Functional response of the Eurasian kestrel (*Falco tinnunculus*) in a season with low vole abundance

Funksjonell respons hos tårnfalk (*Falco tinnunculus*) i en sesong med lav bestand av smågnagere

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Preface

I would like to thank Bjørn E. Foyn and Ole Petter Blestad for letting us use their nest boxes in my thesis, as the study in Trysil would not be possible without their cooperation and help.

I would also give a special thanks to my supervisor Geir A. Sonerud for patiently helping and supervising me through the entire process of writing this thesis, as well as helping me in the field. I would also like to thank supervisor Ronny Steen for great support and company after and during the field work, as well as technical support with the video monitoring equipment. I would also like to thank Vidar Selås for helping identifying prey species.

I would also like to thank Anette Nodeland for cooperation and good company during the field work, as well as Catrine Torjussen for helping collect data.

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Abstract

Understanding a predator’s functional response is an important step in understanding the effect predators have on prey populations. To investigate this five breeding pairs of the Eurasian kestrels (*Falco tinnunculus*) had their nest monitored with motion detection camera and the recordings of prey delivery were used to estimate their diet. The relative abundance of prey was estimated with the use of snap trapping around each nest. The results showed that in a year with low vole abundance the kestrel had a functional response to shrews (Soricidae), with bank voles (*Myodes glareolus*), birds, common lizard (*Zootoca vivipara*) and *Microtus* voles as an alternative prey to shrews. My results suggest that shrews are the preferred prey for the kestrel in a season with low vole abundance. The profitability of voles and shrews seems similar and my results indicate that kestrels focus more in shrews when vole abundance is low. Short term changes in the environment were obtained and related to prey selection. The activity pattern of ectothermic reptiles, such as lizards, is dependent on weather conditions. By model testing and selection I found that the probability that a prey item delivered at a kestrel nest was a lizard increased towards midday and increased with ambient temperature. The probability that a prey delivered at the nest being a bird was best explained by time, and the probability increased later in the day. This may be due to a change in the activity pattern of the prey or a change of focus by the kestrel. The probability that a prey delivered was a *Microtus*-vole was best explained by precipitation, this could be due to of the habitat use of this vole and the negative effect water could have on hunt- and flight ability. The probability that a prey delivered was a bank vole was best explained by temperature, with temperatures having a positive effect. This could be because of the shift in focus away from the primary prey, shrews, which had a higher probability of being delivered at the nest with lower ambient temperature.

Sammendrag

Det å forstå en predators funksjonell respons er et viktig steg i forståelsen av hvilken effekt predatorer har på byttedyrpopulasjoner. For å undersøke dette ble fem hekkende par med tårnfalk (*Falco tinnunculus*) overvåket med kameraer og opptakene ble brukt til å estimere dietten deres. Den relative tettheten av byttedyr ble estimert med fellefangst rundt hvert reier. Resultatene viste at i et år med lav tetthet av smågnagere hadde tårnfalken en funksjonell respons på spissmus (Soricidae), med klatremus (*Myodes glareolus*), fugler, Nordfirfisle (*Zootoca vivipara*) og smågnagere som tilhører *Mictrotus*-slekten som alternativt byttedyr til spissmus. Mine resultater antyder at spissmus er det prefererte byttedyret for tårnfalk når smågnagerpopulasjonen er lav. Lønnsomheten av smågnagere og spissmus ser ut til å være lik for tårnfalk og mine resultater indikerer at tårnfalk fokuserer mer på spissmus i et år med lav bestand av smågnagere. Kortsiktige forandringer i miljøet ble anskaffet og relatert til byttedyrseleksjon. Aktivitetsmønsteret for ektoterme reptiler, som firfisle, er avhengig av værforhold. Med modelltesting og -seleksjon fant jeg at sannsynligheten for at et byttedyr levert på reiret var en firfisle økte nærmere midt på dagen og økte med temperatur. Sannsynligheten for at et byttedyr levert på reiret var en fugl ble best forklart med tid, og sannsynligheten økte senere på dagen. Dette kan være fordi aktiviteten hos byttedyrene forandrer seg igjennom dagen. Sannsynligheten for at et byttedyr levert på reiret var en smågnager i *Microtus*-slekten ble best forklart med mengden nedbør. Dette kan være på grunn av habitatbruken av *Microtus* og den negative effekten vann kan ha på jaktevnen til tårnfalken. Sannsynligheten for at et byttedyr levert på reiret var en klatremus ble best forklart med temperatur, med temperatur som positiv effekt. Dette kan være på grunn av en forandring i fokus bort fra primærbyttedyr, spissmus, som hadde høyere sannsynlighet på å bli levert på reiret ved lavere temperatur.

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Introduction

Understanding functional response and the associated processes are essential for both basic and applied ecology in general. A predator's functional response is how its capture rate is affected by prey abundance (Solomon 1949; Holling 1959), and studying this is an important step in understanding the effects predation has on prey population (Korpimäki & Norrdahl 1991a; Jaksić et al. 1992; Dale et al. 1994; Schenk & Bacher 2002; Millon et al. 2009; Nielsen et al. 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011b). Functional response has been difficult to estimate due to methodological challenges and the complexity of ecosystems, because predators often prey on many species, with complex foraging behaviours which are finely adjusted to maximise energy intake (Sonerud & Steen 2010). Previous studies on functional response in wild predators have often been done either on specialist predators (e.g. Nielsen et al. 2009), or on generalist predators and their relationship to one prey species (Salamolard et al. 2000; Vucetich et al. 2002). I studied a generalist predator, the Eurasian Kestrel (*Falco tinnunculus*), which exploits several prey populations, and investigated further into what response this predator has to changes in prey populations, and tested what effect weather conditions had on the functional response on this predator.

The Eurasian Kestrel, hereafter referred to as the kestrel, is a small raptor with a body mass of approximately 220 g (Village 1990). It is widespread in the Palearctic region and prefers open habitat such as fields, heaths, shrubland and marshland, but also occurs in towns and other human settlements (Cramp et al. 1980). The diet of the kestrel mainly consists of small rodents, especially voles (Cricetidae), but also include shrews (Soricidae), small birds, lizards, snakes, young rabbits, frogs, earthworms, fish, insects and even crabs (e.g. Yalden & Warburton 1979; Korpimäki 1985; Village 1990). The composition of the diet may vary in time and space and reflects the area in which the kestrel lives (Village 1990).

Identifying prey species is difficult when the prey is consumed by the predator at the capture site, and measuring the capture rate of predators in the wild has proven to be very difficult, as it invites plenty of methodological challenges (Sonerud & Steen 2010). Previous studies of the kestrel's diet have been based on evidence of prey captures, such as regurgitated pellets or prey remnants at the nest of the raptor, often in combination with direct observations from a hide. These methods often give coarse and error-prone estimations of delivery rates (Village

1990; Korpimëki & Norrdahl 1991a; Jaksić et al. 1992; Redpath & Thirsgood 1999; Salamolard et al. 2000; Redpath et al. 2001; Millon et al. 2009). For instance; analysing pellets often overestimates small and medium prey (Oro & Tella 1995; Homme 2008) and analysis of prey remains tend to overestimate larger prey (Marchesi 2002; Homme 2008). Recording prey capture by video give a more accurate way to assess the delivery rate and gives more factual information (Lewis et al. 2004; Steen 2009; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b; 2012).

The kestrel is ideal for studying functional response by use of video recording for several reasons. 1) The kestrel is a single-prey loader; carrying a single prey item at the time from the capture site to the nest (Sonerud 1985; 1992). 2) The kestrel has a wide diet, and will take anything it is able to kill (Village 1990; Cramp & Simmons 1980; Korpimäki & Norrdahl 1991a; Sonerud & Steen 2010; Steen et al. 2010; 2011a; 2011b; 2012). It is able to shift between prey species, which allows it to continue to live in one area it would otherwise leave. 3) The kestrel often uses artificial nest boxes (Cramp et al. 1980; Village 1990; Steen et al. 2010; 2011a; 2011b), so installation of video camera and locating the nest is relatively easy. 4) The kestrel is a common raptor and tolerant towards human disturbance (Cramp et al. 1980; Village 1990; Steen et al. 2010; 2011a; 2011b), which allows installing of video camera, banding the chicks and even change the nest box if necessary, without any indications of the kestrel being aggressive or stressed.

The response to differences in prey density may vary among different predator species. The predator might respond numerically, by fluctuations in natality, mortality, immigration and emigration, or it may respond functionally, by changing individual predation rate (Solomon 1949, Holling 1959). To be able to shift to alternative prey in time periods when the main prey is scarce is an advantage in a changing environment. The kestrel is able to respond both numerically and functionally to the fluctuation in prey density (Korpimäki & Norrdahl 1991a).

The aims of my study were to 1) investigate the composition of the diet of the kestrel in a season with low vole abundance, 2) see if the kestrel demonstrated any functional response to any other species which are considered alternative prey, 3) investigate if weather conditions has any effect on the functional response on this predator.

Methods

The study area

The study was conducted in the boreal zone in Trysil municipality in Hedmark County in southeast Norway (61° 12´ - 61° 15´ N; 12° 58´ - 12° 62´ E) during June and July 2012. The forest, which is heavily influenced by forestry, is almost exclusively coniferous forest, primary Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The forestry is based on modern forestry techniques such as un-selective clear cutting of the old forest and regeneration by planting and selective cutting, making the landscape into a variety of tree stands of all ages. The area is interspersed with bogs, and contains only small areas of farmland.

Video monitoring

Five nest boxes with breeding Kestrels were selected for this study, located at Vangen (nest ID 1), Seljefallet (nest ID 2), Gjeddetjønna (nest ID 3), Abbortjønnkoia (nest ID 4) and Bærmyrkoia (nest ID 5). The kestrel's nests were monitored by a motion detection video camera and all deliveries of prey were recorded. The camera was placed in the back, near the sealing of the ceiling; with the lens on the camera pointed towards the opening of the nest box so the arrival of the kestrel with prey was recorded. Via video cable to the base of the tree, the camera was connected to a mini DVR digital video recorder powered by a car battery, and data was collected on SD cards (for further details see Steen 2009). Identification of the prey was done later in the laboratory by watching all the films with the use of projector.

The identified prey was later assigned to five different groups for use in the statistical analysis; common lizard (*Zootoca vivipara*), birds, *Microtus* voles (field vole, *Microtus agrestis* and root vole, *Microtus oeconomus*, pooled), bank vole (*Myodes glareolus*), shrew (Soricidae) and other (containing insects, slow worm (*Anguis fragilis),* frog (*Rana ssp*.) and common toad (*Buflo buflo*)). Some of the prey items were not possible to identify to prey type due to lack of visual information on the video, e. g. the prey items had been handled prior to delivery and delivered in parts, the kestrel hid the prey item from camera view, or the nestlings blocked the camera view. To get an accurate estimate as possible, these prey items were distributed among the possible prey groups in proportion to the distribution of identified prey items for each nest.

