PREY HANDLING BY A GENERALIST PREDATOR, THE GOLDEN EAGLE (*Aquila chrysaetos*)

BYTTEDYRHÅNDTERING HOS EN GENERALISTPREDATOR, KONGEØRN (*Aquila chrysaetos*)

ESPEN GRØNSDAL

NORWEGIAN UNIVERSITY OF LIFE SCIENCES
DEPARTMENT OF ECOLOGY AND NATURAL RESOURCE MANAGEMENT
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Prey handling by a generalist predator, the golden eagle (*Aquila chrysaetos*)

Photo: E. Grønsdal

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Acknowledgments

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Ås, August 2012

Espen Grønsdal

Abstract

Although the golden eagle (*Aquila chrysaetos*) is a well-studied raptor, there is a lack of studies on its prey handling-behaviour, which is important for understanding its prey selection. I extracted data on four individuals of the golden eagle from video footage, where the golden eagles were fed 32 avian prey, 29 mammalian prey, and 4 pieces of pure meat to see whether the golden eagle handled pure meat different than natural prey. I analysed the plucking and feeding behaviour for each feeding trial. Both number of plucks and plucking time for avian prey increased with prey body mass. It was more efficient for the golden eagle to feed on and handle a mammalian prey than to feed on and handle a similar-sized avian prey. Piece size decreased with increasing prey body mass for both prey types, while a piece from a mammalian prey was twice as large as a piece from a similar-sized avian prey. Further, the amount of non-ingested remains increased with increasing prey body mass, and there were more remains from an avian prey than from a similar-sized mammalian prey. Handling efficiency was higher for pure meat than for avian prey but did not differ from mammalian prey, while feeding efficiency were the same for pure meat and for both prey types. The golden eagles were most likely to start feeding from the breast of avian prey, and from the head of small mammalian prey. Further, the golden eagle were more likely to swallow mammalian prey whole than avian prey, due to more amounts of non-ingested parts in avian prey. Smaller prey were more profitable than larger prey, and mammalian prey were more profitable than avian prey. Thus, based on the cost of prey handling, golden eagles should select smaller prey, and mammals rather than avian when self-feeding.

Sammendrag

Kongeørnen (*Aquila chrysaetos*) er en svært utbredt rovfugl, noe som gjør den til en velstudert art. Likevel finnes det svært få studier på artens byttedyrhåndtering, noe som vil være en viktig faktor i viten om kongeørnens byttedyrseleksjon. Gjennom videoopptak har jeg i dette studiet observert fire ulike kongeørners håndtering av til sammen 31 fugler, 29 pattedyr, og 4 porsjoner rent kjøtt for å undersøke om kongeørnen håndterte rent kjøtt annerledes enn naturlige byttedyr. Jeg analyserte plukke- og spiseadferd for hvert måltid, hvor jeg først fant at antall plukk, samt plukketid økte med økende byttedyrmasse hos fugl. Det var mer effektivt for kongeørnen både å spise og å håndtere et pattedyr, enn å spise og håndtere en tilsvarende stor fugl. Videre fant jeg at bitstørrelsen sank med økt byttedyrmasse for både fugl og pattedyr, og at bitstørrelsen fra et pattedyr var dobbelt så stor som bitstørrelsen fra en tilsvarende stor fugl. Andel ufordøyde rester fra byttedyr økte med økt byttedyrmasse, hvor det var mer rester fra fugl enn for et tilsvarende stort pattedyr. Håndteringseffektiviteten for rent kjøtt var høyere enn håndteringseffektiviteten hos fugl, men lik i forhold til pattedyr, mens spiseeffektiviteten var lik hos både rent kjøtt, fugl og pattedyr. Kongeørnen foretrakk å starte spisingen fra brystpartiet hos fugl, mens hos mindre pattedyr startet kongeørnen spisingen fra hodet. Tilslutt fant jeg at kongeørnen svelget pattedyr hel hyppigere enn fugl, som kan skyldes mindre andel ufordøyelige deler i pattedyr enn i fugl. Mindre byttedyr gav en høyere inntaksrate enn større byttedyr, mens pattedyr gav en høyere inntaksrate enn fugl. Basert på kostnadene ved håndtering av byttedyr, burde kongeørnen foretrekke mindre byttedyr, samt foretrekke pattedyr fremfor fugl.

Contents

1. Introduction

The golden eagle is a powerful generalist raptor with a wide distribution in the Northern Hemisphere (Cramp 1980; Seguin et al. 2001; Jacobsen et al. 2011). The predominant prey in the diet of golden eagles usually are leporids such as hares (*Lepus* spp.), and various galliform birds such as black grouse (*Tetrao tetrix*) and willow ptarmigan (*Lagopus lagopus*) (Bramwell et al. 1987; Whitfield et al. 2009; Bourke et al. 2010). However, the prey size ranges from small rodents, reptiles (*Reptilia*) and passerine avian to larger avian species, calf of reindeer (*Rangifer tarandus*) and deer (*Cervidaes* spp.) (Bloom & Hawks 1982; Seguin et al. 2001). In some countries, such as Norway and Finland, domestic sheep and reindeer are significant in the diet of the golden eagle (Haftorn 1971; Cramp 1980; Nybakk et al. 1999; Warren et al. 2001; Norberg et al. 2006; Olav Hjeljord pers. comm.). There are also observations of golden eagles killing other predators such as red fox (*Vulpes vulpes)*, other raptors and even cubs from brown bear (*Ursus arctos*) (Tjernberg 1981; Sulkava et al. 1984; Ellis et al. 2000; Sørensen et al. 2008; Lourenco et al. 2011). While the diet of the golden eagle consist mainly of avian prey by number, it consist of 56 % mammalian prey by mass (Hagen 1952; Tjernberg 1981; Seguin et al. 2001; Slagsvold et al. 2010).

Though numerous studies has estimated the diet of golden eagles (Sulkava & Rajala 1966; Tjernberg 1981; Collopy 1983; Sulkava et al. 1984; Watson et al. 1992; Whitfield et al. 2009), few have observed the prey handling of golden eagles (Slagsvold et al. 2010). Understanding the prey handling and handling efficiency is essential in understanding prey selection of the golden eagle, as well as being important in the management of the main prey species and hence management of the golden eagle per se (Skouen 2012).

Studying prey handling-behaviour among raptors held temporarily in captivity has some advantages over studying prey handling-behaviour of raptors in the wild. Slagsvold et al. (2010) state that for raptors handling their prey in the wild, there are at least four reasons why the prey is not entirely ingested: it is satisfied, the raptors is disturbed during the meal, and flees before being finished; it may be less efficient in extracting more meat from the current carcass, than in finding and capturing a new prey; and the last remains may be difficult to digest, or not be worth eating. For raptors held in captivity will the factors 1-3 be minimize or even eliminated: 1. When satisfied, the raptors can be given the remaining prey at their next meal, 2. Since the raptors are held in captivity, there are no other factors inflicting the handling. When the raptors are disturbed by outside noise like sound from cars or barking from dogs, they could soon continue feeding from the same prey, 3. There is no other food available for the raptors apart from the feed prey giving no option searching for a new prey (Slagsvold et al. 2010). Other advantages of studying prey handling in captivity are that it is easier to identify the prey and quantify the mass and the remaining mass of each eaten prey, while prey in the wild could be plucked one place before it is transported into a new place.

