Partitioning of prey for nestlings by female Eurasian kestrels (Falco tinnunculus): effect of prey type, prey size and brood size.

OPPDELING AV BYTTEDYR FOR REIRUNGENE HOS HUNNER AV TÅRNFALK (*FALCO TINNUNCULUS*): EFFEKT AV BYTTEDYRTYPE, BYTTEDYRSTØRRELSE OG KULLSTØRRELSE.

Nina Berglund Østbye

Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management
Master Thesis 30 credits 2010

Preface

This thesis is the final work of a masters degree at the Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management.

Main supervisor has been Geir Andreas Sonerud at the Department of Ecology and Natural Resource Management. Additional supervisor has been Ronny Steen, also situated at the Department of Ecology and Natural Resource Management.

I want to thank Geir Andreas Sonerud and Ronny Steen for ideas and good supervision during the study, and Ronny Steen for help with the statistics.

Ås, December 13, 2010.

Nina Berglund Østbye

Abstract

I used the video recordings from 19 nests of the Eurasian kestrel (*Falco tinnunculus*) located in south-eastern Norway to investigate allocation of food from parents to nestlings. Prey was both avian and mammalian. The mass of mammalian prey varied from 7-37 g, with an average of 14 g, while mass of avian prey varied from 9-105 g, with an average of 34 g. The female kestrel partitioned the prey items into more pieces when prey items were large than when they were small, and it may be to get the pieces small enough for the nestlings to swallow. When the prey item was large the female tore off larger pieces than when the prey item was small. When brood size increased, the number of pieces each nestling received during a feeding decreased. Prey mass had an effect on the number of pieces each nestling received per feeding in avian prey, but not in mammalian prey. One reason may be the larger range of prey mass in avian than in mammalian prey. Prey preparation in the Eurasian kestrel varies with prey size, prey type and brood size.

Sammendrag

Jeg brukte videoopptak fra 19 reder hos tårnfalk (*Falco tinninculus*) i sør- øst Norge til å undersøke fordeling av føde fra foreldre til fugleunger. Byttedyrene var både små pattedyr og fugler. Massen av små pattedyr varierte fra 7-37 g, med en gjennomsnittsverdi på 14 g, mens massen av fugler varierte fra 9-105 g, med en gjennomsnittsverdi på 34 g. Tårnfalk hunnen delte byttedyrene i flere biter når byttedyrene var store enn når de var små. Dette kan ha blitt gjort for å få bitene små nok til at ungene skal være i stand til å svelge dem. Når massen til byttedyrene var høy rev hunnen av større biter til ungene enn når massen til byttedyrene var lav. Når kullstørrelsen økte, minket antall biter hver unge mottok i løpet av en fôring. Hos byttedyr av typen fugl hadde masse av byttedyr en effekt på antall biter hver unge mottok i løpet av en fôring, men det var ingen effekt hos byttedyr av typen pattedyr. En grunn til dette kan være forskjellen i variasjonsbredde hos massen til fugler i forhold til små pattedyr. Oppdeling av byttedyr hos tårnfalk varierer med byttedyr type, størrelse på byttedyr og kullstørrelse.

TABLE OF CONTENTS

Introduction

Allocation of food from parents to offspring is an important aspect of parental care, and parents are expected to allocate resources in order to maximize the benefit from their investment (Winkler, 1987). Many birds prepare the food for their nestlings, and this is also prevailing for the Eurasian kestrel (*Falco tinnunculus*) (Steen et al. 2010). Prey preparation is time-consuming, and will therefore be traded for other activities, as for example food searching (Barba et al. 1996). Prey preparation must therefore be done for a reason, and one reason may be that the prey item is too large for the nestlings to swallow (Slagsvold and Wiebe 2007, Steen et al. 2010a). Other reasons can be that parts of the prey are toxic or physically dangerous, or that the parents remove low- quality parts of the prey (Barba et al. 1996). There are several factors that can affect food allocation from parents to offspring, and Andersen (2003) found that nestling age, brood size, prey mass and nestling size did influence food allocation in the European Sparrowhawk (*Accipiter nisus*).

