings, where p and q is the proportion of prey items identified as bank vole and *Microtus* vole, respectively, among prey items from the actual nest identified as bank vole, *Microtus* vole or wood lemming. No prey items was identified to mammal only, and prey that was un-identifiable were excluded from the statistical analysis.

In some cases, the parent bird would arrive at the nest with a prey item without providing it to the nestlings and instead flew off with the prey item again. Such cases were not counted as prey delivered to the nestlings, and not included in the statistical analysis.

According to several studies (Lehikonen et al. 2009; McDonald et al. 2004; Sonerud & Steen 2010; Steen et al. 2011a) weather conditions may influence the foraging success of a raptor because the weather conditions may alter the prey encounter rate or the raptors ability to attack successfully. Weather conditions may also influence on the breeding success of the kestrel (Carillo & González-Dávila 2009; 2010a; 2010b, and references therein). Steen et al. (2011a) found that the probability of a lizard being delivered at the nest increased with ambient temperature and solar height, indicating that weather conditions should be included in the statistical analysis. The ambient temperature was therefore calculated for each prey by using the time of delivery. Temperature information was gathered from Trysil Vegstasjon official meteorological station, located in the study area (61º29'N, 12º27'E, at 360 m elevation), and provided the ambient air temperature for each hour of the day (measured once each hour throughout the day. The ambient temperature of each prey delivery was estimated from a linear interpolation between recorded temperatures.

Estimating small mammal abundance

To be able to relate prey selection to the abundance of small mammals, the abundance of small mammals in each kestrel territory was estimated. The area surrounding each of the 6 monitored nests was set with 120 snap traps for two consecutive days and nights, which resulted in a maximum of 240 trap nights per nest. The traps was put out approximately 10 m apart, and this was done in each of the four cardinal directions from the nest, with 30 traps on each direction. Cocoa fat (commercial brand “Delfia matfett”) was used as bait.

All the traps were checked on the first morning and all released traps (either due to trapped animals or other causes) were reset. On the second day of trapping all the traps were collected. To correct for accidental releases (traps that were released without catching an animal) 0.5 trap nights were subtracted from these traps. For each small mammal prey type (mentioned above) a trap index was calculated as the number of individual captured per 100 trap nights. In order to correct for trap saturation, the number of trap nights was subtracted by 0.5 trap nights for each individual caught of other small mammal prey types than the one in question, and thereafter subtracting *n-1* trap nights for *n* trapped animals of the prey type in question. Permission to conduct trapping of small mammals was given by the Directorate for Nature Management.

The snap trapping resulted in a total of 448 small mammals captured; 3 shrews, 87 *Microtus* voles (field voles and root voles pooled), 89 bank voles, 3 grey-sided voles, 264 wood lemmings and 2 Norway lemmings (*Lemmus lemmus*), thus an average of 75 small mammals trapped in each of the six kestrel territories.

Statistics

The statistical analysis was performed with the software JMP® version 9.0.0 (SAS 2010) and the software R version 2.14.1 (R Development Core Team 2011). Linear regression was done in JMP, and logistic multilevel regression was done in R. In the logistic multilevel regression the response variable changed between the five tests, and was whether or not (frequency) a prey item delivered at the nest was a lizard (test 1), a bank vole (test 2), a wood lemming (test 3), a *Microtus* vole (test 4), or a bird (test 5). The number of shrews delivered at the nest (n=2) was insufficient for statistical analysis. Explanatory variables were ambient temperature at the time the prey item was delivered at the nest (Temp), the number of hours from solar midnight (HSM) at the time the prey item was delivered, whether a prey item was delivered in the morning or in the evening (Time), the hour of the day the prey item was delivered (Hour), and the interaction term. Nest ID was included as a random effect (Pinheiro & Bates 2000) to control for any individual differences in prey items delivered due to differences in prey availability or individual prey preference among the breeding pairs. The global model had different combinations, and in order to find the model with the lowest Akaike's information (AIC) all the combinations were tested and the one with the lowest AIC value was selected. The most parsimonious model was kept if Δ AIC was ≤ 2.0 after adding a variable (Burnham 2002). Only the models with a trend, $p \leq 0.11$ are discussed and shown graphically. The 12 models are shown in Table 1.

Table 1: The different models and combinations that best explained whether a prey item delivered at the nest was a lizard (test 1), a bank vole (test 2), a wood lemming (test 3), a *Microtus* vole (test 4), a bird (test 5). Model number corresponds to the model number listed in Appendix 2.

Model number	Model
6	HSM + Nest ID
7	Time + Nest ID
8	Temp + Nest ID
12	Hour + Nest ID
3	Temp + HSM + Nest ID
4	Temp + Time + Nest ID
5	HSM + Time + Nest ID
10	Temp + Hour + Nest ID
11	Hour + I(Hour^2) + Nest ID
2	Temp + HSM + Time + Nest ID

9	Temp + Hour + I(Hour^2) + Nest ID
1	Temp + HSM * Time + Nest ID

Results

A total number of 284 prey items was recorded delivered at the six kestrel nest during the filming for my study. The number of prey species delivered at the nest was 9, including 2 shrews, 183 *Microtus* voles (field voles and root voles), 32 wood lemmings, 22 bank voles, 22 common lizards and 5 birds (Table 2).

Table 2: Prey delivered on the nests of the kestrel. Field vole (*M. agrestis)* and root vole (*M. oeconomus)* are pooled. Shrews are pooled, and not identified to species. Each nest is given a number: Storflendammen (1), Storfallet (2), Bryn Nord (3), Flenvoll (4), Husfliden (5) and Tøråsen (6).

Prey	1	2	3	4	5	6	Sum
Shrews (*Sorex sp.*)	1	1	0	0	0	0	2
Field vole (*Microtus agrestis*)	26	15	23	16	31	25	136
Root vole (*Microtus oeconomus*)	4	1	6	4	14	0	29
Microtus sp.	3	1	1	1	11	1	18
Wood lemming (*Myopus schisticolor*)	2	7	4	9	1	9	32
Bank vole (*Myodes glareolus*)	2	3	2	6	4	5	22
Common lizard (*Zootoca vivipara*)	0	5	0	0	5	3	13
Song thrush (*Turdus philomelos*)	0	1	0	0	1	0	2
Chaffinch (*Fringilla coelebs*)	0	0	0	0	0	1	1
Redwing (*Turdus ilacus*) or Song thrush	0	0	1	0	1	0	2
Wood lemming or *Microtus sp.*	2	3	0	0	1	2	8
Bank vole or *Microtus sp.*	1	0	0	0	2	0	3
Vole (Microtinae)	0	5	1	0	2	6	14
Unidentified prey	0	0	0	0	0	2	2
Sum	41	42	38	36	73	54	284

The trapping indices of each small mammal prey type (Appendix 1) suggest that the populations of the different prey types did not vary synchronously between the kestrel territories. During my study the bank vole and *Microtus* vole populations were at a medium level, while the wood lemming population was very high and the shrew population very low.

The delivery rate of *Microtus* voles (Table 3) was positively correlated with the log-transformed *Microtus* vole trapping index (Figure 1: $R^2=0.76$, $p=0.024$), suggesting that *Microtus* voles were more likely to be delivered at the kestrel nest with increasing abundance in the kestrel territory, i. e. the kestrels showed a functional response to *Microtus* voles. This suggests that *Microtus* voles are the preferred prey for kestrels. There was no trend towards an increase in delivery of bank voles with increasing abundance of bank voles (Figure 1: R^2=0.20, p=0.37) or of wood lemmings with increasing abundance of wood lemmings (Figure 1: R^2=0.015, p=0.82). There was no negative and significant relationship between delivery rates of lizards and the log-transformed trapping index of voles (Figure 2: R^2=0.03, p=0.74), or between the delivery rates of birds and the log-transformed trapping index of voles (Figure 2: R^2=0.015, p=0.82), suggesting that the delivery of lizards and birds were not affected by the vole abundance in the kestrel territories. The number of shrews delivered at the nest was very low (n=2), precluding any statistical analysis of the relationship between delivery rate and abundance.

To see if any of the prey types delivered at the nest was an alternative prey to *Microtus* voles for the kestrel when the abundance of *Microtus* voles were low, the delivery rates of bank vole, wood lemming, birds and common lizard were related to the log-transformed *Microtus* vole trapping index. This relationship was negative and significant for wood lemming (Figure 3: R^2=0.78, p=0.020), negative and non-significant for bank vole (Figure 3: R^2=0.50, p=0.11), positive and non-significant for birds (Figure 3: R^2=0.51, p=0.11) and positive and non-significant for common lizard (Figure 3: R^2=0.002, p=0.93). Thus wood lemming was alternative prey to *Microtus* voles and bank vole tended to, while lizard and birds were not.