In this study I examined the prey handling-behaviour of golden eagles held in temporal captivity and fed various types of prey, by analyzing video footage. I aimed to test the following hypotheses: 1) Number of plucks and plucking time increases with increasing prey body mass,

2) Feeding efficiency, handling efficiency and piece size decreases with increasing prey body mass, 3) The mass of non-ingested remains of prey increases with increasing prey body mass, 4) Feeding efficiency and handling efficiency is higher for handling a piece of pure meat than a natural prey, 5) Prey mass affects the golden eagles choice in where to start feeding on a prey, and 6) Were there any difference among the different prey types (i.e. mammalian and avian) in these hypothesis?

2. Methods

2.1 Study design

My study was based on video footage conducted by H. Grønlien at a facility for rehabilitation of injured raptors at Fåberg in Norway during 2007 – 2012. The rehabilitation is in accordance with the institutional guidelines from National Authorities (Salmila 2011). In my study, I have included video footages of two golden eagles used in a previous study (Slagsvold et al. 2010), and added two other individuals which were found and recorded respectively in March - April 2011 and in February 2012. The four golden eagles used in this study were three males (in their second, third and fourth calendar years) and one female (in her fifth calendar year), and are hereafter identified as 2KM, 3KM, 4KM and 5KF. Sex and age was determined from plumage colour, wing length and body mass (Slagsvold et al. 2010; H. Grønlien pers comm.). The two oldest golden eagles (4KM and 5KF) were found injured alongside railroad tracks, plausibly hit by train (H. Grønlien pers obs.), while the two youngest golden eagles were found unable to fly due to injuries of unknown reasons (2KM) and from of emaciation (3KM).

2.2 Prey

There were a total of 61 prey that were given to the eagles, split into 32 avian prey and 29 mammalian prey with a wide range in both species and size. Each prey were presented on a pallet, where medium-sized prey (i.e. magpie (*Pica pica*), red squirrel (*Sciurus vulgaris*) and Norway rat (*Rattus norvegicus*)) occasionally were tied (n = 8) at the pallet to prevent the golden eagle from removing the prey from the recording spot. When a golden eagle finished a meal of a large prey, remains of the prey were removed and kept in a refrigerator until the next feeding trial (Slagsvold & Sonerud 2007; Slagsvold et al. 2010). Prey were presented repeatedly until the golden eagle finished or refused the prey. Slagsvold & Sonerud (2007) stressed that biological realistic prey were used for each different raptors in their material, which also was represented in the prey being fed to the golden eagles, although realistic prey is a wide term when it comes to a golden eagle. The avian prey size differed from Eurasian siskin (*Carduelis spinus*) at 9.6 g to grey heron (*Ardea cinerea*) at 1402 g, while the mammalian prey size differed from wood mouse (*Apodemus sylvaticus*) at 12.9 g to red fox at 7500 g. In addition, two eagles were given 4 pieces of pure meat without bones, from moose (*Alces alces*) and roe deer (*Capreolus capreolus*) to see how they handled food with minimal handling costs and to compare the feeding efficiency and handling efficiency with avian prey and mammalian prey. No external or alternative food was available during the feeding study. All prey were either found dead in traffic or brought by hunters and volunteers whom found them dead in nature (Slagsvold et al. 2010; H.Grønlien pers. comm.). Each prey was identified to species and weighed before and after the presentation to find the ingested mass. Ejected pellets were not controlled because it is difficult to measure and assign pellets to prey (Slagsvold & Sonerud 2007; Salmila 2011).

2.3 Video analysis

The observation and examination of the video recordings were made by watching videotapes of the four individual golden eagles being fed. I counted the number of plucks the golden eagles made during preparation of the prey, and the number of pieces the eagles tore apart from each prey. I then measured feeding time and plucking time to find the feeding efficiency (i.e. prey mass (g) ingested per feeding time (min)) and handling efficiency (i.e. prey body mass (g) ingested per handling time (min) (plucking time and feeding time pooled)) of each prey. Ingested prey mass was used in calculating feeding efficiency, whereas prey body mass was used in calculating handling time. During observation of the prey handling, pauses which extended >5 s were excluded from the result to avoid any effect of disturbance. The body mass of different prey that were fed to the golden eagles were already recorded, both before and after the meals (Slagsvold & Sonerud 2007; Slagsvold et. al 2010; H. Grønlien unpublished data). From this I found the mean mass of each torn piece, by first measuring the mass of the prey that were ingested and then dividing the ingested mass by the number of pieces which was torn off. Non-ingested prey remains were calculated based on weighting prey body mass before and after feeding. Further, I observed on which part of the prey the golden eagles first started to feed, to find from which part of the prey the golden eagle preferred to start feeding.

For further details of prey and prey types, see appendix.

2.4 Statistics

The analyses were performed by the program R version 2.14.2 (R Development Core R Development Core Team 2012). In the tests with the continuous data as response, I used a linear mixed effect model (LME from the package “NLME”) were each variable were $\log_{10}$ transformed to attain a normal distribution. The response variables were: (1) plucking time, (2) feeding efficiency, (3) handling efficiency, (4) piece size, and (5) mass of non-ingested prey remains. Since there were few mammalian prey that were plucked, the mammalian prey plucking time were excluded from the test. For all the five tests the explanatory variables were prey mass, prey type (avian or mammalian) and the interaction between prey mass and prey type. The identities (ID) of the golden eagles were included as a random effect to control for repeated measurements and variation associated with each of the individuals.

Further, when comparing pure meat versus avian prey and mammalian prey, regarding feeding efficiency and handling efficiency, the explanatory variables were prey type (meat or avian prey, and meat or mammalian prey) and the response variable were feeding efficiency and handling efficiency.

I also tested if prey swallowed whole differed in size body mass compared to prey being eaten in pieces (mammalian prey only, because too few avian were swallowed whole (n = 4)). Further, I tested if the mass of mammalian prey differed between whether the golden eagle start feeding from the head or other body parts (mammalian prey only, because too few avian prey was started from the head (n = 2)). The response variable was for both tests prey mass, and explanatory variables were swallowed whole versus consumed in pieces for the first test, and start feeding from the head versus other body parts for the latter. ID was included as random effect.

For count data (poisson distribution), I used a generalized linear mixed effect model (GLMM (LMER) from the lme4 package) with the number of plucks as a response variable, where avian prey body mass were used as explanatory variable. Mammalian prey were excluded from the number of plucks as a results of few data (n = 4). ID was included as random effect.

Logistic regression model was also used for testing the binominal data. I tested if the golden eagle was more likely to start feeding from the breast compared to other body parts of the prey when feeding on avian prey compared to mammalian. Explanatory variable were avian versus mammalian prey type, while ID was included as random effect. Logistic regression was only used in testing the feeding start from breast, because the wide distribution on few data made it impossible in testing feeding start from the head or swallowed whole by logistic regression, and was thus used in a linear mixed effect model.

