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A telemetry study of the social organization of a tawny owl (*Strix aluco*) population

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Abstract

The spatial dispersion and social interactions were studied in 11 neighbouring pairs of radio-tagged tawny owls *Strix aluco* in a deciduous wood in Denmark from 1998–2001. The numbers and shapes of territories were stable throughout the survey and similar to a mapping made 40 years earlier. The home ranges of mates were of equal size and overlapped 82% in summer and 56% in winter. The inter-mate distances were on average 2.7% shorter than expected by chance. The activity distribution of neighbouring pairs overlapped 9% (95% CI: 2–15%) on average. Males and females did not differ in overlap with neighbours, and there was a similar overlap between neighbours of the same and opposite sex. Both sexes vocalized more often in the peripheries than in the centres of their territory. The vocal activity during May–September varied extensively among years and months in accordance with variation in the density of juvenile floaters. Males and females vocalized equally often and were involved in disputes with neighbours at similar rates. Usually, neighbouring disputes involved either one individual from each pair or all four. Disputes involving all four owls more often involved chasing and fighting than those involving one owl only from each pair. The dispute rate between neighbouring pairs correlated positively with home-range overlap. The total annual mortality was 21% (95% CI: 6–33%). Dead owners were usually replaced within 1–2 months. Two out of four cases of radio-tagged owls disappearing from their territory because of natural causes was due to take-overs by invading owls, suggesting that the risk of losing fitness resulting from eviction was important. The apparent co-operative territorial behaviour of tawny owl pairs is probably due to improved resource holding potential of pair coalitions compared to single individuals.

Key words: *Strix aluco*, tawny owls, radio-tracking, territoriality, home range

INTRODUCTION

Territoriality is a widespread strategy to secure prior access to resources, and a variety of forms of territoriality exist in accordance to the prevailing costs and benefits of attempting to monopolize a given resource (Davies, 1978; Davies & Houston, 1984), not least among birds (Newton, 1998). The tawny owl *Strix aluco* provides an extreme example of life-long resource holding, not only because it defends a small territory throughout the year, but also because it normally appears to defend jointly by pair coalitions (Southern, 1970; Hirons, 1985; Galeotti & Pavan, 1993; Appleby *et al.*, 1999). This makes it an excellent subject for studying investment in territory display with regard to measures of habitat quality, individual quality, sex or the assessed threat of the intruder (e.g. Galeotti & Pavan, 1993; Galeotti,

1994, 1998; Redpath, 1994, 1995; Appleby *et al.*, 1999; Redpath, Appleby & Petty, 2000; Sunde *et al.*, 2001). In addition, in population ecology, the tawny owl has long been used as a key example of a species deliberately regulated by territoriality (e.g. Lack, 1954; Sutherland, 1996; Newton, 1998), as it appears to fulfil all criteria for a social organization following the ideal despotic distribution (Fretwell & Lucas, 1970).

Despite its popularity for studies of territorial behaviour, the spatial dispersion and social interplay among territorial tawny owls have never been comprehensively studied using telemetry, which is the only method that can achieve unbiased spatial information in this strictly nocturnal species. Currently, most published information about dispersion of neighbouring territories is either based on mapping of owls (mostly males) that are vocalizing (spontaneously or responding to playback; e.g. Andersen, 1961; Southern, 1970; Hirons, 1985; Galeotti, 1990, 1994) or from tags recovered in pellets from prey caught at known locations (Southern & Lowe, 1968). In addition to providing incomplete information that is subject to bias,

