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Post-fledging parental care in the female great grey owl (*Strix nebulosa*): a trade-off between provisioning and guarding

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Preface

This master's thesis is written as the final part of my master's degree in general ecology on the Norwegian University of Life Sciences (NMBU). My fieldwork was financially supported by the Norwegian Environment Agency, and I am grateful for their support.

I want to thank my supervisor Geir A. Sonerud, for allowing me to participate in the exciting research project of great grey owls. He provided good help and gave me constructive feedback during the whole process of working with the thesis, which has been really useful. I also want to thank Cathrine S. Torjussen for helping and guiding me a lot during the fieldwork, for reading and commenting my draft, and for good cooperation and company in the field. I really enjoyed the summer spent with the owls in Elverum! Thanks to Trond Berg who provided good help in the field with all his knowledge about the great grey owl, and let us stay in his cabin, he made the fieldwork much easier. Also thanks to the local ornithologists in Elverum who put a lot of effort in finding nests and building nesting platforms, for sharing their locations and allowing us to study the owls in their nests. I would also like to thank Ronny Steen for answering my statistical questions.

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Abstract

Post-fledging parental care is generally little studied in birds. By use of radio telemetry, I studied the post-fledging parental behaviour of female great grey owls (*Strix nebulosa*), measured as number of prey deliveries from males and females and female aggressiveness and brood defence. I also observed the behaviour and movement patterns of the dependent fledged juveniles. The females provided care by staying near the young to guard them and assisting the males with food provisioning. No female deserted the male and offspring before the study was terminated. The males provided more than twice as many prey items for the offspring than the females did in the post-fledging dependence period, and the probability of a female delivering a prey tended to increase with brood size. Females also delivered more prey items when the ambient temperature was low. When a male had captured a prey, he delivered it directly to the fledglings in 83% of the cases, and if he delivered it to the female instead, it was usually under stressful situations. The female spent much time near the fledglings, but the probability of her being absent increased with increased fledgling age and brood size. When intruders were approaching the fledglings, the female could show an extremely aggressive behaviour, and female aggressiveness depended on observer behaviour and decreased with increasing fledgling age. An alternative defence strategy of the female was to perform distraction displays, and the probability of her doing so decreased with brood size. The fledglings moved away from the nest as they aged, and the distance from the nest significantly increased with increasing fledgling age. However, the siblings stayed close to each other during the entire post-fledging dependence period. The juvenile mortality rate from fledging until the fledglings could fly and escape predators was 38%, and the highest mortality rate occurred the first time after fledging. Increasing perching height, staying near siblings and moving towards the parent's hunting area might be strategies the juveniles used to increase their survival chances. I suggest that the female great grey owl faces a trade-off between guarding offspring and provisioning prey for them. Brood size, and the vulnerability of the fledglings, the latter determined by perching height and flying skills, decide how she should balance her effort.

Sammendrag

Ungeomsorg hos fugl etter at ungene har forlatt reiret er generelt lite studert. Ved hjelp av radiotelemetri har jeg studert hunnens bidrag til ungeomsorgen hos lappugle (*Strix nebulosa*) etter at ungene har hoppet ut av reiret, målt i antall byttedyr levert til ungene fra hannen og hunnen og hunnens aggressivitet og ungeforsvar. Jeg har også studert ungenes bevegelsesmønster og atferd i den samme perioden. Hunnen bidro til ungeomsorgen ved å hjelpe hannen med å jakte og med å forsvare ungene. Ingen av hunnene forlot hannen og ungene før studiet ble avsluttet. Hannen leverte mer enn dobbelt så mange byttedyr til ungene som hunnen gjorde i perioden etter utflygning, og sannsynligheten for at et byttedyr var levert av en hunn hadde en tendens til å øke med antall unger i kullet. Hunnene leverte også flere byttedyr ved lave temperaturer. Når en hann hadde fanget et byttedyr, leverte han det direkte til ungene i 83% av tilfellene, og hvis han leverte det til hunnen i stedet var han vanligvis utsatt for stressende omgivelser. Hunnen tilbragte mye tid i nærheten av ungene, men sannsynligheten for at hun ikke var tilstede økte med ungenes alder og med antall unger i kullet. Hunnen kunne vise svært aggressiv atferd når noen nærmet seg ungene, og aggressivitetsnivået var avhengig av observatørens atferd og minket med økende ungealder. Ungene flyttet seg rundt i terrenget etter at de hadde forlatt reiret, og avstanden fra reiret hadde en signifikant økning med økende ungealder. Søsken i samme kull holdt sammen hele perioden. Ungedødeligheten var på 38% i perioden fra utflygning til ungene kunne fly og unnslippe predatorer på egenhånd, og den høyeste dødeligheten fant sted de første dagene etter utflygning. Å velge høytliggende greiner å sitte på og å flytte seg mot jaktområdene til foreldrene kan være strategier ungene brukte for å øke overlevelsessjansene sine. Jeg argumenterer for at lappuglehunnen balanserer ungeomsorgen sin mellom å forsyne ungene med mat og å forsvare dem mot predatorer. Hvordan hun balanserer innsatsen avhenger av kullstørrelse og sårbarheten mot predatorer. Sistnevnte avhenger av hvor høyt de sitter over bakken og hvor godt de kan fly.

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Introduction

In birds, parental care is an important life-history trait that has developed to increase offspring survival (Clutton-Brock 1991; Westneat & Sherman 1993). Avian parental care is most easy to study while the juveniles still are nestlings, but many birds care for their young also outside the nest (Gruebler & Naef-Daenzer 2010; Tarwater & Brawn 2010). The post-fledging dependence period (PFDP) denotes the period from when the offspring have left the nest until they no longer receive care from the parents (Bustamante & Negro 1994; Delgado et al. 2009). This is a crucial life stage with high mortality, and the early post-fledging phase is a survival bottleneck for many birds (Naef-Daenzer & Grüebler 2016). Despite the importance of the post-fledging dependence period for survival, several aspects of this period is generally understudied (Greig-Smith 1980; Montgomerie & Weatherhead 1988; Eldegard & Sonerud 2012; Cox et al. 2014).

Biparental care and social monogamy is the dominating strategy of offspring care among birds, especially when help from both parents is necessary for successful breeding (Cockburn 2006; Korpimäki et al. 2011). In birds of prey, meaning hawks (*Accipitriformes*), falcons (*Falconiformes*) and owls (*Stringidae*), the parental duties are asymmetric between the male and the female in the incubation period and the early nestling stage (Sonerud et al. 2014a). The female usually incubates, broods and dismembers prey for the nestlings, while the male provides the female and the nestlings with prey (Zárybnická & Vojar 2013). In the late nestling stage and the fledgling stages, however, the offspring can keep warm themselves and ingest the food unassisted. This changes the parental duties of the female, and how the female participates in the parental care in these stages varies between different species of birds of prey and depends on prey type (Sonerud et al. 2014a) and environmental factors (Brodin et al. 2003).

Raptors and owls in general have lower survival rates in their first year than in subsequent years (Newton et al. 2016). In most owl species, the chicks leave the nest before they are able to fly, and may therefore suffer high predation rates the first time after fledging (Duncan & Hayward 1994). Parents can increase the survival rate of their offspring by guarding and provisioning food, but offspring care has high energetic costs for the parents, and this results in parental conflicts over the amount of care (Clutton-Brock 1991). Most models regarding parental conflicts over care are based on species with equal parental duties

between the mates, which makes analyses of parental conflicts in raptors and owls with strictly divided roles more complicated (Houston et al. 2005).

For this thesis, I studied the female's contribution to parental care and the fledglings' movement and behaviour in the post-fledging dependence period in the great grey owl (*Strix nebulosa*). Recently, great grey owls have rapidly become more abundant in southern Norway (Berg 2016), and this makes it possible to do more studies on their biology. To the best of my knowledge, no study has been done on the post-fledging parental care in this species. However, some aspects of the post-fledging period has been studied in both this species and in other owl species, so one aim of this study was to compare the behaviour of the great grey owl to other owl species.

When the female great grey owl does not need to brood or dismember prey for the young anymore, her options are to either assist the male with food provisioning, stay near the fledglings to guard them, or desert and leave the remaining parental duties to the male. Despite the fact that offspring benefit from parental care from both parents, polygyny is known from several European raptors and owls (Korpimäki 1988). Female desertion, or sequential polyandry, is common in some species, where the female's benefit from having the opportunity to re-mate or increase her body mass and condition for the next breeding season compensates for the reduced survival of the first brood (Eldegard & Sonerud 2009; Béziers & Roulin 2016). The female Tengmalm's owl (*Aegolius funereus*) deserts her first brood in nearly two out of three nesting attempts (Eldegard & Sonerud 2012), and the male compensates by increasing his food delivery rate. Both polygyny and female desertion in owls become more common with increased food abundance (Eldegard & Sonerud 2009; Korpimäki et al. 2011).

In many bird species, nest predation is the most important variable affecting fitness, and brood defence is an adaptation to reduce the vulnerability of the offspring (Montgomerie & Weatherhead 1988). Predation from mammalian and avian predators is the single most important cause of death in dependent tawny owl (*Strix aluco*) fledglings (Overskaug et al. 1999; Sunde 2005), and Kontiainen et al. (2009) showed that aggressive Ural owl (*Strix uralensis*) females have better offspring survival than non-aggressive females. Whereas the female Tengmalm's owls do not appear to guard their young at all (Eldegard & Sonerud 2012), the female great grey owl can show an extremely aggressive behaviour around the nest (Cramp 1985; Bull & Henjum 1990). If the benefits from defending the young are similar in

the great grey owl as in the Ural owl, the great grey owl female would pay the cost of lack of defence if she deserts.

The level of offspring guarding is highly variable between and within bird species, and the optimal defence level maximizes the difference between fitness benefits measured in increased offspring survival and fitness costs that reduce the probability of parent survival (Montgomerie & Weatherhead 1988). Parental investment theory predicts that parents should defend large broods more than small broods, and invest more in older offspring than in young offspring (Rytkönen 2002; Svagelj et al. 2012). However, most studies of brood defence regard the nestling period, so the defence of fledglings is understudied. It is likely that the parents reduce their defensive effort when the fledglings are old enough to escape dangers on their own.

Since the post-fledging dependence period is a crucial period with high mortality in most altricial birds (Naef-Daenzer & Grüebler 2016), more knowledge of movement patterns and behaviour of fledglings in this period would be useful to evaluate possible risks and to estimate reproductive success, especially for conservation of endangered species (Keedwell 2003; Delgado et al. 2009). Owl fledglings usually stay close to the nest the first time after fledging, and then start moving away from the nest, directional or unoriented (Delgado et al. 2009; Tome 2011; Frye & Jageman 2012; Eldegard et al. 2014). Siblings in a brood usually stay together during the whole post-fledging dependence period (Penteriani et al. 2005; Frye & Jageman 2012; Sunde & Naundrup 2016), which could be an anti-predator strategy as parents may defend aggregated offspring better (Sunde & Naundrup 2016). However, the size and location of the post-fledging area of juvenile great grey owls is unknown.

