Norges miljø- og
biovitenskapelige
universitet

Master's Thesis 2019 30 ECTS
Faculty of Environmental Sciences and Natural Resource Management
Geir A. Sonerud

Post-fledging parental care in the great grey owl (*Strix nebulosa*): female contribution and fledgling movement

Tina Forsnes
Master in Natural resource management

Preface

This master thesis marks the end of my journey at the Norwegian University of Life Sciences (NMBU), giving me a master's degree in nature management. Thanks to the Norwegian Environment Agency for financial support for my field work. I would like to thank my supervisor Geir A. Sonerud for answering all my questions, reading through my drafts, giving constructive feedback and for letting me participate in this project. To Cathrine S. Torjussen, thanks for reading through my thesis and answering my questions, and for some fantastic, and sleepless, experiences during the field work, as well as driving me around. Also thanks to Kari Hegtun for helping out during the field work, giving me the R script and answering my questions regarding the scripts. Thanks to Trond Berg for helping out during the field work, for allowing me to use your owls and to stay in the cabin. I will also thank the rest of the ornithologist in the Norwegian ornithological association in Elverum for allowing me to use their owls and letting me participate in the ringing project.

And of course, thanks to my friends and classmates, what a boring five years it would have been without you! Thanks to my family, I am grateful for having you, sorry I moved so far away. Lastly, but not least, I will give my gratitude to someone who's supported have been important to me. You know who you are. I look forward to years to come in your company!

So I guess this is the end. After five years with learning and great experiences, I am ready to explore the world with new knowledge and new friends. Thank you for the experience Ås, you have been great!

Norwegian University of Life Sciences

May 2019

Tina Forsnes

Abstract

In owls and birds of prey male and female have distinctive roles in parental care. Our knowledge about these roles mostly concerns the pre-fledging period, because in the post-fledging period fledglings move about and are thus harder to locate and follow. The great grey owl (*Strix nebulosa*) is expanding its range in Norway, providing a unique opportunity to study the post-fledglings period, as the resilience of this owl towards disturbances is high. Four adult great grey owls from four different pairs, two males and two females, were equipped with a tail-mounted radio-transmitter that allowed me to distinguish between the parents at prey deliveries and to help locate the fledglings. Field observations were carried out between 21 June and 27 July in the southeastern part of Norway (61°N, 12°E). Most prey items were delivered in the hour blocks of 07.00-10.00 and 18.00-21.00. The male delivered more prey items than the female, 62 and 19 respectively. Of prey captured by the male, fledglings received 59 and the female 2. The probability that the female rather than the male had captured a prey increased with increasing brood size. The female was present in 57% of the cases when an observer approached the brood. The probability of the female being present decreased throughout the season and with fledgling age. Female level of aggressiveness decreased with fledgling age. The female performed distraction display in 75% of the cases where an observer approached. The maximum distance I recorded between a fledgling and the nest it had fledged from was 2791 m. This distance increased with increasing fledgling age. Movement per day for fledglings ranged from 0 m to 602 m, with a mean of 141 m, and increased with increasing fledgling age. The distance between siblings ranged from 0 m to 136 m, with a mean of 28 m, and was independent of fledgling age. The fledglings perched higher with increasing age. All of the 11 fledglings I observed survived throughout the observation period. In the great grey owl, parental care in the post-fledging period is divided between the male providing food for the fledglings, while the female balances her effort between foraging and guarding the fledglings. The fledglings may move a substantial distance from the nest and thus may use quite a large area. More information on the behaviour in the post-fledging period of great grey owls will contribute to the knowledge of sex-roles in parental care and sexual size dimorphism in owls and birds of prey. Information on fledglings' use of the habitat and movement within it will help mangers to take the correct decisions when balancing interests between owls and forestry in Norwegian forests.

Sammendrag

Hos ugler og andre rovfugler har hanner og hunner tydelig rollefordeling i foreldreomsorgen. Vår kunnskap om disse rollene gjelder for det meste perioden mens ungene er i reiret, fordi fugleunger som har forlatt reiret flytter seg rundt og er vanskeligere å finne og følge. For tiden utvider lappugle (*Strix nebulosa*) leveområdet sitt i Norge, og siden lappugla har høy toleranse for forstyrrelser gir dette en unik mulighet til å studere dem etter at ungene har forlatt reiret. Fire voksne lappugler fra fire forskjellige par, to hanner og to hunner, ble utstyrt med radiosendere festet på halefjærene, hvilket gjorde det mulig å skille mellom foreldrene ved byttedyrleveringer og lokalisere ungene. Feltobservasjoner ble gjennomført fra 21. juni til 27. juli i sørøstre deler av Norge (61°N, 12°E). De fleste byttedyrene ble levert i tidsrommet 07.00-10.00 og 18.00-21.00, og hannen leverte flere byttedyr enn hunnen, hhv. 62 og 19. Av de byttedyrene som ble fanget av hannen, mottok ungene 59 og hunnen 2. Sannsynligheten for at hunnen i stedet for hannen fanget byttedyr økte med økende kullstørrelse. Hunnen var tilstede i 57% av tilfellene hvor en observatør nærmet seg ungene, og sannsynligheten for at hun var tilstede avtok utover i sesongen og med ungenes alder. Hunnens aggressivitetsnivå avtok med ungenes alder, og hunnen spilte skadet i 75% av tilfellene når en observatør nærmet seg. Den lengste avstanden jeg registrerte mellom en unge og reiret den hadde forlatt var 2791 m, avstanden økte med ungenes alder. Ungenes daglige forflytning varierte fra 0 m til 602 m, med et gjennomsnitt på 141 m, og økte med deres alder. Avstanden mellom kullsøsken varierte fra 0 m til 136 m, med et gjennomsnitt på 28 m, og var uavhengig av ungenes alder. Ungene satt høyere over bakken med økende alder. Alle de 11 ungene jeg observerte overlevde gjennom perioden med feltobservasjoner. Hos lappugla er foreldreomsorgen etter at ungene har forlatt reiret delt mellom hannen som leverer bytte til ungene, og hunnen som balanserer innsatsen mellom å jakte etter byttedyr og å vokte ungene. Ungene kan flyttet seg en betydelig avstand fra reiret og kan dermed trenge et ganske stort areal. Mer informasjon om atferden hos lappugla etter at ungene har forlatt reiret vil bidra til økt kunnskap om rollefordelingen mellom hunnen og hannen i foreldreomsorgen, og om størrelsesforskjellen mellom kjønnene hos ugler og rovfugler. Informasjon om ungenes bruk av habitat og forflytning i habitatet vil hjelpe forvalter til å ta riktige avgjørelser når interessene mellom ugler og skogsdrift i norske skoger må balansere.

Table of content

Introduction

Biparental care occurs in more than 80% of bird species, including owls and birds of prey (Cockburn 2006). In owls and birds of prey there is a clear distinction between the sex roles; typically the male provides food for the whole family while the females incubate, keep the young warm, dismember prey and feed the young as long as necessary (Sunde et al. 2003; Sonerud et al. 2014a).

In sexual conflict theory parents face conflicts between them, i.e. who should care and how much care to provide (Davies et al. 2012). For the parents there is a cost in making sure their offspring survive. By caring for their young they invest time and energy, which influences their own survival and chance at further reproduction (Olson et al. 2008). According to Houston et al. (2005) a parent would heighten its own chance of survival and remating by making the other parent take most care of their young. Olson et al. (2008) found that parents adjusted their care according to the other parent; if one parent did less, the other also did less. Furthermore, Olson et al. (2008) found that as mating opportunities increased for one of the parents, this parent reduced its effort of parental care compared to the other parents' effort. Eldegard and Sonerud (2009) found, through a field experiment, that the female Tengmalm's owl (*Aegolius funereus*) desert the offspring when food abundance increased, and that the male then was able to take care of the offspring alone.

In addition to the conflict between parents, there is also a conflict between parents and offspring (Trivers 1974). Care and protection from the parents increases the young's chances of survival, and the offspring would benefit from this period being as long as possible. For the parents a longer period of care will reduce their own chance of survival as well as their future fitness (Trivers 1974). Trivers (1974) stated that while having a conflict with the parents, the offspring also have conflicts with its siblings, both with current sibling and future siblings, which most likely will not be equally related. The most important point derived from Triver's theory is that this sibling-rivalry is the very reason for the occurrence of parent-offspring conflict (Davies et al. 2012).

One of the duties of a parent is to protect its offspring. In owls the task of defending the offspring during the pre-fledging period appear to be allocated to one of the parents. In Ural owl (*Strix uralensis*), the female is the one to protect the offspring and is known to be the most aggressive owl (Kontiainen et al. 2009). Similarly, in the great grey owl (*Strix nebulosa*) the female is fearless when protecting her offspring and might attack an intruder (Cramp

1985). In comparison, the male is the most aggressive when protecting the nestlings in snowy owl (*Nyctea scandiaca*) (Wiklund & Stigh 1983), and in burrowing owl (*Athene cunicularia hypugaea*) (Fisher et al. 2004). While the owls might show aggressive behaviour, they also have a milder form of protecting their offspring, called distraction display. The adult owl then displays her wing as broken and thus distracts the predator, luring it away from the offspring (see Armstrong 1954; Sonerud 1988).

Sex roles in parental care have mostly been studied during the pre-fledging period, thus knowledge of these roles in the post-fledging period is scarce (Eldegard & Sonerud 2012). The reason for this might be that fledglings are not restricted to the nest, but move about and are more difficult to observe because of cryptic behaviour and plumage (Eldegard & Sonerud 2012). Studies on the behaviour in the post-fledging period in great grey owl will contribute to the knowledge of sex-roles in parental care and sexual size dimorphism in owls and birds of prey.

I studied the post-fledging parental care of the great grey owl, which is ideal to study due to its resilience towards disturbances from humans. As other owls and birds of prey, the great grey owl also exhibits reversed sexual size dimorphism, where the female is larger than the male. The body mass ranges from 900 g for the male to 1100 g for the female (Cramp 1985).

Across the world, the great grey owl is found in the northern parts of Europe and Asia, Canada and in Alaska (Cramp 1985). It is widely spread in Finland and Sweden, and have in recent years spread to southeastern Norway, its numbers rapidly increasing during the last decade (Berg 2016). In 2009 one nest was found in Hedmark County, and the number has steadily increased each year, apart from the low vole years 2012 and 2015 with no breeding owls known. Berg (2016) concluded that the peak of voles in 2010/2011 was the likely reason for the establishment and the further expansion of the great grey owl in Hedmark County. From being a sporadic visitor, the great grey owl is now considered regular in the forests of Hedmark, with 120 known attempts of nesting in 2017 (Hegtun 2018) and 104 attempts in 2018 (Trond Berg, pers.comm). The breeding density has been high in Elverum municipality.

The great grey owl is included in the Norwegian red list, listed as vulnerable (VU) (Artsdatabanken n.d.). While on the red list of International Union for Conservation of Nature (IUCN), it is listed as least concern (LC) (BirdLife International 2016). The difference is due to the rather low number of great grey owls in Norway, as a whole.

