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Prey handling and consumption by northern goshawks (*Accipiter gentilis*): a feeding experiment

Bjørn Sæther

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Håndtering og konsum av byttedyr hos hønsehauk (*Accipiter gentilis*): et foringseksperiment

Foto by: Bjørn Aksel Bjerke

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PREFACE

This thesis is the final work of a master’s degree of Natural Resource Management at the department of Ecology and Natural Resource Management at Norwegian University of Life Science (NMBU).

Geir A. Sonerud has been my main supervisor and Ronny Steen has been my additional supervisor, both at the Department of Ecology and Nature Resource Management (INA).

I would first like to thank my main supervisor Professor Geir A. Sonerud for all his time, ideas and tremendous supervising during the master period. I wish to thank Ronny Steen for all help with supervision, statistics and help at the fieldwork. Bjørn Aksel Bjerke and Johnny Steen deserve great thanks for giving me the opportunity to record goshawks on their photo sites, and giving me the prey. Further, I thank Kjersti Botten for constructive comments on the language and layout.

Ås, 12 May 2014.

Bjørn Sæther

ABSTRACT

Although the northern goshawk (*Accipiter gentilis*) is a well-studied raptor, little is known about its prey handling behaviour and food requirement in different temperatures. Such knowledge is important for understanding its prey selection. I collected data on four wild female goshawks by video monitoring their handling of presented prey, 9 mammalian prey and 31 avian prey. I also conducted eight feeding trials, where I presented a mammalian and avian prey simultaneously, to see what the goshawk preferred to feed on. In each of these feeding experiments the goshawk fed on avian prey. The goshawks were more likely to start feeding from the head on small avian prey, and from the breast of larger avian prey. The goshawks were more efficient when feeding on a small avian prey than a large avian prey, and more efficient at high temperature and when proportion of remains was high. The piece size decreased with increasing prey body mass, with lower temperatures, and with lower proportion of remains left. Both the feeding efficiency and piece mass decreased when the mammalian prey was frozen. The goshawks ingested more meat when temperatures were sub-zero. Based on this study, to have the highest handling efficiency, the goshawk should select a small prey, particularly on cold days when the prey would freeze fast.

SAMMENDRAG

Selv om hønsehauken (*Accipiter gentilis*) er en godt studert rovfugl, er det gjort få studier på dens byttedyrhåndtering og mat konsum på forskjellige temperaturer. Dette er viktig for å forstå hønsehaukens byttedyrvalg. Jeg studerte fire ville hønsehaukehunner ved å videofilme deres atferd på åte, 9 pattedyr og 31 fugler ble lagt ut. Jeg gjennomførte 8 foringsforsøk hvor det ble lagt ut ett pattedyr og en fugl samtidig, for å se hva hønsehauken valgte å spise. I hvert forsøk valgte hønsehauken å spise fuglen først. Hønsehauken hadde større sannsynelighet for å spise hode til småe fugler først. Hos store fugler var sannsynligheten størst for å begynne å spise brystmuskelen. Hønsehauken var mer effektiv når den spiste på små fugler, enn når han spiste på store. Den var også mer effektiv ved høye temperaturer og når det var mye rester av åte igjen. Bit størrelsen minket med økende vekt på byttet, ved fallende temperaturer og med en lavere andel av rester. Både spise effektiviteten og bit størrelsen minket når pattedyret ble frossent. Hønsehauken konsumerte mer kjøtt når temperaturen var under frysepunktet. Basert på dette studie; for å ha den høyest mulige byttedyrhåndteringen, bør hønsehauken velge et lite byttedyr, og da spesielt på kalde dager hvor byttet vil fryse fort.

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1. INTRODUCTION

A predator should select the most profitable prey, considering the net rate of energy intake in a future perspective, this depends on the handling time and the energy gain the predator obtains from its prey (Stephens & Krebs 1986). Therefore, the prey handling can effect prey selection. Handling time is defined as the total time the predator use to capture, prepare, and ingest its prey (Kaspari 1990). A raptor will prepare the prey to maximize the energy gain, by feeding on the profitable parts and removing the indigestible, toxic, distasteful parts of the prey (Kaspari 1990, Sodhi 1992, Andersen 2003, Slagsvold et al. 2010, Steen et al. 2010). The time needed to prepare a prey will influence the choice of prey through its effect on handling time (Sherry & McDade 1982).

Raptors like owls (Strigiformes), hawks (Accipitriformes) and falcons (Falconiformes), have evolved the ability to capture prey with their feet (Slagsvold & Sonerud 2007, Slagsvold et al. 2010). This has led the bill to become a specialized tool for tearing prey a part. Compared to other birds, raptors take very large prey for their size (Slagsvold et al. 2010) because other birds usually capture their food with the bill. In these birds the prey selection is strongly constrained by swallowing capacity (Slagsvold et al. 2010). Raptors are ingesting relatively small pieces, this causes the meals to be very extended (Slagsvold & Sonerud 2007, Slagsvold et al. 2010). Therefore a strong selection for efficient prey handling is expected (Slagsvold et al. 2010).

In this thesis I explore the handling and feeding behaviour of the northern goshawk *(Accipiter gentilis),* hereafter termed goshawk.

The goshawk is common and widely distributed raptor species throughout the northern hemisphere (Brown & Amadon 1968), with many sub-species (Grønlien 2004, Kenward 2006). The goshawk typically hunts in mature forest using a short-stay, perched technique (Kenward 1982, 2006, Widen 1987, Beier & Drennan 1997). Food is one of the most important limiting factors of raptor species (Newton 1979). For the goshawks this factor is more important than processes acting over large spatial and temporal scales, such as large scale modern forestry and climate changes (Sunde 2002, Johansen 2006).

The goshawk is a long-lived, medium-sized avian predator (Cramp & Simons 1980, Kenward 2006). The mean body mass of Norwegian goshawks is 865 g for males and 1414 g for females (Hagen 1952, Cramp & Simmons 1980), which make this species notable for its sexual size dimorphism (Kenward 2006). This difference in body mass may enlarge the food niche of the goshawk (Kenward 2006). Slagsvold & Sonerud (2007) suggest that reversed sexual dimorphism may be an evolutionary adaption for the male to forage optimally on small avian prey in the breeding season.

The feeding ecology is well studied throughout Europe (Kenward et al. 1981, Selås 1989, Tornberg 1997, Toyne 1998, Rutz 2003, Kenward 2006, Johansen et al. 2007). The goshawk is adapted to hunt medium-sized to large prey, and it has a broad specter of species in the diet, especially during the breeding season (Cramp & Simmons 1980, Widèn 1987, Marcström et al. 1990, Grønnesby & Nygård 2000, Kenward 2006, Johansen et al. 2007). In northern Europe, earlier studies indicated that the goshawks diet consist mainly of avian prey like grouse (Tetraonidae), thrushes (*Turdus*), corvids (Corvidae.), and pigeons (Columbidae), but also mammals like red squirrels (*Scirius vulgaris*) and lagomorphs (Lagomorpha) (Kenward et al.1981, Selås 1989, Tornberg 1997). The mammals are probably most important prey in winter (Tornberg et al. 2006).

Slagsvold et al. (2010) reported that 88 % of the goshawk's diet is avian prey, calculated as the mean value from three different areas (Wikman & Tarsa 1980, Widen 1987, Selås 1989). The size of the prey can vary a lot from small mammals weighing 5 g up to the size of mountain hare (*Lepus timidus*) and capercaillie (*Tetrao urogallus*) males weighing 4 kg. The diversity of prey in the goshawks diet may depend on the abundance and availability of the local bird and mammal fauna (Opdam et al. 1975, Salafsky et al. 2005).

One specialization of the goshawk is its relatively small bill, which it uses to prepare and pluck its prey for self-feeding or feeding offspring (Kenward 2006, Slagsvold & Sonerud 2007, Slagsvold et al. 2010). Studies have shown that plucking makes the prey more aerodynamic, so plucking before transport gives a lower flight cost, which results in higher energy gain (Rutz 2003). Sodhi (1992) found that wild merlins (*Falco columbarius*) often removed 20 % of the prey by plucking before transport. The bill shape prevents the goshawk from swallowing a prey whole, this limit the mass of each bite ingested and makes the feeding a time-consuming activity (Slagsvold & Sonerud 2007, Slagsvold et al. 2010). The swallowing threshold model shows that preparation is a step function of prey mass and predicts preparation of large prey that are impossible to swallow whole (Kaspari 1990).

Another specialization of the goshawk is its short digestive tract with a relative small gizzard, stomach and intestine, just like the sparrowhawk (*Accipiter nisus)* (Barton & Houston 1996, Hillton et al. 1999). The food mass ingested at once is determined by the size of the stomach, and the size can prevent the goshawk from swallowing a prey whole. A shorter digestive tract has a shorter retention time which leads to a lower absorption efficiency (Hilton et al. 1999). This explains why the goshawk does not carry undigested food in the stomach for a long time (Hilton et al. 1999), and why a goshawk should prefer the prey with the highest nutritious value (Barton & Houston 1993).