Table 3: Delivery rates (items per hour) at the kestrel nests. Field vole (*M. agrestis*) and root vole (*M. oeconomus*) are pooled. For calculation of delivery rate see text. Each nest is given a number: Storflendammen (1), Storfallet (2), Bryn Nord (3), Flenvoll (4), Husfliden (5) and Tøråsen (6).

Prey	1	2	3	4	5	6
Shrew	0.02	0.02	0.00	0.00	0.00	0.00
Microtus sp.	0.72	0.39	0.64	0.46	0.82	0.50
Wood lemming	0.04	0.14	0.09	0.20	0.02	0.17
Bank vole	0.04	0.06	0.05	0.14	0.04	0.11
Common lizard	0.00	0.08	0.00	0.00	0.08	0.06
Bird	0.00	0.02	0.02	0.00	0.03	0.02

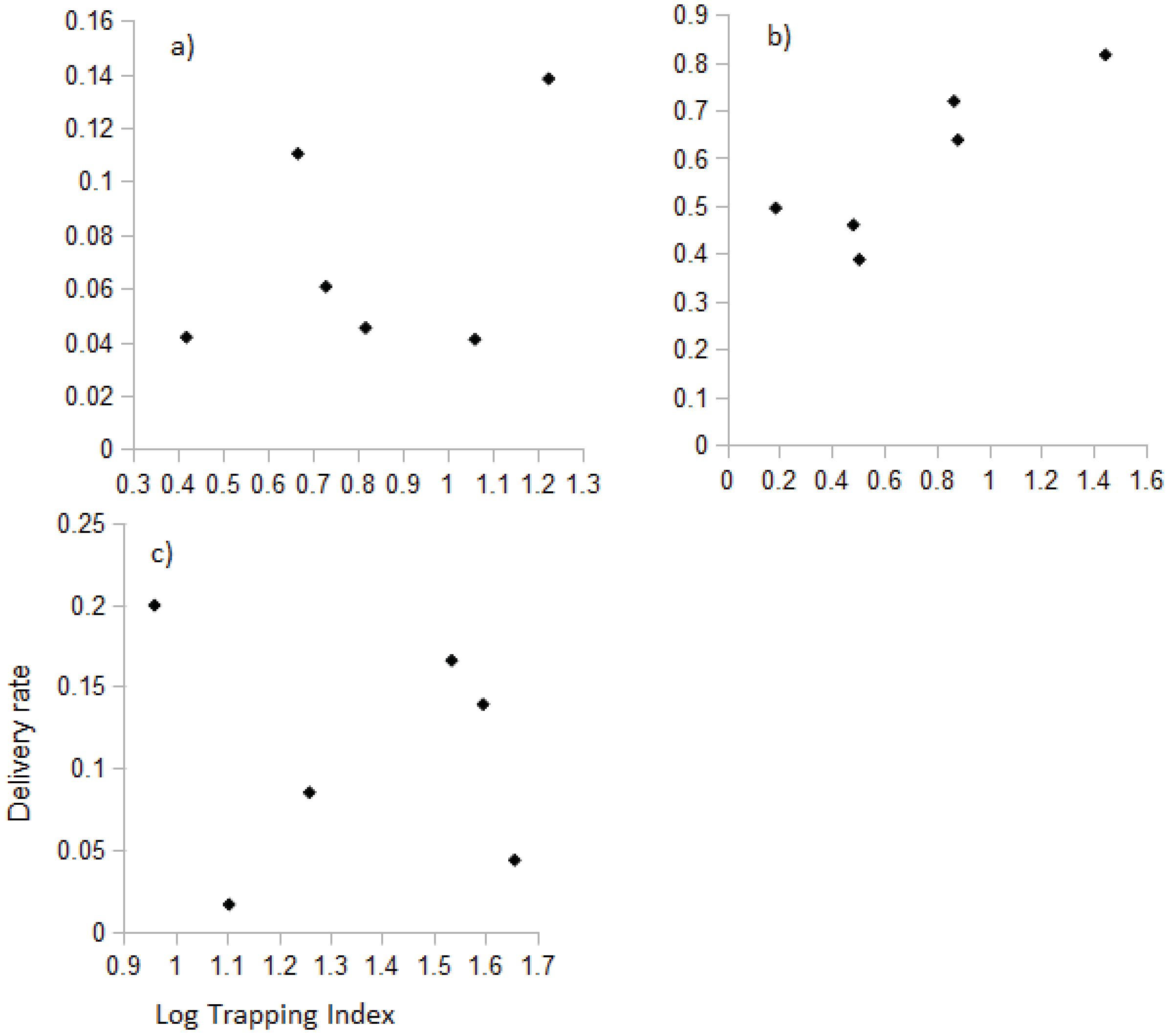

Figure 1: Relationship between delivery rates at kestrel nests and trapping indices of small mammals around the kestrel nests (see text for explanation). a) Bank vole. b) *Microtus* voles (field vole (*M. agrestis*) and root vole (*M. oeconomus*) pooled). c) Wood lemming.

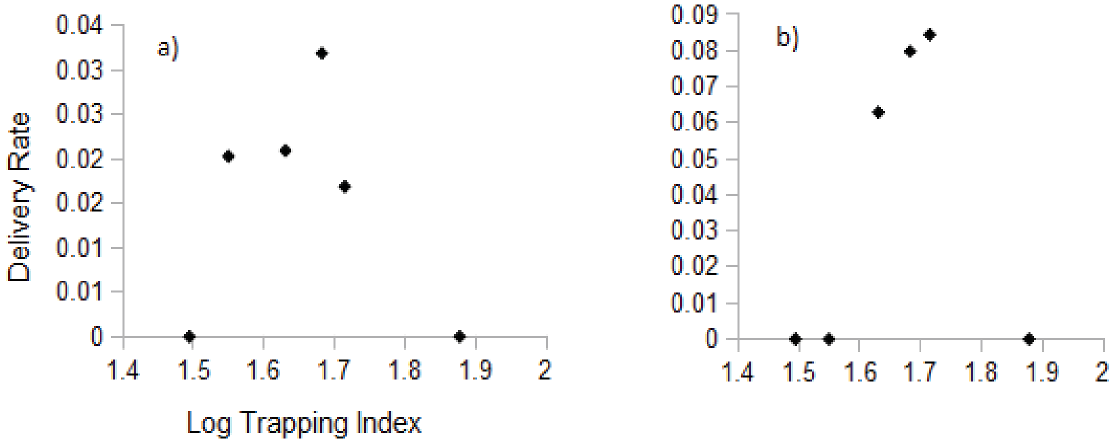

Figure 2: Relationship between delivery rates at kestrel nests and trapping indices of voles around the kestrel nests (see text for explanation). a) Frequency of bird. b) Frequency of common lizard.

