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spatial dispersion and social interplay of mates and neighbours

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Published in:
Ornis Fennica

Publication date:
2013

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Jacobsen, L. B., Sunde, P., Rahbek, C., Dabelsteen, T., & Thorup, K. (2013). Territorial calls in the Little Owl (*Athene noctua*): spatial dispersion and social interplay of mates and neighbours. *Ornis Fennica*, *90*(1), 41-49.

Ornis Fennica 90:41–49. 2013

Territorial calls in the Little Owl (*Athene noctua*): spatial dispersion and social interplay of mates and neighbours

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Received 30 January 2012, accepted 25 June 2012

With the aim of quantifying spatio-temporal and social factors affecting territorial calls in Little Owls, we collected data on the calling behaviour of radio tracked individuals from a low-density population in Northern Jutland, Denmark. There was considerable seasonal variation in calling activity. During the breeding season, males calling away from the nest were located in the direction of the neighbouring nesting site, and males with a neighbour within hearing distance called more often than those with a longer distance to the nearest neighbour. Call posts were on average closer to the nest than telemetry observations, but did not appear to be related to mate distance. With a sound pressure level of 82 dB(A) at 1-m distance, the territorial calls were estimated to be audible to a distance of 4.4 km. Call posts were on average 4.1 m above the ground, which probably maximizes the transmission distance.

1. Introduction

In nocturnal species such as owls (Strigiformes), vocalisations constitute one of the most common ways of long-range signalling during the night. However, very little is known about the spatial behaviour of these birds in connection with calling (Delgado & Penteriani 2007).

Generally, the vocal signals of owls play a role (*i*) in ensuring access to sufficient food and thereby maintaining their fitness (Newton 1979), and (*ii*) are a way to defend the territory and to attract mates (Hirons 1985). The location of call posts in the territory may not be chosen at random (Delgado & Penteriani 2007, Campioni *et al*. 2010). As many owl species are living in year-round territories (Génot *et al*. 1997, Hansen 1952), their calls can be heard throughout the year, and for a number of species the calling activity increases prior to mating (Delgado & Penteriani 2007, Ritchison *et al.* 1988, Lundberg 1980), after which the calling activity decreases (Arsenault *et al.* 2002, Lawless *et al.* 1997). In territorial owl species, population density affects vocal activity (Tome 1997, Galeotti 1994). Relatively isolated pairs often call less, because they do not interact vocally with neighbour pairs (Penteriani 2003).

The Little Owl (*Athene noctua*) is widespread over most of Europe, but has been declining over much of its range in the past 30–40 years, including in Denmark (Thorup *et al.* 2010, Jacobsen 2006). It is a territorial, monogamous, nocturnal raptor that lives in the same area throughout the year and throughout its life (Génot *et al.*1997). It frequently engages in vocal interactions, particularly during the breeding season and when breeding in dense populations (Hardouin *et al*. 2006).

Vocalizations have been studied in detail in Little Owls, and up to 22 types of vocalizations have been described (Exo & Scherzinger 1989). Here we focus on male hoots as the territorial calls, and quantify a number of aspects of territorial calling in a highly fragmented population in northern Jutland, Denmark. We used radio telemetry to locate calling individuals. Radio telemetry provides presumably unbiased information about spatial interactions and interrelationships between mates and neighbours, at periods when they are not vocalising. We estimated the males' distances to the nest, mate, and neighbours during calling. We quantified calling activity during and outside the mating period, and of males with and without successful breeding attempts. Finally, we quantified the gradual fall in the sound-pressure level (SPL) of calls with distance. This, together with knowledge of hearing thresholds for owls (below 0 dB [SPL] in both the Barn Owl *Tyto alba* and the Great Horned Owl *Bubo virginianus*; Fay 1988), allowed us to estimate the calling range for the Little Owls and hence to evaluate the options for owl individuals for being in vocal contact with each other at the estimated distances within and between pairs.