The studies on the goshawk in the recent years, have found an average prey body mass around thrush-size (Grønnesby & Nygård 2000, Johnsen 2007, Johansen et al. 2007), especially during the nestling period (Johansen et al. 2007). Opdam (1975) found an average prey body mass of 277 g for adult males and 505 g for adult females during March in Netherland (Cramp & Simmons 1980), which is much heavier than a thrush. Kenward (2006) found a food demand of 169 g per day for a female goshawk. Tornberg et al. (2013) reported that Slagsvold et al. (2010, unpublished) recorded a maximum meal of 290 g in their feeding experiment, and Kenward (2006) reported the largest meal for a female goshawk to be 569 in another study.

By analysing videos of feeding goshawks I studied the difference in preparation and feeding between small and large prey, and between two different prey types, avian prey (corvids) and mammalian prey (rabbits, *Oryctolagus cuniculus*). Based on previous studies (Andersen 2003, Rutz 2003, Østbye 2010, Salmila 2011, Grønsdal 2012), I first predicted that a goshawk would feed on corvids if it could choose between rabbits and corvids, because the goshawk has been found to be a bird specialist in Europe (Cramp & Simmons 1980, Selås 1989, Rutz 2003, Johansen et al. 2007). Second I predicted the goshawk to start feeding from the head of small avian prey, and that the probability of starting with the head would decrease with increasing prey body mass (Grønsdal 2012), because the skull on large avian prey would be more difficult to break through. Therefore, it would be more difficult to ingest the head of large prey. It may be a nutrient gain in start feeding on the head, because of nutritious part in the brain. Third I predicted that the goshawk would have a lower handling efficiency with increasing prey body mass and decreasing temperatures below freezing, because a larger prey has more feathers, larger bones and unprofitable body parts (Slagsvold & Sonerud 2007), and because the prey may freeze during feeding sessions at sub-zero temperatures. I also predicted the handling efficiency to be higher when there are a high proportion of remains left. Larger prey has more meat concentrated in parts of the body, which may increase the mass of a piece (Götmark & Post 1996). Fourth I predicted the piece mass to be larger at warmer temperatures, and with a high proportion of remains, because it is easier to tear the meat apart at high temperatures, and it is easier to tear larger pieces from a more concentrated piece of meat.

Some of the prey that where fed over several days became frozen. Fifth, I predicted the feeding efficiency to be higher on day one than on day two and three when the prey was frozen. This was tested only with rabbits as prey. And since the rabbits where frozen day two and three, I predicted the piece mass to be smaller when the prey was frozen.

When it is cold on the other hand, I predicted the goshawk to consume more meat, because it will need more energy to maintain the body temperature.

In sum I wanted to answer the following questions: 1) What will a goshawk choose to eat, corvid or rabbit? 2) Where does the goshawk start to eat from an avian prey, the head or the breast muscle, and was it depending on prey body mass? 3) Will handling efficiency increase with increasing temperature, with increasing proportions of remains, and with decreasing prey body mass? 4) Will the piece mass increase with increasing temperature, with a higher proportion of remains and with small prey? 5) Will feeding efficiency and piece mass decrease when a prey becomes frozen? 6) Will the goshawks eat more when the temperature is below zero?

2. METHOD

2.1 Study design

I video monitored four adult wild female goshawks feeding on dead prey in two different time periods, and at three different locations. Location I was in Øyer municipality in Oppland County (61° 17´ N, 10° 21´ E), where the recordings were done in March 2007 (six recordings on six different prey). Location II and III were in Eidsberg municipality in Østfold County (59° 33´ N, 11° 16´ E), where the recordings were done in January and February 2014 (55 different recording days of which 39 recording-days were successful for 33 different preys). The two feeding sites were located 7.3 km apart.

The goshawks filmed were identified to sex and age from pictures taken from a photo hide nearby the feeding places (Bjørn Aksel Bjerke, pers. comm.). The four individuals studied were one 4K+ female (goshawk ID 1, location I), one 7K+ female (goshawk ID 2, location II), one 6K female (goshawk ID 3, location III), and one 4K+ female (goshawk ID 4, location III).

To avoid disturbing the goshawks I put out new prey before dawn when it still was dark, and collected the remains after dusk. I conducted an experiment, where I put out one rabbit and one corvid simultaneously, to see if the goshawk chose to eat the rabbit or the corvid. At location II the prey were put out on a dead three, and during the feeding experiments the preys was nailed with 25 cm apart (Figure1.a). At locations III the prey were put out on a natural moveable dead three (Figure 1.b), and during the feeding experiments the prey were nailed with 15 cm apart. The corvids were placed with the thorax facing up, and the rabbits were placed with the side of the body facing up.

Figure 1. The camera view during the feeding experiments: a) Locality II goshawk ID 2. b) Locality III goshawk ID 4

The goshawks were left alone to feed uninterrupted with minimal interference from humans. I fed the hawks with avian prey that had been killed by traffic, or hunters, and with rabbits that were purchased from a farm that breeds rabbits for commercial sale to restaurants and food stores. The body mass of the rabbits put out were in the weight ranged 500-1900 g. I used rabbits because they are similar to the mountain hare, and wild hares are difficult to obtain. All prey fed in my study were judged to be regular prey for goshawks in winter (Tornberg et al. 2006 and references therein). The temperature was collected from the nearest weather station to the locations II and III (Norwegian Meteorological Institute 2014) where the effect of temperature was tested.

Before being put out each prey was weighed and identified to species, but not aged. The leavings after one feeding session were weighed to record the mass ingested that day. If the prey had not been fully consumed, and there still were eatable parts left, the prey was weighed and put back for the next day. This was the case for almost all rabbits. Each prey item was offered the hawk for three successive days. If there were any leavings after three days, the leavings were collected and weighed. Most rabbits were fed on days with sub-zero temperature, so on the second day the rabbit was completely frozen and more difficult to consume. This was not the case for corvids, because the goshawks consumed all corvids on the first day.

The typical remains from the avian prey were wings, bill, tarsi, sternum and feathers. Remains after the rabbits were vertebra, skin, fur, head, entrails and feet. Both avian and mammalian prey had remains such as whole head, spine, internal organs and stomach.

2.2 Video recording

Prey handling of goshawk ID 1 was recorded with an analogue VHS camcorder with time lapse, and taped on 8 VHS cassettes with a total of 5 hours and 34 minutes handling time. Prey handling of goshawks ID 2, ID 3 and ID 4 was recorded with a digital mini recorder (data stored on SD cards), and later transferred to an external hard drive (see below, Steen 2009), with a total of 130 hours and 5 minutes were the goshawks visited the prey. The camera I used for filming goshawk ID 2, ID 3 and ID 4 was the same as used in studies of prey deliveries at the nest of kestrel *(Falco tinnunculus)* (Steen 2009). At location II the recordings were done slightly tilted from above, where the camera was placed on a stump. At location III the camera was placed so that the recordings were almost from a horizontal view (Figure 1 a, b.). The camera was connected with a video cable to a mini digital video recorder (mini DVR), which stored data on SD cards. The mini DVR recorder and the battery were located in photo hides, nearby the feeding places.

During the recordings of handling time, the prey was tied with a nail to prevent it from being carried by the raptor out of view from the camera. This was not always successful, and the hawk flew away with several of the prey.

Number of prey presented differed between the four goshawks, and not all attempts were successful (Table 1).

Table 1. Number of feeding attempts separated on successful and unsuccessful recordings.

	Corvid			Rabbit		
	Successful	Unsuccessful	Attempts	Successful	Unsuccessful	Attempts
1	6	0	6	0	0	0
2	14	11	25	5	3	8
3	5	4	9	1	2	3
4	5	2	7	3	1	4
Total	30	17	47	9	6	15

2.3 Video analysis

In the video analysis I followed the methods used by Salmila (2011) and Grønsdal (2012). Each bite and pluck from the prey was counted using a manual counting device. A pause was registered if there was no plucking or feeding activity for more than 5s. probably due to interference. The interference could be other raptors flying close by, sound of a train, airplane, car or other anthropogenic sound in the surroundings. Interference may have caused the goshawk to try to flee from the setup with the prey. Therefore, pulling the prey was registered as pause time. In many of the pauses the goshawk seemed calm and relaxed, as it just was digesting.

Sometimes it could be difficult to see exactly what the goshawk was doing with the prey, especially when the hawk turned its back to the camera. In the recordings where the hawk had turned away from the camera I had to judge what it was doing by interpreting its physical movements. When the goshawk bent down, rose up again and had a pulling movement, I assumed it to be eating, but if pieces were thrown away or the hawk had a fast frequency I counted it as plucking.

For each prey I measured plucking time and feeding time to find the feeding efficiency, taken as prey mass (g) ingested per feeding time (min), and the handling efficiency, taken as prey mass (g) ingested per handling time (min), where handling time is plucking time and feeding time pooled (Grønsdal 2012).