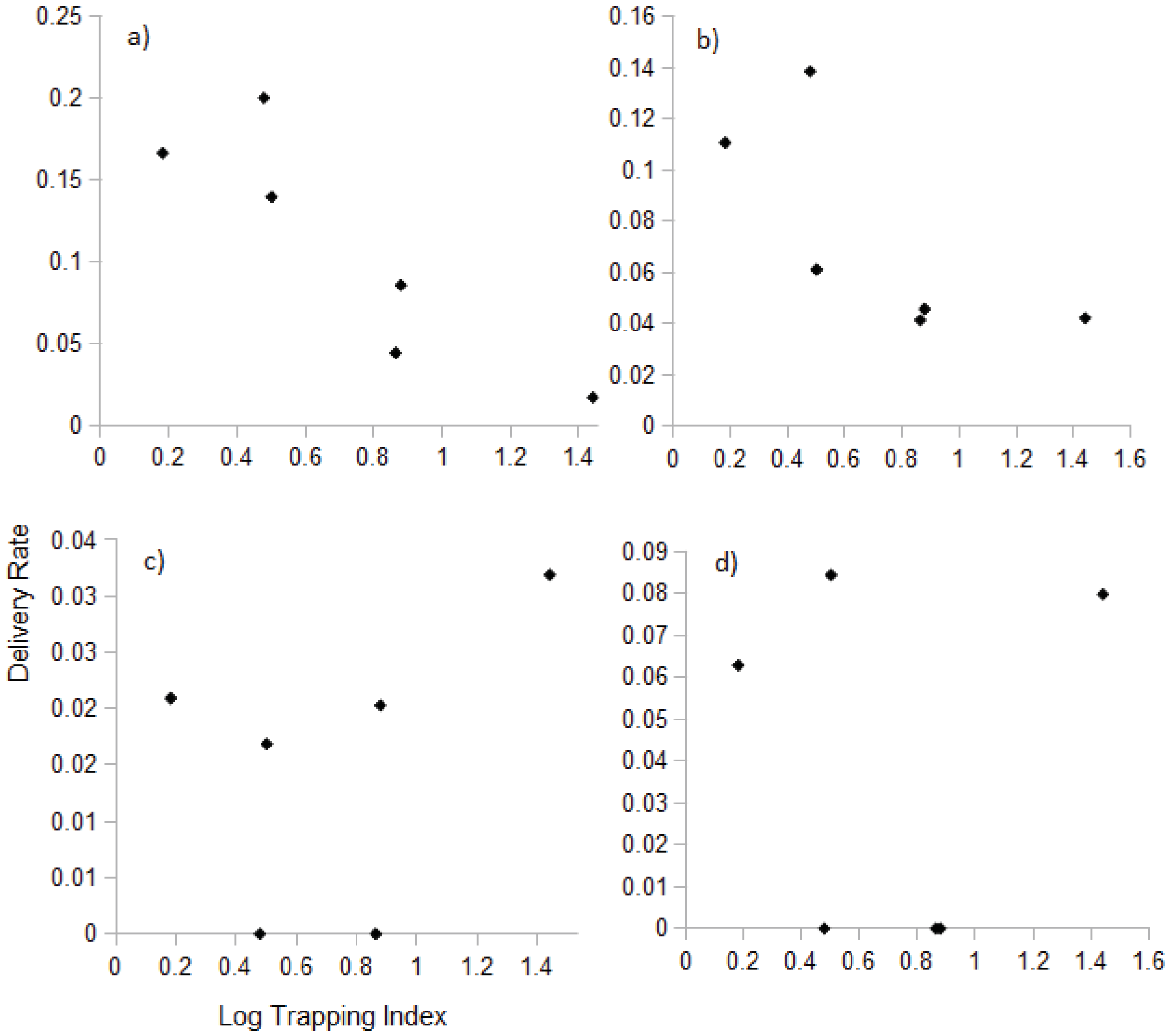

Figure 3: Relationship between delivery rates at kestrel nests and trapping indices of *Microtus* voles around the kestrel nests. a) Delivery of wood lemming. b) Delivery of bank voles. c) Delivery of birds. d) Delivery of common lizards.

To see if the frequency and type of prey delivered at kestrel nests was affected by ambient temperature at the time the prey item was delivered at the nest (Temp), number of hours from solar midnight (HSM) when the prey item was delivered, whether a prey item was delivered in the morning or in the evening (Time), and the hour of the day the prey item was delivered (Hour), a logistic multilevel regression analysis was performed. The resulting AIC values are found in Appendix 2. The best model found for test 1 (Lizard) was model 11 with AIC = 96.403, the best model found for test 2 (Bank vole) was model 7 with AIC = 157.12, the best models found for test 3 (Wood lemming) were model 7 and model 12 with AIC = 190.07 and AIC = 190.54, respectively, the best model found for test 4 (*Microtus* vole) was model 8 with AIC = 321.28, and the best model for test 5 (Bird) was model 6 with AIC = 52.943. Parameter estimates of the best fitted model for the delivery of lizards on the nest (Table 4, Figure 4) suggest that the probability that a prey delivered at the nest was a lizard was highest between 9 am and 1 am (probability = 0.06 for range 9-12 am), and this probability decreased both earlier and later in the day. No lizard was delivered between 5 pm and 7 am.

Table 4: Parameter estimates from a logistic multilevel regression model with the probability of a prey item delivered to kestrel nests being a lizard as response variable, and hour (hour of the day the prey item was delivered) and hour^2 as explanatory variables (n= 284). The estimates are corrected for the random effects of breeding pair identity (n=6).

	Estimate	SE	z	P
Intercept	-7.76	3.27	-2.37	0.02
Hour	0.96	0.59	1.64	0.10
I(Hour^2)	-0.05	0.03	-1.8	0.07

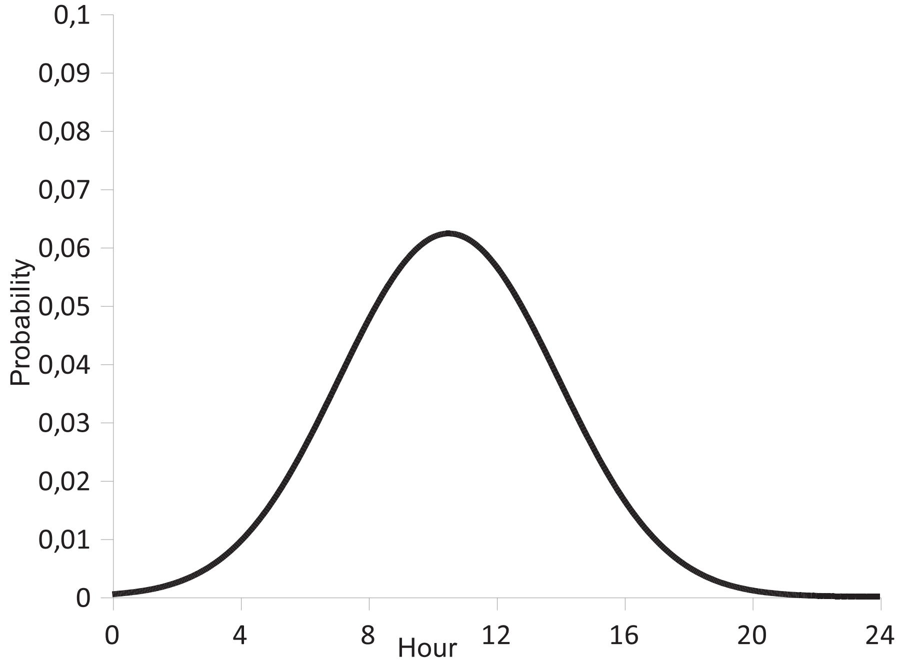

Figure 4: The probability of a prey item delivered at kestrel nests being a lizard as a function of hour of the day the prey item was delivered and of hour^2 (n= 284).

Parameter estimates of the best fitted model for the delivery of birds on the nest (Table 5, Figure 5) show that the probability that a prey delivered at the nest was a bird increased with number of hours since solar midnight (HSM). The probability of a bird delivery increased from 9 HSM (probability = 0.02) and reached the highest probability at 12 HSM (probability = 0.06). No bird was delivered between 6 pm and 8 am.

Table 5: Parameter estimates from a logistic multilevel regression model with the probability of a prey item delivered to kestrel nests being a bird as response variable, and hour since solar midnight (HSM) as explanatory variable (n= 284). The estimates are corrected for the random effects of breeding pair identity (n=6).

	Estimate	SE	z	p
Intercept	-7.01	2.14	-3.28	0.001
HSM	0.35	0.22	1.59	0.110

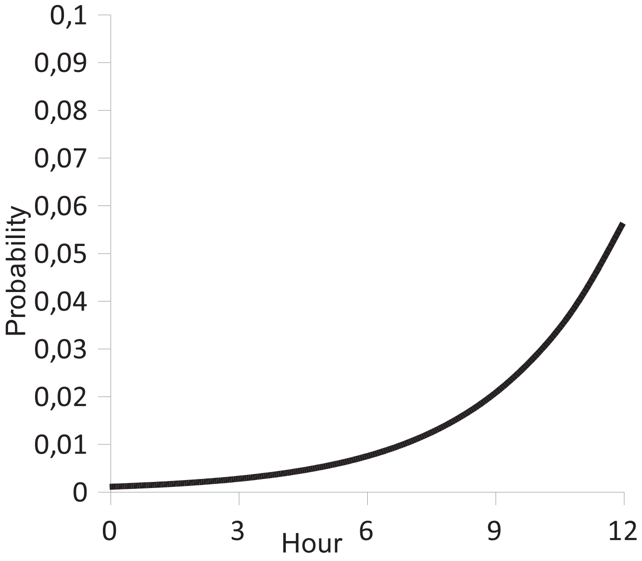

Figure 5: The probability of a prey item delivered at kestrel nests being a bird as a function of hour of the day the prey item was delivered (n= 284).

The probability that a prey delivered at the nest was a wood lemming increased throughout the day (Table 6, Figure 6). The probability of a wood lemming being delivered at the nest was twice as high in the evening (probability = 0.14) as in the morning (probability = 0.07) (Table 6 b). Both models show that there was a higher probability of a wood lemming being delivered at the nest in the evening than earlier in the day. No wood lemming was delivered between 11 pm and 4 am.

The best model(s) for the delivery of bank vole and *Microtus* voles are not further analyzed because they were insignificant (> 0.11). The values of the best models for birds (p=0.11), lizards (probability=0.10 and p = 0.07) and wood lemmings (p=0.099 and p=0.077) are rather high (p > 0.05), and should be interpreted as trends only.