2. Material and methods

2.1. Study area, and recording of vocal behaviour

Data were collected during 2005–2007 within a 27 ´ 30 km area in Northern Jutland, Denmark (56° N, 9° E), with a population of 40–50 pairs (i.e., 0.05–0.06 pairs/km^2). The area is intensively agriculturally managed, with over 80% of the total area being farmland (Sunde *et al*. 2009). Data for the present analyses were collected from 11 radio-tagged Little Owl males, of which 10 were mated with radio-tagged females over the entire course of the survey period. One of the males remained without a mate during the survey. The owls were captured with mist-nets or nest-box traps, and equipped with a back-pack radio transmitter (Bio Track Ltd., 7g including Teflon harness) with expected battery life being 12 months. After the survey, the owls were trapped again and transmitters were removed.

Little Owls make extensive use of acoustic communication (Schönn *et al.* 1991). During the breeding season, two call types predominate: the chewing call, produced by both males and females, and the hoot, produced only by males (Hardouin *et al.* 2008, Exo 1984). We focused on the hoots because they are used by males to defend their territories (Schönn *et al.* 1991), but included chewing calls in cases where territorial calls, beginning with hoots, ended with chewing calls (Hardouin *et al.* 2008).

All locations were obtained by radio tracking, i.e., triangulation within a 50–200 m distance using a VHF receiver (RX 98 from Televilt Int.) with an external directional antenna. The locations of the owls were spatially-referenced to a map (1:10,000) or registered with GPS navigators. Before locating an owl, light scaled from 1 (bright daylight) to 9 (pitch black), wind (Beaufort's scale), temperature, and precipitation (from 1 for no rain to 6 for heavy rain) was recorded.

2.2. Vocalisation data

We used two different datasets to evaluate factors affecting the vocalisations of male Little Owls. The first included up to three locations per night of males separated by at least one hour (hereafter "spot observations"), collected between April 2005 and June 2007 (Appendix 1). Autocorrelation analyses conducted with the Home Range Tools for ArcGIS software (HRT; Rodgers *et al.* 2007) showed that the spatial locations sampled following this protocol were not significantly spatially autocorrelated. For each spot observation, we registered whether or not the male was calling, and also recorded the position of its mate.

The second dataset focused on the breeding season, and consisted of one-hour periods during which all calls and movements of owls were registered (surveillance; Appendix 2). Up to five one-hour surveys were conducted monthly per individual, starting no later than half an hour before sunset and finishing by the sunrise at latest. For each one-hour period, we recorded the number of calls made by a given male, and the bird was located every time it changed its position. If also radio-tagged, a male's mate were located just before the start and immediately after each one-hour survey.

2.3. Statistical analysis of vocalisations

2.3.1. Variation in male calling during the year

We collected spot observations throughout the study years, for which we registered whether a given male was calling or not calling. To identify the probability for an owl to call, we considered the following explanatory variables: (1) month, (2) a four-category division of months (December–March, April–May, June–August, September–November), (3) a three-phase division according to breeding phase (non-breeding, incubation, and nestling/fledging), (4) the male's distance from nest, (5) the male's distance from his mate, and (6) the distance from the male's nest to the nearest neighbouring nest with a territory-holding male. We analysed the vocalisation probability as a binary response variable (calling or silent) with Generalised Linear Mixed Model (GLIMMIX procedure in SAS 9.2) with a logit link function and a binomial error distribution, with each owl and the different observation nights nested within owl as random variables. With regard to the male's distance from nest, we determined the distance between the nesting site and calling position at every locality where it had been calling.

In addition to the above-described whole-season analyses, we tested for effects of the female's assumed (7) fertility status and (8) mating status (mated or widowed) within the season of aroused vocal activity, i.e., March–May. We divided the data into three measuring intervals: the pre-fertile period (from January when the males begin to call to 14 days before the first egg was laid), the fertile period (from 14 days before until 14 days after the first egg was laid), and the post-fertile period (from 14 days after the first egg was laid until 15 August, i.e., the last date of fledged young heard begging for food). We used a paired *t*-test to test for the similarity between presumed fertile and infertile periods.

