

Seasonal dynamics in social behaviour and spacing patterns of the Little Owl *Athene noctua*

Iñigo Zuberogoitia, Jabi Zabala, José Antonio Martínez, Sonia Hidalgo, José Enrique Martínez, Ainara Azkona & Iñaki Castillo

I. Zuberogoitia: Estudios Medioambientales Icarus s.l., Oficina Técnica, Apd. 106, E-48940 Leioa, Bizkaia, Spain. Zuberogoitia@icarus.es (* Correspondence autor)

J. Zabala: Sociedad para el Estudio de las Aves Rapaces (SEAR), C/ Kart Marx 15, 4°F, 48950 Erandio, Bizkaia, Spain

S. Hidalgo: Sociedad para el Estudio de las Aves Rapaces (SEAR), C/ Kart Marx 15, 4°F, 48950 Erandio, Bizkaia, Spain

A. Azkona: Sociedad para el Estudio de las Aves Rapaces (SEAR), C/ Kart Marx 15, 4°F, 48950 Erandio, Bizkaia, Spain

I. Castillo: Sociedad para el Estudio de las Aves Rapaces (SEAR), C/ Kart Marx 15, 4°F, 48950 Erandio, Bizkaia, Spain

J.A. Martínez: C/ Juan de la Cierva 43, El Campello, E-03560 Alicante, Spain. qvcociers@hotmail.com

J.E. Martínez. Departamento de Ecología e Hidrología, Universidad de Murcia, E-30100 Murcia, Spain

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Most owl species exhibit territorial behaviour in order to have sufficient resources to maintain their fitness and biological success. The Little Owl (*Athene noctua*) has been considered a territorial species, although some authors have pointed to movements and social interactions outside a particular territory. We hypothesise that the spatial behaviour and social organisation of Little Owl follows a complex pattern, which varies throughout the year. We radio-tracked nine Little Owls in an area of 10 km² over nine months, paying particular attention to home range variation, social interaction and vocal behaviour. Home range size and overlap varied markedly throughout the year, with maximums in winter, and minimum size and overlap during the breeding season. Little Owls showed exclusive home ranges during the breeding season, whereas home range overlap was frequent in winter. Owls which had lost clutches increased their home ranges and shared the same foraging areas with other owls. Vocal activity was low all year round, except in the months immediately prior to courtship. Increase of vocal behaviour was therefore also associated with a reduction in home range.



1. Introduction

Most owls, like most raptors, exhibit territorial behaviour in order to maintain sufficient resources to improve their fitness (Newton 1979). However, territorial behaviour only takes place under certain conditions and, depending on environmental conditions, a species may show different spatial behaviour, ranging from group-living territories to nomadism (Newton 1979, Macdonald 1983, Kruuk 1989, Donazar 1993, Powell 1994, Arroyo *et al.* 2001, Sergio & Newton 2003). Territory holders have exclusive or priority access to potentially limited resources and, under certain circumstances, some species may develop high levels of intraspecific aggressive behaviour in order to keep and enjoy all the resources of a given area (Southern 1970, Rohner 1997, Zuberogoitia & Martínez 2000, Sunde & Bolstad 2004). Although settlement models predict that individuals will eschew conspecifics to avoid negative density-dependent effects on fitness (Fretwell & Lucas 1970), aggregated distributions may favour access to mates (Serrano 2001), exclusive or preferential use of food or other resources (Donazar 1993), enhance information flow regarding protection against predators or the maintenance of social interaction (Galeotti & Pavan 1993, Appleby & Redpath 1997, Van Nieuwenhuysse & Bekaert 2002) and help individuals to assess habitat quality (Serrano 2001, Sergio & Penteriani 2005). Among the disadvantages of territoriality is the net cost of defending a territory after taking into account energy expenditure and risk of injury etc. (Powell 1994). Therefore, if territoriality takes place, benefits to individuals must outweigh costs (Davies 1978, Powell 2000, Begon *et al.* 2006). Accordingly, when the main limiting factor is the nesting site and definitely not food, higher levels of territorial behaviour would be expected around the nest and its intensity would decrease with distance from the nest (Adams 2001). Many of the variables that influence territoriality change markedly throughout the year (e.g. food availability and nest requirements) and could therefore result in changes in territorial behaviour (Powell 2000).

