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

Hannens bytteleveringer og hunnens aggresjon hos tårnfalk (Falco tinnunculus)

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Master Thesis 60 credits 2013

Acknowledgements

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

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

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

Anette Nodeland Ås, May 2013

Abstract

I studied the foraging strategy in a generalist raptor, the Eurasian kestrel (*Falco tinnunculus*), in a year with low *Microtus* vole and bank vole (*Myodes glareolus*) populations. This was done by video filming prey delivered at the nest, and by simultaneous observing the prey allocation behavior outside the nest. The most common prey type delivered at the five nests studied was the common lizard (*Zootoca vivipara*), followed by birds, voles (*Microtus* and *Myodes*), and shrews (*Soricidea*). I found that the probability that the kestrel returned with items of the same prey type repeatedly differed between prey types, but also depended on weather conditions. The common lizard was more likely to be delivered repeatedly with higher temperature, shrews were more likely to be delivered repeatedly with lower temperatures. For birds no measure weather variable had an effect, and almost always nestlings or newly fledged young were the avian prey delivered repeatedly. This indicated that the kestrel is a central place forager with a win-stay strategy, concentrating on prey types with high availability at specific climatic conditions. In my study I found that there was an increased chance, though not significant, for aggression with higher wind speed and more rainfall. Surprisingly, I also found that the female was more aggressive the heavier body mass the previous prey had, contrary to my theory that the female will be more aggressive if she is hungry.

Sammendrag

jeg undersøkte hvordan fødesøket hos en rovfugl generalist, tårnfalken (*Falco tinnunculus*) var i et år med liten populasjon av *Microtus* og klatremus (*Myodes glareolus)*. Dette gjorde jeg ved å videofilme byttedyr levert på redet, samtidig som jeg observerte atferden når byttet ble overlevert fra hann til hunn. Det vanligste byttedyret levert på de fem studerte reirene var nordfirfisle (*Zootoca vivipara)*, fulgt av fugl, stumpmus (*Microtus* og *Myodes*) og spissmus (*Soricidea*). Jeg fant ut at sannsynligheten for at tårnfalken vil komme med samme type byttedyr etter hverandre var forskjellig mellom type byttedyr, men også avhengig av været. Det var mer sannsynlig at firfisle ble levert flere ganger etter hverandre hvis det var høy temperatur, og flere spissmus etter hverandre ved lave temperaturer. Fugl så ut til å ikke være påvirket av vær, men da fugl ble levert flere ganger etter hverandre var det som regel reirunger, eller unger som nylig hadde forlatt redet. Dette tyder på at tårnfalken vet hvor den skal finne flere av et gitt byttedyr, og støtter opp om at tårnfalken er en central place forager med en vinn-vent strategi. Den konsentrerer seg om spesielle typer byttedyr som er lette å få tak i, enten på grunn av vær eller tilgjengelighet. Under oppgaven fant jeg ut at det var en økt sjanse, men ikke signifikant, for aggresjon ved økt vindstyrke og mer nedbør. Til min overraskelse fant jeg ut at hunnen var mer aggressiv hvis forrige byttedyr var stort, noe som er motsatt av hva jeg hadde forventet meg. Jeg hadde trodd at hunnen ville være mer hissig hvis hun var sulten, noe hun ville vært hvis forrige byttedyr var lite.

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Introduction

The Eurasian kestrel (*Falco tinnunculus*), from now on called the kestrel, has reversed sexual dimorphism as many other raptors have, meaning that the females are larger and heavier than the male (Mueller, 1990; Andersson, 1994; Massemin et al., 2000; Krüger, 2005). In many raptors with reversed sexual dimorphism, aggression is seen between the sexes when the male returns with a prey (Cramp & Simmons, 1980; Cramp, 1985; Sonerud et al., 2013). There are theories saying that the reason for reversed sexual dimorphism are so the kestrels can exploit different niches, and therefore reduce the competition between male and female (Selander, 1966; Snyder & Wiley, 1976; Newton, 1979), but not all results support this theory (Eldegaard & Sonerud, 2011). Because the female is both larger and heavier, she has an excellent possibility to exploit the male for resources, hence increase her own fitness. One would also expect the larger females to have higher fitness than small ones, but a study by Massemin et al. (2000) showed that smaller females produced more nestlings in a year with few voles. It is believed that the reason and maintenance for reversed sexual dimorphism may be the reproductive roles between the sexes (Slagsvold & Sonerud, 2007; Sonerud et al., 2013). In my study I perceived the larger females to be more bossy and aggressive than the smaller ones, making the male work harder and feeding the female in a larger degree than the young. When feeding the young, the female will eat some, or all, of the prey delivered by the male (Kristiansen, 2003; Brodin et al., 2003). The male should therefore give captured prey directly to his young if he want to maximize his own fitness, instead of wasting prey by delivering and feeding the female (Sonerud et al. 2013). At the same time the male should maximize his foraging time, and therefore deliver prey to the female and leave her to dividing the prey and feed the young. Some females will desert the nest and her young, after being fed by the prey items the male has delivered, either to ensure her own survival (Dawson & Bortolotti, 2002; Eldegaard & Sonerud, 2009; Eldegaard & Sonerud, 2010; Sonerud et al., 2013) or to get a new brood with another male (Kelly & Kennedy, 1993; Eldegaard & Sonerud, 2009). The desertion by the female will not have severe consequences if the young are old enough to eat for themselves (Kristiansen, 2003; Sonerud et al. 2013).

The aggression a female kestrel shows towards the brooding male when he returns from hunting, is seen between many other raptors with reversed sexual dimorphism. Still, the reason for why the female sometimes shows aggression, and sometimes not, is unknown.

The fieldwork triggered my interest for bird behavior and the reasons for aggression between the male and female, hence leading me to formulate the following question: “What causes the aggression between the parents, and is the aggression an alternative fitness strategy, plain dominance or a result of hunger?”
It would also be interesting to see if the foraging behavior was affected in a year with few *microtus* voles and bank voles (*Myodes glareolus*). Will they change their tactics and will the female contribute more in finding food to their young?