I recorded which part of the prey the goshawk started to eat from, to find which part of the prey the goshawk preferred to start feeding from.

For more details of the prey types and prey body mass, see appendix 1.

2.4 Statistics

The statistical analyses were performed with the software R, version 3.0.3 (R Development Core Team 2014). For count data (poisson distributed), and for logistic regression binomial distribution of data, I used a generalized linear mixed effect model (GLMM) by Laplace approximation in the lme4 package. For the continuous data (normally distributed), I used a linear mixed effect model (LME) in the lnme package (Pinherio & Bates 2000). In all tests performed goshawk ID was included as random effect to control for individual differences. Because the data on the rabbit was scarce, and there was no overlap in prey mass between the corvids and the rabbits, I had to split the data. Therefore, I could not compare the data on the corvids with the data on the rabbits.

The figures were constructed with back transformed values by using Sigma-Plot 10.0 Estimates are presented as average ± SE. All tests were considered statistically significant when $p \leq 0.05$.

For the logistic regression variables, were whether the goshawk started to eat from the head or from other body parts, while explanatory variables were prey mass. This was only conducted for the avian prey, because there were too few observations on the rabbits.

For the continuous data on consumption of corvids, all variables except temperature were $\log_{10}$-transformed to obtain approximately normal distribution of the model. The response variables were piece mass, i.e. mass (g) ingested divided by the number of pieces for each prey, and handling efficiency, i.e. mass consumed per plucking time and feeding time pooled, (g min^{-1}). Here the explanatory variables were prey mass, proportion of remains, and temperature.

For the continuous data on consumption of rabbits, variables were $\log_{10}$-transformed to obtain approximately normal distribution of the model, except the categorical variable not frozen (prey fed for one day) or frozen (prey fed for two or three days). Rabbits were fed on cold days, when the ambient temperature was below -3 °C, so on the second and third feeding session the prey was frozen. The response variables were feeding efficiency (mass ingested per feeding time) and piece mass (mass ingested divided by the number of pieces for each prey). Here the explanatory variables were original prey mass and if the prey was frozen (put out for two or three days or not).

I did not perform any estimates on the handling efficiency on rabbits because the second and third day, when the prey was frozen the goshawk did not pluck the prey. The goshawk made a hole in the prey the first day (pers. obs.), so the second day the goshawk did not need to pluck the prey to get access to the meat on the rabbit. Therefore, it was more appropriate to compare the feeding efficiency on frozen versus not frozen meat.

Finally, one test was conducted to find the average daily food consumption for the goshawk. Here the response variable was mass consumption (g^{-day}), and the explanatory variable were temperature. In this test I included only prey with remains weighing > 50 g, because when there are > 50 g remains the goshawk is probably satiated when it leaves the prey. The feeding session with < 50 g of remains was not included in the statistical analyses, because the goshawk was probably not satiated.

3. RESULTS

3.1 Did the goshawk eat the corvid or the rabbit first if it could choose?

In all eight food choice experiments the goshawk started to eat the corvid rather than the rabbit. This is significantly different from random (binomial test, p= 0.0039, Table 2). The goshawks also chose to consume the whole bird before it moved over to the mammal to start feed on it (pers. obs.). Even when the goshawk landed on the mammal it walked over the avian prey to feed on that instead.

Table 2. Results from the prey selection experiment on goshawks.

Number of experiment	Prey presented			Prey selected	Location
	Avian	Avian	Mammal		
Date	(Hooded) crow)	(Western Jackdaw)	(Rabbit)		
1) 20. January 2014	X		X	Avian	II
2) 22. January 2014	X		X	Avian	II
3) 23. January 2014		X	X	Avian	II
4) 28. January 2014		X	X	Avian	II
5) 23. January 2014		X	X	Avian	III
6) 24. January 2014		X	X	Avian	III
7) 28. January 2014		X	X	Avian	III
8) 29. January 2014		X	X	Avian	III

3.2 Which body part of the avian prey did the goshawk start to eat from?

From which part of an avian prey the goshawk started to feed was significantly affected by prey mass, where the probability of starting to feed from the head decreased with increasing prey mass (Table 3. Figure 2).

Table 3. Parameter estimates from the GLMM model of where on an avian prey the goshawk started feeding from as a function of prey body mass (n=31, ID=4).

Explanatory variable	Estimate	SE	Z	p
Intercept	3.64	1.512	2.403	0.0163
Prey mass	-0.008	0.003	-2.16	0.0308

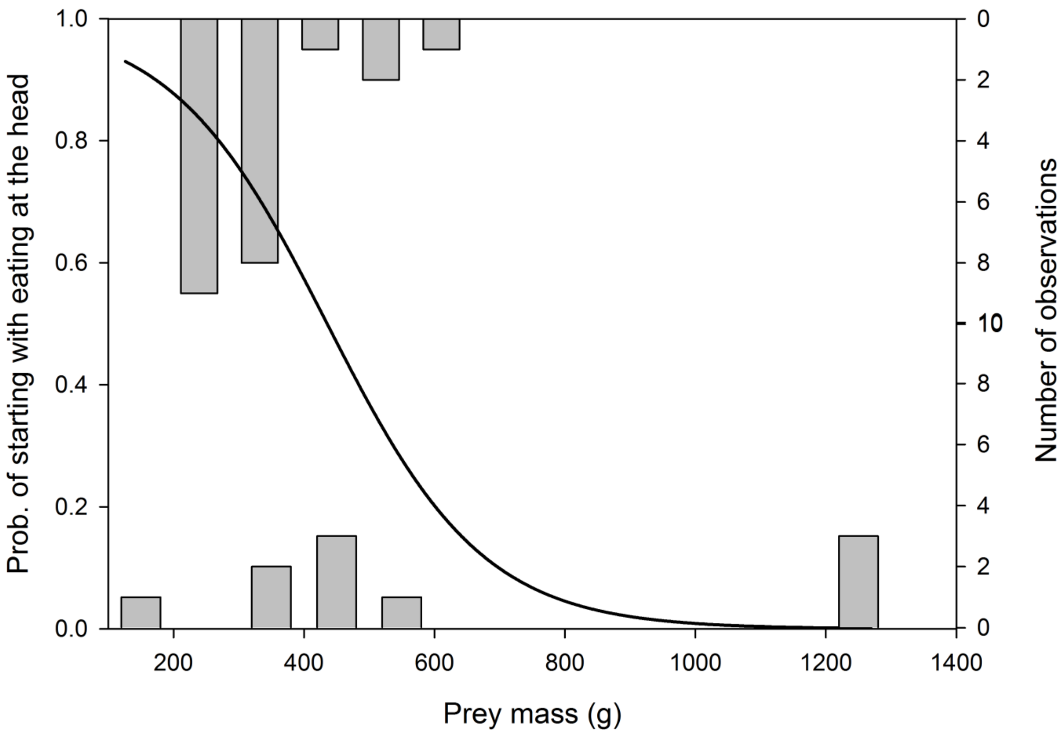

Figure 2. The probability that the goshawk started feed from the head of an avian prey, as a function of prey body mass. Bars represent the raw data (clustered for better visualizing), upper bars denote head (n=21), lower bars breast muscle (n=10). The regression line is from the estimated probability that the goshawk started feeding from the head.

Based on the parameters, the probability of starting with the head on a small prey (126 g) was 93 %, and the probability of starting with the head on a large prey (1269 g, black grouse, *Tetrao tetrix*) was 1 %. The estimated body mass of a prey where the goshawk by chance (50%) started feeding on the head was estimated to be 435 g.

3.3 Effect of prey mass, temperature and proportion of remains on handling efficiency for avian prey

Based on the parameters in the LME model factors affected the handling efficiency of avian prey. The handling efficiency decreased significantly when prey mass increased and the proportion of remains decreased, while the effects of temperature was not significant (Table 4, Figure 3 & 4).

Table 4. Parameter estimates from LME model (n= 22) with the handling efficiency (mass consumed per plucking time and feeding time pooled, g min^{-1}) of avian prey handled by goshawks, as response variable and prey body mass (log_{10} transformed), temperature (°C), and proportion of prey remains (log_{10} transformed) as explanatory variables (n= 22). The estimates are corrected for the random effect of goshawk ID (n=3).