The delivery rate for each prey group at each nest was calculated as the number of prey items delivered per hour. As the kestrel do not hunt at night, the daily period of foraging was set to 20.5 hours, based on estimates done at previous studies at the same area (Sonerud and Steen 2010).

Estimation on prey abundance

In order to investigate the functional response in kestrels, an estimate of prey density has to be obtained. To measure the actual abundance of each prey species is an impossible task (Village 1990), so the relative abundance of each small mammal was measured by the use of snap trapping. To estimate the relative prey abundance snap traps were placed in the area surrounding the five monitored kestrel nests. In each four cardinal directions 30 traps were put out at 10 m interval from the nest making a total of 120 snap traps surrounding each nest. The traps were set up for two consecutive days and nights giving a maximum total of 240 trap nights. A trapping index was calculated for each group of small mammals as a number of individuals trapped per 100 trap nights. Some species are easier to trap than others (Village 1990) and may compromise the effectiveness of the method. However it is a helpful tool in interspecific comparisons between sites and detecting fluctuations in small mammal populations (Hörnfeldt et al. 2006; Homme 2008)

Weather conditions

A web portal (eKlima 2013) provided free access to the climate database of the Norwegian Meteorological Institute, which contains data from past weather conditions. The data were obtained from “Trysil Vegstasjon” official meteorological station situated central in our study area (61°29’N, 12°27’E, at 360 m elevation), were the database contained temperature, wind speed at 10 m above ground, and precipitation every hour of the day. Each delivery of prey item recorded on the video was linked to the respective temperature and wind speed at the time of delivery, as well as the precipitation the last hour before delivery of a prey item. The mean temperature during a prey delivery was 15.15 ± 0.13°C with a minimum and maximum of 5.1°C and 23.7°C, respectively. The mean wind speed was 2.6 ± 0.1 ms^{-1}, with a minimum and maximum of 0.2 and 6.5 ms^{-1}, respectively. The 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 0 and 4.0 mm.

Statistical analysis

Statistical analysis was performed with the software JMP® Pro 10.0.0 and the software R Development Core 2013 2.15.2. Linear regression was done in JMP. Relations between prey data from video monitoring and the snap-trapping results were investigated using Spearman's rank-order correlation test. For model fitting a generalized linear mixed model (lmer) was used in the lme4 package in R (i.e. logistic regression, binomial distribution). I tested if environmental factors affected the type of prey being delivered at the nest. The probability of a prey item being a lizard, bird, *Microtus*, bank vole or a shrew was used as response variable and temperature, rainfall, wind speed and time of the day as explanatory variables (Table 1). Nest ID and nestling age classes were included as a random effects (Pinheiro and Bates 2000; Steen et al. 2012) to control for individual differences in the breeding pairs and for the differences in delivery rate each due to nestling age, respectively. Among all models tested, the model with the lowest AIC-value together with the lowest number of variables (Burnham and Anderson 1998) was selected. Models with AIC-values lower than 2.0 from the best fitted model were considered competing models (Burnham 2002).

Table 1: The different combinations of environmental factors that were used to find the model that best explained whether a prey item delivered at the nest was a lizard, bird, *Microtus* vole, bank vole or shrew.

Model number	Model
1	Temperature + Precipitation + Wind speed + Time + Time^2
2	Temperature + Precipitation + Wind speed
3	Temperature + Precipitation + Time + Time^2
4	Temperature + Wind speed + Time + Time^2
5	Precipitation + Wind speed + Time + Time^2
6	Temperature + Precipitation
7	Temperature + Wind speed
8	Precipitation + Wind speed
9	Temperature + Time + Time^2
10	Precipitation + Time + Time^2
11	Wind speed + Time + Time^2
12	Temperature
13	Precipitation
14	Wind speed
15	Time + Time^2

Results

Prey items delivered at the nest

A total of 443 prey items was recorded through 868 hours of video monitoring at the five nest boxes. The prey types being delivered most often were common lizards, birds, common shrews, field voles and bank voles (Table 2 and 3). The average rate of delivery per nest was 0.59 ± 0.2 prey items per hour (Table 3).

Table 2. Prey delivered at the five kestrel nests as recorded by the video monitoring. For nest ID, see Methods.

Prey type	1	2	3	4	5	Total
Insect	2	0	0	0	0	2
Common lizard *Zootoca vivipara*	2	52	7	73	5	141
Slow worm *Anguis fragilis*	0	0	0	2	0	2
Frog *Rana ssp*.	0	1	0	1	0	2
Common toad *Bufo bufo*	1	0	0	0	0	1
Bird	5	31	24	42	7	108
Common shrew *Sorex araneus*	22	19	11	25	1	78
Eurasian water shrew *Neomys fodiens*	1	0	0	0	0	1
Field vole *Microtus agrestis*	4	7	4	26	4	45
Microtus vole indet	0	0	0	1	0	1
Bank vole *Myodes glareolus*	2	11	7	22	3	45
Vole indet	1	1	1	3	0	6
Mammal indet	2	1	0	1	0	4
Mammal or small passerine	0	0	1	0	0	1
Prey indet	1	4	0	1	0	6
Sum	43	127	55	197	20	443

Table 3: Prey delivery rates at the kestrel nest (items per hour). For nest ID see Methods.

Nest	1	2	3	4	5	Average ± SE
Shrew	0.253	0.084	0.082	0.136	0.024	0.12 ± 0.04
Bank Vole	0.037	0.051	0.057	0.127	0.073	0.12 ± 0.04
Field Vole	0.086	0.033	0.033	0.156	0.097	0.07 ± 0.02
Bird	0.054	0.133	0.179	0.226	0.171	0.15 ± 0.03
Lizard	0.021	0.224	0.051	0.392	0.122	0.16 ± 0.07
Other prey	0.032	0.004	0.000	0.016	0.000	0.01 ± 0.01
Sum	0.450	0.529	0.400	1.053	0.490	0.59 ± 0.12

The functional response to the abundance of small mammals

The relative abundance of small mammals in each kestrel territory was estimated with snap traps. The population of shrews and bank voles was at a medium level. The population of field voles was low, as the field vole was only captured at one site (Table 4).

Table 4: Trapping indices of small mammals (animals trapped per 100 trap nights) at each kestrel nest. For nest ID see Methods.

Nest	1	2	3	4	5	Average + SE
Shrew	2.62	1.34	1.38	0.00	1.33	1.33 ± 0.41
Bank Vole	0.43	2.69	1.84	1.26	0.88	1.42 ± 0.39
Field Vole	0.43	0.00	0.00	0.00	0.00	0.09 ± 0.09

There was no correlation towards an increase in delivery rate of *Microtus* vole with an increasing abundance of *Microtus* vole ($r_s = 0.00$, $p = 0.96$) (Fig 1c), nor of bank vole with increasing abundance of bank vole ($r_s = 0.10$, $p = 0.98$) (Fig 1b). The delivery rate of shrews increased with the abundance of shrews, but the relationship was far from significant ($r_s = 0.30$, $p = 0.43$) (Fig 1a).

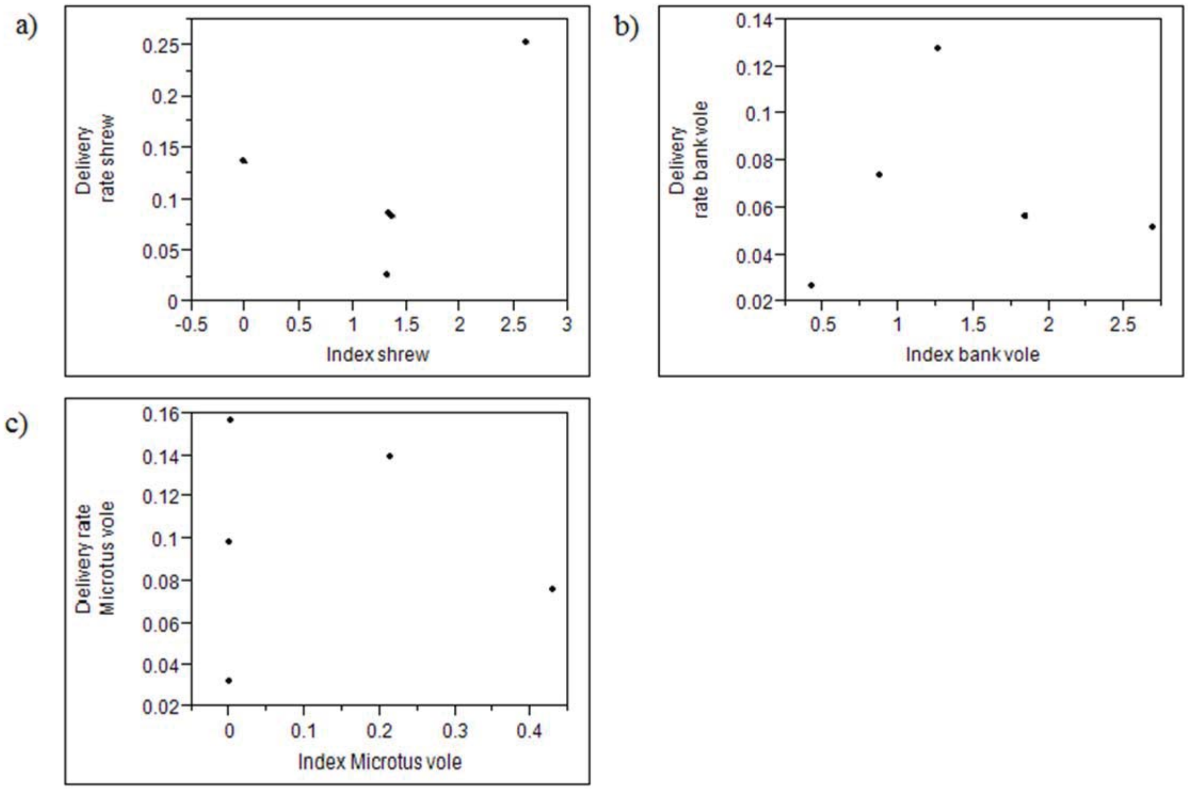

Fig 1: Relationship between delivery rate (items per hour) and the trapping index of the same prey type for each kestrel nest, with a) common shrew (*Sorex araneus*), b) bank vole (*Myodes glareolus*) and c) *Microtus* vole.

