Effects of food provisioning and habitat management on spatial behaviour of Little Owls during the breeding season

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The population of Little Owls in Denmark is close to extinction. The main cause is food limitation during the breeding season. Efforts to improve breeding success include providing breeding pairs with supplementary food and attempts to improve foraging habitats by creating short grass areas near the nests. In addition to increasing the reproductive output, feeding and habitat management may cause parents to work less hard improving their future reproductive value. We studied working efforts of five radio-tagged Little Owl pairs in years of absence and presence of food provisioning, and/or access to short sward vegetation areas near to the nest. We quantified movement as the minimum flight distance hour^{-1} (MFD), using the mean distance from the nest (DN) as a supplementary index. Under unmanipulated conditions, males had higher MFD and DN than females. If provided with food and/or areas with short sward vegetation, males but not females reduced their MFD and DN significantly. If MFD was adjusted for DN (the two measures correlated positively), both sexes reduced their DN-adjusted MFD as response to food provisioning but not to habitat provisioning. Food provisioning therefore had similar proximate effects on the foraging effort of males and females, whereas provisioning of short sward habitats had an indirect effect on male but not female MFD, because of decreased commuting distances between nest and foraging sites. The results indicate that food provisioning not only leads to increased reproductive output in an endangered raptor, but also to decreased working effort, which in turn may improve adult survival.

1. Introduction

Supplementary feeding can be used as a conservation action to reduce the risk of starvation and enhance reproductive performance (Newton 1998, Thorup *at al.* 2010, Ruffino *et al.* 2014). Because parental investments represent a trade-off between the benefits of investment in current offspring and the costs to future reproduction (Harding *et al.* 2009), improvement of the energetic situation may not only increase survival of offspring, but also improve the future reproductive value of the parents by lowering the total reproductive investment. Experimental food provisioning has been shown to improve survival of adults (Robb *et al.* 2008, Seward *et al.* 2013), advance breeding dates of the subsequent breeding attempt (Reynolds *et al.* 2003, Brommer *et al.* 2004, Ruffino *et al.* 2014), decrease parental effort (Wiehn & Korpimäki 1997, Granadeiro *et al.* 2000, Dewey & Kennedy 2001), reduce nestling mortality (Byholm & Kekkonen 2008), increase number of fledglings per brood (Korpimäki 1989, Wellicome *et al.* 1997, González *et al.* 2006, Perrig *et al.* 2014) and influence post-fledgling dispersal (King 1996, Kennedy & Ward 2003). As a conservation action, improvement of the feeding situation of food constrained pairs may therefore not only boost the current reproductive outputs but also result in longer term benefits mediated through lowered reproductive costs.

The Little Owl (*Athene noctua*) is a generalist predator that has shown a steep decline in Denmark during the last 40 years and the population is close to extinction. In 2005–2007, a telemetry based population study aimed to reveal the reasons for the population decline. The study identified the main proximate cause of the population decline as food limitation after egg laying, associated with lack of suitable foraging habitats with vegetation height below 10 cm (Thorup *et al.* 2010, Sunde *et al.* 2014). Experimental food supplementation increased the proportion of eggs that resulted in fledged young from 27% to 79% (Thorup *et al.* 2010). Increased movement (Holsegård-Rasmussen *et al.* 2009) and adult mortality rates (Thorup *et al.* 2013) during the breeding season compared to the non-breeding period indicated high parental investments in pairs not subject to conservation efforts.

In 2009–2014, a local NGO undertook a population conservation programme, aimed at increasing reproductive success through supplementary feeding and habitat improvements. Since 2010, a number of Danish Little Owl pairs have been fed systematically during the breeding season, and/or grass has been mowed or grazed close to their nests to increase natural foraging conditions.