The great grey owl is listed as vulnerable (VU) on the Norwegian red list because of few reproductive individuals (Kålås et al. 2015), so more knowledge about this species is important for conservation management. Raptor and owl research is also relevant because of such species' roles as indicator species or flagship species for nature conservation (Newton et al. 2016). My research objective was to examine the female's contribution in the post-fledgling offspring care of the great grey owl, and to identify the factors explaining her behaviour. To answer this, I collected data on three main aspects of the post-fledging period, namely prey deliveries from males and females, female aggressiveness and offspring guarding, and fledgling movement and behaviour. My hypothesis was that females face a trade-off between food provisioning and offspring guarding, and benefit from staying with their mate and offspring rather than deserting.

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Methods

Study area and study species

The fieldwork took place in Elverum municipality in Hedmark County, southeast Norway (61°N, 12°E) at altitudes of 220 – 400 m. The study area is dominated by coniferous forest, mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and is heavily influenced by modern forestry, making the landscape a mosaic of planted forest stands of different ages, clear-cuts, bogs and forest roads.

The fieldwork was done from 27 May until 26 July 2017, and covered the late nestling stage and the fledgling stages, but ended before the juveniles reached independence. The vole abundance was high in 2017 after a low in 2015 and an increase in 2016 (Geir A. Sonerud pers. comm.). This resulted in 120 documented great grey owl breeding attempts within Hedmark County, of which almost half were in the municipality of Elverum (Trond Berg pers. comm.). Until 2009, great grey owl breeding attempts used to be sporadic and rare in southern Norway (Berg 2016), so Elverum has recently become a hotspot for this species.

The great grey owl is a large owl (male body mass about 900 g) distributed in the boreal forest around the whole Northern Hemisphere (Cramp 1985). This owl is a typical small mammal specialist, while birds, frogs and invertebrates are rarely found in the diet (Cramp 1985). They do not build their own nests, but usually nest in old nests of hawks, in Norway mainly goshawk (*Accipiter gentilis*) and common buzzard (*Buteo buteo*) (Berg 2016). They may also nest in large stumps, on the ground, on man-made nest platforms, and more rarely on other man-made structures such as hunting towers (Sulkava & Huhtala 1997; Berg 2016). Local ornithologists have mounted artificial nesting platforms for the great grey owl all over Elverum municipality, and these platforms were frequently used for breeding in 2017. The nests occupied by the great grey owl are usually located in the old forest with shadow and shelter, but near open habitats where the owls can hunt field voles (*Microtus agrestis*) easily (Sulkava & Huhtala 1997). The great grey owl is described as nomadic and opportunistic, and it may benefit from forest logging because this increases the availability of small mammal prey, as long as the nest locations remain (Bull et al. 1988). However, conservation of the great grey owl would benefit from a forestry practice that leave retention stands near nest sites, as juveniles prefer tree cover after fledging, and leaning trees for juvenile perching (Duncan 1997). Most nests observed during my fieldwork were located in old forests, but some owls had also occupied nests at the edge of bogs and clear-cuts.

Radio tagging

Six adult great grey owls, three males and three females, were captured near their nests and fitted with radio tag in conjunction with bird ringing done by local ornithologists. These males and females belonged to different nests, so individuals from six pairs were radio tagged. The process of ringing, radio tagging and making measures took approximately 60 minutes from the bird was caught until it was released, and was done with permission from the National Animal Research Authority in Norway and the Norwegian Environment Agency.

The radio tagging followed the standardized methods of tail-mounting radio transmitters on birds (Kenward 1978). A radio transmitter (TW-4, Biotrack, England) was glued to the proximal end of one of the mid-tail feathers, and then sewed on. It was also tied to a neighbouring feather for stabilization, and the antenna was tied along the feather. The transmitter weighed only 4 g, which made up about 0.4% of the male body mass of 900 g, and even less of the 20 – 25% heavier female's body mass (Cramp 1985). There was no need for re-capturing the birds to remove the transmitters, because they would shed in the fall when the birds moult their tail feathers (Kenward 1978).

Tracking and observation

My data collection included observations of prey deliveries from the parents, the female's behaviour around the offspring, and the location and behaviour of the fledglings. To locate the fledglings the first time after fledging, I searched around the nest, and located them by listening to their begging calls. Later in the season, when the fledglings moved further from the nest, I tracked the radio tagged parent until I could hear begging calls from the fledglings. To track the radio tagged owls, I used a radio receiver (SIKA Radio Tracking Receiver, Biotrack, England) and a hand-held Yagi-antenna (flexible Yagi, Biotrack, England), and the strength and the directions of the signals were used to locate the birds. When the fledglings were found, I plotted the location of each of them by use of a GPS (Garmin eTrex).

The prey deliveries when the chicks were still in the nest was studied by use of cameras on the nests in a separate study, so my observations on prey deliveries started after fledging. After having located the fledglings, I sat down hiding in a camouflage tent or under another type of cover and observed prey deliveries. I used the signals from the radio-receiver to know if the tagged parent was present or not, and when a parent delivered food, I could use

the signals to identify the parent. The most important information during delivery was which parent had captured the prey, and whether the prey was delivered directly to the offspring or to the other parent. I noticed the time of the delivery and the temperature when possible. Some of the observations were made in stressful situations for the birds, for example during attempts to catch and tag the owls or on occasions when observers were near the fledglings. Because this could affect the behaviour of the owls, a stress parameter was included in the analysis. This parameter had three values: no or little (0), moderate (1) and highly stressful (2) circumstances for the owls during the prey delivery. At my observation distance, it was difficult to distinguish between the different prey species, as all of them were small mammals. However, European water voles (*Arvicola amphibius*) could be recognized because of their large size. Therefore, the prey parameter has two values, water vole and other small mammal.

I also made measurements of the female's behaviour around the offspring. I noted whether the female was present near the offspring when I first approached them, if she performed distraction display to lure me away from the offspring, and scored her aggressiveness on a scale from 0 to 5 (table 1). This scale was based on an aggressiveness score table for the Ural owl (Kontiainen et al. 2009), but was adjusted to suit the great grey owl in the post-fledging period, also in situations where observers did not climb the nest tree or handled the chicks. I also included how many observers were present, and the behaviour of the observers, meaning if they were handling the chicks or observing them from short (<10 m), medium (10-50 m) or long (>50 m) distance.

Table 1: The aggressiveness scores for the behaviour of great grey owl females when an intruder approached the offspring in the post-fledging dependence period. The score table is modified from Kontiainen et al. (2009).

Behaviour	Score	Description
Not present	0	The female was not present near her offspring during the observation.
Silent	1	The female was present, but showed no aggressive behaviour.
Click or bark	2	The female made clicking or barking sounds, but from 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 did not hit.
Hit	5	The female attacked and hit the intruder.

The age of the great grey owl offspring was estimated by local ornithologists when ringing, and later I controlled these estimates by comparing photos of the juveniles with own photos of chicks with known age and photos from literature (Stefansson 1997). I also included the perching substrate and the perching height of the fledglings for each observation. Because it was not always possible to measure the accurate perching height, the observations were put into the categories nest, ground, near ground (<2 m), low (2-5 m), medium (5-10 m), high (10-15 m) and very high (>15 m) perching posts.

Great grey owls can be active at all times of the day and night (Duncan & Hayward 1994), so I varied which hours during a day and night I did the observations. The goal was to cover all 24 hours for each of the pairs studied. Because of logistical challenges, this goal was reached for only three of the pairs, but in total, all of the daily hours were covered at least four times, some hours up to 16 times in total. As far as possible, I tried to visit each brood at least every fourth day, but the observation frequency varied between the broods. At one of the locations, the tagged female was found dead halfway through the study (the cause of death was emaciation according to the necropsy report from the Norwegian Veterinary Institute), and therefore the observation was terminated earlier for this brood. Another brood was difficult to study at the early fledgling state, because the only fledgling usually perched in very dense vegetation and I was thus unable to perform the observations. In the analysis of the female's behaviour around the brood, observations from six other broods in addition to the six broods with marked birds are included. However, these additional broods have fewer observations.

Statistical analyses

All statistical analyses and plots were performed with the software R version 3.1.2 (R Core Team 2014). In the data analysis, my observations are split into three main parts that are analysed separately. These parts are 1) prey delivery from males and females, 2) female behaviour around the offspring and 3) fledgling movement, behaviour and mortality.

Prey delivery

Analyses of the prey delivery were performed by using generalized linear mixed-effects models (GLMMs) with binomial distribution in the lme4 package in R. When the response

variable was whether the female or male delivered the prey, the explanatory variables considered were brood size, fledgling age (days), perching height of fledglings, time of day, hours from solar midnight and number of days after 1 June, hereafter called day number. The number of hours away from solar midnight was calculated as a number between 0 and 12 (Steen et al. 2011), and the time of the day was a categorical variable measured as night (darkness), twilight (light, but the sun below the horizon), morning (from sunrise until 09.00), day (from 09.00 until 18.00) or evening (from 18.00 until sunset). Since fledgling perching height was a categorical parameter with several levels, I also ranked it with continuous values and tested the models with both continuous and categorical values. In addition, the same models were tested with temperature included as an explanatory variable. The models with and without temperature had different sample size, and were therefore considered separately. Then, I used the dataset considering only prey items delivered by the male, and analysed what happened after the male brought a prey to the fledgling area. First, I tested whether the male ate the prey himself or delivered it, with the prey eaten by the male rather than by the female or by a fledgling as response variable. Fledgling age in days and stress (0, 1 or 2) were the only fixed variables considered. Second, I removed the cases where the male ate the prey himself from the dataset, and then tested whether the male delivered the prey directly to a fledgling or to the female. The response variable was whether the female or a fledgling received the prey from the male, and the explanatory variables were fledgling age in days, stress and prey type (water vole or other prey). Analyses of what happened with a prey after being delivered from the male to the female were not possible due to low sample size.

All competing models were ranked after the Akaike information criterion corrected for small samples (AICc). To find the best fitted model, the comparable models were ranked according to the parsimony criteria, which in statistics is a trade-off between bias and variance (Johnson & Omland 2004). Here, all models within two AICc-values away from the model with the lowest AICc-value are ranked after simplicity. This kind of model selection is sufficient when the goal is qualitative understanding rather than quantitative prediction (Bolker et al. 2009).

Nest ID was included in all the models as a random variable to control for nest-specific variations. The normal distribution of the random effect was tested by using the SjPlot (R-version 3.1.3) package in R. Plots of the predicted values based on the GLMMs corrected for nest ID were also created using the SjPlot package.

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The probability of the female being present near her offspring when I first approached either the female or the fledglings was analysed using a GLMM in the lme4-package with binomial distribution. I considered the explanatory variables fledgling age, day number, brood size and fledgling perching height, and made models with all combinations, ranked after AICc-values and parsimony.

The aggressiveness of the female had scores between 0 and 5, and I made linear mixed-effect models in the nlme-package to analyse what decided the aggressiveness. I considered the explanatory variables fledgling age, brood size, day number, fledgling perching height, observer behaviour, and number of observers in the analysis. The categorical parameters fledgling perching height and observer behaviour were also ranked with continuous values and the models were tested with both continuous and categorical values. The models were tested for normal distribution of the residuals by using the qqnorm-function that creates scatterplots that should be fitted against a straight line, and the mean standardized residual should be zero. This function also tested the normal distribution of the random effect.