Explanatory variable	Estimate	SE±	Df	t	p
(Intercept)	1.82	0.48	16	3.82	0.002
Temperature	0.01	0.01	16	1.54	0.142
Prey mass	-0.63	0.21	16	-2.30	0.009
Proportion of remains	0.42	0.18	16	2.40	0.029

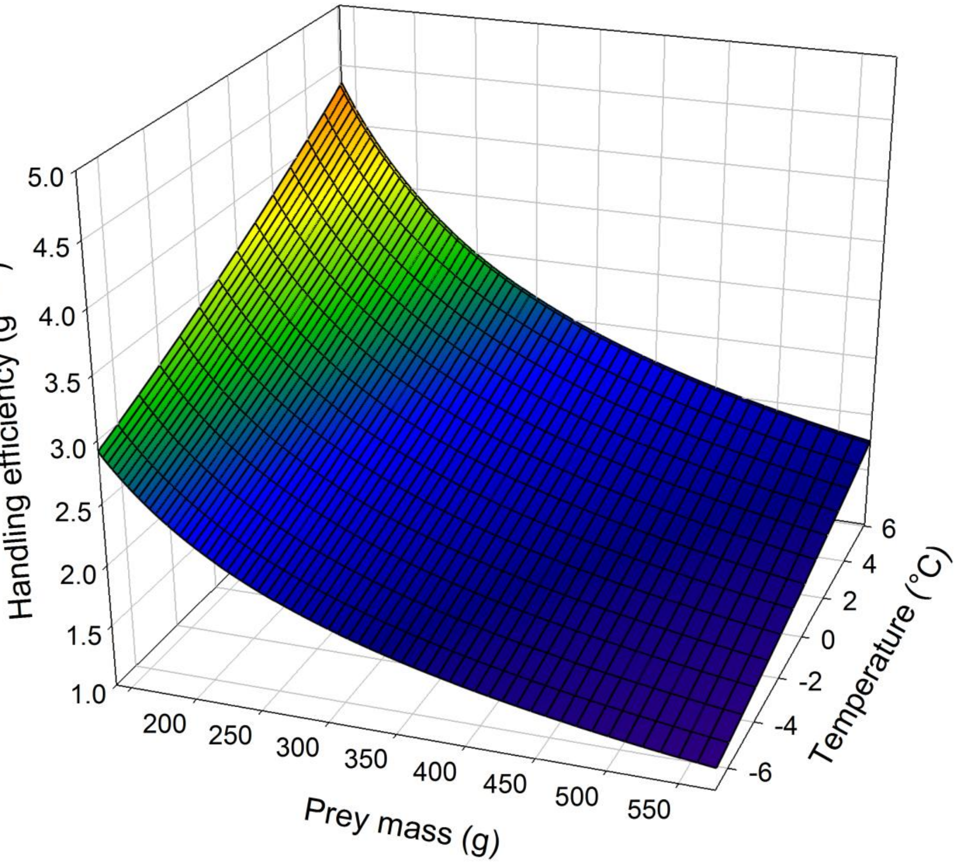

Figure 3. Handling efficiency (mass consumed per plucking time and feeding time pooled, g min^{-1}) of avian prey handled by goshawks, as function of prey body mass (g) and ambient temperature (°C), with the plane describing the complete LME model (calculated from parameter estimates). Note that prey mass and handling efficiency are back-transformed from the log_{10} transformed in the estimates.

Based on the parameters, the highest predicted handling efficiency for a corvid prey was 4.35 g min^{-1} for a prey body mass of 138 g and a temperature of 6.1 °C. In comparison, the predicted handling efficiency for a prey of 575 g with the same temperature (6.1 °C) was 1.76 g min^{-1}. The lowest predicted handling efficiency for a corvid prey was 1.17 g min^{-1} for a prey body mass of 575g and a temperature of -6.9 °C. Based on the estimated mean body mass of prey (244 g), and the mean temperature (-1°C) during the feeding trials, the predicted handling efficiency was 2.5 g min^{-1}. All these predictions are given for a mean proportion of remains of 21%.

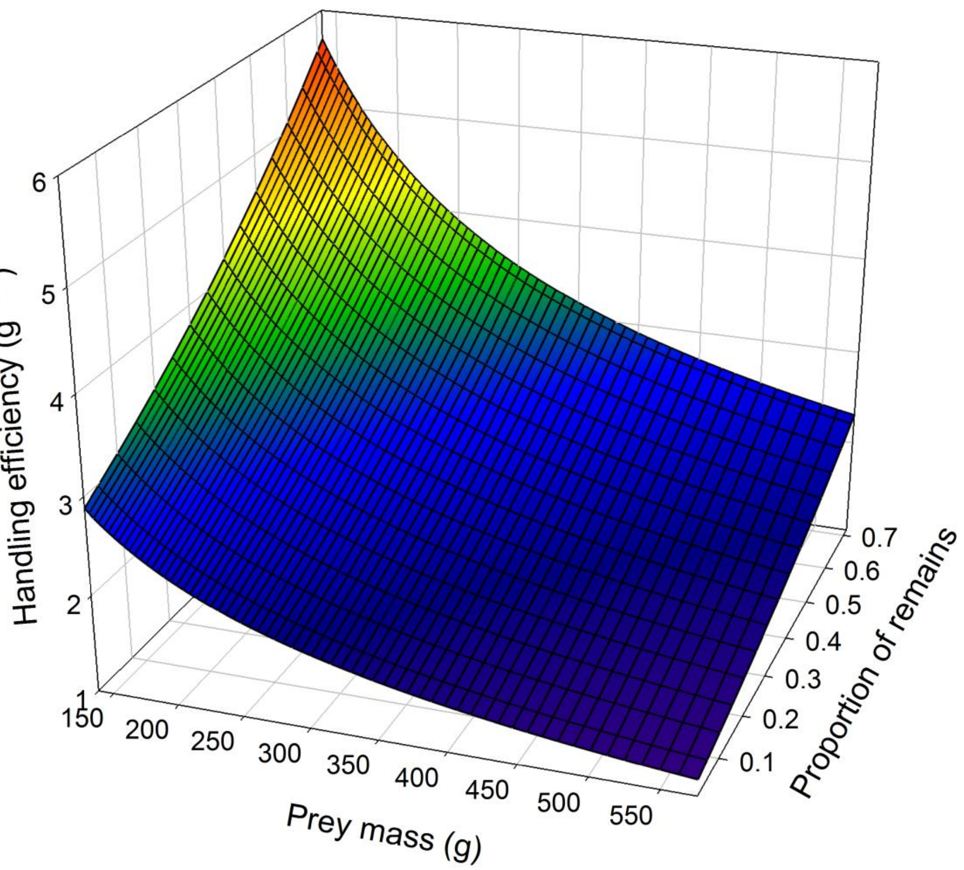

Figure 4. Handling efficiency (mass consumed per plucking time and feeding time pooled, g min^{-1}) of avian prey handled by goshawks as function of prey body mass (g) and proportion of remains, with the plane describing the complete LME model (calculated from parameter estimates). Note that the prey mass and handling efficiency are back-transformed from the log_{10} transformed in the estimates.

Based on the parameter estimated, the highest predicted handling efficiency for corvids prey was 5.7 g min^{-1} for a prey body mass of 138 g when the proportion of remains was 72%. The lowest predicted handling efficiency for corvids was 1.16 g min^{-1} for a prey body mass of 575 g when the proportion of remains was 2%. Based on the estimated mean body mass of prey (244 g) and the mean proportion of remains (21%) the predicted handling efficiency was 2.56 g min^{-1}. All these predictions is given for a mean temperature during the feeding trials (-1 °C).

3.4 Effect of prey mass, temperature and proportion of remains on piece mass

Based on the parameters in the LME model of factors affecting the piece mass. The piece mass decreased significantly when prey mass increased, while the effects of temperature and proportion of remain was not significant (Table 5, Figure 5 and 6).

Table 5. Parameter estimates from a LME model (n=22) with the mass (g) of each piece ingested as response variable, and temperature, prey mass (log_{10} transformed) and proportion of remains (log_{10} transformed) as explanatory variables (n=22). Estimates are corrected for the random effect of goshawk ID (n=3).

Explanatory variables	Estimate	SE±	Df	t	P
(Intercept)	0.33	0.43	16	0.76	0.45
Temperature	0.01	0.01	16	1.73	0.10
Prey mass	-0.41	0.19	16	-2.13	0.04
Proportion of remain	0.21	0.16	16	1.29	0.21