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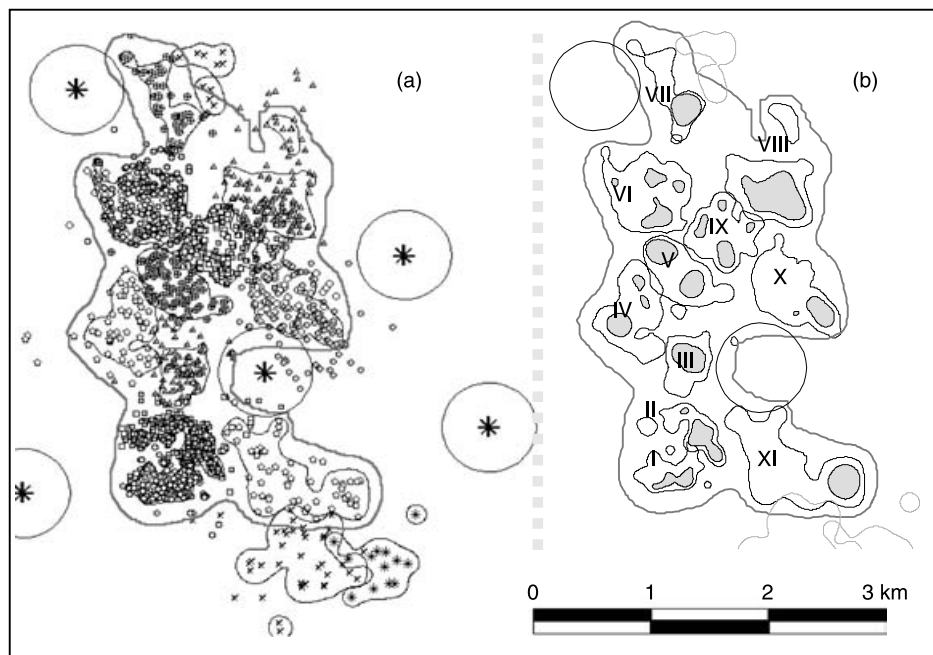


Fig. 1. The spreading of 11 tawny owl *Strix aluco* territories (Table 1) that comprise the study area. In (a), the spacing of telemetry locations of non-breeding individuals for all seasons is shown. The different pairs are represented with different marker types (light for females, dark for males) and the approximate territory borders of the different pairs are indicated as the extension of 80%-kernel home range polygons. The thick line indicates the 95%-kernel isopleths (7.2 km²) for all 11 territories (each pair weighted equally). The grey polygons show the approximate spreading of three territories of radio-tagged owls represented with too few locations during the non-breeding season to be included in the spatial analyses. The asterisks surrounded by 400 m buffer zones indicate the approximate location of the five nearest most territories with untagged owls. In (b), the 11 territories (80%- and 50%-kernel isopleths) are numbered in accordance with information about the different pairs given in Table 1.

these methods offer little information about the spatial interrelationship and interactions between the mates and neighbours when they are not displaying.

In the present study, we describe the dispersion and social behaviour of 23 radio-tagged tawny owls from 11 neighbouring territories in a deciduous forest in Denmark. In particular, we aim to test the general assumption that tawny owl home ranges are actually exclusive and stable among subsequent seasons and years. As the territory structure in some of the present study area was mapped long ago (Andersen, 1961), we are even able to assess the spatial stability of territories over a 40-year period. Furthermore, we want to quantify the extent to which the mates associate or disassociate within their assumedly collective home range in the light of the possible cost of territory sharing in terms of impoverished foraging efficiency (Davies & Houston, 1984; Tobias, 1997). Next, we explore the degree of communal versus individual territorial defence and whether males and females should differ in investment in territorial display. Finally, we aim to test whether the frequent vocalization of this species is a territorial display addressed towards potential usurpers from the pool of non-territorial floaters and to evaluate the actual eviction risk on the basis of the fates of the radio-tagged territory owners.

Having described the owls' breeding behaviour elsewhere (Sunde, Bølstad & Møller, 2003), this paper will primarily focus on the 7.5–12 months of the year

when the mates are not reproductively active and expected to allocate all their effort on holding the territory.

MATERIALS AND METHODS

Study area

The study took place in the southern part of the Gribskov Forest (56 km²), Denmark, including the Strødam Scientific Reserve (55°57' N, 12°16' E). The primary study area (hereafter 'study area'), covered approximately 7.2 km² and consisted of 11 territories, all held by monogamous pairs (Fig. 1). All territories were sited in a continuous forest of primarily planted tree stands (age up to 150 years) of beech *Fagus silvaticus*, oak *Quercus robur*, birch *Betula pendula* and Norway spruce *Picea abies*, interspersed with open areas (for more information see Sunde, Bølstad & Møller, 2003). In the Strødam reserve, where tawny owl territories were mapped during 1957–59, the landscape was virtually the same as during the first study 40 years earlier (see Andersen, 1961).