During the work on this thesis, several hypothesis appeared, but I ended up with a) larger females show more aggression, b) larger prey lead to more aggression, c) longer time between deliveries lead to more aggression, d) the kestrel will hunt similar prey types with similar climatic conditions, e) some prey types are easier to catch at specific conditions, f) if the last prey item was large, there will be less aggression and g) the kestrel depends on small mammals in a large degree.

Methods

Study area

The fieldwork took place in Trysil, Hedmark county, in south-eastern Norway (61° 12´ - 61° 15´ N; 12° 58´ - 12° 62´ E) during June and July in 2012. Even though the corresponding habitats differed from each other, the five different nest sites were all in the boreal zone, primary containing Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The habitat around nest site 305 and OP20 where quite similar; large clear-cuts with scattered pine trees left as seed trees, and a small lake 1-2 km away. Nest site 079 was on a small hill in the middle of a clear-cut, with denser pruce forest around. Nest site 085 was on the edge of a pine forest towards a bog. Nest site 072 was in the overgrown pine plantation after clear-cutting some years ago, near both a farm and a little stream. All nest sites were in short distances (50-150 m) from small and secluded forest roads.

Study species

With a wing-span on 71-80 cm, and a body mass of males ca. 210 g, the Eurasian Kestrel (*Falco tinnunculus*) is a relatively small raptor, with the female only a little larger than the male (Village, 1990). The kestrels breeding in Norway, and other Nordic countries, are migratory, but longer south they are resident, breeding even in cities (Village, 1990; Forsman, 1999). The kestrel is a generalist predator, with a diet consisting mostly of birds, lizards, rodents, shrews and insects. Kestrels adapt their diet to what is available, and show a functional response to voles (Korpimäki, 1985; Village, 1990). The kestrel is an excellent study species because of its use of artificial nest boxes, toleration towards humans and disturbance, its wide diet, and the fact that it is a single-prey loader (Cramp & Simmons, 1980; Village, 1990; Forsman, 1999)

Data collecting and monitoring

I videotaped prey deliveries at the kestrel nests in order to monitor prey deliveries in a year with low *Microtus* vole and bank vole (*Myodes glareolus*) populations (Zarybnicka et al., 2010; Steen et al., 2011b). A small camera was attached in the top of the nest box, with the lens towards the opening of the nest box. The camera was connected to a DVR digital video recorder placed on the ground at the base of the nest tree. The camera had a motion detector, and started recording a 10 s interval after being triggered. All data was collected and saved on a SD card, and the camera was powered by a car battery (for more information see Steen, 2009). Therefore, I was able to monitor all of the nests even when I was not present.

I also collected data on the aggression part of the female when the male returned with prey, by sitting in a hide and monitoring each nest over several hours and days, varying from early morning to early afternoon. During the same time, the prey deliveries at the nest were recorded on video. The kestrel started the hunting at around 05 hours, and continued hunting until a mean at 21 hours. I had a mean observation period of 3-8 hours a day, where my fellow student (Stine Espe) and I switched place after approximately four hours. I took note of every observed prey delivery at the nest, every handover from the male to the female, and every accompanying noise, in addition to observations on the weather. I put up the hide within a radius on 100-200 m from the nest, and limited the motion and noise around the nest to a minimum, in order to avoid scaring and disturbing the kestrels.

Data

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

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

To estimate the small mammal prey abundance around each nest site, there were placed out 30 snap traps in each of the four cardinal directions (north, south, east and west), with an interval of 10 m. The traps were left out over the two following days, making a total of 240 trap nights per nest. This method is not optimal, because not all small mammal species are equally trappable, but it can be a helpful tool to give an approximate number of individuals per species (Village, 1990). During snap trappings it was confirmed that 2012 was a low year for wood lemming (*Myopus schisticolor*) and *Microtus* voles (for more information on trapping results, see Espe (2013)). Therefore, there were very few breeding attempts by the kestrel in the study area. Contrary to previous years, it took several days before I found enough successful breeding attempts to get sufficient data.

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

Since a large part of this thesis concerns what and where the kestrel hunts, in relation to the weather conditions, all data on the weather variable were collected from the Norwegian Meteorological Institutes web portal (eKlima 2013). Their data were collected by the official meteorological station: “Trysil Vegstasjon”. These data were downloaded by Stine Espe, who later passed them on to me (for more information, see Espe (2013)).

Several happenings caused my data to be reduced. First I caught on tape a marten (*Martes martes*) killing and removing all three nestlings in one of the kestrel nests that I studied (nest OP20). Second, ca. two weeks later I found the closest kestrel nest studied, only 1 km away (nest 305), to be empty. So I suspect that the same marten individual visited that nest as well. Unfortunately the camera was not recording when this happened, and I can therefore not be sure if the marten was the predator or not. Third, the female on nest 079 deserted her nest right after being marked with a radio transmitter, but the male continued caring for the brood even after her desertion.

As for another previous study, one of video filming prey deliveries at kestrel nests in Trysin (Steen & Sonerud, 2012), one of the kestrels that I studied delivered a bank vole with total leucism, meaning that this now has occurred more than twice in Trysil county.

Statistical analysis

All analysis where first run with JMP Pro 10.0.0 in order to see what stood out, and to know which test to run in the statistical software program R 2.15.2 in order to save time, and to get an idea of what our data could tell me. Most of the analyses were simple logistic regression (Y by X), Chi-squared test and Z-test. The analysis on win-stay strategy were all run with nestling age and the nest ID as random effects (Pinheiro & Bates, 2000; Steen at al., 2012). This is done to control for differences between the broods and the breeding pairs. The aggression analysis were all run in JMP, and therefore without random effects.

The analysis run in R were first run in order to find the best model, and thereafter testing this model with the three main prey types. I included all weather conditions and interaction between these as response variables, and then selected the model with the lowest AIC-value and fewest variables as the best model (Burnham & Anderson, 1998). Other models with an AIC-value 0-2.0 lower than the best model were competing models (Burnham, 2002), and further analyzed if necessary.