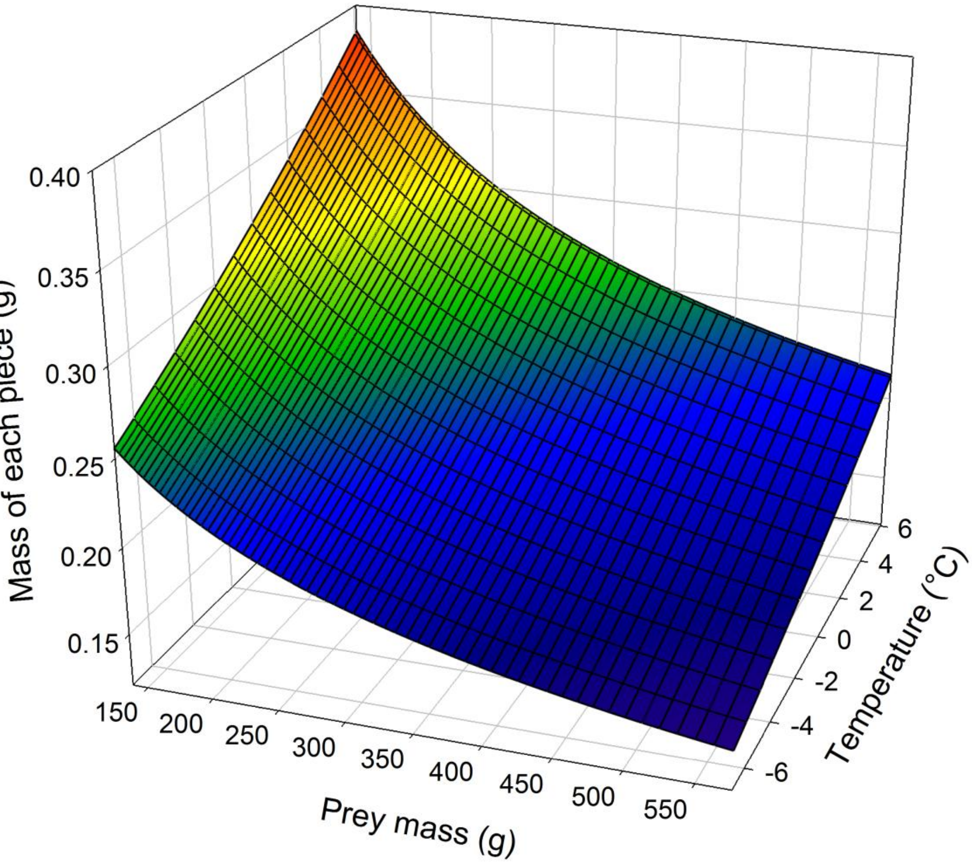

Figure 5. Mass of each piece ingested (g) by goshawks as function of prey body mass (g) and ambient temperature (°C), with the plane describing the complete LME model (calculated from parameter estimates). Note that prey mass and mass of each piece are back-transformed from the $\log_{10}$ transformed in the estimates.

Based on the parameter estimates, the goshawk was predicted to ingest the largest pieces from a small prey (138 g) when the temperature was high 6 °C, and each piece weighed on average 0.39 g. In comparison, with a large prey (575 g) and same temperature (6 °C) the predicted mass of the piece was 0.21 g. The smallest predicted piece mass, was from a large prey (575 g) when it was cold (-6.9 °C) and weighted 0.14 g. For mean prey body mass of 244 g and mean temperature (-1°C), the predicted piece mass was 0.24 g. All these predictions are given for the mean proportion of remains 21%.

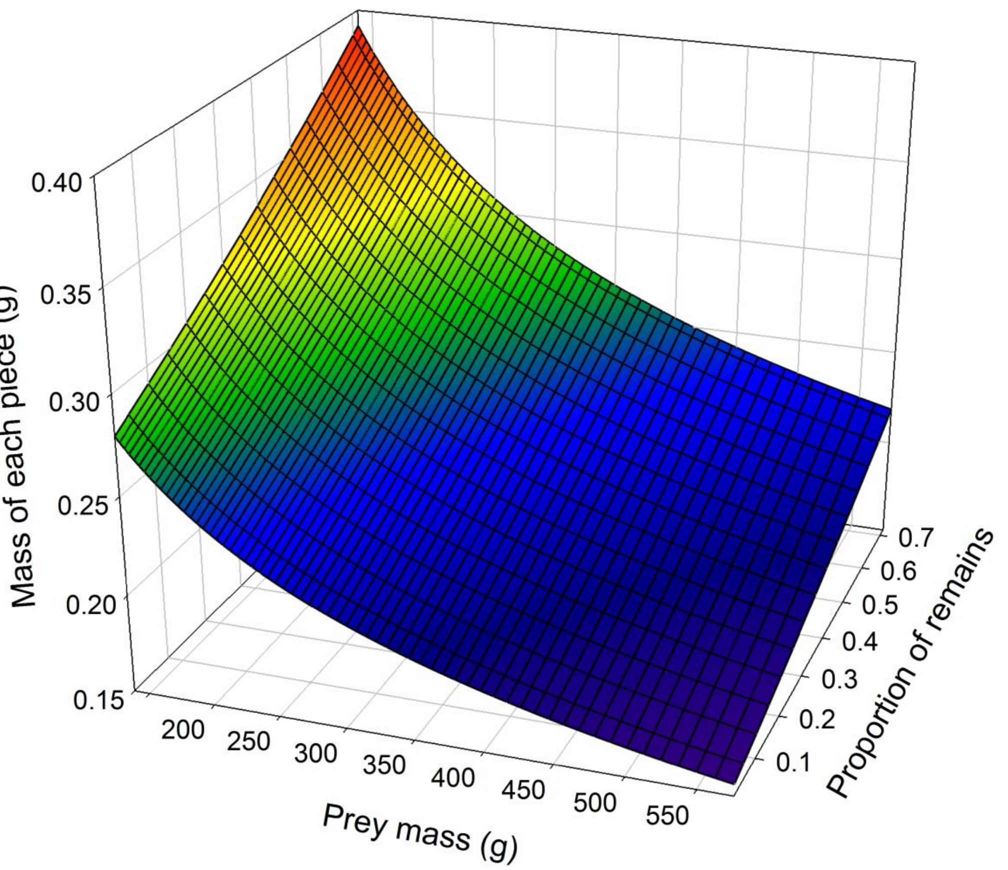

Figure 6. Mass of each piece ingested (g) by goshawks as function of prey body mass (g) and proportion of remains, with the plane describing the complete LME model (calculated from parameter estimates). Note that the prey mass, size of each piece and proportion remains are back-transformed from the log_{10} transformed in the estimates.

Based on the parameter estimates, the goshawk obtained the largest pieces from a small prey (138 g) when the proportion of remains was high 72%, and each piece weighed on average 0.39 g. In comparison, with a large prey (575 g) and same proportion of remains, the predicted mass of the average piece mass was 0.22 g. The smallest predicted piece mass was (0.16 g) and came from a large prey (575 g) when the proportion of remains was low 2%. For a mean prey body mass of 244 g and a mean proportion of remains (21%) the predicted piece mass was 0.24 g. All predictions are given for the mean temperature of -1°C during the feeding trials.

3.5 Effect of feeding efficiency on a frozen rabbit

Based on the LME model factors affected the feeding efficiency the first day versus the second or third day of a feeding trial, feeding efficiency decreased significantly as prey became frozen, while the effect of the original prey mass was not significant (Table 6).

Table 6. Parameter estimates from LME model (n=18, ID= 3) of feeding efficiency (mass consumed pr feeding time) of goshawks as function of original prey mass and whether the prey had been present at sub-zero temperatures for one day or 2-3 days.

Explanatory variable	Estimate	SE±	DF	t	p
(Intercept)	-0.78	0.94	8	-0.83	0.427
Frozen or not	-0.28	0.10	8	-2.70	0.027
Original prey mass	0.48	0.31	3	1.53	0.223

The feeding efficiency in the first day was predicted to be 4.7 min^{-1} compared to 2.5 min^{-1} the second or third day. This prediction was calculated from the mean mammalian body mass of 1068 g.

3.6 Effect of piece mass on a frozen rabbit

Based on the LME model factors affected the mass of piece from a rabbit from day one until day two, the piece mass decreased significantly from day one until day two. The effect of the original prey mass was not significant (Table 7).

Table 7. Parameter estimates from the LME model (n=18, ID=3) of piece size (g) of prey handled by goshawks as function of original prey mass and whether the prey had been present at sub-zero temperatures for one day or 2-3 days.

Explanatory variables	Estimates	SE	DF	t	P
(intercept)	-1.92	1.02	8	-1.88	0.096
Frozen or not	-0.33	0.10	8	-3.23	0.012
Original prey mass	0.47	0.34	3	1.37	0.263

The piece mass the first day was predicted to be 0.314 g. and 0.144 g. on the second and third day. This prediction was calculated from the mean mammalian body mass of 1068 g.

3.7 Effect of temperature on prey mass consumption

Based on a LME model of factors affecting prey mass consumption (g^{-day}), temperature had a significant effect on total mass ingested (Table 8, Figure 7).

Table 8. Parameter estimates from a LME model, with prey mass consumption (g^{-day}) by goshawks as function of temperature with total mass ingested as intercept (n=27, ID=3).