Table 6: Parameter estimates from a logistic multilevel regression model with the probability of a prey item delivered to kestrel nests being a wood lemming as response variable, and Hour (Table a) or morning or evening delivery (Table b) as explanatory variables (n= 284). The estimates are corrected for the random effects of breeding pair identity (n=6).

a)	Estimate	SE	z	p
Intercept	-2.98	0.68	-4.37	0.000
Hour	0.06	0.04	1.65	0.099

b)	Estimate	SE	z	p
Intercept	-1.8	0.43	-4.22	0.000
Morning or evening	-0.72	0.41	-1.77	0.077

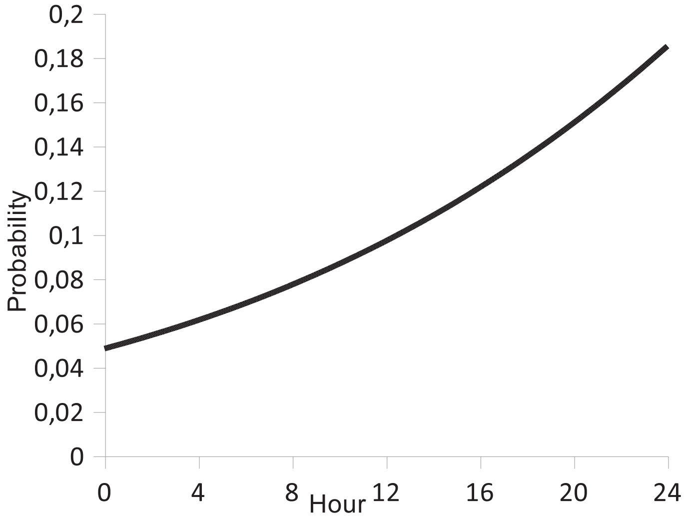

Figure 6: The probability of a prey item delivered at kestrel nests being a wood lemming as a function of hour of the day the prey item was delivered (n= 284).

Discussion

Diet and delivery rate

Of the 284 prey items recorded delivered at kestrel nests voles were the most abundant prey type and *Microtus* voles (Field vole and Root vole pooled) the most abundant of the separate vole species. The following prey types by number were lizards, birds and shrews. Frogs and insects were not recorded delivered at the nests, but may have been captured and eaten by the adult birds. Also previous studies have found a dominance of voles among prey taken by kestrels during the breeding period, and have all suggested a high proportion of *Microtus* voles (Village 1990; Korpimäki 1986; Korpimäki & Norrdahl 1991a; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2011b; 2012). Several studies have indicated that alternative prey are delivered more frequently as the abundance of voles decreases, and that such alternative prey are lizards, shrews and birds (Korpimäki & Norrdahl 1991a; 1991b; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2011b; 2012). The low delivery rate of such prey types in my study supports this. The high delivery rate of large prey such as voles and low delivery rate of small alternative prey such as lizards and shrews may be due to the load-size effect (see Sonerud 1992 and references therein), which predicts that large prey should be more frequently delivered at the nest while small prey should be eaten at the capture site, leading to an overestimation of large prey and underestimation of small prey in the kestrel diet by collecting data at the nest (Sonerud 1992). Sonerud (1989) found that kestrels selectively consumed smaller prey such as lizards and insects at the capture site, while larger prey were mostly delivered at the nest, suggesting that the kestrel's diet includes more small prey than the delivery rates at the nest indicate. Other factors than the load-size effect influence the delivery rates and probably decreases the difference between real functional response and those calculated from delivery rates on the nest (Sonerud 1992; Korpimäki et al. 1994), suggesting that my results are a good estimate of the kestrel's diet and functional response.

The delivery rates in my study are based on video monitoring when the nestlings were 6-15 days old, and dependent on the female to feed them (Cramp & Simmons 1980; Village 1990; Korpimäki & Wiehn 1998; Fargallo et al. 2003; Steen et al. 2010; 2012). According to Sonerud & Steen (2010) and Steen et al. (2012) it is expected that the number of small prey delivered at the nest will increase as the nestlings become older and able to feed unassisted. This is not corresponding to the findings of Slagsvold & Wiebe (2007), who found that larger prey were more frequently delivered to nestlings as the age increased due to increased swallowing capacity. As kestrels and other raptors are able to dismember prey and feed the nestlings smaller parts of the prey (Cramp & Simmons 1980; Village 1990; Fargallo et al. 2003; Steen et al. 2010; 2012), they are not as dependent on the nestlings swallowing capacity as other birds. That larger prey such as voles is delivered more frequently when the nestlings were young may suggest that the parents adjust their feeding efforts in relation to the nestlings age (Steen et al. 2012), and that the diet and prey delivery rates may differ in response to the nestlings age. This is not surprising as nestlings at different age stages have different food acquirement due to differences in growth, energy demands and activity level (Masman et al. 1989; Fargallo et al. 2003; Slagsvold & Wiebe 2007; Ydenberg 2007; Steen et al. 2010; 2012). This may explain the low number of small prey delivered at the kestrel nests in my study and the high number of large prey such as voles. Food monopolizing by dominant nestlings may be avoided by delivering several small prey instead of fewer large prey (Fargallo et al. 2003), indicating that older nestlings should be fed small prey to ensure that all the nestlings acquire enough food. Kestrel nestlings have a peak food demand when they are 15-17 days old (Steen et al. 2012), and Steen et al. (2012) found that the delivery rate of prey items were lower both before and after this age. This means that the delivery rates of my study may be lower than at the peak food demand of the nestlings as the nestlings in my study were up to 15 days old. All the nestlings in my study were close in age between the six nests and should therefore receive approximately the same amount of food.

Millon et al. (2009) found that some of the largest prey species of the European sparrowhawk (*Accipiter nisus*) were caught only by the larger female, and therefore not delivered on the nest during the first half of the breeding period when the male is the sole provider of food to the nestlings. This may also be true for to the kestrel, although it has a smaller degree of sexual-dimorphism than the sparrowhawk, indicating that very large prey species such as mountain hare (*Lepus timidus*) are less likely to be delivered at the nest as long as the male is the sole provider. This assumption may suggest differences between the recorded diet and the actual diet of the kestrel, but based on the high availability of suitable prey in the kestrel territories (Appendix 1) I suggest that such differences are negligible. Sonerud et al. (2010) did not find any differences in captured prey size between the sexes of the kestrel, and state that delivery of large prey caught by the male to the female for dismembering before feeding the nestlings may have given the impression that females deliver larger prey than the male. Small prey caught by the male are delivered directly to the nestlings by the male when the nestlings can feed unassisted (Sonerud et al. 2010). Slagsvold and Sonerud (2007) and Steen et al. (2012) states that in predatory birds were the female dismembers and feed the young there is a negative effect on provisioning due to the fact that the female cannot contribute in provisioning. It may therefore be a tradeoff between delivering several small and easily swallowed prey provisioned by both parents or provisioning of fewer large preys that the female dismember.

Food availability may differ from year to year because the abundance of certain prey (such as voles) varies between years (Sonerud 1986; 1988; Bondrup-Nielsen & Ims 1988; Korpimäki & Norrdahl 1991a; 1991b; Soneud 1992; Boonstra et al. 1998; Klemola et al. 1998; Korpimäki & Wiehn 1998; Eskelinen et al. 2004, and references therein). The results from the trapping of small mammals during my study suggest that the abundance of *Microtus* voles and bank vole was moderate, the abundance of shrews was very low, and the abundance of wood lemming was very high. They also suggest that the abundance of each small mammal species differed between the kestrel territories and the delivery rate of each prey item should therefore differ between the kestrel pairs. The delivery rates support this. There was a large variation in the abundance of the specific vole species between the different kestrel territories, which corresponds to the findings of Sonerud

& Steen (2010) from the same area for 2001-2009. The vole species differ in their habitat preferences (Sonerud 1986, Sonerud & Steen 2010), making habitat composition probably the most contributing factor to differences in abundance between the different kestrel territories. The different territories that I studied also differed in altitude, with Bryn Nord highest and Storfallet lowest, which in turn influence the habitat proportions of the kestrel territories. Sonerud (1980) and Arroyo et al. (2009) found that the height and density of the vegetation protects the voles against raptors. This differs between the kestrel territories and will increase with season as the vegetation grows, and may reduce the amount of suitable hunting area (Sonerud 1980; Arroyo et al. 2009). Sonerud (1980) found that the kestrel were forced to switch from hunting in rich habitat with high prey abundance in the spring to poorer habitat with lower prey abundance later in the season due to increased growth of the vegetation and this may affect the hunting success and delivery rate of prey at kestrel nests. Such affect have been found by Steen et al. (2012) who found that prey delivery rate and prey size at kestrel nests decreased with season. They suggest that the dependency of hunting in close distance to the nest may deplete the habitat of the most suitable prey and therefore reduce the delivery rate and prey size at the kestrel nests. My results were collected relatively early in the breeding season and the amount of suitable prey were high, suggesting that depletion of suitable prey did not occur or affect the delivery rate and prey size delivered at the kestrel nests.