Results

Prey delivered at the nest

A total of 443 prey items were delivered during video monitoring at the five nests, of which 141 lizards, 3 frogs, 79 shrews, 46 *Microtus* voles, 45 bank voles, 108 birds, 2 slow-worms were identified, while 5 items were categorized as a mammal, 6 items as a vole, and the remaining 8 items were unknown. In 68 cases we were also present and watched the deliveries. Most prey items were taken by the males, and I only registered 3 prey items taken, for sure, by the females (for more information, see Espe (2013)).

Win-stay strategy for the three main prey types pooled

I was interested in testing if the kestrel hunted specific prey items at specific times, depending on time of day, and the weather variables ambient temperature, rainfall and wind speed. Before I ran the tests I sorted the dataset and excluded deliveries of *Microtus* voles, bank vole, unidentified mammals, other (insects, slow worm, frog and toad), female being the hunter, hunter of unknown sex, two NA values on time, NA values on temperature, and NA values on the response referring an item being of the same or different as the last one. I removed female being the hunter because there were only three cases of this, and hunter of unknown sex was removed to ensure that I followed the same individual on the hunting trips. After excluding these two, the datasets on bank vole and *Microtus* voles were too small, and were therefore excluded. I remained with a total of 161 prey items, segregated on 49 birds, 29 shrews, and 83 lizards.

Model 173 had the variables prey type, ambient temperature, and the interaction between these two. Model 246 had the same variables, but also rain, while model 198 had wind instead of rain. I ran all three models, but model 246 had autokorrelation, and was therefore excluded from further analysis (Table 1).

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

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

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

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

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

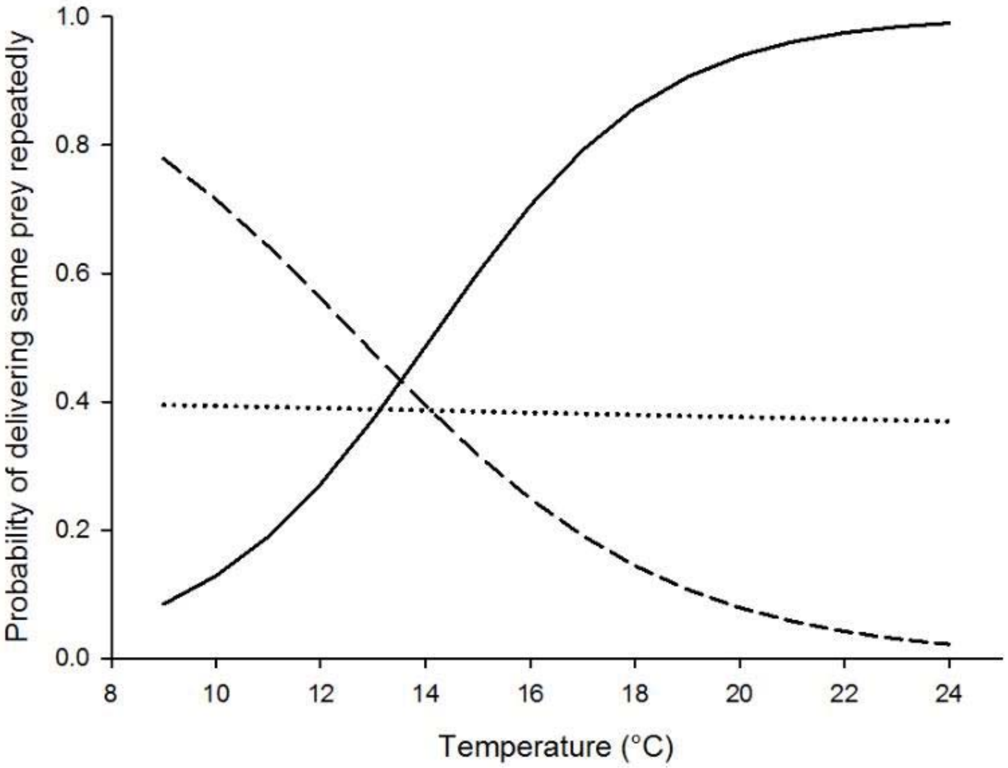

Figure 1. The probability of items of the same prey type being delivered repeatedly to the nest as a function of ambient temperature, for lizard (whole line), shrew (dashed line), and bird (dotted line). Results from model 173.

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

Table 3. Parameter estimates from the best fitted generalized linear mixed-effect model with binominal distribution, corrected for the random effect of nests (N=5), for the probability that a prey item delivered was of the same type as the previous item delivered. Model 173.