The Little Owl (*Athene noctua*) is a declining species across Europe (Génot & Van Nieuwenhuysse 2002). Although it is still abundant in Spain, housing developments, habitat fragmentation and

extensive road building are degrading preferred habitats and causing sharp declines in local populations (Martínez & Zuberogoitia 2004a, Zabala *et al.* 2006). Distribution is typically uneven in many areas of the north and east of Spain, where high-density clusters are found in a matrix of very low density stretches (Zuberogoitia 2002, Martínez & Zuberogoitia 2004a, b). As some authors suggest, this pattern is partly the result of habitat fragmentation (Martínez & Zuberogoitia 2004a, Cornulier & Bretagnolle 2006), and partly due to the intensity and importance of social interaction (Van Nieuwenhuysse & Bekaert 2002, Hardouin *et al.* 2006).

In the present paper we studied the spatial behaviour of Little Owls by radio-tracking and recording vocal activity patterns throughout the year. Our aim was to measure variations in the spatial behaviour of the Little Owl, particularly concerning social interaction. Our main hypothesis was that the social behaviour and organisation of the Little Owl follows a complex pattern, varying during the year in accordance with changes in its bio-ecological needs, including the establishment and disestablishment of territories.

2. Study area and methods

2.1. Study area

The Little Owl population in Bizkaia (Northern Spain) is divided among small heterogeneous distribution patches, whose densities vary with the predominant vegetation types, but which are higher in areas of open fields (Zabala *et al.* 2006, Zuberogoitia & Campos 1997, 1998). We selected one of these patches according to the following characteristics: 1) a high density of Little Owls: in the study area some fields contained seven pairs/km² and the average density in the valley was 2.24 pairs/km² (Zuberogoitia & Campos 1998), 2) knowledge of the Little Owl population size and distribution, which had been censused previously (Zuberogoitia & Campos 1997, 1998). This population was located in the Mungia valley, a 10 km² area dominated by pasture for cattle, and smallholdings. The climate is rainy oceanic, with annual rainfall ranging between 1200 and 2200 mm, and annual average temperatures varying from 13.8°C

Table 1. Sex (M = male, F = female), age (following Euring code: 5 = 2nd calendar year, 4 = 2nd cy or older, 6 = 3rd cy or older, 8 = 4th cy or older, H = 8th cy see i.e. Martínez *et al.* 2002), breeding success and home range, monthly and total home range (ha) of the nine radio-tracked Little Owls over the monitoring period. The home-range estimator used was the 95% minimum convex polygon. In order to establish differences between methods to obtain the home range area, it was also calculated the total home range using the Kernel 95% and 50% probability function.

| | Age | Breeding | Monthly home range (ha) | | | | | | | | | Home range (ha) | | | |
|----|-----|-----------|-------------------------|-------|------|------|-----|-----|------|------|------|-----------------|-------|------|-----|
| | | | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Mean ±SD | MCP95 | K95 | K50 |
| M1 | 6 | 2 owlets | 4.6 | 4.4 | 19.3 | 7.8 | 3.3 | 7.7 | 8.2 | 6.5 | 6.7 | 7.6±4.7 | 15.0 | 10.9 | 1.3 |
| M2 | 8 | Failed | – | 2.2 | 10.8 | 29.1 | 5.3 | 6.6 | 23.1 | 1.9 | 13.1 | 11.5±9.9 | 15.3 | 13.1 | 1.4 |
| M3 | 5 | No paired | – | 4.9 | 17.4 | 8.7 | 9.9 | 7.4 | 7.0 | 7.2 | 10.0 | 9.1±3.8 | 33.3 | 33.5 | 4.5 |
| F1 | 4 | Failed | 6.8 | 9.4 | 10.8 | 13.1 | 4.1 | 7.1 | 13.0 | 5.0 | 8.4 | 8.6±3.3 | 16.0 | 17.6 | 1.6 |
| F2 | H | 2 owlets | – | – | – | 3.9 | 0.1 | 1.3 | 8.9 | 15.0 | 4.0 | 5.5±5.5 | 18.6 | 7.2 | 0.9 |
| F3 | 6 | 1 owlet | 19.5 | 5.6 | 6.4 | 1.2 | – | – | – | – | – | 8.2±7.9 | 15.6 | 2.5 | 0.6 |
| F4 | 6 | Failed | – | 18.8 | 10.9 | 9.7 | 5.3 | 3.7 | 5.9 | 8.0 | 11.7 | 9.2±4.8 | 14.6 | 13.2 | 1.0 |
| F5 | 8 | 3 owlets | 0.4 | 6.8 | 10.9 | 7.1 | 1.6 | 1.1 | 1.6 | 1.4 | 3.0 | 3.8±3.6 | 10.3 | 6.6 | 0.7 |
| F6 | 6 | 2 owlets | 13.5 | 221.2 | 57.3 | 35.5 | 5.0 | 1.0 | 37.6 | 65.4 | 5.8 | 49.2±68.6 | 123.2 | 88.4 | 7.5 |