When I used the parameters from different analyses to predict different values (e.g. handling efficiency), I estimated values based on the median prey body mass in both avian and mammalian prey, along with the maximum and minimum prey body mass in both prey types. Because the wide distribution of body mass for both prey types, a mean value would have been less accurate than using the median. Further, I used a prey mass of 300 g to compare different values from the parameters of avian prey and mammalian prey. This prey body mass was chosen because both mammalian prey (i.e. red squirrel, 299 g) and avian prey (i.e. feral pigeon, 297 g) were represented, and because the prey body mass fits with the required daily ration of an adult golden eagle (Fevold & Craighead 1958; McGahan 1967).

3. Results

3.1 Effect of avian prey mass and prey type on number of plucks

When the golden eagles plucked avian prey, prey body mass affected the number of plucks, where the number of plucks increased with avian prey body mass (Table 3.1, Fig. 3.1). Based on the parameters, the predicted numbers of plucks for avian prey were 15 for a prey with body mass of 9.6 g and 648 plucks for a prey with body mass of 1402 g. The predicted number of plucks for an avian prey with median mass (481 g) was 290.

Table 3.1 Parameter estimates from the GLMM model of number of plucks as function of avian prey body mass, with avian prey mass ($\log_{10}$ transformed) as intercept (n = 32, ID = 4 t).

Explanatory variable	**Estimate**	**SE**	**z**	**p**
Intercept	1.03	0.11	9.09	<0.001
Prey mass	1.73	0.03	51.47	<0.001

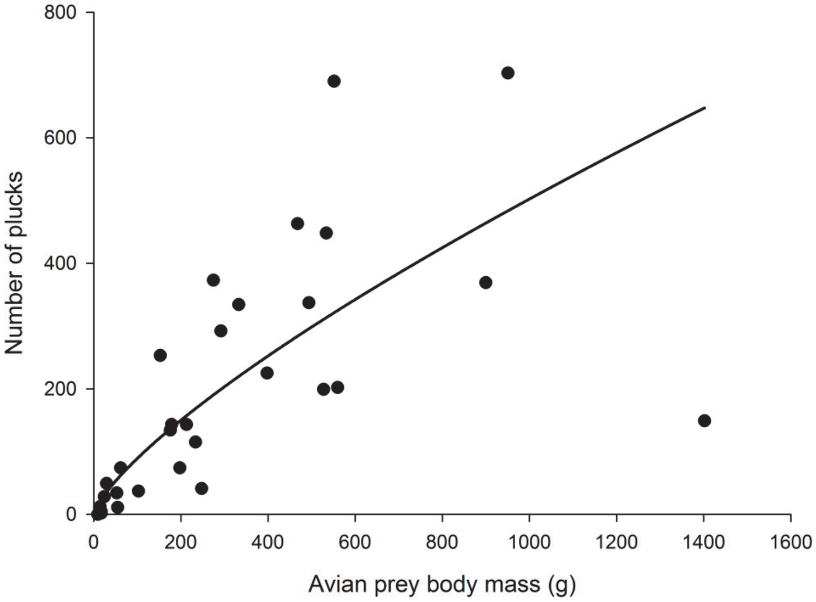


Figure 3.1 Number of plucks as function of avian prey body mass (g) ($\log_{10}$ transformed), with regression line calculated from the GLMM model (y = 1.03 + x*1.73, n = 32, p = <0.001).

3.2 Effect of avian prey mass on plucking time

Based on a LME model of factors affecting plucking time ($\log_{10}$ transformed), prey body mass had a significant effect for avian prey (Table 3.2, Fig. 3.2).

Table 3.2 Parameter estimates from the LME model. Plucking time (min) as function of prey body mass ($\log_{10}$ transformed), with avian prey as intercept (n = 32, ID = 4).

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	-2.15	0.27	27	-8.05	<0.001
Prey mass	1.15	0.12	27	9.61	<0.001

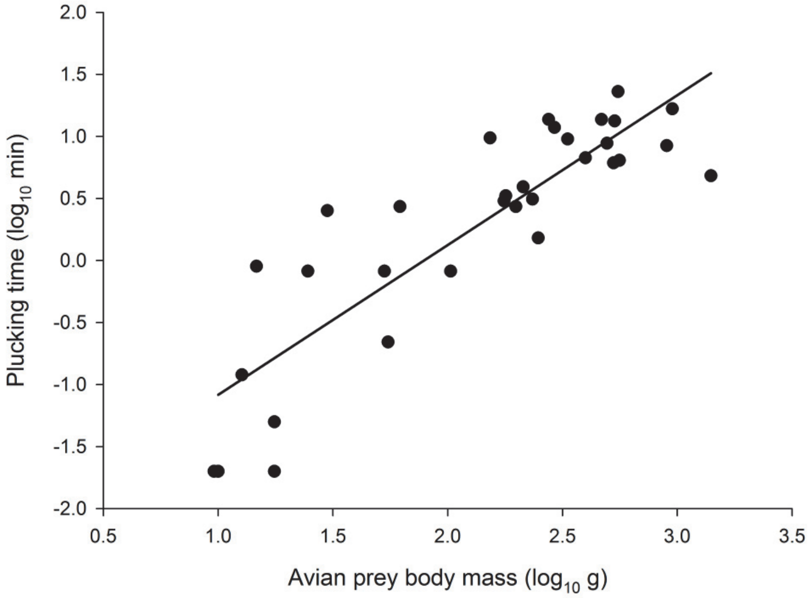


Figure 3.2 Plucking time (min) as function of avian prey body mass (g) ($\log_{10}$ transformed), with regression line calculated from the LME model (y = -2.15 + x*1.15, n = 32, p = <0.001).

Plucking time increased with avian prey body mass (Fig. 3.2). The parameters predicted a plucking time of 0.07 min for a prey body mass of 9.6 g and 30.0 min for a prey body mass of 1402 g. The predicted plucking time for a median-sized avian prey (481 g) was 8.7 min.

3.3 Effect of prey mass ingested and prey type on feeding efficiency

Based on a LME model of factors affecting feeding efficiency ($\log_{10}$ transformed), feeding efficiency decreased with prey mass for both avian and mammalian prey, and the effect of prey mass on feeding efficiency did not differ between the two prey types (Table 3.3., Fig. 3.3).

Table 3.3 Parameter estimates from the LME model (n = 61, ID = 4) of feeding efficiency (mass consumed per feeding time) as function of prey mass ($\log_{10}$ transformed), with a) avian prey as intercept (n = 32), and b) mammalian prey as intercept (n = 29).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	2.31	0.17	54	13.58	<0.001
Prey mass	-0.41	0.07	54	-5.49	<0.001
Prey type (mammal)	0.57	0.21	54	2.75	0.01
Prey mass x prey type (mammalian)	-0.10	0.09	54	-1.05	0.30

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	2.88	0.14	54	21.18	<0.001
Prey mass	-0.50	0.06	54	-8.54	<0.001
Prey type (avian)	-0.57	0.21	54	-2.75	0.01
Prey mass x prey type (avian)	0.10	0.09	54	1.05	0.30