2.4.2. Variation in male calling during the breeding season

For each one-hour surveillance period, we modelled both whether the male was calling or not calling, and the number of calls (including zero observations). To identify the probability that an owl would call during a given surveillance period, we considered the following explanatory variables: (1) Julian day and Julian day^2 (to account for possible non-linear relationships), (2) light intensity, (3) the male's distance from nest, and (4) the male's distance from his mate. With regard to the latter, we used the distance between male and female at the end of the one-hour period if the male had not been calling.

We modelled the number of times a male was calling during each one-hour period using Poisson regression or Generalised Linear Model (with GLIMMIX procedure in SAS 9.2) with a log link function and Poisson error distribution adjusted for overdispersion. We identified final models by removing non-significant variables from the full model (backward elimination), except Owl ID which was included in all models.

To test whether calling was influenced by the distance from a male's nest to the nearest neighbouring nest with a territory-holding male, we compared estimated parameters of calling by each male from the final models with a neighbour within and outside hearing distance from the nest (here, set to 2 km) using a *t*-test. To estimate the distance between a nest of a given male and the nearest known neighbouring nest with a territory-holding male, we used ArcView GIS 3.3. We tested if the calling post were located in the direction (= 0°) of the nearest neighbouring pairs nest. We used two pairs of neighbouring males, from two localities, breeding 800 and 1200 m from each other, respec-

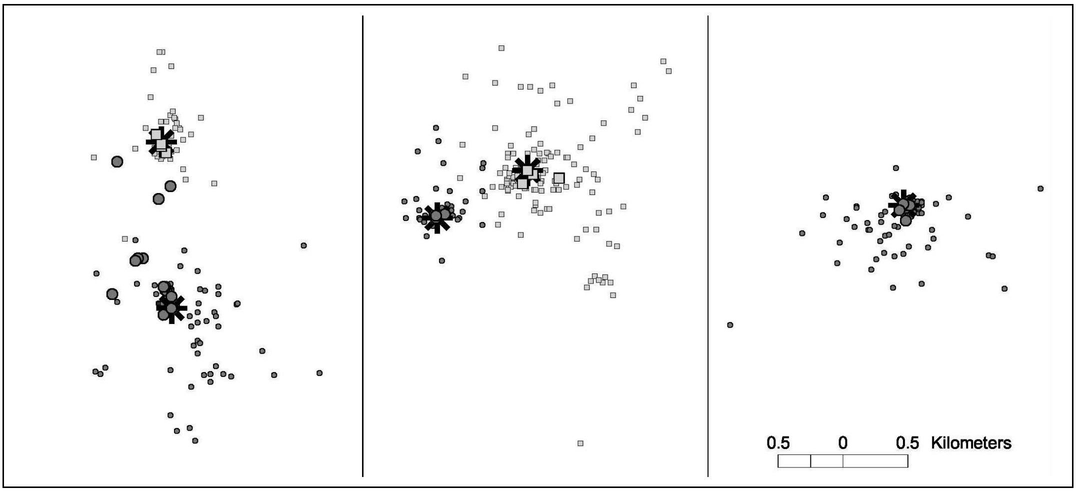

Fig.1. Examples of nocturnal locations of male Little Owls. (a–b) Locations of two neighbouring males as indicated by pale squares and dark circles. (c) Locations of a male with more than 3 km to the nearest neighbour. Large symbols show call posts, and nests are indicated with asterisks.

tively. The effects were evaluated using Oriana 2.02e (Copyright Kovach Computing Services).