The Eurasian kestrel, hereafter called kestrel, is a medium-sized falcon which hunts from perches or by hovering flight (Village, 1990). Kestrels mainly feed on small rodents, but they have a flexible diet which enables them to live in many kinds of environment (Village, 1990). Kestrels are predominately open-country birds, and are absent from dense woodland unless there are clearings where they can hunt (Village, 1990). Diurnal voles of the genus *Microtus* are their most important prey, but besides other small mammals, alternative prey can be birds, lizards, insects and earthworms (Village, 1990). Kestrels take the most abundant prey at the time, and switching to alternative prey when the main prey is scarce allows them to persist in areas they otherwise would abandon (Village, 1990). During the first two weeks after hatching the male hunts and brings prey to the female who portions the prey for the nestlings. Later in the nestling period both parents hunt and bring prey to the nestlings who then consumes the prey on their own (Village, 1990).

Several studies have been done on food provisioning in raptors, and in an earlier study on food allocation in the European Sparrowhawk Andersen (2003) found that the number of pieces a prey item was partitioned into increased as the prey mass increases. Also, smaller prey were partitioned into smaller pieces than larger prey, and bite size tended to increase as the nestlings grew older (Andersen, 2003). Steen et al. (2010a) found that prey preparation in kestrels increased with increasing prey mass. In a study on the American kestrel (*Falco sparverius*) Dawson and Bortolotti (2003) found that the parents delivered a similar amount of food independent of brood size, which gives the nestlings in small broods more food than nestlings in large broods.

In this thesis I will study food allocation from parent to offspring in the kestrel. The male or female kestrel brings the prey to the nest where the female feeds the nestlings with pieces she tears off the prey with her bill. The questions asked in this thesis are: 1) Does number of pieces per prey differ with the size of the prey? One would think that when prey mass increases, the number of pieces also increases. 2) Does bite size increase as prey mass increases? One might assume that the female tears off larger pieces for the young when the prey is larger. 3) Does the amount of food each nestling receives decrease as brood size increases? In larger broods one may expect that each nestling receives less food because there are more nestlings per prey. 4) Does prey size influence how much food each nestling receives? One might assume that the amount of food each nestling receives will increase when prey size increases as there are more food for the female to allocate amongst the nestlings. 5) Does the allocation of food as outlined in questions 1)-4) differ between prey types i.e. mammals and birds?

Methods

Study area and species

The study was conducted in the boreal zones in Trysil municipality in Hedmark county, in south-eastern Norway (61˚ 07 - 61˚ 28´ N; 12˚ 43´ E), in June- July 2003 and May- July 2005. In 2003 nine nests and in 2005 ten nests of the Eurasian kestrel were videotaped. The nests were in nest boxes located in bogs and clear-cuts, surrounded by coniferous forest with only small scattered patches of agricultural areas at altitudes of 300-700 m above sea level (Steen, 2004, Løw 2006).

Video recording

In 2003 the nests were videotaped with a digital camcorder, Canon MV550i, with a WD-30.5 wide-angle lens. The camcorder was mounted on the top of the nest boxes with the lens towards the open front. The broods were video recorded in two periods, the first when brood age was 8-13 days and second when brood age was 21-26 days. The brood were recorded for an average of 10 h 40 min (between 6 AM to 5 PM) in both periods (Steen, 2004).

In 2005 a digital camcorder, Canon MV850i, was used to film the nest boxes. The camcorder was positioned in an angle that made it possible to see the adult kestrel with its prey, and also the nestlings when they were fed by the mother or when self-feeding. The different broods were video recorded for an average of 10 h (from 6 AM to 4 PM) on two subsequent days. One brood was recorded at two separate days at three days interval (Løw, 2006).

Video analysis

I recorded the number of pieces the kestrel female fed the nestlings by watching the videotapes on a TV and count each piece by using a birdcounter. The female held the prey in her talons and tore off bite-sized pieces with her bill and fed the nestlings one piece at a time. Each of the bites she tore off were counted, and also the number of nestlings that were fed during each feeding. Feeding bouts where the nestlings self-fed and feeding bouts where the prey mass was unknown were excluded from the analysis.

The prey items brought to the nests by the kestrels were birds, voles, shrews, unidentified small mammals and lizards, and they had previously been identified to type (Steen 2004, Løw 2006). Prey mass had been estimated previously (Steen 2004, Løw 2006). Based on estimated prey mass and number of pieces recorded I could calculate the average mass of each bite the female tore off the prey.

Statistics

Statistical analyses were performed with the software R, version 2.11.1 (R Development Core Team 2010), by using a generalized linear mixed-effect model (GLMM) for count data (Poisson distribution) from the package ”lmer”, with log-link function. The Poisson loglinear model has the following form:

$$\log \mu = \alpha + \beta x \qquad (1)$$

For this model the back-transformed values were used when constructing the graphs with the relationship between number of pieces and prey mass, given by the formula:

$$\mu = e^{\alpha} (e^{\beta})^{x} \qquad (2)$$

The response variable was the number of pieces a prey was dismembered into by the female. Explanatory variables were prey mass, prey type (i.e. mammalian prey or avian prey), brood size, and the interaction term between prey mass and prey type and brood size.