Great grey owls can be both resident and nomadic (Cramp 1985), though during the breeding season the adult owls keep close to the nest until the nestlings fledge. Hegtun (2018) recorded a fledgling 2.7 km from the nest at an age of younger than 80 days. Great grey owls can utilise various nest types (Wu et al. 2015; Berg 2016). According to Sulkava and Huhtala (1997) great grey owls commonly use nests made by birds of prey, mostly nests of Northern goshawk (*Accipiter gentilis*) and Common buzzard (*Buteo buteo*). Forestry affects nesting habitat of hawks making it harder for them to find suitable nesting places (Sulkava & Huhtala 1997). Consequently, forestry may indirectly affect the population of great grey owl through access to nests. Though great grey owls also use manmade wooden platforms and artificial nests made of twigs (Berg 2016). In other words they are not fastidious on nesting places (Sulkava & Huhtala 1997).

Preferred habitats of great grey owls are forested areas, primarily with coniferous forest. They mainly hunt in open parts of the forest, such as bogs and clear-cuts. When hunting, the owl perches, waiting for prey to appear. Great grey owls mostly hunt during the morning and evening, though they have been observed hunting both day and night, and might hunt around the clock in the breeding season (Cramp 1985). Clear-cuts left by forestry are ideal areas to hunt for the most common prey of the great grey owl (Sulkava & Huhtala 1997), namely voles of the genus Microtus and Myodes (Cramp 1985). However, water vole (*Arvicola terrestris*), shrews (*Sorex*) and birds may also be taken (Cramp 1985). Though forestry most likely has increased the availability of prey to the great grey owl, it might pose a problem as well; as fledglings probably need forest to hide and move around in and the adults need forest to perch when relaxing (Sulkava & Huhtala 1997).

The overall objective of my study was to document the parental care in great grey owls by observing the parents delivering prey to their young. I aimed to answer the following questions: (I) When the male returns with prey, how often does he deliver it to the female who subsequently delivers it to the fledglings, and how often does he deliver it directly to the fledglings? (II) How large proportion of prey delivered has been captured by the female? (III) How does the female behave when an observer approaches the offspring in the post-fledgling period? (IV) How far from the nest does the fledglings move while still accompanied by the female?

Methods

Study area

The study area is located in the boreal zone in Elverum municipality, Hedmark County, in southeastern Norway (61°N, 12°E), at altitudes of 300-500 m. It is dominated by coniferous forest, mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and constitutes of large bogs between forests heavily affected by forestry. Blankets of blueberry covers the ground together with other heaths. The climate is dry year round, although cold in winter and warm in summer. The summer of my field work was exceptionally warm in the entire southern Norway, which led to dry bogs and heaths.

Radio tagging

To find and distinguish between the owls, one of the adult owls in each pair was equipped with a radio transmitter (TW-4 and PIP 3, Biotrack, England**)**. In total four owls from four different pairs were tagged, two males and two females. The transmitter was attached by tail-mounting, following Kenward (1978), at the same time as ringing by local ornithologist. The transmitter was glued to the mid-tail feather and sewed on to this and a neighbouring feather. By attaching it to a tail feather, the transmitter was close to the bird’s centre of gravity and would fall of when the owl moulted at the end of the breeding season (Kenward 1978). Thus, the owl would not have to be recaptured in order to remove the transmitter. The transmitter weighed only 4 g, which is 0.4% the body mass of a male, and even less of the female’s body mass (Cramp 1985). Permission from the National Animal Research Authority in Norway and the Norwegian Environment Agency was acquired in advance.

Field work

The field work was conducted from 21 June until 27 July. The initial objective was to follow each brood until the fledglings no longer received food, and that in the end each brood had been observed at each hour block around the clock. I also tried to visit each brood every fourth day to spread the observations evenly through the field period and to not loose track of the fledglings. As the hatching was late in 2018, approximately between 17 May and 25 May, I was unable to follow the fledglings until they became independent. Furthermore, some hours at night were too dark to carry out any observations, consequently the darkest hour blocks could not be observed. Observations of two broods had to be terminated before the end of the field work due to unforeseen trouble with signals from the radio tag. On the last day of observations the third radio tag was also starting to fail. Consequently, brood 1 and 2 were followed for 35 and 32 days, respectively. While brood 3 and 4, where observations had to be terminated earlier, were followed for 29 and 19 days, respectively.

In the beginning of the field work I found the fledged young close to the nest. Later I started to look for them where I last observed the fledglings. I listened for begging calls, and if I did not hear any, I tracked the tagged parent until I would hear begging calls. To track the parents I used a portable receiver (SIKA, Biotrack, England) and a flexible handheld Yagi antenna (Biotrack, England). Strength and direction of the signal was used to locate the tagged owl.

When observing I hid under camouflage until the female was comfortable with me sitting in plain sight, or she was not present at all. Depending on what the individual female seemed comfortable with, I kept a distance of 20-50 m from the fledglings. I also made sure to not make any disturbing sounds or movements.

I recorded which of the parent that had captured the prey that was delivered, who they delivered it to, and who consumed the prey. Time of delivery and weather conditions were recorded. At the time of delivery I also recorded the value of a stress variable with three levels; observers at a distance (0), observer close, possible disturbance (1), or unnatural situations with a lot of stress from disturbance (2). The latter variable was mostly used when the owls were captured and ringed. To distinguish which parent delivered the prey I used the radio signal. I also tried to identify the species of the prey, but this was challenging. In most cases I either did not see the prey or could only classify it as a small mammal. The distance between the observer and the nearest fledgling (henceforth called observer behaviour) and number of observers were recorded as well.

For each session when first approaching the fledglings, I recorded the behaviour of the female; whether she was present, whether she performed distraction display and her level of aggressiveness. The aggressiveness was scored on a scale from 0 to 5, following Kontiainen et al. (2009) and adjusted by Hegtun (2018). Descriptions of the scores are given in table 1.

As the fledglings became older and the female was not present, the parent delivering food would occasionally fly past me, maximum 5-10 m away. This mostly happened after the first prey was delivered after I had sat down. At later deliveries the parents usually came and went from other directions than where I was sitting, or kept some distance from me.

***Table 1**: Scoring of female aggressiveness when an intruder approaches the offspring of great grey owl in the post-fledgling period. Adopted from Hegtun (2018), which was modified from Kontiainen et al. (2009), description of some scores are slightly changed from Hegtun (2018).*

Behaviour	Score	Description
Not present	0	The female was not present at the time the offspring were found.
Silent	1	The female was present, but showed no aggressive behaviour.
Click or bark	2	The female made clicking or barking sounds, but from a long distance with no or little movement.
Chase	3	The female moved a lot around the intruder and made clicking and barking sounds, but showed no attempt to attack.
Attack	4	The female attacked the intruder within 3 m radius, but veered of.
Hit	5	The female attacked and hit the intruder (a miss is included)

Perching height and perching substrate for the fledglings were recorded and the coordinates of their location saved on a handheld GPS (Garmin eTrex 10). I also recorded the number of fledglings in the brood at each visit. If I later observed a larger brood size, I corrected earlier observations of the brood size to the latest number observed. The broods I followed had 1-4 chicks. Photos of the chicks were taken when local ornithologists were ringing them. To estimate the age of the fledglings I compared these photos with photos of nestlings from a nest with date of hatching known. I then estimated the date of hatching for each of the nests that I followed.

Statistical analysis

Statistical analyses were done with the software R version 3.5.2 (R Core Team 2018). To ease the comparison with the master thesis of Hegtun (2018), I divided the statistical analysis in the same three parts and order, namely 1) prey delivery rates, 2) female behaviour and aggressiveness and 3) fledgling movement and behaviour.

I used the R script made by Hegtun (2018) to make sure that I did the same analysis and ran the same models. There are some differences in the models in part 1 as I have excluded some variables and added some other due to differences in what was sampled during the field work. As Hegtun (2018) I ranked the models after the Aikaike information criteria corrected for small samples (AICc). Models with the lowest AICc value and an ΔAICc <2 were selected and ranked where the best model had the fewest degrees of freedom (df). This is the most parsimonious criterion that is a trade-off between bias and variance (Johnson & Omland 2004). According to Bolker et al. (2009) this type of ranking will be adequate when the objective is qualitative understanding rather than quantitative prediction.

Prey delivery

When analysing prey deliveries I used generalized linear mixed effects-models (GLMMs) with binomial distribution from the lme4-package in R. The response was whether the female or the male had captured the prey, and explanatory variables were fledgling age (days), brood size, hours from solar midnight, day number, time of day and temperature (°C). Hours from solar midnight were calculated as described in Steen et al. (2011a), with a number between 0 and 12, while day number was set from 1 June as day 1. Time of day was set as a categorical variable with morning between 01.13 (solar midnight) and 13.13 (solar midday) and evening between 13.13 and 01.13, and as a numerical variable with hours from solar midnight as a number between 0 and 23. For easier comparison with the master thesis of Hegtun (2018), I considered the models with and without the temperature variable separately, although I had recorded temperature for all of my observations. Brood ID was included as a random variable in the entire analysis to correct for brood specific variation.

The data for who received prey from the male was too skewed to analyse by GLMM. Thus I used a two-sided binomial test to test whether the distribution was random or not. A Fisher's combined probability test corrected for brood ID. The same test was used for the response of female captured prey. I could not test the response of who consumed prey delivered by the male due to too small sample and skewed data for GLMM. All figures were made in R.

Female behaviour and aggressiveness

For models predicting «female distraction display» I used GLMM from the lme4-package with binomial distribution. The variables I considered were fledgling age, aggressiveness, fledgling perching height (both categorical and numerical), brood size and observer behaviour (both categorical and numerical). The categorical variable for perching height was divided in ground, near ground (0.5-2 m), low (2-5 m), medium (5-10 m), high (10-15 m) and very high (>15 m), while the numerical variable had a number from 1 to 6. Observer behaviour was set to far (>50 m), medium (10-50 m) or close (<10 m) observer distance, or to catch (handling the chicks), with the corresponding numerical variable with numbers from 1 to 4.

Combinations of all variables were made. I also included brood ID as a random variable in all models of the analysis.

For models predicting female aggressiveness I used linear mixed-effect models from the nlme-package. Predictor variables considered were fledgling age, fledgling perching height (both categorical and numerical), brood size, day number, number of observers and observer behaviour (both categorical and numerical).

For predicting «female present», I used GLMM from the lme4-package with binomial distribution. The variables I considered were fledgling age, fledgling perching height (both categorical and numerical), brood size and day number. Normal distribution of residuals and random effects for the models were tested with the qqnorm-function in R.

Fledgling movement and behaviour

Distance from nest, movement per day and distance between siblings were calculated from the UTM coordinates sampled during the field observations. The distance was calculated by use of Pythagoras. When calculating distance from nest I used coordinates of only one of the fledglings for each day I had registered coordinates. Movement per day was calculated by dividing distance between two coordinates observed successively with number of days elapsed between observations. Distances between siblings in broods of two or more were calculated for each sibling in the brood that I had coordinates for.

When analysing the relationship between distance from nest and fledgling age, I used a linear-mixed-effect model from the nlme-package in R. Values of the distance from the nest were log-transformed. Both movement per day and distance between siblings were analysed in the same way, though only movement per day with log-transformed values. The relationship between perching height and fledgling age was also tested with a linear mixed model (LMM).