Several studies state that in altricial birds such as the kestrel the type of prey selected by parents for their nestlings have a major effect on the amount of time and energy spent on food collection (hunting), prey preparation and feeding of the nestlings (Slagsvold & Sonerud 2007; Slagsvold & Wiebe 2007; Millon et al. 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011b; 2012). Parents have to minimize the constraints set by time spent on self-feeding and hunting and at the same time maximize the delivery of prey at the nest (Ydenberg 2007), and should therefore focus their hunting on the most optimal prey that best covers the daily energy and nutritional needs for the nestlings (Steen et al. 2011b; 2012). According to Steen et al. (2011b) the most optimal prey for the kestrel are voles, and kestrels can potentially rear young exclusively on voles in years with high vole abundance (Steen et al. 2011b). This is not a likely scenario for other prey items such as insects, lizards and shrews, as the delivery rate would have to be higher than what is possible in Fennoscandian boreal forests (Steen et al. 2011b).

Functional response

Several studies have been conducted on a predator's functional response, ranging from insects (Schenk & Bacher 2002) to mammals (Jaksić et al. 1992; Dale et al. 1994; Nilsen et al. 2009) and birds (Korpimäki & Norrdal 1991a; Jaksić et al. 1992; Redpath & Thirsgood 1999; Salamolard et al. 2000; Millon et al. 2009; Sonerud & Steen 2010). The studies conducted on birds, with the exception of Sonerud & Steen (2010), did not use video to record prey deliveries and may therefore be more affected by errors and miscalculations in their approximations on prey delivery rates. In my study the kestrels showed a functional response to *Microtus* voles, but not to bank vole or wood lemming. The abundance of lizard and birds in the kestrel territories were not estimated due to logistic and time constraints, and I was then unable to test whether the kestrel had a functional response to these prey or not. My results suggest that the delivery rate of lizard and birds were not affected by the abundance of voles. Several studies indicate that the kestrel may adopt a functional response or a numerical response to the abundance of voles, depending on the abundance of such prey (Village 1987; Korpimäki & Norrdahl 1991a; Fargallo et al. 2003; Sonerud & Steen 2010). My findings of functional response to voles are comparable to findings by Korpimäki & Norrdal (1991a), who found that the kestrel showed both functional and numerical response to *Microtus* voles, but not to common shrews. Their results tended for a functional response to bank vole, but the relationship was not significant. Korpimäki & Norrdal (1991a) presented no data on the wood lemming, which may be due to a low abundance of wood lemmings in the study area as it is mainly dominated by agricultural fields. Korpimäki & Norrdal (1991a) also stated that the kestrel's functional response was primarily linked to the changes in the vole abundance, and only partly explained by alterations in their hunting behavior such as changing hunting areas to were the most abundant prey are located.

Sonerud & Steen (2010), who used video surveillance techniques, suggested that the kestrel may have a non-selective multi-functional response to small mammals and found that bank vole, *Microtus* voles and wood lemming were captured in proportion to their abundance in the kestrel territories (functional response), but results from my study suggest that wood lemmings were captured only when the abundance of *Microtus* voles were low. Jaksić et al. (1992) found that of the ten studied predators in their Neotropical study area only the Austral pygmy owl (*Glaucidium nanum*) showed a functional response to the changes in the abundance of available small mammal prey, and that several of the other predators shoved a numerical response to the abundance of small mammals. According to Korpimäki (1986) and Korpimäki & Norrdal (1991a) it is more common with functional response to voles in lower altitudes in southern Fennoscandia due to more stable communities, than in higher altitudes or further north were predators usually show numerical response to voles as the prey tend to fluctuate more strongly. Salamolard et al. (2000) found that the Montague's Harrier (*Circus pygargus*) in France have a strong numerical response to vole abundance, contradicting the assumption of Korpimäki (1986) and Korpimäki & Norrdal (1991a), and also found a functional response to vole abundance as vole biomass in pellets increased with increasing abundance of voles.

Habitat preference and delivery rate

Differences in habitat preferences between the vole species may influence the delivery rate of prey items at the kestrel nests because kestrels predominantly hunt in open habitat (Cramp & Simmons 1980; Korpimäki 1986; Sonerud 1986; Village 1990). *Microtus* voles are predominantly found in open habitats such as clear-cuts and agricultural fields (Sonerud 1986; Korpimäki & Norrdahl 1991b; Sonerud & Steen 2010), which makes them more vulnerable to attack from kestrels. This may explain the high delivery rate of *Microtus* voles in kestrel territories with medium to low abundance of such voles. The low delivery rate of grey-sided voles can be explained by the low abundance of such voles, only 3 individuals were caught in the snap-traps, and only some locations (such as Bryn Nord) include the preferred habitat of the grey-sided vole which is old and open mountainous birch- and spruce forest (Hörnfeldt et al. 1990, and references therein). Studies in the same area suggest similar use of clear-cuts as the *Microtus* voles (Sonerud and Steen 2010), a frequently used area for hunting kestrels (Løken 2009), which suggest that more grey-sided voles would be delivered if the abundance was higher. Several studies state that bank voles and wood lemmings occur at higher densities in forest habitats than in more open habitats, and that forest habitat may act as source populations for the bank voles and wood lemmings hunted by the kestrels in open habitat (Sonerud 1986; Sonerud & Steen 2010). The different vole species also differ in their vulnerability to being captured by avian predators as they differ in agility and physiology (Nishimura & Abe 1988). *Microtus* voles have a larger digestive system than the bank vole in order to digest folivorous material, making the *Microtus* vole less agile and more prone to capture than the bank vole (Sonerud 1986; Sonerud & Steen 2010). This corresponds well with the findings of Nishimura & Abe (1988) and Village (1990), which both found that agile mice (*Apodemus* ssp.) escaped better than the less agile voles (mainly *Microtus* voles) from hunting Ural owls (*Strix uralensis*) and kestrels, respectively.

Several studies state that wood lemmings are predominantly found in old coniferous boreal forest, and that they have a specialized diet containing several species of green mosses that are tightly associated with such habitats (Bondrup-Nielsen 1993; Eskelinen 2002; 2004; Federov et al. 2008). The high abundance of wood lemming during my study may have forced wood lemmings into more open habitats than preferred due to competition for resources, which in turn may have made wood lemmings more susceptible to hunting kestrels. This may also occur for the bank vole in years with high abundance. According to Steen et al. (2011b) the wood lemming is on average heavier than both *Microtus* voles and bank voles, and the increased size may be linked to the diet. As moss is hard to digest (Saarela & Hissa 1993; Eskelinen 2002, and references therein), and contain several secondary compounds (Seigler 1998), the wood lemming may need a larger intestinal system to digest successfully. Larger size and increased intestinal weight may reduce the wood lemming's agility, and make it more susceptible to avian predators. The secondary compounds may make the wood lemming less attractive to the kestrels (a form of aposematism), or potentially have lower nutritional value. To the best of my knowledge, studies who investigate this idea has not been published. In order to avoid such secondary compounds the kestrel may have to increase the handling time when feeding the nestlings with wood lemmings, as most of the secondary compounds may be found in the digestive system, perhaps indicating that this should be removed before consumption. These assumptions may explain the low delivery rate of wood lemmings. Wood lemmings spend a long time at the same feeding place (Eskelinen 2002; 2004). This suggest that the wood lemming is more stationary and less likely to travel frequently between several feeding places, making it more difficult to locate for hunting kestrels.

Alternative prey and delivery rate

According to the terminology of Sonerud (1992), *Microtus* voles were the kestrels' main prey in my study and the remaining prey types (bank vole, wood lemming, lizard, birds and shrews) should be alternative prey to the kestrel. Linear regression analysis verified wood lemming as alternative prey, and there was a negative, but insignificant relationship for the bank vole. Meaning that the bank vole tended to be an alternative prey to the kestrel, but the results from my study can only be interpreted as a trend. Birds and lizards was not alternative prey to *Microtus* voles.