The probability of the female performing distraction display was tested by using a GLMM with binomial distribution in the lme4-package. Because I regarded this as an alternative strategy to aggressive behaviour, aggressiveness was one of the predictor variables in the analysis. Other predictor variables were fledgling age, brood size, observer behaviour and fledgling perching height. The plot showing the probability of the female distracting display was constructed with the SjPlot-package in R. Nest ID was included as a random effect in all the analyses of female behaviour.

Fledgling movement, behaviour and mortality

Based on the sampled UTM coordinates of the fledgling locations, I calculated the distance from each fledgling location to the respective nest, the distance from a fledgling plot to the last sampled fledgling plot of that brood, and the mean distance between the siblings in a brood. The mean distance the brood had moved per day was calculated by dividing the distance between two consecutive plots on the number of days elapsed between the observations. Fledgling mortality rate was calculated in three different fledgling stages, based on the fledgling phase division for tawny owl fledglings in Overskaug et al. (1999). Phase 1 was the first 10 days from fledging until the fledglings reached safe positions above the ground, phase 2 was the period when they improved their flying skills, up to 30 days after fledging. Phase 3 was the remaining part of the dependence period when the fledglings could

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fly and escape predators, but since the study was terminated in the middle of this period, mortality rates are calculated for phase 1 separately and for phase 2 and the early phase 3 together.

The relationship between the fledgling's distance from the nest and fledgling age was analysed using a linear mixed-effect model with the nlme-package in R. The log-transformed values of the distance from the nest was the response variable and fledgling age was the explanatory variable. The log-values were chosen because they gave a better linear relationship for the data and excluded negative prediction values. The data on mean movement per day was analysed in the same way with log-transformed values. The relationship between the distance between siblings in a brood and fledgling age was also analysed with a linear mixed-effect model. Another LMM tested the perching height as a numeric value against fledgling age. Nest ID was included as a random variable in all the analyses to control for nest-specific variation. The normal distribution of random effects and of the residuals were tested with the qqnorm-function.

Figures were made in R, and all the scatterplots show the distribution of the raw data. The regression lines and their confidence intervals in the figures showing the log-transformed data and the figures showing the distance between siblings and fledgling perching height are based on the estimates from the linear mixed-effect models, so the contribution of random effects are taken into account. The non-linear prediction lines and the confidence intervals for these predictions are constructed with the splines-package in R. These predictions are based on simple linear regressions in the splines-package, where the fledgling age parameter is split into two categories, and nest ID is not corrected for.

Ethical note

The great grey owl is a species that is particularly tolerant towards human beings and robust to handling and ringing (Berg 2016). However, human disturbance of nests known to the public has been a problem in Elverum (Berg 2016), so I followed the agreed procedure among local ornithologists of keeping all nest locations secret. In addition, radio tagging was done at the same time as ringing, to avoid catching and handling a bird more than once. During the observations, I tried to minimize the disturbance by observing silently from a distance tolerated by the owls.

Results

Prey delivery rates

During the observation period, I recorded 109 prey deliveries and delivery attempts. Of the associated items, 74 had been captured by the male and 35 by the female (figure 2a). Most of the prey items carried to the fledgling locations were eaten by the fledglings, but both the male and the female ate a few items each. As expected, a female never delivered a prey item to the male, but the male delivered prey items to the female on some occasions (figure 2b). I observed eight prey deliveries from a male to a female, of which the female ate three prey items herself (figure 2c), and delivered four items further to the fledglings, while it is unknown what happened to the last item. However, in some of these events, it looked more like the female stole the prey from the male's beak rather than the male delivered the prey to the female voluntarily. All the observations of a prey delivery from the male to the female happened in the same breeding pair, which also had the nest with the most human disturbance.
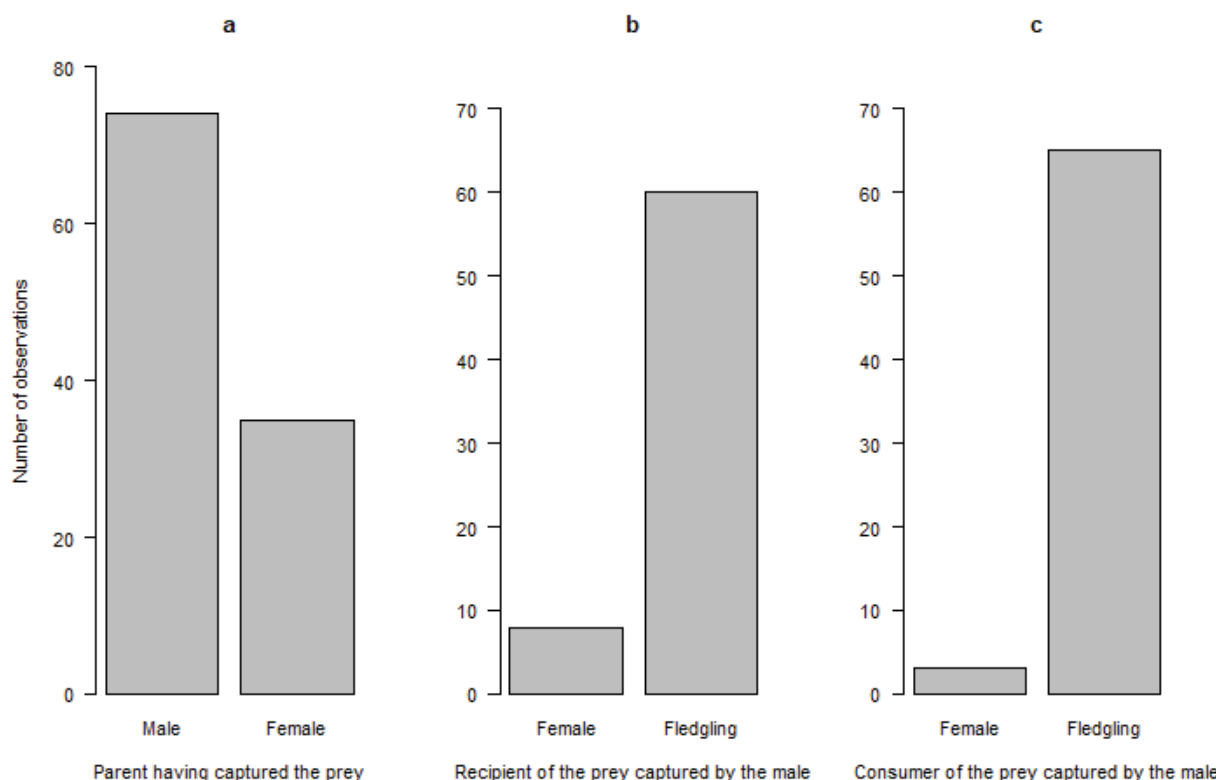
Figure 1: The distribution of the prey deliveries: a) number of prey delivered by males and females, b) prey received by the female or a fledgling after having been captured by the male, and c) prey consumed by the female or a fledgling after having been captured by the male and carried to the Fledgling perching height.

The female was often hunting for prey near the fledgling locations. I observed her capturing 14 prey items for the young near the fledglings, in addition to foraging for herself in the fledgling area. In comparison, I observed the male hunting near the fledglings only twice.

Table 2: The most parsimonious models for the probability of the female rather than the male having captured the prey with a) temperature excluded (n=109) and b) temperature included (n=72). Nest ID is included as a random factor in all the analyses. The most parsimonious models are the models within ΔAICc< 2 with the fewest degrees of freedom (df), and all competing models are listed in appendix 1.

Model	df	AICc	ΔAICc
a)			
Brood size	3	133.41	0.13
Brood size + Day number	4	133.84	0.56
Brood size + Fledgling age	4	133.94	0.70
Brood size + Hours from solar midnight	4	134.83	1.55
Brood size + Time of day	6	133.41	0.00
b)			
Temperature	3	81.07	0.00
Temperature + Hours from solar midnight	4	82.31	1.23
Temperature + Fledgling age	4	82.91	1.84
Temperature + Brood size	4	82.96	1.89

The most parsimonious model explaining the probability of the female rather than the male having captured a prey when temperature was excluded from the analysis had brood size as the only predictor variable (table 2a). The second and third best models included day number and fledgling age, respectively, in addition to brood size (table 2a). The additional models with temperature included, but lower sample size, had temperature as the only predictor variable as the most parsimonious model, followed by the model including temperature and brood size (table 2b).
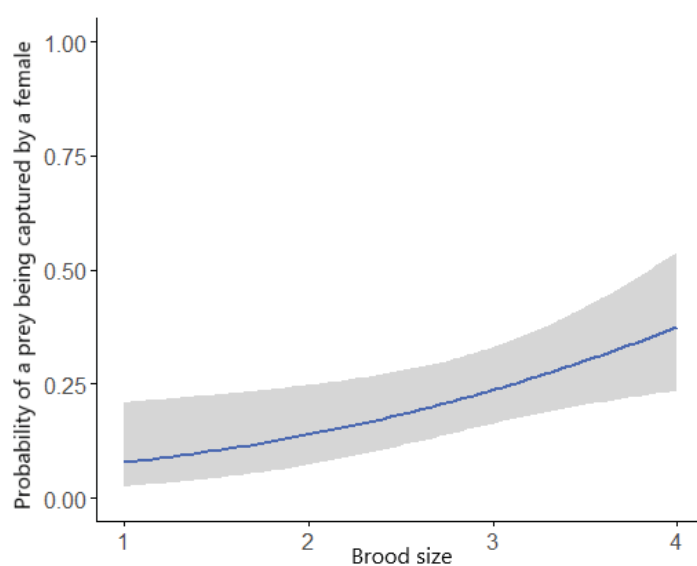

Figure 2: The predicted probability of a delivered prey had been captured by the female rather than by the male as a function of brood size. Nest ID is included as a random effect in the analysis.

The model parameter brood size had a marginally non-significant effect (p=0.089), and the probability of a female delivering a prey tended to increase when brood size increased in the three best-fitted models when the models were corrected for random effects of nest ID and temperature was excluded (figure 2). Brood size may also be regarded as the best predictor variable, as it was included in the best 16 competing models, with

significant effect in some of them. Fledgling perching height was also a variable included in several of the best models, and the categorical parameters low and very high fledgling perching height showed a significant positive estimate in several models. The best models included the categorical rather than continuous values of perching height. Day number and fledgling age are correlated variables with positive estimates, but showed non-significant effects in most models. Time of day and hours from solar midnight had no effect.
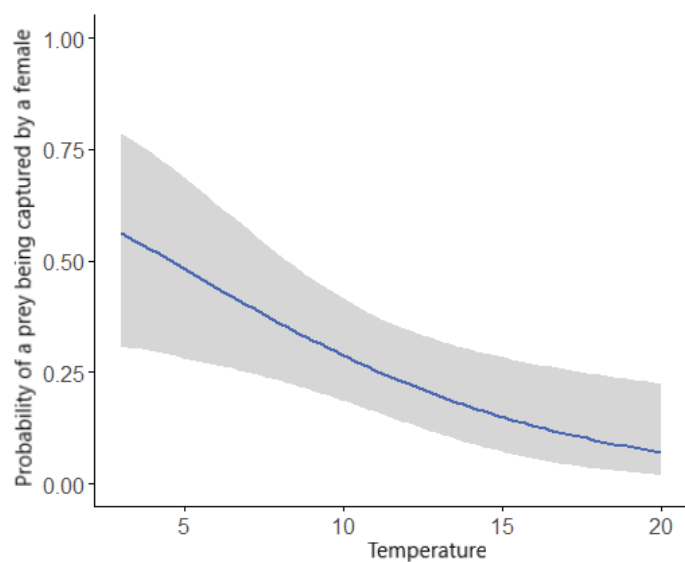

Figure 3: The predicted probability of a delivered prey having been captured by the female rather than by the male as a function of ambient temperature. Nest ID is included as a random effect in the analysis.

