Prey handling and in a generalist and specialist raptor: the Eurasian kestrel (*Falco tinnunculus*), and the Peregrine falcon (*Falco Peregrinus*)

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Abstract

I used video footage of feeding trials to study prey handling in five Eurasian kestrels *(Falco tinnunculus*) and five peregrine falcons (*Falco peregrinus)* kept in temporal captivity. The trials were filmed between 2008 and 2016. A total of 130 prey items (57 dead birds, 59 dead mammals and 14 pieces of pure meat) were offered to the raptors. I analysed plucking and feeding behaviour for each feeding bout in each trial. I found that kestrels and peregrines preferred feeding from head of prey first for both mammalian and avian prey. Plucking time increased with prey mass and was higher for avian prey than mammalian prey of the same size. The difference in plucking time between avian and mammalian prey was larger in kestrels than in peregrines. Handling efficiency decreased with prey mass but was not affected by prey type. Smaller prey were more profitable to ingest than larger prey, and for kestrels, mammalian prey were more profitable than avian prey. I found that kestrels were less efficient when handling larger prey in the last feeding bout than the first or middle bouts. For peregrines, there was no difference in handling efficiency between feeding bouts. The amount of non-ingested remains after a meal increased with increasing prey mass in both kestrels and peregrines, but the proportion of remains relative to prey size left by kestrels was constant. Based on my results, kestrels should select small mammalian prey rather than avian prey and extract meat from prey until the profitability of the prey item drops below a threshold. Peregrines should feed from prey until the remaining carcass is depleted by digestible body parts.

Contents

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1. Introduction

For a raptor preying almost only on birds, such as the peregrine (*Falco peregrinus*), excellent flight hunting skills are required in order to capture vigilant and agile prey, and thus body mass must be kept low in order to hunt efficiently (Hagen 1952, Anderson and Nordberg 1981). To meet these requirements, such raptors restrain their digestive capacity by having a lighter digestive tract and a smaller gut and gizzard than raptors preying mainly on voles and other small mammals, and food are absorbed faster to decrease retention time (Barton and Houston 1996). Morsels ingested are relatively small, as the bird's beak is long and narrow, specialized for handling avian prey, thus resulting in extended meals (Barton and Houston 1996). Vole feeders, on the other hand, such as the kestrel (*Falco tinnunculus*), hunt from elevated perches, and may hover mid-air before pouncing prey on the ground. This hunting technique requires less manoeuvrability than of catching prey mid-air, thus body weight is less constrained by foraging ecology in kestrels (Slagsvold el al. 2010). These anatomical differences between vole feeders and bird feeders suggest interspecific variation in optimal prey selection and consumption between kestrels and peregrines as their digestive capacity and retention time differ (Barton and Houston 1993; Hilton et al. 1999; Tornberg and Reif 2007).

The Eurasian kestrel is a generalist predator, which occupy a wide geographical range and can be seen throughout most of Europe, Africa and Asia during breeding season (Village 1990). Kestrels are most successful where vole populations are abundant; however they are highly adaptable feeders allowing them to occupy a wide range of habitats. Small mammals such as field vole (*Microtus agrestis*), bank vole (*Myodes glareolus*) and wood mice (*Apodemus sylvaticus*) are predominant prey, and prey selection depends heavily on vole abundance (Hagen 1952, Village 1982a). Larger mammals are rarely killed by kestrels, but young individuals of hares, rabbits, squirrels and rats are eaten occasionally (Village 1990). Avian prey includes various species of open-country birds such as European starling (*Sturnus vulgaris*) and skylarks (*Alauda arvensis*). Young, fledglings or old and dying individuals of larger birds such as ducks and waders are at risk of predation from kestrels as they are slow and less wary and thus more vulnerable to attacks (Newton et al 1982a). Avian prey made up 4.3% among the total vertebrate prey consumed by kestrels during breeding season in Norway, which classifies them as vole feeders (Hagen 1952, Slagsvold et al. 2010). Kestrels also feed on slow, ground-living invertebrates such as earthworms and beetles, especially during spring when snow is melting which make prey migrate to the surface. (Village 1990) Fish, crabs and carrion have also been killed by kestrels on rare occasions (Cave 1968).

The peregrine falcon is a specialist predator including almost exclusively birds (99%) in their diet. Peregrines thrive in open country habitats such as coast lines, river valleys, mountain ranges and increasingly in cities all over the world where food supplies are high (Ferguson-Lees 2001, Ratcliffe 1980). Domestic pigeons (*Columba livia domestica*) are predominant prey, but pairs of peregrines might develop fondness for specific prey that is in good local supply or at a certain time of year as prey selection is dependent on availability (Ratcliffe 1980, Rejt 2001, Dixon et al 2018). Avian prey size range from hummingbirds (~3g) to medium sized birds such as starlings, gulls and doves, and large birds such as sandhill cranes >3000 g (*Grus canadensis*) (Cramps et al. 1980; Brown 1986). Peregrines frequently attack and kill other raptors such as sparrowhawks (*Acciptier nisus*) and barn owls (*Tyto alba*), and even remains of other peregrines have been found in pellets. However, attacks on other raptors are often actions of nest defence resulting in fatality (Ratcliffe 1980). (Ratcliffe 1980) stated that most birds are vulnerable to attack from peregrines and only swans and eagles seem to exempt from predation. Frogs, toads, fish and carrion from dead sheep have also been reported killed by peregrines, as well as young of rabbits. (Village 1990)

A comparison of prey handling and handling efficiency in kestrels and peregrines is important in order to understand the underlying mechanisms of optimal prey selection in a generalist raptor to a bird feeding raptor, and how these factors affect foraging ecology (Village 1990, Slagsvold et al 2010). Studying prey handling is also of importance for the management of predominant prey species included in a raptor’s diet and hence management of the kestrel and peregrine population per se (Grønsdal 2012; Skouen 2012)

Several studies have investigated prey handling and feeding efficiency in other raptors such as common buzzard, goshawks and merlin (*Falco columbarius*) (Aanonsen 2003; Slagsvold and Sonerud 2007; Slagsvold et al 2010; Salmila 2011). However, to my knowledge, the profitability of feeding from the same prey item in multible bouts rather than capturing and feeding on a new prey has not been investigated earlier.

In this study, I aimed to test the following hypotheses: 1) Prey mass and type affect the falcons´ choice in where to start feeding on prey. 2) Time spent plucking increases with prey mass and is higher for avian prey than mammalian prey. 3) Handling efficiency differs between peregrines and kestrels and is affected by prey mass and type. 4) Handling efficiency differs between feeding bouts, and decreases from the first to the last bout. 5) The proportion of non-ingested prey remains increases with increasing prey mass and is higher for avian prey than mammalian prey.

2. Material and methods

2.1 Reasons for studying raptors in captivity

In the wild, prey handling-behavior in raptors might be influenced by environmental factors such as competition or attacks from other predators or other natural interruptions (Slagsvold et al. 2010, Salmila 2011, Grønsdal 2012). (Slagsvold et al 2010) stated that a raptor in the wild might not completely ingest a prey item for at least four reasons; (1) it is disturbed while feeding and leaves prey behind, (2) it is satisfied, (3) capturing and feeding on a new prey might be more beneficial than extracting meat from current prey, and (4) the energetic or nutritional value of prey captured drops to a point where it is no longer worth ingesting, or the remains are too difficult to ingest or digest.

Since raptors were kept in temporal captivity, at least three of these factors were minimized; factor (1) was minimized as the raptor was left alone with prey and could quickly resume feeding from the same prey item if disturbed by noise from outside. Factor (2) was eliminated as the raptor, if temporarily satisfied, could be offered the remains of the same prey item later in a new feeding bout. Since raptors where fed only one prey item at once, factor (3) was eliminated as no optional food sources were available. (Slagsvold et al. 2010)

(Slagsvold et al. 2010) stated that studying prey handling in raptors kept in temporal captivity is advantageous because we could control the type and size of offered prey, and the prey remains left by raptors after a meal are easy to collect and identify. In the wild, a raptor may handle prey elsewhere than the killing site, and prey remains may be cached in hidden places, making it logistically difficult to find and quantify them. (Village 1990, Slagsvold et al. 2010) Also, identifying prey remains simply based on recordings at raptor nest sites may give rise to biases as parts of prey might be removed by parents prior to nest delivery, e.g. by plucking feathers from avian prey (Rutz 2003, Village 1990), and prey remains may also be removed from the nest after feeding. (Slagsvold et al. 2010)

2.2 Study and study species

Five common kestrels were used in this study; two juvenile males in their first calendar year (1KM, 1KM_08), one juvenile female in its first calendar year (1KF) and two adult males in their second and third calendar year, respectively (2KM, 3KM). Two female peregrine falcons were in their first and eight calendar year, respectively (1KF, 8KF), while three male peregrine falcons were in their first, second and third calendar year, respectively (1KM, 2KM and 3KM). Thus, among the birds studied, three kestrels and two peregrines were juveniles, while two kestrels and three peregrines were adults. The birds were found in the wild by volunteers and brought to a rehabilitation facility for injured raptors. All raptors were given care in accordance with institutional guidelines from National Authorities (Salmila 2011) to recover from injury. Age was determined by plumage colour, bar width, difference in outermost primary feathers (pinions), wing length and body mass. (Slagsvold et al. 2010, Sonerud pers. comment 2012) The age of the common kestrel 2KM was a bit uncertain as the tail plumage was grey and the bar narrow, indicating 2K, but indifference between old and new pinions indicate 3K or older. In this study it was identified as 2KM. It was found alongside a road unable to fly, possibly due to emaciation, but might also have been struck by a car. One of the juvenile male kestrels (1KM) was also found alongside a road with signs of cerebral injuries and unable to fly. The other juvenile male kestrel (1KM) was found sitting outside a shop, probably emaciated due to low body mass, but had no physical injuries. The other individuals were brought to the rehabilitation facility for unknown reasons. All raptors were in good physical condition before the trials started. The raptors were fed regularly to prevent starvation between trials as unequal hunger between trials may bias the relationship between prey size and ingestion rate. (Slagsvold and Sonerud 2007)

2.3 Prey and prey presentation

Kestrels were fed a total of 70 dead prey items in various sizes divided into 28 avian prey, 36 mammalian prey and 6 pieces of pure meat (control). Peregrines were fed a total of 60 prey items size divided into 29 avian, 23 mammalian and 8 pieces of pure meat. Mammalian prey ranged from a 6.6 g common shrew (*Sorex araneus*) to a 263 g red squirrel (*Sciurus vulgaris*), while avian prey ranged from a 4.8 g goldcrest (*Regulus regulus*) to a 545 g hooded crow (*Corvus corone*). Avian prey (juveniles or adults from late summer, autumn or winter) were either shot by hunters, killed in traffic or in other accidents. Mammalian prey were trapped in the wild, lab-reared or killed in traffic. All prey items were biologically realistic (Slagsvold and Sonerud 2007). Prey items were kept frozen for a maximum of two years before being thawed and presented on a wooden plate, in direct view in front of the camera. One prey item at a time was randomly selected with respect to prey size, type and availability and offered the focal raptor per bout. Mammalian prey of the same species but of different size, were offered 1-4 times per individual falcon while avian prey only included one individual per raptor. Pure beef/fillet from roe deer (*Capreolus capreolus*) without non-digestable body parts such as bones, were used as control items as this prey type requires minimal preparation before ingestion. Some prey items, often large prey, were nailed to the platform either before or during feeding bouts as some raptors attempted to remove the prey away from the camera spot. If the attempt was successful, the bird was interrupted and chased away from the prey, and the prey item was presented again on the wood bench. One of the raptors swallowed the string attached to the nail, but this did not affect handling efficiency as it was ingested at the end of a meal, and the raptor did not show any sign of injury or displeasure afterwards. If there were edible leftovers after a meal, prey remains were stored in a refrigerator and presented once again a few hours later or the following day in a new feeding bout (Slagsvold and Sonerud 2007; Slagsvold et al. 2010). Feeding bouts were repeated until the entire prey item was consumed or the focal raptor no longer showed any interest in feeding. The prey remains after each meal were collected, identified and weighed. Ejected pellets were excluded from the study as they are hard to measure and assign to prey (Slagsvold et al. 2007; Salmila 2011)

For further information about prey items see Appendix I, table 1 a-b.