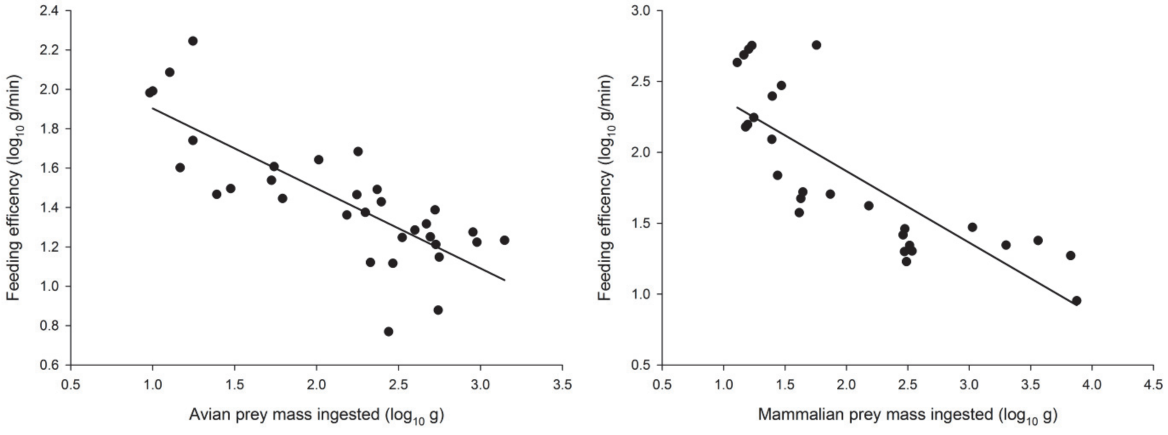

a) b)

Figure 3.3 Feeding efficiency (mass consumed per feeding time) as function of prey mass (g) (log$_{10}$ transformed), with regression line calculated from the LME model. a) Avian prey (y = 2.31- x*0.41, n = 32, p = <0.001), and b) mammalian prey (y = 2.88-x*0.50, n = 29, p = <0.001).

From the parameters, the predicted feeding efficiency for an avian prey was 81.2 g ingested per min for an ingested prey mass of 9.6 g, 10.7 g ingested per min for an ingested prey mass of 1402 g, and 15.6 g ingested per min for a median avian prey (481 g). For mammalian prey the predicted feeding efficiency was 207.1 g ingested per min for an ingested prey mass of 12.9 g, 8.6 g ingested per min for an ingested prey mass of 7500 g and 32.9 g ingested per min for a median mammalian prey (494 g). For an ingested prey mass of 300 g, the feeding efficiency was predicted to be 20.1 g per min for an avian prey, and 42.4 g for a mammalian prey.

For prey that were swallowed whole, feeding efficiency increased with ingested prey mass, as shown by the data points to the upper left in Fig. 3.3.

3.4 Effect of prey mass and prey type on handling efficiency

Handling time was measured as plucking time and feeding time pooled. Based on a LME model of factors affecting handling efficiency ($\log_{10}$ transformed), handling efficiency decreased with prey body mass for both avian and mammalian prey, and the effect of prey body mass on handling efficiency did not differ between the two prey types (Table 3.4, Fig. 3.4).

Table 3.4 Parameter estimates from the LME model (n = 61, ID = 4) of handling efficiency (mass consumed per plucking time and feeding time pooled) as function of prey body mass ($\log_{10}$ transformed), with a) avian prey as intercept (n = 32), and b) mammalian prey as intercept (n = 29).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	1.98	0.21	54	9.54	<0.001
Prey mass	-0.35	0.09	54	-3.81	<0.001
Prey type (mammal)	0.91	0.25	54	3.58	<0.001
Prey mass x prey type (mammalian)	-0.17	0.12	54	-1.48	0.14

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	2.89	0.17	54	17.50	<0.001
Prey mass	-0.52	0.07	54	-7.14	<0.001
Prey type (avian)	-0.91	0.25	54	-3.58	<0.001
Prey mass x prey type (avian)	0.17	0.12	54	1.48	0.14

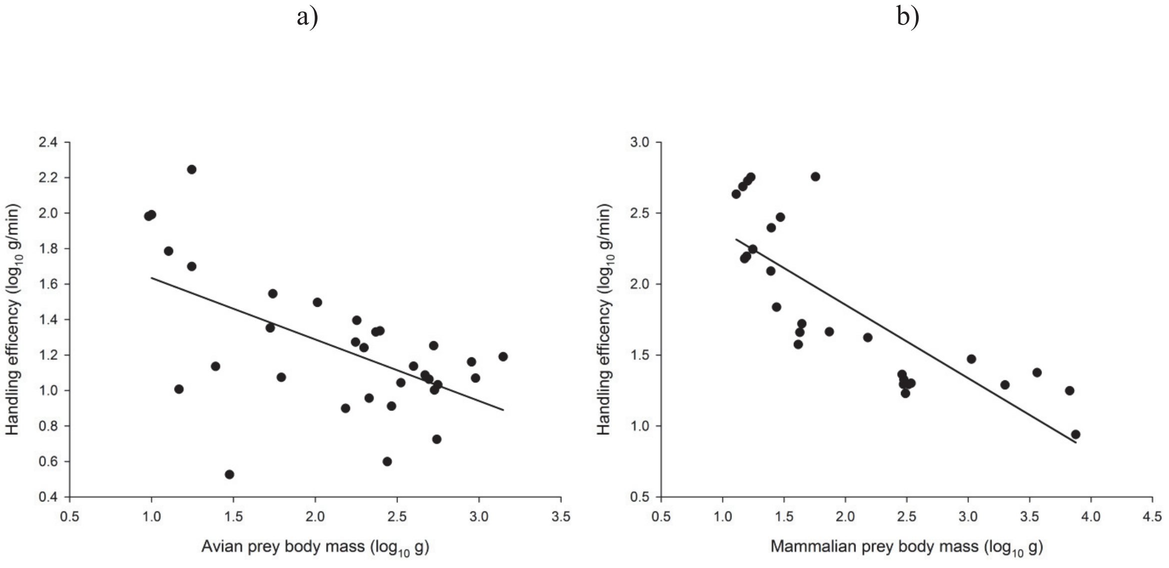


Figure 3.4 Handling efficiency (mass consumed per plucking time and feeding time pooled) as function of prey body mass (g) (log$_{10}$ transformed), with regression line calculated from the LME model. a) Avian prey ($y = 1.98\text{-}x*0.35$, $n = 32$, $p = <0.001$), and b) mammalian prey ($y = 2.89\text{-}x*0.52$, $n = 29$, $p = <0.001$).

Based on the parameters, the predicted handling efficiency for avian prey was 43.7 g ingested per min for a prey body mass of 9.6 g, 7.8 g ingested per min for a prey body mass of 1402 g, and 11.3 g ingested per min for a median avian prey (481 g). For mammalian prey the predicted handling efficiency was 206.4 g ingested per min for a prey body mass of 12.9 g, 7.6 g ingested per min for a prey body mass of 7500 g and 31.3 g ingested per min for a median mammalian prey (494 g). For prey body mass of 300 g, the handling efficiency was predicted to be 13.3 g per min for an avian prey, and 40.5 g for a mammalian prey.

3.5 Effect of prey mass ingested and prey type on piece size

From the LME model of factors affecting piece size ($\log_{10}$ transformed), piece size decreased with prey mass for both avian and mammalian prey, and the effect of prey mass on piece size did not differ between the two prey types (Table 3.5, Fig. 3.5).