The probability of a female delivering a prey decreased significantly (p=0.012) with increasing ambient temperature (figure 3). When temperature was included in the analysis, no other variable showed any trend or significant effect. Temperature was correlated with the time of the day, and probably also to seasonal temperature differences during the summer. Thus, the results may be affected by the date I measured the temperature.

Table 3: The most parsimonious models explaining what happened after a male arrived with a prey, with a) the probability of the male eating the prey rather than delivering it to the female or fledglings as response (n=72), and b) the probability of the male delivering a prey to the female rather than to a fledgling as response (n=68). Nest ID is included as a random factor in all the analyses. All competing models are listed in Appendix 2.

Model	df	AICc	ΔAICc
a)			
Fledgling age + Stress	4	16.37	0.00
Stress	3	18.72	2.35
Fledgling age	3	28.17	11.80
b)			
Stress + Prey	4	28.33	1.08
Stress + Prey + Fledgling age	5	27.25	0.00
Stress + Fledgling age	4	29.87	2.61

The male in the pairs was observed to arrive with prey on 74 occasions, of which two were excluded from the analysis because it was unknown what happened to the prey, and 60

(83.3%) were delivered directly to the fledglings. The male ate four of the prey items himself. Because the male did not eat these prey items immediately after he had captured them, but carried them to the chicks, I assume that they were intended for the offspring. Among the models of the probability of a male eating the prey himself rather than delivering it to the female or the chicks, the one with the lowest AICc value included fledgling age and stress (table 3), but none of the parameters showed a significant effect (table 4a). However, the male ate the prey himself only under stressful circumstances, and this happened only early in the fieldwork period. It is likely that the sample size was too low to get a significant effect.

Similarly, in the models showing the probability of a male delivering a prey to the female instead of directly to the fledglings, increased stress level significantly increased the probability of a delivery to the female (table 4b). The prey type was also included in the most parsimonious model, but the effect of delivering a water vole compared to another small mammal was not significant. This might be a result of low sample size, as I only observed a water vole delivery twice, and the male delivered it to the female in both cases.

Table 4: The estimates for the most parsimonious models where the responses are a) the probability of the male eating the prey himself rather than delivering it to the female or a fledgling, and b) the probability that the female rather than a fledgling receiving a prey captured by the male.

Model Explanatory variables	Estimate	Standard error (SE)	z-value	p-value
a)				
Intercept	-19.43	14113.60	-0.001	1.00
Fledgling age	-0.60	0.44	-1.36	0.17
Stress	21.50	7056.82	0.003	1.00
b)				
Intercept	-6.44	2.35	-2.74	0.0061
Stress	2.32	0.86	2.71	0.0068
Prey: water vole	34.61	8.23e+06	0.00	1.00

Female behaviour and aggressiveness

When I first approached the fledglings, the female was present near her offspring in 71.4% of the cases, and when I tracked and found the female away from the fledglings, she was either hunting or resting. According to the most parsimonious model (table 5a), the probability of the female being absent increased significantly with both fledgling age (p=0.008) and brood size (p=0.028), as well as with day number, but the latter variable was strongly correlated to fledgling age. Fledgling perching height had no effect.

Table 5: The most parsimonious models explaining the female behaviour near the offspring: a) the probability of the female being present when I first approached the fledglings (n=80), b) the estimation of female aggressiveness level when observers entered the fledgling area (n=75), and c) the probability of the female performing distraction display (n=84). Nest ID is included as a random factor in all the models. All competing models are listed in Appendix 3.

Model	df	AICc	ΔAICc
a)			
Brood size + Fledgling age	4	86.43	1.03
Brood size + Day number	4	86.45	1.05
Brood size + Fledgling age + Fledgling perching height + Day number	11	85.40	0.00
b)			
Fledgling age + Observer behaviour	7	198.09	0.00
Observer behaviour + Fledgling perching height (continuous)	7	198.66	0.57
c)			
Brood size	3	107.92	0.00
Number of observers	3	108.85	0.93

Aggressive behaviour from the female included clicking with the beak, barking, chasing and attacking. During the whole observation period, little or moderate aggressiveness was observed more frequently than highly aggressive behaviour (figure 9). The most parsimonious model predicting the aggressiveness level (see description in table 1) included fledgling age and observer distance (table 5b). The predicted aggressiveness declined with fledgling age (figure 10, p<0.001), and the females were clearly most aggressive when observers were catching and
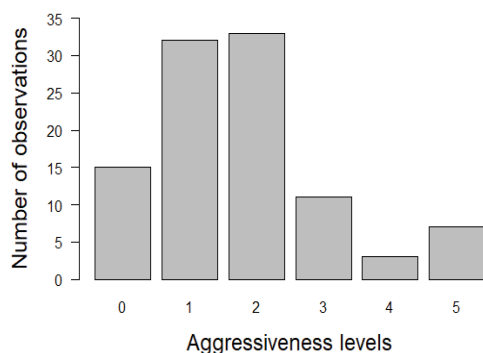

Figure 9: The distribution of observations on the different aggressiveness levels. See table 1 for explanation of aggressiveness levels.
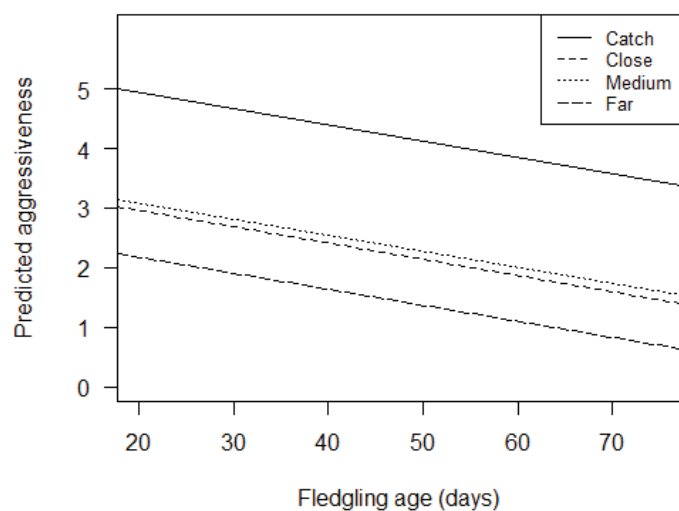
Figure 10: The predicted aggressiveness as a function of fledging age and observer behaviour towards the fledglings (n=75). "Catch" means catching and handling the fledglings, "close" is observation from <10 m distance, "medium" is observation from 10-50 m distance and "far" means observation from >50 m distance. From the top, the lines in the figure show the predicted aggressiveness for behaviour "catch", "medium", "close" and "far".

handling the chicks (p<0.001). Still, some females were hitting and attacking the observers also when they stayed close or medium close to the fledglings, mainly in the early fledging stages. The predicted aggressiveness was slightly higher at medium observer distance than at close distance (figure 10). Note that the distance categories measured the distance to the tree or substrate where the chick was perching, and perching height was not included.

In some of the competing models, fledgling perching height and number of observers also had significant effects on aggressiveness. Higher perching height reduced the aggressiveness and more observers increased it. However, there were strong correlations between fledgling perching height and fledgling age, and between number of observers and observer behaviour, and these additional variables had no significant effects in models where the correlated variable also was included. Brood size had no significant effect on aggressiveness in the best models.

The female also had another approach to lead the attention away from the fledglings; distraction display. She then usually located herself in the opposite direction of the observer than the fledglings were, made a lot of noise, and sometimes acted as if her wing was broken. The female performed distraction display on 37.2% of the occasions she was observed near her offspring, and the most parsimonious model explaining the probability of female distraction display had brood size as the only predictor variable (table 5c). The probability of the female performing distraction display decreased marginally non-significant with increased brood size (figure 11, p=0.058). None of the models showed significant effects of fledgling age, observer behaviour or fledgling perching height, but some of the models showed a trend that aggressive behaviour made it less likely that the females distracted display.
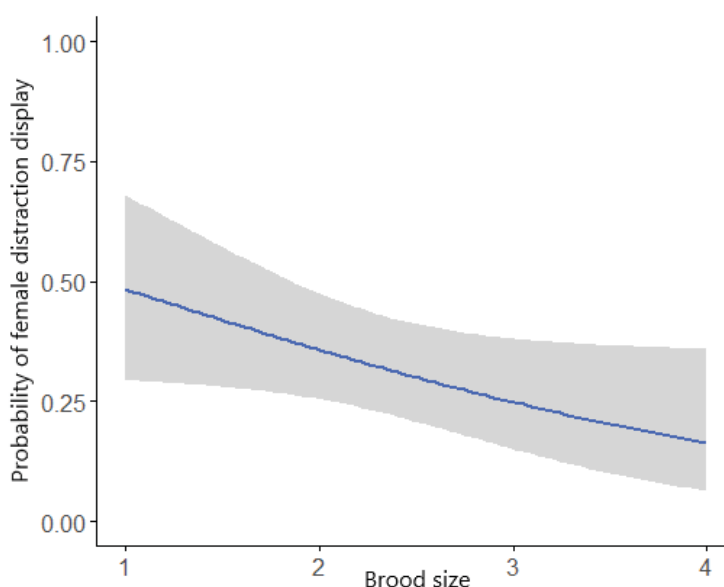

Figure 11: The predicted probability of a female performing distraction display as a function of brood size (n=84). Nest ID is included as a random factor in the analysis.

Aggressive behaviour towards other species was also observed on some occasions. A female owl was barking when a roe deer (*Capreolus capreolus*) was passing, and once I

observed a male and a female cooperating in chasing away a raptor from the area where the fledgling was located. Then, the female was both clicking with the beak, chasing and making some of the same noises as when she performed distraction display. On the other hand, some other bird species were mobbing and making alarm calls when great grey owls were present, especially the Eurasian jay (*Garrulus glandarius*) was mobbing aggressively and the great-spotted woodpecker (*Dendrocopos major*) made loud alarm calls.