The number of shrews delivered at the kestrel nests was very low, which corresponds well with the low abundance of shrews in the kestrel territories. Several studies have found that shrews appear to be an alternative prey to voles for the kestrel (Korpimäki & Norrdal 1991a; 1991b; Sonerud & Steen 2010). My results did not suggest this, probably due to the high abundance and delivery rate of voles at all kestrel nests studied, and the corresponding low abundance and delivery rate of shrews at all kestrel nests, resulting in limited statistical possibilities to investigate how shrews interact with voles and other prey species to effect on kestrel capture rate and diet. According to Sonerud & Steen (2010) and Steen et al. (2011b) shrews and voles are quite similar in profitability to the kestrel. Both prey groups would be expected to be preyed upon by kestrels when encountered, and this suggest that more shrews would have been delivered if if the abundance of shrews had been higher. Several studies state that when the abundance of voles increase, the number of shrews delivered at the nest decreases (Korpimäki & Norrdal 1991a; Sonerud & Steen 2010). Experimental removal of avian predators such as kestrels and Tengmalm's owls increased the abundance of shrews in periods with a declining vole population, but not when the vole population increased (Norrdal & Korpimäki 2000). This suggests that more shrews are captured when the vole abundance declines. According to Sonerud & Steen (2010) and Steen et al. (2012) the number of shrews delivered at kestrel nests should increase when the nestlings become able to ingest shrews unassisted, which is when they are 15 days old.

While the delivery rate of bank vole and *Microtus* voles was quite constant throughout the day, the delivery rates of birds, lizard and wood lemming were not. Common lizards were delivered more frequently between 9 am and 1 pm, suggesting that the kestrel more frequently hunted, or had higher hunting success, for lizards at this time of the day. Because common lizards are ectothermic, prevailing weather conditions will strongly affect their activity pattern, sprint speed, foraging success and capacity to escape from predators (Van Damme et al. 1987; Verwaijen & Van Damme 2007), and Steen (et al. 2011) found that the probability of a lizard being delivered at the nest increased with both ambient temperature and solar height independently. Ambient temperature is positively linked with solar height which increase in the time interval 9 am to 1 pm, thus indicating that common lizards may have a higher activity level and therefore be more vulnerable to hunting kestrels when leaving their hide to forage and become more easily spotted by hunting kestrels.

Larger prey caught by a raptor are generally delivered at the nest while smaller prey are consumed at the site of capture (Sonerud 1992), and according to Sonerud (1992) and Steen (et al. 2011) this suggest that the size distribution of the prey delivered at raptor nests may be a biased estimate of the size distribution of the prey captured by the raptor. As the lizard is a small prey it may be consumed more frequently at the capture site than larger prey (Sonerud 1989), suggesting that the proportion of lizards captured in the study area was most likely higher than the proportion of lizards among the prey items delivered at the kestrel nests. The capture rate of lizards in the study area may be regarded as a functional response (Steen et al. 2011), and according to Sonerud (1992) the number of lizards delivered at the nest will increase if a certain threshold is reached and more lizards are caught than the kestrel needs to fulfill its own energy requirements. According to Steen et al. (2012) there is no effect of nestling age or season on the delivery rate of lizard at kestrel nest. Lizards and insects are generally more important in the kestrel's diet further south in the species range (Cramp & Simmons 1980; Village 1990; Carillo et al. 1994; Carillo & Aparicio 2001; Carillo & González-Dávila 2010a; 2010b), and smaller prey such as lizards and shrews may be delivered more frequently as the nestlings get older and both parents hunt (Steen et al. 2012).

The probability that a prey item delivered at a kestrel nest was a bird increased with increasing proximity to midday compared to earlier and later in the day, suggesting that the kestrel more frequently hunted, or had a higher hunting success for birds at midday. Four out of the five birds delivered at the kestrel nests were thrushes, which are small to medium sized passerines that mainly feed on invertebrates and fruit (Cramp et al. 1988). The two species delivered were the Song thrush (*Turdus philomelos*) and the Redwing (*Turdus ilacus*) which both search for food in the ground litter, and frequently forage in open habitats (Cramp et al. 1988). Their nestlings usually leave the nest before they are fully able to fly (Cramp et al. 1988). These characteristics make them susceptible to hunting kestrels, and it is very likely that some of the thrushes delivered were young birds that were unable to fly or effectively escape avian predators. As both thrushes and the kestrel are diurnal birds, it is not surprising that I found birds more likely to be delivered at the kestrel nests at mid-day than earlier and later in the day as this is most likely a time of increased activity. Millon et al. (2009) suggested that the song thrush is highly vulnerable to predation by the sparrowhawk, which may strengthen my assumption of increased vulnerability to predation from the kestrel. Several studies state that birds are alternative prey to voles for the kestrels (Cramp & Simmons 1980; Village 1990; Korpimäki & Norrdahl 1991a; 1991b; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2011b), but this was not found in my study. A possible explanation may be the low number of birds delivered at the kestrel nests resulting in a less robust statistical analysis, combined with the high abundance of more profitable prey such as voles in all of the six kestrel territories. Several have found that when the abundance of voles increase, the proportion of avian prey delivered at the nest decreases (Korpimäki & Norrdal 1991a; 1991b; Sonerud & Steen 2010; Steen et al. 2010; 2011b). This corresponds well with the results of my study. It was not possible to estimate the abundance of avian prey in the kestrel territories due to logistic constraints. According to Steen et al. (2012) there is no effect of nestling age or season on the delivery rate of birds at kestrel nest.

Korpimäki & Norrdal (1991a) found that birds were more frequently killed by kestrels than by the Short-eared owl (*Asio flammeus*) and the Long-eared owl (*Asio otus*), which suggest that kestrels hunt birds more effectively than these owls do. According to Redpath & Thirgood (1999), the hen harrier (*Circus cyaneus*) mainly feed on field voles, meadow pipit (*Anthus pratensis*) and chicks of the red grouse (*Lagopus lagopus*), and had a higher delivery rate of each of these prey types when the abundance of the specific prey type increased. The kestrel and the hen harrier are both generalist predators, which suggest that they may have the same functional response to avian prey. For the kestrel birds have a lower profitability than voles (Village 1990; Sonerud & Steen 2010; Steen et al. 2010) due to increased handling time (Sonerud & Steen 2010; Steen et al. 2010), plucking prior to delivery at the nest (Steen 2004; Løv 2006) and lower attack success when aiming at birds compared to voles (Village 1990). The low attack success suggest that the kestrel have to spend more time for successful hunting on birds compared to the time spent on voles, and that birds should only be predated when the vole densities are lower than a critical threshold and the kestrels are forced to hunt any available prey in the territories.

Studies on the interaction between kestrels and wood lemmings are rare, and the results from my study suggest that wood lemmings are an alternative prey to *Microtus* voles. Kestrels hunting in territories whit high abundance of *Microtus* voles delivered fewer wood lemmings on the nest than kestrels hunting in territories with lower abundance of *Microtus* voles. *Microtus* voles may then be preferred over wood lemming, and I suggest that wood lemming is caught only when the abundance of *Microtus* voles is low and the abundance of wood lemming is high. The bank vole also tended to be delivered more frequently as the abundance of *Microtus* voles decreased, and the abundance of bank vole was high, but the relationship was statistically insignificant. More data on the interactions between the kestrel and the wood lemming are needed to support my assumptions. The probability that a prey delivered at kestrel nests was a wood lemming increased throughout the day, and was twice as high in the evening as earlier in the day. According to Saarela & Hissa (1993) the wood lemming appears to be active both day and night, and the high activity pattern and non-rhythmic behavior is an adaptation to the poor diet, which may force the animal to forage frequently both day and night. Such behavior may mask a potential circadian rhythm (Saarela & Hissa 1993). If the wood lemming is nocturnal or most active at dusk and dawn, it is less likely to be caught by kestrels that need daylight to be able to hunt. This may partially explain why the delivery rate of wood lemming was independent of wood lemming abundance and inversely related to *Microtus* vole abundance, and why the delivery of wood lemming increased with later hour of the day. It is also possible that when the daylight fades in the evening more wood lemming are caught as they become harder to distinguish from *Microtus* voles and bank vole, and therefore more frequently delivered at the nests.

Limitations and future research

Although the observational approach used in my thesis gives the most accurate measure of the kestrel's diet, several limitations such as errors in prey identification or selective transport of prey to the nest by the kestrels may have biased the data and therefore biased the recorded diet from the actual diet composition. Several studies state that estimating prey delivery rates by using video recordings at the nest is more advantageous than other techniques (Lewis et al. 2004; Steen 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b; 2012), such as direct observations from a hide (Redpath & Thirgood 1999; Redpath et al. 2001) or analysis of prey remnants and the content of pellets (Korpimäki & Norrdal 1991a; 1991b; Jaksić et al. 1992; Carillo et al. 1994; Redpath & Thirgood 1999; Redpath et al. 2001; Salamolard et al. 2000; Millon et al. 2009; Carillo & González-Dávila 2010a). Most importantly the level of errors and level of unidentified prey is lower than for the other techniques (Lewis et al. 2004; Steen 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b; 2012). Direct observations are the most time consuming method to estimate diet (Redpath et al. 2001), and video monitoring greatly diminish the amount of time needed and at the same time causes less disturbance (Steen 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b; 2012).