Table 3.5 Parameter estimates from the LME model (n = 61, ID = 4) of piece size (g) as function of prey mass ($\log_{10}$ transformed), with a) avian prey as intercept (n = 32), and b) mammalian prey as intercept (n = 29).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	1.35	0.16	54	8.43	<0.001
Prey mass	-0.48	0.07	54	-6.88	<0.001
Prey type (mammalian)	0.35	0.19	54	1.79	0.08
Prey mass x prey type (mammalian)	-0.01	0.08	54	-0.06	0.95

b)

Explanatory variable	Estimate	SE	DF	t	p
Intercept	1.70	0.13	54	13.29	<0.001
Prey mass	-0.48	0.06	54	-8.71	<0.001
Prey type (avian)	-0.35	0.19	54	-1.79	0.08
Prey mass x prey type (avian)	0.01	0.09	54	0.06	0.95

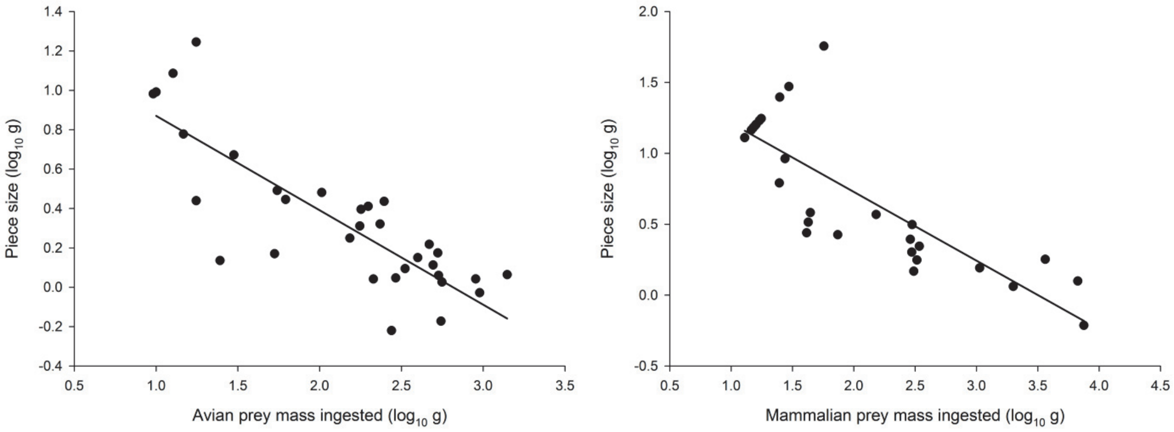

a) b)

Figure 3.5 Piece size (g) as function of prey mass (g) ($\log_{10}$ transformed), with regression line calculated from the LME model. a) Avian prey (y = 1.35-x*0.48, n = 32, p = <0.001) and b) mammalian prey (y = 2.89-x*0.52, n = 29, p = <0.001).

Based on the parameters, the predicted piece size for avian prey was 7.6 g for an ingested prey mass of 9.6 g, 0.7 g for an ingested prey mass of 1402 g, and 1.2 g for a median avian prey (481 g). For mammalian prey the predicted piece size was larger than 12.9 g for an ingested prey mass of 12.9 g, which can be explained that smaller prey were swallowed whole, 0.7 g for an ingested prey mass of 7500 g and 2.5 g for a median mammalian prey (494 g). For an ingested prey mass of 300 g, the piece size was predicted to be 1.5 g for an avian prey, and 3.1 g for a mammalian prey. The average piece size for pure meat was 3.6 ± 1.1 g (range 2.2 – 4.9 g, n = 4).

For prey swallowed whole, piece size by definition increased with prey body mass, as shown by the data points at the upper left in Fig. 3.5.

3.6 Effect of prey mass and prey type on the mass of non-ingested prey remains

Based on a LME model of factors affecting the mass of non-ingested remains ($\log_{10}$ transformed), the mass of non-ingested remains increased with prey body mass for both avian and mammalian prey, and the effect of prey body mass on the amount of remains did not differ between the two prey types (Table 3.6, Fig 3.6).

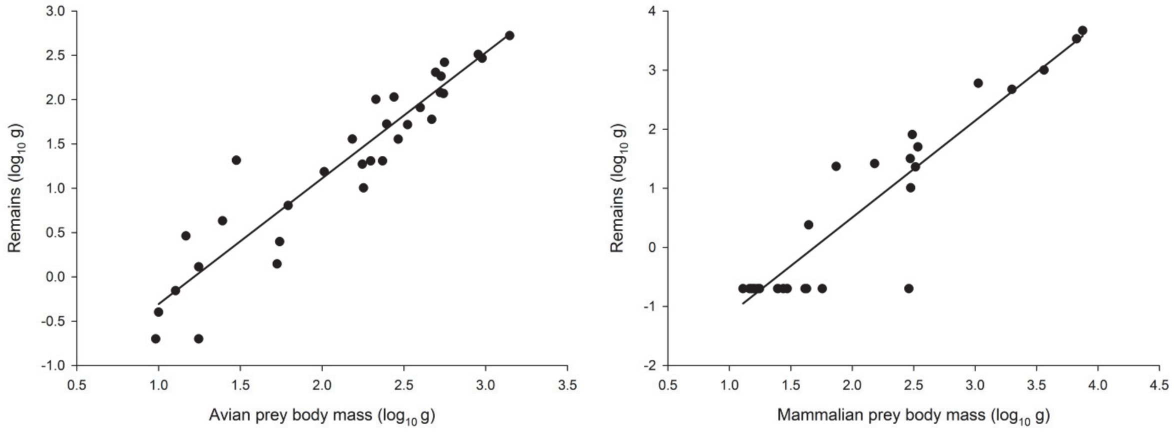
Table 3.6 Parameter estimates from the LME model (n = 61, ID = 4) of remains (g) as function of prey body mass, with a) avian prey as intercept (n = 32), and b) mammalian prey as intercept (n = 29) (all $\log_{10}$ transformed).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	-1.73	0.29	54	-6.00	<0.001
Prey mass	1.42	0.13	54	11.23	<0.001
Prey type (mammalian)	-1.04	0.35	54	-2.95	0.005
Prey mass x prey type (mammalian)	0.22	0.16	54	1.36	0.18

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	-2.77	0.23	54	-12.15	<0.001
Prey mass	1.64	0.10	54	16.26	<0.001
Prey type (avian)	1.04	0.35	54	2.95	0.005
Prey mass x prey type (avian)	-0.22	0.16	54	-1.36	0.18


a)

b)

Figure 3.6 Mass of non-ingested remains (g) as function of prey body mass (g) ($\log_{10}$ transformed), with regression line calculated from the LME model. a) Avian prey ($y = -1.73+x*1.42$, $n = 32$, $p = <0.001$), and b) mammalian prey ($y = -2.77+x*1.64$, $n = 29$, $p = <0.001$).

There were more remains from an avian prey than from a mammalian prey. Based on the parameters, an avian prey median mass (481 g) was predicted to give 25.3% of the mass as remains, while a median mammalian prey (494 g) was predicted to give 8.8% of the mass as remains. At 300 g prey body mass for both prey types, the prediction was 20.5% of the mass as remains for avian prey and 6.4% of the mass as remains for mammalian prey.

3.7 Effect of pure meat and prey type on feeding efficiency and handling efficiency

Based on the parameters in the LME model, no significant differences was found in feeding efficiency when comparing pure meat from avian or mammalian prey (Table 3.7).