The delivery rates of bank vole, field vole, lizard and birds were, however, negatively correlated with the trapping index of shrews, showing that these prey types was less likely to be delivered at the nest with the increasing abundance of shrews (Fig 2). The relationship was significant for bank vole (r_s = -0.90, p = 0.012), lizard (r_s = -0.90, p = 0.047) and birds (r_s = -0.70, p=0.018), but not for *Microtus* voles (r_s = -0.70, p = 0.32).

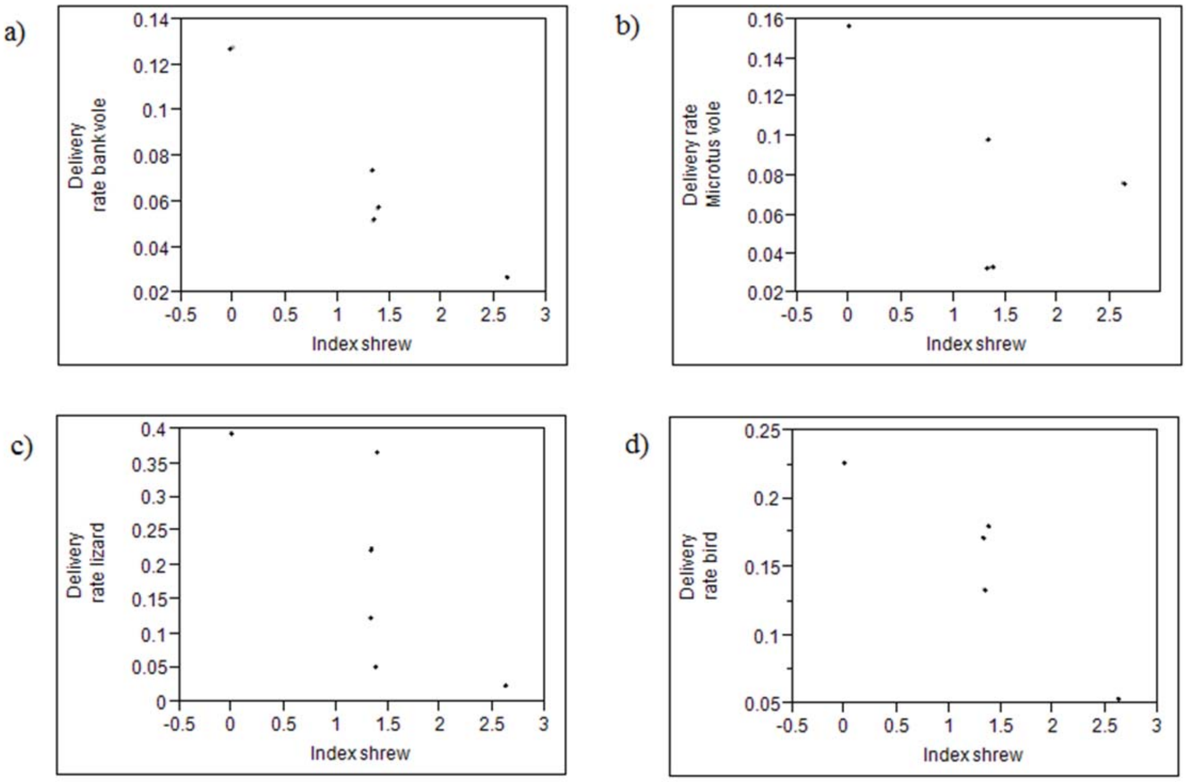

Fig 2: Relationship between delivery rate for a) bank vole (*Myodes glareolus*), b) *Microtus* voles, c) common lizard (*Zootoca vivipara*) and d) birds and the trapping index of shrew (*Sorex araneus*) for each kestrel nest.

Environmental factors affecting the probability of prey type delivered

The probability of a prey item delivered at the nest being a lizard (lizard vs. other prey) was best explained by model 9, which included ambiant temperature at the time of delivery and the time of the day (Table 5a). The delivery rate of lizards increased with increasing ambient temperature and was highest at noon (Figure 3). There were two competing models which included rainfall the last hour and wind speed, respectively, but the effect of these variables were not significant (Table 5a).

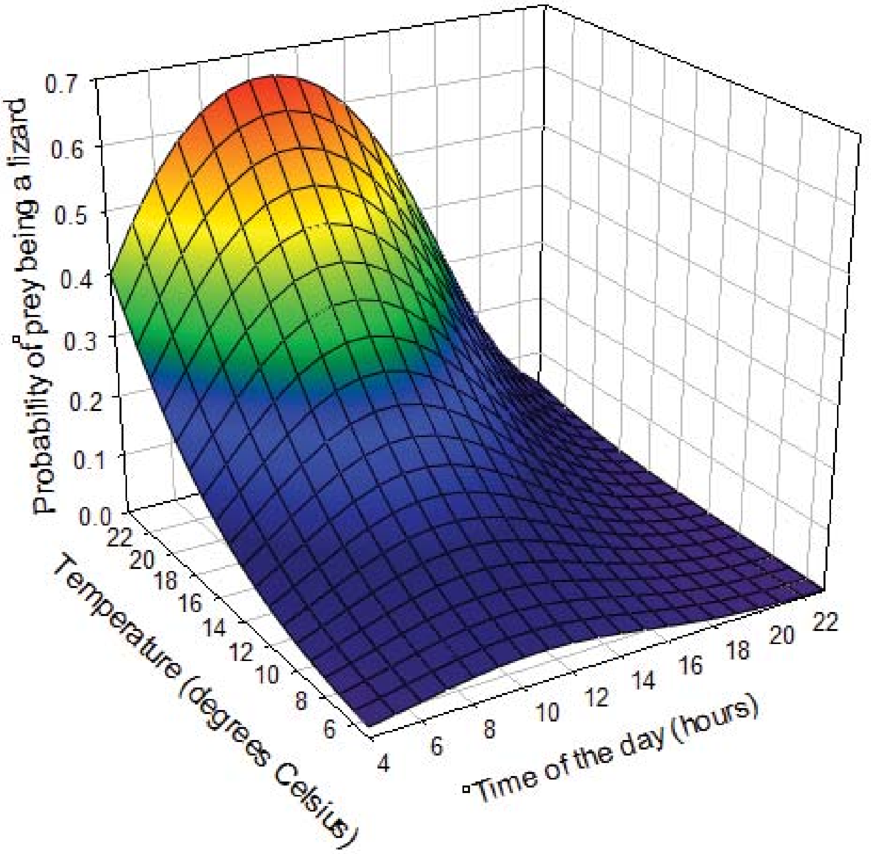

Figure 3: The probability of a prey item delivered at a kestrel nest being a lizard (*Zootoca vivipara*) as a function of hour of the day and ambient temperature at delivery.

The probability of a prey item being a bird (bird vs. other prey) was best explained by model 15 which included time of the day (Table 5b), where the delivery rate increased with time of the day (Figure 4), but the effect was not significant (Appendix 2). There were two competing models which included temperature and the other rainfall (Table 4b).

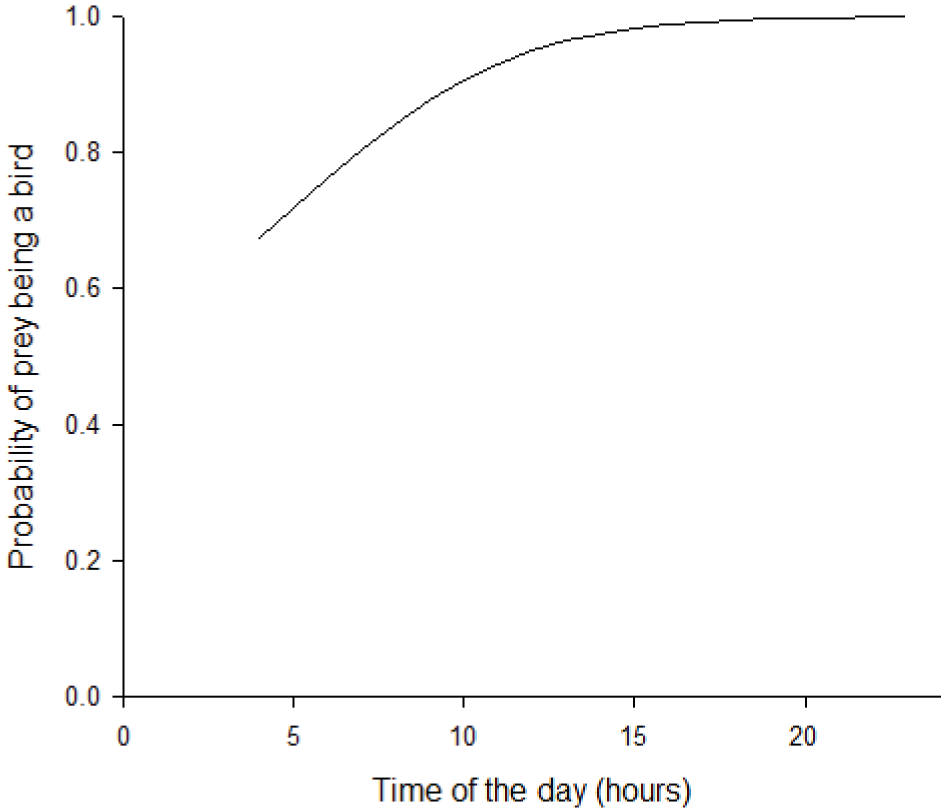

Figure 4: The probability of a prey item delivered at a kestrel nest being a bird as a function of hour of the day at delivery.