Table 1. The number of 60-min telemetric surveys of nocturnally active Little Owls during the breeding season, divided by pair, year, breeding phase and sex. Presence of feeding and/or habitat improvement initiatives (mowing or grazing) as well as the number of nestlings are also indicated.

| | | Number of 1-h surveys | | | | | Conservation action | | |
| | | | Male | | Female | | | | |
Pair ID	Year	Incub	Nest	Fledg	Nest	Fledg	Feeding	Habitat	Young
1	2005	6	4	1	4	1			2
	2006	1	4	5	3	5			1
	2011	6	15	1	15	0	x	x	3
7	2006	1	7	0	4	0			3
	2011	0	7	7	8	8	x	x	6
8	2006	4	0	0	0	0			0 *
	2007	0	0	0	3	0			3
	2011	0	10	5	7	5	x	x	2
14	2006	0	3	2	4	2		x	1 **
	2007	0	3	0	0	0	x	x	5
15	2006	0	0	4	0	5		x	5
	2011	1	11	2	14	2	x	x	1

* Eggs deserted; ** 5 unhatched eggs

Here, we investigate how movements and activity distance in Little Owl pairs with severely food constrained breeding success is affected by management actions (food supplementation and habitat improvement) aimed at improving their feeding situation during the breeding period. We hypothesize that Little Owl parents will reduce working effort if the reproductive burden is lowered. We predict that parents should (1) move shorter distances per time unit, and (2) stay closer to nest when receiving extra food and/or provided with foraging habitat close to the nest.

2. Material and methods

2.1. Study species, population and study area

The Little Owl is a 170–210 g, primarily nocturnal owl, inhabiting various types of open, cultural landscapes. It is a resident, generalist mesopredator with a diverse prey spectrum ranging from earthworms (Lumbricidae) and insects, to amphibians, mammals and birds up to 50 g (Van Nieuwenhuyse *et al.* 2008). It captures its prey from perches or by walking on the ground (Tomé *et al.* 2011), and is reliant on its prey items being exposed on bare soil or grass vegetation shorter than 10 cm (Grzywaczewski 2009, Šálek *et al.* 2010, Sunde *et al.* 2014). Little Owls form monogamous pairs with biparental care. The species is widespread in south-central Europe, but has declined considerably due to agricultural intensification (Tucker *et al.* 1994, Van Nieuwenhuyse *et al.* 2008, Thorup *et al.* 2010). In Denmark, the species has declined steadily from a minimum of 1,000 breeding pairs in 1970 to less than 100 in 2007 (Thorup *et al.* 2010).

2.2. Field study

The study population represents the last population stronghold in the intensively managed agricultural landscape of northern Jutland, Denmark (56°N, 09°E). The area is 0–60 m.a.s.l. with an Atlantic climate resulting in mild winters (for more information about the study area see Sunde *et al.* 2009).

Several pairs received supplementary food during 2010–14. Supplemented food consisted of dead one day-old (30 g) poultry chicken (*Gallus*

gallus domesticus) from a commercial poultry hatchery and laboratory mice (*Mus musculus*). The food was provided from March until August every day or every second day at a rate of approximately 90–210 g nest^{-1}day^{-1}. Habitat improvement initiatives consisted of provisioning short sward vegetation (mowed or grazed) 50–200 m from the active nests during the entire breeding period. We monitored the brood size until fledging. The number of nestlings was recorded as the number of young at age of ringing, and the numbers of fledglings were recorded as the number of young seen or heard around the nest soon after fledging (Thorup *et al.* 2013).