Division of the year

The non-breeding phase of the tawny owls was divided into a 'summer' (1 June–31 October) and a 'winter'

Table 1. The owls *Strix aluco* (M, male; F, female) surveyed as possessors of the 11 territories in the study (Fig. 1). The time intervals indicate the total duration of the telemetry surveys. Number of selected telemetry fixes from the non-breeding period is given. In individuals surveyed in the same season in different years, the number of fixes in the first and the second season are separated with '/'. Numbers in parentheses indicate that the numbers of fixes were too small to allow any kind of spatial analysis. If no other information is given, the end of the survey was due to ceased radio function. Of the 19 owls with ceased radio function, 17 were later caught and had their tags removed and two died before recapture

| Pair | Owl | Survey period | Number of selected fixes | | | Comments |
|------|-----|------------------------------------|--------------------------|----------|---------|--|
| | | | All | June–Oct | Nov–Mar | |
| I | 05M | May 98–April 00 | 158 | 37/39 | 51/39 | Raised three young to independence in 1998. 12F hit by car. 25F expelled by 31F 2 weeks after capture. Raised three young to independence in 1999 and two in 2000. |
| | 12F | June 98 | – | – | – | |
| | 25F | Nov 98 | – | – | – | |
| | 31F | Mar 99–Jan 00 | 69 | 43 | 29 | |
| II-A | 01M | April 98–Oct 98 | 35 | 35 | – | Raised three young to independence in 1998. Both mates diseased after prolonged period of challenge from alien pair |
| | 10F | May 98–Oct 98 | 42 | 42 | – | |
| II-B | 26M | Nov 98–Dec 00 | 174 | 44/22 | 62/38 | This pair took over territory II after 01M and 10F died. One unhatched egg in 1999. Two young died after fledging in 2000. Raised three young to independence in 2001. |
| | 24F | Nov 98–Oct 00 | 188 | 46/24 | 60/44 | |
| | | Dec 00–May 01 | | | | |
| III | 02M | April 98–Aug 99 | 93 | 29/21 | 43 | Raised two young to independence in 1998. Four unhatched eggs in 1999. |
| IV | 23F | Oct 98–Sep 99 | 62 | (5)/19 | 35 | Three unhatched eggs in 1999. |
| V | 38M | Jan 00–Jan 01 | 79 | 31 | 33 | Took over the territory in Aug 1999, 2 months after being independent. No breeding in 2000. |
| VI | 13M | Nov 98–Feb 01 | 169 | 32/41 | 26/40 | Raised one young to independence in 1998. Two nestlings died in 1999. 07F caught by goshawk. No breeding in 2000. Raised three young to independence in 2001 |
| | 07F | May 98–Jan 00 | 117 | 22/39 | 31/17 | |
| | 61F | April 00–Mar 01 | 44 | 34 | – | |
| VII | 50F | April 99–Jan 00 April 01–Sep 01 | 54 | 23/20 | (11) | Two young died after fledging in 1999. No breeding in 2000. Raised three young to independence in 2001. |
| VIII | 57M | April 99–April 00 | 82 | 27 | 52 | Raised two young to independence in 1999. 50F hit by car. No breeding in 2000. |
| | 51F | April 99–Nov 99 | 30 | 26 | (4) | |
| | 60F | Jan 00–Nov 00 | 30 | (1) | 18 | |
| IX | 46M | April 99–Jan 00 | 60 | 32 | 29 | Raised three young to independence in 1999. No breeding in 2000. Two young died after fledging in 2001. |
| | 33F | April 99–Mar 00 | 118 | 33/28 | 48 | |
| | | Dec 00–Sep 01 | | | | |
| X | 32M | April 99–July 00 | 122 | 43/17 | 48 | Raised one young to independence in 1999. No breeding attempt in 2000. 32M killed by goshawk. |
| | 06F | April 99–Jan 00 | 74 | 49 | 23 | |
| XI | 40F | April 99–Jan 00 | 58 | 31 | 22 | Single female held the territory in spring 1998. Raised two young to independence in 1999. No breeding in 2000. |

period (1 November–31 March). The 'summer' period was characterized by mild weather conditions and the annual peak in prey abundance (Bølstad, 2001), but it was also the time of year when juveniles tried to attain their own territories. During 'winter', very few floaters were left in the study area (Sunde, 2001) and prey densities reached their annual low (Bølstad, 2001).