The probability of a prey item being a *Microtus* vole (*Microtus* vole vs. other prey) was best explained by model number 13 including rainfall the last hour before delivery at the nest (Table 5c), but the effect was not significant (Appendix 3) The delivery rate decreased with amount of rainfall (Figure 5). There were two competing models which had temperature and wind speed as the only explanatory variable (Table 5c)

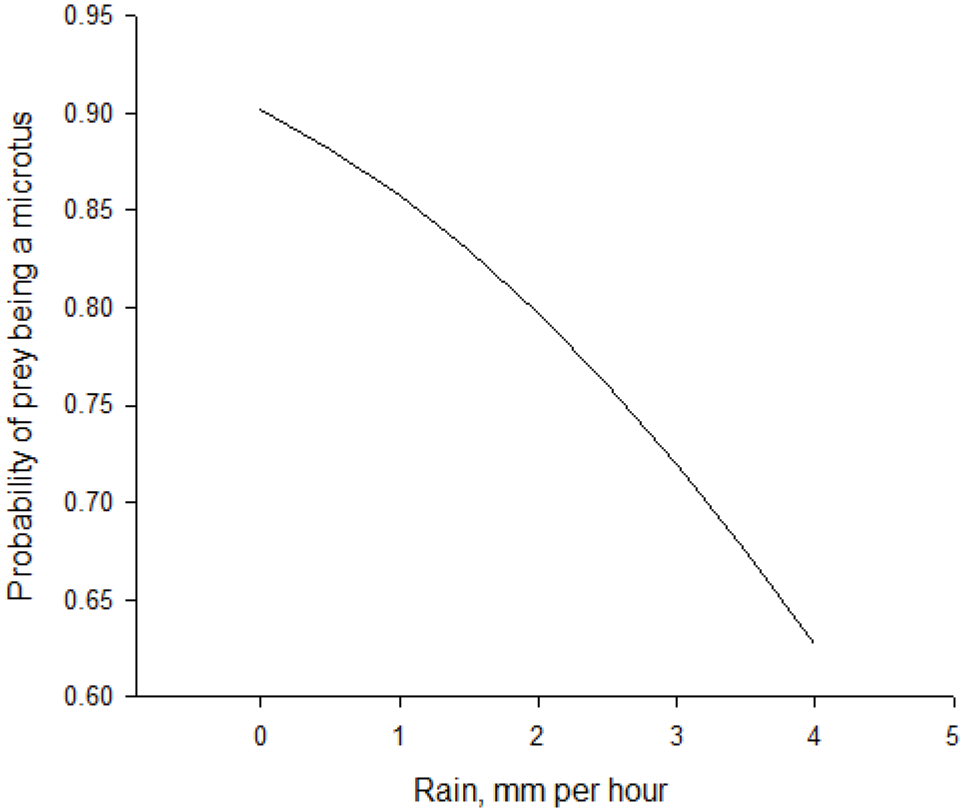

Figure 5: The probability of a prey item delivered at a kestrel nest being a *Microtus* vole as a function of rainfall the last hour before delivery.

The probability of a prey item being a bank vole (*Myodes glareolus*) (bank vole vs. other prey) was best explained by model 12 including ambient temperature at the time of delivery (Table 5 d), but the effect was not significant (Appendix 4). The delivery rate increased with increasing temperatures (Figure 6). The second best model had a lower AIC (ΔAIC -1.0), but one additional variable, rainfall (Table 5d). To be a better fitted model with one additional variable, ΔAIC number would have to be - 2.0.

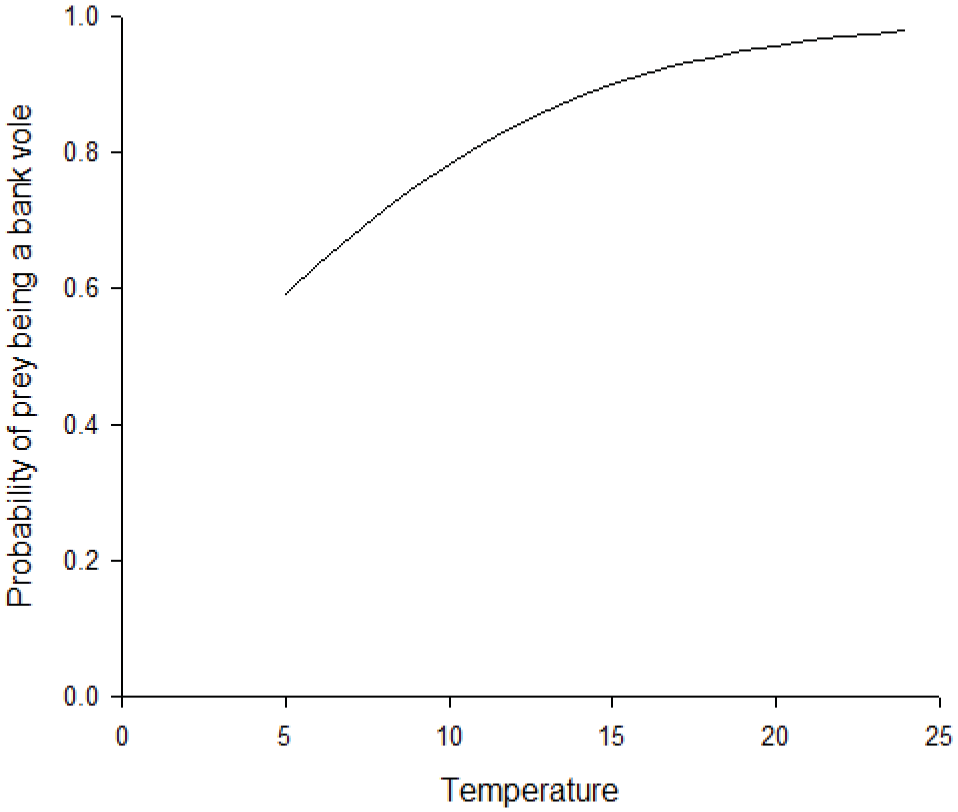

Figure 6: The probability of a prey item delivered at a kestrel nest being a bank vole (*Myodes glareolus*) as a function of ambient temperature at the time of delivery.

The probability of a prey item delivered being a shrew (*Sorex* ssp.) (Shrew vs. other prey) was best explained by model 12, where the ambient temperature was the explanatory factor (Table 5e), but the effect was not significant. The delivery rate decreased with increasing temperature (Figure 7). There were no competing models (Table 5e).

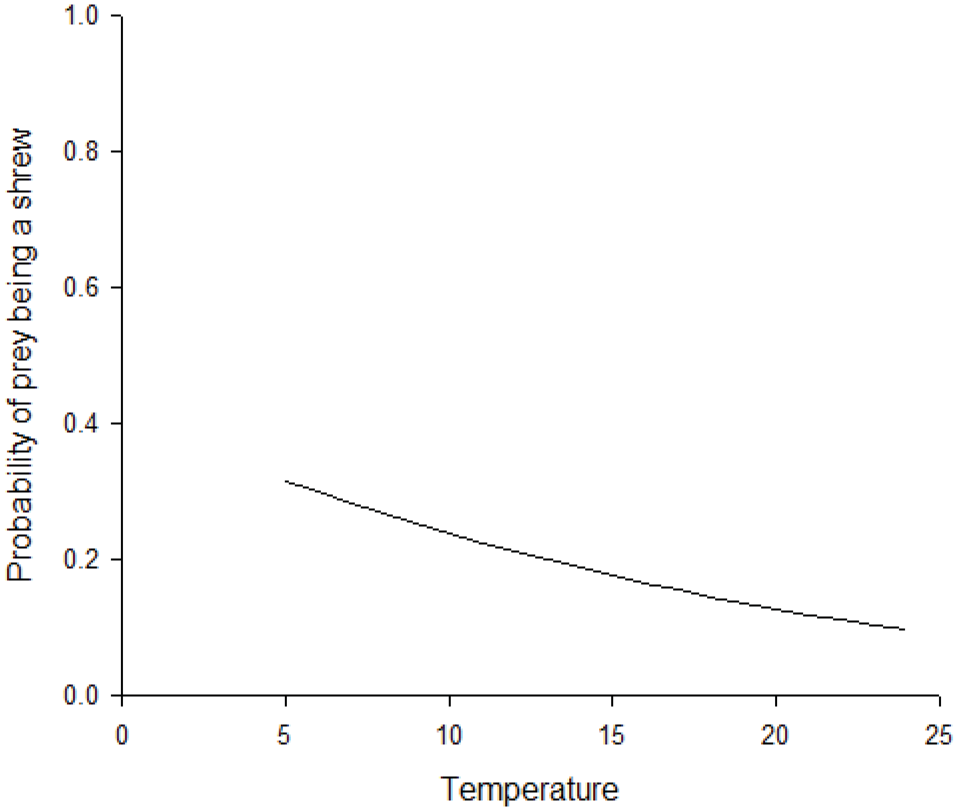

Figure 7: The probability of a prey item being delivered at a kestrel nest being a shrew (*Sorex* ssp.) as a function of ambient temperature at the time of delivery.

Table 5. Model selection with the probability of a prey item delivered being a a) lizard (*Zootoca vivipara*), b) bird, c) *Microtus* vole, d) bank vole (*Myodes glareolus*) or e) shrew (*Sorex* ssp.) as response variable, and temperature, rainfall, wind speed and time of the day as explanatory variables, where x_1 denotes the temperature before delivery, x_2 denotes rainfall the last hour, x_3 denotes wind speed and x_4 denotes the time of the day. ΔAIC is the difference between the best fitted model and a model after adding or removing a variable, thus the model with ΔAIC = 0.00 is the best model. Sample size: n = 442, and random effect: ID = 5 and nestling age class from 5 to 23 days.

Test	Model nr.	Model	AIC	ΔAIC
a)	9	$f(x) = \beta_0 - \beta_1 x_1 - \beta_2 x_4 + \beta_3 x_4^2$	440.6	0.0
	3	$f(x) = \beta_0 - \beta_1 x_1 + \beta_2 x_2 - \beta_3 x_4 + \beta_4 x_4^2$	441.6	1.0
	4	$f(x) = \beta_0 - \beta_1 x_1 + \beta_2 x_3 - \beta_3 x_4 + \beta_4 x_4^2$	442.6	2.0
b)	15	$f(x) = \beta_0 + \beta_1 x_4 - \beta_2 x_4^2$	469.2	0.0
	9	$f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_4 - \beta_3 x_4^2$	469.4	0.2
	10	$f(x) = \beta_0 + \beta_1 x_2 + \beta_2 x_4 - \beta_3 x_4^2$	469.4	0.4
c)	13	$f(x) = \beta_0 - \beta_1 x_2$	289.1	0.0
	12	$f(x) = \beta_0 + \beta_1 x_1$	289.8	0.7
	14	$f(x) = \beta_0 + \beta_1 x_3$	290.4	1.3
d)	12	$f(x) = - \beta_0 + \beta_1 x_1$	284.9	0.0
	6	$f(x) = - \beta_0 + \beta_1 x_1 - \beta_2 x_2$	283.9	-1.0
	7	$f(x) = - \beta_0 + \beta_1 x_1 - \beta_1 x_3$	286.8	1.9
e)	12	$f(x) = - \beta_0 - \beta_1 x_1$	392.8	0.0
	14	$f(x) = - \beta_0 - \beta_1 x_3$	395.4	2.6
	13	$f(x) = - \beta_0 - \beta_1 x_2$	395.8	3.0

Discussion

Functional response

From the 443 filmed deliveries at the nest, common lizard was the most abundant by number, followed by birds, shrews and voles. There were also a few insects, frogs, slow worms, and one toad. This combination of prey types corresponds to other estimates of the diet of the Eurasian Kestrel in northern Europe in seasons with low abundance of *Microtus* voles and bank voles (Korpimäki 1985a; Village 1990; Korpimäki & Norrdahl 1991a; 1991b; Sonerud & Steen 2010; Steen et al. 2011b; 2012). Previous studies have found that the diet varies considerably between years, and that the proportion of voles found in the diet of kestrels strongly reflect the abundance of voles in the area (Korpimäki 1986; Village 1990; Korpimäki & Norrdahl 1991a; Sonerud & Steen 2010; Steen et al. 2011b; 2012), suggesting a functional response to voles. Several studies have also indicated that alternative prey such as lizards, birds and shrews are delivered more frequently as the abundance of voles decreases (Korpimäki & Norrdahl 1991a; 1991b; Sonerud & Steen 2010; Steen et al. 2011b; 2012).