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

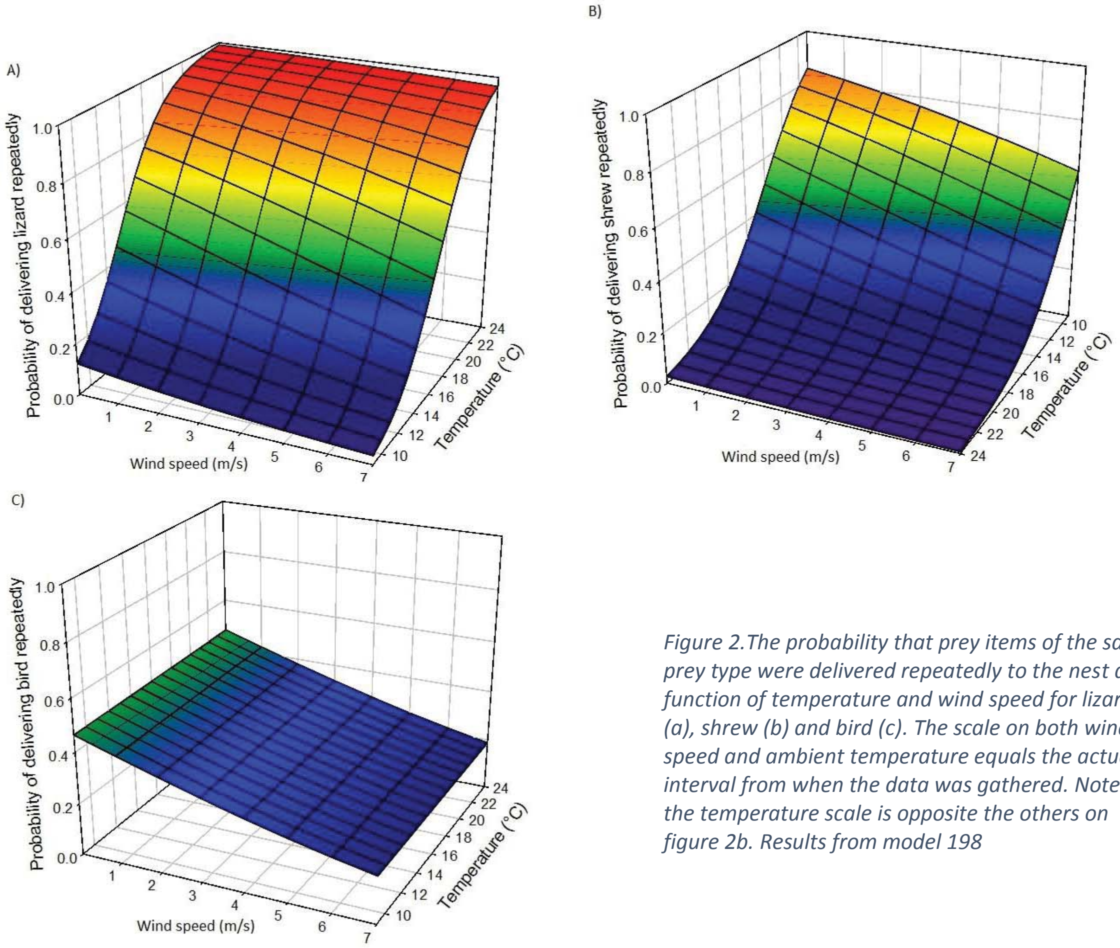

Figure 2.The probability that prey items of the same prey type were delivered repeatedly to the nest as a function of temperature and wind speed for lizard (a), shrew (b) and bird (c). The scale on both wind speed and ambient temperature equals the actual interval from when the data was gathered. Note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

Win-stay strategy for the three main prey types separately

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

Lizard

The three best models all contained ambient temperature, and model 18 and 19 had additionally the variable unknown sex of previous hunter, meaning that the sex of the kestrel delivering the previous prey was unknown. Model 19 also included day delivery, meaning that the prey was either delivered on the same day as the previous prey item, or on the day after the previous prey item. This variable is also the second variable in Model 17. Model 19 had the lowest AIC, but was far from being significant, and is therefore not included in this thesis.

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

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

For lizard, all variables were significant, and especially temperature stood out, and support the results I found in the analysis where all prey items were included. Because I was interested in studying win-stay strategy, I considered model 18 to be the best one to study further (table 5).

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

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

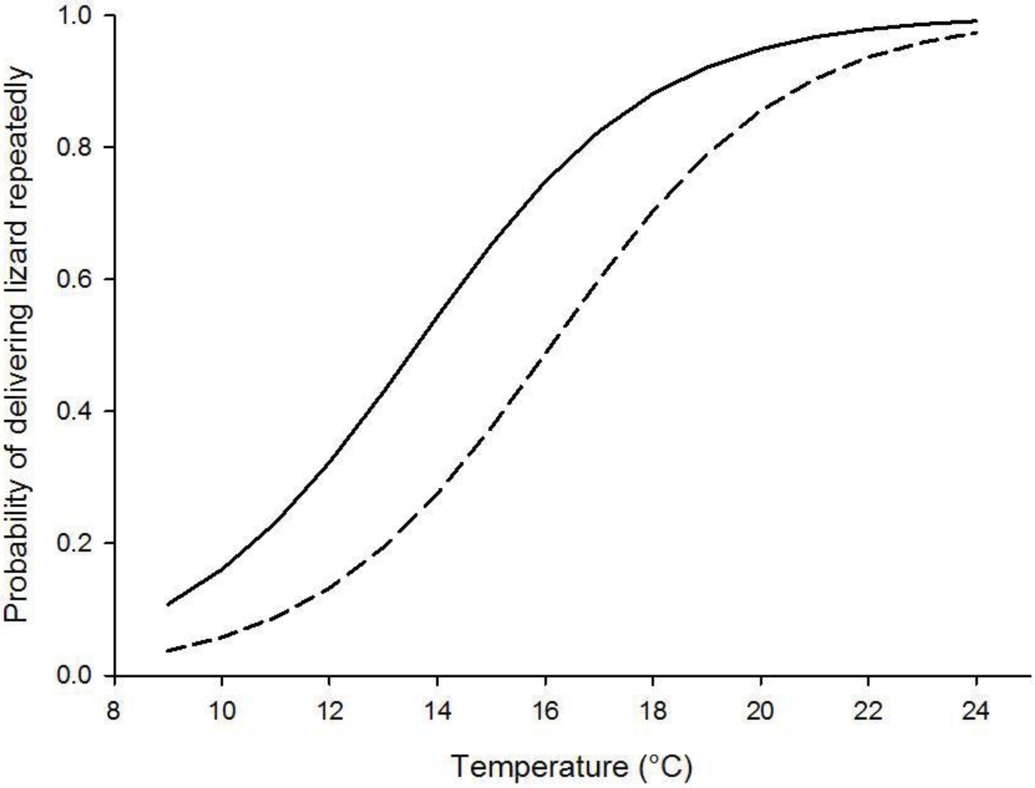

Figure 3. The probability of lizards being delivered repeatedly as a function of ambient temperature, where known previous hunter is represented with the whole line, and unknown previous hunter as dashed line. The temperature scale represents the temperatures when lizards were delivered at the nests.