Table 3.7 Parameter estimates from the LME model (n = 65, ID = 4), of feeding efficiency (mass consumed per feeding time) ($\log_{10}$ transformed) as function of prey type; mammalian prey (n = 29), avian prey (n = 32), and pure meat (n = 4), with prey types as intercepts.

Explanatory variable	**Estimates***	**SE**	**DF**	**t**	**p**
Mammalian prey vs. avian prey	0.42	0.11	59	3.88	<0.001
Pure meat vs. avian prey	0.34	0.22	59	1.55	0.13
Pure meat vs. mammalian prey	-0.07	0.22	59	-0.32	0.75

* Difference in the intercept

Handling efficiency, however, was significantly higher for pure meat than for avian prey, but did not differ significantly between mammalian prey and pure meat (Table 3.8).

Table 3.8. Parameter estimates from the LME model (n = 65, ID = 4), of handling efficiency (mass consumed per handling time) ($\log_{10}$ transformed) as function of prey type; mammalian prey (n = 29), avian prey (n = 32), and pure meat (n = 4) with prey types as intercepts.

Explanatory variable	**Estimates***	**SE**	**DF**	**t**	**p**
Mammalian prey vs. avian prey	0.60	0.12	59	5.23	<0.001
Pure meat vs. avian prey	0.54	0.24	59	2.25	0.03
Pure meat vs. mammalian prey	-0.07	0.24	59	-0.27	0.79

* Difference in the intercept

3.8 From which part of the prey did feeding start?

3.8.1 Feeding start from the breast

From the parameters in the GLMM model (Table 3.9), the probability that the golden eagles started feeding from the breast of their prey was significantly higher for avian prey than for mammalian prey. From the parameters estimates the probability of feeding start from the breast was predicted to be 74 % for avian prey and 13 % for mammalian prey. Prey body mass were excluded from the test, due to minor effect of prey body mass from both prey types.

Table 3.9 Parameter estimates from the GLMM model (n = 58, ID = 4), of the probability that feeding started from the breast of the prey as function of prey type, with a) avian prey as intercept, and b) mammalian prey as intercept.

a)

Explanatory variable	**Estimate**	**SE**	**z**	**p**
Intercept	-1.05	0.44	-2.39	0.02
Prey type (mammalian)	3.00	0.87	3.42	<0.001

b)

Explanatory variable	**Estimate**	**SE**	**z**	**p**
Intercept	1.95	0.76	2.57	0.01
Prey type (avian)	-3.00	0.87	-3.43	<0.001

3.8.2 Feeding start from the head

Based on the parameters from the LME models, the mammalian prey the golden eagle started to feed from the head were significantly smaller than mammalian prey where the golden eagles started from other body parts (Table 3.10). Mammalian prey where the golden eagle started to feed from the head was predicted to weigh 60.1 g, while mammalian prey where the golden eagles started from other parts of the body were predicted to weigh 1159.2 g.

Table 3.10 Parameter estimates from the LME model (n = 27, ID = 4) of difference in prey body mass ($\log_{10}$ transformed) between mammalian prey where the golden eagles started to feed from the head and those where the golden eagles started to feed from other body parts, with a) feeding start from the head as intercept, and b) feeding start from other body parts as intercept.

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	1.78	0.19	11	9.61	<0.001
Feeding start (other)	1.28	0.26	11	4.91	<0.001

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
Intercept	3.06	0.19	11	16.55	<0.001
Feeding start (head)	-1.28	0.26	11	-4.91	<0.001

3.8.3 Swallowed whole

Based on the parameters from the LME models, the mammalian prey that the golden eagle swallowed whole were significantly smaller than mammalian prey being consumed in pieces (Table 3.11). From the parameters, predicted prey body mass was 19 g when mammalian prey were swallowed whole, and 317 g when mammalian prey were consumed in pieces.

Table 3.11 Parameter estimates from the LME model (n = 27, ID = 4) of difference in prey body mass ($\log_{10}$ transformed) between mammalian prey that the golden eagles swallowed whole and those that the golden eagles consumed in pieces, with a) swallowed whole as intercept, and b) consumed in pieces as intercept.

a)

Explanatory variable	Estimate	SE	DF	t	p
Intercept	1.27	0.24	22	5.39	<0.001
Consumed in pieces	1.23	0.27	22	4.50	<0.001

b)

Explanatory variable	Estimate	SE	DF	t	p
Intercept	2.50	0.20	22	12.28	<0.001
Swallowed whole	-1.23	0.27	22	-4.50	<0.001

4. Discussion

4.1 Sources of biases

The golden eagles that were fed in temporally captivity were shielded from natural factors, such as competition from other predators or other natural interruptions. The golden eagles also had no other available food sources and had to focus on the prey being fed, instead of leaving and finding a new prey (Slagsvold et al. 2010). These factors could affect an increased proportion of ingested prey and a shorter handling time, due to the decreased need for vigilance: when the golden eagles were interrupted in their feeding, they could continue after a short break (Slagsvold et al. 2010; pers. obs.). However, it is plausible that the four golden eagles had not adapted to the safe environment in this short period being fed, and was still behaving like wild golden eagles (cf. Salmila 2011).

It is possible that the eight prey that were tied made the prey less efficient to handle and thus less profitable than it would have if not being tied (R. Steen pers. comm.). Because some prey were occasionally removed from the recording spot, the associated remains may therefore have been spread around and left out from the weighing and analyses of the prey remains, resulting a possible underestimation of the remains. Larger prey, such as mountain hare (*Lepus timidus*) and red fox, were not tied because they were too heavy for the golden eagles to remove, while passerines and smaller rodents were not tied since they were ingested right away, often by being swallowed whole.

Depending on prey selection in an area, some golden eagles may adapt to be more specialized on particularly prey categories which could lead to different prey handling-behaviour (Tjernberg 1981). However, the four golden eagles in my study were found in Southeast Norway, leaving minor or no differences in the natural prey selection.

Being a large raptor with a voluminous plumage, the feeding behaviour of the golden eagles was often difficult to observe when the golden eagles were positioned with their back to the camera. Separating between counting plucks and counting pieces was in some cases entirely dependent on separating the plucking sound from the tearing sound. There were no recorded sounds in the video of the two most recent golden eagles that were video recorded, due to complications with new video recording equipment. Hence, for these two golden eagles it was even more challenging to separate plucking and feeding, where I had to interpret the handling behaviour to separate plucking from feeding. I assume that my counting was both valid and correct, though it may be some minor biases in some of the counting. The difficulty in observing the golden eagles when they were positioned away from the camera also inflicted the sample for the test of where the golden eagles started to feed from the prey, leaving fewer prey in these tests than the other tests.

One of the golden eagles was fed and recorded in an outdoor aviary during winter. Sunshine on a snow-covered ground, made a very bright light on the video, which made it difficult to see details in the video.

The predicted values based on the parameters were in some cases inflicted by the wide distribution of prey body mass in the data set. In number of plucks for instance, the model predicts that a golden eagle used 15 plucks to finish preparation of a 9.6 g avian prey. However, no avian prey that were plucked 15 times fell below a body mass of 24.6 g (pers. obs.).