2.4 Video analysis

The video analysis was made by watching video recordings of the kestrels and peregrines handling the prey item given. I measured the duration of each feeding session starting from the first to the last observed ingested bite made by the focal raptor. Plucking sessions started from first deliberate attempt, successful or not, to remove unfavourable parts from prey and ended when the bird started feeding or lost interest in the prey item completely. The total number of plucks and ingested morsels from prey during trials were registered by using a click counter to minimize human error, as these numbers could be high and difficult to remember. Single plucks during a feeding session were not registered as pauses as they usually lasted 3 seconds or less and had a negligible effect on feeding efficiency. The video recordings were without sound, so, when the falcon turned its back against the camera, I determined behaviour by carefully observing head movements and looking for parts of prey being removed. Fast and vigorous head movements indicated plucking behaviour while slower movements without shaking its head indicated feeding behaviour. Behaviour was registered respectively to these assumptions. To minimize the effect of disturbance, inactivity or irrelevant behaviour such as pellet ejection lasting 5 s or more during a feeding or plucking session, were registered as pauses (Slagsvold and Sonerud 2007; Slagsvold et al. 2010; Grønsdal 2012). Plucking sessions during feeding were registered as pauses in total feeding time. I also observed at which part of prey the falcons started feeding or plucking to investigate any individual or general preference in where to initiate these behaviours at different prey type and/or size. Handling efficiency was measured as mass ingested (g) divided by feeding time and plucking time pooled.

2.5 Statistical analysis

The statistical analysis was performed with the program R version 3.4.4 (R development core team 2018). There were a total of 130 trials in 10 focal raptors; 5 kestrels, and 5 peregrines in the overall model. Handling efficiency, amount of prey mass remains, plucking time, average meal size and handling efficiency in feeding bouts were analyzed by linear mixed-effects regression, as implemented by the lme-function in the nlme-library of R. All continuous variables, both response and explanatory, were log10 transformed before analysis to obtain a normal distribution. To account for body size in raptors when comparing kestrels and peregrines, I used the relative size of offered prey, taken as the percentage of the focal raptors body mass. To determine any preference regarding at which part of the prey item the raptors chose to start feeding, I used a generalized linear mixed model (GLMM) fit by maximum likelihood (Laplace Approximation) ['glmerMod'] with a binominal distribution. Response variables included in the two logistic regression models (GLMM) were whether 1) raptors started feeding from the head or from other part of the prey and 2) feeding started from the breast or from other part of the prey. Pieces of pure meat were fed the raptors and classified as control to estimate the cost of plucking a prey. Raptor ID was set as a random effect to control for repeated measurements and unexplained variation associated with each individual raptor. Age and sex was eliminated as factors in all tests. To predict values based on the parameters from the LME/GLMM models (e.g. handling efficiency for a given prey size), I estimated the minimum, maximum and median prey mass in avian and mammalian prey for kestrels and for peregrines. When testing effects of feeding bouts; min., max, and median values were based on items included in this study only. To calculate the probability of raptors starting to feed from the head or breast of prey, I back transformed the output estimates given by the best GLMM model in R, then multiplied the result by 100 to get the predicted percentage.

When estimating average meal size, prey items consumed in only one feeding bout was excluded from the study, as well as the very last feeding bout, as the raptor might not be satisfied with little to no edible remains to feed from at the end of the meal. Since pieces of pure meat required minimal preparation before ingestion, raptors could spend all energy on food consumption, increasing handling efficiency to a maximum (Salmila 2011; Grønsdal 2012). Therefore, I estimated feeding and gut capacity based on the average amount of mass of pure meat consumed.

When investigating handling efficiency in different bouts, I classified the first bout as "first, intermediate bout(s) as between, and the last bout as "last". Pure meat (control) was excluded from these tests as it was of no biological interest.

3. Results

3.1 Probability of starting to feed from the head of prey

3.1.1 Kestrels

For kestrels, there was a non-significant difference between the effects of avian and mammalian prey on the probability of starting to feed from the head. Prey type, prey mass and the interaction between prey type and prey mass did not affect the probability of kestrels starting to feed from the head. (Table 3.1.1)

Table 3.1.1 Parameter estimates from the best GLMM model (AIC = 47.4, n = 56, ID = 5) of factors affecting the probability that kestrels started feeding from the head of prey items, calculated as a function of prey type with avian prey set as intercept.

Explanatory variable	Estimate	SE	z	p
(Intercept)	1.56	0.55	2.83	<0.001 **
Prey type mammalian	0.74	0.82	0.91	0.363

Based on the parameters estimates from the GLMM model, and after correcting for ID and prey mass, the probability that kestrels started to feed from the head was 82.6% for avian prey and 90.9% for mammalian prey.

3.1.2. Peregrines

Prey mass did not affect the probability of peregrines starting to feed from head of mammalian prey first ($p = 0.86$), (table 3.1.2.) From observing raw data, peregrines started to feed at the head of all mammalian prey, even large prey with massive skulls such as the squirrel (262 g).

For avian prey items, there was no significant effect of prey mass on the probability of starting to feed at the head. (Table 3.1.2)

Table 3.1.2 Parameter estimates from the best GLMM model (AIC = 46.4, n = 31, ID = 5) of factors affecting the probability of peregrines starting to feed from the head of prey items, calculated as a function of prey mass (log 10 transformed).

Explanatory variable	Estimate	SE	z	p
(Intercept)	-0.45	0.71	-0.64	0.521
Prey mass	0.0005	0.002	0.18	0.855

From the parameter estimates in the GLMM model, the probability of peregrines starting to feed at the head of avian prey after correcting for prey mass and ID was 40.7%.

3.2 Probability of starting to feed from the breast of prey

3.2.1 Kestrels

Kestrels started to feed from the breast of its prey in only three cases, which was too small for a meaningful analysis.

3.2.2 Peregrines

None of the mammalian prey items handled by peregrines were eaten from the breast first. The probability of starting to feed from the breast on avian prey was not influenced by prey mass ($p = 0.734$) (Table 3.2.1).

Table 3.2.1 Parameter estimates from the best GLMM model (AIC = 67.5, n = 58, ID =5), of factors affecting the probability of peregrines starting to feed from the breast of avian prey as a function of prey mass.

Explanatory variable	Estimate	SE	z	p
(Intercept)	1.47	0.57	2.58	0.01
Prey mass	-0.001	0.003	-0.34	0.734

Based on the parameters estimates from the GLMM model, and after correcting for ID and prey mass, the probability that peregrines started to feed from the breast was 79.4% for avian prey.

3.3 Time spent plucking

3.3.1 Kestrels

Based on the chosen LME model, prey mass had a positive effect on time spent plucking both avian and mammalian prey by kestrels ($p = 0.002$, $p = 0.003$), (Table 3.3.1 a-b). The regression slopes for plucking time for avian and mammalian prey in relation to prey mass were identical (0.58), indicating a similar positive response to increasing prey mass. However, the estimated intercept values for avian prey (-0.14) and mammalian prey (-0.76) predicted that kestrels spent longer time plucking avian prey than mammalian prey of the same size ($p < 0.001$ (Table 3.3.1, Figure 3.3.1).

Table 3.3.1 Parameter estimates of variables in the best LME model (AIC = 71.88, n = 64, ID = 5) describing plucking time (min) (log10 transformed) as a function of prey mass (g) (log10 transformed) for kestrels, where intercept is set as a) avian prey (n = 28) and b) mammalian prey (n = 35).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	-0.14	0.25	57	-0.55	0.58
Prey mass	0.58	0.19	57	3.11	0.002
Prey type (mammalian)	-0.62	0.09	57	-6.56	<0.001

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	-0.76	0.25	57	-3.02	0.004
Prey mass	0.58	0.19	57	3.11	0.003
Prey type (avian)	0.62	0.09	57	6.56	<0.001

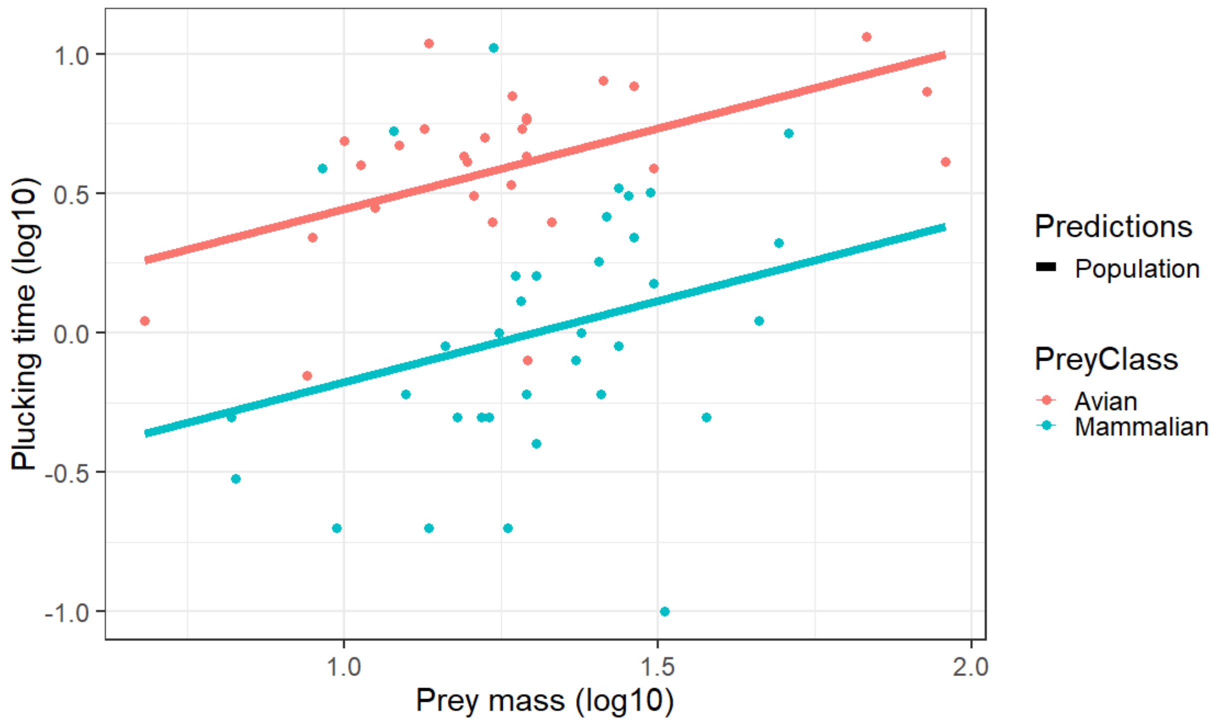

Figure 3.3.1 Time spent plucking prey (min) (log 10 transformed) by kestrels as a function of prey mass (g) (log 10 transformed), with regression lines for avian prey (red) and mammalian prey (blue) calculated by the LME model fitted by REML. Red line denotes avian prey ($y = -0.14 + x*0.58$, $p = 0.002$), and blue line denotes mammalian prey ($y = -0.76 + x*0.58$, $p = 0.003$).