In the entire analysis brood ID was included as a random variable to control for nest-specific variation. Normal distribution of residuals and random effects for the models were tested with the qqnorm-function in R. All figures were made in R and scatterplots were used to show the distribution of the raw data.

To take the contribution of random effects into account, regression lines and confidence intervals were estimated from the linear mixed-effects model. This applies to the log-transformed data and the figures showing distance between siblings and fledgling perching height. To create the non-linear prediction lines and confidence intervals I used the splinespackage in R. Here brood ID was not corrected for and the predictions are based on simple linear regression. Also the fledgling age parameter was split into two categories.

Ethical note

The great grey owl is quite resilient to handling by humans, though there have been problems with disturbances from the public in Elverum (Berg 2016). All handling, ringing and radio tagging were done with care and according to professional procedures. Radio tagging was done at the same time as ringing to avoid handling the owl more than once. As agreed between local ornithologists I have kept the locations secret to avoid disturbances of the owls. During observations I avoided making any disturbing sounds or movements and kept at a distance the female seemed comfortable with.

Results

Prey delivery

In total I observed 81 prey deliveries, 19 from the female and 62 from the male (figure 1). Prey captured by the male was either delivered directly to a fledgling (n=59) or to the female (n=2). The receiver of one of the prey items captured by the male was not recorded, but in the end a fledgling consumed it. The female did not consume any of the two prey items received from the male. She delivered both to a fledgling, but one of the prey items was lost on the ground and was not recovered during the observation session. Fledglings thus consumed 61 prey items captured by the male.

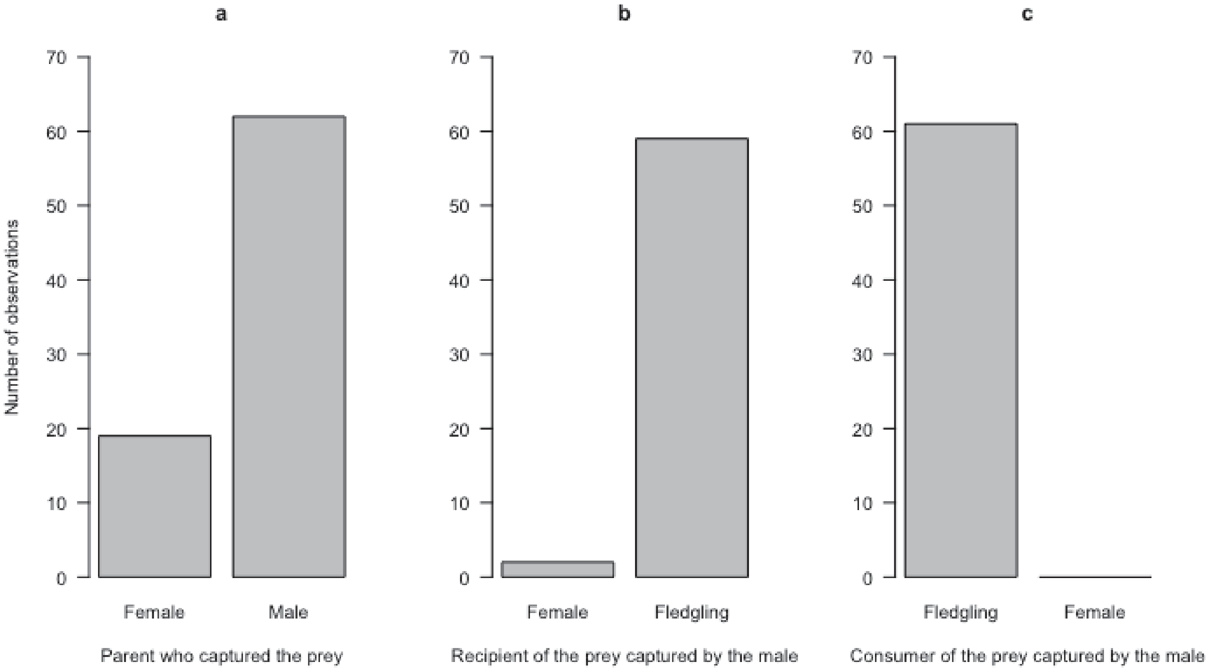

Figure 1*: Allocation of prey a) captured by either female or male great grey owl (n=81), b) received from the male (n=62) and c) thereafter consumed (n=61).*

In total each 24 hours-block of the day was covered by observations at least twice, although I had few observation hours at two of the locations, because observations were terminated early due to technical problems. At the other two locations I observed almost every hour. Most prey items were delivered in the morning, between 07.00 and 10.00 hours, and in the evening between 18.00 and 21.00 hours (figure 2). The results are not entirely representative as these peaks also represent the time when most of the observations were made. There is also a difference between the two locations observed most. At one location prey were delivered more often in the morning while at the other location it were delivered more often in the evening.

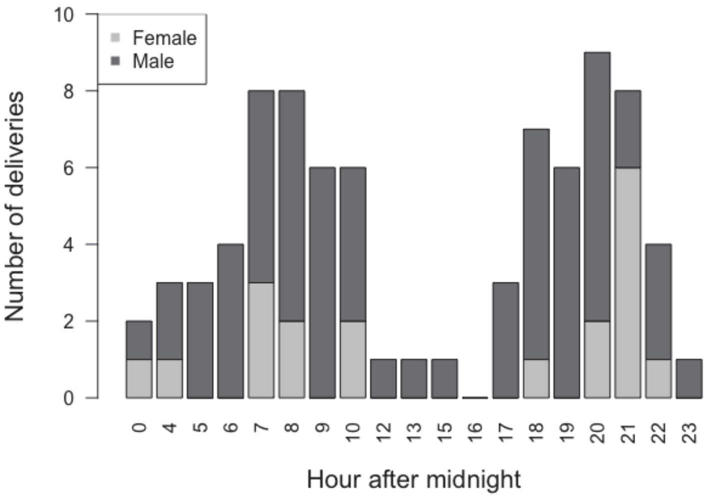

***Figure 2**: Daily distribution of prey delivered by female (light) and male great grey owl (dark) (n=81).*

The distribution of prey captured by the male and female differed significantly from random (table 2). The best model predicting why female rather than the male had captured the prey delivered, included the variable brood size, when temperature was excluded from the analysis (table 3a). The second, third and fourth best models included the variables hours from solar midnight, time of day and age in different combination with brood size in all models (table 3a). The probability of the female rather than the male capturing a prey increased significantly with increasing brood size (table 4a, figure 3).

***Table 2**: Distribution of captured prey by male and female great grey owl, tested with binomial test for each brood and for all broods pooled, both not corrected for brood ID and corrected for brood ID with Fisher's combined probability test.*

Brood ID	Captured by male	Captured by female	df	P
1	27	9	1	0.0046
2	27	10	1	0.0086
3	3	0	1	0.25
4	5	0	1	0.062
All (not corrected)	62	19	1	< 0.0001
All (corrected)	62	19	8	< 0.005

When temperature was included in the analysis, the best predictor model, after AICc-value and parsimony, included the variables temperature, brood size and hours from solar midnight (table 3b). While the second best model included age together with the other three variables mentioned. The effect of temperature was marginally non-significant, while both brood size and hours from solar midnight had a significant effect (table 4b).

***Table 3**: The most parsimonious models predicting female rather than male capture of prey in the great grey owl, when a) temperature was excluded from the analysis (n=74), and b) temperature was included in the analysis (n=74). Brood ID is included as a random variable. Models are ranked by AICc and parsimony with ΔAICc <2 and fewest degrees of freedom (df).*

Model	df	AICc	ΔAICc
a)			
Brood size	3	85.22	1.31
Brood size + Hours from solar midnight	4	83.91	0.00
Brood size + Time of day (categorical)	4	85.53	1.62
Brood size + Hours from solar midnight + Age	5	85.63	1.72
b)			
Temperature + Brood size + Hours from solar midnight	5	82.57	0.00
Temperature + Brood size + Hours from solar midnight + Age	6	84.30	1.73

***Table 4**: Estimates from the most parsimonious models predicting female rather than male capture of prey in the great grey owl, when a) temperature was excluded from the analysis (n=74), and b) temperature was included in the analysis (n=74). Brood ID is included as a random variable.*

Explanatory variables	Estimate	Standard error (SE)	Z	P
a)				
Intercept	-4.49	1.74	-2.58	0.0099
Brood size	1.01	0.49	2.06	0.039
b)				
Intercept	-4.63	2.31	-2.00	0.045
Temperature	0.16	0.09	1.80	0.072
Brood size	1.15	0.49	2.35	0.019
Hours from solar midnight	-0.55	0.23	-2.40	0.016

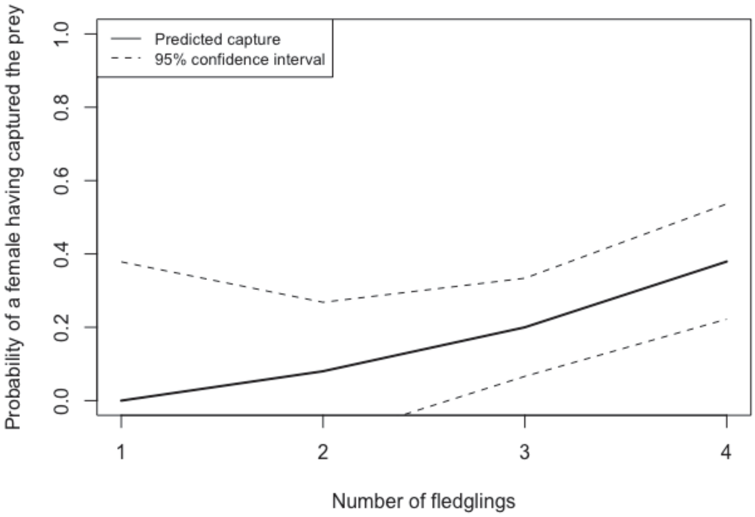

Figure 3*: Predicted probability of female great grey owl having captured the prey as a function of brood size, when temperature was excluded from the model (n=74).*

The fledglings received 59 prey items from the male, while the female received only 2 items. There is one item captured by the male where the recipient is unknown, though a fledgling consumed it. The allocation of prey received by the female or fledglings from the male was significantly different from random (table 5). During the field work, I did not observe any male consume a prey that he had captured. Most likely he consumed them while out hunting. In total, fledglings consumed 79 prey items captured by either the male or female. On two occasions late in the field work, I observed a fledgling dismember the prey instead of swallowing it whole. This happened at two different locations.

Table 5*: Prey received by fledglings or the female from the male great grey owl. The distribution is tested with binomial test for each brood and for all broods pooled, both not corrected for brood ID and corrected with Fisher's combined probability test.*

Brood ID	Received by fledgling	Received by female	df	P
1	26	1	1	< 0.0001
2	27	0	1	< 0.0001
3	3	0	1	0.25
4	4	1	1	0.38
All (not corrected)	60	2	1	< 0.0001
All (corrected)	60	2	8	< 0.005

Female behaviour and aggressiveness

When I approached the fledglings, the female was present in 57% of the cases (n=75). Day number was the only variable in the best model according to AICc and parsimony (table 6a), but this variable was highly correlated with fledgling age. The female was significantly more absent with increasing day number (table 7).