to 12°C. Winters are mild and there is no summer drought.

2.2. Trapping and handling Little Owls

We chose a sample unit of 1 km² where we located seven territories, and set up three trapping points 100 m apart. These points were an equal distance from three known nests. We started to trap owls in the second half of December 2003 and continued until March 2004. Trapping took place at only one point per day, where we set up two mist nets and a tape recorder, playing three different recordings of Little Owl voices, changing them between days. One of the nets was placed perpendicularly to the cattle fences, and the tape recorder was located on the ground below this net. Another net was set perpendicularly to the first, parallel to the fence and 4 m away. In addition, we trapped three Little Owls by setting up a net immediately in front of their roosting places. The age and sex of every Little Owl was assessed following Martínez *et al.* (2002).

We captured and fitted nine Little Owls with radio tags, which were slung over the back using a Teflon harness (Biotrack, Dorset, UK).

2.3. Radio-tracking

Radio-tracking took place at night, three to four times every week over nine months (January to

September). We used the point sampling method, recording the same number of locations for each individual, at the same times of night, thus avoiding bias due to autocorrelation and timetabling seasonal changes (Kenward 2001). The same author suggested that this method provides not only a standard range, but is also useful in other analyses such as examining sociality based on relationships between simultaneous locations of adjacent individuals. The monitoring schedule began at dusk and lasted for one to four hours, starting at a different place each night so as to avoid bias related to usual behaviour of the individuals. A hand-held 3-element Yagi antenna, a TRX-1000S receiver (Wildlife Materials Inc. Carbondale, USA), a Sika model receiver (Biotrack, Dorset, UK) and a RX8910 receiver (Televit International AB) were deployed on foot by three teams using walky-talkies. We tried to find the nine Little Owls at the same time in order to study social interaction accurately (Kenward 2001). First, we scanned the main fields so as to obtain a preliminary estimate of the approximate position of all the owls, and subsequently monitored every Little Owl located in the same place at the same time. Fixes were taken within 50 m of the animal using the homing technique (White & Garrot 1990) with an accuracy of 4 m². During the study period we obtained 1223 different fixes for the nine Little Owls (122.8 ± 30.8, range 61–160). The artificial lights around the study area and vocal activity sometimes helped us confirm the precision of the telemetry locations.

Diurnal roosts were located two or three times every month.

During the radio-tracking activities we also monitored Little Owl vocalization. For this purpose, we noted every call (song, contact voice, alarm voice and others) produced by a Little Owl, and recorded the amount of time (in seconds) spent vocalizing. Moreover, every time a Little Owl was heard we scanned radio-frequencies in order to know which individual was calling.

2.4. Data treatment

Fixes were plotted on high resolution aerial photographs (0.5 m pixel) implemented in a Geographic Information System (GIS) with an estimated accuracy of 4 m². The home-range estimator used was the 95% minimum convex polygon and was calculated for each month (MCP, White & Garrot 1990). The degree of home range overlap among Little Owls was calculated monthly by measuring the surface area (ha) that individuals shared and values between non-overlapping home ranges were also considered. Arcview Spatial software was used for the analysis.