From the parameters in the LME model, the predicted plucking time for avian prey handled by kestrels was 2.5 min for a prey mass of 8.7 g, 3.8 min for a median sized prey (17.8 g) and 5.1 min for a prey mass of 28.9 g.

The predicted plucking time for mammalian prey handled by kestrels was 2.2 min for a prey mass of 6.6 g, 4.1 min for a median sized prey (19.9 g) and 7 min for a prey mass of 49.2 g.

3.3.2 Peregrines

Based on the parameters from the LME model, prey mass had a positive effect on plucking time on both avian and mammalian prey ($p < 0.001$), (Table 3.3.2). The regression slopes for plucking time in relation to prey mass for peregrines were identical for avian and mammalian prey (0.85), indicating a similar increase in plucking time in response to increasing prey mass regardless of prey type. However, the estimate of intercept was slightly larger for avian prey

(-0.75) than for mammalian prey (-1.15), predicting that peregrines spent longer time plucking avian prey than mammalian prey of the same size. (Table 3.3.2, figure 3.3.2) The difference between intercept of avian and mammalian prey was 0.4 in peregrines, while in kestrels the difference was 0.62. Thus, the difference between time spent plucking on avian prey compared to mammalian prey of the same size was smaller in peregrines than kestrels.

Table 3.3.2 Parameter estimates from the best LME model (AIC = 75.46, n = 53, ID = 5) describing plucking time (min) (log10 transformed) as a function of prey mass (g) (log10 transformed) for peregrines, with intercept set as a) avian prey (n = 28) and, b) mammalian prey (n = 24).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	-0.72	0.26	46	-2.71	<0.001
Prey mass	0.85	0.11	46	7.73	<0.001
Prey type (mammalian)	-0.43	0.11	46	-3.76	0.001

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	-1.15	0.24	46	-4.69	<0.001
Prey mass	0.85	0.11	46	7.73	<0.001
Prey type (avian)	0.43	0.11	46	3.76	<0.001

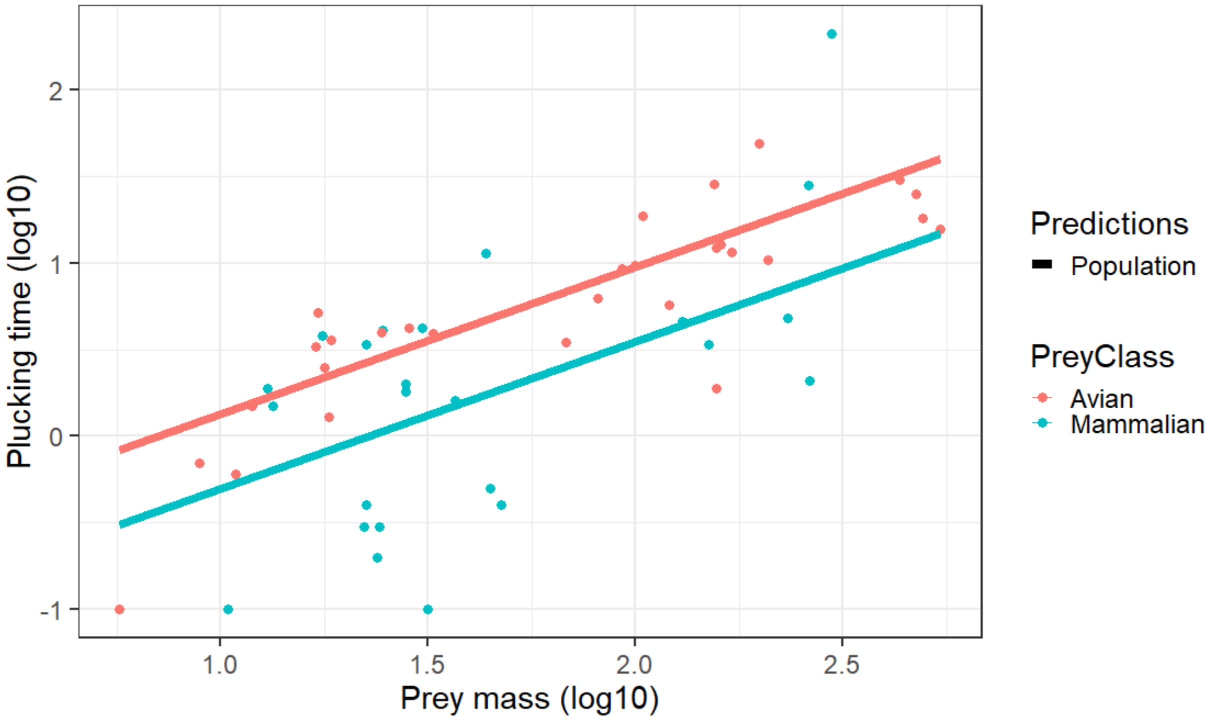

Figure 3.3.2 Time spent plucking prey (min) (log10 transformed) by peregrines as a function of prey mass (log10 transformed), with regression lines calculated by the LME model fitted by REML. Red line denotes avian prey (y = -0.72 + x*0.85, p <0.001), and blue line denotes mammalian prey (y = -1.15 + x*0.85, p = <0.001).

For peregrines handling avian prey, the predicted plucking time from the parameters in the LME model was 48 s for a prey mass of 5.7 g, 9.0 min. for a median sized prey (93 g), and 40.6 min. for a prey mass of 545 g.

For mammalian prey, the predicted plucking time was 1.4 min for a prey mass of 10.5 g, 3.3 min. for a median sized prey (28.0 g), and 24.0 min. for a prey mass of 297.0 g.

3.4 Meal size

3.4.1 Meal size in kestrels

Based on the parameters given by the LME model, the estimated average meal size for the kestrels was 15.7 g for avian prey, 17.9 g for control and 13.6 g for mammalian prey (table

3.4.1 a-c), figure 3.4.1). The average amount of pure meat consumed by the female kestrel during a meal was equivalent to 7.3 % of her body weight (246 g), while pure meat ingested by male peregrines was calculated to be 4.3% of their average body weight (186 g).

Table 3.4.1 Parameter estimates from the LME model (AIC = 261.4) describing average meal size in kestrels (g) as a function of prey type, where intercept is set as a) avian prey (n = 15), b) control items (n = 6), and c) mammalian prey (n = 18).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	15.67	2.41	32	6.51	<0.001
Prey type (control)	2.22	3.47	32	0.64	0.528
Prey type (mammalian)	-2.17	2.55	32	-0.83	0.413

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	17.89	3.18	32	5.63	<0.001
Prey type (avian)	-2.22	3.47	32	-0.64	0.528
Prey type (mammalian)	-4.33	3.26	32	0.11	0.19

c)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	13.56	2.22	32	6.11	<0.001
Prey type (control)	4.33	3.26	32	1.33	0.19
Prey type (avian)	2.12	2.55	32	0.83	0.41

3.4.2 Meal size in peregrines

Based on the parameter estimates given by the LME model, the estimated average meal size for the peregrines was 51 g for avian prey, 78 g for control food and 37 g for mammalian prey (table 3.4.2 a-c, figure 3.4.2). The amount of pure meat ingested by female peregrines was equivalent to 8% of their average body weight (1000g), while pure meat ingested by male peregrines was calculated to be 13% of their average body weight (577g).

Table 3.4.2 Parameter estimates from the LME model (AIC = 486.5, n = 54, ID =5) describing average meal size in peregrines as a function of prey type, where intercept is set as a) avian prey (n = 29), b) control food (n = 8) and c) mammalian prey (n = 17).

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	51.39	12.82	47	4.01	<0.001
Prey type control	26.09	8.96	47	2.91	0.006
Prey type mammal	-14.84	7.29	47	-2.04	0.048

b)

Explanatory variable	Estimate	SE	DF	t	p
(Intercept)	77.48	14.5	47	5.34	<0.001
Prey type avian	-26.09	8.96	47	-2.91	0.006
Prey type mammal	-40.93	10.16	47	-4.03	<0.001

c)

Explanatory variable	Estimate	SE	DF	t	p
(Intercept)	36.54	13.23	47	2.76	0.008
Prey type (control)	40.93	10.16	47	4.03	<0.001
Prey type (avian)	14.84	7.29	47	2.04	0.048

3.5 Handling efficiency

3.5.1 Handling efficiency in kestrels and peregrines compared

The best fitted global LME model (AIC = 1.38) excluded any interaction between the explanatory variables as none were significant. Prey type did not affect handling efficiency, nor did the interaction between prey type and relative prey mass. Based on the parameters from the LME model, there was a trend that handling efficiency was negatively correlated with relative prey mass, but this was not significant ($p = 0.071$) (Table 3.5.1).

The regression slope values for peregrines and kestrels were identical ($r = -0.13$), which indicated a similar rate of decrease in handling efficiency in response to increasing relative prey mass. However, the intercept for peregrines had a higher value (0.34) than for kestrels

(-0.15), which indicated a stronger ability to handle larger prey relative to raptor body mass efficiently in peregrines ($p = 0.016$) (Table 3.5.1, Figure 3.5.1).

Table 3.5.1 Parameter estimates from the LME model (AIC = 1.38, n = 57, ID = 10), describing handling efficiency as a function of relative prey mass (log10 transformed) with kestrel set as intercept.