A linear mixed-effect model (lme) from the package ”lmer” was used for continuous data (normal distribution). The response variable was an index of amount of bites that each nestling obtained, i.e. number of pieces the prey was dismembered into by the female divided on number of nestlings that achieved food. Explanatory variables were prey mass, prey type (i.e. mammalian prey or avian prey), brood size, and the interaction term between prey mass and prey type. The index of amount of bites that each nestling obtained, prey mass and brood size were log10 transformed to obtain approximate normal distributions. Back-transformed values were used when constructing the graphs from the parameter estimates.

In both models brood size was treated as a cofactor, and only included if being significant at level 0.10. The variable breeding pair was included as random effect (Pinheiro and Bates 2000) to control for any individual differences in prey handling behaviour. Averages are shown with one standard error (SE).

Results

Prey mass, number pieces and bite size

Average body mass of prey was 14.0 ± 1.1 g (range 7-37 g, n= 38) for small mammals, and 34.0 ± 2.5 g (range 9-105 g, n= 81) for birds. The average number of pieces a prey item was partitioned into was 35.1 ± 2.3 (range 4-68, n= 38) for mammals, and 68.0 ± 6.2 (range 13-272, n= 81) for birds. The average bite size was 0.49 ± 0.07 g (range 0.15-0.63 g, n= 38) for small mammals, and 0.69 ± 0.07 g (range 0.09-4.77 g, n=81) for birds.

Effect of prey size and prey type on number of pieces and bite size

The generalized linear model included type of prey, mass of prey and the interaction between mass and prey (Table 1, Fig 1). Brood size did not contribute in this model.

Table 1) Parameter estimates from the GLMM model of variables explaining the number of pieces a prey was partitioned into when kestrel females fed their nestlings, with breeding pair as random effect (n= 119 (81 birds and 38 mammals) , number of breeding pairs = 18, years = 2)
a) Prey type bird as intercept. b) Prey type mammal as intercept.

a)

	Estimate	**Std. Error**	**z value**	**p value**
(Intercept)	3.14	0.09	34.88	<0.001
Prey mass	0.03	<0.01	7.21	<0.001
Prey type (mammal)	0.59	0.08	7.22	<0.001
Prey mass x prey type (mammal)	-0.02	<0.01	-4.48	<0.001

b)

	Estimate	**Std. Error**	**z value**	**p value**
(Intercept)	3.73	0.07	57.13	<0.001
Prey mass	0.01	<0.01	17.02	<0.001
Prey type (bird)	-0.59	0.08	-7.22	<0.001
Prey mass x prey type (bird)	0.02	<0.01	4.48	<0.001