The food availability for kestrels varies between years because the abundance of each prey type changes from year to year (Sonerud 1986; 1988; Bondrup-Nielsen & Ims 1988; Korpimäki & Norrdahl 1991 a; 1991b; Sonerud 1992; Korpimäki & Wiehn 1998). In my study the relative abundance of small mammals was measured by the use of snap trapping around the kestrel nests. According to Village (1990), this method may not reflect the actual abundance, as some species may be easier to trap than others and trappability may vary between seasons, but it will reflect a rough temporal change in prey abundance. The results from my study showed a moderate population of shrews and bank voles and a low population of field voles. In addition they also showed a variation in abundance of small mammas between the nests, suggesting that there would be a difference in delivery rate between kestrel pairs. This is supported by the fact that the delivery rates varied between the nests.

I found no increase in delivery rate of *Microtus* voles or bank voles with an increasing abundance of the same species in the field, which does not correspond to previous studies done in seasons with high vole abundance (Village 1990; Korpimäki 1986; Fargallo et al. 2003; Sonerud & Steen 2010; Steen et al. 2011b; 2012), or the fact that Korpimäki &

Norrdahl (1991a) found the proportion of prey body mass of *Microtus* voles in the kestrel's pellets to reflect the abundance of *Microtus* voles in the field. This difference could be due to the kestrels hunting elsewhere where the trapping was done; however without radio-tracking the kestrels, it is impossible to tell where they hunted. It is reasonable to think that a kestrel uses a larger hunting area with lower prey availability, and thus hunted outside our snap-trapping area. The snap-trapping index may therefore not represent the abundance of small animals where the hunting took place, so much as giving us an indication of the prey population. Supporting this, Village (1982) found a negative correlation between food supply and kestrel home range, suggesting that a trapping index such as recorded in my study may be of more importance in seasons with high vole abundance.

My findings could, however, be due to low sample size (n=5), lacking the statistical power necessary to detect these effects, and give outliers a greater statistical influence. There was, however, an increase in delivery rate of shrews with the trapping index of shrews, and a significant negative correlation between the delivery rate of bank vole, birds and lizards and the trapping index of shrews. This indicates that the kestrel was less likely to deliver a bank vole, bird or lizard at the nest with an increasing density of shrews in the area, suggesting that the kestrel had a functional response to shrews.

To study the functional response of an animal is to reveal how its capture rate is affected by prey abundance (Solomon 1949; Holling 1959), and several studies have been conducted to recognize this effect (Jaksić et al. 1992; Gross et al. 1993; Dale et al. 1994; Korpimäki & Norrdahl 1991a; Millon et al 2009; Sonerud & Steen 2010). Several studies on the kestrel suggest a functional response to *Microtus* voles (Korpimäki 1986; Village 1990; Korpimäki & Norrdahl 1991a; Sonerud & Steen 2010; Steen et al. 2011b; 2012). However in my study voles appeared to be an alternative prey to shrews for the kestrel, as the delivery rate of voles decreased with an increasing abundance of shrews in the area. In years with high abundance of voles, studies have found the kestrel to deliver more voles with increasing vole abundance and alternative prey, such as lizards, birds and shrews to be inversely related to vole abundance. (Korpimäki 1986; Village 1990; Korpimäki & Norrdahl 1991a), indicating voles to be primary prey and lizards, birds and shrews to be alternative prey. My study shows, however, that kestrels captured more shrews with increasing shrew abundance, and that voles, birds and lizards were inversely related to shrew abundance. This is supported by a study done in Scotland, where there was a higher proportion of remnants from shrews found in kestrel’s pellets when the vole abundance was low, even though the relative abundance of shrews was unchanged (Village 1982), as well as a study done in Finland where the shrew population increased with the decline of the vole population, when they experimentally removed birds of prey (Norrdahl & Korpimäki 2000). Another study done in Norway supporting my results, demonstrated a strong positive relationship found between the proportion of shrews in prey remains and their estimated abundance in the field (Homme 2008).

The overall profitability of voles and shrews for kestrels seems to be quite similar (Sonerud & Steen 2010). During our filming, voles was often decapitated or partitioned, before the they were fed to the kestrel nestlings, while shrews were eaten whole and unassisted by the nestlings as soon they were able to, which was at the age of about 14 day. This is supported by a study done by Steen et al. (2011), which found that voles were handled prior to delivery in 52 % of the cases, while shrews were only handled in only 1 % of the cases prior to delivery. The ingestion rate of voles was about 40 % higher than for shrews. If we assume the attack success of voles and shrews are about the same, the overall profitability seems to be quite similar for the kestrel nestlings (Sonerud & Steen 2010). If we assume the profitability of voles and shrews are roughly the same, the kestrel may focus less on voles when shrews are more abundant, thus making shrews the primary prey in seasons of low vole abundance. In support of this, Sonerud & Steen (2010) found the delivery rate of shrews increased with increasing abundance of shrews, and the most parsimonious model of variables explaining the delivery rate of shrews included both vole and shrew abundance, with a negative and positive effect respectively.

In my study, shrews seemed to be the primary prey of the kestrel, as there was a tendency towards an increase in shrew delivery with increasing abundance of shrews, as well as a significant negative effect of shrew abundance on the deliver rate of voles, birds and lizards. Many studies have suggested that voles are the primary prey for the kestrel in years with high vole abundance (Village 1990; Korpimäki 1986; Korpimäki & Norrdahl 1991a; Steen & Sonerud 2010; Steen et al. 2011b; 2012). This may be because of the “load-size effect” (Sonerud 1992 and references therein). When single-loading raptors have young in a nest, they have to decide which prey to consume themselves at the capture site, and which to bring back to the nest. According to foraging models the predator should carry larger prey to the nest and eat smaller prey at the capture site, depending on the distance from the capture site

(Stephens & Krebs 1986). The kestrel has been found to consume smaller prey such as lizards and shrews at the capture site and carry larger prey, such as voles and birds, to the nest (Sonerud 1989). Thus, in years with high vole abundance, video recording at the nest may lead to an overestimation of large prey and underestimation of smaller prey in the kestrel's diet (Sonerud 1992). My results on the delivery rate, however, may better reflect the diet of the kestrel based on the delivery rate, as the vole abundance was low.

Birds appeared to be an alternative prey for the kestrels in my study, because the delivery rate of birds declined with increasing abundance of shrews. This result is supported by another study done in Norway, where the delivery rate of birds, recorded with video camera in the kestrels nest, declined with increasing abundance of voles (Sonerud & Steen 2010). In Finland, a study found that the proportion of remnants of birds found in kestrel's pellets declined with increasing abundance of voles (Korpimëki & Norrdahl 1991a). In both of these studies, unlike my study, the vole abundance was high and the kestrel had a functional response to voles, instead of shrews. As the profitability of shrews and voles are quite similar for the kestrel (Sonerud & Steen 2010; Steen et al. 2011b), it would likely that avian prey still remained an alternative prey, even when the vole abundance is low.

Prey preparation before feeding is an important part of the handling time for the kestrel and it has been found to increase with prey size (Steen 2004). The female usually plucks and feeds avian prey to the nestlings, as well as using time and energy to handle the avian prey before delivering it to the nest (Steen & Sonerud 2010 and references therein). By the use of video monitoring the avian prey were often seen decapitated, parted or plucked when delivered at the nest (Steen 2004, Sonerud et al. 2010). The handling time of shrews, however, are virtually zero; it has been found that only 1 % of the shrews delivered to the nest were decapitated (Homme 2008; Steen & Sonerud 2010) and the nestlings become able to ingest shrews unassisted at about 14 days old (Steen et al. 2012). The attack success of avian prey is lower than of other prey, such as voles or shrews (Village 1990), this together with the handling time makes the overall profitability of avian prey low (Sonerud & Steen 2010), and an alternative prey to shrews. So even though the shrews are smaller in size (9.6 g; Steen 2010), than avian prey (37.8 g; Steen et al. 2010), the kestrel had a functional response to shrews, supporting that shrews have a higher overall profitability for the kestrel, and the kestrel should therefor focus their time and energy on hunting shrews in a year with low vole abundance, and not birds.

Lizards also appeared to be alternative prey to shrews in my study, as the delivery rate of lizards declined with increasing abundance of shrews. Lizards and shrews are similar in the way that both prey types require little handling, and the nestlings can feed on them unassisted (Sonerud & Steen 2010), and the ingestion rate of shrews and lizard as a unit for the nestlings is also similar (5.3 vs. 4.8 g/min; Steen et al. 2011a). Sonerud & Steen (2010) states the kestrel will probably hunt both shrews and lizards indiscriminately, but may focus less on lizards when shrews are abundant, and in years with high abundance of voles lizards appeared to be alternative prey to voles, as the overall profitability of voles is higher compared with lizards.

Model testing with environmental factors

By model selection I was able to test which of the recorded environmental factors had most impact on the delivery rate of the different prey types. I tested for ambient temperature, precipitation, wind speed and time of the day, because all this information was easily accessible. The probability of a prey item delivered at a kestrel nest being a lizard was best explained by hour of the day and ambient temperature at delivery, where the probability of a prey being a lizard increased with increasing ambient temperature and proximity to midday. This agrees with an earlier study done in the same area on 55 kestrel nests over a period of six years, where the probability of lizards being delivered to kestrels was determined by solar height and ambient temperature (Steen et al. 2011a). The lizards need to increase body temperature by external heat to maximize physiological functions, and the activity level is known to vary with hydrological conditions and ambient temperatures (Lorenzon et al. 1999). This function makes lizards more active during high ambient temperatures, either foraging or spending time exposed in the sun, which makes them more vulnerable to predation by kestrels because they may be easier to spot. This fits with my results, where the probability of a prey being a shrew decreased with increasing temperature. The kestrel may switch foraging tactic if lizards become more abundant during warm and sunny days, by focusing more on lizards or restrict their search effort to microhabitats where lizards are more abundant (Steen et al. 2011a). Out of fifteen models on the probability of a lizard being delivered at the nest, two were competing (ΔAIC < 2.0) for the best fit, one included rainfall the last hour and the other included wind speed, but none of these were significant. Many reptiles can absorb sufficient solar heat to raise their body temperature above air temperatures, even on cool days, but this depends on solar radiation and the cooling effect on the wind (Brattstrom 1965). Therefore, with higher wind speed the kestrel may be less likely to deliver a lizard at the nest, because of the low availability of lizards. One may also think that the ambient temperature is connected to the amount of precipitation, because there is lower solar radiation during heavy rainfall and the activity level of the lizards may be affected.