Explanatory variables	Estimate	SE±	DF	t	P
(Intercept)	2.3	0.08	23	28.92	<0.0001
Temperature	-0.04	0.02	23	-2.33	0.029

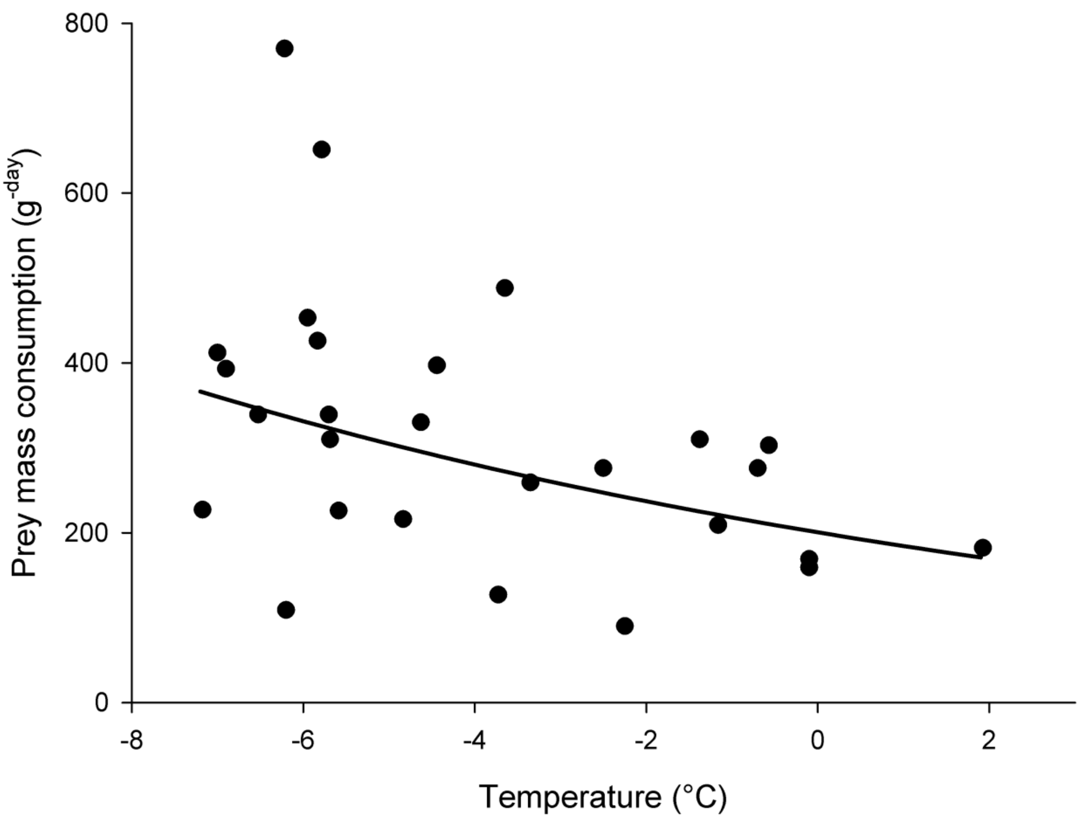

Figure 7. Prey mass consumption (g^{-day}) as function of temperature (°C), with the regression line calculated from the LME model (f(x) = 2.30 (±0.08) - 0.04 (±0.02)x, df = 23, F = 5.44, p = 0.029, n = 27, ID = 3)

Prey mass consumed per day decreased with increasing temperature (Figure 7). The parameter estimates predicted a daily prey mass consumption of 279 g at the average temperature of -3.9°C. The predicted consumption on a cold day at -7.2 °C was 366 g. The predicted consumption at 0 °C was 200 g and the predicted consumption on 1.9 °C was 171 g.

4. DISCUSSION

4.1 Biases due to methods

I did not age the prey, so I cannot exclude the possibility that some prey items would have been easier to consume than others. Small and juvenile prey have fewer feathers and a more fragile body with softer and smaller bones that are easier to swallow (Slagsvold & Sonerud 2007, Slagsvold et al. 2010). Different parts of a prey may have different nutritional value, and may differ in profitability. The goshawks may have consumed more prey parts, and fewer and larger pieces, from a juvenile prey than an adult prey (Kaspari 1991, Steen et al. 2010).

I found it difficult to find all the remains after a goshawk had fed on a prey. The goshawk threw the feathers and other remains on the ground, and some remains may have blown away or become snowbound. It was difficult to find all remains in the vegetation, especially small parts of feathers and fur. In these cases some of the leavings may have been lost, so that the mass of the leavings may have been underestimated.

On the videos it seemed that the goshawks were not much disturbed or driven to flight by threats. Only a couple of times the hawks on locality III protected the prey when it seemed as if another raptor was flying over them (pers. obs.). I therefore assume that when there were remains left after a meal, the goshawk were satisfied, whereas when there were no remains left, the goshawk flew away for hunting or digesting. I could not know if the goshawk consumed other food, but it seems like the goshawks preferred to eat the whole prey presented instead of start hunting a new one. It is important to bear in mind the fact that hunting a new prey may be costly and possibly dangerous (Kenward 2006), and that this may be the reason why the goshawks consumed the whole prey.

Another bias may be the different camera layouts. It was difficult to determine what a hawk was doing when it turned its back to the camera. Ideally I should have had several cameras filming the goshawks from different angles.

All prey were tied to the feeding place to avoid the hawk carrying the prey away. This may also have caused larger variance in the result, because the goshawk may have been prevented from swallowing the last pieces whole, which would have forced the hawk to take more pieces than necessary to finish the meal.

Originally the handling efficiency includes time for capturing the prey, i.e. the time elapsed from an attack is launched until the prey has been captured. Because the goshawk was fed, this factor was excluded from the handling efficiency in my study.

4.2 Goshawk preferred to consume corvids rather than rabbits

The goshawk chose to eat on a corvid rather than a rabbit, and the goshawk consumed the whole corvid before it started feeding on the rabbit. To the best of my knowledge there are no other food choice experiments on the goshawk, but there are studies on the diet (Kenward et al. 1981, Selås 1989, Tornberg 1997, Toyne 1998, Rutz 2003, Kenward 2006, Johansen et al. 2007), and these reported that the goshawk feed most on avian prey. Slagsvold & Sonerud (2007) suggested that it could have been more beneficial to choose a mammalian prey instead of an avian prey because the plucking is a time and energy consuming activity.

Before I started the prey choice experiment I fed the goshawk with rabbits only, to make sure that the goshawk would eat a rabbit if it had no alternatives. I thus eliminated the argument that rabbit was an unfamiliar prey for the goshawk. The goshawk is capable of catching and feeding on rabbits elsewhere in Europe (Kenward 2006).

The goshawk's adaption to catch and eat avian prey makes it more successful in catching avian prey than mammalian prey compared to other raptors (Kenward 2006). This may be the reason for why the goshawk chose the corvid first, because in this way it would avoid competition in its food niche. The nutritional value of the meat may be higher in avian than mammalian prey (Barton & Houston 1993), and this could be another reason for why the goshawk chose the avian prey first.

The nutritional value could also be the reason for why the goshawk chose to eat the whole corvid before it started feeding on the rabbit. Therefore, goshawks would gain more energy by feeding on the corvids than the rabbits, although the corvids needed more plucking and had a longer handling time.

If the goshawk's behaviour is in accordance with the optimal foraging theory (Stephens & Krebs 1986), the corvid is much more profitable than the rabbit, even when there is a low proportion of meat remaining.

4.3 Part of prey where the feeding session started

The probability that the goshawk started eating from the head increased with decreasing prey mass. The reason why the goshawk started with the head is probably that there is a nutrient and energy advantage in the brain of the prey. The reason for why the probability was higher of starting with the head on small prey may be that it is more difficult to break through skull of larger prey.

Another factor affecting the goshawks choice of where to start feeding may be that there is more food on the breast muscle on larger prey than smaller ones. I also observed that the hawk sometimes started to feed from other places of avian prey, for instance where the wing is attach to the breast muscle.

To the best of my knowledge there is only one previous study of which part of the prey a raptor starts to feed. Grønsdal (2012) found that the golden eagle (*Aquila chrysaetos*) started to eat from the head on smaller mammalian prey, but did not find the same pattern on avian prey. This can be explained with the fact that the golden eagle is larger than the goshawk, and may not have the same problem with breaking through the skull of the prey. Grønsdal (2012) also found that the head was eaten on all the small avian prey, but not always first, which indicates that the head nutritionally is an important part of the prey. The goshawk is more specialized to feed on avian prey than the golden eagle, so the goshawk may utilize the avian prey better.

4.4 Effect of prey mass, temperature and proportion of remains on handling efficiency for corvid prey

The handling efficiency (mass consumed per plucking time and feeding time pooled, g min^{-1}) decreased with increasing prey mass, decreasing proportion of remains, and decreasing temperature.

From the parameters a corvid prey of 138 g was handled 2.5 times more efficient than a corvid prey of 575 g. My findings are in line with those of Slagsvold & Sonerud (2007) and

Grønsdal (2012). Who also found that handling efficiency of avian prey decreased with increasing prey mass. The reason for why the small corvids are easier to ingest, may be from the fact that larger corvids have more feathers and indigestible parts. Slagsvold & Sonerud (2007) suggested that the negative trend in ingestion rate with increasing prey mass may lead to a lower energy gain per unit feeding time, when feeding on a large prey.