Fledgling movement and behaviour

Most of the chicks left the nest when they were between 30 and 36 days old, the youngest chick observed on the ground was 30 days old and the oldest chick observed in a nest belonged to a 38 days old brood. The chicks left the nest before they were able to fly and stayed near the nest the first time after fledging, but started jumping and climbing immediately. The predicted relationship between a fledgling's distance from the nest and its age had an exponential slope, but also older fledglings could be located close to the nest (figure 4a). There was a significant increase in predicted distance from nest with increasing fledgling age, with a slope on 0.035 ± 0.0030 times the fledgling age on the log-transformed scale ($p<0.001$) when corrected for nest ID (figure 4b).
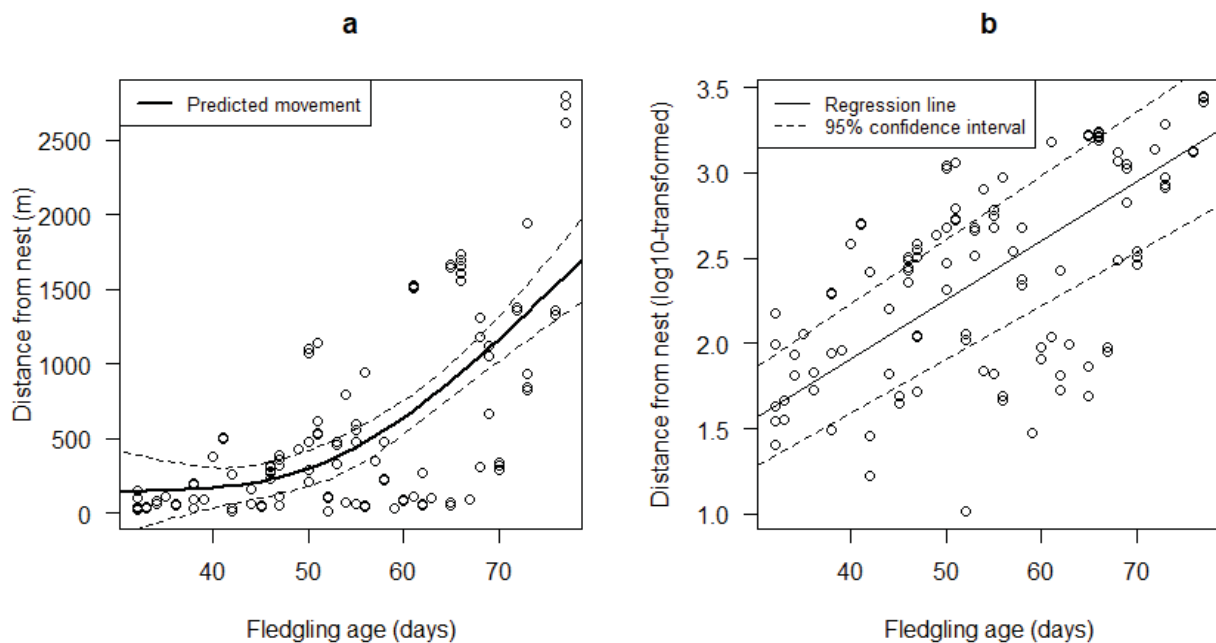

Figure 4: a) Relationship between the fledglings' distance from the nest and fledgling age, with prediction line and confidence interval for the prediction. b) The same relationship, but with data on a log-transformed scale and a linear regression line. Nest ID is included as a random factor in the regression analysis.

The five great grey owl broods that I followed moved in different speeds and directions (figure 5). The fledglings in nest 1 stayed less than 300 m from the nest until they reached almost 70 days, and then they dispersed abruptly, while the fledglings in nests 3 and 4 moved a lot between each observation and left the natal area earlier. The distance between nest 1 and nest 2 was only 230 m, and neither of the fledglings moved in the direction of the neighbouring nest. There were few observations on fledgling location for nest 5 early in the study, so the true movement pattern of this brood might differ from the figure. The fledglings did not always move in the same direction (figure 5), and one brood could be located in all directions from the nest. The maximum distance away from the nest that I observed a fledgling younger than 80 days was 2792 m.
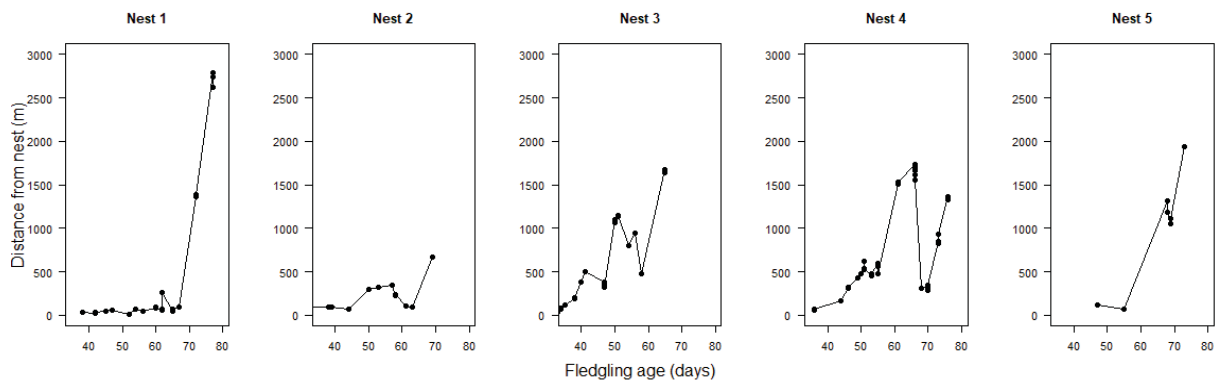
Figure 5: Distance from nest at each day with observation for each of the five broods with most observations of Fledgling perching height.

The estimated distance the fledglings had moved per day ranged from 1.8 m to 669.3 m (mean 118.5 m, median 73.3 m) (figure 6a). There was a significant increase in movement per day with increasing age, and the slope was 0.034±0.0049 times the fledgling age on the log-scale (p<0.001) when corrected for nest ID (figure 6b). Still, also older fledglings sometimes moved only short distances (figure 6). The exact age at which the fledglings became able to fly is uncertain, but the youngest fledglings I observed flying were 44 days old, and all fledglings could fly at the age of 50 days. After the fledglings became able to fly, they tended to start moving just after a prey delivery, often in the direction to where the delivering parent came from.
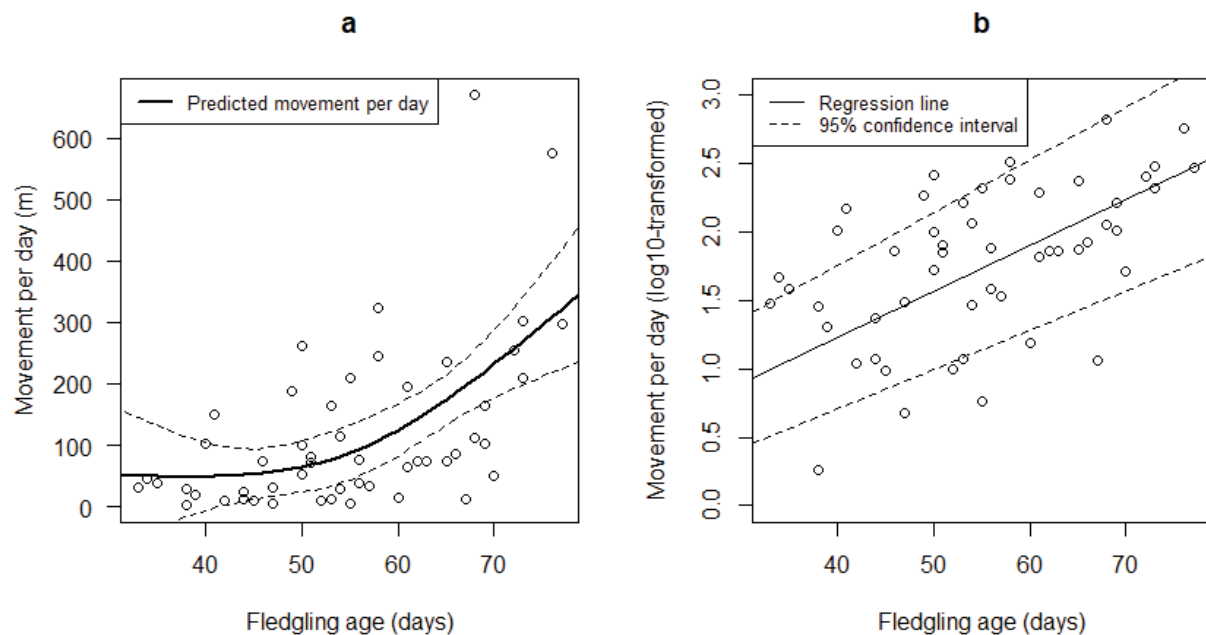
Figure 6: a) Relationship between the fledglings' movement per day and fledgling age, with prediction line and confidence interval for the prediction. b) The same relationship, but with data on a log-transformed scale and a linear regression line. Nest ID is included as a random factor in the regression analysis.

Brood mates were usually located close to each other, and the measured distance between siblings in a brood ranged from 1 m to 112 m (mean 31.0 m, median 21.7 m). The distance between the siblings tended to increase with increasing age, though not significantly (figure 7, p=0.10) with an estimate for the slope of 0.62±0.37. Fledglings able to fly were more often located further from each other (>50 m) than were younger fledglings, but also the older fledglings frequently stayed close to each other (figure 7), and several were often found perching in the same tree or in neighbouring trees, regardless of age.

The fledglings could be located on the ground or close to the ground until the age of almost 50 days, but fledglings that were 40 days or older were usually found perching in trees, and the perching height increased significantly with increasing age (figure 8, p<0.001).

Figure 7: Relationship between the distance between the siblings in a brood and fledgling age. Nest ID is included as a random factor in the regression analysis.

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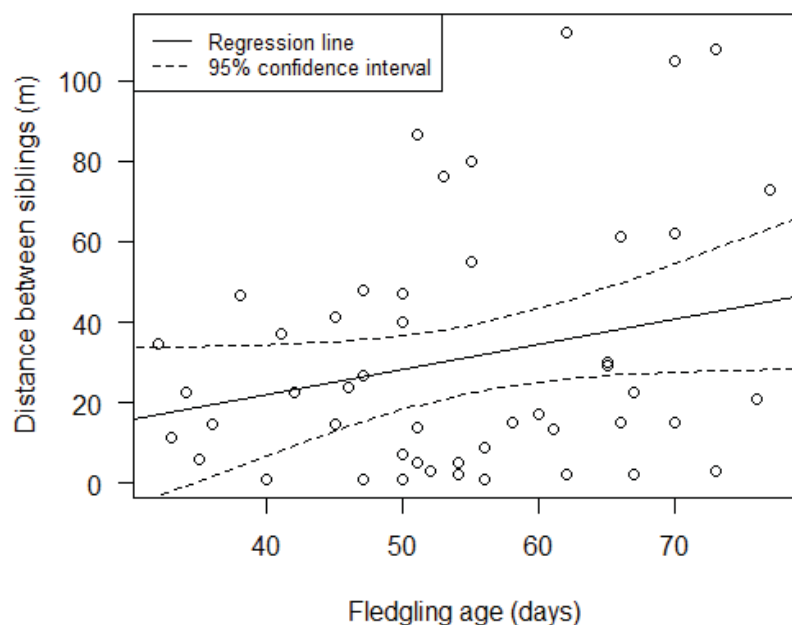However, older fledglings that were able to fly also sometimes perched low, at heights of 2-5 m, but they were never found on the ground (figure 8). Fledglings started to perch in trees before they became able to fly, usually because they were climbing leaning trees or trees with low branches.
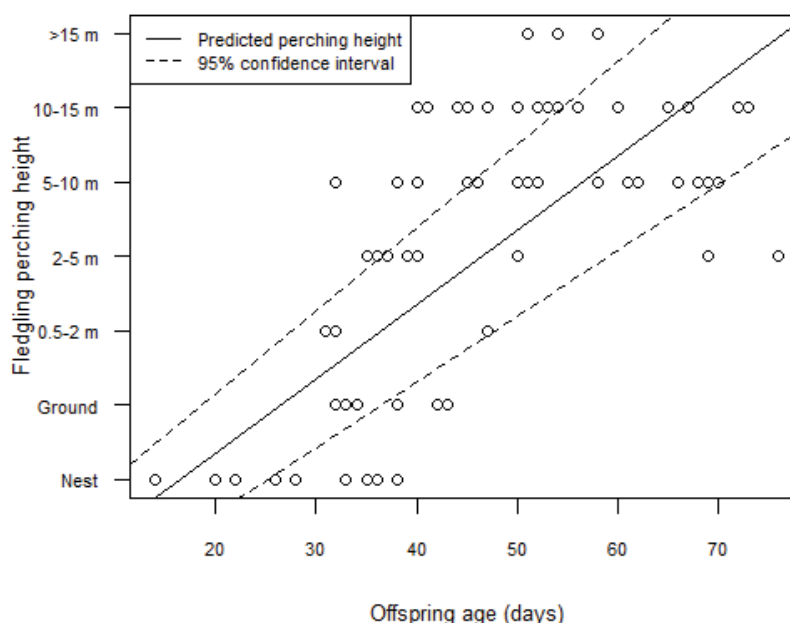
Figure 8: Relationship between fledgling perching height and offspring age. Nest ID is included as a random factor in the regression analysis.