Shrew

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

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

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

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

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

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

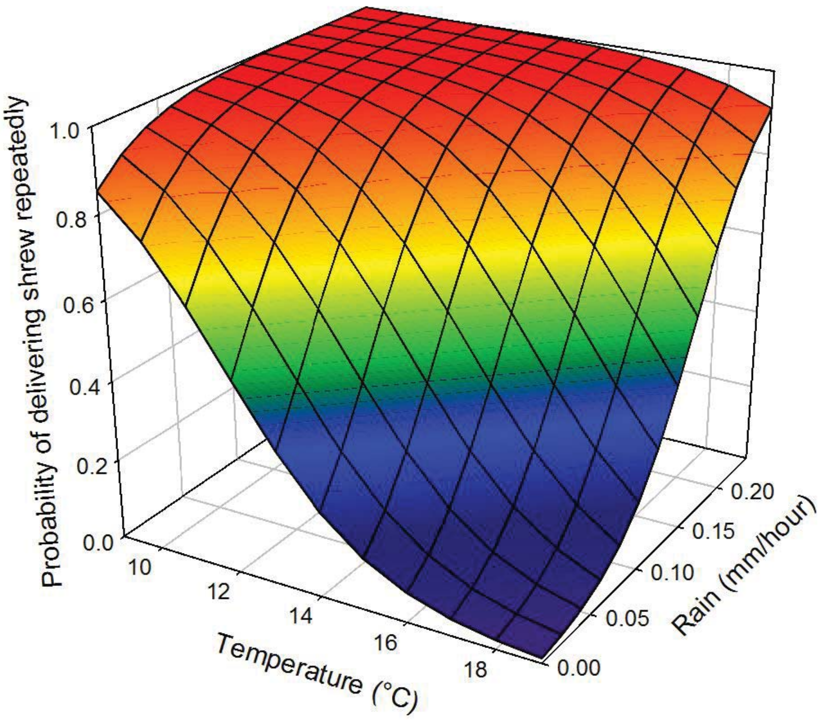

Figure 4. The probability of shrew being delivered repeatedly at kestrel nests as a function of ambient temperature and rainfall. Both variables are in the actual interval when shrews were delivered.

Bird

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

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

The two best models had only one variable. Model 4 contained wind speed, and Model 8 rainfall.

None of the models (4 and 8) were significant for any of the weather variables, but both showed a trend. The trend was greater for wind, than for rain (Tables 9 and 10).

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

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

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

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

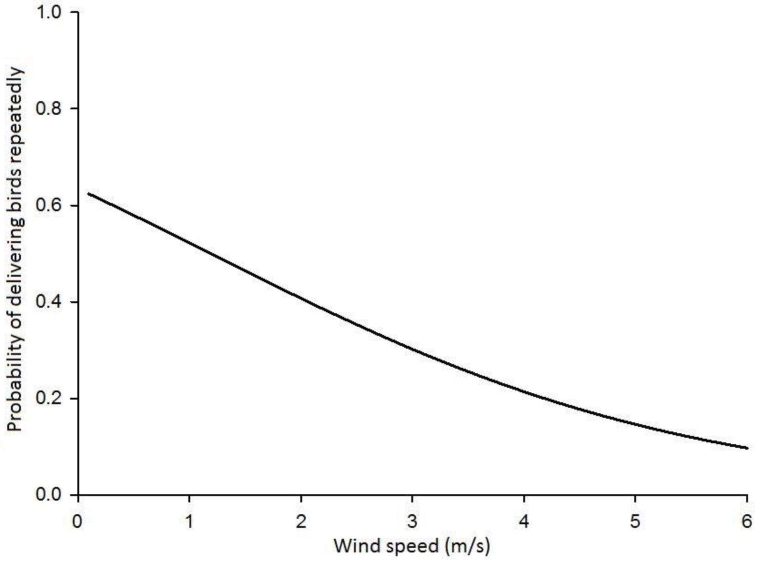

Figure 5. The probability of delivering birds repeatedly as a function of wind speed. The wind interval represents the actual interval when birds were delivered.

Aggression

I was interested in testing which variables affected the aggression level during prey delivery. As for all the other tests, I first ran the analysis in JMP, before I tested further in R. Unfortunately no variables stood out as significant in R, and in order to save time I decided not to test this further. For simplicity I have only included the results from the analysis in JMP in this thesis. All analysis are simple logistic regression (Y by X), and there were a total of 48 cases of either aggression or no aggression.

Table 11. AIC table for the single-variable models, for the probability that the female showed aggression towards the male when he returned to the nest with a prey.

Model	Variables	AIC	Rank
Wind	1	61.2	1
Rain	1	61.6	2
Body mass of previous prey	1	62.8	3
Body mass of current prey	1	63.4	4
Temperature	1	64.4	5

Wind speed was in the model with the lowest AIC and was almost significant, and in order to know if wind led to more or less aggression I included Figure 6. The higher the wind speed the more likely aggression occurred from the female towards the male during prey deliveries (Figure 6).

Table 12. Model with the response variable aggression, and the explanatory variable wind speed.

Explanatory variables	Estimate	SE	X^2	**P**
Intercept	-1.86	0.69	7.48	0.007
Wind	0.36	0.20	3.24	0.07

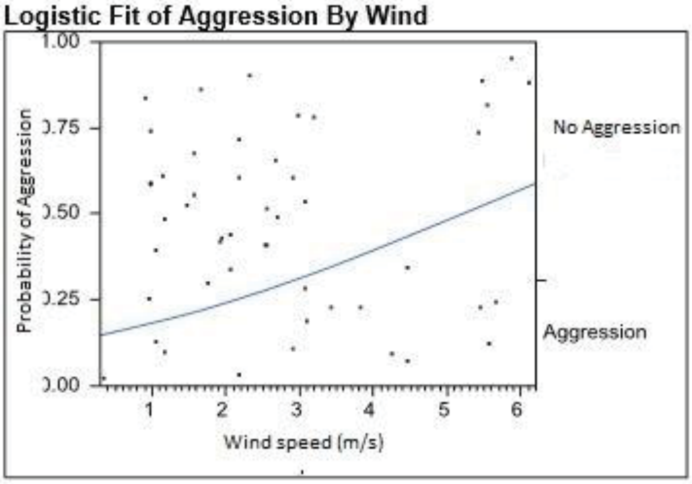

Figure 6. The probability of female aggression towards the male when he returned with prey, as a function of wind speed.