The probability of a prey item delivered at the nest being a *Microtus* vole was best explained by a non-significant effect of precipitation the last hour before delivery, and the delivery rate decreased with amount of rainfall. This could be explained by fact that the habitats of *Microtus* voles are clear-cuts and agricultural fields with predominantly high field vegetation in summer (Sonerud 1986; Korpimäki & Norrdahl 1991b; Sonerud & Steen 2010). With heavy rainfall the kestrel will become wet by attacking the prey in dense, high grass, which in turn may affect flight or hunting ability. To the best of my knowledge there is no published data testing this hypothesis, but in the field I observed the female kestrel spending more time in the nest or in sheltering forest during heavy rain. There were also two competing models which included temperature and wind speed, but one may think these two factors as linked to rainfall.

The probability of a prey delivered at the nest being a bank vole was best explained by a non-significant model which included ambient temperature, with the probability increasing with temperature. This may be because the kestrel was less focused on shrews at high temperatures, suggested by the indication that the kestrel switched hunting tactic during warm periods of the day to hunt lizards. This shift in focus away from the primary prey may have affected the probability that the kestrel captured other prey as well, such as bank voles. To the best of my knowledge there has not been published anything addressing this idea, so I can only speculate, and urge further research on the subject.

The probability of a prey item being delivered at the nest being a bird was best explained by a non-significant model which included time of the day, with higher probability later in the day.

As there is no published study for comparison I can only speculate what this means. It may indicate a shift in focus of the kestrel; the kestrel may have be more focused on prey with high profitability, such as shrews in the beginning of the day, and shifted their focus to lizards around noon. As there is less likely that a lizard would be caught later in the day, the focus of the kestrels may have shifted yet again and perhaps towards birds.

Conclusion

My study was done in a year with low vole abundance, reflected both by the trapping data and the diet of the kestrel. In my study the kestrel showed a functional response to shrews, indicating that the main prey for the kestrel was shrews. Alternative prey were voles, lizards and birds. Voles and shrews seemed to be similar in profitability and the most profitable prey for the kestrel in my study, but because the density of voles was low, it appeared that the kestrel focused more on shrews, which seemed to be more plentiful at the time, and thus had a functional response to shrews. This confirms that kestrels are able to respond functionally in a changing environment, where the prey availability changes between seasons. The kestrels were also able to change their hunting tactic during the day in response in changing availability of prey during a day. This was shown by the significant best-fit model of the delivery of lizards, where the probability increased towards noon and temperature had a positive effect. The probability of a prey item delivered at the nest being a bird was best explained by time, and the probability increased later in the day. This may be because of the activity pattern of the prey and the change of focus for the kestrel. The probability of a prey delivered being a *Microtus*-vole was best explained by precipitation, this could be due to of the habitat use of this vole and the negative effect water could have on hunting ability. The probability of a prey item delivered being a bank vole was best explained by temperature, with temperatures having a positive effect. This could be because of the shift in focus away from the primary prey, shrews, which had a higher probability to being delivered at the nest with lower temperatures. What effects other factors have on functional response on kestrels, such as weather conditions, have to the best of by knowledge rarely been studied, and I urge more research on this issue.

References

Bondrup-Nielsen, S. & Ims, R. A. (1988) Demography during a population crash of the wood lemming, *Myopus schisticolor*. *Canadian Journal of Zoology* 66: 2442-2448

Brattstom, B. H., (1965) Body temperatures of reptiles. *American Midland Naturalist* 73: 376-422

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

Burnham, K. P., Anderson, D. R. (1998) Model selecting and inference:a practical informtion-theoretic approach. Springer, New York

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 western palearctic. Vol. II. Oxford: Oxford University Press.

Dale, B. W., Adams, L. G. & Bowyer, T. (1994) Functional response of wolves preying on barren ground caribu in a multiple-prey ecosystem *Journal of Animal Ecology* 63: 644-652

eKlima (2013) Available at: eklima.met.no (accessed: 25.01.2013)

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. *Evolutionary Ecology Research* 5:549-558

Gross, J. E., Shipley, L. A., Hobbs, N. T., Spalinger, D. E. & Wunder, B. A. (1993) Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology* 74:778-791.

Holling, C. S. (1959) The components of predation as revealed by a study of small-mammal predation on the European pine sawfly. *Canadian Entomologist* 91: 293-320

Homme, G. (2008) Estimating the diet of the Common kestrel (Falco tinnunculus): a comparison between video recording at the nest and traditional analysis of pellets and prey remains. Master thesis. Ås: Norwegian University of Life Sience, Department of Ecology and Natural Resource Management. 34 pp.

Hörnfeldt, B., Christensen, P., Sandström, P., & Ecke, F. (2006) Long-tern decline and local extinction of *Clethrionomys rufocanus* in boreal Sweden. *Landscape Ecology*. 21: 1135-1150

Jaksić, F. M., Jimenz, J. E., Castro, S. A & Feinsinger, P. (1992) Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. *Oecologia* 89: 90-101

Korpimäki, E. (1985a) Diet of the kestrel *Falco tinnunculus* in the breeding season. *Ornis Fennica* 62: 130-137.

Korpimäki, E. (1985b) 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

Korpimäki, E. (1986) Seasonal changes in food of the Tengmalm's owl *Aegolius funerus* in western Finland. *Ann Zool Fenn* 23: 339-344

Korpimäki, E. & Norrdahl, K. (1991a) Numerical and functional response of kestrels, short-eared owls, and long-eared owls of 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. & Wiehn, J. (1998) Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos* 83: 259-272.

Lewis, S. B., Falter, A. R. & Titus, K. (2004) A comparison of 3 methods for assessing raptor diet during the breeding season. *Wildlife Society Bulletin* 32:373-385.

Lorenzon, P., Clobert, J., Oppliger, A., & John-Alder, H. (1999) Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). *Oecologia* 118: 432-430

Marchesi, L., Pedrini, P., & Sergio, F. (2002) Biases associated with diet study methods in the Eurasian Eagle-Owl. *Journal of Raptor Research* 36:11-16

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. *Journal of Animal Ecology* 78: 741-751

Nilsen, E. B., Linnell, J. D. C., Odden, J. & Andersen, R. (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: Eurasian lynx. *Journal of Animal Ecology*. 78: 741-751

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

Oro, O. & Tella, J. L. (1995) A comparison of 2 methods for studying the diet of the Peregrine Falcon. *Journal of Raptor Research* 29: 207-210

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

Redpath, S. M., Thirgood, S. J. (1999) Numerical an functional response in generalist predators: han harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology*. 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

Salamolard, M., B. 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

Schenk, D. & Bacher, S. (2002) Functional response of a generalist predator to one of its prey species in the field. *Jounal of Animal Ecology*. 71: 524-531

Solomon, M. E. (1949) The natural control of animal populations. *Journal of Animal Ecology* 18: 1-35

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

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. *Holarctic Ecology* 9: 33-47

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

Sonerud, G. A. (1992) Functional-response of birds og 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. 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. theses, Agricultural University of Norway, Ås

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., Selås, V. & Slagsvold, T. (2010) The feeding constraint hypothesis: prey preparation as a function of nestling age and prey mass in the Eurasian kestrel. *Animal Behaviour* 80: 147-153

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 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*) *Journal of Ornithology* 153: 1087-1099

Stephens, D. W. & Krebs, J. R. (1986) Foraging theory. Princeton University Press, Princeton. New Jersey, USA

Village, A. (1982) The home range and density of kestrels in relation to vole adundance. *Journal of Animal Ecology* 51: 413-428

Village, A. (1990) The Kestrel. Poyser, London

Vucetich, J. A., Peterson, R. O. & Schaefer, C. L. (2002) The effect of prey and predator densities on wolf predation. *Ecology* 83: 3003-3013

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

Appendix 1

Model testing; which factors best explain whether a prey item delivered at the nest was a lizard. For model selection, see model 5.

Model 1:
AIC: 441.2

	Estimate	Std. Error	t-value	p-value
Intercept	6.65168	1.43252	4.643	0.0001***
Temp	-0.17273	0.07629	-2.264	0.0236 *
Rain	1.01210	1.35258	0.748	0.4543
Wind	0.02640	0.12915	0.204	0.8380
Time	-0.57694	0.28404	-2.031	0.0422 *
Time^2	0.02645	0.01040	2.544	0.0110 *

Model 2:
AIC: 464.5

	Estimate	Std. Error	t-value	p-value
Intercept	4.65467	0.92449	5.035	0.0001 ***
Temp	-0.19443	0.05214	-3.729	0.0002 ***
Rain	1.09152	1.24358	0.878	0.3801
Wind	-0.10754	0.12324	-0.873	0.3829

Model 3:
AIC: 441.6

	Estimate	Std. Error	t-value	p-value
Intercept	6.81477	1.42831	4.771	0.0001 ***
Temp	-0.17984	0.07632	-2.356	0.0185 *
Rain	0.99487	1.32892	0.749	0.4541
Time	-0.58504	0.27949	-2.093	0.0363 *
I(Time^2)	0.02690	0.01023	2.630	0.0085 **

Model 4:
AIC: 442.6

	Estimate	Std. Error	t-value	p-value
Intercept	6.857054	1.425998	4.809	0.0001 ***
Temp	-0.198703	0.073630	-2.699	0.0070 **
Wind	0.003953	0.127752	0.031	0.9753
Time	-0.542996	0.277333	-1.958	0.0502
Time^2	0.025576	0.010205	2.506	0.0122 *

Model 5:
AIC: 447.5

	Estimate	Std. Error	t-value	p-value
Intercept	6.905351	1.459800	4.730	0.0001 ***
Rain	1.723430	1.431085	1.204	0.2280
Wind	0.023371	0.129675	0.180	0.8570
Time	-1.006674	0.230544	-4.367	0.0001 ***
Time^2	0.041080	0.008798	4.669	0.0001 ***

Model 6:
AIC: 463.2

	Estimate	Std. Error	t-value	p-value
Intercept	4.50940	0.90985	4.956	0.0001***
Temp	-0.20047	0.05224	-3.837	0.0001 ***
Rain	1.18091	1.25516	0.941	0.3468