2.5. Sound-pressure measurements

To estimate the sound-pressure level (SPL) of intensively-calling males as a function of distance, we first stimulated the measured subject with playback of rival calls. The output level of the CD player used for playback was set slightly lower than estimated SPL by listening to calling males to decrease the possibility for a scaring effect of an unnaturally high SPL (Dabelsteen 1981).When a male started to call in response to the playback, we stopped the recording and measured the SPL of the calls using a Brüel & Kjær Precision Sound Level Meter Type 2206 (A-filter, Fast setting) at a gradually decreasing distance from the calling male. We

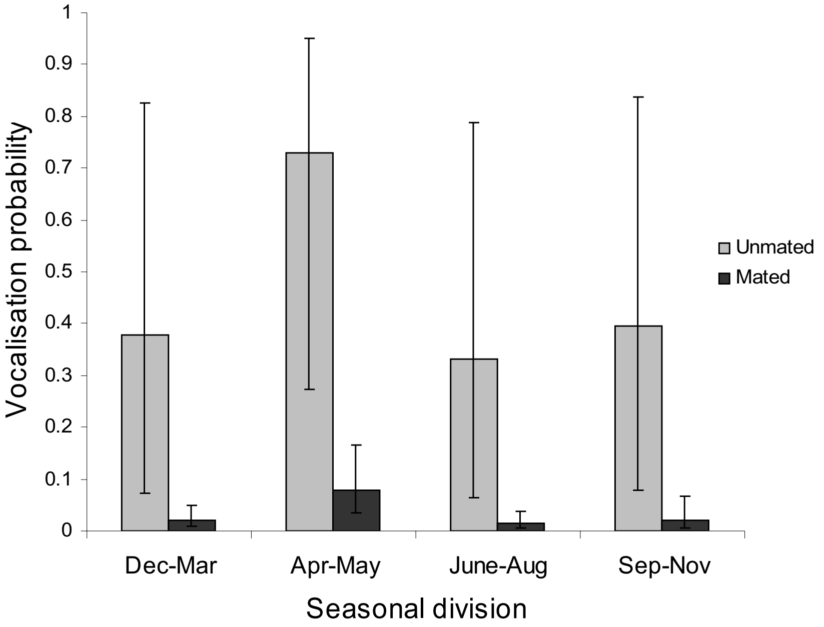

Fig. 2. Vocalisation probability of male Little Owls (least-square mean estimates from model presented in Table 1) along a seasonal gradient, with 95% CI.

marked each measuring position with a stick, and the next day measured the distance between each stick and the position of the calling male. We performed SPL measurements on six different males for eight different nights between 22 April and 7 May 2006. They all had incubating females. As we measured a different number of calls (1–28) at different distances, we calculated an average SPL for each distance and used these averages in a regression of SPL on distance.

3. Results

3.1. Spatial locations of call posts, and sound pressure of calls

The call posts were 4.1 ± 2.0 (mean ± SD) m above the ground. Of 70 call posts, 36% were trees, 23% roofs of buildings, 21% fence posts, and 14% hedge rows. Call posts were located 84 ± 121 m from the nest (range 3–603 m, $N = 64$). The distance between duet-calling males was 730 ± 334 m (range 365–1,182 m, $N = 24$). For all males, the average size of the minimum convex polygon based on call posts was 2.3 ha (1.1 SE, range 0.3–5.3).

The sound-pressure level (SPL) decreased as a function of distance following y = –22.5 [log10 (distance)] + 82. Thus, according to the regression, 0 dB (A) was reached at 4.4 (95% Confidence interval: [1.1, 15]) km distance. The average decrease in SPL was 7 dB (A) per doubling of distance, which is slightly more than the 6 dB expected from the distance law (Bradbury & Vehrencamp 2011).

3.2. Seasonal variation in calling rates

Radio-tagged individuals vocalised 44 times out of a total number of 791 spot observations, and 14 out of 346 spot observations where the mate distance was established (Fig. 1). In terms of temporal scale, vocal activity was higher in April–May than during the rest of the year (Fig. 2), and higher for unmated than for mated males (Table 1). However, it did not vary significantly between the breeding and non-breeding seasons (Table 1). Within the fertile period, there was no significant difference in calling rate between fertile and unfertile periods of the female ($t_6 = 0.77$, $P = 0.47$). In terms of spatial scale, the vocalisation frequency correlated negatively with the distance to the nest (Table 1, Fig. 3a), but was independent of the distance to the mate (Table 1).