Table 6*: The most parsimonious models for the probability of a great grey owl a) female being present (n=53), b) female being aggressive (n=52) and c) female performing distraction display (n=53). Brood ID is included as a random variable. Models are ranked by AICc and parsimony with ΔAICc <2 and fewest degrees of freedom (df).*

Model	df	AICc	ΔAICc
a)			
Day number	3	34.91	0.00
Day number + Brood size	4	35.79	0.87
Fledgling age + Brood size	4	36.14	1.23
b)			
Fledgling age + Observer behaviour (categorical)	7	155.98	0.00
Fledgling age + Observer behaviour (categorical) + Brood size	8	156.22	0.24
Fledgling age + Observer behaviour (numeric)	5	158.60	2.62
c)			
Observer behaviour (numeric)	3	38.57	0.00
Fledgling age	3	38.75	0.18
Aggressiveness	3	38.86	0.29
Brood size	3	40.10	1.53
Aggressiveness + Observer behaviour (numeric)	4	40.11	1.54

Table 7*: Estimates from the most parsimonious models for the probability of female great grey owl being present (n=53). Brood ID is included as a random variable.*

Explanatory variables	Estimate	Standard error (SE)	Z	P
Intercept	16.12	4.96	3.25	0.0011
Day number	-0.34	0.104	-3.28	0.0011

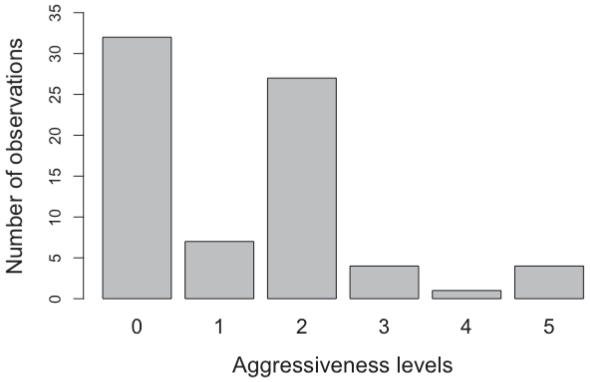

***Figure 4**: Distribution of observation of female great grey owl on levels of aggressiveness (n=75). Levels are described in table 1.*

During the field work I registered mostly no or moderate aggressiveness more often than highly aggressive behaviour from the female (figure 4). Aggressive behaviour from the female included clicking with the beak, barking, chasing or attacking (see table 1). I did not observe the male displaying any aggressive behaviour. The most parsimonious model had fledgling age and observer behaviour as predictor variables (table 6b). Fledgling age had a significant effect on aggressiveness, while observer behaviour had no significant effect (table 8). The aggressiveness decreased with increasing fledgling age (figure 5).

***Table 8**: Estimates from the most parsimonious models for the probability of a female great grey owl being aggressive when approached (n=52). Brood ID is included as a random variable.*

Explanatory variables	Estimate	Standard error (SE)	T	P
Intercept	6.37	0.83	7.73	<0.0001
Fledgling age	-0.09	0.01	-7.07	<0.0001
Observer behaviour FAR	-0.07	0.88	-0.08	0.94
Observer behaviour MEDIUM	-0.91	0.67	-1.39	0.18
Observer behaviour CLOSE	-0.07	0.66	-0.10	0.92

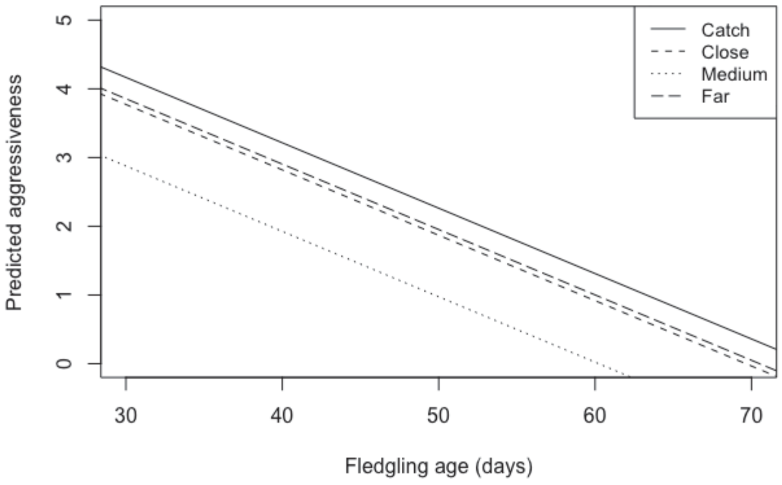

***Figure 5**: Predicted aggressiveness by female great grey owls as a function of fledgling age (n=52). «catch» is catching and handling the fledglings, «close» is observing or saving coordinates on the GPS <10 m from a fledgling, «medium» is observing a fledgling at a distance of 10-50 m, and «far» is observing the fledglings at a distance >50 m. Level of aggressiveness are described in table 1.*

In order to remove attention from her offspring the female used distraction display, where she pretended to have a broken wing and made loud calls to distract the intruder. In these cases she would place herself in the opposite direction of the fledglings compared to the intruder. The females performed distraction display in 75% of the cases (n=40) when I approached and she was present. The best model predicting the occurrence of distraction display had the numerical variable observer behaviour (table 6c). The best model was marginally better than the second and third best models with the variables fledgling age and aggressiveness, respectively (table 6c). The variable observer behaviour had no significant effect (table 9).

Table 9: *Estimates from the most parsimonious models for the probability of female great grey owl performing distraction display (n=53). Brood ID is included as a random variable.*

Explanatory variables	Estimate	Standard error (SE)	Z	P
Intercept	-0.93	1.63	-0.57	0.57
Observer behaviour (numeric)	0.88	0.65	1.36	0.18

During the field work I once observed a female chasing away an Eurasian jay (*Garrulus glandarius*), which was perching in the same tree as one of the fledglings. Another female barked at a car passing some few hundred meters off. The latter female also barked at and chased away something unknown to me twice when I was observing the fledglings.

Fledgling movement and behaviour

The chick that left the nest first was 27 days old at the time. By the age of 38 days all of the chicks were out of the nest. At the time the chicks left the nest, they were not able to fly, but moved around by jumping on the ground and climbing sloping trees and trees with low branches. With age they moved away from the nest, but the distance they moved varied (figure 6). The fledglings from brood 1 kept a distance of 300-400 m from the nest up to an age of 54 days, before they suddenly at the age of 58 days moved far off in just a few days. In general, brood 1 moved in one direction away from the nest. The fledglings from brood 2 moved quickly away from the nest, and by the age of 48 days they had moved 1 km. The fledglings from brood 2 and 3 kept moving back and forth in their respective forest area. Fledglings from brood 3 and 4 did not move further than 450 m from the nest during the observation period. The maximum distance I recorded from the nest was for brood 1, the fledgling had then an age of 57 days. For all the broods, the maximum distance from the nest was 2791 m (842 m, ±97 on average, and median 469 m).

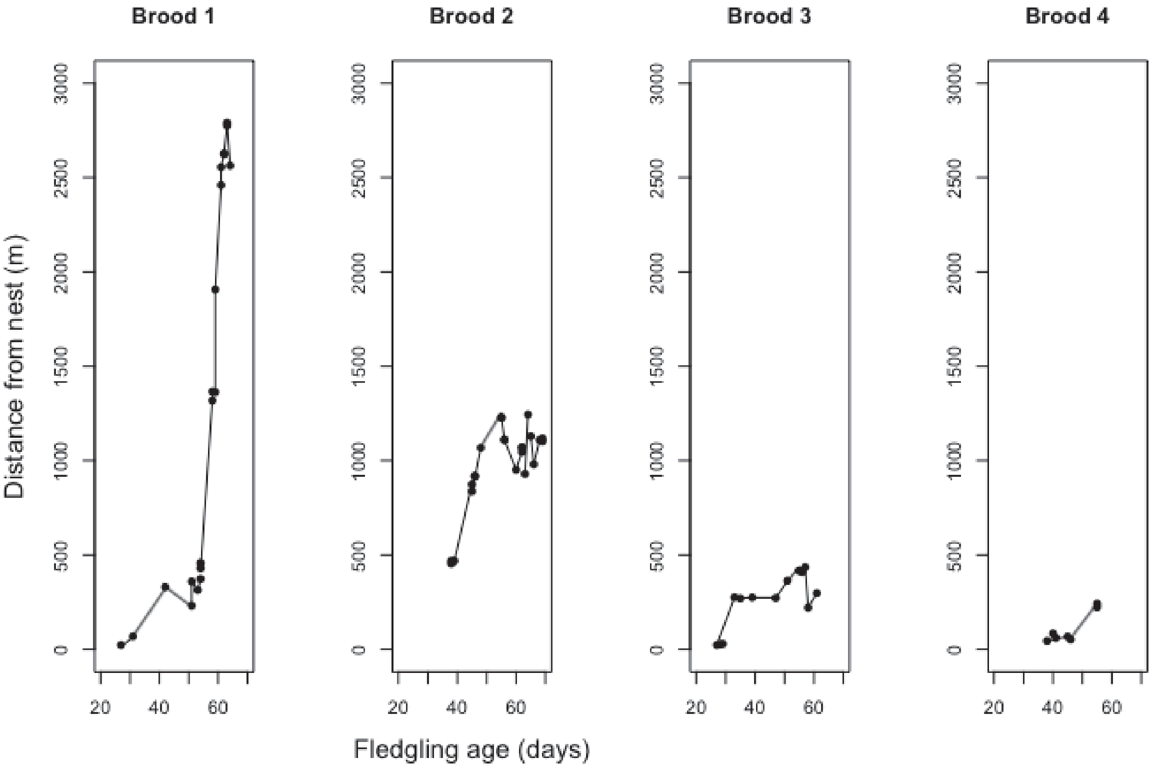

***Figure 6**: Distance from nest as a function of fledgling age for four broods of great grey owl. Brood 1 and 2 were followed until the age of 64 and 69 days, respectively. While brood 3 and 4 were followed until the age of 61 and 55 days, respectively.*

The relationship between a fledgling’s distance from the nest and its age had an exponential slope (figure 7a). There was a significant increase in distance from nest with increased fledgling age (table 10a, figure 7b).

