Prey preparation and feeding of nestlings in the goshawk (*Accipiter gentilis*)

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PREFACE

The present study constitutes my Master thesis at the Norwegian University of Life Sciences. My main supervisor has been Geir A. Sonerud, and I am very grateful for all the time he has devoted helping me with this thesis. Vidar Selås has also been a helpful, and contributing supervisor. The study has received financial support from the Norwegian Directorate for Nature Management, Akershus county municipality and Buskerud county municipality.

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ABSTRACT

Prey preparation and feeding of nestlings in the goshawk (Accipiter gentilis)

Foraging is the main behaviour for survival. An efficient exploitation of available food is therefore important. I explored prey handling and feeding behaviour of the goshawk (Accipiter gentilis). Prey deliveries and feedings were recorded by video filming at seven goshawk nests in Buskerud and Akershus county during June and July 2005. During the 327 hours taped, a total of 146 prey items were delivered to the nest. The dominating prey group was thrushes (*Turdus*), constituting 55.5 % of all prey delivered. The type of prey being delivered was affected by previous prey delivered. The probability of a juvenile thrush being delivered decreased as the season progressed. If the brood was large, the possibility of the male delivering prey to the nest sites himself increased. The variables which best explained decapitation of avian prey were prey mass, whether the prey was a juvenile or an adult bird, and sex of the supplier. Both the amount of plucking and the probability of decapitation of prey increased with prey mass. The probability of a juvenile prey being decapitated was less than for an adult prey. Females delivered a higher frequency of decapitated prey than the males. Prey mass was the best predictor of the time needed to consume a prey (feeding time). Feeding time decreased with nestling age, while feeding efficiency increased with nestling age. To my knowledge, the finding related to distinct decapitation of juvenile and adult prev is new, and should be further examined.

SAMMENDRAG

Bytterdyrhåndtering og fóring av unger hos hønsehauk (Accipiter gentilis)

Furasjering er en essensiell atferd for overlevelse. Effektiv utnyttelse av tilgjengelig føde er derfor viktig. Jeg utforsket håndterings- og föringsatferd hos hønsehauk (Accipiter gentilis). Byttedyrleveringer og spisetid ble registrert ved videofilming av sju hønsehaukreir i Buskerud og Akershus fylke i løpet av juni og juli 2005. I løpet av de 327 timene som ble filmet, ble 146 byttedyr levert på reiret. Den dominerende byttedyrgruppen var trost (Turdus), som utgjorde 55.5 % av alle byttedyr levert. Hva slags byttedyr som ble levert var påvirket av det foregående byttedyret som ble levert. Sannsynligheten for at juvenil trost ble levert som byttedyr minsket utover i perioden etter 1. juni. Dersom kullstørrelsen var stor økte sjansen for at hannen leverte byttedyret på reiret selv. Variablene som forklarte dekapiteringsatferden for fugler var byttedyrvekt, om det var en voksen eller juvenil fugl, og hvilket kjønn som leverte byttedyret på reiret. Både sannsynligheten for dekapitering og ribbegraden av et byttedyr økte med vekt, og sannsynligheten for at et byttedyr var dekapitert ved levering var mindre for juvenile enn for voksne byttedyr. Hunner leverte en høyere frekvens av dekapiterte byttedyr enn hva hannene gjorde. Byttedyrvekt var den beste forklaringsvariabelen på hvor lang tid det tok å spise et byttedyr (spisetid). Spisetiden minsket med ungenes alder mens spiseeffektiviteten økte med ungenes alder. I forhold til min kunnskap er funnet vedrørende ulik dekapiteringspraksis av unge og voksne byttedyr ny, og bør utforskes mer.

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INTRODUCTION

In altricial birds, parental care is essential for the survival of the nestlings. Raptors are altricial, with incubation and nestling periods lasting up to 31 weeks, which is among the longest known in birds (Newton 1979). When raptors hatch they are relatively well developed compared to other altricial birds (Newton 1979). On hatching their eyes are open, their body completely covered in down, and they are able to take food directly from the female's bill (Newton 1979). Because the nestlings are dependent on food provisioning from the adults for such a long time, the portioning of the parents time is essential. During the breeding period raptors practice marked labour-division (Newton 1979, Brodin and Jönsson 2003).

During provisioning little of the prey is ingested by the capturer, instead the majority is fed to e.g. the nestlings (Ydenberg 1994). It is important to segregate between feeding and provisioning, because the energy intake and expenditure are different (Ydenberg and Welham 1992). Studies on food provisioning are rarer than foraging (Ydenberg 1994). Prey preparation is characterized by the time and energy spent handling a prey prior to ingestion (Kaspari 1990). The time needed to prepare a prey will influence the choice of prey through its effect on handling time (Sherry and McDade 1982). In the present study I try to explore the handling and feeding behaviour of the goshawk (*Accipiter gentilis*).

The goshawk is a long-lived, medium-sized avian predator with reversed sex dimorphism (Cramp and Simmons 1980). Male and female body mass in Norway is respectively ca. 865 g and ca. 1414 g (Cramp and Simmons 1980). It breeds in large parts of the Holarctic. Fennoscandia is the northernmost area where goshawks stay throughout the year (Cramp and Simmons 1980). The goshawk feeds opportunistically on birds and mammals, and individuals commonly start breeding when they are between 1 and 4 years old (Cramp and Simmons 1980).

As a forest-dwelling raptor, the goshawk prefers to nest in old forest with elements of old and large mature coniferous trees (Squires and Ruggiero 1996). The Norwegian goshawk population is not as numerous as earlier. The decline was rapid due to hunting, previous of the all-year protection of raptors which came in 1971 (Nygård et al. 1998). More recently the

modern forestry has had a negative impact on the population (Selås 1997, Nygård et al. 1998). Today the cause of population decline is probably both the reduction in preferred hunting habitat and a reduction of prey (Selås 1997). The goshawk is today a red-listed specie and the population estimates was 1765 pairs in 2000. (Grønlien 2004).

The goshawk is mainly a solitary bird, except in the breeding season (Cramp and Simmons 1980) and it also hunts alone (Opdam et al. 1977). When hunting, the goshawk often sits and watches from a hidden perch, then by using surprise attack and a short flight pursuit it catches and kills the prey with its claws (Opdam et al. 1977).

During the goshawks nestling period the male hunts most of the prey delivered to the nest, while the female is responsible for all direct parental care (brooding, guarding and feeding the nestlings) (Cramp and Simmons 1980). When the goshawk has killed a prey it often plucks it near the capture site (Rutz 2003), but the prey might also be plucked near the nest. Prey handling is carried out by both male and female (Schnell 1958, Tornberg 1997). Late in the nestling season the female will start hunting, but the timing is very variable (Cramp and Simmons 1980).

The aim of my study was to get a better knowledge of the goshawks behaviour during the nestling period. I studied the prey delivered to the nest and the sex of the adult supplying it. Different prey types may be delivered during the course of the study and the sex of the supplier may be influenced by the brood size and nestling age. I also looked at prey handling, plucking and decapitation of prey, and hypothesised that large prey would be more thoroughly handled before delivery. Moreover, variables affecting feeding time and feeding efficiency were investigated.