Explanatory variable	**Value**	**SE**	**DF**	**t**	**p**
(Intercept)	-0.15	0.1	46	-1.42	0.162
Prey mass	-0.13	0.07	46	-1.85	0.071
Species (peregrine)	0.34	0.11	8	3.04	0.016

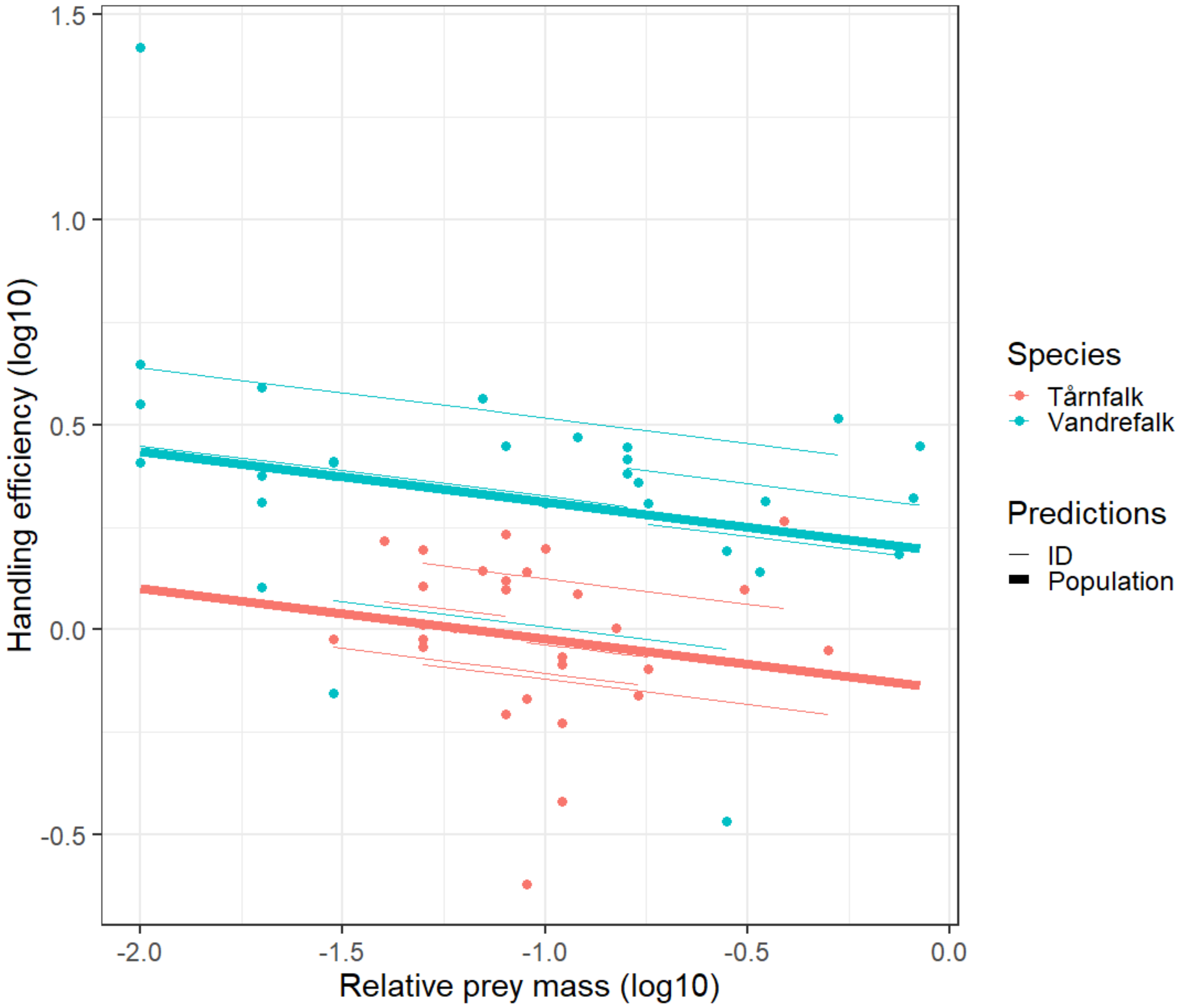

Figure 3.5.1 Handling efficiency (log10 transformed) as a function of relative prey mass (log10 transformed), with regression lines calculated by LME fitted by maximum likelihood for kestrels (red) (y = -0.15 - x*0.13, p = 0.16, n =) and peregrines (blue) (y = 0.34 - x*0.13, p = 0.02, n = 57).

Based on the parameters from the global LME model, handling efficiency in kestrels was predicted to be 0.5 g/min for a prey type of 8.7 g, 0.48xg/min for a median sized prey (19.85g) and 0.39 g/min for a prey mass of 95 g.

From the LME model, handling efficiency in peregrines was predicted to be 1.7 g/min for a prey mass of 5.7 g, 1.2 g/min for a median sized prey (96.5 g) and 0.96 g/min for a prey mass of 545 g.

3.5.2 Handling efficiency in kestrels

Based on the parameters from the LME model, there was a trend that the interaction between prey mass and prey type had an effect on handling efficiency, however, it was non-significant (avian prey; p = 0.110, mammalian prey; p = 0.108). For mammalian prey, increasing relative prey mass had a significant negative effect on handling efficiency (p = 0.019), (Table 3.5.2, Figure 3.5.2).

Table 3.5.2 Parameter estimates from the best LME model (AIC = -27.47 , n = 64 , ID = 5), describing handling efficiency in kestrels as a function of prey mass and the interaction of prey mass with prey type, where intercept is set as a) avian prey, and b) mammalian prey.

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	<0.001	0.14	56	<0.001	1.000
Prey mass	-0.02	0.11	56	-0.17	0.866
Prey type (mammalian)	0.54	0.21	56	2.57	0.013
Prey mass * Prey type (mammalian)	-0.26	0.16	56	-1.63	0.110

b)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	0.54	0.16	56	3.42	<0.001
Prey mass	-0.28	0.12	56	-2.42	0.019
Prey type (avian)	-0.54	0.21	56	-2.57	0.013
Prey mass * Prey type avian)	0.26	0.16	56	1.64	0.108

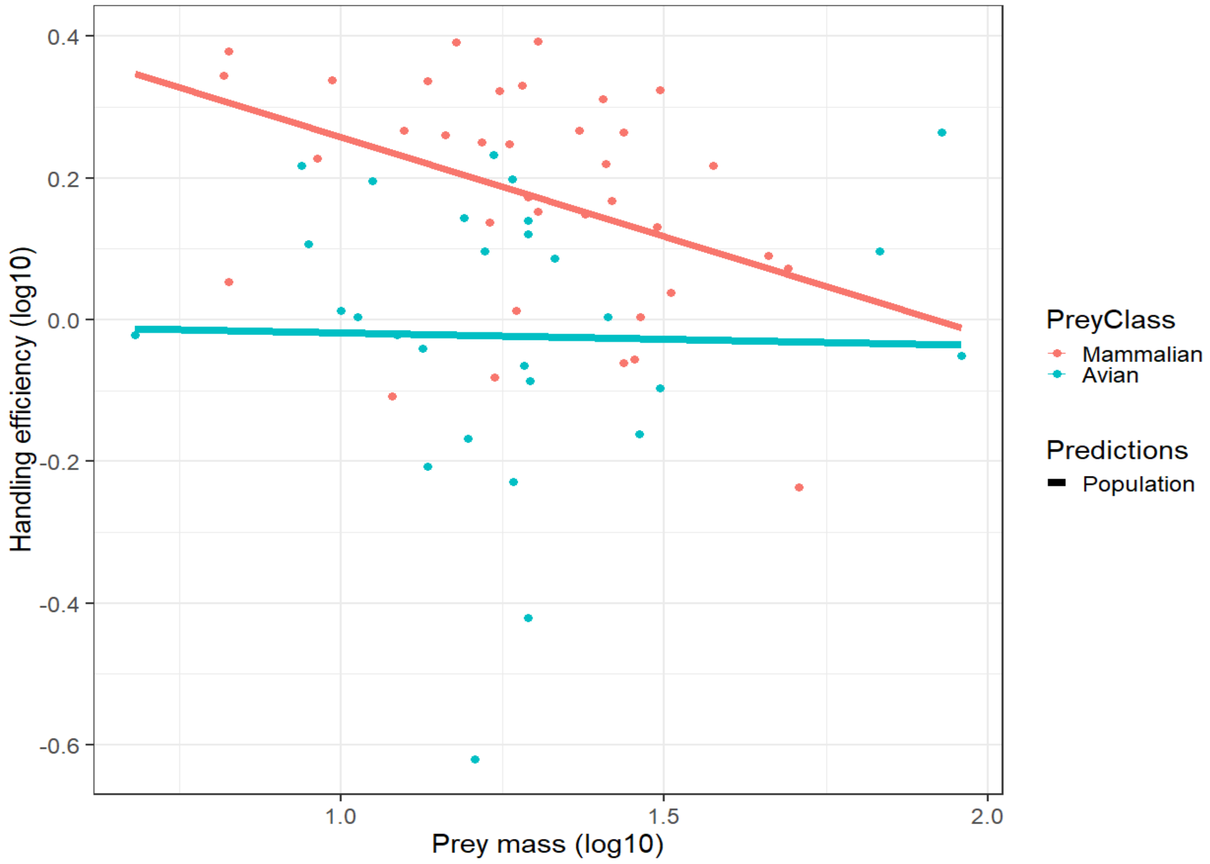

Figure 3.5.2 Handling efficiency (log10 transformed) of kestrels, as a function of prey mass (g) (log10 transformed), in mammalian prey (red line), and avian prey (blue line) with regression lines calculated by LME model fitted by REML. Red line denotes mammalian prey ($y = 0.54 - x*0.28$, $p = 0.019$), and blue line denotes avian prey ($y < 0.001 - x*0.02$, $p = 0.87$)

Based on the parameters given by the LME model, the predicted handling efficiency of kestrels for avian prey was 0.96 g/min for a prey mass of 8.7 g, 0.94g /min for a median sized prey (17.8 g) and 0.90 g/min for a prey mass of 95 g.

The predicted handling efficiency of kestrels for mammalian prey was 2.0 g/min for a prey mass of 6.6 g, 1.5 g/min for a median sized prey (19.9 g), and 1.2 g/min for a prey mass of 49.2 g.

3.5.3 Handling efficiency in peregrines

There was no significant effect of prey type on handling efficiency in peregrines. The best model included only prey mass as explanatory variable ($p = 0.012$) (table 3.5.3, figure 3.5.3).

However, the QQ – plot revealed a problem with normality, and the estimates from the LME model need to be interpreted with caution. (Appendix table 3, Figure III.)

Table 3.5.3 Parameter estimates based on the best fitted LME model (AIC= 38.6, n = 53, ID = 5) describing handling efficiency of peregrines (g/min, log10 transformed) as a function of prey mass (log10 transformed).