Fledgling mortality

In total, I observed 24 fledged great grey owl offspring from eight different nests, of which 20 survived through phase 1, which was the first ten days after fledging when they were still located near the ground. Thus, there was 16.7% mortality in the first fledgling phase. Three of these broods were not followed long enough to reach the phase where they became good flyers and could escape a predator, one brood because the tagged female was found dead and two because they hatched late and the fieldwork was terminated before they reached this phase. In the remaining five broods, ten out of twelve fledglings survived from phase 1 until the study was terminated in phase 3, giving a mortality of 16.7% from the beginning of phase 2 until the middle of phase 3. It is likely that the true estimate would be slightly higher, since my sample only includes broods where both parents were alive during the whole study period. The total mortality from fledgling until the middle of phase 3 was 37.5% in these five broods. All of these estimates are based on a small sample size.

Discussion

Prey delivery rates

In general, the great grey owl males delivered more than twice as many prey items to the offspring than the females did. The male is the main provider of food in raptors and owls, but the female might assist him in the later part of the rearing period (Sonerud et al. 2014a). In great grey owls this occures from the offspring are 45 – 60 days old (Cramp 1985). In Tengmalm's owl, males delivered more prey items than the female in all offspring stages, and a proportion of females did not assist the male in food provisioning at all, but deserted after the end of the brooding period (Eldegard & Sonerud 2012; Zárybnická & Vojar 2013). On the contrary, there were no difference in provisioning rates between male and female eastern screech owls (*Megascops asio*) in the post-brooding period (Courter et al. 2017). No great grey owl female was observed to desert the male in my study, but the hunting contribution varied among females. How early in the rearing period a female raptorial bird starts to provide food depends on prey type and size (Sonerud et al. 2014b). Screech owls often feed on invertebrates, which makes the female able to contribute earlier than e.g. great grey owls that feed on mammals. The energy requirement of a brood also depends on offspring size, so a brood of great grey owls would need more food than for example a brood of the smaller Tengmalm's owl. This could make female contribution to foraging more necessary in great grey owls than in other species.

The probability of a prey item being captured by a female rather than by a male increased with increasing brood size. Similarly in the Tengmalm's owl, the female showed a stronger increase in number of prey deliveries than the male did with increased brood size (Eldegard & Sonerud 2012). Food supplementation of Tengmalm's owls reduced the food delivery rates of both parents, but females showed a stronger reduction (Eldegard & Sonerud 2010), indicating that females can adjust their foraging effort after the brood's need. Brood size was also the factor with greatest influence on provisioning rate for both parents in great tits (*Parus major*), where the male in general had highest food delivery rate (Hinde & Kilner 2007). Whether the female should assist the male in food provisioning or not in raptorial birds would depend on the hunting success of the male, the energy requirement of the brood and environmental stochasticity (Brodin et al. 2003). This might explain the difference in foraging activity between individual great grey owl females. Increased brood size increases the energy

requirement of the brood, so it is likely that the female great grey owl adjusts her hunting effort with brood size to maximize offspring survival.

Despite the common view of males providing food early in the rearing period and females assisting him later, I found no significant trend showing that the probability of a female delivering a prey increased with increased fledgling age, considering the period after fledging. A possible explanation for this is that the trend would be visible if the nestling stage was included in the analysis, because females may assist in foraging as soon as the offspring can keep warm themselves and ingest their food unassisted. At what time the female started to hunt also varied among the broods, so brood size and individual variations are probably important explanations. Increased ambient temperature decreased the chance of a prey delivery from the female. I suggest that the females prefer to hunt in the early morning hours when the temperatures are low, while the males spread their deliveries more evenly. A possible explanation for this is that the male needs to spend most of his time hunting to satisfy the brood's energy requirement, while the female only assists the male when necessary. Therefore, she is free to forage mainly when she finds it most comfortable.

The female did more often than the male hunt for prey near the location where the fledglings were perching. The same pattern was found in a study of tawny owls, the females foraged close to the fledglings while males could travel far to hunt (Sunde et al. 2003). This might suggest a general higher foraging effort for the smaller and more agile male (Courter et al. 2017), so considering the number of prey deliveries from each parent alone might over-estimate the female's energetic contribution in foraging for the offspring. On the other hand, having females foraging close to the fledglings could be an offspring defence strategy that minimizes the costs in the female's trade-off between foraging and guarding.

I observed a male arriving with a water vole twice, and both times, he delivered it to the female rather than to the fledglings. Male kestrels (*Falco tinnunculus*) tended to deliver small prey items directly to the offspring, and large prey items to the female so she could assist the feeding, and prey type affected the probability of a prey being delivered directly to the nestlings (Sonerud et al. 2013). In northern pygmy owls (*Glaucidium gnoma*), the male usually delivered all kinds of prey to the female and only rarely to the offspring also after fledging (Frye & Jageman 2012). The great grey owl fledglings were old enough to ingest their main prey, small mammals, unassisted after fledging, but they probably needed help with consuming the large water vole. It is likely that the size of the prey compared to the size of the offspring affects the ability to ingest prey unassisted, and the large great grey owl

ingests relatively small prey compared to the little northern pygmy owl. More observations on water vole deliveries to great grey owl fledglings is needed to examine the significance of this.

When a male arrived with a prey, but consumed it himself near the fledglings, it was only under stressful circumstances. Increased stress level increased the probability of the male delivering the prey to the female rather than to the young. In some of the prey deliveries from the male to the female, it looked more as if the female stole the prey from the male's beak rather than the male delivered it to her voluntarily. In kestrels, females are larger and dominant over the male, and controlled the transfer of prey from male to female, and often grabbed prey from the male and chased him away (Sonerud et al. 2013). In the case of the great grey owl, it looked like the female grabbed this opportunity only when the male lingered to deliver directly to the offspring because of stressful surroundings.

Female behaviour and aggressiveness

The probability of the female being absent from the fledglings increased with increasing fledgling age and increased brood size. This suits the data on prey deliveries as females with large broods foraged more. Tawny owl females have been reported to stay within a few meters from the fledglings the first 30 days after fledging (Sunde & Naundrup 2016), and because the fledglings usually do not need assistance in ingesting prey after fledging, the females are present mainly to guard the offspring. When the fledglings grow older, the need of guarding is reduced, so the female can spend more time self-feeding or hunting for the offspring.

The female great grey owl was clearly more aggressive than the male and only females were observed to attack or hit intruders. This pattern is previously known for the great grey owl (Cramp 1985; Bull & Henjum 1990). Also in the other *Strix* species tawny owl (Wallin 1987) and Ural owl (Kontiainen et al. 2009), females take more risks in the defence of their young and show more aggressive behaviour than males towards intruders. On the other hand, the males were more aggressive than the females towards humans in snowy owls (*Bubo scandiacus*) (Wiklund & Stigh 1983), and male kestrels were more aggressive than females towards a stuffed pine marten (*Martes martes*) put near the nest (Tolonen & Korpimäki 1995). In contrast, the Tengmalm's owl does not seem to guard their offspring at all (Eldegard & Sonerud 2012). In an interspecific comparison of aggressive offspring defence in waders,

parent body mass and number of parents present were the most important factors explaining variation in aggressive nest defence (Larsen et al. 1996). This can relate to behaviour differences explained by size difference among owl species. The large size of the great grey owl and the other European *Strix* species makes them actual threats to predators, in contrast to the smaller Tengmalm's owl, and this makes nest defence more profitable. Furthermore, snowy owls breed and hunt in open tundra (Therrien et al. 2014), and a foraging male can detect intruders from long distance, making both parents available for brood defence. Because great grey owls breed in forested habitats, a foraging male is usually not available for brood defence, which selects for brood defence performed mainly by the female.

The aggressiveness of the female was at highest right after fledging, and declined when the fledglings grew older. Great grey owl females are known to be at their most aggressive at hatching and right after fledging (Cramp 1985), so my observations fits the general pattern. In general, the survival of fledglings of altricial tree-nesting birds is substantially lower during the first post-fledging weeks than in both the nestling period and in later post-fledging stages (Naef-Daenzer & Grüebler 2016). Owl fledglings are at their most vulnerable the first days after fledging, and the early post-fledging dependence period has been recorded as a period with high mortality due to predation in e.g. tawny owls (Sunde 2005), long-eared owls (*Asio otus*) (Tome 2011), little owls (*Athene noctua*) (Perrig et al. 2017) and burrowing owls (*Athene cunicularia*) (Todd et al. 2003). According to the theory of optimal nest defence, the offspring become more valuable for the parents as they grow older, but after fledging, the benefits from a defensive act decreases as the fledglings become better in recognizing and escaping danger (Montgomerie & Weatherhead 1988). Therefore, the net benefit of aggressive nest defence in the great grey owl is at its highest when the juveniles have fledged, but not yet reached high perching heights or become able to fly.

The brood size of the observed great grey owls had no effect on the female aggressiveness in the post-fledging dependence period. The theory of optimal nest defence predicts that the intensity of nest defence should increase with increased brood size (Montgomerie & Weatherhead 1988), and the aggressive brood defence increased with brood size in the female Ural owl (Kontiainen et al. 2009), male and female tawny owl (Wallin 1987), female kestrels (Tolonen & Korpimäki 1995) and male and female great tits (Rytkönen 2002). On the contrary, the aggressiveness of snowy owl parents was not affected by brood size (Wiklund & Stigh 1983). An explanation of this is that long-lived birds with high adult survival that are unable to nest again the same breeding season will put maximum investment

in the breeding independently of brood size (Wiklund & Stigh 1983). Like the snowy owl, great grey owls only breed in high vole years (Hipkiss et al. 2008), and will therefore gain from high parent investment in these years.

Observer behaviour affected the aggressiveness level. Obviously, the parents were most aggressive when the observer posed a direct threat by handling the young and least aggressive when the observer kept long distance, but there was almost no difference between close and medium observer distance. Actually, the model predicted a slightly higher aggressiveness score at medium distance rather than short distance. A possible explanation for this trend is that I did usually not approach fledglings on the ground from less than 10 m distance, but more often stayed close to trees where fledglings were perching to plot the GPS coordinates. Because the female was generally more aggressive right after fledging when the fledglings often were on the ground, this might affect the predicted aggressiveness more than the difference between short and medium observer distance.