METHODS

Study area

This study was conducted at seven goshawk nests between 1 June and 1 July 2005. Six of the nest sites are in the boreo-nemoral zone, while one (Løken) is in the southern boreal zone. Three nests were located within Buskerud county $(59^{\circ} 40' - 59^{\circ} 56' \text{ N}, 9^{\circ} 41' - 9^{\circ} 48' \text{ E})$, two of them in Øvre Eiker municipality and one in Modum municipality. The landscape around these nests is dominated by forest. Four nests were located within Akershus county $(59^{\circ} 36' - 59^{\circ} 42' \text{ N}, 10^{\circ} 39' - 10^{\circ} 52' \text{ E})$, three of them in Ås municipality and one in Frogn municipality (appendix 1). This area is dominated by agricultural and developed areas. All the nests in Buskerud county were in pine trees (*Pinus sylvèstris*), ca. 15 - 20 m above the ground. The nests in Akershus county were also built in pine trees, except for one nest which was located in a spruce (*Picea àbies*). Brood size varied from 2 to 4 (appendix 1). Only one of the 23 nestlings died during the course of the study.

Data collection

During the study period, 327 hours of video were taped (appendix 1 and 2 for details). Each goshawk nest was studied in two periods. In each period the nest was studied two days in a row. The recording was normally done from 06 hours to 18 hours, except at the three nests in Buskerud county where the filming was distributed over several days. The length of the filming was approximately the same at all nests (appendix 1). The recording was done by mounting a water proof lens (wired 18LED night vision colour CCTV camera, size: 50 X 45 X 45(mm)) to a branch 0.5 - 1.5 m. above the nest. A 100 m long modified RCA video cable was used to connect the lens to the video camera (digital camcorder: Canon MV700i.). While recording, the observers stayed in a tent where they had the video-camera and the power supply (12 voltages lead battery (10 Ah)). Digital video cassettes of the type DVC mini cassettes were used, these lasted 2 hours in the long play mode. The cassettes were changed inside the tent to avoid disturbing the goshawks.

Analysing the videocassettes

The video tapes were analysed by connecting the video-camera to a 32-inch colour TV (Grundig ST84-794 TOP). When watching the videos of prey items delivered to nest, the following variables were noted: the supplier (male or female), whether the prey was decapitated, the plucking category, and species of prey. Most of the prey delivered was plucked and decapitated. This made the identification of species difficult. The species

identification was done by comparing the size and colour of the body and feet of the prey with stuffed specimen. A couple of plucked specimens were also used to facilitate the identification. The plucking categories used were the same as those used by Aasen (2004). Prey in plucking category 1 was either not plucked, or at most, the feathers on one wing and tail had been removed. The prey in category 2 had feathers from both wings and from the tail removed, and the body was slightly plucked. The prey in category 3 were completely plucked with no feathers left, and had only small amounts of down.

A total of 146 prey items were recorded delivered to the nests on the video tapes. Of these prey items, the entire feeding sequence was recorded for the 70 which were fed to the nestlings by the female. Only prey fed by the female was studied because these feedings were more continuous and made it easier to compare the length of the feeding sequences of different prey species. The feeding time was defined as the time elapsed from when the female bent her head down to take the first piece of a prey item, until she had finished the last piece (Aasen 2004). Feeding pauses > 5 seconds were subtracted from the feeding time. The feeding sequences included both the female feeding her brood and the female self-feeding. The brood age was determined by comparing pictures of goshawk broods (Holstein 1942) with the recordings.

Estimating body mass of delivered prey

The body mass of delivered prey was estimated from body mass given in literature (appendix 6) (Cramp and Simmons 1980, Cramp 1988, Cramp and Perrins 1994, Selås 2001), taken as the mean of male and female body mass, but not separating between juvenile and adult prey. The body mass of unidentified thrushes was estimated as the mean mass of all the thrush species among prey delivered to the nest. The head was estimated to constitute 12.9 % of total body mass (T. Slagvold and G. A. Sonerud unpublished), and subtracted from the total body mass to determine the correct mass of decapitated prey (body mass * 0.871). For 22 of the 146 delivered prey, it was impossible to decide whether the head had been removed or not. When estimating the mass of these prey, the probability of a prey delivered to the nest being decapitated was calculated by dividing the amount of prey delivered with head on the total amount of prey delivered. This probability (68.5 %) was then subtracted from one and multiplied by 12.9 %. The answer was then subtracted from the preys total body mass (weight * 0.912). Prey body mass was not corrected for plucking.

Statistics

All statistical analysis and graphics were made by using the software JMP (2000). For most of the statistical tests only avian prey was included, because mammalian prey only consisted of red squirrels (*Sciurus vulgaris*), and were too few to analyse. Where the red squirrels are included in the statistical tests, it is especially noted. Whether nest locality had any effect was tested by adding nest locality to the test as a random factor.

Logistic regression and stepwise regression (backward elimination of variables) were used to analyse the data. Only variables with significant effects were included in the models. In the stepwise regression the residuals were tested for normality. Logistic regression was used to test which variables affected the plucking degree of a delivered prey. Before running the model, the plucking categories were transformed from an ordinal to a nominal variable by pooling plucking category 2 and 3, leaving us with only two plucking categories. Logistic regression was also used to test which variables affected the probability of a prey being delivered decapitated or not.

Logistic regression was further used to test the relationship between currently delivered prey and the previously delivered prey. Squirrels were included in the test. Before testing the relationship, avian prey were split into two groups, thrushes (*Turdus*) and others. This was done because there was a high number of thrushes (n = 80) among the prey items compared to the other bird species (n = 66).

Stepwise regression (backward elimination) was used to test which factors affected feeding time and feeding efficiency. Prior to the tests, the prey mass, feeding time and feeding efficiency were log-transformed for normal distribution of the residuals. Only prey items completely handled by the adult (adult female feeding the nestlings), was included in the tests. Efficiency was calculated by dividing prey mass (g) with feeding time (min.).

Logistic fit, contingency analysis and oneway analysis were used for further testing of the significant effects in the models and for making figures. Means are given with one standard error.

In logistic probability plots, the points do not represent actual observations, but are interpreted as differences from the average over both levels (JMP 2000).

RESULTS

Types of prey delivered to the nest

A total of 146 prey items were recorded delivered to the seven goshawk nests. The mean number of prey delivered during a day, including squirrels, was 3.3 ± 0.17 , ranging from 1 to 11 (n = 146). There was no significant difference in prey delivery rate (prey items per day, respectively) between the first and the second period (3.2 ± 0.24 and 3.4 ± 0.25) (Oneway Anova; n = 146, t = -0.63, p = 0.53). Of all the prey items, 55.5 % were classified as thrushes, 26.7 % as corvids, 11.0 % as other birds, 4.8 % as mammals and 2.1 % as unidentified (appendix 3 and 4 for details on prey types). The only mammal prey was the red squirrel. The most common avian prey were the redwing (*Turdus iliacus*) and the song thrush (*Turdus philomelos*), making up 32.2 % of the number of prey delivered. There was no significant difference in the proportion of adult and juvenile prey delivered to the nests during the two filming periods, 66 adults and 9 juveniles in period one and 63 adult and 8 juveniles in period two (Likelihood ratio test; n = 146, x² = 0.02, p = 0.89, the test included squirrels).

The mean body mass of all prey items was 167.6 g (table 1). The largest prey delivered was a common raven (*Corvus corax*, 1254 g), but it was parted when delivered to the nest. The smallest prey delivered was a decapitated passerine (17.4 g) (appendix 6 for details on prey mass). The thrushes was the prey group with the lowest mean body mass, while birds other than thrushes had the largest mean body mass (table 1). The mean body mass of birds other than thrushes exceeded that of squirrels by only 7.3 g (table 1), which was not significant (Oneway Anova; n = 65, $R^2 = 0.0001$, p = 0.93).