To analyse the social interactions and the possibility of dynamic territoriality (dominant individuals having preferential, not exclusive, use of resources), we followed the method proposed by Kenward (2001) for dynamic interaction: if there are n pairs of locations x_{1j}, y_{1j} and x_{2j}, y_{2j} for each dyad, the observed mean distance is

$$D_0 = \sum \frac{\sqrt{(x_{1j} - x_{2j})^2 + (y_{1j} - y_{2j})^2}}{n} \quad (1)$$

The distances between Little Owls were then compared using Mann-Whitney test with the expected mean distance obtained by randomising all possible pairs of locations at which the animals were detected (Kenward 2001).

3. Results

3.1. Individual data

We monitored nine Little Owls: two established pairs, four adult resident females and a 1-yr-old

male. Four females bred successfully and the other two lost the clutches (Table 1). The 1-yr-old male did not mate. The average nearest neighbour distance, considering nesting sites, was 739.42 ± 421.88 m (range 99–1,698 m).

3.2. Home ranges

The annual home range of Little Owls was 15.1 ha \pm 2.46 (range 10.3–18.6 ha) for every paired owl, although 123.2 ha for one paired female (Table 1). The only unpaired Little Owl had a home range twice as large (33.3 ha) as its neighbours.

The home range area varied over the months (Kruskal-Wallis Test, $H = 16.63$, d.f. = 8, $P = 0.034$). The home range was larger during winter-time (February) than in any other season, decreasing during the pre-courtship and increasing again just after the breeding period (Fig. 1).

The extension of the mean home range of successful owls during the breeding months (3.42 ± 2.84 ha, $n = 5$) was significantly lower (Mann-Whitney test, $U = 21$, $n = 21$, $P = 0.019$) than the home range of the owls that failed to breed (9.33 ± 7.98 ha, $n = 3$).

The home range overlap varied with the time of year (Kruskal-Wallis test, $H = 99.85$, d.f. = 8, $P < 0.001$). Overlap was maximum in late winter and minimum during the breeding season and summer (Fig. 1).

3.3. Dynamic interaction

During the study period we obtained 1,223 high resolution fixes (4 m² accuracy) for the nine Little Owls. The average distance between owls was 560 ± 371 m (range 0–2689 m). Distances between owls were obviously shorter than expected when pairs were considered (Mann-Whitney test, $P < 0.01$). The female with the largest home range spent more time than expected (Mann-Whitney test, $P < 0.01$) far from the other Little Owls, although during winter we detected her sharing the same foraging sites twice with one male and four times with three different females. The subadult male was always at a shorter distance than expected with respect to all the Little Owls except the latter female. His home range overlapped exten-

Fig. 1. Monthly variation of the home range (mean \pm S.D.) of the nine radio-tracked Little Owls during the monitoring period (black squares). Percentages (mean \pm S.D.) of home range overlap between the nine radio-tracked Little Owls during the monitoring period (grey circles).