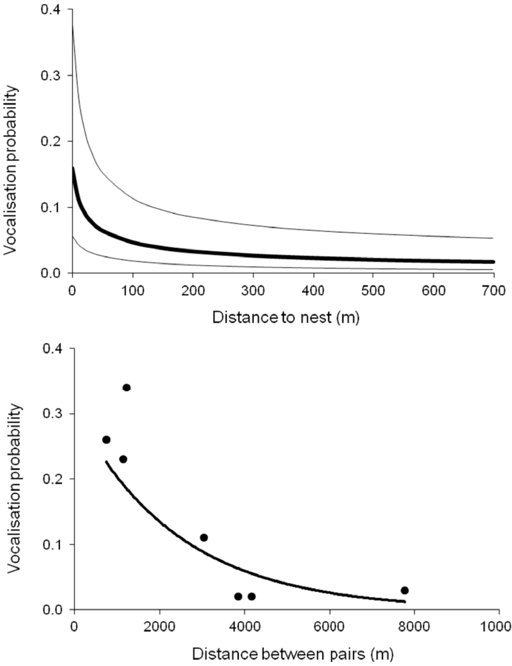

Fig. 3. (a) Vocalisation probability in the Little Owl, as a function of distance to nest estimated from logistic regression (see Table 1); thin lines indicate 95% CI. (b) Vocalisation probability of radio-tagged males plotted against distance from nest to the nearest known neighbour.

3.3. Variation in calling rates during the breeding season

Radio-tagged Little Owls vocalised in 27 out of a total of 222 one-hour surveillance periods between January and July in 2006 (average 2.9 ± 13.3 SD; max. 129 calls hour^{-1}). Vocal activity both in terms of whether an owl called or not and the number of calls varied within this period (Table 2). The vocalisation rate correlated negatively darkness score (Table 2). We did not find significant effects of distance to the nest or mate during this period (Table 2). Males with nests within 2 km from other males (a conservative estimate of hear-

Table 1. Generalised linear mixed model for the influence of selected model parameters on the vocalisation probability of radio-tagged male Little Owls. Logit link function was applied; individual testing for univariate and type III effects in the least adequate model, comprised by significant terms only. Variables in italics did not correlate significantly with the vocalisation probability. For data, see Appendix 1.

	Univariate effects			Type III effects			Predicted relation		
Effect	*F*	*df*	*P*	*F*	*df*	*P*	Parameter	*B*	SE (*B*)
							Intercept	–0.561	0.906
Nest distance	11.58	1, 786	0.0007	17.16	1, 688	< 0.0001	log(x + 1)	–1.566	0.378
Mate status	28.12	1, 205	< 0.0001	17.27	1, 6.16	0.0056	Single	3.446	0.829
							Paired	0.000	
Season	4.23	3, 518	0.0057	4.7	3, 389	0.0031	Dec–Mar	–0.077	0.672
							Apr–May	1.407	0.665
							June–Aug	–0.279	0.682
							Sep–Nov	0.000	
Breeding status	0.45	2, 686	0.63	0.05	2, 355	0.95			
Mate distance	0.90	1, 333	0.34	0.00	1, 329	0.98			
Month*	0.93	11, 776	0.51						
Owl identity								0.273	0.390
Date (Owl ID)								0.687	0.553

* Not adjusted for owl identity in order to achieve model convergence

Table 2. Generalised linear mixed model for the influence of selected model parameters on the number of calls of radio-tagged male Little Owls surveyed during one-hour periods (see text for details). Log link function and Poisson error distribution were applied, owl identity was included as a fixed effect. Variables in italics did not correlate significantly with vocalisation probabilities. For data, see Appendix 2.