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	0.66	0.17	47	3.84	<0.001
Prey mass	-0.20	0.07	47	-2.60	0.012

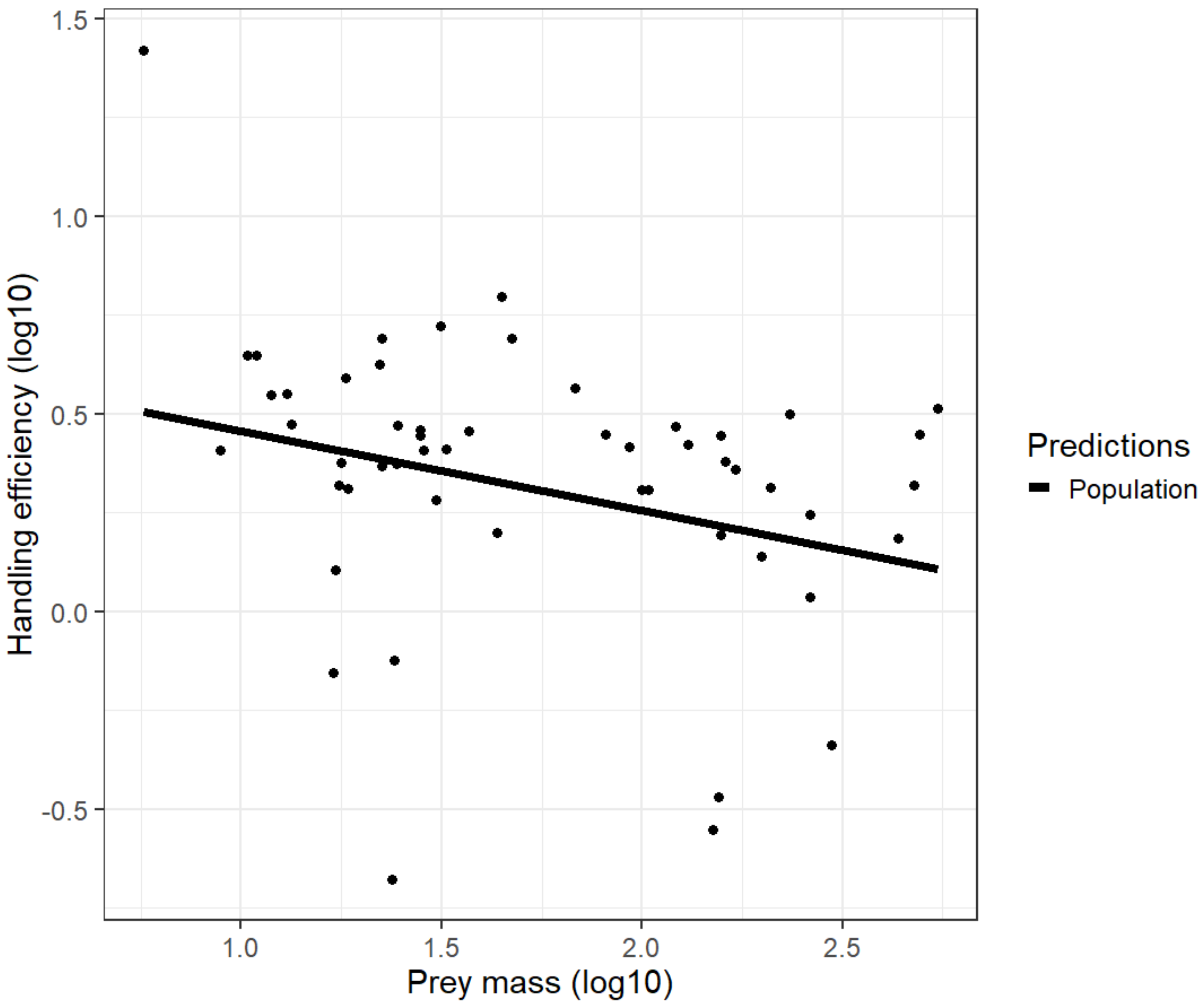

Fig. 3.5.3 Handling efficiency (log10 transformed) of peregrines as a function of prey mass (g) (log10 transformed), with regression line calculated by the best LME model fitted by REML ($y = 0.66 - x*0.2$, $n = 53$, $p = 0.012$**)**

Based on the parameters given by the LME model, the predicted handling efficiency of peregrines was 3.22 g/min for a prey mass of 5.7 g, 1.84 g/min for a median sized prey (96.5 g), and 1.29 g/min for a prey mass of 545 g.

3.6 Handling efficiency in different feeding bouts

3.6.1 Feeding bouts in kestrels

For kestrels, there was an interaction between relative prey mass and the last feeding bout (p = 0.027); handling efficiency decreased significantly in the last feeding bout compared to the first and middle bouts when initial relative prey mass (mass of prey when first bout started) increased (table 3.6.1, figure 3.6.1). Prey type and the interaction between prey type and prey mass had no significant effect on handling efficiency and were excluded from the model. (Table 3.6.1)

Table 3.6.1 Parameter estimates from the best LME model (AIC = -15.6, n = 56, ID = 5) of handling efficiency (log10 transformed) as a function of the interaction between prey mass (log 10 transformed) and feeding bouts, where intercept is set as a) first bout, b)bout(s) between the first and the last bout, c) last bout and d) anova table

a)

Explanatory variable	Value	SE	DF	t	p
(Intercept)	0.15	0.23	46	0.66	0.514
Prey mass	-0.07	0.15	46	-0.44	0.66
Bouts between	-0.42	0.44	46	-0.97	0.339
Last bout	0.22	0.25	46	0.9	0.375
Prey mass *bouts between	0.28	0.28	46	1	0.323
Prey mass *last bout	-0.32	0.19	46	-1.7	0.096

b)

Explanatory variable	**Value**	**SE**	**DF**	**t**	**p**
(Intercept)	-0.26	0.39	46	-0.68	0.5
Prey mass	0.20	0.24	46	0.87	0.39
First bout	0.42	0.44	46	0.95	0.35
Last bout	0.67	0.39	46	1.62	0.112
Prey mass * first bout	-0.27	0.28	46	-0.98	0.333
Prey mass * Last bout	-0.59	0.26	46	-2.28	0.027

c)

Explanatory variable	**Value**	**SE**	**DF**	**t**	**p**
(Intercept)	0.37	0.12	46	3.06	0.004
Prey mass	-0.38	0.11	46	-3.41	0.001
First bout	-0.22	0.25	46	-0.9	0.375
Bouts between	-0.64	0.39	46	-1.64	0.108
Prey mass * first bout	0.32	0.19	46	1.7	0.096
Prey mass * bouts between	0.59	0.26	46	2.3	0.026

d)

Explanatory variable	**numDF**	**denDF**	**F**	**p**
(Intercept)	1	46	0.53	0.47
Prey mass	1	46	1.88	0.177
Bouts	2	46	2.28	0.114
Prey mass * Bouts	2	46	3.26	0.04

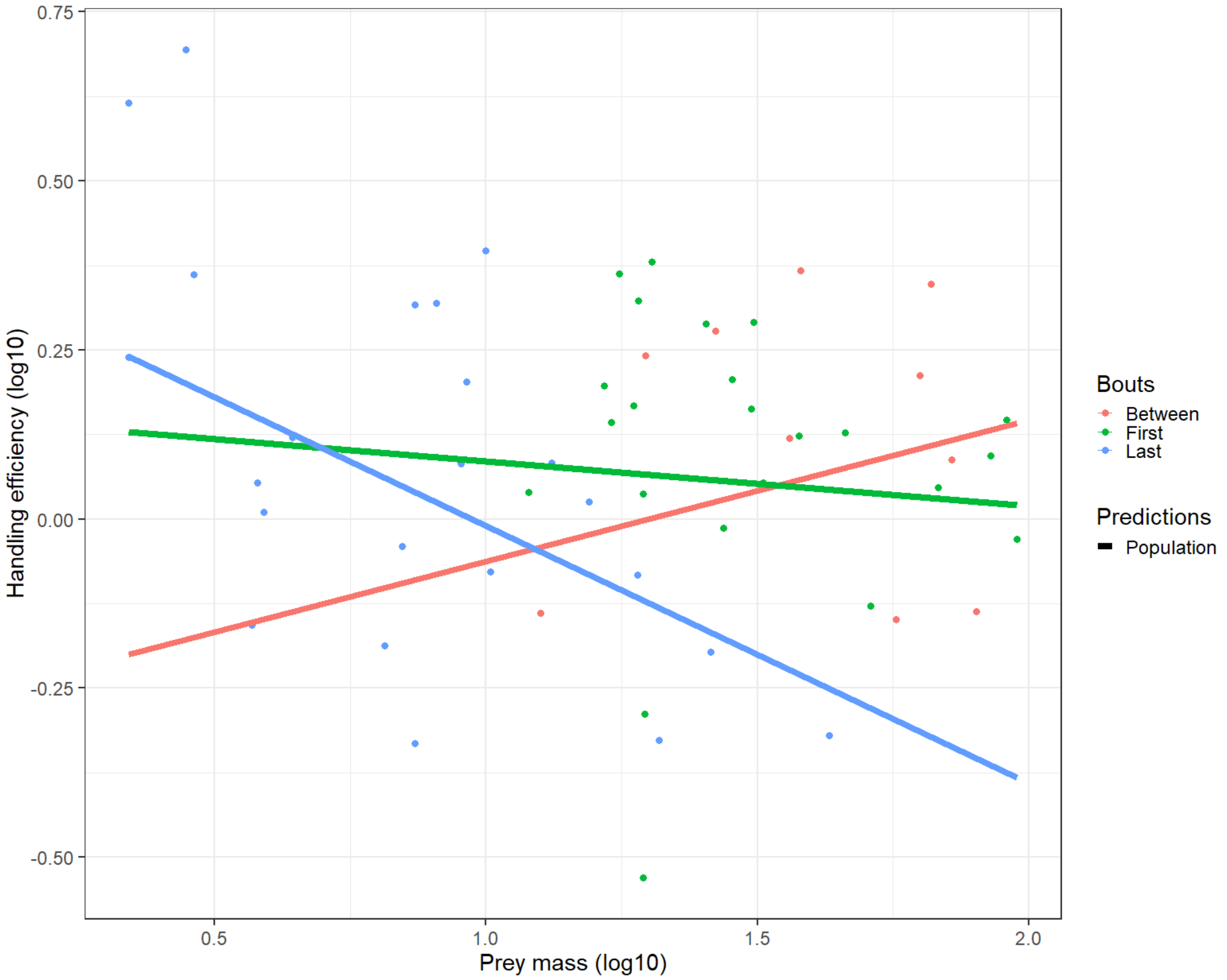

Figure 3.6.1 Handling efficiency (log10 transformed) of kestrels in different feeding bouts as a function of prey mass (log10 transformed) with regression lines fitted from the LME model. Green line denotes first bout (y = 0.15 -x*0.07, p = 0.66), red line denotes bouts between first and last bout (y = -0.27 + x*0.21, p = 0.377), and blue line denotes last bout (y = 0.37 – x*0.38, p = 0.001)

Based on the parameters from the LME model, the predicted handling efficiency of kestrels handling prey in the last bout was 0.13 g/min for a prey mass of 12 g, 0.08 g/min for a median sized prey (26.4 g) and 0.04 g/min for a prey mass of 95 g.

3.6.2 Feeding bouts in peregrines

From the parameter estimates given by the LME model, handling efficiency in peregrines did not differ between the three categories of feeding bouts (p = 0.346), and there was no effect of prey type, prey mass or the interaction between prey type and prey mass (table 3.6.2 a-b).