Most of the great grey owl females did only attack human intruders climbing nest trees or handling chicks, but some females also attacked observers who were close or medium close to the fledglings in the early post-fledging period. Previously, large individual differences between breeding pairs in aggressiveness towards human intruders in the great grey owl have been observed (Cramp 1985). Some Ural owl mothers were more aggressive across year than others (Kontiainen et al. 2009) and this phenotypic variation suggests that aggressive behaviour could be heritable. It is therefore likely that individual variations in temperament is an important factor explaining aggressive behaviour. Further studies on great grey owl aggressiveness could if possible evaluate the effect of female age and identity.

The female great grey owl was observed to perform distraction displays on 37% of the occasions I approached her near her offspring. Distraction display is an alternative and less risky offspring defence strategy to aggressive behaviour (Montgomerie & Weatherhead 1988), and Holarctic waders are known to meet mammalian predators with distraction displays while they might attack and chase avian predators (Larsen et al. 1996). The profitability of distraction display also depends on the experience of the predator, unexperienced predators would be distracted while experienced predators may ignore the distraction and start searching for the brood, so the proportion of experienced predators in an area decides whether grouse hens should distract display or not (Sonerud 1988). In great grey owls, there are individual differences in distraction display behaviour, and it may mainly be performed by shyer birds (Cramp 1985). In contrast to the waders and grouse facing

mammalian predators, the great grey owl is capable of attacking and harming the predator if the distraction display does not lure it. Therefore, I expect individual differences among the owls to be more important than the experience and behaviour of the predators in the habitat.

The probability of the female performing distraction display decreased with brood size, while fledgling age and observer behaviour had no effect. Because the cost of performing distraction display is relatively low for great grey owls, the net benefit of this behaviour could be high enough to select for the behaviour also when the fledglings are old. The probability of the female performing distraction display may be related to her presence near the young, so females that spend much time foraging are less likely to distract display. This may explain the trend that increased brood size reduced the probability of female distraction display, because the profitability of hunting for the offspring is higher. Females with few fledglings, on the other hand, are less likely to hunt and would spend more time near the young in all fledgling stages.

None of the females in my study deserted the male before the study was terminated, which is in contrast to Tengmalm's owls, where the female deserted the male in 63% of studied broods (Eldegard & Sonerud 2012). The suggested explanation for female desertion is the opportunity to remate, and a study of barn owls (*Tyto alba*) found that females nested twice within the same season more often than males did (Béziers & Roulin 2016). The parental role asymmetry in raptors and owls makes female desertion more likely than male desertion, because the females are not as strictly required as the males for successful rearing in the later rearing stages (Korpimäki et al. 2011; Béziers & Roulin 2016). However, aggressive nest defence would select for monogamy, as two parents are needed for efficient defence (Larsen 1991). Therefore, presence of females could be more beneficial for offspring survival for a longer period in the great grey owl than female presence is for smaller and less aggressive owl species. Despite this, a study of great grey owls in Oregon showed that most females deserted and left the remaining offspring care to their mate 3-6 weeks after fledging (Bull et al. 1989). Still, these females deserted later in the season than Tengmalm's owls and barn owls did, and they did not remate. The advantages of guarding the fledglings during the first weeks after fledging might explain this delay in desertion, and it could partly explain why some females did not desert at all. However, the North American great grey owls had smaller clutch sizes than what is reported in Scandinavia, despite high prey abundance (Bull et al. 1989). Because female desertion in great grey owls is only reported from small broods in North America, it is possible that the main objective for females to stay with old fledglings

is foraging for the brood rather than defending it. To understand the dynamics of female desertion in great grey owls better, it would be necessary to study female parental care in years with higher vole abundance than in my study.

Fledgling movement and behaviour

The fledgling's distance from the nest increased with increased fledgling age, and I observed fledglings younger than 80 days old up to 2.7 km from their nest. To compare, long-eared owls in Slovenia stayed less than 100 m from the nest up to 45 days after fledging (Tome 2011) and little owls in Denmark moved up to 250 m before dispersal (Pedersen et al. 2013). Burrowing owls in North Dakota had a nest-centred dispersal and the observed maximum distance from the nest before dispersal was 300 m (Davies & Restani 2006). Eagle owls (*Bubo bubo*) in Spain dispersed up to 1.5 km from the nest at 85 days of age (Penteriani et al. 2005). Tengmalm's owl fledglings were recorded up to 2 km from the nest in the Czech Republic (Kouba et al. 2013) and 3 km from the nest in Norway (Eldegard et al. 2014) before reaching independence, while northern pygmy owl family groups in the Rocky Mountains dispersed up to 3.3 km (Frye & Jageman 2012). Dispersal distance probably depends on territoriality of the species, food abundance and breeding density. These results show that great grey owl fledglings in southeast Norway are capable of dispersing several km before they reach independence, which is relatively far compared to other owls.

Different great grey owl broods dispersed in different speeds, and the different broods did not always move in the same direction. Older fledglings sometimes returned to the area near the nest. Great grey owl fledglings are known to move towards the hunting area of the male, and switch direction if the male changes hunting area (Cramp 1985). Juvenile eagle owls also move unoriented, and one study showed that the nest represented a focal point in the post-fledging dependence period (Delgado et al. 2009). A possible explanation for fledgling movement is that the fledglings will maximize the chance of being fed by minimizing the distance to the parents and begging siblings (Sunde & Naundrup 2016). This explanation suits my data on great grey owl movement as the offspring often moved in the same direction as the parent delivering food after a prey delivery. Great grey owls are less territorial than e.g. tawny owls and Ural owls (Bull & Henjum 1990) and can therefore easily move without crossing the borders to other territories. This makes it possible for great grey owl fledglings to disperse several km before independence, while fledglings in territorial species need to stay

within the territory of their parents. However, the fledglings from nests with short distance to their neighbouring nests did not move towards their neighbours. The fledglings from the two nests located 230 m from each other moved in general less than the fledglings from the other broods during the first time after fledging, indicating that juveniles keep some distance to other broods or nests. However, two great grey owl broods from adjacent nests were observed to perch together in a mix after fledging (Trond Berg, pers. comm.)

The daily movement of the brood increased with increased fledgling age, and the increase was more rapid after the fledglings became able to fly short distances at the age of about 45 days. This is similar to the movement of eagle owl fledglings, which moved only short distances during the first 20 days after fledging, but then they increased their step length and maximized it close to dispersal (Delgado et al. 2009). Movement in the post-fledging dependent period is important for experience and learning (Delgado et al. 2009), and it is also selected for if predators are likely to return to locations where they previously have captured prey (Sonerud 1985). Overskaug et al. (1999) suggested that high predation pressure might induce movement of tawny owl broods in central Norway, and this might also be the case for great grey owls.

Siblings in a brood stayed close to each other during the whole observation period, but older fledglings were more frequently observed further from each other than young fledglings were. Eagle owl fledglings increased the distance to their siblings with increasing age, and fledglings younger than 100 days old could stay up to 698 m from each other (Penteriani et al. 2005). Tawny owl fledglings, on the other hand, had short inter-sibling distance during the whole post-fledging dependence period (Sunde & Naundrup 2016). Similarly, northern pygmy owl fledglings stayed less than 100 m from each other until independence, usually with a distance of 0 – 30 m (Frye & Jageman 2012). Short distance between the siblings could be an anti-predator strategy because the female can guard aggregated offspring better, and short distance to begging siblings could also increase the chance of receiving food from the parents (Sunde & Naundrup 2016).

Unsurprisingly, the perching height of the fledglings increased with increasing fledgling age. Older great grey owl juveniles in North America also perched higher than young juveniles did, and dependent fledglings able to fly perched higher than adults did (Whitfield & Gaffney 1997). Near-independent fledglings started perching at heights similar to adult perching heights (Whitfield & Gaffney 1997), and in my observations, some juveniles started to perch lower when they became older. Very high perching heights is probably an

anti-predator strategy, but as the fledglings become older and advance their flying skills, lower perching heights are advantageous to practice hunting.

Fledgling mortality

The calculated mortality from fledging until the middle of phase 3 where the fledglings could fly and escape predators was 38% based on my limited sample. High mortality rates for juvenile great grey owls were also recorded in North America (Bull et al. 1989; Whitfield & Gaffney 1997). I found that the highest mortality rate per day occurred the first time after fledging, when the fledglings were at their most vulnerable. The same pattern was found for tawny owls (Coles & Petty 1997; Overskaug et al. 1999; Sunde 2005), burrowing owls (Todd et al. 2003; Davies & Restani 2006) and long-eared owls (Tome 2011). The mortality rate of great grey owls in my study was similar to the mortality rate of 36% in tawny owl offspring from fledging until independence (Coles & Petty 1997; Sunde 2005), but because of low sample size, my calculated mortality rate is uncertain and further studies on fledgling survival is necessary to find a better estimation. Fledgling age is in general the most important predictor for juvenile survival in birds, and fast growing individuals have higher survival probability than slow-growing individuals (Maness & Anderson 2013). Supplemental feeding of little owl nestlings increased their post-fledging survival rate, indicating that physical condition may increase the fledgling's ability of escaping predators (Perrig et al. 2017).

Conclusion

The female great grey owl contributed to post-fledging parental care by food provisioning and offspring guarding, and she seemed to balance her effort after what would be the most profitable for offspring survival. Because the male usually delivered prey items directly to the fledglings and the female rarely had to assist in prey handling, I suggest that the main objectives for the female to stay with the brood were offspring guarding and assisting in prey provisioning. Aggressive brood defence was an efficient anti-predator strategy in this large owl, and was most profitable early after fledging when the fledglings were most vulnerable, which also was a period with relatively high offspring mortality. The fledglings maximized their benefit of the brood defence by staying close to their siblings, increasing their perching heights and moving towards the hunting area of the parents. Females with large broods started hunting earlier and provided more food for the offspring than females with small broods did, which suggests that the profitability of hunting was higher than the profitability of guarding in large broods. Increased brood size had no effect on aggressiveness, but reduced the probability of female distraction display, which also supports the theory of a trade-off between foraging and guarding, where guarding is favoured when the male can satisfy the brood's food requirement alone. Further studies on this relationship in years of different prey abundance would be needed to test the hypothesis that the female balances her effort based on the brood's need. The movement of the broods was relatively high compared to owl fledglings of other species, which can be regarded as strategies for avoiding predators, maximizing the chance of being fed and improving flying and hunting skills.