	Univariate effects			Type III effects			Predicted relation		
Effect	*F*	*df*	*P*	*F*	*df*	*P*	Parameter	*B*	SE (*B*)
Owl ID	0.80	6, 215	0.57	1.32	5, 210	0.25	Intercept	0.76	2.26
Julian day	0.09	1, 220	0.76	8.92	1, 210	0.0032	Julian day	0.145	0.047
Julian day^2	0.38	1, 220	0.54	9.85	1, 210	0.0019	Julian day^2	–0.0007	0.0002
Light level	4.59	1, 220	0.03	7.71	1, 210	0.006	Light level	–0.52	0.190
Distance mate	1.34	1, 220	0.25	2.77	1, 210	0.097	Owl 2	–2.79	1.11
Distance nest	3.50	1, 220	0.063	0.12	1, 210	0.73	Owl 7	–3.71	1.21
							Owl 15	–2.39	1.13
							Owl 19	–5.47	2.36
							Owl 21	–4.73	5.29
							Owl 22	0	0

ing distance) apparently called more than those without ($t_5 = –3.473$, $P = 0.018$; Fig. 3b). Call post locations more than 50 m from the nest for the two males with neighbouring nests within 1200 m, were located in the direction of the nest of neighbouring pairs (Rayleigh test: $N = 16$, $Z = 5.30$, $P = 0.004$; CI = [322°, 25°]; $N = 5$; $Z = 4.81$, $P = 0.002$; CI = [335°, 7°]). The directions from the nest to call post locations (> 50 m) could not be distinguished from random in one male with three neighbours within 1,200 m or in one male with only a floater as neighbour.

4. Discussion

The height of call posts probably maximizes the transmission distance (Marten & Maler 1977). However, Dabelsteen *et al*. (1993) have suggested that the main reason for a male to sing at an elevated position is to increase their ability to hear responses of other individuals, rather than to maximize the transmission. A call posts close to a nest may be used to draw attention to a suitable nesting site (Klatt & Ritchison 1996), and high levels of territorial behaviour are to be expected near the nest. The more distant the call posts were from the nest, the closer they were to the nests of neighboring breeding pairs, suggesting that calls may have a territorial function, even in very low densities of the focal species.

Under optimal conditions, Little Owls are likely to be able to hear each other further away than 4 km distance. With an average home range size (90% Minimum Convex Polygons of 41 ha (Sunde *et al*. 2009) and an inclination to primarily vocalise adjacent to their nests (this study), territorial calls should be audible for the female for most of the time, and hence be an effective means of communication across the home range.

The strong seasonality in calling frequency, and the fact that calling was concentrated to the vicinity of the nest indicate that Little Owl males mainly attempt to defend the nest and their mate when calling. This is in contrast to some other owl species that are most vocally active in the peripheries of their home range (Sunde & Bølstad 2004). The negative correlation between calling rates and presence of neighbouring pairs close by suggest that social display may be stimulated by the presence of neighbours, a result similar for several owl species (Penteriani 2003, Zuberogoitia *et al*. 2007, Sunde 2011). We did not find evidence for males being more aggressive during the fertile period of their mate, as could have been expected had they been concerned about extra-pair copulations (Birkhead & Møller 1992, Birkhead 1979). This is also in line with reports of very low rates of extra-pair paternity in Little Owls in much higher population densities than in the present study (Müller *et al.* 2001). Elevated rates of calling in single males suggest that calling also served in mate attraction.

Population census protocols for Little Owls and other owl species assume equal probability of detection regardless of population density (Hardey *et al.* 2006, Thompson 2002; but see Penteriani *et al.* 2002). However, if willingness to respond to playback correlates with population density, relatively more pairs will remain undetected in thin populations, unless playback surveys are repeated several times.

Acknowledgements. The telemetry study was funded by the Villum-Kann Rasmussen Foundation. Thanks to Monika Chrenkova for comments on a previous version of the manuscript.