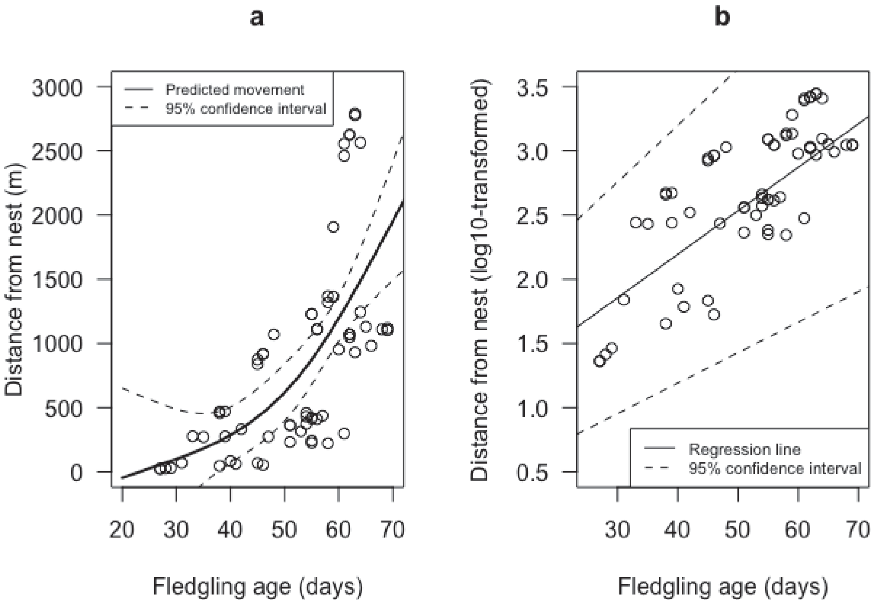

***Figure 7**: Distance from great grey owl fledglings to the nest they fledged from as function of their age, with prediction line on a a) non-transformed scale, and b) log10-transformed scale and a linear regression line. Brood ID is included as a random variable in the regression analysis.*

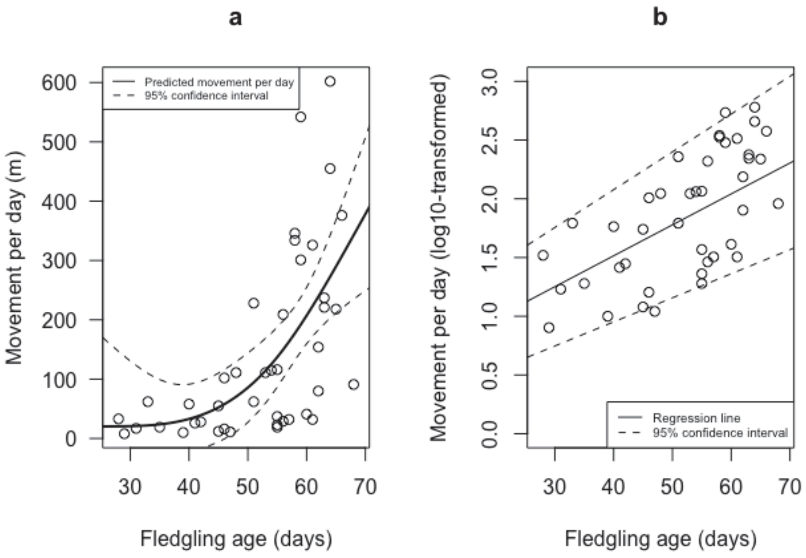

Figure 8*: Movement per day of great grey owl fledglings as a function of their age, with prediction line on a) non-transformed scale, and b) log10-transformed scale and a linear regression line. Brood ID is included as a random variable in the regression analysis.*

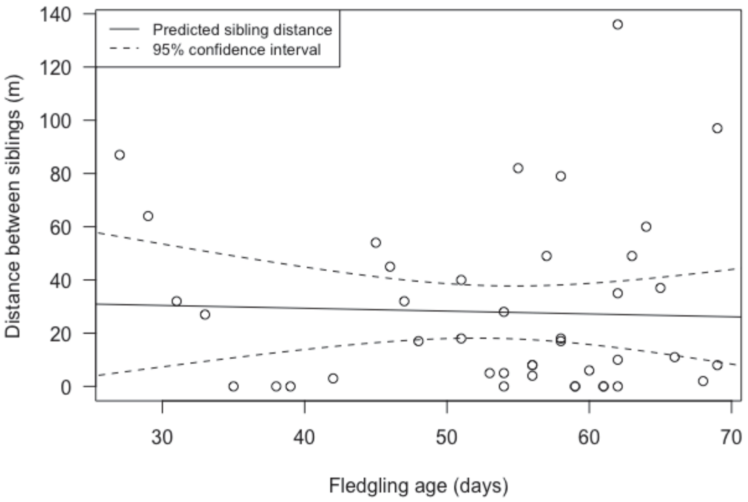

Figure 9*: Distance between siblings in a brood of great grey owl fledglings as a function of their age, with prediction line. Brood ID is included as a random variable.*

The estimated distance that the fledglings moved per day ranged from 0 m to 602 m (141 m, ±24 on average, and median 71 m) (figure 8a). I once happened to find the fledglings in the same tree two days in a row, they were then at an age of 39 days. There was a significant increase in movement per day with increasing age on a log-transformed scale (table 10b, figure 8b). After the fledglings became able to fly, they tended to start moving just after a prey delivery, often in the direction of where the delivering parent came from.

The distance between siblings ranged from 0 m to 136 m (28 m, ±5 on average, and median 17 m). The distance between siblings did not change significantly with increasing age (table 10c, figure 9). Regardless of age, several fledglings could be found perching in the same tree or neighbouring trees.

After the fledglings were 31 days old I did not observed any of them on the ground, with one exception; one fledgling was perching on the ground at the age of 45 days. Perching height increased significantly with increasing age (table 10d, figure 10). Fledglings were perching in trees before they were able to fly because they climbed sloping trees and trees with low branches.

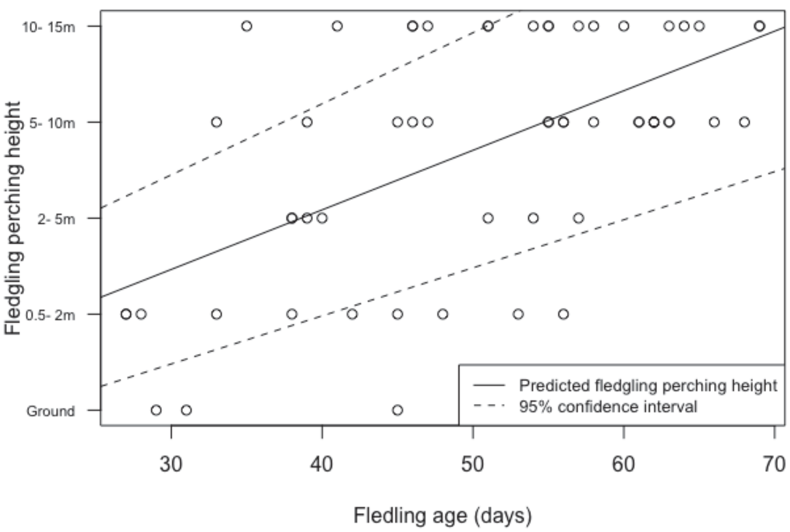

Figure 10*: Perching height of great grey owl fledglings as a function of their age, with prediction line. The perching height is set as intervals; ground, near ground (0.5-2 m), low (2-5 m), medium (5-10 m) and high (10-15 m). Brood ID is included as a random variable in the regression analysis.*

Table 10*: Estimates from a model of a) distance from great grey owl fledglings to the nest they fledged from as function of their age, on log10-transformed scale, b) movement per day of fledglings as a function of their age, on a log10-transformed scale, c) distance between siblings in a brood as a function of their age, and d) perching height of fledglings as a function of their age. Brood ID is included as a random variable.*

Explanatory variables	Estimate	Standard error (SE)	T	P
a)				
Intercept	0.84	0.60	1.40	0.17
Age	0.03	0.01	3.34	0.0015
b)				
Intercept	0.46	0.33	1.40	0.17
Age	0.03	0.01	4.51	0.0001
c)				
Intercept	33.62	24.80	1.36	0.18
Age	-0.11	0.46	-0.24	0.82
d)				
Intercept	2.61	0.63	4.17	0.0001
Age	0.06	0.01	5.18	<0.0001

Fledgling mortality

In total I followed 11 fledglings of great grey owl from four different broods. During the field work, from the time the chicks left the nest until the last day I followed them, no fledgling disappeared or was found dead. The oldest brood was then at an age of 69 days. The mortality was therefore 0% during my observation period.

Discussion

Prey delivery

Time of delivery

Prey were delivered to great grey owl fledglings day and night, though most were delivered in the morning and the evening, between 07.00 and 10.00 hours and 18.00 and 21.00 hours, respectively. In comparison, the nocturnal Tengmalm's owl had most deliveries at the nest between 22.00-02.00 (Eldegard & Sonerud 2012), while in the diurnal Eurasian Kestrel (*Falco tinnunculus*), prey was delivered at the nest between c 03.00 in the morning and c 23.30 in the evening (Steen et al. 2011b).

According to Cramp (1985) great grey owls usually hunts around the clock in the breeding season, which my results supports. At high northern latitudes days are long during summer, which may make it easier for the owls to hunt. The owls are reported to locate prey by sound alone beneath snow cover in the winter, and the placement of the ears combined with the facial plate, which gives the owl enhanced hearing, makes the great grey owls also capable hunters in the dark (Cramp 1985).

The hot and dry weather during my field work might have forced the owls to remain calm and relax in the shadows during the warmest hours of the day, thus leaving them to hunt in the morning and the evening when the temperature was lower. Also, I had less observations hours outside the time where most prey deliveries was observed, and most of the data were from two broods. Adult owls might hunt at different hours at different broods, and the weather condition might affect the hunting times. It is also likely that the owl hunted at the same time as their prey were active, as the prey then would be easier to locate. Steen et al. (2011a) found that there was an increased probability of Common Lizard (*Zootoca (Lacerta) vivipara*) to be delivered at a Eurasian Kestrel nest with increasing temperature and hours from solar midnight, i.e. when the lizards were most active and easy to locate. More observations are needed, preferably in different weather conditions; to stronger specify when great grey owls deliver prey during the day and if the weather actually affects the deliveries.

In the hours between 01.00 and 03.00 I did not observe the fledglings as it was too dark, but the owls might still have delivered prey. Compared to Tengmalm's owl, the great grey owl is larger and thus less vulnerable to predation (see estimated survival rates in Eldegard and Sonerud (2009) and Bull et al. (1989), respectively). By hunting at night the Tengmalm's owl may have a lower risk of predation, while the great grey owl is probably not limited by the risk of predation. Thus, the great grey owl can hunt at any time that is beneficial, though probably limited by other unknown factors. This may be the reason to the difference in time of deliveries between the two species.

Female capture

Male great grey owls had captured more of the prey delivered than females (77% and 23%, respectively). There was an increased probability of female capturing prey when brood size increased, when temperature was excluded from the analysis. When temperature was included in the analysis female capture was increased by brood size and temperature, and decreased with hours from solar midnight. Similarly, Hegtun (2018) found that the male great grey owl captured more prey than the female (68% and 32%, respectively). Sunde et al. (2003) observed that in tawny owl (*Strix aluco*) the male provided most of the food through the post-fledgling period, and Eldegard and Sonerud (2012) found the same for Tengmalm's owl. When Hegtun (2018) included temperature in the analysis, temperature was the only predictor variable, and the probability of female capture decreased with increasing temperature. In Tengmalm's owl deliveries of prey increased for both parents when brood size increased, but the female responded stronger than the male to increased brood size (Eldegard & Sonerud 2012).

In parental care, parents face the conflict of who should care, and how much to care (Davies et al. 2012). Caring for the offspring derives energy of the parent, and this affects future survival and reproduction of the parent (Houston et al. 2005). Thus one parent would benefit from the other parent doing the hard work (Houston et al. 2005), maximizing its own survival and reproduction. In owls and birds of prey the parental care is divided between the sexes (Sunde et al. 2003; Sonerud et al. 2014a). According to Sunde et al. (2003) the female tawny owl balances her effort between guarding the offspring and capturing prey. If both parents were out hunting, the fledglings would be an easy prey to other predators. With a larger brood the female might have to assist the male in providing food so the fledglings do not starve. Eldegard and Sonerud (2012) suggested that the female Tengmalm's Owl may keep her effort low to deter the male from leaving to breed with a second female; instead he would be occupied with feeding their offspring and it is the female who might have the chance to an extra-pair copulation (Eldegard & Sonerud 2012).