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Appendix 1

<u>Female capturing prey: temperature excluded</u>

A list of all competing models (GLMM with binomial distribution) explaining the probability of a female rather than a male having captured a prey, with temperature excluded. Nest ID is included as a random variable in all the models. The continuous version of fledgling perching height gave higher AICc values, and these models are excluded from the table. n=109

Model	df	AICc	ΔAICc
Brood size + Time of day	6	133.27	0.00
Brood size	3	133.41	0.13
Brood size + Day number	4	133.84	0.56
Brood size + Fledgling perching height	9	133.86	0.59
Brood size + Fledgling age	4	133.94	0.70
Brood size + Hours from solar midnight	4	134.83	1.55
Brood size + Hours from solar midnight + Fledgling perching height	10	135.15	1.88
Brood size + Fledgling perching height + Day number	10	135.34	2.07
Brood size + Fledgling age + Time of day	7	135.38	2.11
Brood size + Fledgling perching height + Time of day	12	135.47	2.20
Fledgling age	3	135.55	2.28
Brood size + Fledgling age + Hours from solar midnight	5	135.70	2.43
Brood size + Fledgling perching height + Fledgling age	10	133.71	2.44
Fledgling age + Time of day	6	135.94	2.67
Brood size + Fledgling perching height + Fledgling age + Day number	11	135.95	2.67
Brood size + Fledgling perching height + Fledgling age + Hours from solar midnight	11	137.36	4.09
Fledgling age + Hours from solar midnight	4	137.46	4.19
Brood size + Fledgling perching height + Day number + Time of day	13	137.77	4.49
Brood size + Fledgling perching height + Fledgling age + Time of day	13	137.92	4.65
Brood size + Fledgling perching height + Fledgling age + Day number + Time of day	14	138.89	5.62
Fledgling age + Fledgling perching height	9	139.85	6.58
Brood size + Fledgling perching height + Day number + Time of day + Hours from solar midnight	14	140.28	7.01
Fledgling age + Time of day	12	140.94	7.66
Brood size + Fledgling perching height + Fledgling age + Day number + Hours from solar midnight + Time of day	15	141.42	8.14
Fledgling age + Hours from solar midnight + Fledgling perching height	10	141.67	8.39
Fledgling age + Fledgling perching height + Day number	10	142.26	8.99
Fledgling age + Fledgling perching height + Day number + Time of day	13	143.51	10.24
Fledgling age + Fledgling perching height + Day number + Time of day + Hours from solar midnight	14	145.83	12.56

Female capturing prey: temperature included

A list of all competing models (GLMM with binomial distribution) explaining the probability of a female rather than a male having captured a prey, with temperature included. Nest ID is included as a random variable in all the models. The continuous version of fledgling perching height gave higher AICc values, and these models are excluded from the table. n=72

Model	df	AICc	ΔAICc
Temperature	3	81.07	0.00
Temperature + Time of day	6	81.98	0.91
Temperature + Hours from solar midnight	4	82.31	1.23
Temperature + Fledgling age	4	82.91	1.84
Temperature + Brood size	4	82.96	1.89
Temperature + Day number	4	82.99	1.92
Temperature + Brood size + Time of day	7	83.80	2.73
Temperature + Brood size + Hours from solar midnight	5	84.13	3.05
Temperature + Fledgling age + Time of day	7	84.29	3.22
Temperature + Time of day + Day number	7	84.36	3.28
Temperature + Time of day + Hours from solar midnight	7	84.42	3.35
Temperature + Fledgling age + Hours from solar midnight	5	84.54	3.46
Temperature + Day number + Hours from solar midnight	5	84.58	3.51
Temperature + Brood size + Day number	5	84.86	3.79
Temperature + Fledgling age + Fledgling perching height	5	84.87	3.80
Temperature + Brood size + Fledgling age	5	84.87	3.80
Temperature + Fledgling age + Day number	5	85.19	4.12
Temperature + Brood size + Day number + Time of day	8	86.26	5.18
Temperature + Brood size + Hours from solar midnight + Fledgling age	6	86.43	5.36
Temperature + Brood size + Fledgling perching height	10	89.70	8.63
Temperature + Hours from solar midnight + Fledgling perching height	10	90.99	9.92
Temperature + Brood size + Fledgling perching height + Day number	11	91.81	10.73
Temperature + Brood size + Fledgling perching height + Fledgling age	11	92.02	10.94
Temperature + Day number + Fledgling perching height	10	92.13	11.05
Temperature + Fledgling age + Brood size + Fledgling perching height + Hours from solar midnight	12	93.08	12.00
Temperature + Time of day + Fledgling perching height	12	94.23	13.16
Temperature + Brood size + Fledgling age + Time of day + Fledgling perching height	14	95.08	14.01
Temperature + Fledgling age + Brood size + Day number + Fledgling perching height + Hours from solar midnight	13	95.73	14.66

Appendix 2

<u>Male delivers prey to the female</u>

All competing models (GLMM with binomial distribution) explaining the probability of a prey captured by a male is delivered to the female rather than directly to the fledglings. Nest ID is included as a random variable in all the models. n=68

Model	df	AICc	ΔAICc
Stress + Prey + Fledgling age	5	27.25	0.00
Stress + Prey	4	28.33	1.08
Stress + Fledgling age	4	29.87	2.61
Stress	3	31.26	4.01
Prey	3	37.71	10.46
Prey + Fledgling age	4	38.29	11.04
Fledgling age	3	40.00	12.75

Appendix 3

<u>Female being present</u>

All competing models (GLMM with binomial distribution) explaining the probability of the female being present near her offspring when I first approached the fledglings. Nest ID is included as a random variable in all the models. n=80

Model	df	AICc	ΔAICc
Fledgling age + Brood size	4	86.96	0.00
Brood size + Day number	4	86.98	0.02
Fledgling age + Brood size + Day number	5	88.72	1.76
Fledgling age + Fledgling perching height + Brood size + Day number	11	89.28	2.32
Fledgling age	3	90.09	3.12
Fledgling age + Fledgling perching height	9	90.19	3.23
Fledgling perching height + Day number	9	91.25	4.29
Day number	3	91.31	4.34
Fledgling age + Day number	4	92.31	5.34
Fledgling perching height	3	92.37	5.40
Fledgling age + Fledgling perching height + Day number	10	92.58	5.62
Brood size	3	92.72	5.76

<u>Female aggressiveness</u>

All competing models (GLMM with logistic distribution) explaining the predicted female aggressiveness level. Nest ID is included as a random variable in all the models. n=75. The continuous version of fledgling perching height and the factor version of observer behaviour had lower AICc values and were more significant than the alternatives.

Model	df	AICc	ΔAICc
Fledgling age + Observer behaviour	7	198.09	0.00
Observer behaviour + Fledgling perching height (continuous)	7	198.66	0.57
Fledgling age + Observer behaviour + Brood size	8	200.91	2.82
Observer behaviour + Number of observers + Fledgling perching height (continuous)	8	201.85	3.75
Fledgling age + Observer behaviour + Number of observers	8	202.15	4.06
Observer behaviour	6	202.25	4.15
Observer behaviour + Fledgling perching height (continuous) + Brood size	8	202.68	4.59
Fledgling age + Fledgling perching height (continuous) + Observer behaviour	8	203.44	5.35
Observer behaviour + Brood size	7	204.77	6.68
Fledgling age + Brood size + Number of observers + Observer behaviour	9	204.91	6.82
Fledgling age + Brood size + Fledgling perching height (continuous) + Observer behaviour	9	205.41	7.32
Brood size + Number of observers + Observer behaviour + Fledgling perching height (continuous)	9	205.62	7.53
Observer behaviour + Number of observers	7	206.03	7.94
Fledgling age + Observer behaviour + Number of observers + Fledgling perching height (continuous)	9	207.29	9.20
Observer behaviour + Brood size + Number of observers	8	208.75	10.66
Brood size + Fledgling age + Fledgling perching height (continuous) + Observer behaviour + Number of observers	10	208.94	10.85
Observer behaviour (continuous) + Fledgling perching height (continuous)	5	210.92	10.83
Fledgling age + Observer behaviour (continuous)	5	212.06	13.97
Fledgling age + Brood size + Fledgling perching height (continuous) + Observer behaviour (continuous) + Number of observers	8	220.75	22.66
Brood size + Observer behaviour (continuous)	5	223.30	25.21
Observer behaviour (continuous)	4	223.89	25.80
Fledgling age + Number of observers	5	224.40	26.31
Observer behaviour (continuous) + Number of observers	5	226.58	28.49
Fledgling age	4	226.86	28.77
Fledgling age + Brood size + Number of observers	6	227.06	28.97
Number of observers + Fledgling perching height (continuous)	5	227.13	29.04
Fledgling age + Brood size	5	228.68	30.59
Fledgling perching height (continuous)	4	228.82	30.73
Fledgling age + Fledgling perching height (continuous) + Number of observers	6	229.65	31.56
Brood size + Fledgling perching height (continuous) + Number of observers	6	230.79	32.70
Fledgling age + Fledgling perching height (continuous)	5	231.64	33.55
Fledgling age + Brood size + Fledgling perching height (continuous) + Number of observers	7	231.64	33.55
Number of observers	4	231.82	33.73
Brood size + Fledgling perching height (continuous)	5	231.93	33.84
Fledgling age + Brood size + Fledgling perching height (continuous)	6	232.43	34.33
Number of observers + Brood size	5	232.61	34.52

| | 4 | 236.74 | 38.65 |

Model	df	AICc	ΔAICc
Brood size	4	236.74	38.65

Female distraction display

All competing models (GLMM with binomial distribution) explaining the probability of the female performing distraction display. Nest ID is included as a random variable in all the models. n=84

Model	df	AICc	ΔAICc
Brood size	3	107.92	0.00
Number of observers	3	108.85	0.93
Fledgling perching height (continuous)	3	109.55	1.63
Brood size + Fledgling age	4	109.79	1.87
Aggressiveness + Brood size	4	109.98	2.07
Fledgling age	3	110.06	2.14
Brood size + Observer behaviour (continuous)	4	110.07	2.16
Fledgling perching height	8	110.48	2.56
Brood size + Fledgling perching height	9	110.64	2.72
Aggressiveness	3	110.74	2.82
Aggressiveness + Fledgling perching height (continuous)	4	110.77	2.85
Observer behaviour (continuous)	3	110.95	3.04
Brood size + Observer behaviour	7	111.14	3.22
Aggressiveness + Fledgling perching height	9	112.30	4.38
Brood size + Aggressiveness + Observer behaviour	8	112.33	4.42
Fledgling age + Fledgling perching height	9	112.73	4.82
Aggressiveness + Observer behaviour (continuous)	4	112.94	5.03
Brood size + Fledgling perching height + Aggressiveness	10	113.03	5.11
Brood size + Fledgling perching height + Fledgling age	10	113.05	5.13
Aggressiveness + Observer behaviour	7	113.41	5.49
Brood size + Fledgling age + Observer behaviour	8	113.53	5.61
Fledgling perching height + Aggressiveness + Fledgling age	10	114.14	6.23
Brood size + Aggressiveness + Fledgling age + Observer behaviour	9	114.19	6.27
Aggressiveness + Fledgling age + Observer behaviour	8	114.20	6.28
Fledgling perching height (continuous) + Observer behaviour	7	114.26	6.35
Brood size + Aggressiveness + Observer behaviour + Fledgling perching height	14	114.50	6.58
Aggressiveness + Fledgling perching height + Observer behaviour	13	114.64	6.72
Brood size + Aggressiveness + Fledgling age + Fledgling perching height	11	115.34	7.43
Brood size + Fledgling age + Observer behaviour + Fledgling perching height	14	115.78	7.87
Aggressiveness + Fledgling age + Observer behaviour + Fledgling perching height	14	116.27	8.35
Brood size + Aggressiveness + Fledgling age + Observer behaviour + Fledgling perching height	15	116.48	8.57