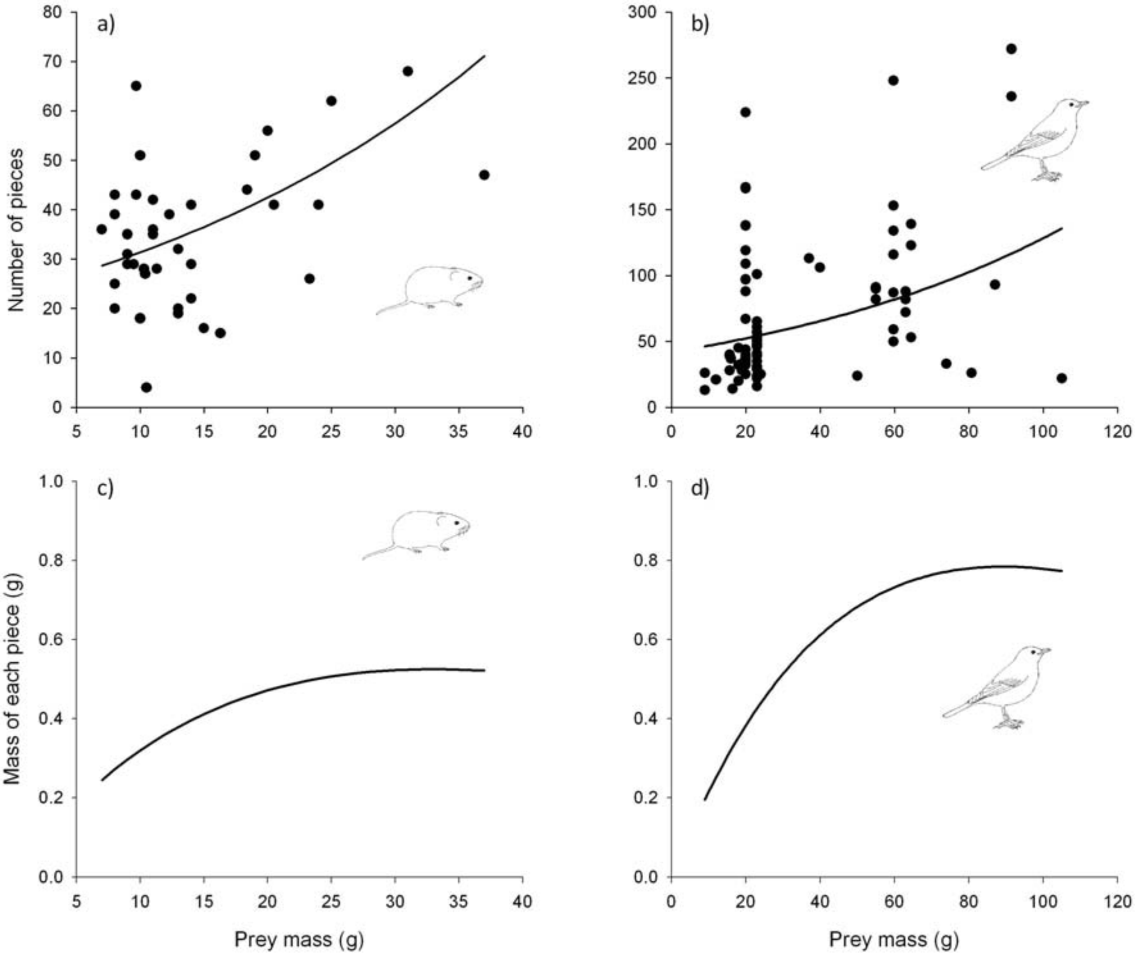

Figure 1. Prey partitioning by female kestrels feeding nestlings. a) Number of pieces that mammals were dismembered into in relation to prey mass. b) Number of pieces that birds were dismembered into in relation to prey mass. c) Estimated mass of each piece of mammals in relation to prey mass. d) Estimated mass of each piece of birds in relation to prey mass. Graphs calculated from the parameter estimates (back-transformed).

The number of pieces a prey was partitioned into increased with increasing prey mass, both for mammalian and avian prey (Fig 1 a, b). Larger prey was partitioned into larger pieces than smaller prey, both for small mammals and birds (Fig 1 c, d). The average body mass of mammalian prey was 14.0 g. At that mass a mammal was partitioned into 35.4 pieces, each piece weighing 0.40 g. At the minimum mass of mammalian prey, which was 7 g, the prey was partitioned into 28.6 pieces, with a mass of 0.24 g per piece. At the maximum mass of 37.0 g a mammalian prey was partitioned into 71.1 pieces, each weighing 0.52 g. Avian prey had an average mass of 34 g, and was at this mass partitioned into 61.2 pieces, each weighing

0.56 g. The minimum mass of avian prey was 9 g, and at this mass avian prey was partitioned into 46.3 pieces which weighed 0.19 g each. The maximum mass of avian prey was 105 g, and at this mass avian prey was partitioned into 135.9 pieces with a weight of 0.77 g per piece.

Effect of prey size and brood size on number of pieces per nestling

The linear mixed-effect model included prey mass, prey type and the interaction between prey mass and prey type, while brood size was included as a cofactor (Table 2, Fig. 2). In this model brood size was significant and therefore included in the model.

Table 2) Parameter estimates from the LME model, with breeding pair as random effect (n= 119 (81 birds and 38 mammals), number of breeding pairs = 18, years = 2). a) Prey type bird as intercept. b) Prey type mammal as intercept.

a)

	Estimate	SE	DF	t	p
(Intercept)	1.06	0.17	98	6.26	<0.001
Log Mass	0.43	0.11	98	3.93	<0.01
Log Brood	-0.80	0.12	16	-6.86	<0.001
Prey type (mammal)	0.19	0.29	98	0.66	0.51
Log Mass x Prey type (mammal)	-0.24	0.24	98	-0.97	0.33

b)