Weather conditions might affect the hunting activity of the female. In the middle of the day, the female usually rested in the shadows (personal observation). Prey captured by the female was mostly delivered during the cooler hours of the day. Temperatures are seasonal and vary frequently with hours from solar midnight in the summer. Hegtun (2018) suggested that the date the temperature was measured might have affected her results; this might apply to my results as well. My sample size was small, so the differences in the effects of predictor variables compared with those found by Hegtun (2018) might be due to chance. Further research on variables affecting female capture of prey is needed.

Recipient of male capture

Of the prey items delivered by the male, the fledglings received 97% and the female 3%. Hegtun (2018) found the male to deliver 83% of the prey items to the fledglings and 11% to the female. In both studies the male delivered by far most of the prey items to the fledglings. In contrast, Frye and Jageman (2012) observed that the male northern pygmy-owl (*Glaucidium gnoma*) rarely delivered prey to the fledglings (12%) in the post-fledgling period, but mostly to the female who subsequently delivered to the fledglings (88%). Frye and Jageman (2012) suggested that the period of attendance to the brood by the female determined the allocation of prey deliveries. According to Sonerud et al. (2014b) the female attendance might depend on the fledglings need to having the prey item dismembered.

When the great grey owl young are still in the nest, the female receives the prey from the male and dismember it while the male leave to forage (Cramp 1985), thus they avoid arriving at the nest with a prey while the other parent are feeding the nestlings (Sonerud et al. 2014b). At this point the female is able to control the food delivered to the nestling and eat some of it herself (Eldegard & Sonerud 2009; Sonerud et al. 2013). When the chicks have fledged, they are able to swallow a prey whole and the male can then deliver directly to the fledglings. The female is no longer in control of the division of food, and the male can better ensure that his hunting efforts benefit his offspring directly. The fledglings would benefit from receiving the prey directly and consume it themselves, other than having the female consume it.

In the parent-offspring conflict the offspring would benefit from receiving care longer than what the parent would benefit from (Trivers 1974). Thus there is a constant tug of war between parent and offspring that leads to coadaptation between the parties (Hinde et al. 2010). The fledglings use begging calls to induce their parents to retrieve food for them. If one fledgling started to beg, at least one more would also make begging calls (personal observation). Thus there is also a conflict between offspring, sibling rivalry, concerning who should receive the prey being delivered. Roulin et al. (2009) suggested that young barn owls

(*Tyto alba*) adjust their begging calls to their siblings. Siblings call when the parents are not present as well, to decide who will bee trying hardest to get the prey next time (Roulin et al. 2009). My sample size was too small and skewed to analyse which variables that might have effected who received prey captured by the male.

Female behaviour and aggressiveness

Presence of female

The female was present in 75% of the cases when I approached the fledglings, and with increasing day number she was more often absent; though day number is highly correlated with fledgling age. Hegtun (2018) found the female great grey owl to be present in 71% of the approaches, and that both fledgling age and brood size affected the probability of the female being present. Similarly, female tawny owls kept close to their offspring both day and night the first 1-2 weeks after leaving the nest (Sunde et al. 2003).

The female seem to balance her effort between foraging and guarding the offspring (Sunde et al. 2003). As newly fledged the young fledgling move around on the ground and can climb only sloping trees, being exposed to a greater danger of predators than at older age (Sunde 2005). When the fledglings get older, they usually perch higher and are more able to fly (Sunde 2005; Hegtun 2018), thus the female do not have to be present at all time to guard her offspring. This might be the reason as to why the female is increasingly more absent as the days passes.

The female might also have been resting in a tree away from the fledglings, especially at the warmest hours of the day, though this would not explain the increasing absence as the days passes. In accordance with the parent-parent conflict, the female may keep a distance to the fledglings in order to rest and make sure she is in a good condition until next years breeding season, leaving the male to expend his energy on foraging for the fledglings.

Female aggressiveness

The aggressiveness of the female decreased with increasing fledgling age. Hegtun (2018) found the same decline in aggressiveness from the female with increasing fledgling age, and also that aggression was affected by the distance to the observer. I did not find the latter difference, but this could be due to smaller sample size. In tawny owl, the level of nest defence by the female increased with increasing brood size (Wallin 1987). Likewise, in the

Ural owl, Kontiainen et al. (2009) found that the timing of reproduction and brood size affected the aggressiveness of the female at the nest; females nesting earlier and having larger broods were more aggressive. In comparison, Fisher et al. (2004) reported that the aggressiveness of male burrowing owls was affected by weather conditions; in windy and warm conditions the male reduced his defence.

Kontiainen et al. (2009) found that aggressiveness in Ural owl was important to the recruitment of offspring, as offspring recruitment increased in years with noticeable defence of the nest. Thus aggressive females recruited more offspring to the population (Kontiainen et al. 2009). The survival of female Ural owl was not affected by her aggressiveness according to Kontiainen et al. (2009), though a male's survival might be affected because of his smaller body size. Thus, female Ural owl seems to be more adapted than the male in defending the brood and she may presumably be as aggressive as she need. I observed a change in the female aggressiveness with offspring age, which is in accordance with Kontiainen et al. (2009) who suggested that the aggressive behaviour is plastic, and that there are individual differences between the females. With age the fledglings have a decreased risk of predation (Sunde 2005), and the female does not need to defend her offspring as intensively as earlier (Brodin et al. 2003). The female seemed to habituate to an observer's presence, this is shown to be possible at least for the burrowing owl in rural and urban Argentina (Cavalli et al. 2018). Thus, habituation might be a possible explanation to the decreased aggressiveness of the female with increasing day number, which is correlated to fledgling age.

Female distraction display

When I approached the fledglings and the female was present, she performed distraction display in 75% of the cases. The behaviour of the observer was the best predictor variable, but was not significant. In comparison, female great grey owl performed distraction display in only 37% of the approached cases in Hegtun (2018), and the best predictor variable was brood size. In the snowy owl, Wiklund and Stigh (1983) found that there was a higher chance of the male than the female attacking a human intruder, and that the female was the one most likely to perform distraction display if this was done.

Distraction display is a milder form of protecting the offspring and affects the survival of the adult owl less than more aggressive behaviour such as attacking. Why a female choose to distract than rather attack might also be affected by her individual level of aggressiveness, or, as suggested by Brodin et al. (2003), the predation risk of the female and the fledglings. At a larger risk for the female or a decreased risk for the fledglings, the female decreases her guarding (Brodin et al. 2003).

With larger brood size, there might be a higher chance of the female being out hunting when the observer arrived, thus making it seem like it is a connection between brood size and distraction display (Hegtun 2018). In contrast a female with only one offspring may not have to contribute to the feeding of the fledgling, and thus can rest close to her offspring and be ready to defend it whenever needed. Most broods I followed were large, and according to Hegtun (2018), the female should more often be out hunting, but I observed her performing more distraction display than did Hegtun (2018). It would be interesting to look into the differences of distraction display as function of brood size, but more data need to be collected.

According to Armstrong (1954) there is a higher chance of distraction display being performed if the species is primarily subject to diurnal predation and lives at high northern latitudes. This is the case with the great grey owl. The distance from the observer, which is a potential predator, to the fledgling is critical to the survival of the fledgling. Likely the female must balance between letting a potential predator know that she, and possibly the fledgling, are in close proximity and thus perform distraction display to lure the predator away, or keep quiet, hoping the predator does not find the fledglings (Sonerud 1988). The closer the predator get, the larger threat it poses. Thus, there is probably some threshold where the female decides to distract or to outright attack the intruder.

Fledgling movement and behaviour

Distance from nest

The distance from nest increased with increasing fledgling age and the maximum I recorded was c 2.8 km for a fledgling at the age of 57 days. The distance varied between broods, and two of them did not move farther than 450 m during my field period (these broods were followed for the shortest time, 19 and 29 days). Similarly, Hegtun (2018) recorded the fledglings of great grey owl to have moved just as far during her observation as I did, 2.7 km, and that the distance from nest also varied between broods. For eagle owl (*Bubo bubo*) in Spain the maximum recorded distance from nest before dispersal was 1.5 km for fledglings older than 85 days (Penteriani et al. 2005). Kouba et al. (2013) recorded Tengmalm’s owl in the Czech Republic at a distance of 2 km from the nest, and Eldegard et al. (2014) recorded fledglings of Tengmalm’s owl in Norway up to 3.7 km from the nest. Fledglings of the northern pygmy-owl in Montana, USA, was recorded up to 3.3 km from the nest (Frye & Jageman 2012). In comparison, burrowing owl in Idaho, USA, moved only up to 350 m from the nest before dispersal (King & Belthoff 2001). As Kouba et al. (2013) found, there seem to be a difference in the movement pattern of small and large species of owls; smaller species, such as Tengmalm’s owl move farther from the nest during the post-fledging period than larger species of owls, such as the great grey owl. Though the pattern is not definite.

The non-directional movement of the fledglings that I observed might be associated with fledglings moving in the direction from which the delivering parent arrived. This pattern of movement was also observed by Hegtun (2018) and Geir A. Sonerud (pers. comm.) for great grey owl and Tengmalm’s owl, respectively. Kouba et al. (2013) suggested that this pattern of movement in Tengmalm’s owl shortens the distance to the hunting grounds. The location of hunting grounds varies between nests. At one nest the hunting grounds might be located in approximately the same direction and thus the fledgling will constantly move in this direction. This might be the case with brood 1 in my study, which generally moved in one direction. At other nests the hunting grounds might be located in different directions and the fledglings are thus moving back and forth, according to which direction the parent arrives from. This might explain the pattern of movement observed in brood 2 and 3, which were moving around in their respective forest area.

By moving around the fledglings might also try to avoid predators, though the variation in distance from nest might suggest that this is unlikely. The female protects her offspring, and keeps close just after they have left the nest. Also, the loud sound of the begging calls might be heard from more than 100 m off in good weather conditions (personal observation). A predator would not have a problem locating the fledglings, so I believe moving away from the nest is not a strategy for hiding from predators.

Delgado et al. (2009) suggested three reasons for why eagle owl fledglings move around in a non-directional pattern after leaving the nest, and these may be applied to the great grey owl as well. Firstly, because they receive food from their parents and are protected by the female, they do not have to find a shelter to hide in. Secondly, the fledglings need to learn about their surroundings, and moving around and exploring is the best way of doing this. Last, jumping on the ground and gliding from tree to tree is the best way to explore since their flying abilities is not yet fully developed.

Movement per day

As the great grey owl fledglings grew older, their movement per day increased. The same was found by Hegtun (2018). In the eagle owl, Delgado et al. (2009) observed a similar increase in movement per day.

With age the fledglings ability to fly improves, thus they are able to move further (Delgado et al. 2009). Their increased mobility makes it possible for them to shorten their distance to their provider's hunting grounds (Kouba et al. 2013). An animal's perceptual range is suggested by Delgado et al. (2009) to be short in the beginning, and might be why the fledglings move short distances just after leaving the nest. As the fledglings learn about their surroundings and improve their flying abilities, the perceptual range is increased (Delgado et al. 2009), and the fledglings' movements increase.