Prey type	Во	Body mass (g)		
Thrushes (Turdus)	72.8	±	1.4	80
Birds other than thrushes	285.2	±	27.9	58
All birds	162.1	±	14.7	138
Mammals (squirrels)	277.9	±	7.8	7
All prey	167.6	±	14.2	145

Table 1. Body mass $(\pm SE)$ of prey types delivered at the goshawk nests.

Variables with a significant effect on the type of prey delivered (either thrush or other prey types) were days after 1 June, previous prey type, prey age (adult or juvenile), and days after 1 June * prey age (table 2). Squirrels were included in the test. The interaction between

nestling age, supplier (male or female) and prey number that day and their interactions with each other and with the variables in table 2 were not significant. The variables not significant were eliminated in the following order: previous prey type * supplier, previous prey type * prey age, days after 1 June * nestling age, prey number that day * prey age, nestling age * prey age, prey number that day * supplier, prey age * supplier, days after 1 June * supplier, nestling age * supplier, supplier, days after 1 June * previous prey type, nestling age * previous prey type, days after 1 June * prey number that day, nestling age * prey number that day * prey number that day, nestling age, prey number that day * previous prey type, days after 1 June * previous prey type, prey number that day and nest locality (random factor).

Table 2. Nominal logistic fit of significant effects on the type of prey delivered. Whole model: n = 113, $x^2 = 17.25$, df = 4, p = 0.0017, $R^2 = 0.11$.

Variable	df	x ²	Р
Days after 1 June	1	5.58	0.018
Previous prey type	1	8.72	0.032
Prey age (adult or juvenile)	1	0.17	0.680
Days after 1 June * Prey age	1	8.74	0.003

The parent goshawks were more likely to provision a thrush when the previous prey provisioned also was a thrush (figure 1).



Figure 1. Type of prey delivered in relation to the type of the previously delivered prey, when there are two prey types thrushes (*Turdus*) (1) and the rest (other birds and squirrels) (2). Likelihood ratio test: n = 113, $x^2 = 8.43$, df = 1, p = 0.004.

Type of prey delivered was not significantly affected by prey age i.e. adult or juvenile (figure 2).



Figure 2. Type of prey delivered in relation to prey age (adult or juvenile), when there are two prey types thrushes (*Turdus*) (1) and the rest (other birds and squirrels) (2). Likelihood ratio test: n = 146, $x^2 = 0.46$, df = 1, p = 0.50.

Season (days after 1 June) had no significant effect on prey type delivered to the nest alone, when both adult and juvenile prey were included (figure 3).



Figure 3. Type of prey delivered in relation to days after 1 June, when there are two prey types thrushes (*Turdus*) (1) and the rest (2) (other birds and squirrels) Both adult and juvenile prey are included in the analysis. Whole model: n = 146, $x^2 = 0.015$, p = 0.90, df =1, $R^2 = 0.0001$.

Also, season had no significant effect on prey type delivered to the nest alone, when only adult prey were included (figure 4).



Figure 4. Type of prey delivered in relation to days after 1 June, when there are two prey types; thrushes (*Turdus*) (1) and the rest (2) (other birds and squirrels). Only adult preys are included in the analysis. Whole model: n = 129, $x^2 = 0.58$, p = 0.45, df = 1, $R^2 = 0.0032$.

In contrast, season had a strong significant effect on prey type delivered to the nest, when only juvenile prey were included (figure 5). The probability of a (juvenile) thrush being delivered decreased with number of days after 1 June.



Figure 5. Type of prey delivered in relation to days after 1 June, when there are two prey types; thrushes (*Turdus*) (1) and the rest (2) (other birds and squirrels). Only juvenile preys are included in the analysis. Whole model: n = 17, $x^2 = 5.73$, p = 0.017, df =1, $R^2 = 0.24$.

Sex of the supplier which delivered prey to the nest

The supplier was recorded for 133 prey items delivered to the goshawk nests. Of these the female delivered 84 (63.2 %) and the male 49 (36.8 %). Probably the male had caught most of the prey items, as the majority of the prey delivered to nest by the female, was handed to her by the male (pers. obs.). In the statistical test of factors affecting the sex of the supplier (male or female) the squirrels were included. The only variable with significant effect was brood size (table 3). The following variables were not significant and were eliminated in the following order: original body mass * nestling age, nestling age, prey age, prey type delivered, original body mass and code locality (random).

Table 3. Nominal logistic fit of significant effects on the adult delivering prey to the goshawk nest (male or female). Whole model: n = 133, $x^2 = 4.12$, df = 2, p = 0.04, $R^2 = 0.024$.

Variable	df	x ²	Р
Brood size	1	4.12	0.04

When brood size increased, there was a higher probability that the male goshawk delivered the prey to the nest himself (figure 6).



Figure 6. The effect brood size had on the adult sex delivering the prey to the goshawk nest (male or female). Squirrels are included. Whole model: n = 133, $x^2 = 4.12$, p = 0.04, df = 1, $R^2 = 0.024$.

Plucking of prey

The plucking category was noted for the 130 of the prey items. The plucking categories used were the same as in the study by Aasen (2004). Of the prey items, 19 were of plucking category one, either not plucked, or at most, feathers on one wing and tail had been removed, 57 were of category two, feathers from two wings and from the tail were removed, and the body was slightly plucked, and 54 were of category three, completely plucked with no feathers left, only small amounts of down. Of the six squirrels with noted plucking degree, four were of category one. Of the 124 birds, 15, 55 and 54 were of plucking category one, two and three respectively. There was no significant difference between the plucking degrees in filming period one and two (Likelihood ratio test, n = 130, $x^2 = 4.12$, p = 0.13, df = 2).

In the statistical test of factors affecting plucking degree, the numbers of plucking categories were reduced from three to two; 1 was retained while category 2 was the original category 2 and 3 pooled. The original prey body mass was used; i.e. body mass not corrected for decapitation. Variables with a significant effect on the plucking degree of avian prey were prey body mass and decapitation (table 4). The nestling age, brood size, supplier (male or female) and prey age with their interactions with each other, and with the variables in table 4, were not significant. The non significant variables were eliminated in the following order: nestling age * brood size, original prey body mass * with or without head, supplier * with or without head, supplier * prey age, nestling age * with or without head, nestling age * supplier, brood size * prey age, brood size * supplier, supplier * original prey body mass, supplier, nestling age * original body mass, nestling age * prey age, nestling age, brood size * with or without head, brood size * original body mass, brood size, with or without head * prey age, original body mass * prey age, nest locality as random factor. The variable brood size * original body mass (p = 0.022) was taken out despite of significant value because thought reasonable.

Table 4. Nominal logistic fit of the significant effects on the plucking degree of avian prey. Whole	e model: n =
116, $x^2 = 14.27$, $df = 2$, $p = 0.0008$, $R^2 = 0.17$.	

Variable	df	x ²	Р
Original prey body mass	1	3.13	0.077
Decapitation	1	7.00	0.008

Larger prey were delivered more thoroughly plucked than smaller prey, the probability of more plucking increased with increasing prey mass (figure 7).



Figure 7. The probability of a prey being plucked on delivery at nest, in relation to prey body mass (g). Whole model: n = 122, $x^2 = 7.27$, p = 0.007, df =1, $R^2 = 0.08$. Squirrels are excluded from the test.

Prey that was decapitated on delivery at nest was more likely to be plucked (figure 8).