Catching, survival estimation and radio tracking of owls

We caught territorial tawny owls by netting them during daytime in nest boxes or tree cavities; by night we caught them in swing door traps in the nest box or in mist nets when attracted to playbacks of calls. The owls were fitted with a backpack radio transmitter (Biotrack, Wareham, U.K.) weighing 8–13 g (including harness: 1.5–3% of the birds' body weight), which was mounted on the body beneath the plumage with 6 mm Teflon ribbon. The radios

lasted for 10–12 months. We attempted to tag all owls until June 2000. In addition, 3 females were re-tagged prior to the 2001-breeding season. All surviving owls were caught and had their tags removed within 2 years after the completion of the telemetry study. In 6 territories, both mates were radio-tagged, in 3, we only caught the female and in 2, only the male (Table 1, Fig. 1). We also included survival data from another 9 territorial owls (6 territories) with insufficient telemetry data to be included in the spatial analyses. Cause-specific mortality rates were calculated on the basis of Heisey & Fuller's (1985) method, using the program MICROMORT 1.3 (courtesy of D. M. Heisey). In addition to the adult owls, we radio-tagged 11–28 juveniles each year, allowing us to estimate, approximately, the density of non-territorial floaters in the study area each month in summer/early autumn. The young were defined as being independent when they ceased begging for food, this occurred at 55–83 days after fledging. When independent, the young

usually stayed in the vicinity of the natal territory for 1–2 months or longer (Sunde, 2001).

As the owls were usually inactive during the day (Sunde, Bølstad & Desfor, 2003), all analyses are based on observations obtained during the night. On 2 to 4 nights per week, throughout the year, the owls were located by triangulation at 10–200 m (normally 20–50 m) distances by 1 of us. A network of roads and trails on which we could bike, usually allowed us to locate any owl (± 5 –25 m) within 5–15 min from the beginning of the search. Even though only 1 person at a time located the owls, it was rarely a problem to triangulate the owls as they usually perched for several minutes at each place. Owls vocalizing or being observed while triangulated, regularly confirmed the precision of the telemetry locations. We could always receive the signals even when the owls occasionally moved 1–2 km outside their normal range. Each night, the owls from the different territories were tracked in a predetermined order. Usually we registered 1 location per owl per night. These ‘primary’ fixes constituted an unbiased sample of the owls’ spatial dispersion and behaviour. Sudden engagements in territory disputes or other conspicuous activities of interest were also registered. These opportunistically obtained ‘secondary’ fixes were used in specific analyses of possible sex-differences in territorial disputes. During April–August, all times of the night were sampled with approximately the same intensity. During the rest of the year, the owls were primarily tracked during the first 5–8 h of the night.

Analyses of range use

Home-range size was measured as 95%, 80% and 50% fixed kernels (Worton, 1989) with ad hoc estimation of the smoothing parameter, using the Animal Movement extension version 2.2 (Hooge & Eichenlaub, 1997) for ArcView (version 2.3, ESRI). Total range size was estimated as the 100% minimum convex polygon (100% MCP) corrected for the underestimation bias due to varying numbers of telemetry fixes (100% MCP_c = 100% MCP $\times \exp[6/n^{0.7}]$; n = number of telemetry fixes; Gaustad & Mysterud, 1993). We tested for differences in home-range size among mates and between seasons by means of a 3-way ANOVA, correcting for differences between pairs.

Analyses of range overlap

Home-range overlaps were calculated between seasonal home ranges of individual owls, between mates and between neighbours (individual owls or complete pairs). Individual owls or pairs were defined as neighbours if they had adjacent ranges, i.e. if the pairs’ 99%-kernel home ranges overlapped, the contact zone not being buffered by a third territory. We indexed the home-range overlaps as the proportional overlap between 95%-kernel polygons ($O_p = 2A_o/[A_a + A_b]$, A_o being the overlap area of the two polygons, covering the areas A_a and A_b).

To directly quantify the proportional overlap between 2 samples of fixes, we weighted the proportional share of 100×100 m squares as:

$$O_s = 1 - 1/2 \sum (|P_{iA} - P_{iB}|)$$

where P_{iA} and P_{iB} is the proportion of primary fixes in sample A and B located in square i . Owing to stochastic variation, even when there is a complete overlap in the underlying distribution of the 2 samples of fixes, the value of O_s will be smaller than 1 unless the number of fixes is infinitely large. To adjust for this error, a corrected overlap ($O_{sc} = O_s/\bar{O}_{sr}$, where \bar{O}_{sr} is the mean value of 100 of randomized overlap estimates) was applied. If the 2 samples had the same underlying distribution (no partitioning), O_{sc} would be distributed around 1 (the variance approaching 0 as the number of fixes approaches infinity). We tested whether the mean O_{sc} -value was significantly smaller than 1 with a 1-tailed t -test. As the method of calculating proportional share of 1-ha squares demanded a large number of telemetry fixes to be reliable, we only used this method in within-pair comparisons that could be expected to overlap entirely, and to compare the total overlap of complete, neighbouring pairs (> 150 fixes from each sample).