Table 3.6.2 Parameter estimates of variables from the LME model (AIC = 113.61, n = 65, ID = 5), describing handling efficiency (log 10 transformed) of peregrines as a function of prey type and feeding bouts, where a) avian prey is set as intercept and b) anova table

a)

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	0.15	0.16	57	0.95	0.346
Prey type mammal	0.25	0.15	57	1.73	0.089
First bout	0.22	0.16	57	1.31	0.195
Last bout	0.10	0.16	57	0.63	0.532

b)

Explanatory variable	**numDF**	**denDF**	**F**	**p**
(Intercept)	1	57	8.6	0.005
Prey type	1	57	2.44	0.123
Bouts	2	57	0.86	0.428

3.7 Mass of prey remains

3.7.1 Kestrels

Prey type did not have an effect on mass of prey remains left by the kestrels after handling prey, and was removed from the final model, leaving prey mass as the only explanatory variable in the best fitted LME model. The mass of prey remains was positively correlated with prey mass ($p = 0.009$) (table 3.7.1, figure 3.7.1). However, the regression slope was less than, but not significantly different from, one ($r = 0.82$, $SE = 0.30$), thus within the range of the confidence interval ($CI = 0.22$-1.42), indicating a constant proportion of remains with increasing prey mass.

Table 3.7.1 Parameter estimates from the best LME model (AIC = 131.5, n = 64, ID = 5) describing the proportion of non-ingested prey remains (g) (log10 transformed) as a function of prey mass (g) (log10 transformed) for prey handled by kestrels.

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	-0.88	0.41	58	-2.16	0.035
Prey mass	0.82	0.30	58	2.71	0.009

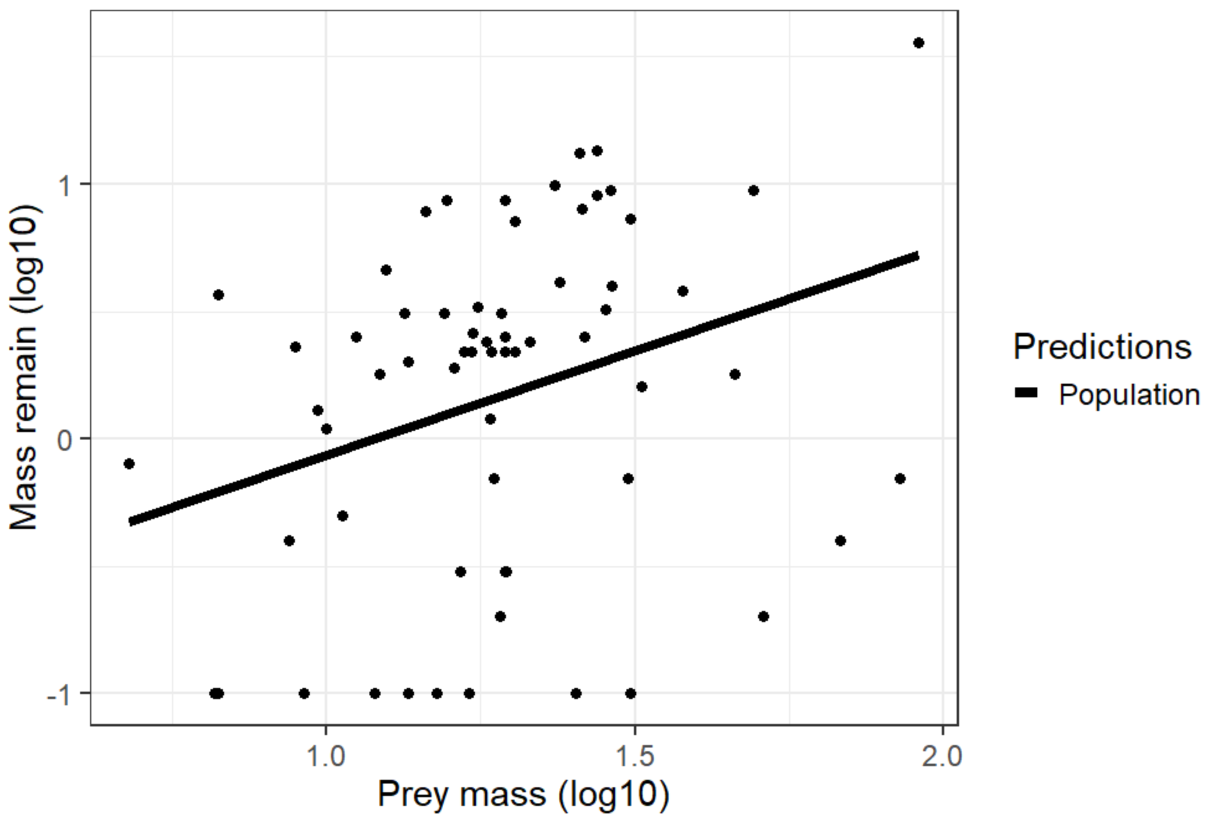

Fig.3.7.1 Mass of prey remains (g) (log10 transformed) as a function of prey mass (g) (log10 transformed) for kestrels, with regression line calculated by the LME model fitted by REML ($y = -0.88 + x*0.82$, $n = 64$, $p = 0.009$).

Based on the parameters from the LME model of avian prey handled by kestrels, a prey of 8.7 g was predicted to give 0.78 g remains (9.0 %), a median sized prey (17.8 g) was predicted to give 1.4 g remains (8%), and a prey of 95 g was predicted to give 5.5 g remains (5.8 %).

A mammalian prey of 6.6 g was predicted to give 0.62 g remains (9.4 %), a median sized prey of 19.9 g was predicted to give 1.53 g remains (7.7 %), while a prey of 49.2 g was predicted to give 3.27 g remains (6.5 %).

3.7.2 Peregrines

Prey type did not affect the mass of prey remains of prey handled by peregrines, and was excluded from the model. Based on the outputs given from the selected LME model, prey mass had a significant positive effect on mass of prey remains ($p < 0.001$) (Table 3.7.2). The regression slope was significantly larger than one ($r = 1.39$, $SE = 0.14$, $CI = 1.21 – 1.57$), indicating an increase in proportion of remains with increasing prey mass (Table 3.7.2, Figure 3.7.2).

Table 3.7.2 Parameter estimates of variables in the best LME model (AIC = 99.433, n =53, ID = 5), describing the mass of prey remains (g) (log10 transformed) as a function of prey mass (log10 transformed) for prey handled by peregrines**.**

Explanatory variable	**Estimate**	**SE**	**DF**	**t**	**p**
(Intercept)	-1.49	0.30	47	-5.03	<0.001
Prey mass	1.39	0.14	47	9.80	<0.001

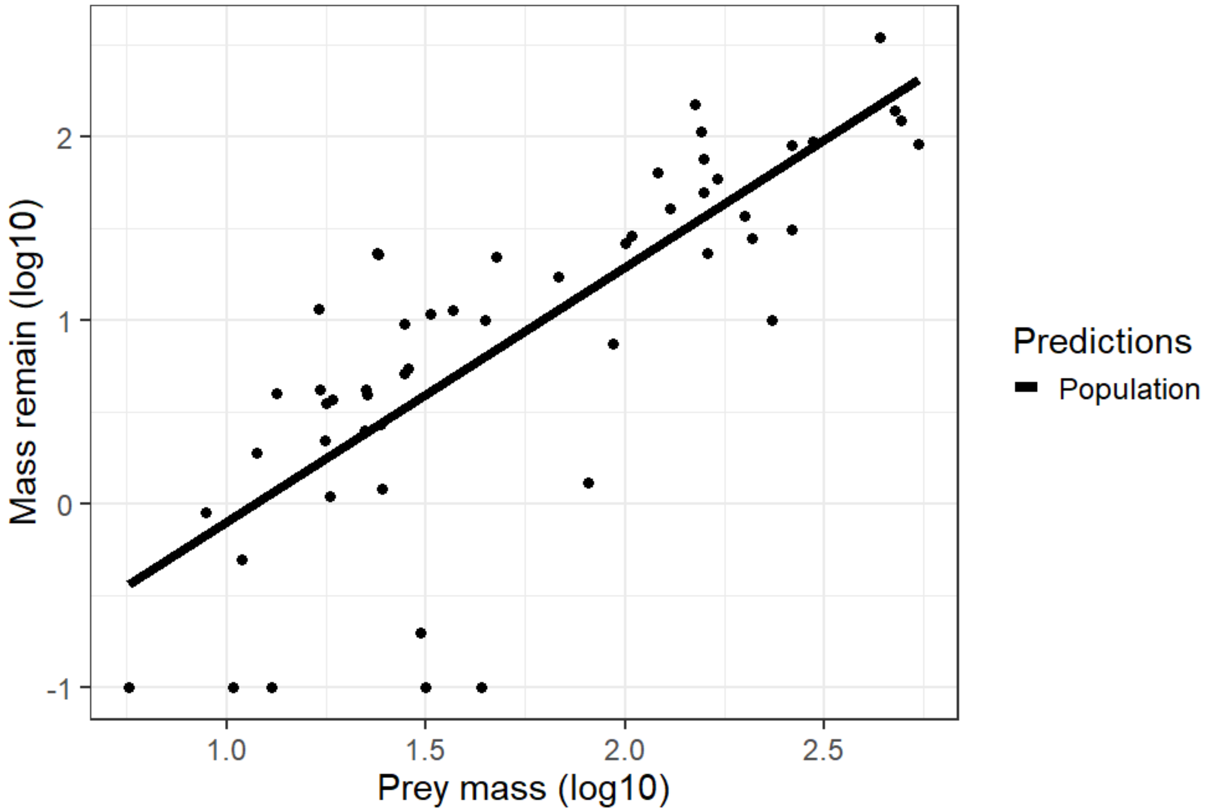

Figure 3.7.2 Mass of prey remains (g) (log 10 transformed) as a function of prey mass (g) (log10 transformed) for peregrines, with regression line calculated by the LME model fitted by REML (y = -1.49 + x*1.39, n = 53, p <0.001).

For avian prey handled by peregrines, the parameters from the LME model predicted a prey of 5.7 g to give 0.37 g of its initial mass as remains (6.5 %), a median sized prey (93 g) to give 17.7 g remains (19.0 %), while an prey of 545 g was predicted to give 208.3 g remains (38.2 %).

For mammalian prey handled by peregrines, the LME model predicted a prey of 10.4 g to give 0.85 g of its initial mass as remains (8.2 %), a median sized prey (28 g) to give 3.35 g remains (12.0 %), while prey of 297 g was predicted to give 87.8 remains (29.5 %).

4. Discussion

4.1 Probability of starting to feed from head of prey

When handling mammalian prey, peregrines fed exclusively from the head first in all prey items, even in the largest prey with a massive skull such as the squirrel, while the kestrels fed from the head first in 91% of the mammalian prey. When handling avian prey, kestrels fed from the head first in 83% of the total prey items, while peregrines fed from head first in 41% of prey items.

The sample size for this analysis of peregrines was low (n = 31), compared to the sample size for the analysis of the probability of peregrines starting at the breast of prey (n = 59) (see 4.2), and this might have biased the result. The difference in sample size was a result of observation bias; in some of the trials, the raptors started feeding in areas in vicinity of the head such as the neck and throat, thus making it harder to determine the exact part of prey that feeding started. These uncertain observations were excluded from the study.