	Estimate	SE	DF	t	p
(Intercept)	1.25	0.25	98	5.06	<0.001
Log Mass	0.19	0.22	98	0.88	0.38
Log Brood	-0.80	0.12	16	-6.86	<0.001
Prey type (bird)	-0.19	0.29	98	0.66	0.51
Log Mass x Prey type (bird)	0.24	0.24	98	-0.97	0.33

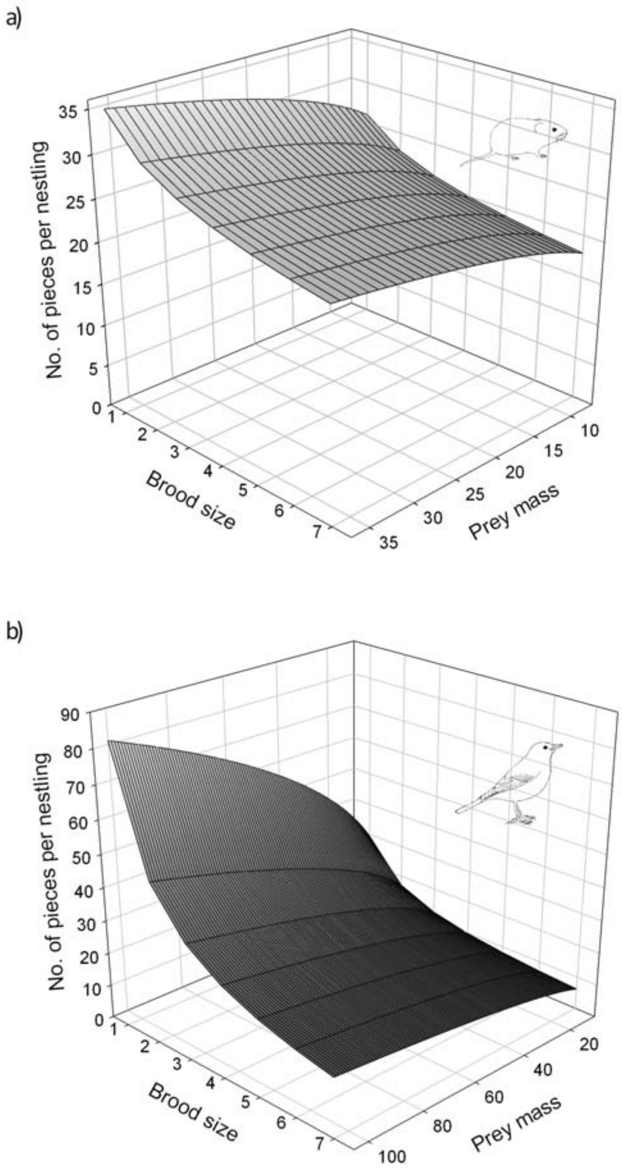

Figure 2. a) Number of pieces per nestling that voles were dismembered into in relation to prey mass and brood size. b) Number of pieces per nestling that birds were dismembered into in relation to prey mass and brood size. Graphs calculated from the parameter estimates (back-transformed).

The number of pieces that each nestling received per feeding decreased as brood size increased, both for mammalian and avian prey. Prey mass had a significant effect for avian prey, where the nestlings received more pieces per feeding when prey mass increased, but not for mammalian prey. The effects of prey type and the interaction between prey type and prey mass were not significant (Table 2).

Discussion

Effect of prey size and prey type on number of pieces and bite size

Larger prey, both mammalian and avian, were partitioned into more pieces than smaller prey. Avian prey were on average partitioned into more pieces than mammalian prey, but avian prey had on average a higher prey mass than mammalian prey. When prey are heavier there are more food for the female to allocate to the nestlings, and she can tear the prey into more pieces. Larger prey may be partitioned into more pieces so that the pieces are small enough for the nestlings to swallow. In early stages of the nestling period nestlings will only be able to swallow small and soft food items, and the female have to spend more time preparing large prey than smaller prey (Slagsvold and Wiebe 2007). This is consistent with the feeding constraint hypothesis (Slagsvold and Wiebe 2007), which predicts that prey preparation will increase with increasing prey mass (Steen et al. 2010a). When studying prey preparation as a function of nestling age and prey mass Steen et al. (2010a) found that the probability of a prey being decapitated increased as prey mass increased, which is consistent with my findings that kestrels increase prey preparation with larger prey. Prey size may not be the only factor influencing number of pieces a prey is partitioned into; nestling begging and nestling age could also have an influence. If the nestlings are hungry and therefore begging intensely the female may partition the prey into fewer pieces to feed the nestlings more efficiently. Nestlings that have been recently fed may be calmer and the female may take more time to prepare the prey, and then divide it into more pieces.