Rain was the second best model (Table 11), and the result show that there was a trend towards either more or less aggression with increasing rain (Table 13). I therefore needed to include Figure 7 to know whether rain caused aggression. As for wind speed, more rain increased the probability of aggression (Figure 7).

Table 13 .Model with the response variable aggression, and the explanatory variable rainfall..

Explanatory variables	Estimate	SE	X^2	**P**
Intercept	-1.15	0.38	9.16	0.003
Rainfall	12.45	7.41	2.82	0.09

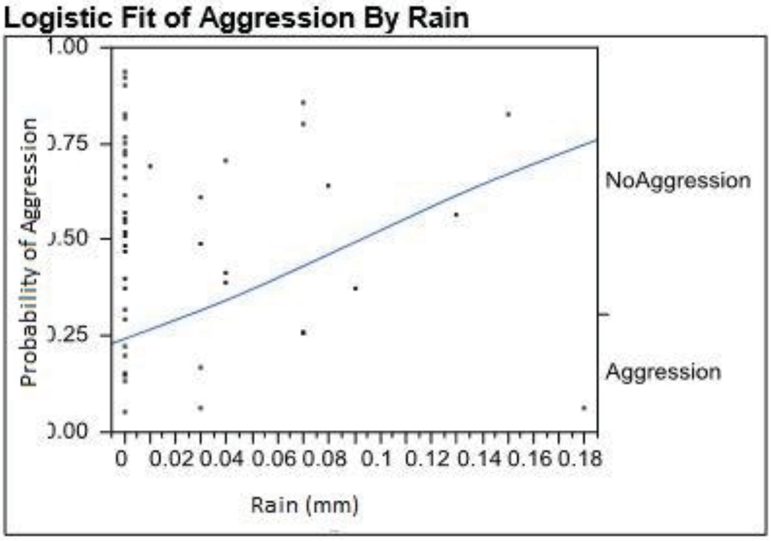

Figure 7.The probability of female aggression towards the male when he returned with prey, as a function of rainfall.

There was a weak trend towards increasing probability of aggression with increasing body mass of the previous prey delivered to the nest (Table 14, Figure 8).

Table 14.Model with the response variable aggression, and the explanatory variable body mass of previous prey.

Explanatory variables	Estimate	SE	X^2	P
Intercept	-1.25	0.45	7.55	0.006
Body mass of previous prey	0.021	0.016	1.86	0.2

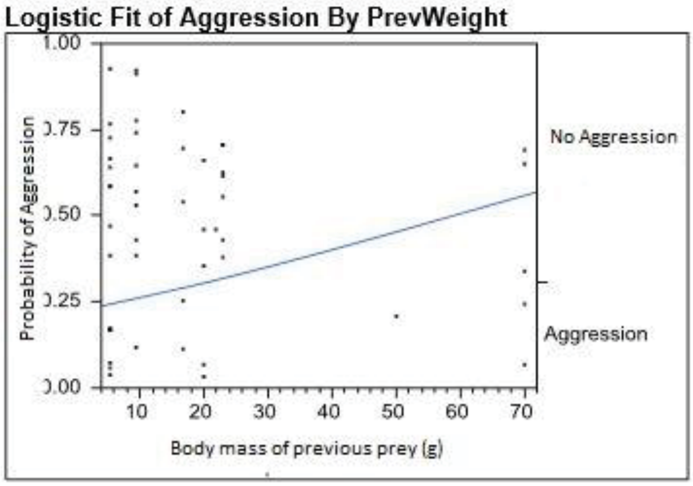

Figure 8.The probability of female aggression towards the male when he returned with prey, as a function of body mass of previous prey.

Table 15. Model with the response variable aggression, and the explanatory variable body mass of current prey.

Explanatory variables	Estimate	SE	X^2	P
Intercept	-0.97	0.42	5.38	0.02
Body mass of current prey	0.009	0.013	0.46	0.5

Since none of the two variables were significant, or showed a trend, I cannot say anything about the effects of body mass and ambient temperature, on the probability of aggression from the female towards the male during prey deliveries.

Table 16. Model with the response variable aggression, and the explanatory variable ambient temperature.

Explanatory variables	Estimate	SE	X^2	P
Intercept	0.016	1.97	0.0	1.0
Ambient temperature	-0.057	0.13	0.18	0.7

Discussion

Win-stay strategy

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

The ambient temperature, seemed to affect what type of prey, and probably also where, the kestrel hunted. I found that the probability of repeated deliveries of lizards increased, and that the probability of repeated deliveries of shrews decreased, with increased ambient temperature. Higher temperature led to more lizards being delivered (Yalden & Warburton, 1979; Løw, 2006; Steen et al., 2011a; Espe, 2013) and also made it more likely that the next prey would be a lizard. When the ambient temperature is high the lizards become more active and look for food, and are therefore easier targets for the kestrel (Craig, 1978). Because lizards may have a clumped distribution, it will pay the kestrel to remember where to go to capture more (Sonerud, 1985). The opposite happens when the ambient temperature is low. Then the shrews becomes an easy target since they are more active during colder periods. This support the fact that the kestrel is indeed hunting different prey types at different temperatures.

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

It is more efficient to return to a previously successful site, than to hunt randomly, and my results confirm that the kestrel is a central place forager with a win-stay strategy (Tinbergen, 1981; Sonerud, 1985).