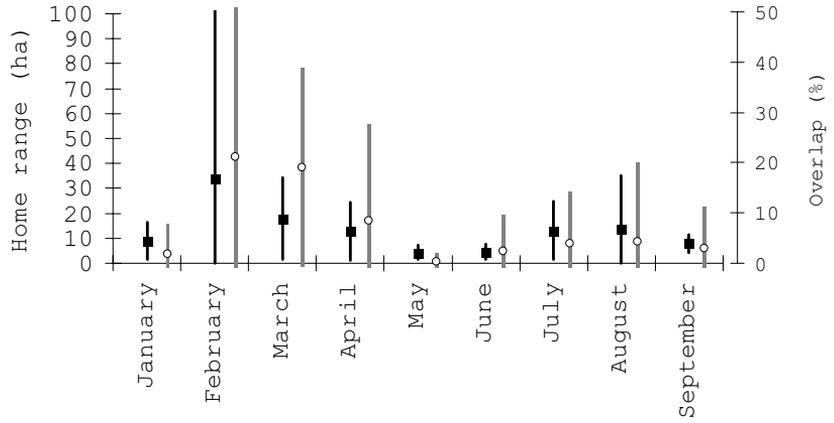
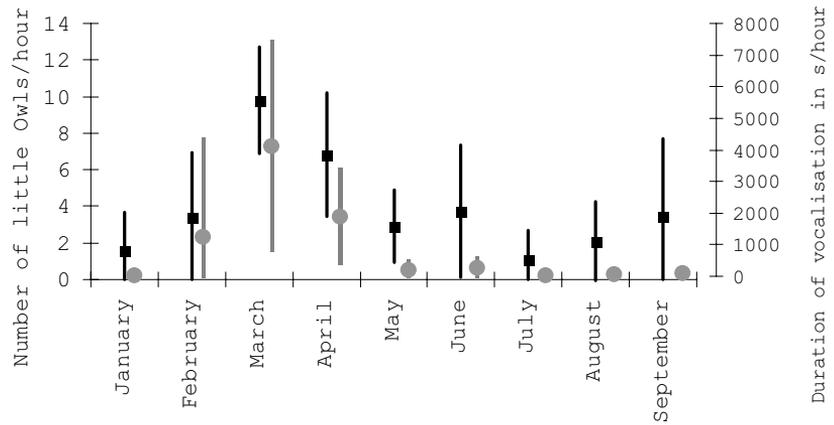


Fig. 2. Monthly variation in the number of Little Owls heard per hour (mean \pm S.D., black squares) and in the vocal activity, summarizing the amount of seconds (mean \pm S.D.) per hour that every Little Owl were singing (grey circles), during the nine monitoring months in the study area.



sively with all of them, although he only shared the same places simultaneously with one male ($n = 8$) and one female ($n = 3$).

One of the pairs was closer than expected (Mann-Whitney test, $P < 0.01$) to the neighbouring female, but this female only shared the same place twice with the male and never with the female. The other pair was closer than expected (Mann-Whitney test, $P < 0.01$) to two females.

Two females shared the same roost (barn) five times in March. Moreover, one of these females was once recorded close to the other female.

The analysis of interactions between every Little Owl and the other owls, considering the average data for every month, revealed significant differences (Friedman test for paired samples, X^2_6 range between 26.06 and 34.57, $P < 0.001$). Obviously, the established pairs had the lowest distances between two owls when the interactions between them were considered. However, consider-

ing all the interaction data the minimum value was obtained for the 1-yr-old male and the highest value for the female with the greater home range.

3.4. Vocal activity

On average, during 250 hours of listening effort, 1.87 Little Owl/hour (S.D. = 2.18) produced vocalisations, with an average 414 seconds/hour of vocal activity (S.D. = 1248).

The vocal activity of Little Owls varied seasonally. The number of Little Owls recorded every hour was lowest during winter and summer, whilst the highest number of owls calling was detected in March and April, when the mating season started (Kruskal-Wallis test, $H = 38.92$, $d.f. = 8$, $P < 0.001$, Fig. 2). Likewise, the amount of time spent singing was much higher during these months (Kruskal-Wallis test, $H = 52.97$, $d.f. = 8$, $P < 0.001$, Fig. 2).

4. Discussion

The average annual home range recorded in the study area, 15 ha, was similar to that obtained in other high-density areas (Exo 1992, Finck 1988, Van Nieuwenhuysse *et al.* in press). Also in agreement with these authors, home range varied throughout the year, being larger in winter, especially in March (Exo 1992, Génot & Wilhelm 1993). Exo (1992) suggested that this increase was due to courtship behaviour, although in our study area the courtship season starts in April (Zuberogoitia & Torres 1997), when both home range and overlap were minimal. The smallest home range was obtained in May (4.3 ha), during the laying period, followed by June when the chicks were being reared. We suggest that the reduction in home range during the breeding period is due to the high energy demands of courtship, laying, hatching and rearing of chicks. During this time, both adults must forage close to the nest in order to minimise the energy expended in frequent trips from the nest to foraging fields and *vice versa* (Rosenberg & McKelvey 1999, Adams 2001, Génot & Lecomte 2004, Verhaeghe *et al.* 1996). This seems to be reinforced by our finding that home ranges were significantly smaller for successfully breeding Little Owls than for unsuccessful pairs during the breeding season. Having failed to breed, these pairs started to move longer distances, which further supports our hypothesis. As these did not need to return to the nest with prey, they could eat *in situ*, which allowed them to use more intensive foraging areas.