Figure 8. Plucking category in relation to decapitation of avian prey. Likelihood ratio test: n = 116, df = 1, $x^2 = 11.42$, p = 0.0008, $R^2 = 0.13$. Squirrels are excluded from the test.

Because plucking and decapitation may be part of the same decision taken by the hawk; i.e. decapitation may not be a factor affecting the decision to pluck, the logistic regression analysis for plucking degree was repeated with the same variables except decapitation. Prey body mass remained significant, while brood size entered as a new significant effect (table 5).

Variable	df	x ²	Р
Original prey body mass	1	7.96	0.005
Brood size	1	4.35	0.037

Table 5. Nominal logistic fit of significant effects on the plucking degree of avian prey. Whole model: n = 122, $x^2 = 11.62$, df = 2, p = 0.003, $R^2 = 0.128$.

Brood size had a significant effect on the plucking degree. As brood size increased prey was more likely to be plucked on delivery (figure 9).



Figure 9. The influence brood size had on the plucking degree of a prey. Whole model: n = 122, df = 1, $x^2 = 3.66$, p = 0.06, $R^2 = 0.04$. Squirrels are excluded from the test.

Decapitation

A total of 85 prey were decapitated (n = 124) on delivery, constituting 68.5 % of all preys delivered. Of the mammals 57.1 % were decapitated (n =7), and of the birds 69.0 % (n =117). This difference was not significant (Likelihood ratio test; n = 124, $x^2 = 0.43$, p = 0.51). The original prey body mass was used in the test, i.e. body mass not corrected for decapitation. Whether an avian prey was decapitated or not on delivery, was affected by plucking category, original body mass, prey age (adult or juvenile), supplier (male or female) and nest locality (table 6). The insignificant variables were as follows, and eliminated in the following order: nestling age * plucking category, brood size * original body mass, supplier * original body mass, brood size* prey age, brood size * plucking category, original body mass * prey age, nestling age * prey age, plucking category * original body mass, nestling age * original body mass, plucking category * prey age, nestling age * brood size. The variable nestling age * brood size (p = 0.04) was taken out despite of significant value because thought reasonable.

Table 6. Nominal logistic fit of significant effects on the probability of avian prey being decapitated or not. Whole model: n = 117, $x^2 = 45.0$, df = 6, p < 0.0001, $R^2 = 0.31$.

Variable	df	x ²	Р
Plucking category	2	10.69	0.005
Original body mass	1	7.39	0.007
Prey age (adult or juvenile)	1	6.05	0.014
Supplier (male or female)	1	3.96	0.047
Nest locality (radom factor)	1	5.98	0.014

When avian prey were more thoroughly plucked, the likelihood of the prey being delivered decapitated increased (figure 10).



Figure 10. The probability of decapitation in relation to plucking category of avian prey. Likelihood ratio test: n = 117, df = 2, $x^2 = 20.59$, p < 0.0001.

The probability that an avian prey was delivered decapitated increased with its body mass (figure 11).



Figure 11. The effect body mass (g) had on the probability that avian prey was delivered decapitated. Whole model: n = 117, df = 1, $x^2 = 18.47$, p < 0.0001, $R^2 = 0.128$.

Adult avian prey were significantly more often delivered to the nest decapitated than juvenile avian prey (figure 12).



Figure 12. The probability of decapitation for adult and juvenile prey. Likelihood ratio test: n = 117, df = 1, $x^2 = 6.35$, p = 0.012, $R^2 = 0.044$. Squirrels are excluded from the test.

The sex of the hawk delivering prey to the nest had significant effect on the decapitation of prey (figure 13). Females delivered significantly more often decapitated prey than did males.



Figure 13. The relationship between decapitation and supplier (male or female), delivering prey to the nest. Likelihood ratio test: n = 117, df = 1, $x^2 = 5.02$, p = 0.025, $R^2 = 0.035$. Squirrels are excluded from the test.

Nest locality had a significant effect on the probability that a prey was decapitated on delivery (table 6). This means that the habit of decapitating prey differed between the different goshawk pairs.

Because decapitation and plucking may be part of the same decision taken by the hawk; i.e. plucking may not be a factor affecting the decision to decapitate, the logistic regression analysis was repeated with the same variables except plucking degree. Original body mass, prey age, supplier and locality remained significant in this test, too (table 7).

Table 7. Nominal logistic fit of significant effects on the probability of avian prey being decapitated or not. Whole model: n = 117, $x^2 = 34.3$, df = 4, p < 0.0001, $R^2 = 0.24$.

	-		
Variable	df	\mathbf{x}^2	Р
Original body mass	1	16.46	< 0.0001
Prey age (adult or juvenile)	1	7.77	0.0053
Supplier (male or female)	1	3.77	0.0522
Nest locality (random factor)	1	3.97	0.0047

Feeding time

The feeding time of 70 prey items fed to the nestlings by the female was recorded. The shortest feeding time was 68 sec. and the longest was 2233 s (37 min, 13 s). The mean feeding time for all prey items were 411 ± 46 s, for all avian prey 375 ± 38 s, for thrushes 284 \pm 27 s, for all birds excluding thrushes 626 ± 102 s, and for squirrels 1222 ± 544 s (appendix 7 for details). There was a significant difference between the feeding time of thrushes and that of other avian prey (Oneway Anova n = 67, R² = 0.13, p = 0.0027). There was also a significant difference between the feeding time of squirrels (Oneway Anova n = 70, R² = 0.098, p = 0.0085). There was no significant difference in feeding time between birds other than thrushes and tree pitpit (*Anthus trivialis*) and that of squirrels (Oneway Anova n = 25, R² = 0.102, p = 0.12).

In the statistical test of factors affecting feeding time, two plucking categories were used; category 1 was retained while category 2 was the original category 2 and 3 pooled. Only avian prey were included. The duration of the time the female goshawk spent feeding the nestlings was affected by prey mass and nestling age (table 8). In the stepwise regression the following variables were also tested but not included in the final model: prey age, brood size, plucking category, log10 body mass * nestling age, nestling age * prey decapitated or not, nestling age * prey age, log10 body mass * plucking category, nestling age * plucking category, prey decapitated or not * prey age, log10 body mass * prey age. Nest locality had no significant effect.

Table 8. Stepwise regression model of variables significantly affecting the feeding time of avian prey, when
goshawk females were feeding their nestlings (Log10 transformed, s). Whole model: $n = 67$, $R^2 = 0.509$, $p < 0.509$,
$0.0001 \mathrm{df} = 2.$

Response	Variable	Estimate	SE	df	F	Р
Feeding time	Intercept	1.2917	0.186	1	0.000	
	Prey body mass	0.714	0.09	1	62.87	< 0.0001
	Nestling age	- 0.014	0.0044	1	10.46	0.0019

Feeding time increased with prey body mass (figure 14), and decreased as the nestlings grew older (figure 15).



Figure 14. The effect of prey body mass (g) on feeding time (Log10 transformed, s) for female goshawks feeding their nestlings. Log10 feeding time (s) = $1.13 (\pm 0.19) + 0.66 (\pm 0.09)$ Log10 body mass (g). R² = 0.43, n = 67. Squirrels are excluded from the test.



Figure 15. The effect of nestling age (days) on feeding time (Log10 transformed, s) for female goshawks feeding their nestlings. Log10 feeding time (s) = $2.603 (\pm 0.12) - 0.008 (\pm 0.01)$ nestling age. R² = 0.026, n = 67. Squirrels are excluded from the test.

Feeding efficiency

The prey group with the highest mean feeding efficiency was birds other than thrushes (29.1 g/min), followed by thrushes (23.2 g/min) and squirrels (22.3 g/min). The prey item with the highest feeding efficiency was a juvenile thrush (73.3 g/min) and the prey with the lowest feeding efficiency was a tree pitpit (*Anthus trivialis*) (5.0 g/min) (appendix 7 for details). There was nearly a significant difference between the feeding efficiency of thrushes and that of the other avian prey (Oneway Anova n = 67, R² = 0.057, p = 0.051). The difference between the feeding efficience between the feeding efficience between the feeding efficience between the feeding efficience between the feeding efficiency of all bird prey and that of squirrels was not significant difference between the feeding efficience between the feeding efficience between the feeding efficiency for birds other than thrushes and tree pitpit and that of squirrels (Oneway Anova n = 25, R² = 0.1014, p = 0.12)

In the statistical test of factors affecting feeding efficiency, two plucking categories were used; category 1 was retained, while category 2 was the original category 2 and 3 pooled. Only avian prey were included. The feeding efficiency (g/min.) was only significantly affected by the nestling age (table 9). In the stepwise regression the following variables were also tested but not included in the final model: prey age, log10 body mass, prey decapitated or not, brood size, plucking category, log10 body mass * nestling age, nestling age * prey decapitated or not, nestling age * prey age, log10 body mass * plucking category, nestling age * prey age, log10 body mass * prey age. Nest locality had no significant effect.

Table 9. Stepwise regression model of variables affecting the efficiency of the goshawks feeding on avian prey
(Log10 transformed, g/min). Whole model: $n = 67$, $R^2 = 0.17$, $p < 0.0006$.

Response	Variable	Estimate	SE	df	F	Р
Log10 efficiency	Intercept	1.0114	0.0913	1	0.0	
	Nestling age	0.0168	0.0046	1	13.085	0.0006

There was a positive relationship between feeding efficiency and nestling age (figure 16), as the nestlings became older they were able to consume prey faster.



Figure 16. The relationship between feeding efficiency (Log10 transformed, g/min) and nestling age (days). Log10 efficiency = $1.011 (\pm 0.09) + 0.017 (\pm 0.005)$ Nestling age. R² = 0.168, n = 67. Squirrels are excluded from the test.

Although prey body mass was included in the efficiency estimate, efficiency was still plotted against body mass to visualise the relationship (figure 17).



Figure 17. The relationship between feeding efficiency (Log10 transformed, g/min) and body mass (g) Log10 efficiency = $0.65 (\pm 0.192) + 0.34 (\pm 0.095)$ Log10 body mass. R² = 0.16, n = 67. Squirrels are excluded from the test.

DISCUSSION

Types of prey delivered to the nest

A total of 146 prey items were delivered to the goshawk nests during the study period, 93.1 % birds and 6.9 % mammals. The majority of the prey species were thrushes and corvids, the only mammal species delivered was the red squirrel. The findings are similar to what other studies have found concerning goshawk diet during the nestling period (Opdam et al. 1977, Selås 1989, Tornberg 1997). The fact that 56 % of avian prey items were thrushes contrasts with the dominating share of grouse in the summer diet in the study of Widén (1987), conducted in coniferous forest in central Sweden. The results are, on the contrary, consistent with the results reported by Grønnesby and Nygård (2000), who found thrush-sized birds to be the dominating prey group. The latter study dealt with goshawk nests in mixed forested and agricultural areas, and is therefore more comparable to this study. Squirrels were not very numerous among the prey items in this study. This is probably due to the fact that squirrels are more important to the goshawk's diet in the winter than in the summer (Widén 1987). It is also known that goshawks may act as generalists, taking prey according to availability (Grønnesby and Nygård 2000). Prey delivered to the nest may therefore be looked upon as a sub sample of what is available in the territory (Bañbura et al. 1999).

The female delivered most of the prey to the nest, but the male probably made most of the kills, as it was observed that the male often delivered prey to the female near the nest (pers. obs.). This type of labour division is consistent with current knowledge of the social pattern and behaviour of goshawks (Cramp and Simmons 1980), and with the reversed sexual size dimorphism hypotheses; the female guard the nest while the smaller males forage more energy efficient (Newton 1979).

The proportion of juvenile prey delivered to the nests was less than expected (11 %). It is reasonable to think that nestlings are easy to find and that fledglings are easier to catch due to their lack of experience, as for example broods of corvids are noisy and easy detectable (Tornberg 1997). There may have been some incorrect classification of prey because it is difficult to distinguish between adult and juveniles birds. It should also be noted that most of the juveniles classified are actually recent fledglings. An earlier study of the common buzzard (*Bueto bueto*) also found that few (22 %) juveniles were taken (Tveiten 2004). In contrast, Selås (2001) showed that the majority (59 %) of avian prey, taken by common buzzards were juveniles. Tornberg (1997) have shown that goshawk males have the capability to learn where

nests of their avian prey are situated within their territory. This type of behaviour may enhance nest predation. When looking beyond the difficulties separating between fledglings and adult birds, it may be assumed that the proportion of juveniles in each filming period is comparable. There was only one more juvenile delivered at the nests in period 1 compared to period 2. Selås (1993) also failed to find difference between early and late summer delivery of juveniles in the sparrowhawk (*Accipiter nisus*). At the same time, the probability that a juvenile avian prey delivered was a thrush decreased as the season progressed, i.e. in relation to the number of days after 1 June. At the same time, the probability that an adult avian prey was a thrush remained constant as the season progressed. This result can be explained by the fact that later in the season, it becomes more difficult to catch juvenile prey, as they become better at flying (Newton 1986).

The probability of a thrush being delivered increased when the previous prey delivered was a thrush, and the same was the case for other prey. Steen (2004) also found that the previous delivered prey had an influence on the prey delivered by Eurasian kestrels (*Falco tinnunculus*). This type of behaviour has also been observed in spotted flycatchers (*Muscicapa striata*), where the birds were more likely to return to a specific site if a quick and successful catch had been made there (Davies 1977). This behaviour, where a predator chooses to return to the previous capture site, is not restricted to birds, but has also been observed among mammals (Sonerud 1985). Broods of birds form food patches, and may thus act as such return-sites (Tornberg 1997).

It is possible that not all prey caught by the goshawks were brought to the nest in order to save energy. The goshawk is a single-prey loader, which only carries one prey item per trip to the nest. This type of behaviour favours the delivery of large prey, while smaller prey to a higher frequency would be consumed at the capture site (Bull 1989, Sonerud 1992), as found in the Eurasian kestrels (Sonerud 1989). It is thought that this, to some extent, will overestimate the number of large prey items caught (Sonerud 1992). Selås (1989) on the contrary believes that, in the goshawk's case, the hunting parent will kill a certain proportion of prey too large to carry without eating parts of it, and due to this other animals will take some of the prey items before the prey can be transported to the nest site.

Sex of the supplier which delivered prey to the nest

When the brood size was large, it was more likely that the male goshawk delivered the prey to the nest himself. This labour division between male and female, may indicate that adults with larger broods have a higher food demand which forces the female away from the nest to hunt. Because of this the female is not accessible to receive the prey from the male and the male has to deliver the prey item to the nest himself.

Plucking of prey

When the goshawk has caught and killed a prey it usually plucks the prey on the ground or on a small elevation before bringing it back to the nest (Cramp and Simmons 1980). There are many reasons for plucking the prey outside the nest, among them reducing the risk of diseases and the exposure of the nest site (Rands et al. 2000). Plucking is also an important behaviour that maximises the energy consumption when removing the inedible parts that in some cases, even might be toxic (Kaspari 1990, Rands et al. 2000). When dividing the time available, raptors have to choose between spending more time handling prey or rather spend time searching for more prey (Kaspari 1990).

Processing prey in the field gives the advantage of reduced travelling costs for a single-prey loader (Sodhi 1992). This is supported by Sodhi's (1992) study on merlin (*Falco columbarius*) males, which were more likely to prepare a prey far away from, than near the nest. The study of Booms and Fuller (2003) on the gyrfalcon (*Falco rusticolus*) also found evidence that only certain prey parts were delivered to the nest; prey parts difficult to transport and with little nutrients were more seldom brought to the nest.

I found that as brood size increased, goshawks had the tendency to pluck the prey more thoroughly, the opposite of Barba et al. (1996). This is not in agreement with the fact that time and food demands increase with increased brood size. In a study on great tits (*Parus major*) the preparation increased with prey size and decreased with brood size (Barba et al. 1996). It should, however, be noted that in the study of Barba et al. (1996), the relationship between prey preparation and brood size was not significant when they removed the effects of other variables. Kaspari (1990) makes a prediction in the gut encounter model (a model primarily made with insectivore birds in mind) that preparation should increase with increasing encounter rate. If there is a high density of prey available in the goshawks territories and goshawks in these quality territories have larger broods (Eldegard et al. 2003), this could be an explanatory factor for its plucking behaviour. Aasen (2004) also found that large broods

received decapitated prey more often than small ones, and decapitation of prey can be viewed as a type of plucking behaviour.

I found that prey with large body mass was more thoroughly plucked. This is in agreement with the findings of Aasen (2004), Ponz et al. (1999). The gut encounter model (Kaspari 1990) also predicts that preparation of prey should be more thorough for large prey. Preparation and removal of indigestible parts save room in the gut for more prey (Kaspari 1991). Plucking of larger prey also reduces the transport costs.

Goshawk prey were not less plucked as the nestling became older. Similarly, Sodhi (1992) found that prey preparation did not differ between breeding periods. Newton (1979), on the contrary, found the opposite. I found that the female goshawk continued to feed the young, after they could feed themselves (pers. obs.). This was also observed in the study of Aasen (2004) on the sparrowhawk, and was also found by Newton (1979). A reason for not seeing any tendency of decreased plucking with nestling age may lie in the fact that the female continues to feed the nestlings, and that plucking behaviour facilitates the feeding. Reasons for the female to continue the feeding may be to reduce the aggression between the nestlings (Aasen 2004), and to ensure an even distribution of food (Schnell 1958).

In the present study prey which were thoroughly plucked were more likely to be decapitated. This seems reasonable because the head is often the first part to be removed during plucking of prey (Schnell 1958).

Decapitation

Of the prey delivered to the goshawk nests, 69 % were decapitated. These values are similar to those on the sparrowhawk where 70 % of all prey was decapitated (Aasen 2004). In the Eurasian kestrel only 38 % of avian prey was decapitated (Steen 2004). The goshawks' diet is more similar to the diet of sparrowhawks than to the diet of the Eurasian kestrel, so it is more relevant to compare the values of the goshawk and the sparrowhawk.

The results from the present study showed that females were more likely than males to deliver a decapitated prey at the nest. As gender of the bird catching the prey was not observed in this study, the female deliveries at the nest constitute a combination of prey caught by the female herself, and prey caught by the male. Likewise, the decapitation may have been performed by the male prior to the prey-trade or by the female after the prey-trade. In a study on food habits of goshawks, Schnell (1958) found that if a prey was delivered to the nest without being decapitated, the female would tear off the head first. Male goshawks are also known to often consume parts of large prey, such as grouse heads, prior to delivery at the nest (Tornberg 1997). In the cases were the male goshawks delivered non-decapitated prey to the female, the male may have plucked the prey prior to delivery and the female may have decapitated the prey prior to nest delivery, or the prey may have been neither plucked or decapitated by the male, and the female was left to carry out all the prey handling. In merlins the energy costs of plucking prey constitutes about 50 % less than the flight costs involved with a non-handled prey (Warketin and West 1990). Consequently, the male will profit from decapitating a prey before carrying it back to the nest, but it becomes a trade-off between how to allocate the time and energy.

A predator should feed on the most profitable parts of a prey (Sih 1980). The head of a prey item should therefore be consumed, and the plucking of feathers and feet should rather be left behind, as seen in the behaviour of male sparrowhawks (Aasen 2004). A reason for not delivering the prey's head to the nest may be that it is difficult for the nestlings to consume it.

I found that the probability of decapitation was not affected by nestling age. Aasen (2004) found the same in the sparrowhawk. In contrast, Newton (1986) observed that sparrowhawk males decapitated prey only in the early nestling stages.

In this study, large prey were more often decapitated on delivery than were small prey. Moreover, when a prey was thoroughly plucked it was more likely to be decapitated. These results are identical to those of Aasen (2004) on the sparrowhawk. Decapitation of large prey was also found by Steen (2004) and Barba et al. (1996). One reason for decapitating large prey is the same as for plucking a prey, namely a reduction of travelling costs.

Although raptors tear and dismember a prey item, and thereby are able to consume larger prey than birds which swallow prey items intact, there may be some restrictions on the swallowing capacity of the nestlings. The grasshopper sparrow (*Ammodramus* savannarum) overcomes gap-size limitations through prey preparation (Kaspari 1990). The width-reduction hypothesis predicts that a prey's body parts contributing most to prey width should be removed, because they obstruct swallowing (Kaspari 1990). The skull of a prey item is probably the hardest part for a goshawk nestling to swallow, consequently it should be removed.

Adult avian prey were significantly more often delivered decapitated compared to the juvenile avian prey. Skull hardness may have influenced the decision of whether to decapitate a prey. It is probably easier for the nestlings to handle and swallow the head of juvenile prey due to the fact that the skulls of juvenile prey contain more cartilage, and thus is more pliable than an adult skull (Sonerud pers. comm.). Another reason for not decapitating juvenile prey is the fact that the juvenile beak is short and soft and thereby easier to swallow than an adult beak (Sonerud pers. comm.). Sodhi (1992) failed to find a correlation between prey mass and the transport distance in the merlin. There may be many factors affecting decapitation and transport of prey, and the ability of nestlings to consume certain prey parts and not others may be one of them.

Nest as a random factor turned out to have an effect on the probability of decapitating a prey before delivery. This inter- nest variation in the probability of decapitating may be the distance from the nest at which the goshawks hunt. Goshawks hunting far away from the nest may be more likely to deliver decapitated prey, compared to adults hunting near the nest. The hunting distance from the nest was not recorded in my study, but Sodhi (1992) found that merlins prepared prey more thoroughly when the distance to the nest was large.

Feeding time

The duration of the 70 feeding sequences recorded ranged, from 68 s to 2233 s, with a mean of 411 s. Schnell (1958) recorded 79 feeding sequences of goshawks in Sierra Nevada, ranging from 15 s to 61 min (3660 s), with a mean of 11.5 min (690 s). Feeding time in my study was defined as the time elapsed from when the female bent its head down to take the first piece of a prey item until having finished the last piece (Aasen 2004), and feeding pauses > 5 seconds were subtracted from the feeding time. Schnell (1958) did not define the feeding time. Therefore, a strict comparison of the feeding times, between this study and that of Schnell (1958) is impossible, but the estimates are similar. If Schnell's definition of feeding time failed to subtract feeding pauses > 5 seconds, the estimates from this study and his study would be even more similar.

How much time an individual uses on the different daily tasks is essential for the rearing and survival of offspring. A time budget is fundamental because carrying out one task is a lost opportunity to perform other acts. When measuring the costs related to prey handling behaviour, time is a more appropriate currency than energy (Rovero et al. 2000).

The variation in goshawk feeding time was best explained by prey mass, as it took longer to consume large prey. This agrees with many earlier findings (Kaspari 1990, Bañbura et al. 1999, Kristiansen 2003, Steen 2004, Aasen 2004). A study on the Tengmalms owl (*Aegolius funereus*) also found a longer feeding time when feeding on avian prey compared to other prey types (Kristiansen 2003). This is partly inconsistent with my results, which showed a shorter feeding time for avian prey than for squirrels. It should be noted that there were very few squirrels in my study, and that the diet of the Tengmalms owl is very different from that of the goshawk, never the less, the difference in feeding time between mammals and avian prey is stressed.

The feeding time in my study decreased as the nestlings grew older. Other studies have also found that older nestlings eat faster than younger ones (Kristiansen 2003, Aasen 2004). Reasons for the feeding time to decrease with nestling age may be that the nestlings get more feeding experience, and are able to swallow larger pieces and more hard prey parts, also the female may choose to increase the bite sizes fed to older nestlings. Bañbura et al. (1999) states that, "the ability of chicks to swallow items is certainly size-dependent and changes with age". Aanonsen (2003) found that bite size increased with nestling age in common buzzard. In the sparrowhawk, Andersen (2003) did not find any such increase, while Newton (1986) claimed that pieces did become larger as the young grew. Usually the entire carcass is fed to the nestlings, except a few hard parts that are eaten by the female (Schnell 1958). Prey parts not eaten by small young, such as prey legs, are eaten without problems when they become older (Newton 1979). Aasen (2004) found that the female used less time to feed the nestlings if the brood was large. I found no such pattern, and neither did Booms and Fuller (2003) for gyrfalcons.

Feeding efficiency

Foraging is the main behaviour for survival, and it is reasonable to assume that predators should feed in such a manner as to obtain the greatest possible energy reward per unit time (Schoener 1971 sited in Freeland 1980). An efficient exploitation of available food is, therefore important, and there are many ways of solving the task. Some may prefer prey that, when abundant, gives the greatest energy intake, or some may ignore prey that is difficult to handle or capture (Davies 1977). Ydenberg and Welham (1992) distinguish between the terms "feeding" and "provisioning", and states that the best solution for birds provisioning altricial nestlings is to try to maximize the daily delivery of food.

Many models of foraging behaviour and energy intake look at the relationship between time spent catching, handling and consuming the prey (e.g. Sih 1980, Ydenberg and Welham 1992). There are many definitions of feeding efficiency. In this study, feeding efficiency is defined as grams consumed per minute feeding time (feeding time is taken as defined above).

Whereas the feeding time was shorter for avian prey than for squirrels, feeding efficiency did not differ between these two prey types. Feeding efficiency \approx profitability, given that feeding time equals handling time. However, since handling time which includes plucking, and plucking increased with body mass, the profitability of birds were lower than squirrels and the profitability of larger birds may be overestimated compared to small birds. My findings differ from Aasen's (2004) study on the sparrowhawk, which found that, mammals had a much higher efficiency than avian prey. In this study, efficiency is defined as the ratio between mass eaten and handling time.

The feeding efficiency in this study increased with nestling age, which seems reasonable as the nestlings ate faster as they grew older. My results also fit well with those of Steen (2004) for the Eurasian kestrel, where nestling mass had a positive effect on the handling efficiency, when the female fed the nestlings. In Steen's (2004) study, the handling efficiency included the pooled time spent preparing, feeding and cleaning (Steen 2004). A study by Weathers and Sullivan (1991) also found a positive relationship between foraging efficiency and age, as did that of Aasen (2004). Foraging efficiency in Weathers and Sullivan's (1991) study was defined as the rate of energy gained per hour spent foraging. The current study and those of Aasen (2004), Steen (2004) and Weathers and Sullivan (1991), use different definitions of efficiency, but are still comparable due to the fact that they all include the feeding sequence.

It seems natural that the handling efficiency increases with nestling age, as the young gain proficiency at foraging and become more adapted to feeding. Another explanatory factor is the nutrient demand which increase with age, while the nestlings manage to consume larger pieces of prey (Newton 1979).

Aasen (2004) found that the efficiency was highest for the largest broods. I found no such relation. The reason for this might be that the female fed the nestlings, and that her ability to tear off meat in a certain speed is constant, independent of the brood size.

CONCLUSION

The most important findings of the present study were i) that prey type delivered was affected by the previous prey type delivered to the nest, ii) the chance of the male delivering prey to the nest himself, increased with brood size, iii) plucking and decapitation of prey increased with prey mass, while the probability of a juvenile prey, being decapitated was less than for an adult prey, and females delivered a higher frequency of decapitated prey compared to the males, iv) feeding time increased with prey mass and decreased with nestling age, and v) feeding efficiency also increased with nestling age. There are many factors influencing the decisions made by the goshawk parents. Some of them we partly understand, but many remain to be explored. To my knowledge, the finding related to distinct decapitation of juvenile and adult prey is new, and should be further examined.

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Appendix 1: Hatching date, brood size and hours of filming at each goshawk nest studied

Data on nests

Nest number	Locality	County	Haching date	Brood size period 1	Brood size period 2	Total hours of filming
1	Solbergstrand	Akershus	25 May	4	3	42
2	Tierud	Akerhus	27 May	ю	ς	47
3	Torsnes	Akerhus	18 May	4	4	46
4	Slørstad	Akerhus	2 June	ю	ς	48
5	Himsjø	Buskerud	27 May	ю	ω	49
6	Lurdalen	Buskerud	26 May	7	7	46
7	Løken	Buskerud	31 May	4	4	49
All						327

1							1					
	Period 1		Video					Period 2		Video		
			recordings							recordings		
Locality	Date	Age	Start	Stop	Start	Stop	Hours	Date	Age	Start	Stop Start Stol	Hours
Solbergstrand	1 June	8	08.00	10.00	16.00	20.00	6	25 June	32	00.00	18.30	12
Solbergstrand	3 June	10	00.00	18.00			12	26 June	33	00.00	18.00	12
Tierud	9 June	14	00.00	18.00			12	20 June	25	00.00	18.00	12
Tierud	10 June	15	06.30	18.00			11	21 June	26	00.00	18.00	12
Torsnes	4 June	18	00.00	18.00			12	19 June	33	00.00	18.00	12
Torsnes	5 June	19	00.00	18.00			12	20 June	34	00.00	16.00	10
Slørstad	7 June	9	00.00	18.00			12	27 June	26	00.00	18.00	12
Slørstad	8 June	٢	00.00	18.00			12	28 June	27	00.00	18.00	12
Himsjø	10 June	15	14.00	16.00	20.00	22.00	4	27 June	32	00.00	18.00	12
Himsjø	11 June	16	05.00	18.00			13	28 June	33	00.00	19.00	13
Himsjø	12 June	17	00.00	13.00			7					
Lurdalen	13 June	19	16.00	20.00			4	24 June	30	15.00	17.00 17.30 21.3	05
Lurdalen	14 June	20	13.30	21.30			8	25 June	31	00.00	14.00 15.00 20.3	0 13
Lurdalen	15 June	21	07.00	11.00			4	26 June	32	07.00	13.00	9
Lurdalen	17 June	23	00.00	12.30			9					
Løken	16 June	17	13.00	19.30			9	29 June	30	07.00	15.30	8
Løken	17 June	18	6.00	11.00			5	30 June	31	00.00	18.00	12
Løken	18 June	19	00.00	18.00			12	1 July	32	00.00	12.00	9

Appendix 2: Timetable for video recording and nestling age for the goshawk nest

Appendix 3:

Prey data

		Feeding time	
Species	Recorded	Not recorded	Total
Tree Pitpit, Anthus trivialis	1	0	1
Song Thrush, Turdus philomelos	4	4	8
Redwing, Turdus iliacus	1	1	2
Fieldfare, Turdus pilaris	3	1	4
Common Blackbird, Turdus merula	11	5	16
Mistle Thrush, Turdus viscivorus	1	0	1
Redwing/Song Thrush	16	21	37
Common Blackbird/ Fieldfare	1	1	2
Thrushes Turdus unid.	7	3	10
Eurasian Jay, Garrulus glandarius	5	13	18
Hooded Crow, Corvus cornix	6	9	15
Eurasian Jackdaw, Corvus monedula	0	0	0
Black-billed Magpie, Pica pica	1	3	4
Common Raven, Corvus corax	0	1	1
Corvidae unid.	1	0	1
Great Spotted Woodpecker, <i>Dendrocopos major</i>	1	0	1
Common Wood Pigeon, columba palumbus	2	3	5
Hazel Grouse, Bonansa bonasia	0	1	1
Black Grouse, <i>Tetrao tetrix</i> \bigcirc	0	1	1
Capercaillie, Tetrao urogallus	2	1	3
Grouse unid	0	3	3
Small passerines, Passeriformes	2	0	2
Red Squirrel, Sciurus vulgaris	3	4	7
Unid.	2	1	3.
Sum	70	76	146

Appendix 4: Distribution of prey

Number	%
81	55.5
39	26.7
16	11.0
7	4.8
3	2.1
146	100 .
	Number 81 39 16 7 3 146

Appendix 5: Prey with feeding time

Species	Period 1	Period 2	Total
Tree Pitpit, Anthus trivialis	1	0	1
Song Thrush, Turdus philomelos	3	1	4
Redwing, Turdus iliacus	0	1	1
Fieldfare, Turdus pilaris	2	1	3
Common Blackbird, Turdus merula	10	1	11
Mistle Thrush, Turdus viscivorus	1	0	1
Redwing/Song Thrush	15	1	16
Common Blackbird/ Fieldfare	0	1	1
Thrushes, <i>Turdus</i> unid	6	1	7
Eurasian Jay, Garrulus glandarius	3	2	5
Hooded Crow, Corvus cornix	4	2	6
Eurasian Jackdaw, Corvus monedula	0	0	0
Black-billed Magpie, Pica pica	0	1	1
Common Raven, Corvus corax	0	0	0
Corvidae unid.	0	1	1
Great Spotted Woodpecker, <i>Dendrocopos major</i>	1	0	1
Common Wood Pigeon, columba palumbus	1	1	2
Hazel Grouse, Bonansa bonasia	0	0	0
Black Grouse, <i>Tetrao tetrix</i> \bigcirc	0	0	0
Capercaillie, Tetrao urogallus	2	0	2
Grouse unid.	0	0	0
Small passerines, Passeriformes	2	0	2
Red Squirrel, Sciurus vulgaris	2	1	3
Unidentified	1	1	2.
Sum	54	16	70

Appendix 6: Estimated prey body mass of species recorded as prey at seven goshawk nest in Norway 2005

After Cramp and Simmons (1980), Cramp (1988) and Cramp and Perrins (1994):

	C	2	-
<u> Dpecies</u>	Country	Season	body mass g
Tree Pitpit, Anthus trivialis	Germany	Breeding season	23
Song Thrush. Turdus philomelos	England	May-June	74
Redwing Turdus iliacus	Netherlands	Anril-Mav	63
Fieldfare Turdus nilaris	Norway	All vear	105
Common Blackbird. Turdus merula	Great Britain/Norway	Spring	95
Mistle Thrush, Turdus viscivorus	England	April/August	119
Eurasian Jay, Garrulus glandarius	Norway	Outside breeding season	161
Hooded Crow, Corvus cornix	Norway	August/May	500
Eurasian Jackdaw, Corvus monedula	Netherlands	March/June	235
Black-billed Magpie, Pica pica	England	June/August	213
Common Raven, Corvus corax	Poland	All year	1254
After Selås (2001):			
Great Spotted Woodnecker. Dendrocono	smaior		06
Common Wood Pigeon, <i>columba paluml</i>	Shi		495
Hazel Grouse, Bonansa bonasia			372
Black Grouse, Tetrao tetrix 🖓			925
Red Squirrel, Sciurus vulgaris			300
Estimated:			
Trushes, (Turdus)			84
Redwing/Song Thrush			68
Small passerines, Passeriformes			20
Common Blackbird/ Fieldfare			100
Capercaillie, <i>Tetrao urogallus</i> 2 (partiti	ion off)		500

Category	Ν	Max	Min	Mean	SE
Prey number per day		11	1	3.34	0.18
Feeding time all prey (sec.)	70	2233	68	411.79	45.64
Feeding time, avian prey sec.	67	1464	68	375.48	37.51
Mass, all prey (g.)	145	1254	17.4	167.64	14.18
Mass, avian prey (g.)	138	1254	17.4	162.10	14.74
Feeding time, thrushes Turdus (sec.)	44	818	68	284.93	27.26
Feeding time, other birds (sec.)	26	2233	83	626.50	101.90
Feeding time, squirrels (sec.)	3	2233	365	1222.70	544.62
Feeding efficiency, all prey (g/min)	70	73.26	5.02	25.09	1.85
Feeding efficiency, squirrels (g/min)	3	42.95	7.02	22.26	10.72
Feeding efficiency, avian prey (g/min)	67	73.26	5.02	25.22	1.89
Feeding efficiency thrushes <i>Turdus</i> (g/min)	44	73.26	5.38	23.20	2.46
Feeding efficiency, other birds (g/min)	23	65.16	5.02	29.08	2.77

Appendix 7: Number of prey delivered, feeding time, feeding efficiency and prey body mass

Appendix 8: Prey delivered, supplier, plucking category and decapitation

Category			Ν
Supplier (female or male)	Female = 84	Male = 49	133
Prey type (thrushes <i>Turdus</i> or other birds	Thrushes $= 80$	Other = 59	139
Plucking category	1 =19	2 = 57 3 = 54	130
With or without head	With $= 39$	Without $= 85$	124
Bird or mammal	Bird = 139	Mammal = 7	146
Prey age	Adult = 129	Juvenile =17	146

Appendix 9: Variables used in the analyses

Nominal variables:

Period (1 or 2) Supplier (male or female) Prey species Prey type (thrushes *Turdus /* others) Previous prey type (thrushes *Turdus /* other) New plucking category (1 or 2) Decapitation Bird or mammals Prey age (adult or juvenile)

Continuous variables:

Days after 1 June Nestling age Brood size Prey mass Prey number that day Code locality Feeding time Original mass (not corrected for decapitation) Feeding efficiency (mass / feeding time)

Ordinal variables:

Plucking category (1, 2 or 3)