Aggression

The female kestrel became more aggressive towards the male during prey deliveries if the last prey was smaller, if it was longer since last prey delivery, if it rained more, if the wind was stronger, or it was colder. These results were as I expected. None of the results were significant, however, but wind speed and rainfall showed trends. A surprising result was that the aggression tended to increase with larger body mass of previous prey delivered. This is opposite to what I had expected: if the last prey item was heavy, there should be less aggression because the female kestrel and the young are less hungry. But again, it would be a waste to spend a lot of energy on a small prey item. As mentioned by Sonerud et al. (2013) smaller prey items may not be worth the energy spilled by being aggressive.

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

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

On four occasions other kestrels were observed visiting the nests, and they may have been doing this as a nest prospecting for breeding the next year (cf. Eadie & Gauthier, 1985; Zicus &

Hennes, 1989; Pärt & Doligez, 2003). Aggression was also seen between the kestrels that I studied, and these nest-prospecting kestrels.

Unfortunately my observation and videotape data on aggression were quite limited, with only 15 cases of aggression when either a bird, a shrew or a lizard was delivered. On the other hand, I had 33 cases where I knew for sure that the kestrels showed no aggression towards each other, still including the three main prey types; bird, shrew or lizard. This means that almost a third of my observations involved aggression. In addition, I had to remove some observations of aggression in order to limit the statistical disturbance, this was aggression when the prey were either bank vole or a *Microtus* vole. Again, the fact that I collected data a low year for voles, and in a summer with cold and rainy weather, restricted the number of observations and thus influenced the statistical tests on this thesis.

Conclusion

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

There was a tendency to more aggression from the female towards the male during prey deliveries with worsening weather conditions. Due to the low vole populations there were very few breeding attempts during my study season, and the few females that bred were probably withholding their contribution to the nestlings and focused on their own survival. It would be interesting to study the female kestrels' aggression behavior in a year with high prey abundance.

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Appendix

Appendix I: Model 173, three main prey pooled

```
            linear      mixed       model       fit         by          the         Laplace     approximation
Formula:                Prey        ~           PreyID2     *           Temp        +           (1          |           Nest)
            Data:       malehunt
            AIC         BIC         logLik      deviance
            205,4       226,9       -95,69      191,4
Random                  effects:
            Groups      Name        Variance                Std.Dev.
            Nest        (Intercept)             0,21687                 0,46569

Number                  of          obs:        161,        groups:     Nest,       5

Fixed       effects:
            Estimate                Std.        Error       z           value       Pr(>|z|)
(Intercept)             -6,5591     2,146       -3,056      0,00224                 **
PreyID2Bird             6,1986      2,7252      2,275       0,022931                *
PreyID2Shrew            10,8554                 3,3277      3,262       0,001106                **

Temp        0,4645      0,1345      3,454       0,000553                ***
PreyID2Bird:Temp                    -0,4717     0,1694      -2,785      0,005361                **

PreyID2Shrew:Temp                   -0,8021     0,2297      -3,492      0,00048                 ***

---
Signif.     codes:      0           ‘***’       0,001       ‘**’        0,01        ‘*’         0,05        ‘.’         0,1         ‘

Correlation             of          Fixed       Effects:
            (Intr)      PrID2B      PrID2S      Temp        PID2B:
PreyID2Bird             -0,774
PreyID2Shrw             -0,639      0,506
Temp        -0,985      0,777       0,638
PryID2Brd:T             0,774       -0,988      -0,509      -0,79
PryID2Shr:T             0,575       -0,459      -0,985      -0,586      0,47
```

Appendix II: Model 173

Lizard	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-6,5591	2,146	-3,056	0,00224	**
PreyID2Bird	6,1986	2,7252	2,275	0,022931	*
PreyID2Shrew	10,8554	3,3277	3,262	0,001106	**
Temp	0,4645	0,1345	3,454	0,000553	***
PreyID2Bird:Temp	-0,4717	0,1694	-2,785	0,005361	**
PreyID2Shrew:Temp	-0,8021	0,2297	-3,492	0,00048	***

Shrew	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	4,2962	2,5602	1,678	0,09333	.
PreyID2Lizard	-10,8554	3,3277	-3,262	0,00111	**
PreyID2Bird	-4,6567	3,0526	-1,525	0,12714	
Temp	-0,3376	0,1862	-1,813	0,06978	.
PreyID2Lizard:Temp	0,8021	0,2297	3,492	0,00048	***
PreyID2Bird:Temp	0,3303	0,2119	1,559	0,11897	

Bird	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-0,36051	1,724379	-0,209	0,8344	
PreyID2Lizard	-6,19864	2,725172	-2,275	0,02293	*
PreyID2Shrew	4,656732	3,052621	1,526	0,12714	
Temp	-0,00728	0,103854	-0,07	0,94411	
PreyID2Lizard:Temp	0,471741	0,169416	2,784	0,00536	**
PreyID2Shrew:Temp	-0,33034	0,211871	-1,559	0,11896	

Appendix II: Model 198 three main prey pooled

```
Formula:  Prey      ~         PreyID2*  Temp      +         Wind      +         (1        |
Nest)
          Data:     malehunt
          AIC       BIC       logLik    deviance
          205       229,6     -94,5     189
Random              effects:
          Groups    Name      Variance            Std.Dev.

          Nest      (Intercept)         0         0
Number              of        obs:      161,      groups:   Nest,     5

Fixed     effects:
          Estimate            Std.      Error     z         value     Pr(>|z|)

(Intercept)         -5,9645   2,1576    -2,764    0,005703            **

PreyID2Bird         5,8003    2,7095    2,141     0,032295            *

PreyID2Shrew        10,9264             3,2755    3,336     0,000851            ***

Temp      0,4456    0,1334    3,341     0,000834            ***
Wind      -0,1943   0,1222    -1,591    0,111678
PreyID2Bird:Temp              -0,443    0,1677    -2,641    0,008259            **

PreyID2Shrew:Temp             -0,801    0,2256    -3,55     0,000385            ***

---
Signif.   codes:    0         ‘***’     0,001     ‘**’      0,01      ‘*’       0,05      ‘.’       0,1       ‘

Correlation         of        Fixed     Effects:
          (Intr)    PrID2B    PrID2S    Temp      Wind      PID2B:
PreyID2Bird         -0,779
PreyID2Shrw         -0,634    0,505
Temp      -0,977    0,777     0,642
Wind      -0,188    0,058     -0,008    0,014
PryID2Brd:T         0,782     -0,989    -0,51     -0,795    -0,035
PryID2Shr:T         0,567     -0,456    -0,986    -0,59     0,05      0,468
```