Our analyses use telemetry based movement data from five territories (both mates tagged) studied in breeding seasons with and without food provisioning and/or nearby access to short sward vegetation (Table 1). The five pairs represent a subsample of a total of 14 pairs surveyed in 2005–2006 under unmanipulated conditions in the sense that no particular action was taken to improve their breeding conditions (Holsegård-Rasmussen *et al.* 2009, Sunde *et al.* 2009). In 2007, one of the pairs received additional food (dead laboratory mice and day-old poultry chickens) after egg laying as a part of a scientific experiment, testing for effects of food limitation on breeding success (Thorup *et al.* 2010). In 2011, a follow-up study was conducted on four other previously studied pairs. Hence, in total five pairs were surveyed in years with and without food supplementation (Table 1): in one pair all birds were surveyed in both years, in three pairs one of the mates had been replaced in the second study year, and in one pair mates had been replaced in the second study year. Two of the pairs had access to > 1 ha of short sward vegetation within 100 m from the nest before 2011. Even though these areas were not maintained for the purpose of helping the Little Owls, their structure and appearance was so similar to those areas that were managed for Little Owls in 2011, that they were coded as "habitat improved". Accordingly, three of five pairs experienced breeding situations with and without access to short sward habitat close to the breeding site. As follows from the design (Table 1) dictated by circumstances, effects of feeding and habitat improvement were somewhat confounded and could therefore not be definitely separated statistically. The complete dataset (60-

min surveys, $n = 200$) is available in Supplement 1. Five of the ten birds originally surveyed in the first control year were replaced before the year of food addition; hence the total number of individuals tracked was 15, of which five were studied during both control and food supplementation situations.

We captured the Little Owls with mist-nets or in nest-boxes. In 2005–2007, captured owls were fitted with backpack VHF radio transmitters (7 g including Teflon harness, TW-4 tags, Biotrack Ltd), with an expected battery life of 10–12 months. In 2011, the owls were followed only during the breeding season, we therefore used tail-mount radio transmitters (1.8 g, BD-2 transmitters, Holohil Systems Ltd) with an expected battery life of four months. After completion of the survey in 2005–2007, owls were recaptured and their tags removed. The tail-mounted tags fell off at moult shortly after the breeding season.

The tracking was conducted from incubation until fledging, between April and August. We concentrated our sampling to the nocturnal period (defined as the period from 30 min before sunset until 30 min after sunrise) when the owls were truly active, i.e. moving away from diurnal roosting quarters to open land. Following the procedure described by Holsegård-Rasmussen *et al.* (2009) we radio tracked the different individuals continuously for 60-min periods, one time per night, at various starting times, registering every detectable displacement during this interval. We located the individuals with triangulation. Signals were normally detectable from 200–500 m, and geographical positions of owls were usually determined with triangulations from 50–100 m distance. The estimated positions were drawn on topographical maps (1:10,000), or registered with a GPS-navigator. We estimated the accuracy of positions to be 5.0 m (SE 3.6 m) by comparing location assessed by triangulation with their real position (obtained with a GPS; $n = 6$).

Breeding phases were categorised as incubation (egg laying to hatching), nestling (hatching to fledging) and fledging (from fledging to cessation of begging).

2.3. Statistical analyses

To quantify movement and activity distance, we used the minimum flight distance per hour (MFD),

calculated as the total linear distance between all observed consecutive telemetry fixes during one-hour surveys, and the mean distance to the nest (DN), calculated as the mean distance to the nest from each telemetry fix, as defined by Holsegård-Rasmussen *et al.* (2009). Each one-hour period was considered an independent statistical unit. To obtain normally distributed data these were log-transformed prior to the statistical analyses.

We analysed variation in MFD and DN by means of mixed models (MIXED procedure in SAS 9.4, SAS Institute) with sex, breeding phase, brood size, presence or absence of feeding, and presence or absence of habitat improvement initiatives as fixed effects. We used territory identity as subject identifier (experimental "blocking unit" as random effect) because the territory embraced all relevant environmental variation except the experimental treatments. Owl identity was not used as subject identifier because only five of the 15 owls were studied during control years as well as during years of feeding (half of the owls from the first study year were exchanged before the second study season) and thus would result in partial disconnection of territory-information between control and treatment years in the statistical design. If owls of the same sex within the same territory (in different years) were given the same identity code, the covariance parameter of owl ID nested within territory was estimated to zero, indicating no relevant random variation to be accounted for in addition to territory ID. Degrees of freedoms of fixed effects were calculated by means of Satterthwaite's approximation (Littell *et al.* 2006).

Fixed effects were estimated in base models with the effects of sex (S), breeding phase (BP) and (if statistically significant) the interaction S*BP. We also tested for additional variation explained by brood size, temperature and presence/absence of rain, but because none of these nuisance variables explained additional variation ($p > 0.05$), they were not included. Effects of food supplementation (F) and habitat improvements (H) were tested in relation to the base model with and without inclusion of the other experimental variable (because of the effects of F and H confounded, effect estimates of F adjusted for H and vice versa shall be interpreted with caution). From these models, we derived the predicted relative differences in MFD and DN in relation to feeding

Table 2. Statistical significance of fixed effects, explaining variation in minimum flight distance (MFD) and mean distance from nest (DN) in Little Owls during 60-minute telemetric surveys, adjusted for other explanatory variables as indicated. Significance levels; °: $p < 0.1$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ****: $p < 0.0001$. F = Feeding, H = habitat improvement, S = sex, BP = Breeding phase.

Fixed effect	Controlled for/ other terms in model	MDF			DN		
		F	df	sign	*F*	df	sign
BP	S, S*BP	3.52	2, 190	*	1.78	2, 130	
S	BP, S*BP	12.52	1, 191	***	16.68	1, 191	****
S*BP	S, BP	2.51	1, 192		9.38	1, 190	**
F	S, BP, S*BP	8.82	1, 35.7	**	20.70	1, 49.3	****
F*S	S, BP, S*BP, F	2.82	1, 171	°	12.12	1, 171	***
F*BP	S, BP, S*BP, F	0.55	2, 167		0.27	2, 131	
H	S, BP, S*BP	7.02	1, 62.9	*	29.65	1, 97.4	****
H*S	S, BP, S*BP, H	5.06	1, 175	*	23.51	1, 178	****
H*BP	S, BP, S*BP, H	0.59	2, 188		0.05	2, 135	
F	S, BP, S*BP, H	1.75	1, 8.39		0.05	1, 13.6	
H	S, BP, S*BP, F	0.00	1, 9.97		5.81	1, 15.6	*
Effects adjusted for the other response variable (MFD or DN: "cov"):							
cov + cov2		109	2, 193	****	91.6	2, 166	****
S	cov + cov2	0.06	1, 193		16.83	1, 193	****
F	S, cov, cov2	9.71	1, 189	**	1.44	1, 173	
F*cov	S, F, cov, cov2	6.66	1, 193	*	0.02	1, 194	
F + F*cov	S, cov, cov2	8.13	2, 187	***	0.71	2, 169	
F + F*cov	S, cov, cov2, H	8.35	2, 82	***	1.57	2, 49	
H	S, cov, cov2	2.15	1, 194		9.30	1, 185	**
H*cov	S, H, cov, cov2	6.69	1, 193	*	2.98	1, 194	°
H + H*cov	S, cov, cov2	4.56	2, 192	*	6.10	2, 180	**
H + H*cov	S, cov, cov2, F	8.87	2, 145	***	6.25	2, 49	**

or habitat improvement as least square means (LSMEANS option in SAS). Because behaviour of males and females differed in general and in response to the treatments, effects were derived separately for males and females.

Finally, because the two response variables, MDF and DN, correlated internally, we also constructed a set of models where we tested for the effect of S, D or H on MDF adjusted for DN and DN adjusted for MDF.

3. Results

Both flight (MFD) and activity distances (DN) varied significantly as functions of sex (S) and breeding phase (BP) as well as with feeding (F) and habitat improvement initiatives (H) (Table 2). Statistically significant interaction terms S*F and S*H (Table 2), indicated that males reduced their effort more than females when fed and/or receiving habitat improvements (Fig. 1). Effect estimates divided on gender showed that males responded significantly to F as well as H, whereas females did not (Table 3). When not fed, males moved 3.6 times longer distances per hour and were located 3.3 times further away from the nest than their mates (Fig. 1, Table 3). If fed, males reduced their MFD to 41% and their DN to 43% of the former distances, or 2.2 and 1.7 times the distances of their mates. Similar figures were apparent for breeding situations with and without habitat improvements (Table 3, Supplement 2).

In both sexes, the MFD increased with increasing DN up to 300 m then stabilized (Fig. 2, Table 2). DN-adjusted MFDs interacted with food provisioning, as the MFD adjusted for DN was lower for food-provisioned birds than for non-food provisioned birds during surveys (Fig. 2), as also evident as a significant interaction term between DN and food addition (Table 2). A similar
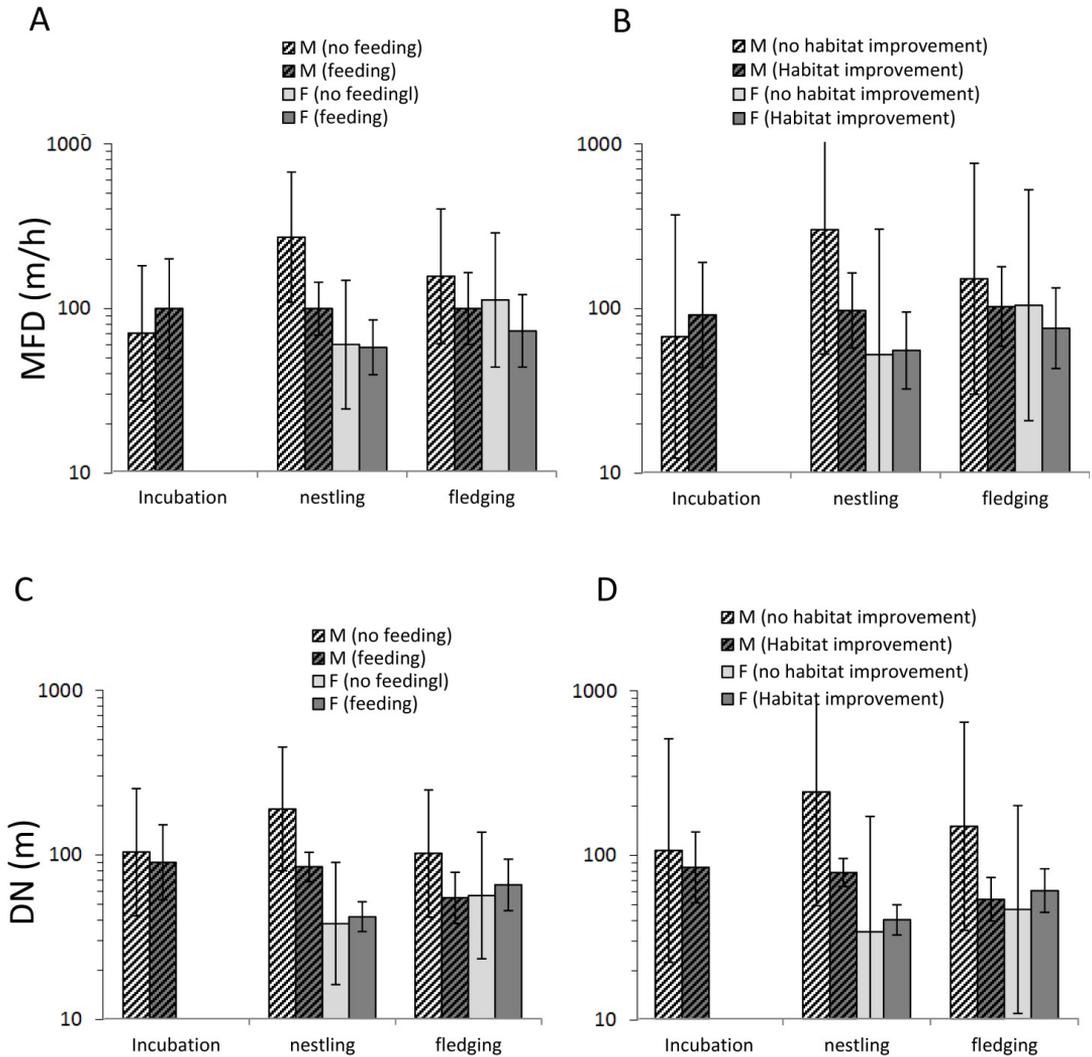
Fig. 1. (A–B) Minimum flight distances per hour (MFD) and (C–D) distances from nest (DN) of male and female Little Owls during different phases of the breeding season divided on whether they were fed or not (A, C) or whether the habitats were attempted improved (C, D). Error bars indicate 95% confidence intervals of the harmonic mean.

effect of habitat improvement was also evident (Table 2). Despite some collinearity between the two predictors, the effects of food provisioning and habitat improvements appeared to operate alongside if included in the same model (Table 2).

Males and females expressed identical functions of MFD in relation to DN (evident as no significant main effect of sex on MFD in a model accounting for effect of DN: Table 2, Fig. 2). Hence, for a given mean distance to the nest, males and females had equal MFD. Any overall difference in MFD between males and females was therefore re-

lated to males operating further afield from the nest than females. If the sex-specific effect of feeding on MFD was adjusted for the owls DN, both sexes reduced their DN-adjusted MFD if food was provided (Table 3).

DN controlled for variation in MFD was higher for males than for females and lower for pairs provided with short sward vegetation close to the nest (also when adjusted for effect of food provisioning), but independent of food provisioning (Table 2). Food provisioning reduced MFD (in males) not only as an indirect effect of in-
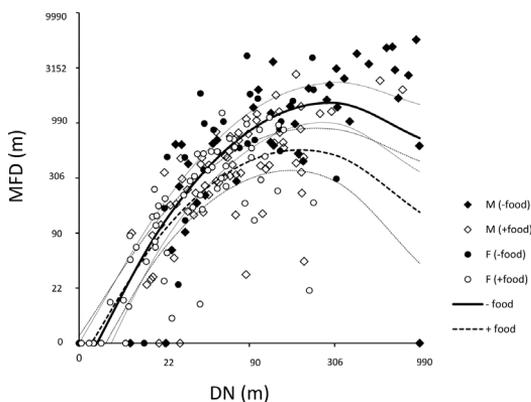
Fig. 2. Minimum flight distance per hour (MFD) of breeding Little Owls plotted against the mean distance from the nest during the 60-min survey (DN) and the quadratic functions in presence and absence of artificial feeding (thin lines indicate 95% confidence zones) predicted from mixed models. Males and females had similar MDFs when controlling for variation in DN.

creased activity range from the nest, but also as a higher movement speed per se.

4. Discussion

As far as the effects of feeding and habitat improvement could be separated, feeding appeared to result in males flying shorter distances from the nest to forage as well as reduce their movement speed per se as indicated by lower MFD adjusted for DN. Provisioning of short sward areas close to the nests appeared mainly to influence the DN likely because of selection for these areas. Provisioning of foraging habitat adjacent to the nest appeared to reduce MFD indirectly through reduced commuting distances between foraging sites and the nest. Short sward areas are used intensively relative to availability during the summer (Grzywaczewski 2009, Šálek & Lövy 2012, Sunde *et al.* 2014, L.B. Jacobsen & M. Chrenková, pers. observation).

Males showed the strongest reduction in MFD as result of food provisioning, apparently because food provisioned males not only reduced their foraging efforts (apparent as MFD adjusted for DN), but also reduced the DNs, leading to less commuting between foraging habitats and the nest site. Females responded to food provisioning by reducing their foraging movements similarly to males, but

Table 3. Relative differences in minimum flight distance per hour (MFD) and distance from nest (DN) of breeding, radio-tagged Little Owls as effects of feeding and habitat improvements (divided on sex), and between sexes (divided on years where the owls were either fed or not received additional food during the breeding season). Effect size is given as the antilog of the coefficients (10^b) and expresses the magnitude of the difference in response values as a function of the fixed effect (e.g. $10^b = 0.41$ as an effect of feeding on MFD in males, indicates that males that receive food during the breeding season reduce their MFD to 41% of the level when not fed). The estimates are based on mixed models that control for variation among territories (random effect) with breeding phase, sex, treatment and sex*treatment as fixed effects. Significance levels; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Effect	Group	MFD	DN
Feeding	Males	0.41 **	0.43 ***
	Females	0.65	0.84
Habitat	Males	0.37 **	0.30 ***
	Females	0.89	1.00
Sex (male)	Fed	2.24 **	1.67 ***
	Not fed	3.58 ***	3.26 ***

kept a constant (short) mean activity distance to the nest irrespective of food supply.