Prey mass did not affect the birds' choice in starting to feeding from head of prey which is in contrast with previous studies (Grønsdal 2012)

4.2 Probability of starting to feed from breast of prey

The sample size for kestrels starting to feed from breast of their prey first was too small for a meaningful test (n = 3). In trials with peregrines, none of the mammalian prey items were eaten from the breast first, while the probability of starting to feed from the breast first on avian prey was predicted to be 79%. The pectorial (flight) muscles in breast of avian prey are highly nutritious in comparison to breast muscles in mammalian prey, which suggests a higher profitability of feeding from breast of avian prey than of mammalian prey (Grønsdal 2012.) In the wild, prey items might get lost, stolen or deteriorate due to environmental conditions. Hence, the raptor should feed from the most nutritious parts of prey first in order so attain highest energetic output from the prey.

4.3 Plucking time

Time spent plucking increased in both kestrels and peregrines in response to increasing prey body mass. These results are in accordance with results from previous studies (Steen et al 2010; Slagsvold et al. 2010; Salmila 2011; Grønsdal 2012) which found that larger prey required longer preparation before being ingested due to solid bones, skull fur and feathers. The smallest mammalian prey were either not plucked, or plucked a few times to create an opening to feed from as (Kaspari 1990) stated that the swallowing threshold suggest prey not to be prepared if its width is narrower than the raptors gap dimensions.

Both kestrels and peregrines spent longer time plucking avian prey than mammalian prey of the same relative size. However, the difference in plucking time between the two prey types was smaller for peregrines than kestrels, indicating that plucking avian prey was much more time consuming for kestrels. These results fit with the assumptions that predominant prey included in the raptors diet require less preparation before ingestion than unfamiliar or unfavourable prey (Slagsvold et al 2010).

4.4 Average prey mass ingested per bout (meal)

During breeding season, the average daily energy intake for kestrel is 400 KJ for males and 317 KJ for females, equivalent to eight and six voles respectively, while during winter this drops to 270 KJ daily for both sexes, which is equivalent to four voles (Masman 1986; Masman et al. 1986) However, in captivity, (Kirkwood 1980a) found that daily energy intake in kestrels was 50-170 KJ, as energy expenditure dropped significantly due to inactivity.

The average daily intake for wild peregrines is 127 g for adults and 157 for young individuals (Ratcliffe 1980). For peregrines kept in captivity, (Stirling-Aird 2015) found that daily energy intake was 100-110 g for males and 140-150 g for females.

These estimates provide information about daily energy requirements in kestrels and peregrines, but they do not explain the average amount of food ingested by raptors during one meal. Assuming raptors in my study stopped feeding when feeling full; the amount of food consumed during a feeding bout gave an estimate of gut capacity. If there were no more edible prey remains after a meal, or if the prey was completely ingested, this assumption was not met as the raptor had no option to continue feeding if still hungry. Therefore, estimates in my study were based on prey items consumed in two or more bouts where food ingested in the last bout were excluded from the study.

The difference in average meal size between avian prey, pure meat and mammalian prey consumed by kestrels was small compared to the averages obtained in trials with peregrines, thus indicating that kestrels feeding capacity were less affected by plucking prey. Peregrines consumed a larger proportion of pure meat compared to their body size during a meal than kestrels, indicating a larger gut capacity in the former species. These findings were in contrast to (Barton and Houston1996) which stated that a bird feeders gizzard and digestive tract are smaller than of a vole feeder.

4.5 Handling efficiency

4.5.1 Handling efficiency in kestrels and peregrines compared

The general handling efficiency model originally included hunting time as a factor, i.e. the duration from the onset of an attack until prey has successfully been captured. In my study, the raptors were fed dead prey items, limiting handling efficiency to measures of mass ingested per unit of handling time (plucking and handling time pooled).

In my global model investigating handling efficiency between kestrels and peregrines, the parameters predicted peregrines to handle prey of the same relative size more efficiently than kestrels. Therefore, the profitability of large prey was expected to be higher in peregrines than in kestrels.

4.5.2 Handling efficiency in kestrels

Kestrels handled mammalian prey more efficient than avian prey, especially small prey. However, the steep regression slope for mammalian prey (-0.28) predicted the difference in profitability of mammalian and avian prey to disappear when prey mass approached 100 g. The largest avian prey given to a kestrel was a fieldfare (*Turdus pilaris*) with a body mass of 95 g, while the next largest was a bullfinch (*Pyrrhula pyrrhula*) with a mass of 31.1g and the largest mammalian prey given a kestrel was field vole (*Microtus agrestis*) with a mass of 49 g. Thus, the prediction that the profitability of large mammalian and avian was similar was not based on actual observations and was not of biological importance as kestrels rarely catch prey of both prey types with a mass of >100 g in the wild.

4.5.3 Handling efficiency in peregrines

For peregrines handling prey, prey mass had a negative effected on handling efficiency. However, the effect of increasing prey mass on handling efficiency in peregrines might have been biased by prey items given as the distribution of residuals in the QQ-plot revealed a problem with normality (see 4.8). However, the problem with normality in the analysis could also be explained by sampling error or random effects, such raptor ID.

4.6 Variation in handling efficiency in different feeding bouts

I found that kestrels handling larger prey were less efficient in the last feeding bout compared to the first or intermediate bout(s). After extracting nutritious parts of prey in the first feeding bout(s), the profitability of the remaining carcass left to feed on in the last bout declined, as it consisted of a higher proportion of non-utilisable and/or unfavourable body parts such as bones, feathers, wool and skull (Slagsvold et al. 2010, Grønsdal 2012). The remaining edible parts of prey might also be hard to extract or tear apart from prey, thus more time consuming to handle. In the wild, the raptor might have discarded the prey item at an earlier stage during feeding bouts as there would often be other food sources available. As seen in other predators such as wolves, when prey availability is high, predators tend to devour only the most nutritious part of prey then move on to the next victim optimizing energetic input compared to expenditure. Thus, the lower threshold of when to abandon a prey item might fluctuate by factors such as prey availability, hunting time and strike success. Juvenile kestrels might benefit from extracting as much meat as possible from their prey before launching attacks at new prey as their strike success are typically lower than of adults (Village 1990).

There were no differences in handling efficiency between feeding bouts for peregrines. These results might reflect that the profitability of prey consumed by peregrines declined at a lower rate during feeding bouts compared to that of kestrels, as peregrines often swallow and completely digest bones of prey leaving less remains (Ratcliffe 1980). According to my results, peregrines should benefit from extracting meat from the same prey instead of finding new prey until the carcass of current prey is completely depleted of edible body parts.

To the best of my knowledge, there are no previous studies on variation in handling efficiency between feeding bouts in raptors. Because I found kestrels to be less effective when handling large prey in the last feeding bout in my study, I suggest further studies on other generalist or vole feeding raptors to investigate if this applies to vole feeders in general or just kestrels. Since I did not investigate any effect of raptor age on handling efficiency, it would also be interesting to study differences in handling efficiency between feeding bouts of birds of different age classes.

4.7 Proportion of prey mass remains

Identifying prey remains left by falcons after a meal have been conducted in several studies however most have focused on determining diet composition, and not quantifying prey remains after a meal (Navjot et al. 1993; Salvati et al.1999, Geng et al 2009). This may lead to severe biases such as overestimating the profitability of large prey, especially avian prey (Slagvold et al. 2010)

The amount of prey remains left by kestrels was predicted to increase with increasing prey mass, however, the proportion of remains was constant. These results contrasts with results obtained in previous studies on mass remains in raptors (Slagsvold et al. 2010; Salmila 2011; Grønsdal 2012), which stated that the proportion of mass remains increased with increasing prey body mass. These results might however been biased by the variation in prey size of prey offered the focal raptors; (see 4.8).

Both the amount and proportion of non-ingested prey mass remains left by peregrines increased in response to increasing prey mass for both avian and mammalian prey, indicating that larger prey were harder to ingest possibly due to a higher proportion of larger and more solid bones, feathers and fur (Tjernberg 1981; Slagsvold et al. 2010; Grønsdal 2012).

Prey type did however not affect the amount of prey remains, which is in disagreement with what Grønsdal (2012) and Salmila (2011) found, namely that an avian prey of a given size leaves more non-ingested remains than a mammalian prey of similar size.

4.8 Possible bias and future studies

The kestrels and peregrines were fed in temporal captivity which shielded them from environmental factors such as competition from other predators or other natural interruptions (Slagsvold et al 2010, Grønsdal 2012). Prey items were kept in a refrigerator between feeding bouts in order to stay fresh and prevent deterioration from bacteria, parasites or weather conditions. The raptors were fed only one prey item at a time with no other food sources available and no option to discard prey in order to find new prey. These factors could affect handling efficiency as the need for vigilance decreased; when interrupted, the raptors could resume activity shortly after a break. (Slagsvold et al 2010, Grønsdal 2012). However, I noted that the raptors continuously stopped handling prey to scan the environment, indicating that they were highly alert and behaving like wild raptors. (see also Slagsvold et al 2010, Salmila 2011).

Some of the videotapes were in poor condition; the picture was blurry with low resolution, and most of the recordings had no sound. This made it harder to distinguish between plucking and feeding behaviour, especially when the raptor was feeding with its back to the camera. If the raptor covered the prey with its body, it was difficult to determine where it started to feed from its prey, and these uncertain observations were all excluded from the analyses resulting in a lower sample size. In a few trials, the focal raptors succeeded in removing prey from the camera spot and continued feeding from a branch, a hay stack or in various positions on the floor behind or in front of the wooden plate they were supposed to perch on while feeding. During these relocations of prey, parts of prey might have been scattered around in the room and not retrieved later when collecting, weighing and quantifying prey remains. Thus, the proportion of ingested prey might be overestimated and the prey remains underestimated as a result in these analyses. (see also Grønsdal 2012)

The camera filmed from only one angle. I suggest future studies use multiple cameras at once from different angles, at least two cameras on opposite sides of the feeding plate to prevent observation bias. Sound is also crucial for distinguishing between feeding and plucking behaviour when the raptors are standing with its back towards the camera. Some of the raptors spent a considerable amount of time attempting to detach tied prey from the wooden plate instead of plucking or feeding from it, which might have influenced handling efficiency.

Mammalian prey were either small or large, e. g. mass of mammalian prey given peregrines had a median mass of 28 g which is less than 10% of heaviest mammalian prey given (297 g). The lack of intermediate mammalian prey relative to raptor body mass given the peregrines might have biased the results in all the analyses, thus predicting a steeper regression slope in the analyses of handling efficiency and prey remains than if intermediate prey were present.. Finding intermediate mammalian prey suitable for scientific research which does not violate ethical law (many are pets such as hamsters etc.) might be hard to find in Scandinavia fauna, but a suggestion might be small rats with body weights from 50 ~ 200 g.

5. Conclusion

I found that both kestrels and peregrines preferred feeding from head of prey first. Kestrels spent longer time plucking avian prey than mammalian prey of similar size. Peregrines also plucked avian prey more than mammalian prey, but the difference was smaller than for kestrels. Peregrines were more efficient than kestrels handling prey of the same relative size regardless of prey type. Handling efficiency did not differ between feeding bouts in peregrines, while kestrels were less effective when handling large prey in the last feeding bout compared to the first and intermediate bouts. I suggest further studies investigating variation between feeding bouts in other generalist or vole feeding raptors to determine if my results apply to vole feeders in general. The amount of mass remains left by kestrels after feeding increased with increasing prey mass, but the proportion of remains relative to prey body mass remained constant. In peregrines, both the amount of- and the proportion of prey mass remains left after feeding increased with increasing prey mass.