The goshawk's handling efficiency was affected by the proportion of remains left during the feeding sessions. When there was a high proportion of remains left, the goshawk ingested more meat per unit time. There are studies on the proportion of remains after the feeding sessions (Slagsvold et al. 2010, Salmila 2011, Grønsdal 2012), but these estimated the different proportions of remains after different prey (mammals and avian) and body mass, and not that the effect the proportion of remains had on handling efficiency. The reason for why the proportion of remains had such a positive effect on the handling efficiency may be that when there are a high proportion remains left, there are still much eatable part of the prey left, and the goshawk ingest the food faster, because of easier availability. Thus the preparing time will be shorter.

I found a mean proportion of remains of 21 % for the avian prey. This finding matches the findings of Slagsvold et al. (2010), who found a proportion of remains of 20 %, in avian prey in general.

The goshawk ingested more meat per time unit when the temperature was high than when it was low. The calculated handling efficiency when the temperature was low (-6.9°C) compared to when it was high (6.1°C) for a mean sized corvid (244 g) was 2.0 g min^{-1} and 3.0 g min^{-1}, respectively. It is important to remember that the effect of the temperature was not significant, but there was a trend in the data. The reason for why the temperature affected the handling efficiency may be that the prey may freeze during the feeding session and causes the piece mass to decrease (see below). Therefore, the goshawk would consume the same number of pieces, but the piece mass would be lower. This would lead to the goshawk needing more time to gain the same amount of meat when the temperature is < 0 °C than when the temperature is > 0 °C. I do not know if there was any difference in number of pieces ingested per minute, when the temperature is < 0 °C compared to > 0 °C, but the temperature may be affecting the goshawk movements, so it became slower when the temperature was sub-zero.

Competition between goshawks may be an important factor in the handling behaviour, because if there is competition for food, the goshawks may ingest the food faster and ingest more food per feeding session. I was also unable to test the effect of age on the handling efficiency, some old experienced goshawks may handle the prey better than juvenile ones.

Because the handling efficiency where higher for smaller corvids than larger corvids, it may be a better choice to feed on small avian prey if the goshawk should feed more efficiently. This applies also when the temperature is sub-zero, because the prey may freeze during the feeding session. In an optimal environment the goshawk will find a new prey when the threshold value of energy gain, drops to a level where the goshawk uses more energy than it is obtaining by feeding (Stephens & Krebs 1986).

4.5 Effect of prey mass, temperature and proportion remains on piece mass

The piece mass decreased with increasing prey mass, decreasing proportion of remain and decreasing temperature degrees. From the parameters the piece from a small corvid was estimated to be nearly twice as heavy as a piece from a large prey given the same temperature and proportion of remains. This is in line with the findings of Grønsdal (2012) and Salmila (2011). The reason for why the piece mass are larger on small prey may be that it is easier to tear off pieces of meat from a small prey, and that small prey are easier to handle.

The piece mass was also affected by the proportion of remains. When there was a high proportion of remains, the piece mass was larger. A prey with a high proportion of remains will have more fleshy body parts, as it is easier to tear larger pieces from it, and the meat is more available.

Also the temperature during the feeding session affected the piece mass. When the temperature was high (6°C) the piece was 1.6 times heavier than when the temperature was low (-6.9°C), given the same body mass and the mean proportion of remain. When the temperature is sub-zero the prey may freeze during the feeding session, and the prey may became more difficult to tear apart.

The swallowing threshold explains why the goshawks did not swallow prey whole. Therefore, the piece cannot be larger than the goshawk can swallow. The swallowing threshold and the specialist bill are why the goshawk needs to prepare its prey, and why the feeding session lasts for a long time (Kaspari 1990, Slagsvold et al. 2010). These findings are similar to my results on handling efficiency. The most profitable prey will be a small prey with high nutrient value, which is easy to handle and easy to ingest

.

4.6 Effect of feeding efficiency and piece mass on a frozen rabbit

Feeding efficiency decreased when the prey became frozen. Based on the parameters on the feeding efficiency the goshawk ingested the meat almost twice as fast the first day compared to the second or third day. The piece mass decreased when the prey became frozen. Based on the parameters on the piece mass the goshawk ingested twice as large pieces the first day compared to the second or third day.

The goshawk is known to feed on carrion, especially in harsh winters and periods with low food abundance (Kenward 2006). Therefore, a goshawk who returns to a previous prey may have to eat from a frozen prey, if the ambient temperature is below zero. The results on the feeding efficiency and piece mass of a frozen prey were conducted to show how much more difficult it could be to ingest meat from a frozen prey. The goshawk used more time and energy to ingest the same amount of meat when the prey was frozen, as when the prey was not frozen (pers. obs.). According to the optimal foraging theory (Stephens & Krebs 1986), the goshawk should choose what is most energetic of hunting for a new prey or eating the frozen prey.

My results show that the goshawk chose to eat carrion instead of hunting new prey. There are several factors affecting this, it could be that the prey abundance was low, or that hunting a new prey may have been very time and energy consuming. Kenward (2006) pointed out that there is always a risk involved for the goshawk when hunting a new prey: the hawk could be wounded or even die. In that context it may be more beneficial to eat the frozen prey.

4.7 Effect of temperature on prey mass consumption

The prey mass consumed per day by a goshawk increased with decreasing temperature. This means that the goshawk needs to find and eat more food when it is cold than when it is warm, probably because the goshawk needs more energy to produce and maintain the body temperature.

I estimated the daily food requirement on a day with ambient temperature of 1.9 °C to be 171 g, which is very similar to the findings of Kenward (2006), who found a daily food requirement of 169 g in female goshawks.

The estimated average size of a meal in my study was 279 g when there was >50 g of remains left, and the estimated average temperature was -3.9°C. This is almost as much food as Slagsvold et al. (2010, unpublished data) have recorded as the largest meal the goshawk can ingest (290 g). My two largest meals recorded were 770 g and 650 g, which are much larger. These recordings were made on two cold days when the temperature was -6.2°C and -5.8°C. This shows that a goshawk is able to ingest a large meal when it has the meat available. Kenward (2006) found the largest estimated meal on female goshawk to be 569 g, which is more similar to my results, than what Slagsvold et al. (2010, unpublished data) found. One reason for why the low values found by Slagsvold et al. (2010, unpublished data) are that their goshawks were held in captivity indoor i.e. with little exercise and high temperature.

The reason for why I have recorded larger meals than Slagsvold et al. (2010, unpublished data) and Kenward (2006) may be because I have studied the feeding behaviour on days with temperatures below zero. The goshawks also used longer time to eat on the two recording days (pers. obs.) this can affect the amount of food ingested. To the best of my knowledge this has not been examined earlier, and my study shows that the food requirement is larger on cold days. The winter is the critical season for the goshawk, due to a lower abundance of prey (Sunde 2002, Kenward 2006) and a climate change with warmer winters may be beneficial for the goshawks that are living at higher latitudes, because of a lower food requirement.

However, Sunde (2002) found no effect of weather or temperature on relative starvation risk in goshawks. The main explanation for the difference in mortality between the goshawks in the north and south of Norway was the prey abundance and not the harsh winter temperature (Sunde 2002). Jiguet et al. (2010) found that the climate change has been associated with increasing populations at the northern limit of bird species range, which may affect the prey availability during the winter. Moreover warmer winters do also advance the arrival of spring migrants and may thus increase the abundance of prey (Newton 1986). Based on data on breeding success in relation to breeding start and arrival of migratory birds Lehikoinen et al. (2012) pointed that they cannot exclude the possibility that the warmer climate could improve the survival of goshawks.

5. CONCLUSION

According to optimal foraging theory, the prey that the goshawks choose to catch and eat should have the highest energy gain per unit handling time. I found that the goshawk preferred to eat corvids over rabbits, and that for smaller avian prey the feeding started from the head, while on larger prey the goshawks started at the breast muscle. Further, it would have been interesting to do feeding experiments with two different avian prey and with a wider variety of prey, to see if the goshawk would have consumed the first prey completely, or if it has switched to the second prey after having eaten the most nutritious and energetic parts of the body. I found that the ambient temperature and proportion of remains affected the handling efficiency and piece mass negatively. This shows the goshawk to struggle more to ingest the food when the temperature is sub-zero, and the prey is frozen. I also found that the food requirements were higher in temperatures sub-zero. To the best of my knowledge, there have been no other similar studies, and it would be interesting to investigate the food requirements on a larger temperature scale, to see if the climate changes would affect the goshawk population to increase due to lower mortality rates, because of less food requirements during the winter. The amount of energy that the goshawk used and gained from ingestion of different prey types, and at different temperatures, was not measured in this thesis, but would be interesting topic for further studies.

REFERENCES

Andersen, L. I. 2003. Food allocation from parent to offspring in the European sparrowhawk (*Accipiter nisus*): impact of relative nestling size. Cand. agric.thesis. Ås: Agricultural University of Norway.

Barton, N. W. & Houston, D. C. 1996. Factors influencing the size of some internal organs in raptors. *Journal of Raptor Research*, 30: 219-223.