If it had been possible to record all prey items captured by the kestrels, and not only prey delivered at the nests, it would have been possible to estimate the actual prey capture rate and investigate functional response of the kestrels prey groups more accurately. Future technological development may make it possible to attach cameras to the kestrel and thereby see all of the prey items captured (Rutz et al. 2007; Sonerud & Steen 2010; Steen et al. 2011), making it possible to estimate the capture rate and investigate the functional response to each prey group more accurately than the techniques available today can. According to Rutz et al. (2007) this should be possible in near future due to the rapid technological development of cameras and wireless data transfer. More studies are needed to find reasons to why the kestrel do not show functional response to wood lemmings, and more studies on the ecology of the wood lemming would be an important part of this.

Conclusion

The kestrels showed a functional response to *Microtus* voles and I suggest that *Microtus* voles are the preferred prey for the kestrel. There was no indication that kestrels showed a functional response towards bank vole or wood lemming. The relatively low delivery rate of bank vole, wood lemming, common lizard and birds suggest that they are alternative prey to *Microtus* voles, but my results suggest that only the wood lemmings was an alternative prey to *Microtus* voles during my study. Bank vole had a negative, but insignificant trend, meaning that the bank vole tended to be an alternative prey to *Microtus* voles. Studies on the interaction between the kestrel and the wood lemming are rare, and I suggest that wood lemmings are caught only when the abundance of wood lemming is high and the abundance of *Microtus* voles is low. More research on the interaction between the kestrel and the wood lemming are needed to support this assumption, and to find an explanation for why the kestrel does not show functional response to wood lemming. Common lizard was most frequently delivered between 9 am and 1 pm, and I suggest that this is due to increased activity of lizards as the temperature increases at this time of the day. The probability of a bird being delivered at kestrel nests increased with the number of hours since solar midnight, suggesting that birds were hunted at midday. This corresponds well with the activity pattern of thrushes, which were the most delivered group of birds. I also suggest that flightless thrush fledglings are particularly vulnerable to predation by kestrels. The probability that a prey delivered at the nest was a wood lemming increased throughout the day and was twice as high in the evening than in the morning. This may suggest that the wood lemming is more active in the evening and therefore more vulnerable to hunting kestrels, or it may be mistaken for a M*icrotus* vole or a bank vole as the daylight fades away.

References

Arroyo, B., Amar, A, Leckie, F., Buchanan, G. M.,Wilson, J. D. & Redpath, S. 2009. Hunting habitat selection by hen harriers on moorland: implications for conservation management. Biol. Conserv. 142: 586-596.

Bondrup-Nielsen, S. & Ims, R. A. 1988. Demography during a population crash of the wood lemming, *Myopus schisticolor*. Can. J. Zool. 66: 2442-2448.

Bondrup-Nielsen, S. 1993. Food preference and diet of the wood lemming (*Myopus schisticolor*). In: The biology of lemmings (eds. Stenseth, N. C. and Ims, R. A.). pp 303-309. Academic Press. London.

Boonstra, R., Krebs, C. J. & Stenseth, N. C. 1998. Population cycles in small mammals: the problem of explaining the low phase. Ecology 79: 1479-1488.

Burnham, K. P. 2002. Model selection and multimodel inference: a practical information-theorethic approach. 2nd ed. Springer. New York.

Carillo, J., Hernández, E. C., Nogales, M., Delgado, G., Garcia. & Ramos, T. 1994. Geographic variation in the spring diet of *Falco tinnunculus* L. on the island of Fuerteventura and El Hierro (Canary Islands). Bonn. Zool. Beitr. 45: 39-48.

Carillo, J. & Aparicio, J. M. 2001. Nest defence behavior of the Eurasian kestrel (*Falco tinnunculus*) against human predators. Ethology 107: 865-875.

Carillo, J. & González-Dávila, E. 2009. Latitudinal variation in breeding parameters of the Common kestrel *Falco tinnunculus*. Ardeola 56: 215-228.

Carillo, J. & González-Dávila, E. 2010a. Geo-environmental influences on breeding parameters of the Eurasian kestrel (*Falco tinnunculus*) in the Western Palearctic. Ornis Fennica 87:15-25.

Carillo, J. & González-Dávila, E. 2010b. Impact of weather on breeding success of the Eurasian kestrel *Falco tinnunculus* in a semi-arid island habitat. Ardea 98: 51-58.

Cramp, S., Simmons, K. E. L., Gillmore, R., Hollom, P. A. D., Hudson, R., Nicholson, E. M., Ogilvie, M. A., Olney, P. J. S., Roselaar, C. S., Voous, K. H., Wallace, D. I. M. & Wattel, J. 1980. The birds of the western palearctic. Vol. II. Oxford: Oxford University Press.

Cramp, S., Simmons, K. E. L., Gillmore, R., Hollom, P. A. D., Hudson, R., Nicholson, E. M., Ogilvie, M. A., Olney, P. J. S., Roselaar, C. S., Voous, K. H., Wallace, D. I. M. & Wattel, J. 1988. The birds of the western palearctic. Vol. V. Oxford: Oxford University Press.

Dale, B. W., Adams, L. G. & Bowyer, T. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. J. Anim. Ecol. 63: 644-652.

Damme, R. Van., Bauwens, D. & Verheyen, R. R.1987. Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. Herpetol. 45: 405-415.

Eskelinen, O. 2002. Diet of the wood lemming *Myopus shisticolor*. Ann. Zool. Fenn. 39: 49-57.

Eskelinen, O. 2004. Studies on the ecology of the wood lemming *Myopus shisticolor*. PhD thesis. University of Joensuu.

Eskelinen, O., Sulkava, P. & Sulkava, R. 2004. Population fluctuations of the wood lemming *Myopus shisticolor* in eastern and western Finland. Acta Theriol. 49: 191-202.

Fargallo, J.A., Laaksonen, T., Korpimäki, E., Pöyri, V., Griffith, S.C. & Valkama, J. 2003. Size-mediated dominance and begging behaviour in Eurasian kestrel broods. Evol. Ecol. Res. 5: 549-558.

Federov, V. B., Goropashinaya, A. V., Boeskorov, G. G. & Cook, J. A. 2008. Comparative phylogeography and demographic history of the wood lemming (*Myopus shisticolor*): implications for the late Quaternary history of the taiga species in Eurasia. Mol. Ecol. 17: 598-610.

Hörnfeldt, B., Carlsson, B.-G., Löfgren, O. & Eklund, U. Effects of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). Can. J. Zool. 68: 522-530.

Jaksić, F. M., Jimėnez, J. E., Castro, S. A. & Feinsinger, P. Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. Oecologia 89: 90-101.

Klemola, T., Korpimäki, E. & Norrdahl, K. 1998. Does avian predation risk depress reproduction of voles? Oecologia 115:149-153.

Korpimäki, E. 1986. Diet variation, hunting habitat and reproductive output of the kestrel *Falco tinnunculus* in the light of the optimal diet theory. Ornis Fenn. 63: 84-90.

Korpimäki, E. & Norrdahl, K. 1991a. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. Ecology 72: 814-826.

Korpimäki, E. & Norrdahl, K. 1991b. Do breeding nomadic avian predators dampen population fluctuations of small mammals? Oikos 62: 195-208.

Korpimäki, E., Tolonen, P. & Valkama, J.1994. Functional responses and load-size effect in central place foragers: data from the kestrel and some general comments. Oikos 69: 504-510.

Korpimäki, E. & Wiehn, J. 1998. Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. Oikos 83: 259-272.

Lehikonen, A., Byholm, P., Ranta, E., Saurola, P., Valkama, J., Korpimäki, E., Pietiäinen, H. & Henttonen, H. 2009. Reproduction of the common buzzard at its northern range margin under climate change. Oikos 118: 829-836.

Lewis, S. B., Falter, A. R., & Titus, K. 2004. A comparison of 3 methods for assessing raptor diet during the breeding season. Wildl. Soc. Bull. 32: 373-385.

Løken, Ø. 2009. Home range, habitat selection and behavior of male kestrels (*Falco tinnunculus*) in boreal forest. MSc thesis. Norwegian University of Life Sciences.