The home range and overlap were higher during the winter, when Little Owls shared pastures regardless of sex, age or status, sometimes being found very close to each other. Such a disruption of home range boundaries outside of the breeding season is probably a consequence of changes in the needs of individuals and of the dispersion and unpredictability of areas with abundant food (Macdonald 1983, Adams 2001).

Little or no aggression was observed among Little Owls found in the same place simultaneously. During winter, it was very common to find 3–6 monitored Little Owls perched along less than 50 m of the same fence at the same time. This behaviour was not sex-related. In fact, one female, which usually rested in the same house, was found

on five different occasions during winter resting during daylight hours in the house of the other female, both sleeping in the same corner, close to a third Little Owl.

During winter and summer the vocal activity of Little Owls was very low, with only a few short duration calls. Only during the pre-courtship and courtship periods did vocal activity increase significantly and Little Owls could be heard frequently producing long calls. Interestingly, as vocal activity increased in frequency and duration, home range and overlap decreased. It seems that Little Owls start to settle territorial boundaries prior to the breeding season, when home ranges become almost exclusive, at least during the care of the breeding mates.

Considering species conservation strategies and population censuses, it is important to identify differences in monthly behaviour. Our study reveals that winter aggregation in some fields could indicate important feeding areas and could help to establish social relationships thus improving neighbourhood knowledge (see Hardouin *et al.* 2006). Meanwhile, further studies focused on the breeding period would be important in order to determine the ecological requirements for successful breeding.

The relevance of social activities in the life-cycle of the Little Owl suggests further conservation possibilities for re-colonising depleted areas or colonising designated areas (Ward & Schlossberg 2004). Firstly, studies must determine the causes of population decline (e.g., Martínez & Zuberogoitia 2004b) allowing remediation of the causes of death. The designation of good-quality areas (both for breeding and communal feeding areas) should follow by modelling habitat preferences (Van Nieuwenhuysse & Leysen 2001, Martínez & Zuberogoitia 2004b, c). Then, reproducing appropriate social clues may enhance the probability of re-colonisation by dispersing individuals. This may hold true especially for short-dispersing species such as the Little Owl (Génot & Van Nieuwenhuysse 2002).

Moreover, conservation efforts on persisting populations should focus on clumps and dispersal areas, rather than on individual territories (Génot & Van Nieuwenhuysse 2002, Van Nieuwenhuysse & Bekaert 2002), which, in turn, implies that studies on habitat preferences or habitat use should

previously determine the appropriate spatial scale (Martínez *et al.* 2003).

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Minervanpöllön sosiaalisen käyttäytymisen dynamiikkaa

Suurin osa pöllöistä on reviirilintuja. Minervanpöllön on reviirilintu, vaikka tiedetäänkin, että minervanpöllöjen reviirien koot vaihtelevat vuodenaikojen mukaan. Seurasimme yhdeksää radiolähettimin varustettua minervanpöllöä 10 km² alueella yhdeksän kuukauden ajan. Erityisesti kiinnitimme huomiota reviirin koon vaihteluun, sosiaaliseen kanssakäymiseen ja ääntelyyn. Reviirien koko ja päällekkäisyys vaihtelivat seuranta-jakson aikana. Suurimmillaan reviirin olivat talvella ja pienimmillään pesinnän aikana. Pesintäreviireillä ei esiintynyt päällekkäisyyttä. Pesinnänsään epäonnistuneet yksilöt laajensivat reviiriään. Tällöin ruokailupaikat saattoivat olla yhteisiä toisten yksilöiden reviirien kanssa. Ääntely oli vuoden ympäri vähäistä lukuunottamatta pesintää edeltävää aikaa.

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