Appendix IV: Model 198

Lizard	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-5,9646	2,1576	-2,764	0,005702	**
PreyID2Shrew	10,9263	3,2755	3,336	0,00085	***
PreyID2Bird	5,8004	2,7095	2,141	0,032294	*
Temp	0,4456	0,1334	3,341	0,000834	***
Wind	-0,1943	0,1222	-1,591	0,111682	
PreyID2Shrew:Temp	-0,801	0,2256	-3,55	0,000385	***
PreyID2Bird:Temp	-0,4431	0,1677	-2,641	0,008258	**

Shrew	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	4,9619	2,535	1,957	0,050308	.
PreyID2Lizard	-10,9264	3,2755	-3,336	0,00085	***
PreyID2Bird	-5,1263	3,0164	-1,699	0,089231	.
Temp	-0,3554	0,1821	-1,952	0,050979	.
Wind	-0,1943	0,1222	-1,591	0,111678	
PreyID2Lizard:Temp	0,801	0,2256	3,55	0,000385	***
PreyID2Bird:Temp	0,358	0,2088	1,714	0,086502	

Bird	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-0,16425	1,699401	-0,097	0,923	
PreyID2Shrew	5,126109	3,016395	1,699	0,08924	.
PreyID2Lizard	-5,80029	2,709471	-2,141	0,03229	*
Temp	0,002526	0,101669	0,025	0,98018	
Wind	-0,19432	0,122158	-1,591	0,11168	
PreyID2Shrew:Temp	-0,35797	0,208836	-1,714	0,08651	.
PreyID2Lizard:Temp	0,443046	0,167738	2,641	0,00826	**

Appendix V: Three main prey types separately

Lizard model 18

```
Generalized            linear      mixed     model     fit       by         the       Laplace   approximation
Formula:               Prey        ~         Temp      +         Previous_ +          (1        |           Nest)
                       Data:       lizard
                       AIC         BIC       logLik    deviance
                            96,19      105,9    -44,09     88,19
Random                 effects:
                       Groups      Name      Variance  Std.Dev.
                       Nest        (Intercept 0,007768  0,088133
Number                 of          obs:      83,       groups:   Nest,                4

Fixed                  effects:
                       Estimate    Std.      Error     z         value      Pr(>|z|)
(Intercept)                  -6,23    2,1762    -2,863  0,004199 **
Temp                        0,4575    0,1375     3,328  0,000876 ***
Previous_hunterUnknown     -1,1423    0,5255    -2,174  0,029741 *
---
Signif.                codes:              0 '***'        0,001 '**'         0,01 '*'          0,05 '.'

Correlation            of          Fixed     Effects:
                       (Intr)      Temp
Temp                        -0,986
Prvs_hntrUn                 -0,003    -0,115
```

Shrew model 25

```
Generalized      linear   mixed    model    fit      by       the      Laplace  approximation
Formula:         Prey     ~        Temp     +        Rain     +        (1       |        Nest)
                 Data:    shrew
                 AIC      BIC      logLik   deviance
                    35,19    40,66    -13,6    27,19
Random           effects:
                 Groups   Name     Variance Std.Dev.
                 Nest     (Intercept 3,0294   1,7405
Number           of       obs:     29,      groups:  Nest,             4

Fixed            effects:
                 Estimate Std.     Error    z        value    Pr(>|z|)
(Intercept)        7,2703    3,834    1,896   0,0579 .
Temp              -0,6124    0,288   -2,126   0,0335 *
Rain              27,8832   17,901    1,558   0,1193
---
Signif.          codes:          0 '***'        0,001 '**'         0,01 '*'         0,05 '.'         0,1 '        '           1

Correlation      of       Fixed    Effects:
                 (Intr)   Temp
Temp               -0,961
Rain                0,379   -0,442
```

Bird model 4

```
Generalized   linear     mixed        model      fit        by        the
Formula:      Prey       ~            Wind       +          (1        |
              Data:      bird
              AIC        BIC          logLik     deviance
              66,45      72,12        -30,22     60,45
Random        effects:
              Groups     Name         Variance   Std.Dev.
              Nest       (Intercept)  4,83E-     2,20E-08
                                      16
Number        of         obs:         49,        groups:    Nest,     5
Fixed         effects:
              Estimate   Std.         Error      z          value     Pr(>|z|)
(Intercept)   0,5514     0,785        0,702      0,482
Wind          -0,4631    0,295        -1,57      0,116
Correlation   of         Fixed        Effects:
              (Intr)
Wind          -0,919
```

```
>                       summary(model8)
Generalized             linear    mixed     model    fit       by       the      Laplace   approximation
Formula:                Prey      ~         Rain     +         (1       |        Nest)
```

Bird model 8

```
                        Data:     bird
                        AIC       BIC       logLik   deviance
                          67,19     72,87    -30,6     61,19
Random                  effects:
                        Groups    Name        Variance  Std.Dev.
                        Nest      (Intercept)  5,49E-17  7,41E-09
Number                  of        obs:      49,      groups:   Nest,             5
Fixed                   effects:
                        Estimate  Std.      Error    z         value    Pr(>|z|)
(Intercept)              -0,8006    0,3308   -2,421   0,0155   *
Rain                      3,1351    2,8379    1,105   0,2693
---
Signif.                 codes:           0  ‘***’      0,001   ‘**’         0,01  ‘*’          0,05  ‘.’
Correlation             of        Fixed     Effects:
                        (Intr)
Rain                      -0,375
```