Barton, N. W. H. & Houston, D. C. 1993. A comparison of digestive efficiency in birds of prey. *Ibis*, 135: 363-371.

Beier, P. & Drennan, J.E. 1997. Forest structure and prey aboundance in foraging areas of northern goshawk. *Ecological Applications,* 7: 564-571.

Brown, L. & Amadon, D. 1968. Eagles, hawks and falcons of the world. Country Life Books, London.

Cramp, S. & Simmons, K. E. L. (eds). 1980. The birds of the western Palearctic. Vol. 2. - Oxford Univ. Press.

Grønlien, H. (ed). 2004. Hønsehauken i Norge. Bestandens status og utvikling siste 150 år. Norsk Ornitologisk Forening Rapport nr. 5.

Grønnesby, S. & Nygård, T. 2000. Using time-lapse video monitoring to study prey selection by breeding Goshawks (*Accipiter gentilis)* in Central Norway. *Ornis Fennica,* 77: 117-129

Grønsdal, E. 2012. Prey handling by a generalist predator, the golden eagle (*Aquila chrysaetos*) Master thesis. Ås: Norwegian University of Life Science. 40pp.

Götmark, F. & Post, P. 1996. Prey selection by sparrowhawks, (*Accipiter nisus)*: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 351: 1559-1577.

Hagen, Y. 1952. Rovfuglene og viltpleien. Oslo: Gyldendal. 603 pp.

Hilton, G. M., Houston, D. C., Barton, N. W. H., Furness, R. W. & Ruxton, G. D. 1999. Ecological constraints on digestive physiology in carnivorous and piscivorous birds. *Journal of Experimental Zoology*, 283: 365-376.

Jiguet F, Devictor V, Ottvall R, van Turnhout C, van der Jeugd H, Lindström A. 2010. Bird population trends are linearly affected by climate change along species thermal ranges. *Proc R Soc B,* 277:3601–3608.

Johansen. H.M.2006. Diet of goshawk (*Accipiter gentilis*) nestlings in south-eastern Norway: A comparison of farmland- and forest-dominated areas. Master thesis. Ås: Norwegian University of Life Science 32pp.

Johansen, H.M, Selås, V., Fagerland, K., Johnsen, J.T., Sveen. B-A., Tapia, L., & Steen, R. 2007. Goshawk diet during the nestling period in farmland and forest-dominatet areas in southern Norway. *Ornis Fennica,* 84: 181-188.

Johnsen. J.T. 2007. Diet and prey selection of breeding goshawks (*Accipiter gentilis)* in eastern Norway. Master thesis. Ås: Norwegian University of Life Sience. 31pp.

Kaspari, M. 1990. Prey preparation and the determinants of handling time. *Animal Behaviour*, 40: 118-126.

Kaspari, M. 1991. Prey preparation as a way that grasshopper sparrows (*Ammodramus savannarum*) increase the nutrient concentration of their prey. *Behavioral Ecology*, 20: 789-796.

Kenward, R.E. 2006. The Northern Goshawk.Poyser Series, A&C Black, London, UK.

Kenward, R.E, 1982. Goshawk hunting behavior, and range size as a function of food and habitat availability. *Journal of Animal Ecology,* 51: 69-80.

Kenward, R.E., Marcström, V. & Karlbom, M. 1981. Goshawk winter ecology in Swedish pheasant habitats. *Journal of Wildlife Management,* 45: 397-408.

Lehikoinen, A., Lindèn. A., Byholm, P., Saurola, P., Valkhama, J., Kaitala, V. & Lindèn, H. 2013. Impact of climate change and prey abundance on nesting success of a top-predator, the goshawk.*Oeceologia*, 171: 283-293.

Marcström, V., Kenward, R. & Karlbom, M. 1990. Duvhöken och dess plats I nature. AB Trycksaker, Norrköping.

Newton, I. 1979. Population biology of raptors. - Poyser, Berkhamsted.

Norwegian Meteorological Institute 2014. Observations and climate statistics: Rakkestad. Retrived 25. March 2014. From: (http://www.yr.no/sted/Norge/%C3%98stfold/Rakkestad/Rakkestad_(H%C3%A5by)_m%C3%A5lestasjon/)

Opdam, P. 1975. Intra- and interspecific differentiation with respect to the feeding ecology in two sympatric species of the genus Accipiter. *Ardea*, 63: 30–54.

Opdam, P., Thissen, J., Verschuren, P. & müskens, G. 1977. Feeding ecology of a population of goshawks (*Accipiter gentilis)*. *Journal of Ornithology,* 118: 35-51

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

R Development Core Team 2014. R: a language and environment for statistical computing. Vienna. Austria.

Rutz, C. 2003. Assessing the breeding season diet of goshawks (*Accipiter gentilis*): biases of plucking analysis quantified by means of continuous radio-monitoring. *J. Zool. Lond*. 259: 209-217.

Salafsky, S. R., Reynolds, R. T. & Noon, B. R. 2005. Patterns of temporal variation in goshawk reproduction and prey resources. *Journal of Raptor Research,* 39: 237-246.

Salmila, K. 2011. Prey preparation and feeding by a bird-hunting predator in temporal captivity: the sparrowhawk (*Accipiter Nisus*). Master thesis. Ås: Norwegian University of Life Science. 37PP.

Selås, V. 1989. Prey selection in the goshawk during the breeding season. - Fauna (Oslo) 42: 104-110.

Sherry, T. W. & McDade, L. A. 1982. Prey selection and handling in two neotropical hover-gleaning birds. *Ecology*, 63: 1016-1028.

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

Slagsvold, T., Sonerud, G. A., Grønlien, H. E. & Stige, L. C. 2010. Prey handling in raptors in relation to their morphology and feeding niches. *Journal of Avian Biology*, 41: 488-497.

Sodhi, N. S. 1992. Central place foraging and prey preparation by a specialist predator, the merlin. *Journal of Field Ornithology*, 63: 71-76.

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. 2010. Food provisioning in a generalist predator: Selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel *(Falco tinnunculus)*. PhD Thesis. Ås: Norwegian University of Life Sciences, Ecology and Natural Rescourse Management, INA.

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.

Stephens, D. W. & Krebs, J. R. 1986. Foraging theory. Princeton, N.J.: Princeton University Press.

Sunde, P. 2002. Starvation mortality and body condition of Goshawks (*Accipiter gentilis*) along latitudinal gradient in Norway. *Ibis,* 144: 301-310.

Tornberg, R. 1997. Prey selection of the Goshawk (*Accipiter gentilis*) during the breeding season: The role of prey profitability and vulnerability *Ornis Fennica*, 74: 15-28.

Tornberg, R., Korpimaki, E. & Byholm, P. 2006. Ecology of northern goshawk in Fennoscandia. *Studies in Avian Biology*, 31: 141-157.

Tornberg, R., Lindèn, A., Byholm, P., Ranta, E., Valkama, J., Helle, P. & Lindèn, H. 2013. Coupling in goshawk and grouse population dynamics in Finland. *Oecologia,* 171: 863-872

Toyne, E.P. 1998. Breeding season diet of Goshawk (*Accipiter gentilis)* in Wales. Ibis 140: 569-579.

Widèn, P. 1987. Goshawk predation during winter, spring and summer in a boreal forest area of central Sweden. - *Hol. Ecol.* 10: 104-109.

Wikman, M. & Tarsa, V. 1980. Food habits of the goshawk during the breeding season in southwestern Finland 1969-77. - *Suomen Riista* 28: 86-96.

Østbye, N. B. 2010. Partitioning of prey for nestlings by female Eurasian kestrels *(Falco tinnunculus):* Effect of prey type, prey size and brood size. Master thesis. Ås: Norwegian University of Life Sciences.

APPENDICES

Appendix 1. Prey species, prey number, number of prey items fed to the goshawk and the body mass of each individual prey item fed to the four individuals of the goshawk. The two right hand columns corresponding that the prey body mass and goshawk ID matches.

Prey species	Prey type	Number of prey items consumed	Body mass (g)	Prey eaten by goshawk ID
Eurasian Jay (*Garrulus glandarius*)	Avian	3	139, 163 and 174.	2, 3 and 3.
Hooded Crow (*Corvus cornix*)	Avian	10	370, 378, 442, 449, 450, 471, 520, 520, 555 and 576.	1, 4, 1, 2, 1, 2, 1, 1, 1 and 2.
Magpie (*Pica pica*)	Avian	4	190, 236, 240 and 241.	2, 3, 3 and 2.
Western Jackdaw (*Corvus monedula*)	Avian	13	165, 179, 180, 180, 180, 192, 200, 201, 204, 206, 210, 219 and 219.	3, 2, 2, 2, 2, 4, 2, 4, 2, 2, 4, 2 and 4.
Rabbit, (*Oryctolagus cuniculus*)	Mammal	9	528, 582, 753, 812, 878, 935, 983, 1779 and 1894.	2, 4, 3, 2, 4, 2, 2, 2 and 4.

Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no