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Appendix

Appendix I

Table 1 Prey species, prey type, prey mass and number of prey items of the same species fed fed the individual raptors in a) kestrels, b) peregrines.

a)

Prey species	Prey type	Mass (g)	Number of prey items	Raptor ID
Bank Vole (*Myodes glareolus*)	Mammal	18.2, 9.2, 26.2, 17.3, 20.2, 19.5, 25.7, 12.5, 14.5, 27.4, 23.4	11	1KM 1KM_08, IKF 2KM
Blue tit (*Cyanistes caeruleus*)	Avian	10	1	3KM
Bullfinch (*Pyrrhula pyrrhula*)	Avian	28.9, 31.1	2	1KM 1KM_08
Coal tit (*Periparus ater*)	Avian	8.9	1	2KM
Common chaffinch (*Fringilla coeleb*)	Avian	18.5	1	1KM_08
Common shrew (*sorex araneus*)	Mammal	6.6, 6.7, 9.7	3	1KM 2KM
Eurasian blackcap (*Sylvia atricapilla*)	Avian	15.7	1	1KM

Eurasian robin (*Erithacus rubecula*)	Avian	13.6, 15.5	2	1KM_08 3KM
Eurasian siskin (*Spinus spinus*)	Avian	13.4	1	1KF
Eurasian wren (*Troglodytes troglodytes*)	Avian	10.6, 8.7	2	1KM_08
European roe deer (*Capreolus capreolus*)	Control	65, 41.6, 124, 136	4	1KM_08, 1KF,
Fieldfare (*Turdus pilaris*)	Avian	95	1	1KM
Goldcrest (*Regulus regulus*)	Avian	4,8	1	1KM_08
Great tit (*Parus major)*	Avian	21.4, 17.2, 11.2	3	1KM 3KM
Iron sparrow (*Prunella modularis*)	Avian	19.6, 19.5, 16.7	3	1KM 1KF 3KM
Lesser whitethroat (*Sylvia curruca*)	Avian	12.2	1	1KF
Short tailed vole (*Microtus agrestis*)	Mammal	49,2	1	1KM_08
Tree pipit (*Anthus trivialis*)	Avian	16.1	1	2KM
White wagtail (*Motacilla alba*)	Avian	18.4	1	2KM
Willow warbler (*Phylloscopus trochilus*)	Avian	19.2	1	1KM_08
Wood mouse (*Apodemus sylvaticus*)	Mammal	13.6, 12, 15.2	2	1KM 1KM_08

Yellow necked mouse (*Apodemus flavicollis*)	Mammal	23.9, 29, 51,	3	1KM 1KF

b)

Prey species	**Prey type**	**Mass (g)**	**Number of prey items**	**Raptor ID**
Bank vole (*Myodes glareolus*)	Mammal	13.4, 24.1, 22.5, 30.7	4	1KM, 8KF
Bullfinch (*Pyrrhula pyrrhula*)	Avian	32.5	1	8KF
Common blackbird (*Turdus merula*)	Avian	100	1	8KF
Common chaffinch (*Fringilla coeleb*)	Avian	22,4	1	3KM
common wood pigeon (**Columba palumbus**)	Avian	493	1	3KM
Eurasian jackdaw (*Coloeus monedula*)	Avian	155, 157	2	1KM, 8KF
Eurasian jay (*Garrulus glandarius*)	Avian	157	1	1KM
Eurasian magpie (*Pica*	Avian	199, 208.5	2	2KM, 3KM

pica)				
Eurasian red squirrel (*Sciurus vulgaris*)	Mammal	150, 262, 263, 297	4	1KM, 2KM 3KM, 8KM
Eurasian robin (*Erithacus rubecula*)	Avian	17	1	1KM
Eurasian siskin (*Spinus spinus*)	Avian	11.9	1	8KF
Eurasian wren (Troglodytes troglodytes)	Avian	8.9	1	8KF
European greenfinch (*Chloris chloris*)	Avian	24.4, 28.5	2	8KF
European water vole (*Arvicola amphibius*)	Mammal	130	1	8KF
Fieldfare (*Turdus pilaris*)	Avian	93, 104	2	2KM, 3KM
Great tit (*Parus major*)	Avian	17.6, 17.2	2	2KM, 8KF
Hooded crow (*Corvus cornix*)	Avian	435, 476	2	2KM, 3KM
Norway lemming (*Lemmus lemmus*)	Mammal	36.9	1	8KF
Tree pipit (*Anthus trivialis*)	Avian	17.8	1	8KF

Tundra vole *(Microtus oeconomus)*	Mammal	47,4, 44.7	2	3KM
Wood mouse (*Apodemus sylvaticus*)	Mammal	13	1	2KM
Yellow necked mouse (*Apodemus flavicollis*)	Mammal	27,9, 43.5, 24.6, 22.2,	4	1KM, 2KM, 3KM

APPENDIX 2

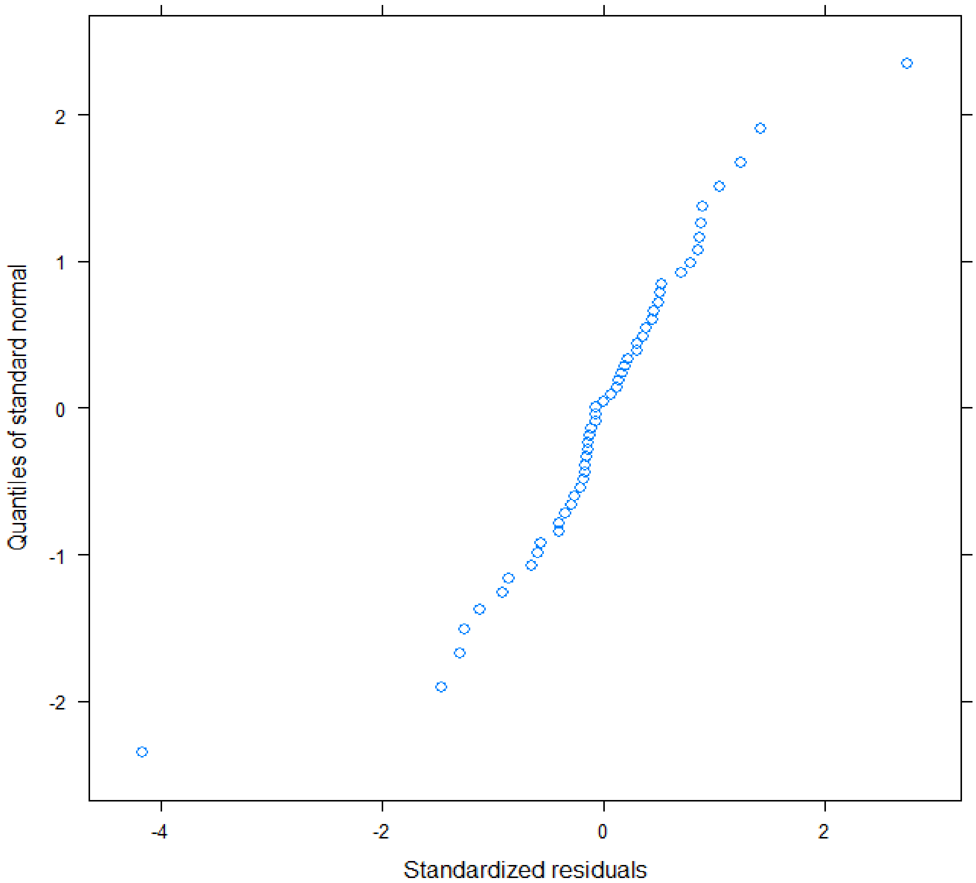

Figure II. The distribution of residuals describing handling efficiency in peregrines

APPENDIX 3

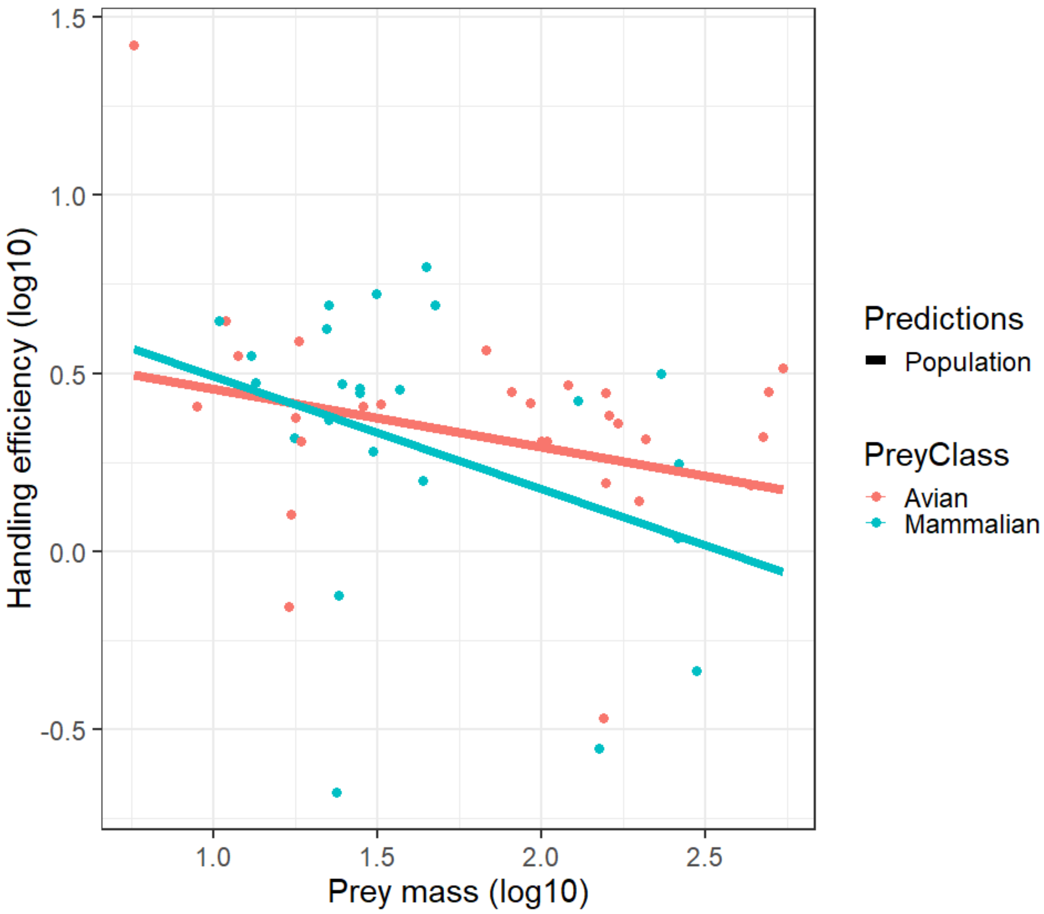

Figure III. Handling efficiency (log10 transformed) as a function of prey mass (g) (log10 transformed), with regression line calculated from the best LME model fitted by REML. Red line denotes avian prey and blue line denotes mammalian prey.