Analyses of mate association

The association of mates was analysed by comparing the mean observed inter-mate distance with the mean distance of 1000 randomized inter-mate distances for each pair. In the case of a random association of the mates, the log-ratio of the two means should be approximately normally distributed around 0, as tested with a 1-sample t -test. To test whether certain inter-mate distances were preferred, the observed inter-mate distances were divided into distance categories of 0–100 m, 1–300 m, 3–500 m and > 500 m. The observed proportional distributions were tested against the random expectations with a compositional analysis (Aebischer, Robertson & Kenward, 1993).

Analyses of vocalization rate

To test whether the vocalization rate varied in accordance to the centre of the territory, for each pair, we calculated the vocalization rate (the proportion of primary fixes where an owl hooted or uttered ‘keewick’ cries) in 3 different territory zones (within the 50%-kernel, between the 50%- and the 80%-kernel and outside the 80%-kernel isopleths) and tested the difference with Friedman’s test. Since the total vocalization frequencies was reasonably normally distributed, even when calculated on for each individual owl, we tested for inter-sexual differences in vocalization rate between the 3 territory zones by means of a repeated-measure ANOVA, entering pair-ID and sex as factors.

Temporal variation in vocalization rate was modelled as a logit link function with a binomial error (PROC

GENMOD in SAS 6.12), i.e. using the telemetry fixes as observation units. As we were interested in testing whether vocalization was an effort to advertise territory ownership against floaters, the analysis was restricted to May–September when no courtship behaviour was expected, and many independent juveniles had still not dispersed from the study area. We also included data from breeding individuals during this period, entering breeding status as a factor in the analysis. The density of independent juveniles was estimated as the number of independent radio-tagged juveniles located in the study area in a given month, divided by the proportion they made up of the total number of juveniles reaching independence in the study area that year. We included data from pairs represented with ≥ 8 observations in a given month. The most parsimonious model was found by starting with a model based on all main effects and second-order interaction terms, gradually removing the least significant terms, as tested by the maximum likelihood criterion (Hosmer & Lemeshow, 1989). In an initial step, data were divided by sex, but as sex did not explain any variation, we pooled the observations across gender in all subsequent analyses. Finally, we tested the additive effects of floater density by adding this variable to the model.

Significance levels

Throughout the paper, we applied $P < 0.05$ as the significance level, except in the model selection procedure of temporal variation in vocalization rate. Here, a $P < 0.01$ was chosen, as 5–6 selection variables were available in each step. In analyses based on < 10 observations (low power), we discuss boarder-line significant results ($P < 0.10$) as ‘tendencies’. Two-tailed tests were standard unless otherwise stated.

RESULTS

Size and stability of home ranges

The average home-range size (entire year for individual owls) was 89, 57, 27 and 6.7 ha for 100% MCP_{cs} , 95%, 80% and 50% kernels, respectively, irrespective of sex (Table 2, Fig. 2). For 100% MCP_{cs} and 80%-kernels, the combined home range of mates was larger than that of males only, suggesting that the mates did not have perfectly overlapping home ranges. The size of the 100% MCP_{cs} and the 95%-kernels did not differ between seasons, whereas the 80%- and 50%-kernels were slightly larger during summer than during winter. The size of the 100% MCP_{cs} and 95%-kernels were larger if estimated for both seasons than for the summer period only, suggesting a somewhat different use of the periphery of the home range in the cold and warm seasons, whereas the centres did not appear to shift position from one season to the next. The dispersion of the territories in the Strødam reserve was similar to Andersen’s (1961) mapping 40 years earlier (Fig. 3).