Model 7:
AIC: 463.8

	Estimate	Std. Error	t-value	p-value
Intercept	4.88096	0.90700	5.381	0.0001 ***
Temp	-0.20283	0.05177	-3.918	0.0001 ***
Wind	-0.11972	0.12268	-0.976	0.3290

Model 8:
AIC: 477.5

	Estimate	Std. Error	t-value	p-value
Intercept	1.9146	0.5265	3.636	0.0003 ***
Rain	1.5774	1.2532	1.259	0.2081
Wind	-0.1634	0.1229	-1.330	0.1835

Model 9:
AIC: 440.6

	Estimate	Std. Error	t-value	p-value
Intercept	6.85709	1.42482	4.813	0.0001 ***
Temp	-0.19865	0.07360	-2.699	0.0070 **
Time	-0.54168	0.27357	-1.980	0.0478 *
$Time^2$	0.02552	0.01006	2.538	0.0112 *

Model 10:
AIC: 445.6

	Estimate	Std. Error	t-value	p-value
Intercept	6.906169	1.455673	4.744	0.0001 ***
Rain	1.704808	1.424782	1.197	0.2310
Time	-0.998276	0.225590	-4.425	0.0001 ***
$Time^2$	0.040760	0.008616	4.731	0.0001 ***

Model 11:
AIC: 448.2

	Estimate	Std. Error	t-value	p-value
Intercept	6.939895	1.452101	4.779	0.0001***
Wind	0.007563	0.129639	0.058	0.9530
Time	-0.992531	0.229312	-4.328	0.0001 ***
$Time^2$	0.040708	0.008758	4.648	0.0001 ***

Model 12:
AIC: 462.7

	Estimate	Std. Error	t-value	p-value
Intercept	4.74062	0.89821	5.278	0.0001 ***
Temp	-0.21037	0.05183	-4.059	0.0001 ***

Model 13:
AIC: 477.1

	Estimate	Std. Error	t-value	p-value
Intercept	1.5587	0.4603	3.386	0.0007 ***
Rain	1.7373	1.2547	1.385	0.1662

Model 14:
AIC: 478.3

	Estimate	Std. Error	t-value	p-value
Intercept	2.0739	0.5192	3.994	0.0001 ***
Wind	-0.1862	0.1222	-1.523	0.1280

Model 15:
AIC: 446.2

	Estimate	Std. Error	t-value	p-value
Intercept	6.939406	1.450572	4.784	0.0001 ***
Time	-0.989757	0.224331	-4.412	0.0001 ***
$Time^2$	0.040602	0.008571	4.737	0.0001 ***

Appendix 2

Model testing; which factors best explain whether a prey item delivered at the nest was a bird. For model selection, see model 5.

Model 1:
AIC: 471

	Estimate	Std. Error	t-value	p-value
Intercept	0.568873	1.055704	0.539	0.590
Temp	0.053029	0.061566	0.861	0.389
Rain	0.669502	0.521791	1.283	0.199
Wind	0.008889	0.108580	0.082	0.935
Time	0.048952	0.218821	0.224	0.823
$Time^2$	-0.005010	0.007711	-0.650	0.516

Model 2:
AIC: 478.4

	Estimate	Std. Error	t-value	p-value
Intercept	0.49552	0.74465	0.665	0.506
Temp	0.02512	0.04472	0.562	0.574
Rain	0.54404	0.50051	1.087	0.277
Wind	0.07166	0.10518	0.681	0.496

Model 3:
AIC: 469

	Estimate	Std. Error	t-value	p-value
Intercept	0.571382	1.054551	0.542	0.588
Temp	0.052881	0.061497	0.860	0.390

Rain	0.665270	0.518063	1.284	0.199
Time	0.052653	0.213763	0.246	0.805
Time^2	-0.005151	0.007504	-0.686	0.492

Model 4:
AIC: 471.4

	Estimate	Std. Error	t-value	p-value
Intercept	0.528651	1.043044	0.507	0.612
Temp	0.022430	0.057972	0.387	0.699
Wind	-0.007277	0.107395	-0.068	0.946
Time	0.137078	0.209642	0.654	0.513
Time^2	-0.007934	0.007430	-1.068	0.286

Model 5:
AIC: 471.4

	Estimate	Std. Error	t-value	p-value
Intercept	0.5743894	1.0363271	0.554	0.579
Rain	0.5704834	0.4997725	1.141	0.254
Wind	-0.0005056	0.1084636	-0.005	0.996
Time	0.1714230	0.1617419	1.060	0.289
Time^2	-0.0090946	0.0058506	-1.554	0.120

Model 6:
AIC: 476.9

	Estimate	Std. Error	t-value	p-value
Intercept	0.60758	0.72215	.841	0.400
Temp	0.02925	0.04430	0.660	0.509
Rain	0.52374	0.49089	1.067	0.286

Model 7:
AIC: 478.1

	Estimate	Std. Error	t-value	p-value
Intercept	0.70467	0.72639	0.970	0.332
Temp	0.01533	0.04406	0.348	0.728
Wind	0.06456	0.10455	0.618	0.537

Model 8:
AIC: 478

	Estimate	Std. Error	t-value	p-value
Intercept	0.87278	0.37797	2.309	0.0209 *
Rain	0.51066	0.49409	1.034	0.3014
Wind	0.07175	0.10432	0.688	0.4916

Model 9:
AIC: 469.4

	Estimate	Std. Error	t-value	p-value
Intercept	0.526709	1.042819	0.505	0.614
Temp	0.022428	0.057968	0.387	0.699
Time	0.134320	0.205370	0.654	0.513
Time^2	-0.007827	0.007249	-1.080	0.280

Model 10:
AIC: 469.4

	Estimate	Std. Error	t-value	p-value
Intercept	0.574227	1.035448	0.555	0.579
Rain	0.570713	0.497705	1.147	0.252
Time	0.171231	0.156778	1.092	0.275
Time^2	-0.009087	0.005643	-1.610	0.107

Model 11:
AIC: 471.2

	Estimate	Std. Error	t-value	p-value
Intercept	0.536419	1.033823	0.519	0.6039
Wind	-0.014137	0.107287	-0.132	0.8952
Time	0.188212	0.161215	1.167	0.2430
Time^2	-0.009606	0.005838	-1.646	0.0999

Model 12:
AIC: 476.4

	Estimate	Std. Error	t-value	p-value
Intercept	0.80109	0.70548	1.135	0.256
Temp	0.01923	0.04361	0.441	0.659

Model 13:
AIC: 476.5

	Estimate	Std. Error	t-value	p-value
Intercept	1.0475	0.2771	3.780	0.0002 ***
Rain	0.4848	0.4833	1.003	0.3158

Model 14:
AIC: 477.5

	Estimate	Std. Error	t-value	p-value
Intercept	0.94037	0.37417	2.513	0.012 *
Wind	0.06247	0.10355	0.603	0.546

Model 15:
AIC: 469.2

	Estimate	Std. Error	t-value	p-value
Intercept	0.532191	1.033719	0.515	0.6067
Time	0.182857	0.156398	1.169	0.2423
Time^2	-0.009397	0.005633	-1.668	0.0953

Appendix 3

Model testing; which factors best explain whether a prey item delivered at the nest was a *Microtus*-vole. For model selection, see model 5.

Model 1:

AIC: 295.9

	Estimate	Std. Error	t-value	p-value
Intercept	0.990424	1.384341	0.715	0.474
Temp	-0.020106	0.087526	-0.230	0.818
Rain	-0.478742	0.354794	-1.349	0.177
Wind	-0.032485	0.151504	-0.214	0.830
Time	0.261959	0.291013	0.900	0.368
$Time^2$	-0.009414	0.010363	-0.908	0.364

Model 2:
AIC: 478.4

	Estimate	Std. Error	t-value	p-value
Intercept	1.7752727	1.0897061	0.438	0.661
Rain	-0.3946279	0.3385606	-1.166	0.244
Wind	0.0009449	0.1453476	0.006	0.995

Model 3:
AIC: 293.9

	Estimate	Std. Error	t-value	p-value
Intercept	0.971476	1.382568	0.703	0.482
Temp	-0.018966	0.087241	-0.217	0.828
Rain	-0.472571	0.353665	-1.336	0.181
Time	0.248074	0.283269	0.876	0.381
$Time^2$	-0.008885	0.010031	-0.886	0.376

Model 4:
AIC: 295.4

	Estimate	Std. Error	t-value	p-value
Intercept	1.030119	1.388450	0.742	0.458
Temp	0.013119	0.083520	0.157	0.875
Wind	-0.018143	0.150136	-0.121	0.904
Time	0.169249	0.281678	0.601	0.548
$Time^2$	-0.006357	0.010038	-0.633	0.527

Model 5:
AIC: 294.1

	Estimate	Std. Error	t-value	p-value
Intercept	0.963932	1.382776	0.697	0.486
Rain	-0.453148	0.334707	-1.354	0.176
Wind	-0.033140	0.150765	-0.220	0.826
Time	0.219685	0.219462	1.001	0.317
$Time^2$	-0.007946	0.008006	-0.992	0.321

Model 6:
AIC: 290.7

	Estimate	Std. Error	t-value	p-value
Intercept	1.77706	1.05774	1.680	0.0929
Temp	0.02918	0.06615	0.441	0.6591
Rain	-0.39479	0.33838	-1.167	0.2433

Model 7:
AIC: 291.8

	Estimate	Std. Error	t-value	p-value
Intercept	1.536135	1.057738	1.452	0.146
Temp	0.041433	0.065063	0.637	0.524
Wind	0.005947	0.145452	0.041	0.967

Model 8:
AIC: 291.1

	Estimate	Std. Error	t-value	p-value
Intercept	2.209158	0.528302	4.182	0.0001 ***
Rain	-0.424734	0.331034	-1.283	0.199
Wind	0.003807	0.145492	0.026	0.979

Model 9:
AIC: 293.4

	Estimate	Std. Error	t-value	p-value
Intercept	1.019202	1.385861	0.735	0.462
Temp	0.013492	0.083412	0.162	0.871
Time	0.162272	0.275578	0.589	0.556
Time^2	-0.006090	0.009772	-0.623	0.533

Model 10:
AIC: 292.2

	Estimate	Std. Error	t-value	p-value
Intercept	0.94599	1.38149	0.685	0.493
Rain	-0.44853	0.33415	-1.342	0.179
Time	0.20800	0.21271	0.978	0.328
Time^2	-0.00749	0.00771	-0.972	0.331

Model 11:
AIC: 293.6

	Estimate	Std. Error	t-value	p-value
Intercept	1.044279	1.385157	0.754	0.451
Wind	-0.022181	0.150600	-0.147	0.883
Time	0.198437	0.218033	0.910	0.363
Time^2	-0.007327	0.007944	-0.922	0.356

Model 12:
AIC: 289.8

	Estimate	Std. Error	t-value	p-value
Intercept	1.54672	1.02818	1.504	0.132
Temp	0.04171	0.06470	0.645	0.519

Model 13:
AIC: 289.1

	Estimate	Std. Error	t-value	p-value
Intercept	2.2186	0.3883	5.714	0.0001 ***
Rain	-0.4252	0.3306	-1.286	0.198

Model 14:
AIC: 290.4

	Estimate	Std. Error	t-value	p-value
Intercept	2.13982	0.52771	4.055	0.0001 ***
Wind	0.01251	0.14573	0.086	0.932

Model 15:
AIC: 291.7

	Estimate	Std. Error	t-value	p-value
Intercept	1.031034	1.382763	0.746	0.456
Time	0.190905	0.211725	0.902	0.367
Time^2	-0.007033	0.007665	-0.918	0.359

Appendix 4

Model testing; which factors best explain whether a prey item delivered at the nest was a bank vole. For model selection, see model 5.