In sibling rivalry the siblings compete with each other over care from their parents (Davies et al. 2012). The first fledgling to meet the delivering parent will have a higher chance of receiving the prey. Thus, the siblings might induce each other to move after a prey has been delivered, so to have a better position next time a delivery is made. As they get better at flying they probably try to keep up with each other and move a lot.

Distance between siblings

There was no pattern in the distance between siblings in a brood, this distance did not change with fledgling age. The only other study on great grey owl sibling distance, Hegtun (2018), did not find any pattern either, though the distance tended to increase with increasing fledgling age. In contrast, Sunde and Naundrup (2016) found that in tawny owl the distance between siblings decreased subsequently after they left the nest, 20-25 days after fledging the distance between siblings slightly increased with increasing fledgling age. In the eagle owl, Delgado et al. (2009) found that the distance between siblings increased with time.

The siblings are constantly in competition with each other over who should get the prey that is being delivered (Davies et al. 2012). Flying off might lead to the fledgling loosing an opportunity to receive prey; it is more profitable to stay close to its siblings. If a fledgling is moving towards the direction the parent delivering food came from, this might lead to the siblings moving after so not to loose their opportunity of receiving a prey at the next delivery. Staying close to siblings might also be an anti-predator strategy, making it easier for the female to defend her offspring when they are aggregated (Sunde & Naundrup 2016).

Fledgling perching height

With age, the fledglings perched higher, though older fledglings could still occasionally be perching close to the ground. Hegtun (2018) also found that the fledglings increased their perching height with increasing age. In tawny owl, Sunde (2005) found that fledglings increased their perching height during the first days after leaving the nest.

As the flying ability of the fledglings improves with age they will be able to perch higher in a tree. It is also safer to perch higher as the risk of predation is associated with staying near the ground (Sunde 2005). Sunde (2005) found that for tawny owl the probability of dying decreased from one day to the next with increasing perching height the first 14 days after fledging. A fledgling should therefore aim to get high up as fast as possible to reduce its own risk of predation. As the fledglings get older the risk of perching on the ground might be lower due to their enhanced ability to fly and thus to escape quicker. This might be the reason as to why fledglings occasionally could be found perching close to the ground. The one I observed had no problem flying off when I was approaching.

Fledgling mortality

The fledgling mortality during my fieldwork was zero the entire period of observation. In contrast, Hegtun (2018) calculated the total mortality of fledglings of great grey owl during her field work to be 38%. In comparison, Bull et al. (1989) found the mortality rate of juveniles great grey owl the first year to be 53%. Though there is a difference in mortality, there is also a difference in the duration of the observation period between the studies. In the burrowing owl most mortality happens during two separate periods in the post-fledgling stage, 0-13 and 22-34 days after the fledglings had left the nest, respectively (Davies & Restani 2006).

Davies and Restani (2006) suggested that predation was the main cause of mortality in fledglings of the burrowing owl. This might also be likely in the great grey owl as Bull et al. (1989) found that seven of the fledglings had died by predation and only two by starvation. Davies and Restani (2006) argued that it is unlikely that fledglings of burrowing owl died because of starvation in the beginning of the post-fledgling stage because their parents fed them.

Both Hegtun (2018) and I followed broods with both parents present. The fledglings in these broods probably benefitted from having both parents present, one to feed them and one to protect them. It might be that it was enough food to feed all the fledglings and that the females were good at defending their offspring, so that all of them at least survived until I no longer were observing. However I do not believe my results are representative for the population of great grey owl, as my sample size was small and mostly contains data from two broods that were followed the entire length of the field work. Most likely there was a coincidence that the broods I followed did not loose any fledglings.

Conclusion

In conclusion parental care in the great grey owls post-fledge period is divided such that the male provides most of the food for the fledglings and the female guards the fledglings, though the female might contribute to provisioning as well. The male delivers most of the prey directly to the fledglings, and all prey items observed captured by the female was delivered to a fledgling. Female great grey owls appear to have individual differences in their level of aggressiveness, though they also seem to habituate to an observer’s presence. In the broods I followed, the female still accompanied the fledglings when I ended observations. During this period the fledglings used an extensive area, though this varied between broods.

Little is known about behaviour of the great grey owl in the post-fledgling period and further research are needed. Though the sample size in this study is small, these results contribute to the knowledge about great grey owls, and hopefully inspire to more research on the field. As the great grey owl has recently expanded to eastern Norway, and appears to expand further towards south and west, it is important to know more about this period of life for the owl. In a management perspective, future research should look more into how large an area the owls use during the breeding season, so that these areas may be managed without conflicts with development and forestry.

References

Armstrong, E. A. (1954). The ecology of distraction display. *The British journal of animal behaviour*, 2: 121-135.

Artsdatabanken. (n.d.). *Strix nebulosa J. R. Forster, 1772*. Available at: https://artsdatabanken.no/Rodliste2015/rodliste2015/Norge/4624 (accessed: 09.04.18).

Berg, T. (2016). Lappuglehekkinger i Hedmark 1989-2015, Rapport: Fylkesmannen i Hedmark.

BirdLife International. (2016). *Strix nebulosa*. The IUCN red list of threatened species 2016. Available at: http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22689118A93218931.en (accessed: 09.04.18).

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24: 127-135.

Brodin, A., Jönsson, K. I. & Holmgren, N. (2003). Optimal energy allocation and behaviour in female raptorial birds during the nestling period. *Écoscience*, 10: 140-150.

Bull, E. L., Henjum, M. G. & Rohweder, R. S. (1989). Reproduction and mortality of great gray owls in Oregon. *Northwest Science*, 63: 38-43.

Cavalli, M., Baladrón, A. V., Isacch, J. P., Biondi, L. M. & Bó, M. S. (2018). The role of habituation in the adjustment to urban life: an experimental approach with burrowing owls. *Behavioural Processes*, 157: 250-255.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proc. R. Soc. B*, 273: 1375-1383.

Cramp, S. (ed.) (1985). *The birds of Western Palearctic*, vol. IV.

Davies, J. M. & Restani, M. (2006). Survival and movements of juvenile burrowing owls during the postfledging period. *Condor*, 108: 282-291.

Davies, N. B., Krebs, J. R. & West, S. A. (2012). *An introduction to behavioural ecology*. 4th ed.: Wiley-Blackwell.

Delgado, M. M., Penteriani, V. & Nams, V. O. (2009). How fledlings explore surrondings from fledging to dispersal. A case study with Eagle Owls *Bubo bubo*. *Ardea*, 97: 7-15.

Eldegard, K. & Sonerud, G. A. (2009). Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. *Proc. R. Soc. B.*, 276: 1713-1721.

Eldegard, K. & Sonerud, G. A. (2012). Sex roles during post-fledging care in birds: female Tengmalm's Owls contribute little to food provisioning. *J. Ornithol.*, 153: 358-398.

Eldegard, K., Vognild, H. & Sonerud, G. A. (2014). Intersexual difference in early natal dispersal: abrupt departure by females and gradual emigration by males in Tengmalm's Owl *Aegolius funereus*. *J Ornithol*, 155: 235-242.

Fisher, R. J., Poulin, R. G., Todd, L. D. & Brigham, R. M. (2004). Nest stage, wind speed, and air temperature affect the nest defence behaviours of burrowing owls. *Can. J. Zool*, 82: 707-713.

Frye, G. G. & Jageman, H. R. (2012). Post-fledging ecology of Northern Pygmy-Owl in the Rocky Mountains. *The Wilson Journal of Ornithology*, 124: 199-207.

Hegtun, K. (2018). Post-fledging parental care in the female great grey owl (*Strix nebulosa*): a trade-off between provisioning and guarding. Ås, Norwegian University of Life Sciences: Faculty of Environmental Sciences and Natural Resource Management.

Hinde, C. A., Johnstone, R. A. & Kilner, R. M. (2010). Parent-offspring conflict and coadaptation. *Science*, 327: 1373-1376.

Houston, A. I., Szekely, T. & McNamara, J. M. (2005). Conflict between parents over care. *Trends Ecol. Evol.*, 20: 33-38.

Johnson, J. B. & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.*, 19: 101-108.

Kenward, R. E. (1978). Radio transmitters tail-mounted on hawks. *Ornis Scand.*, 9: 220-223.

King, R. A. & Belthoff, J. R. (2001). Post-fledging dispersal of Burrowing owls in southwestern Idaho: characterization of movements and use of satellite burrows. *Condor*, 103: 118-126.

Kontiainen, P., Pietiäinen, H., Huttunen, K., Karell, P., Kolunen, H. & Brommer, J. E. (2009). Aggressive Ural owl mothers recruit more offspring. *Behav Ecol*, 20: 789-796.

Kouba, M., Bartos, L. & Stastny, K. (2013). Differential movement patterns of juvenile Tengmalms Owls (*Aegolius funereus*) during the post-fledging dependence period in two years with constrasting prey abundance. *PLoS. ONE.*, 8: 1-10.

Olson, V. A., Liker, A., Freckleton, R. P. & Székely, T. (2008). Parental conflict in birds: comparative analyses of offspring development, ecology and mating oppurtuinties. *Proc. R. Soc. B.*, 275: 301-307.

Penteriani, V., Delgado, M. M., Maggio, C., Aradis, A. & Sergio, F. (2005). Development of chicks and predispersal behaviour of young in the Eagle Owl *Bubo bubo*. *Ibis*, 147: 155-168.

R Core Team. (2018). *R: A language and environment for statistical computing*, 3.5.2 ed. Vienna, Austria: R Foundation for Statistical Computing.

Roulin, A., Dreiss, A., Fioravanti, C. & Bize, P. (2009). Vocal sib-sib interactions: how siblings adjust signalling level to each other. *Anim. Behav.*, 77: 717-725.

Sonerud, G. A. (1988). To distract display or not: grouse hens and foxes. *Oikos*, 51: 233-237.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2013). Size-biased allocation of prey from male to offspring via female: family conflicts, prey selection, and evolution of sexual size dimorphism in raptors. *Oecologia*, 172: 93-107.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2014a). Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian kestrel. *Anim. Behav.*, 96: 31-38.

Sonerud, G. A., Steen, R., Selås, V., Aanonsen, O. M., Aasen, G. H., Fagerland, K. L., Fosså, A., Kristiansen, L., Løw, L. M., Rønning, M. E., et al. (2014b). Evolution of parental roles in provisioning birds: diet determines role assymetry in raptors. *Behav Ecol*, 25: 762-772.

Steen, R., Løw, L. M. & Sonerud, G. A. (2011a). Delivery of Common Lizards (*Zootoca (Lacerta) vivipara*) to nests of Eurasian Kestrels (*Falco tinnunculus*) determined by solar height and ambient temperature. *Can. J. Zool*, 89: 199-205.

Steen, R., Løw, L. M., Sonerud, G. A., Selås, V. & Slagsvold, T. (2011b). Prey delivery rates as estimates of prey consumption by Eurasian Kestrel *Falco tinnunculus* nestlings. *Ardea*, 99: 1-8.