Territoriella läten hos minervaugglan: rumslig fördelning och socialt samspel

Syftet men denna studie var att kvantifiera hur rumsliga, temporära och sociala faktorer påverkar territoriell vokal aktivitet hos minervaugglan. Vi samlade data om revirhävdande vokal aktivitet hos individer märkta med radiosändare i en Nord-Jylländsk population med låg täthet. Årstidsvariationen i aktiviteten var betydande. Hanar som under häckningsperioden ropade långt från boet lokaliserades i grannrevirets riktning. Hanar som hade en granne inom hörbart avstånd ropade oftare jämfört med hanar vars närmaste granne var längre bort. I genomsnitt var ropplatserna närmare boet än telemetriobservationerna, men de verkade inte ha något samband med avståndet till partnern. Utgående från den på 1 m avstånd uppmätta ljudtrycksnivån 82 dB(A) estimerades att de territoriella lätena hörs på 4,4 km avstånd. Ropplatserna var i medeltal på 4,1 m höjd ovanför marken, vilket troligtvis maximerar transmissionen.

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Appendix 1. Seasonal distribution of spot observations (*N* = 791) of 13 Little Owl males; data collected from April 2005 to June 2007.

Owl ID	Vocal	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
2	No	11	24	15	24	12	32	24	7	13	11	7	7	187
	Yes	0	2	0	3	1	0	0	0	0	0	0	0	6
6	No	6	19	8	7	0	9	4	0	8	3	1	2	67
	Yes	0	6	4	4	0	0	0	0	0	0	0	0	14
7	No	8	23	19	13	5	6	5	0	7	3	1	2	92
	Yes	0	0	1	3	2	0	0	0	0	0	0	0	6
9	No	0	0	0	0	0	0	0	0	0	3	1	0	4
	Yes	0	0	0	0	0	0	0	0	0	0	0	0	0
12	No	0	15	10	6	3	7	13	6	7	0	0	0	67
	Yes	0	1	0	1	0	3	0	0	0	0	0	0	5
15	No	0	5	20	12	4	12	2	0	0	0	0	0	55
	Yes	0	0	0	2	0	3	0	0	0	0	0	0	5
17	No	0	0	0	19	5	7	12	2	0	0	0	0	45
	Yes	0	0	0	1	0	0	0	0	0	0	0	0	1
19	No	0	0	0	10	6	14	3	0	0	0	0	0	33
	Yes	0	0	0	0	0	0	0	0	0	0	0	0	0
21	No	0	0	0	0	0	18	5	0	0	0	0	0	23
	Yes	0	0	0	0	0	0	0	0	0	0	0	0	0
22	No	7	1	8	0	0	10	13	9	4	7	4	0	63
	Yes	0	0	0	0	0	1	0	1	1	1	0	0	4
23	No	0	0	0	0	0	10	15	0	0	0	0	0	25
	Yes	0	0	0	0	0	0	0	0	0	0	0	0	0
26	No	7	0	0	0	0	7	12	8	4	10	5	6	59
	Yes	1	0	0	0	0	0	0	0	2	0	0	0	3
30	No	5	1	10	6	0	5	0	0	0	0	0	0	27
	Yes	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2. Seasonal distribution of one-hour surveys (*N* = 222) of 7 Little Owl males; data collected from January to July 2006.

Owl ID	Vocal	Jan	Feb	Mar	Apr	May	Jun	Jul	Total
2	No	4	13	10	8	2	9	11	57
	Yes	0	1	0	3	1	0	0	5
7	No	2	11	13	11	4	0	0	41
	Yes	0	0	0	2	2	0	0	4
15	No	0	3	13	9	4	7	2	38
	Yes	0	0	5	2	0	6	0	13
17	No	0	0	0	9	5	2	0	16
	Yes	0	0	0	1	0	0	0	1
19	No	0	0	0	6	5	13	1	25
	Yes	0	0	0	1	0	0	0	1
21	No	0	0	0	0	0	6	2	8
	Yes	0	0	0	0	0	1	0	1
22	No	0	0	0	0	0	3	7	10
	Yes	0	0	0	0	0	2	0	2