4.2 Effect of avian prey mass on number of plucks and plucking time

The number of plucks increased with avian prey body mass. Due to the swallowing threshold, smaller avian prey were either not plucked or plucked fewer times than a large avian prey. The swallowing threshold state that prey should not be prepared unless it is too large for the predator to ingest whole and preparation time is a function of the prey width (Kaspari 1990). Smaller avian prey have often a more fragile body than a larger avian prey with a stronger skeleton (Salmila 2011), and contributes to the correlated number of plucks and avian prey body mass. The golden eagle only plucked from three larger mammalian prey, for creating an opening in the prey to feed from (pers. obs.).

Plucking time increased with increased avian prey body mass, which fits with results from other studies (Salmila 2011; Skouen 2012), as well as the feeding constraint hypothesis which states that increasing prey body mass will lead to increased preparation (Steen et al. 2010). The amount of undigestible parts of an avian prey, such as feathers, entrails and bones increased with prey body mass, which led to more plucking and thus made the prey less profitable for the golden eagle to ingest (Kaspari 1991; Slagsvold et al. 2010).

4.3 Effect of prey mass and prey type on feeding efficiency and handling efficiency

Feeding efficiency (prey mass (g) ingested per feeding time (min)) decreased with prey mass, both in avian prey and mammalian prey, where mammalian prey were ingested faster than avian prey. Based on the parameters, a mammalian prey of 300 g was ingested 2.1 times faster than an avian prey of 300 g. This finding is supported by Samilas (2010) who found the similar effect of prey body mass and prey type on feeding efficiency for sparrowhawks (*Accipiter nisus*).

Prey that were swallowed whole had a very high feeding efficiency, leaving small prey very profitable. According to optimal foraging theory, golden eagles should always choose the most profitable prey to maximize their net rate of food intake, because increased prey mass leads to lower energy gain per unit feeding time (Barnard 2004; Slagsvold & Sonerud 2007).

Handling efficiency (prey body mass ingested (g) per handling time (min), i.e. plucking and feeding time pooled) originally includes time for capturing the prey, i.e. the time elapsed from the attack is launched until the prey has been captured. Because the golden eagles were fed, this factor was excluded from the handling time in my study. The handling efficiency decreased with increasing prey body mass for both mammalian prey and avian prey. From the parameters, a mammalian prey of 300 g was handled 3.1 times more efficient than an avian prey of 300 g. My findings are in line with those of Skouen (2012), who found that avian prey were less efficient to handle than mammalian prey for golden eagles in their nests. However, my results contrasts with those on the handling efficiency of mammalian prey for the sparrowhawk (Salmila 2011); a large mammalian prey needed more plucking than a similar large avian prey. The differing results could be explained by the fact that few mammalian prey were plucked by the golden eagles, leaving plucking to have less effect on the handling efficiency of mammalian prey for golden eagles than for sparrowhawks.

For a carrion feeder, feeding efficiency and handling efficiency is an important factor in the competition with other predators on carrions. Adult golden eagles seem to ingest food faster than young golden eagles, especially when they are affected by competitors (Halley & Gjershaug 1998). Although I was unable to test the effect of age on feeding efficiency and handling efficiency, competition may be an important factor in the feeding and handling behaviour of the golden eagle.

4. 4 Effect of prey mass ingested and prey type on piece size

The size of each piece decreased with increasing prey mass both for avian prey and mammalian prey. Larger prey may lead to more preparing and thus more and smaller pieces (Slagsvold & Sonerud 2007). Being a large generalist, the golden eagle is also capable of swallow prey in large pieces by pouncing large pieces and whole smaller prey from above such as other specialized vole feeders i.e. owls (*Strigiformes*) (Slagsvold et al. 2010).

A piece from a mammalian prey of 300 g was predicted to be 2.2 times heavier than a piece of an avian prey of 300 g. Mammalian prey required less plucking than avian prey, and could thus be easier swallowed in larger pieces with less included non-ingested parts in their ingestion. The difference in piece size between the two prey types could also be caused by the fact that mammalian prey were more swallowed whole (n = 11) than avian prey (n = 4) because the predicted piece size was affected by whether prey was swallowed whole or not.

Although red fox was the largest prey in my study (7500 g) with a predicted piece size of 0.7 g, Wilmers et al. (2003) found that eagles (golden eagles and bald eagles (*Haliaeetus leucocephalus*)) feeding on carcasses of elk (*Cervus elaphus*) had a piece size of 3.15 g. Based on my findings, the negative correlation between piece size and prey body mass, feeding on an elk should result in a smaller piece size than 0.7 g. I assume, however, that there may be a threshold in this negative correlation, because large ungulate prey (*Ungulata* sp.) may contain more available pure meat than in smaller prey, thus leads to larger pieces. This was supported in my findings on average piece size of pure meat from ungulate species (moose and roe deer) of 3.6 ± 1.1 g.

4.5 Effect of prey mass and prey type on the mass of non-ingested prey remains

The mass of non-ingested remains increased with increasing prey body mass for both prey types, and indicated that larger prey were harder to ingest than smaller prey due to more remains such as feathers, fur and larger bones (Tjernberg 1981; Slagsvold et al. 2010). From a 300 g prey, the golden eagle left 20.5 % of an avian prey as non-ingested remains, and only 6.4 % of a mammalian prey. In agreement with Salmila (2011), my findings state that avian prey with a given mass had more non-ingested remains than an equally sized mammalian prey.

Though there has been many studies on prey remains after golden eagles (Mollhagen et al. 1972; Connolly et al. 1976; Collopy 1983; Watson et al. 1992; Seguin et al. 2001), most used the remains to identify the diet and not to estimate the quantities of the remains after ingested a prey. However, Sulkava and Rajala (1966) found that prey smaller than the willow ptarmigan (about 500 g) occurred half as often among older prey remains as among fresh ones, and thus assumed that larger bones were more harder to decay than smaller bones. This supports my findings that smaller prey leave less non-ingested remains than larger prey.

4.6 Effect of pure meat and prey type on feeding efficiency and handling efficiency

Feeding efficiency did not differ between ingesting pure meat and ingesting avian prey or mammalian prey. Handling efficiency however, was lower for avian prey than for pure meat, but did not differ between mammalian prey and pure meat. My findings indicates that the golden eagle, in being a large generalist, is not affected by preparing natural prey to the same degree as smaller and more specialized raptors. This is supported by the findings of Salmila (2011) on the sparrowhawk; there was a higher efficiency for pure meat than for natural prey both in feeding and handling. Nevertheless, there is an indication that handling an avian prey results in more preparing and thus a lower profitability due to a longer handling time than handling mammalian prey or pure meat.

Because there were only four feedings with pure meat, these data was less valid than the data of feedings of avian and mammalian prey. Pure meat thus only suggest a potential effect of plucking for the feeding efficiency and handling efficiency (Salmila 2011) .

4.7 Part of the prey where feeding started

4.7.1 Feeding start from the breast

The probability that the golden eagle would start feeding from the breast of a prey was predicted to be 74 % for avian prey and 13 % for mammalian prey. The golden eagle started to feed mainly from the breast of an avian prey for at least two reasons: First, the breast is a more nutritious body part of an avian prey than of a mammalian prey, because the breast of an avian prey is mostly made up by the flight muscles (G. Sonerud pers. comm.). Second, because handling an avian prey is less profitable than handling a mammalian prey, hence more non-ingestible and unprofitable body parts from an avian prey, it is possible that the golden eagle primarily would feed from the breast. Further, prey body mass did not affect the golden eagle's choice of whether to start feed from the breast or not.