Sulkava, S. & Huhtala, K. (1997). The great gray owl (*Strix nebulosa)* in the changing forest environment of northern Europe. *J. Raptor Res.*, 31: 151-159.

Sunde, P., Bølstad, M. S. & Møller, J. D. (2003). Reversed sexual dimorphism in tawny owls, *Strix aluco*, correlates with duty division in breeding effort. *Oikos.*, 101: 265-278.

Sunde, P. (2005). Predators control post-fledging mortality in tawny owls, *Strix aluco*. *Oikos*, 110: 461-472.

Sunde, P. & Naundrup, P. J. (2016). Spatial and begging behaviours of juvenile Tawny Owls (*Strix aluco*) from fledging to independence under constrasting food conditions. *J. Ornithol.*, 157: 961-970.

Trivers, R. (1974). Parent-offspring conflict. *Am. Zool.*, 14: 249-264.

Wallin, K. (1987). Defence as parental care in Tawny owls (*Strix aluco*). *Behaviour*, 102: 213-230.

Wiklund, C. G. & Stigh, J. (1983). Nest defence and evolution of reversed sexual size dimorphism in Snowy Owls *Nyctea scandiaca*. *Ornis Scand.*, 14: 58-62.

Wu, J. X., Siegel, R. B., Loffland, H. L., Stock, S. L., Roberts, K. N., Keane, J. J., Medley, J. R., Bridgman, R. & Stermer, C. (2015). Diversity of great gray owl nest sites and nesting habitats in California. *J. Wildl. Manage.*, 79: 937-947.

Appendix 1

***Table A1**: All models predicting that the female rather than the male in great grey owl pairs had captured a prey that was delivered to fledglings (n=74), ranked by AICc. Temperature was excluded from the analysis. Both the categorical and numerical variable of «time of day» are included. Brood ID is included as a random variable in all models.*

Model	**df**	**AICc**	**ΔAICc**
Brood size + Hours from solar midnight	4	83.91	0.00
Brood size	3	85.22	1.31
Brood size + Time of day (categorical)	4	85.53	1.62
Brood size + Fledgling age + Hours from solar midnight	5	85.63	1.72
Brood size + Time of day (numerical)	4	86.27	2.36
Brood size + Hours from solar midnight + Day number + Time of day (categorical)	6	87.07	3.16
Brood size + Day number	4	87.30	3.39
Brood size + Fledgling age	4	87.44	3.54
Brood size + Fledgling age + Time of day (categorical)	5	87.62	3.71
Brood size + Day number + Time of day (categorical)	5	87.76	3.86
Fledgling age + Hours from solar midnight	4	88.29	4.38
Brood size + Fledgling age + Time of day (numerical)	5	88.54	4.63
Brood size + Day number + Time of day (numerical)	5	88.57	4.66
Time of day (categorical)	3	89.79	5.88
Fledgling age	3	90.64	6.73
Fledgling age + Time of day (categorical)	4	91.98	8.07
Fledgling age + Time of day (numerical)	4	92.57	8.66

***Table A2**: All models predicting that the female rather than the male in great grey owl pairs had captured a prey that was delivered to fledglings (n=74), ranked by AICc. Temperature was included in the analysis. Both the categorical and numerical variable of «time of day» are included. Brood ID is included as a random variable in all models.*

Model	**df**	**AICc**	**ΔAICc**
Temperature + Brood size + Hours from solar midnight	5	82.57	0.00
Temperature + Brood size + Hours from solar midnight + Fledgling age	6	84.30	1.73
Temperature + Brood size	4	87.33	4.76
Temperature + Hours from solar midnight	4	87.49	4.92
Temperature + Brood size + Time of day (categorical)	5	87.83	5.26
Temperature + Brood size + Time of day (numerical)	5	88.57	6.01
Temperature + Fledgling age + Hours from solar midnight	5	89.33	6.76
Temperature + Brood size + Day number	5	89.37	6.80
Temperature + Brood size + Fledgling age	5	89.57	7.00
Temperature + Day number + Hours from solar midnight	5	89.62	7.05
Temperature + Time of day (categorical) + Hours from solar midnight	5	89.68	7.12
Temperature + Brood size + Time of day (categorical) + Fledgling age	6	89.88	7.31
Temperature + Brood size + Time of day (categorical) + Day number	6	90.10	7.53
Temperature	3	90.64	8.07
Temperature + Brood size + Time of day (numerical) + Fledgling age	6	90.89	8.32
Temperature + Time of day (numerical) + Day number + Brood size	6	90.94	8.38
Temperature + Time of day (categorical)	4	91.82	9.25
Temperature + Time of day (numerical)	4	92.41	9.85
Temperature + Day number	4	92.85	10.28
Temperature + Fledgling age	4	92.87	10.31
Temperature + Fledgling age + Time of day (categorical)	5	93.80	11.23
Temperature + Time of day (categorical) + Day number	5	93.88	11.31
Temperature + Time of day (categorical) + Time of day (numerical)	5	93.92	11.35
Temperature + Time of day (numerical) + Fledgling age	5	94.64	12.08
Temperature + Time of day (numerical) + Day number	5	94.69	12.12

Appendix 2

Table A3*: All models predicting whether female great grey owl was present (n=53) when the fledglings were approached, ranked by AICc. Brood ID is included as a random variable.*

Model	**df**	**AICc**	**ΔAICc**
Day number	3	34.91	0.00
Day number + Brood size	4	35.79	0.87
Fledgling age + Brood size	4	36.14	1.23
Fledgling age	3	38.77	3.86
Fledgling perching height (categorical) + Brood size + Day number	8	40.96	6.05
Fledgling perching height (categorical) + Brood size + Fledgling age	8	41.65	6.74
Fledgling perching height (categorical) + Fledgling age	7	44.97	10.05
Fledgling perching height (numeric)	3	49.26	14.35
Brood size	3	56.15	21.23

Table A4*: All models predicting whether female great grey owl performed distraction display (n=53) when the fledglings were approached, ranked by AICc. Brood ID is included as a random variable.*

Modell	**df**	**AICc**	**ΔAICc**
Observer behaviour	3	38.57	0.00
Fledgling age	3	38.75	0.18
Aggressiveness	3	38.86	0.29
Brood size	3	40.10	1.53
Aggressiveness + Observer behaviour (numeric)	4	40.11	1.54
Fledgling perching height (numeric)	3	40.20	1.63
Number of observers	3	40.42	1.84
Brood size + Observer behaviour (numeric)	4	40.74	2.17
Aggressiveness + Fledgling perching height (numeric)	4	41.22	2.65
Brood size + Fledgling age	4	41.27	2.69
Aggressiveness + Brood size	4	41.31	2.74
Fledgling age + Aggressiveness + Observer behaviour (categorical)	7	43.41	4.84

Brood size + Aggressiveness + Observer behaviour (categorical)	7	44.39	5.82
Fledgling age + Brood size + Observer behaviour (categorical)	7	44.76	6.19
Fledgling perching height (categorical)	6	47.84	9.26
Fledgling age + Aggressiveness + Fledgling perching height (categorical)	8	49.24	10.67
Aggressiveness + Fledgling perching height (categorical)	7	49.66	11.09
Fledgling age + Fledgling perching height (categorical)	7	49.77	11.20
Brood size + Fledgling perching height (categorical)	7	51.05	12.48
Fledgling age + Aggressiveness + Brood size + Fledgling perching height	9	53.11	14.54
Aggressiveness + Brood size + Fledgling perching height (categorical)	8	53.24	14.67
Fledgling age + Brood size + Fledgling perching height (categorical)	8	53.30	14.73
Fledgling perching height (categorical) + Aggressiveness + Observer behaviour (categorical)	10	53.89	15.32
Fledgling age + Aggressiveness + Observer behaviour (categorical) + Fledgling perching height (categorical)	11	57.57	19.00
Aggressiveness + Brood size + Observer behaviour (categorical) + Fledgling perching height (categorical)	11	58.62	20.05
Fledgling age + Observer behaviour (categorical) + Brood size + Fledgling perching height (categorical)	11	59.48	20.91
Fledgling age + Aggressiveness + Brood size + Observer behaviour (categorical) + Fledgling perching height (categorical)	12	62.70	24.13

***Table A5**: All models predicting female great grey owl aggressiveness (n=52) when the fledglings were approached, ranked by AICc. Brood ID is included as a random variable.*

Modell	**df**	**AICc**	**ΔAICc**
Fledgling age + Observer behaviour (categorical)	7	155.98	0.00
Brood size + Observer behaviour (categorical) + Fledgling age	8	156.22	0.24
Fledgling age + Observer behaviour (numeric)	5	158.60	2.62
Fledgling age + Observer behaviour (categorical) + Number of observers	8	159.59	3.61
Brood size + Fledgling age + Number of observers + Observer behaviour (categorical)	9	160.01	4.03
Fledgling age	4	160.41	4.43
Brood size + Fledgling age + Fledgling perching height (numeric) + Observer behaviour (categorical)	9	160.86	4.88
Brood size + Fledgling age	5	160.87	4.89
Fledgling age + Observer behaviour (categorical) + Fledgling perching height (numeric)	8	161.06	5.08
Fledgling age + Number of observers	5	163.60	7.62
Brood size + Fledgling age + Number of observers	6	164.22	8.24
Brood size + Fledgling age + Fledgling perching height (numeric)	6	164.56	8.59
Brood size + Fledgling age + Number of observers + Fledgling perching height (numeric) + Observer behaviour (categorical)	10	164.77	8.80
Fledgling age + Fledgling perching height (numeric)	5	164.79	8.81
Fledgling age + Observer behaviour (categorical) + Number of observers + Fledgling perching height (numeric)	9	164.79	8.82
Brood size + Fledgling age + Number of observers + Fledgling perching height (numeric) + Observer behaviour (numeric)	8	165.73	9.75
Brood size + Fledgling age + Number of observers + Fledgling perching height (numeric)	7	168.05	12.08
Fledgling age + Number of observers + Fledgling perching height (numeric)	6	168.08	12.10
Fledgling perching height (numeric)	4	177.11	21.13

Fledgling perching height (numeric) + Observer behaviour (categorical)	7	177.25	21.27
Fledgling perching height (numeric) + Observer behaviour (numeric)	5	177.38	21.40
Brood size + Fledgling perching height (numeric)	5	179.47	23.50
Number of observers + Observer behaviour (categorical) + Fledgling perching height (numeric)	8	179.66	23.68
Brood size + Observer behaviour (categorical) + Fledgling perching height (numeric)	8	179.80	23.83
Number of observers + Fledgling perching height (numeric)	5	180.09	24.11
Brood size	4	180.79	24.82
Observer behaviour (categorical)	6	180.90	24.93
Brood size + Observer behaviour (numeric)	5	181.10	25.12
Observer behaviour (numeric)	4	182.06	26.08
Brood size + Number of observers + Fledgling perching height (numeric)	6	182.56	26.58
Brood size + Number of observers + Fledgling perching height (numeric) + Observer behaviour (categorical)	9	182.66	26.68
Brood size + Observer behaviour (categorical) + Number of observers	8	182.95	26.98
Brood size + Number of observers	5	183.68	27.71
Number of observers	4	184.05	28.07
Number of observers + Observer behaviour (numeric)	5	184.08	28.10

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway