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Variation in working effort in Danish Little Owls *Athene noctua*

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Locomotion is costly and should therefore serve a purpose according to the principle of optimal behaviour. In this light, we studied variation in nocturnal activity of radio-tagged Little Owls *Athene noctua* in Denmark where, after a decline of at least 30 years, the species is threatened with extinction. The study is based on 143 one-hour surveys of breeding and 274 surveys of non-breeding Little Owls (27 territorial individuals on 14 territories). Working effort is calculated as the total linear distance between all observed consecutive telemetry fixes during one-hour surveys (Minimum Flight Distance, MFD). The effort peaked during the post-hatching dependency period with males flying longer distances and having fewer inactivity periods than females. This might suggest that also after hatching, males provide more food to the nest than females. Non-breeding owls were completely inactive in 13% of all surveys. Probability of inactivity increased with heavy rain and was highest in the middle of the night. During the non-breeding season, MFD of active owls varied with a peak in March and a low in December, possibly reflecting seasonal variation in metabolic needs and social activity. During the non-breeding season, MFD was slightly higher for males than for females, possibly reflecting lower energetic flight costs due to lower weight, and were highest at the beginning and end of nights.

Key words: Little Owl, *Athene noctua*, working effort, energetic cost, reproduction, seasonal variations, Denmark

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INTRODUCTION

Activity is essential for any animal to acquire vital resources but is also costly in terms of energy expenditure, physiological wear, and exposure to predators and accidents (Flasskamp 1994). According to the principle of optimal behaviour, any activity should therefore serve a purpose (Krebs & Davies 2003), wherefore variation in activity is likely to reflect variation in needs and gains of a certain activity. Thus studies of variation in activity are a well-known method to acquire knowl-

edge about ecological constraints of species (e.g. Sunde *et al.* 2003, Stauss *et al.* 2005).

The Danish Little Owl population has decreased dramatically since the 1970s and is still diminishing, possibly because too few young are produced (Thorup *et al.*, unpubl. data). Information about patterns of individual investment in activity is therefore of utmost importance in order to understand the species' energetic costs during the annual cycle in general and during the breeding period in particular, when reproductive success might be energetically con-

strained. The aim of this study is to quantify the factors influencing working effort, measured as flight distance per time unit, of Little Owls *Athene noctua* with special emphasis on the timing and strength of the reproductive investment. On the assumption that activity level reflects the energetic investment in foraging, the peak period of working effort is likely to reflect the seasonal peak in energetic stress. Working effort of owls during the non-breeding period does not only provide a baseline against which data from the breeding season could be compared, but also reflects how a non-breeding bird adjusts its activity level to seasonal change, during night and as a response to ambient conditions.

METHODS

Study area

Data were collected in the north-western part of Denmark (56°N, 09°E), from 2005 to 2007. The study area (0–60 m a.s.l.) was mainly agricultural managed with 68% of the area within 1 km from Little Owl nests consisting of cultivated fields, 10% pastures, 7% tree vegetation, 7% fallow fields and 8% gardens or built-up areas.

Field observations

Nesting sites of marked Little Owls were all associated with buildings, some in artificial nest boxes and others in cavities within buildings. Little Owls were captured with mist nets or in a fitted trap box and fitted with a backpack radio transmitter (7 g including harness, Bio-track Ltd) with an expected battery life of 11–12 months. Data were collected April 2005 – June 2007, from 27 individuals, representing 14 different territories.

At various starting times, individuals were radio-tracked continuously for a 60-min period between sunset and sunrise, using a VHF-receiver with an external antenna. During the 60-min survey period, every detectable movement was registered by an observer on foot. Initially, the owl was located as precisely as possible (usually within 20 m) by triangulation from 50–200 m distance. During the survey, however, triangulation was not always needed due to sufficient detail on the owl's position and movements. The estimated positions of the owl were either mapped (1:10 000) or registered with a GPS-navigator after the owl had moved on. In addition to displacements, vocalizations and nest visits were registered, as well as whether the owl was active or resting (evident by inconstant or constant signals, respectively).

At the beginning of each survey, weather and light conditions were noted: wind on Beaufort's scale, temperature, precipitation scaling from 1 (no rain) to 6 (heavy rain) and light intensity scaling from 1 (bright daylight) to 9 (pitch black). When sampling was most intense (summer 2006), individual owls were surveyed with regular intervals up to five times per month.

Analyses

The measure of working effort used in this study was calculated as the minimum distance individuals moved during a survey, i.e. the total length measured between all consecutive telemetry fixes during the 60-min survey. This measure is referred to as the *Minimum Flight Distance per time unit* (MFD, m/h), since some movements can remain unobserved. Furthermore, *Mean Distance from the Nest* (DN) was calculated as

$$DN = \frac{\sum DN_i \times t_i}{\sum t_i}$$

where DN_i is distance to the nest from the i^{th} telemetry fix and t_i is the time spent at the i^{th} telemetry fix ($\sum t_i$ was 60 min for all surveys).

Since MFD for non-breeding birds varied significantly over the year (see later), analyses focusing on MFD-variation in relation to breeding status were restricted to observations between 15 April (earliest egg laying) and 15 August (last date of fledged young heard begging for food). We will refer to this period as the breeding period throughout, without including the preceding territorial phase (March). The breeding season was divided into three phases: incubation, nestling and fledgling. Surveys on incubating females were not included. In Little Owls, the female is the only sex incubating (Van Nieuwenhuysen *et al.* 2008), and only very short movements of radio-tagged females were observed during this period. The onsets of incubation, nestling and fledgling phases were determined by backdating the age of young, assuming incubation and nestling periods lasting 30 and 33 days, respectively (Glue & Scott 1980, del Hoyo *et al.* 1999).

As all radio-tagged owls bred, non-breeding individuals in these analyses had either failed or completed their reproductive investment. The analyses of variation in MFD of non-breeding owls were based on data from the entire year.

Because individuals were observed to be completely inactive during a number of surveys, yielding bimodal MFD-distributions (Fig. 1), the analyses of variation in activity were conducted in two steps, representing (1) the choice of whether to move at all and, for those that moved, (2) how far to move during 1 hour. The analy-

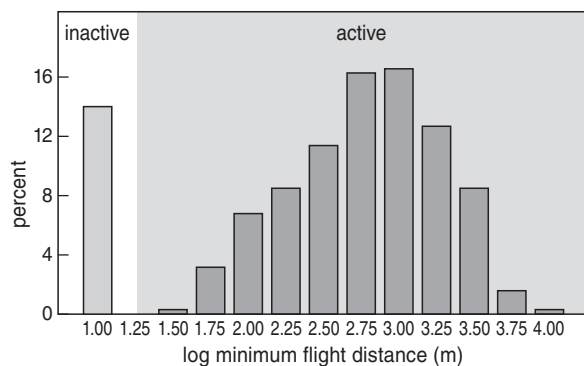


Figure 1. Distribution of log-transformed Minimum Flight Distances per hour, from one-hour nocturnal surveys of breeding and non-breeding radio-tagged Little Owls ($n = 418$).

ses of conditional probabilities of making a move during 1 hour (activity rate, AR) were conducted by means of generalized linear mixed models (PROC GLIMMIX in SAS 9.1) with a logit link and a binomial error distribution. The variation in MFD for those which did move was analysed with a general linear mixed model (PROC MIXED in SAS). To achieve normality, MFD-distances were log-transformed ($\log [MFD+10]$). In all analyses, territory ID was entered as a random effect unless otherwise stated. Significance levels at $P < 0.05$ were used throughout.

RESULTS

Breeding period

Between 15 April and 15 August, the time interval in which breeding activities were observed, the activity

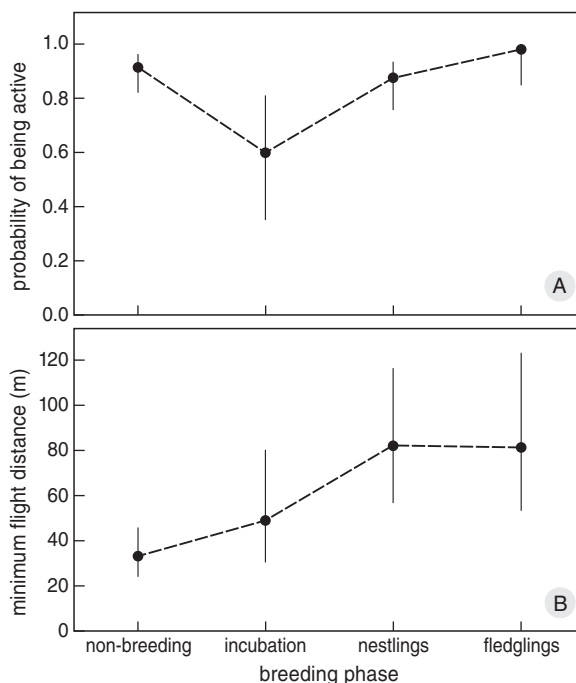


Figure 2. (A) Probability (95% CI) for Little Owls to be active during 1-hour nocturnal surveys during successive breeding phases (including non- and failed breeders). (B) Means (95% CI) of Minimum Flight Distance per hour when Little Owls were active by successive breeding phases (including non- and failed breeders).

rate as well as the distance moved per time unit, varied significantly with breeding status (Table 1 and Fig. 2). Inactivity was most commonly observed during the incubation period (only male observations) whereas the MFDs were highest for parents with nestlings or fledglings and lowest for non-breeding owls.

Table 1. Effects of breeding phase and sex of radio-tagged Little Owls on activity rate (general linear mixed model) and MFD of active owls (mixed model) during nocturnal 1-hour surveys conducted between 15 April and 15 August. All analyses accounted for variation between territories (random effect). Because no data on activity is available for incubating females no interaction term was estimated for AR. Breeding phase: non-breeding (individuals with failed reproduction), incubation (only on males, while females are incubating the eggs), nestlings and fledglings. Territory ID is the identification number of the territories occupied by radio-tagged Little Owls.

Effect	Activity rate (AR)			Minimum Flight Distance (MFD)		
	<i>df</i>	χ^2	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Breeding phase	3	11.75	0.008	3,19	9.98	<0.0001
Sex	1	4.92	0.027	1,19	3.86	0.051
Sex × Breeding phase				2,19	0.51	0.600
Territory ID (random)	12	13.6	0.328	12,19	4.38	<0.0001

In the breeding period, activity rates were higher in males than in females, but this difference was only marginally significant for the MFDs (Table 1). However, looking only at the period between hatching and independence, males were active more often than females ($\chi^2_1 = 5.90$, $P = 0.015$) and activity rate increased slightly with brood age ($\chi^2_1 = 5.97$, $P = 0.015$). When active, males moved significantly longer distances per time unit than females, 1110 and 640 m/h, respectively, and MFD tended to be positively correlated with the initial brood size and the proportion of the brood that stayed alive during the survey. The MFD was not related to the age of the young, neither when entered as a linear or quadratic covariate (Table 2). Moreover, there was no evidence of differential MFD of males and females with brood age (interaction term between sex and brood age: $F_{1,83} = 0.11$, $P = 0.75$). A substantial amount of the variation in MFD could be explained by mean distance of the owl to the nest through the survey (Table 2), overriding the significant effect of sex. Hence, long movement distances per time unit were associated with foraging far from the nest, and the larger MFD in males compared to females were attributable to a larger activity range of males (Fig. 3. Test for difference in DN between males and females with young, controlling for pair, brood size and the proportion of the brood that stayed alive during the survey:

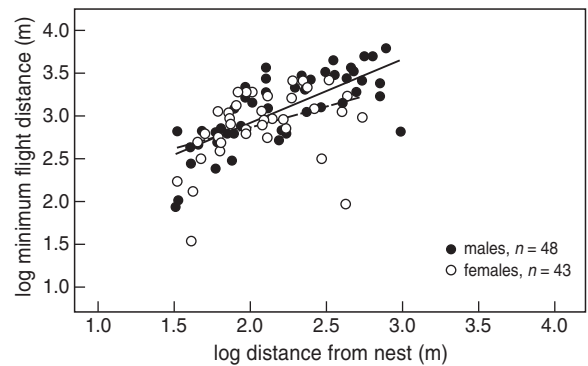


Figure 3. Scatter plot of log-transformed Minimum Flight Distance per time unit against log-transformed distance from nest. Plots are on moving, breeding Little Owls after hatching, separately for males ($n = 48$, $r = 0.41$) and females ($n = 43$, $r = 0.75$).

$F_{1,84} = 26.27$, $P < 0.0001$). The number of nest visits during the survey did not correlate with MFD in general, but tended to be positively correlated with MFD when controlling for the overriding effect of DN (partial effect of log-transformed number of nest visits, adjusted for territorial variation: $b = 1.52$, $F_{1,88} = 3.29$, $P = 0.073$; not adjusted for variation between territories: $b = 1.87$, $F_{1,97} = 5.32$, $P = 0.023$). Males and females attended nests equally often (adjusted for terri-

Table 2. Mixed model effects of various factors on Minimum Flight Distance (MFD) during 102 one-hour nocturnal surveys of radio-tagged Little Owls with dependent young. *Brood age*: Number of days after chicks hatched; *Brood size*: The current number of chicks in the brood; *Brood left*: The reduction in brood size from number of eggs laid to number of current chicks. *DN*: Distance from nest. *Nest visit rate*: Number of times during a 1-hour survey, where either the position of radio tagged Little Owl was at the nest site or/and when increased begging was registered. Univariate effects (though adjusted for the random effect of between-territory differences $F_{7,84} = 2.81$, $P = 0.011$) with an apparent significance of $P < 0.1$, were considered in model B and C as shown in bold. In model C, the ultimate effect of sex is overridden by the effect of DN (because males operated further away from the nest). Ambient conditions during the survey (time of the night, wind, precipitation, temperature and light score) did not correlate with MFD (not shown in Table: all P -values > 0.15).

Effects	A. Univariate effects			B. Additive effects to sex + breeding situation			C. Model including effects of sex, breeding variables and DN				
	df	F	P	df	F	P	df	F	P	B	SE(B)
Sex											
Male	1,89	9.41	0.003	1,85	11.20	0.0012	1,84	2.20	0.14	0.11	0.07
Breeding situation											
Brood age	1,85	0.84	0.36								
Brood age ²	1,85	0.53	0.47								
Brood size	1,87	3.87	0.05	1,85	2.12	0.15	1,84	1.31	0.26	0.07	0.06
Brood left	1,87	3.331	0.07	1,85	3.14	0.08	1,84	4.18	0.04	0.36	0.17
Behaviour											
Nest visits	1,89	0.50	0.48								
DN	1,89	25.96	<0.0001	1,84	19.48	<0.0001	1,84	19.48	<0.0001	0.47	0.11

torial variation only: $F_{1,89} = 0.23, P = 0.63$). There were no indications that MFD of parents with dependent young were conditioned to the time within the nocturnal period, weather conditions or light (Table 2).

Activity variation of non-breeding owls

Of 274 one-hour surveys conducted on non-breeding Little Owls, no movements were detected in 35 cases (13%). Activity rate did not vary across territories, months or between sexes, but decreased late in the night (time passed since sunset; Wald $\chi^2_1 = 3.93, P = 0.047$), and with increasing rain score (Wald $\chi^2_1 = 4.58, P = 0.032$). If these two significant ambient factors, maintained in the final model after forward as well as backward stepwise selection procedures, were removed from the model, increasing wind scores were selected instead as a predictor of inactivity (Wald $\chi^2_1 = 3.87, P = 0.049$; partial effect of wind when also accounting for effect of rain score: $\chi^2_1 = 2.71, P = 0.099$).

There was a considerable seasonal variation in MFD of active, non-breeding Little Owls, moving the longest distances per time unit in late winter and spring, reaching a peak in March after which MFD decreased through autumn to a seasonal low in December (Table 3, Fig. 4).

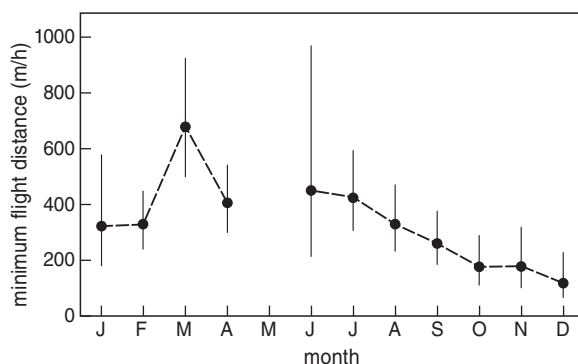


Figure 4. Monthly means (95% CI) of Minimum Flight Distances of active, non-breeding radio-tagged Little Owls during 1-hour nocturnal surveys ($n = 274$). All surveyed owls were actively breeding in May.

Throughout the year, males moved on average 25% longer distances per time unit than females (Table 3). A quadratic relation existed between time after sunset and MDF, Little Owls moving most at the start and least in the middle of the night (Table 3, Fig. 5). An apparent highly significant, positive relation between MFD and light score, disappeared completely after accounting for

Table 3. Mixed model effects of various explanatory variables on Minimum Flight Distance per hour for 242 one-hour surveys of non-breeding Little Owls (all estimates were adjusted for territorial effects as random factor: $F_{14,226} = 0.87, P = 0.59$). Effects are given as (A) isolated (univariate) effects (i.e. only adjusted for territorial variation), (B) additive effects to a model including effects of sex and month (bold) and (C) additive effects to the final model, including all significant effects (bold). DN: Mean distance of owl to nest during the survey.

Variable types	A. Univariate effects				B. Additive effects to sex + month				C. Additive effects to final model			
	df	F	P	Beta	df	F	P	Beta	df	F	P	Beta
Month	10,22	4.68	<0.0001		10,22	4.38	<0.0001		10,21	3.10	0.0011	
Sex												
Male	1,23	5.98	0.015	0.14	1,22	8.46	0.004	0.15	1,21	6.53	0.011	0.12
Month x sex					10,21	1.17	0.31		10,20	1.24	0.27	
Ambient												
Temperature	1,23	5.57	0.019	-0.01	1,22	0.28	0.60	-0.01	1,21	2.10	0.15	-0.01
Wind	1,23	2.80	0.096	-0.03	1,22	0.60	0.44	-0.01	1,21	0.80	0.37	-0.01
Rain score	1,23	0.19	0.66	-0.02	1,22	0.01	0.93	0.00	1,21	0.00	0.97	0.00
Light score	1,23	26.86	<0.0001	-0.11	1,22	16.55	<0.0001	-0.09	1,21	1.73	0.19	-0.04
Night length	1,23	3.75	0.054	-0.43	1,22	1.31	0.25	1.15	1,21	1.57	0.21	1.18
Time after sunset +	1,23	19.48	<0.0001	-2.88	1,21	19.98	<0.0001	-2.81	1,21	18.31	<0.0001	-2.50
Time after sunset ²	1,23	11.77	0.0007	5.46	1,21	13.12	0.0004	5.62	1,21	11.76	0.0007	4.97
Behaviour												
DN (km)	1,23	48.67	<0.0001	0.80	1,22	40.61	<0.0001	0.71	1,21	30.28	<0.0001	0.62
Vocalisation	1,23	4.60	0.033	0.21	1,22	0.76	0.39	0.08	1,21	2.79	0.096	0.14

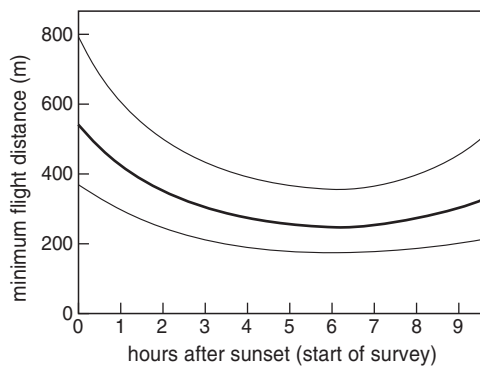


Figure 5. Predicted relation between Minimum Flight Distance during one hour of non-breeding Little Owls as function of hours after sunset at the start of the survey (95% confidence error zones are indicated). Baseline values are estimated for a male owl in February.

the effect of time of the night. Movement distances per time unit was not correlated with any weather variables, but increased with the owl's mean distance to the nest site during the survey (Table 3).

DISCUSSION

Activity in Little Owls exists at two levels: whether to move at all, and if so, how much. Interestingly, we found that these two behavioural processes are influenced by different factors. Furthermore, considerable variation as to the two activity measures could be observed depending on breeding status, time of the year, sex, and ambient conditions during the survey.

Inactivity, in this study measured as no movements during one hour, should pay in situations where the owl's entire needs were saturated (e.g. Sutherland & Moss 1985) or where the expected pay-off of any activity did not outweigh the movement cost. In situations where the owls would be practising pause-travel hunting with long optimal give-up-times (>1 hour) at each perch, apparent inactive owls might actually have been hunting individuals. Apparent inactivity was relatively less common in the late breeding period, especially in males, and, for non-breeding individuals, during heavy rain (and wind) and late in the night. From a cost-benefit perspective, all these correlations make sense as parental duties motivate birds to spend more time foraging, and heavy rain and wind is likely to reduce foraging efficiency and increase thermoregulatory costs (McCafferty *et al.* 1997). A higher inactivity rate of females during the post-hatching period compared to

males might also be motivated by sex-specific parental care duties.

For active individuals, the moved distance per time unit was highly variable between individual surveys, indicating that in the course of a night Little Owls expressed bursts of activity interspersed with periods of fewer movements. As expected, MFD was considerably higher for breeding than for non-breeding birds, with a maximum reached after hatching. After hatching, the age of the brood did not appear to influence MFD as one might expect as chicks grew and so their energy demand, although the frequency of inactivity periods decreased. If activity level is taken as a measure of parental effort, no particular phase within the two-month post-hatching dependency period could be identified as particularly demanding. The fact that MFD within this relatively small sample of territories was positively correlated with initial brood size (marginally significant) and the proportion of the brood that stayed alive during the survey, give some support for the hypothesis that MFD was correlated with parental working effort (e.g. Dawson & Bortolotti 2003).

The increase in MFD with increasing mean distance to the nest during the survey might also indicate that foraging far from the nest was associated with increasing work load. The strong positive correlation between MFD and mean distance to the nest also explains why MFD was not positively correlated with number of nest visits, as the partial correlation between these two variables became positive, when accounting for the confounding effect of mean distance to the nest. With an observed prey spectrum ranging from insects to rodents and birds (Van Nieuwenhuysse *et al.* 2008), it is feasible that owls foraging far from the nest were targeting larger prey items with a higher energetic reward and lower capture rates than those foraging adjacent to the nest. If this is true, this may also explain why males did not attend the nest more often than females albeit on average moving 73% longer distances per time unit. Accordingly, males also operated more distant from the nest than did females.

The observed inter-sexual differences in behaviour, might suggest some level of sex-specific duty division in breeding effort, with males providing more food and females possibly being more active in care and defence of young as observed in several raptorial birds with reversed sexual size dimorphism (Galeotti *et al.* 2000, Sunde *et al.* 2003). Males are 9–10% lighter than females (del Hoyo *et al.* 1999), consequently males can fly longer distances than females for the same amount of energy (Sunde *et al.* 2003, Engel *et al.* 2006, Schmidt-Wellenburg *et al.* 2007). With the male sex

predisposed to invest in foraging effort, the heavier female might be disposed to guard the brood because of higher momentum when striking at a predator approaching the nest (Andersson & Norberg 1981). The need for thermo-regulation of small chicks (Durant *et al.* 2004, Margalida *et al.* 2007) or re-establish muscle mass after incubation (Dietz *et al.* 2007) are not likely explanations for the indicated difference in male and female post-hatching behaviour, as female MFD in that case should increase with chick age. This would have been apparent as a sex x brood age interaction term, which in this analysis was far from significant.

MFD varied seasonally for non-breeding Little Owls, reaching a maximum in March and a minimum in December after a steady decrease during autumn, and males moving slightly (25%) more than females throughout the year. These seasonal differences are likely to be due to seasonal variation in energy needs, social activity or foraging tactics, or a combination of all. Metabolic needs of Little Owls do vary seasonally, being lowest in wintertime (Exo 1988). Social activity level (indexed as social encounters or vocalisation rates) over the year also mirrors the seasonal variation in MFD well as social activity increases from very low levels in autumn to peak in the months before courtship (March–April). In March, the Little Owls also maintained the seasonally largest home ranges and MFD was positively correlated with the mean distance to the nest during the survey (Sunde *et al.* 2009). It is therefore plausible that the annual peak in MFD between January and April should be interpreted in a social context. Differential foraging tactics over the year are less likely to explain the seasonal variation in MFD, as Little Owls' diet choice is temperature sensitive. At temperatures below 0°C, earthworms and insects, which are the most frequent prey items during summer (Hounscome *et al.* 2004), are no longer available, and Little Owls switch to vertebrates, like rodents and birds (Ille 1983, Schön *et al.* 1991, own observations). If a change in hunting strategy influenced activity budgets, we should expect MFD to be correlated with temperature, which was not the case.

Generally higher MFD in males than females throughout the year might be a simple consequence of lower energy expenditure of the lighter males (Sunde *et al.* 2003) but different social roles in the non-breeding season might also be a possibility. The bimodal activity distribution with Little Owls moving more early and late and less in the middle of the night can possibly be explained by a need to forage after and before the diurnal period of inactivity.

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SAMENVATTING

Vliegen is een dure activiteit voor een vogel en zal dan ook alleen plaatsvinden als het optimaal bijdraagt tot het doel waarvoor het wordt uitgevoerd. Met dit in het achterhoofd bestudeerden we met behulp van telemetrie de nachtelijke activiteit van Steenuilen *Athene noctua* in Denemarken. De soort neemt hier al minstens dertig jaar in aantal af en wordt nu met uitsterven bedreigd. Het onderzoek is gebaseerd op 143 uurwaarnemingen van broedvogels en 274 uurwaarnemingen van niet-broedvogels (27 vogels, 14 territoria). Als maat voor de geleverde vlieginspanning is de som van de lineaire afstand tussen opeenvolgende telemetrische bepalingen (MFD) genomen. De MFD bleek het grootst in de periode dat er jongen in het nest waren. Mannetjes legden in deze fase langere afstanden af dan vrouwtjes en rustten minder vaak. Dit duidt erop dat de mannetjes ook na het uitkomen van de eieren meer voedsel naar het nest brengen dan de vrouwtjes. Niet-broedende uilen waren in 13% van alle uurwaarnemingen niet actief. De kans op inactiviteit nam met hevige regenval toe. De vogels waren het minst actief rond middernacht. Buiten het broedseizoen was de MFD van actieve uilen het grootst in maart en het kleinst in december. Dit patroon weerspiegelt wellicht een seizoensmatige variatie in energiebehoefte en sociale activiteit van de vogels. Buiten het broedseizoen was de geleverde inspanning van mannetjes aanzienlijk groter dan van vrouwtjes en het hoogst aan het begin en aan het einde van de nacht. Het verschil tussen de geslachten zou kunnen samenhangen met de geringere vlieggkosten van de mannetjes als gevolg van hun lagere lichaamsgewicht.

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