Larger prey were partitioned into larger pieces than smaller prey. This asserts itself both for avian and mammalian prey. It may be profitable for the female to tear off larger pieces for the nestlings since it will make the feeding more effective. Tearing off small pieces is time consuming, so when the nestlings are able to swallow larger pieces it may be profitable for the female to tear off as large pieces as possible for the nestlings.

Effect of prey size and brood size on number of pieces per nestling

The number of pieces each nestling received per feeding decreased as brood size increased. Nestlings in large broods receive less food per feeding than these in smaller broods. That can mean that there are less beneficial for the nestlings to be raised in large broods. The parents will have to increase their hunting effort to be able to feed nestlings in large broods at the same rate as nestlings in small broods. Tolonen and Korpimäki (1994) found that Eurasian kestrel parents did not invest more in hunting as brood size increased. In a study on the American kestrel (*Falco sparverius*) Dawson and Bortolotti (2003) found that the parents delivered a similar amount of food independent of brood size, which suggests that they have a fixed investment strategy. A fixed investment strategy predicts that there will not be an effect of brood size on parental effort, which gives nestlings in larger broods less food than nestlings in smaller broods (Dawson and Bartoletti 2003). Steen et al. (2010b) also found that there could be a cost to the individual nestling being reared in a large brood because each nestling received less food than when reared in a small brood.

The mass of a prey item had a significant effect on number of pieces per nestling when nestlings were fed with avian prey. When avian prey items were larger, the nestlings received more pieces per feeding than when prey items were smaller. So even though the female tore off larger pieces when prey items were large, she also tore off more pieces for the nestlings. The larger the prey item is, the more food the female can allocate to the nestlings.
Prey mass did not have such an effect in mammalian prey, may be because of less variation in the mass of mammalian prey than avian prey. The results may have been different if the range of mammalian prey mass and the range of avian prey mass had been more similar.

Conclusion

When the kestrel female fed nestlings larger prey items they were divided into more pieces than smaller prey items, and larger prey items were also divided into larger pieces than smaller prey items. The female may partition large prey into more pieces so the pieces will be small enough for the nestlings to swallow. When brood size increased, each nestling received fewer pieces of food from each prey. When prey mass increased each nestling received more pieces from the prey item if it was a bird, but not if it was a mammal. My findings is consistent with earlier studies that have found that prey size has an effect on prey preparation. What could have been interesting to investigate further is how nestling age and nestling size effect the provisioning of food from the female kestrel to the nestlings.

References

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

Barba, E., Lopez, J. A., GilDelgado, J. A. 1996. Prey preparation by adult great tits Parus major feeding nestlings. Ibis. **138:** 532-538.

Dawson R.D., Bortoletti G.R. 2003. Parental effort of American kestrels: the role of variation in brood size. Canadian Journal of Zoology. **81:** 852-860**.**

Løw L.M. 2006. Prey preparation and ingesting rate in breeding Eurasian kestrels, *Falco tinnunculus*. MSc thesis, Norwegian University of Life Sciences, Ås.

Pinheiro, J. C., Bates, D. M. 2000. Mixed-effects models in S and S-PLUS. Springer, New York.

Slagsvold, T., Wiebe, K. L. 2007. Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. Animal Behaviour. **73:** 691-700.

Steen R. 2004. Food provisioning in the Eurasian kestrel (*Falco tinnunculus*): handling efficiency of prey delivered to the nest. Cand. scient. thesis, Agricultural University of Norway, Ås.

Steen R., Løw L.M., Sonerud G.A., Selås V., Slagsvold T. 2010a. The feeding constraint hypothesis, prey preparation as a function of nestling age and prey mass in the Eurasian kestrel. Animal Behaviour. **80:** 147- 153.

Steen R., Løw L.M., Sonerud G.A., Selås V., Slagsvold T. 2010b. Prey delivery rates as estimates of prey consumption by Eurasian kestrel (*Falco tinnunculus*) nestlings. In: Steen R. Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (*Falco tinnunculus*). PhD thesis, Norwegian University of Life Sciences, Ås.

Tolonen P., Korpimäki E. 1994. Determinants of parental effort: a behavioural study in the Eurasian kestrel, *Falco tinnunculus*. Behavioural Ecology and Sociobiology. **35:** 355-362.

Village A., 1990. The Kestrel. T & AD Poyser.

Winkler D.W. 1987. A general model for parental care. The American Naturalist. **130:** 526-543.