Mode 1:
AIC: 289.1

	Estimate	Std. Error	t-value	p-value
Intercept	-0.224385	1.239247	-0.181	0.8563
Temp	0.159241	0.079958	1.992	0.0464 *
Rain	-0.570504	0.322538	-1.769	0.0769
Wind	-0.062790	0.108732	-0.578	0.5636
Time	0.074415	0.265754	0.280	0.7795
Time^2	-0.003548	0.009490	-0.374	0.7085

Model 2:
AIC: 285.7

	Estimate	Std. Error	t-value	p-value
Intercept	-0.09060	0.90726	-0.100	0.92046
Temp	0.16728	0.06041	2.769	0.00562 **
Rain	-0.57271	0.30507	-1.877	0.06048
Wind	-0.05099	0.10653	-0.479	0.63217

Model 3:
AIC: 287.4

	Estimate	Std. Error	t-value	p-value
Intercept	-0.286496	1.235225	-0.232	0.817
Temp	0.162957	0.078936	2.064	0.039 *
Rain	-0.542101	0.317737	-1.706	0.088
Time	0.045939	0.258776	0.178	0.859
Time^2	-0.002485	0.009227	-0.269	0.788

Model 4:
AIC: 289.9

	Estimate	Std. Error	t-value	p-value
Intercept	-0.1574243	1.2368374	-0.127	0.89872
Temp	0.2008923	0.0763595	2.631	0.00852 **
Wind	-0.0355974	0.1027328	-0.346	0.72896
Time	-0.0517048	0.2528741	-0.204	0.83799
Time2	0.0007046	0.0090389	0.078	0.93787

Model 5:
AIC: 295.

	Estimate	Std. Error	t-value	p-value 4
Intercept	0.057168	1.228282	0.046	0.9629
Rain	-0.788366	0.313925	-2.511	0.0120 *
Wind	-0.077824	0.118686	-0.656	0.5120
Time	0.414031	0.201713	2.053	0.0401 *
Time^2	-0.015557	0.007354	-2.115	0.0344 *

Model 6:
AIC: 283.9

	Estimate	Std. Error	t-value	p-value
Intercept	-0.21199	0.87070	-0.244	0.80764
Temp	0.16596	0.06001	2.766	0.00568 **
Rain	-0.55710	0.30247	-1.842	0.06550

Model 7:
AIC: 286.8

	Estimate	Std. Error	t-value	p-value
Intercept	-0.47067	0.86888	-0.542	0.58803
Temp	0.18395	0.05877	3.130	0.00175 **
Wind	-0.03119	0.10136	-0.308	0.75828

Model 8:
AIC: 295.6

	Estimate	Std. Error	t-value	p-value
Intercept	2.31855	0.38419	6.035	0.0001 ***
Rain	-0.74555	0.31498	-2.367	0.0179 *
Wind	-0.02247	0.12074	-0.186	0.8523

Model 9:
AIC: 288

	Estimate	Std. Error	t-value	p-value
Intercept	-0.194606	1.232468	-0.158	0.87454
Temp	0.201617	0.075924	2.656	0.00792 **
Time	-0.063936	0.249311	-0.256	0.79760
Time^2	0.001173	0.008901	0.132	0.89517

Model 10:
AIC: 293.8

	Estimate	Std. Error	t-value	p-value
Intercept	0.005409	1.227272	0.004	0.9965
Rain	-0.764779	0.310425	-2.464	0.0138 *

Time	0.385727	0.196860	1.959	0.0501
Time^2	-0.014472	0.007157	-2.022	0.0432 *

Model 11:
AIC: 299

	Estimate	Std. Error	t-value	p-value
Intercept	0.208522	1.226552	0.170	0.8650
Wind	-0.048490	0.116710	-0.416	0.6778
Time	0.366250	0.198870	1.842	0.0655
Time^2	-0.014027	0.007231	-1.940	0.0524

Model 12:
AIC: 284.9

	Estimate	Std. Error	t-value	p-value
Intercept	-0.54108	0.83893	-0.645	0.51895
Temp	0.18298	0.05848	3.129	0.00175 **

Model 13:
AIC: 293.6

	Estimate	Std. Error	t-value	p-value
Intercept	2.2580	0.2064	10.939	0.0001 ***
Rain	-0.7402	0.3134	-2.362	0.0182 *

Model 14:
AIC: 298.7

	Estimate	Std. Error	t-value	p-value
Intercept	2.1650292	0.3704022	5.845	0.0001 ***
Wind	-0.0003305	0.1188439	-0.003	0.998

Model 15:
AIC: 297.2

	Estimate	Std. Error	t-value	p-value
Intercept	0.169137	1.224175	0.138	0.8901
Time	0.350062	0.194739	1.798	0.0722
Time^2	-0.013404	0.007062	-1.898	0.0577

Appendix 5

Model testing; which factors best explain whether a prey item delivered at the nest was a shrew. For model selection, see model 5.

Model 1:
AIC: 400.4

	Estimate	Std. Error	t-value	p-value
Intercept	-0.376963	1.137820	-0.331	0.740
Temp	-0.080276	0.066389	-1.209	0.227
Rain	-0.117614	0.380138	-0.309	0.757
Wind	-0.062178	0.115635	-0.538	0.591

Time	0.037468	0.228703	0.164	0.870
Time^2	-0.001421	0.008201	-0.173	0.862

Model 2:
AIC: 396.5

	Estimate	Std. Error	t-value	p-value
Intercept	-0.26350	0.85764	-0.307	0.759
Temp	-0.07441	0.05002	-1.488	0.137
Rain	-0.11029	0.36945	-0.298	0.765
Wind	-0.05637	0.11336	-0.497	0.619

Model 3:
AIC: 398.7

	Estimate	Std. Error	t-value	p-value
Intercept	-0.3948397	1.1442846	-0.345	0.730
Temp	-0.0828722	0.0672019	-1.233	0.218
Rain	-0.1169529	0.3758169	-0.311	0.756
Time	0.0169134	0.2264411	0.075	0.940
Time^2	-0.0005915	0.0080956	-0.073	0.942

Model 4:
AIC: 398.5

	Estimate	Std. Error	t-value	p-value
Intercept	-0.3775563	1.1370794	-0.332	0.740
Temp	-0.0742437	0.0639165	-1.162	0.245
Wind	-0.0618150	0.1146111	-0.539	0.590
Time	0.0234175	0.2230360	0.105	0.916
Time^2	-0.0009735	0.0080336	-0.121	0.904

Model 5:
AIC: 400.7

	Estimate	Std. Error	t-value	p-value
Intercept	-0.443108	1.143323	-0.388	0.698
Rain	0.010891	0.365198	0.030	0.976
Wind	-0.060411	0.114762	-0.526	0.599
Time	-0.137056	0.175632	-0.780	0.435
Time^2	0.004558	0.006458	0.706	0.480

Model 6:
AIC: 394.7

	Estimate	Std. Error	t-value	p-value
Intercept	-0.33762	0.85053	-0.397	0.691
Temp	-0.07950	0.05016	-1.585	0.113
Rain	-0.11104	0.36530	-0.304	0.761

Model 7:
AIC: 394.6

	Estimate	Std. Error	t-value	p-value
Intercept	-0.31410	0.84261	-0.373	0.709
Temp	-0.07149	0.04947	-1.445	0.148

Wind	-0.05648	0.11257	-0.502	0.616

Model 8:
AIC: 397.4

	Estimate	Std. Error	t-value	p-value
Intercept	-1.29961	0.48552	-2.677	0.00743 **
Rain	-0.01037	0.36427	-0.028	0.97729
Wind	-0.07972	0.11123	-0.717	0.47355

Model 9:
AIC: 396.8

	Estimate	Std. Error	t-value	p-value
Intercept	0.3937284	1.1434008	-0.344	0.731
Temp	-0.0765983	0.0646685	-1.185	0.236
Time	0.0022197	0.2211220	0.010	0.992
Time^2	-0.0001218	0.0079410	-0.015	0.988

Model 10:
AIC: 398.9

	Estimate	Std. Error	t-value	p-value
Intercept	-0.461788	1.148826	-0.402	0.688
Rain	0.014910	0.360979	0.041	0.967
Time	-0.161781	0.172108	-0.940	0.347
Time^2	0.005522	0.006310	0.875	0.381

Model 11:
AIC: 398.7

	Estimate	Std. Error	t-value	p-value
Intercept	-0.443318	1.143224	-0.388	0.698
Wind	-0.060518	0.114476	-0.529	0.597
Time	-0.136944	0.175375	-0.781	0.435
Time^2	0.004557	0.006454	0.706	0.480

Model 12:
AIC: 392.8

	Estimate	Std. Error	t-value	p-value
Intercept	-0.38957	0.83722	-0.465	0.642
Temp	-0.07651	0.04956	-1.544	0.123

Model 13:
AIC: 395.8

	Estimate	Std. Error	t-value	p-value
Intercept	-1.503506	0.435832	-3.45	0.000561 ***
Rain	-0.003663	0.358288	-0.01	0.991844

Model 14:
AIC: 395.4

	Estimate	Std. Error	t-value	p-value
Intercept	-1.3007	0.4819	-2.699	0.00696 **
Wind	-0.0796	0.1109	-0.718	0.47272

Model 15:
AIC: 396.9

	Estimate	Std. Error	t-value	p-value
Intercept	-0.462337	1.148634	-0.402	0.687
Time	-0.161649	0.171963	-0.940	0.347
$Time^2$	0.005522	0.006308	0.876	0.381