This is probably because Little Owl females vigorously defend the nest site and fledged young against enemies (Van Nieuwenhuyse *et al.* 2008). Our results suggest that the activity distance of females is constrained by brood guarding motives, which prevents flexibility with regard to foraging distance.

The male is the primary caregiver in Little Owls (Nieuwenhuyse *et al.* 2008). As reproductive costs can reduce survival of parents (Eldegard & Sonerud 2010), the decreased parental working effort potentially leads to increased self-maintenance or lower predation risk and thus increased future reproduction. Parents with easy access to food are expected to have enhanced fitness (Dawson & Bortolotti 2002), and thereby probably reduce immune-related responses (Ilmonen *et al.* 2003, Harding *et al.* 2009). The effects of reduced working effort on survival (e.g. see Santos & Nakagawa 2012, Thomson *et al.* 2014) and future breeding condition (e.g. see Brommer *et al.* 2004) in Little Owls remain to be investigated. As the daily mortality rates in Danish Little Owls

were three times higher during the breeding season compared to the non-breeding season (Thorup *et al.* 2013), the decrease in movement and activity distances could have released some of the reproductive burden and may potentially have increased adult survival. Locomotion is also costly in terms of exposure to predators (Flasskamp 1994) and a mesopredator the Little Owl may be at risk of predation from, e.g., Tawny Owls (*Strix aluco*; van Niewenhuyse *et al.* 2008). Access to abundant food sources may lead to less risk taking, e.g., by moving more carefully (reduced movement speed), and reducing time at risk (reduced commuting distance).

Our results underline the importance of prioritizing habitats close to the nest sites when planning improvement of foraging habitats for Little Owls and other species which bring multiple, small, prey items to the nest.

Effekter av matning och habitatskötsel på minervauggans beteende under häckningstiden

Minervauggan är så gott som utdöd i Danmark. Huvudorsaken till dess tillbakagång är begränsad födotillgång under häckningen. För att öka häckningsframgången har man försett häckande par med supplementär föda och förbättrat habitatens kvalitet med tanke på födosök. Det senare har gjorts genom att man skapat lågvuxen ängsmiljö nära boplatserna. Förutom att påverka häckningsframgången kan dessa aktioner minska föräldrarnas arbetsbörda och således öka deras framtida reproduktiva värde.

Vi studerade arbetsbördan hos fem radiomärk-

ta par av minervauggla under år med och utan extra matning och/eller tillgång till lågvuxen äng. Vi kvantifierade rörlighet som den minsta flugna distansen per timme (MFD) och som medeldistans från boet (DN).

Under omanipulerade förhållanden var hanar rörligare än honor i fråga om båda måtten. Om paren matades eller hade tillgång till lågvuxen äng, minskade hanar (men inte honor) sin rörlighet väsentligt. Om MDF korrigeras för DN (de två måtten korrelerade positivt), kunde en minskning av det justerade MDF-värdet observeras hos båda könen hos matade par, men inte hos par som hade förbättrade habitat nära boplatsen. Matning hade därför liknande proximata effekter på båda könens arbetsbördor. Däremot hade habitatskötsel en indirekt effekt på hanars men inte på honors MDF, p.g.a. kortare flygdistanser mellan bo och jaktmarker. Resultaten tyder på att matning leder till både ökad reproduktiv framgång och mindre arbetsbörda, som i sin tur kan öka överlevnaden av vuxna fåglar hos denna utrotningshotade art.

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