Løw, L. M. 2006. Prey preparation and ingestion rate in breeding Eurasian kestrels (*Falco tinnunculus*) in boreal forests. MSc thesis. Norwegian University of Life Sciences.

McDonald P. G., Olsen, P. D. & Cockburn, A. 2004. Weather dictates reproductive success and survival in the Australian brown falcon *Falco berigora*. J. Anim. Ecol. 73: 683-692.

Masman, D., & Klaassen, M., 1987. Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). Auk 104: 603-616.

Masman, D., Dijkstra, C., Daan, S. & Butt, A. 1989. Energetic limitations of avian parental effort-field experiments in the kestrel (*Falco tinnunculus*). J. Evol. Biol. 2: 435-455.

Millon, A., Nielsen, J. T., Bretagnolle, V. & Møller, A. P. 2009. Predator-prey relationships in a changing environment: the case of the sparrowhawk and its avian prey community in a rural area. J. Anim. Ecol. 78: 1086-1095.

Moen, A. 1998. Nasjonalatlas for Norge, vegetasjon. Hønefoss: Statens kartverk. (In Norwegian).

Nilsen, E. B., Linnel, J. D. C., Odden, J. & Andersen, R. 2009. Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. J. Anim. Ecol. 78: 741-751.

Nishimura, K. & Abe, M. T. 1988. Prey susceptibilities, prey utilization and variable attack efficiencies of Ural owls. Oecologia 77: 414-422.

Norrdahl, K. & Korpimäki, E. 2000. Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predators. Oikos. 91: 528-540.

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

R Development Core Team. 2011. R: a language and environment for statistical computing. Vienna, Austria

Redpath, S. M. & Thirgood, S. J. 1999. Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. J. Anim. Ecol. 68: 879-892.

Redpath, S. M., Clarke, R., Madders, M. & Thirgood, S. J. 2001. Assessing raptor diet: comparing pellets, prey remains and observational data at hen harrier nests. Condor 103: 184-188.

Rekdal, Y. 2010. Vegetasjon og beite i Flendalen beiteområde. Rapport frå vegetasjonskartlegging i Trysil kommune. Norwegian Forest and Landscape Institute. Ås. (In Norwegian).

Riegert, J., Fainová, D., & Bystřická, D. 2010. Genetic variability, body characteristics and reproductive parameters of neighboring rural and urban common kestrel (*Falco tinnunculus)* populations. Pop. Ecol. 52: 73-79.

Rutz, C., Bluff, L. A., Weir, A. A. S. & Kacelnik, A. 2007. Video cameras on wild birds. Science.

318: 765.

Saarela, S. & Hissa, R. 1993. Metabolism, thermogenesis and daily rhythm of body temperature in the wood lemming, *Myopus schisticolor*. J. Comp. Physiol. B. 163: 546-555.

Salamolard, M., Butet, A., Leloux, A. & Bretagnolle, V. 2000. Response of an avian predator to variations in prey density at a temperate latitude. Ecology 81: 2428-2441.

SAS 2010. JMP® statistics and graphics guide, version 9.0.0. SAS Institute. Cary, USA.

Schenk, D. & Bacher, S. 2002. Functional response of a generalist predator to one of its prey species in the field. J. Anim. Ecol. 71: 524-531.

Seigler, D. S. 1998. Plant secondary metabolism. Kluwer Academic Publishers. 759 pp.

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

Slagsvold, T. & Wiebe, K. L. 2007. Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. Anim. Behav. 73:691-700.

Sonerud, G. A. 1980. Jaktstrategier hos flyvende småpattedyrpredatorer i barskog. Cand. real. avhandling. Univeritetet i Oslo. (In Norwegian).

Sonerud, G. A. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. Holarct. Ecol. 9: 33-47.

Sonerud, G. A. 1988. What causes the extended lows in microtine cycles? Analysis of fluctuations in sympatric shrews and microtine populations in Fennoscandia. Oecologia. 76: 37-42.

Sonerud, G. A. 1989. Allocation of prey between self-consumption and transport in two different-sized central place foragers. Ornis Scand. 20: 69-71.

Sonerud, G. A. 1992. Functional-responses of birds of prey: biases due to the load-size effect in central place foragers. Oikos 63: 223-232.

Sonerud, G. A. & Steen, R. 2010. Multi-species functional response in a generalist raptor. Manuscript in: Steen, R. 2010. Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (*Falco tinnunculus*). PhD thesis. Norwegian University of Life Sciences.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. 2010. Do females really capture larger prey than males in breeding raptors? Size-dependent prey-allocation by male Eurasian kestrels *Falco tinnunculus*. Manuscript in: Steen, R. 2010. Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (*Falco tinnunculus*). PhD thesis. Norwegian University of Life Sciences.

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. J. Raptor Res. 43: 69-74.

Steen, R., Løv, L. M., Sonerud, G. A., Selås, V. & Slagsvold, T. 2010. The feeding constraint hypothesis: prey preparation as a function of nestling age and prey mass in the Eurasian kestrel. Anim. Behav. 80: 147-153.

Steen, R., Løv, 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. Can. J. Zool. 89: 199-205.

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

Steen, R., Sonerud, G. A. & Slagsvold, T. 2012. Parents adjust feeding effort in relation to nestling age in the Eurasian kestrel (*Falco tinnunculus*). J. Ornithol. (In press).

Verwaijen, D. & Damme, R. Van. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. J. Therm. Biol. 32: 388-395.

Village, A. 1987. Numbers, territory-size and turnover of the short-eared owls *Asio flammeus* in relation to vole abundance. Ornis Scand. 18: 198-204.

Village, A. 1990. The kestrel. Poyser. London.

Ydenberg, R. C. 2007. Provisioning. In: Stephens, D. W., Brown, J. S., & Ydenberg, R. C., editors. Foraging Behavior and Ecology. University of Chicago Press. USA. Pp. 273-304.

Appendix

Appendix 1: Trapping index for each small mammal prey type delivered at the kestrel nests, and for voles pooled calculated as the number of individual captured per 100 trap nights (see text). Each nest is given a number: Storflendammen (1), Storfallet (2), Bryn Nord (3), Flenvoll (4), Husfliden (5) and Tøråsen (6).

Nest	Shrew	Bank vole	*Microtus* vole	Wood lemming	Voles
1	0	11.46	7.30	45.18	75.37
2	0	5.35	3.17	39.25	51.80
3	0	6.55	7.56	18.09	35.43
4	0.48	16.71	3.01	9.07	31.20
5	0	2.62	27.65	12.64	48.08
6	1.01	4.63	1.52	34.12	42.68
Average + SE	0.25 ± 0.19	7.89 ± 2.34	8.37 ± 4.36	26.39 ± 6.74	47.43 ± 7.01

Appendix 2: AIC values listed from lowest to highest. Test 1-5 (frequency of whether a lizard (test 1), a bank vole (test 2), a wood lemming (test 3), a *Microtus* vole (test 4), a bird (test 5) or not (frequency) was delivered at the nest):

Test	Order	AIC	Model	Variables
1	1	96.403	11	2
1	2	98.711	10	2
1	3	97.875	9	3
1	4	99.984	12	1
1	5	100.696	7	1
1	6	101.098	6	1
1	7	100.315	5	2
1	8	100.492	4	2
1	9	102.352	8	1
1	10	103.071	3	2
1	11	101.121	1	3
1	12	101.924	2	3
2	1	157.120	7	1
2	2	157.830	8	1
2	3	156.040	2	3
2	4	158.130	6	1
2	5	158.230	12	1
2	6	157.510	3	2
2	7	157.700	4	2
2	8	158.530	5	2

2	9	159.160	10	2
2	10	159.910	11	2
2	11	157.240	1	3
2	12	159.070	9	3
3	1	190.070	7	1
3	2	190.540	12	1
3	3	191.230	8	1
3	4	190.890	10	2
3	5	191.010	4	2
3	6	193.310	6	1
3	7	191.580	3	2
3	8	192.070	5	2
3	9	192.310	11	2
3	10	192.160	2	3
3	11	192.530	9	3
3	12	194.090	1	3
4	1	321.280	8	1
4	2	322.300	7 and 12	1
4	3	322.310	6	1
4	4	322.290	3	2
4	5	323.160	4	2
4	6	323.210	10	2
4	7	324.240	11	2
4	8	324.300	5	2
4	9	323.910	2	3
4	10	324.690	9	3
4	11	325.900	1	3
5	1	52.943	6	1
5	2	54.587	3	2
5	3	54.863	5	2
5	4	56.078	8	1
5	5	56.136	7	1
5	6	56.186	12	1
5	7	54.770	11	2
5	8	58.044	4	2
5	9	58.049	10	2
5	10	56.299	9	3

5	11	56.434	2	3
5	12	58.401	1	3