4.7.2 Feeding start from the head

Out of 27 mammalian prey, eight of them the golden eagles started feeding from their head. The predicted body mass of prey where feeding started from their head were 60 g, while prey that were started feeding from other body parts were predicted to weigh 1159 g, which state that the golden eagles started feeding from the head more often from smaller prey than from larger prey. This may be because the importance for a large raptor of where to start feeding from mammalian prey decreases with decreased prey body mass, while avian prey that are too large for the golden eagle to swallow whole primarily are started fed from the breast. However, data reveal that heads or skulls only where left as remains in larger prey (i.e. red fox, mountain hare, grey heron and hooded crow (*Corvus cornix*)) while it was ingested in all of the smaller prey (pers. obs.). This may indicate that the head being particular nutritious and thus a profitable body part that is easier to utilize in smaller than in larger prey, and is therefore being ingested first (R. Steen pers. comm.).

4.7.3 Swallowed whole

Kaspari (1990) stressed that the swallowing threshold in a predator drives prey preparation and that a prey should not be prepared unless it cannot be swallowed whole. The predicted mammalian prey body mass for a golden eagle to swallow whole was 19 g, while the heaviest mammalian prey which were swallowed whole was 57 g. This indicates that the swallowing threshold in a golden eagle is at least 19 g for mammalian prey. Only a few (n = 4) avian prey were swallowed whole, probably because small avian prey were less profitable than small mammalian prey due to less meat and more non-ingestible parts, such as feathers. Further, mammalian, prey like small rodents have a more cylindrical form than small avian prey and is thus easier to swallow whole (Skouen 2012).

Although the golden eagle have a taller and narrower bill than specialized vole feeders (Slagsvold et al. 2010), the body size of the golden eagle, hence the esophagus is large enough to swallow smaller prey whole. Because smaller prey were either swallowed whole or torn in larger pieces than larger prey, smaller prey would lead to a higher intake rate for the golden eagle. Being a large and heavy raptor, the golden eagle is less adapted to catch small prey than other raptors such as some buzzards (*Buteo* sp.) and other vole feeders. However, the golden eagle is one of few raptors that are capable to catch larger prey such as hares and foxes, as well as outperform predators larger then themselves (i.e. white-tailed eagles (*Haliaeetus albicilla*) in competition on carcasses (Halley & Gjershaug 1998).

In agreement with previous studies on other raptors (Slagsvold & Sonerud 2007; Salmila 2011), the golden eagle should choose a mammalian prey instead of a similar-sized avian prey due to less plucking and preparing in a mammalian prey. Higher feeding efficiency and handling efficiency, and lower amount ofnon-ingested remains, favors mammalian prey from avian prey in being the most profitable prey of the golden eagle.

5. Conclusion

According to optimal foraging theory, the chosen prey of a golden eagle should have the highest possible energy gain per unit handling time. I found that larger prey lead to decreased feeding and handling efficiency and were thus less profitable for the golden eagle, due to more time spent to prepare the prey. I also found that avian prey were less profitable than a similar-sized mammalian prey, containing more non-ingestible parts such as feathers. Feeding efficiency did not differ between pure meat and avian or mammalian prey, while handling efficiency was lower for avian prey than for both mammalian prey and pure meat, due the time spent for plucking. Further, prey body mass affected a golden eagle's choice of where to start feeding from in a mammalian prey, but not from an avian prey. For smaller mammalian prey, the feeding started from the head, while for avian prey the feeding mainly started from the breast. To the best of my knowledge, there have been no other similar studies, it would thus be interesting to investigate which part of the prey other raptors start to feed, for a better understanding of the prey selection and thus a better knowledge of the feeding behaviour of the species.

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Appendix

Prey species, prey type, number of prey items and prey body mass of each prey which were fed to the four golden eagles.

Prey species	**Prey type**	**Number of prey items**	**Prey body mass (g)**	**Prey fed by golden eagle ID**
Bank Vole (*Myodes glareolus*)	Mammalian	6	14.6, 16, 17 15.1, 15.2 27.5	2KM 3KM 5KF
Blue tit (*Cyanistes caeruleus*)	Avian	1	10	5KF
Bohemian Waxwing (*Bombycilla garrulus*)	Avian	2	53 62	2KM 3KM
Brambling (*Fringilla montifringilla*)	Avian	1	24.6	5KF
Common Blackbird (*Turdus merula*)	Avian	1	103	5KF
Common Crossbill (*Loxia curvirostra*)	Avian	1	29.9	3KM
Common Gull (*Larus canus*)	Avian	1	333	2KM
Eurasian Jay (*Carduelis spinus*)	Avian	1	153	3KM
Eurasian Siskin (*Carduelis spinus*)	Avian	1	9.6	2KM
Eurasian Woodcock (*Scolopax rusticola*)	Avian	2	234 248	2KM 5KF
European Green Woodpecker (*Picus viridis*)	Avian	2	179 198	2KM 3KM
European Magpie (*Pica pica*)	Avian	2	213 176	4KM 5KF
European Water Vole (*Arvicola amphibius*)	Mammalian	3	57, 152 74	2KM 5KF

European Herring Gull (*Larus argentatus*)	Avian	1	951	2KM
Feral Pigeon (*Columba livia*)	Avian	2	275, 292	3KM
Goosander (*Mergus merganser*)	Avian	1	900	4KM
Great tit (*Parus major*)	Avian	2	17.6 14.7	3KM 5KF
Grey Heron (*Ardea cinerea*)	Avian	1	1402	3KM
Hooded crow (*Corvus cornix*)	Avian	5	468 552, 560 494 534	2KM 3KM 4KM 5KF
Mountain Hare (*Lepus timidus*)	Mammalian	2	3640 1993	4KM 5KM
Norway rat (*Rattus norvegicus*)	Mammalian	2	289 342	3KM 4KM
Red Fox (*Vulpes vulpes*)	Mammalian	2	7500 6700	3KM 5KF
Red Squirrel (*Sciurus vulgaris*)	Mammalian	4	327 297 308 289	2KM 3KM 4KM 5KF
Redwing (*Turdus iliacus*)	Avian	1	55	2KM
Robin (*Erithacus rubecula*)	Avian	2	12.7 17.6	3KM 5KF
Rock Ptarmigan (*Lagopus muta*)	Avian	1	398	3KM
Roe deer (*Capreolus capreolus*)	Mammalian	1	1062	4KM
Willow Ptarmigan (*Lagopus lagopus*)	Avian	1	528	3KM
Wood mouse (*Apodemus sylvaticus*)	Mammalian	5	15.7, 17.6 24.9 12.9, 24.7	2KM 3KM 5KF
Yellow-necked Mouse (*Apodemus flavicollis*)	Mammalian	4	29.6 41.3, 42.5, 44.2	3KM 5KF

Pure meat ingested				
Moose (*Alces alces*)	Mammalian	3	1102, 279 1983	2KM 3KM
Roe deer (*Capreolus capreolus*)	Mammalian	1	760	4KM