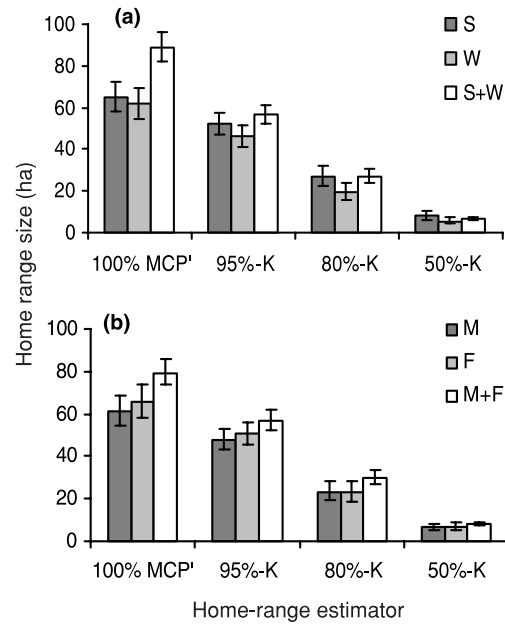


Fig. 2. Estimated marginal means and 95% CI error bars of home-range size from three-way ANOVAs (Table 2) including the effects of gender, seasons and pair ID and the second-order interactions between these variables. The home-range size are calculated as 100% Minimum Convex Polygons (MCP) corrected for underestimation bias (100% MCP_c), and 95%-, 80%- and 50%-kernels (95%-K, 80%-K and 50%-K). (a) The mean range size of non-breeding owls during summer (S: 1 June–31 October), winter (W: 1 November–31 March) and the entire survey period (both S and W represented). (b) The mean range sizes of males (M), females (F) and the pairs’ shared range (M + F).

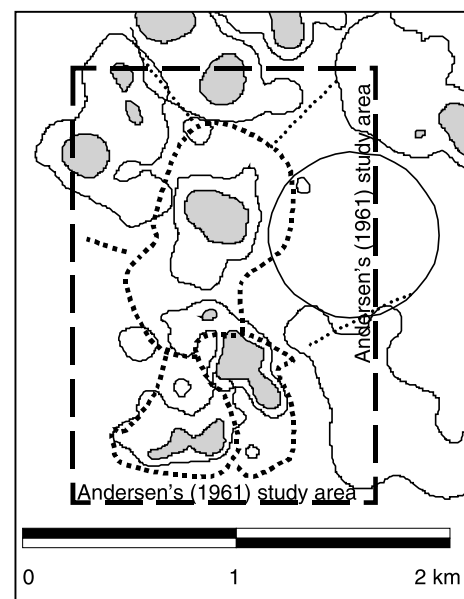


Fig. 3. The extension of home ranges of territories I–IV and XI from Fig. 1(b), compared to the territory borders 40 years earlier (dotted lines). Redrawn from Andersen (1961).

Table 2. F-statistics from three-way ANOVAs of differences in home-range size (log-transformed), in relation to sex and seasons for tawny owls *Strix aluco*. Home-range sizes are calculated as 100% Minimum Convex Polygons corrected for underestimation bias (100% MCP_c), and 95%-, 80%- and 50%-kernels (95%-K, 80%-K and 50%-K). To correct for between-territory variation, the first- and second-order effects of Pair-ID on home-range size are also included in the model (given in *italics*). Analysis A tests the difference in range size of non-breeding birds between males (M) and females (F) and between summer (S, June–October) and winter (W, November–March). Analysis B tests for differences in range size when calculated for the entire pair as opposed to the male only and for the entire year (S + W) as opposed to the summer season only (S). The latter analysis is sensitive to area segregations between mates and different periods of the year. Abbreviations for significance levels: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; R^2 (adj) indicates the amount of variation explained by the independent variables

| | | Home-range estimators | | | |
|--|------|----------------------------|------------|------------|------------|
| | d.f. | Log(100%MCP _c) | Log(95%-K) | Log(80%-K) | Log(50%-K) |
| A. Tests for differences between M/F and S/W (based on data from six pairs surveyed through both seasons, two pairs surveyed during S and two M and two F with untagged mate surveyed through both seasons) | | | | | |
| Sex (M vs. F) | 1,5 | 0.229 | 0.286 | 1.337 | 1.015 |
| Season (S vs. W) | 1,5 | 0.901 | 3.632 | 9.206* | 8.020* |
| Sex × season | 1,5 | 0.077 | 2.025 | 0.698 | 0.541 |
| Pair ID | 11,5 | 9.393* | 10.415** | 3.977 | 3.365 |
| Pair ID × sex | 7,5 | 1.670 | 1.331 | 1.761 | 1.525 |
| Pair ID × season | 9,5 | 3.999 | 3.651 | 2.084 | 2.325 |
| R ² (adj) | | 0.78 | 0.80 | 0.62 | 0.58 |
| B. Tests sensitive for range segregation between sexes and seasons (six pairs surveyed through both seasons and two pairs only surveyed during S and two M with untagged mate surveyed through both seasons) | | | | | |
| Sex (M vs. M+F) | 1,5 | 18.041** | 6.445 | 9.494* | 4.222 |
| Season (S vs. SW) | 1,5 | 62.955*** | 6.751* | 0.381 | 5.404 |
| Sex × season | 1,5 | 0.298 | 1.308 | 0.001 | 5.181 |
| Pair ID | 9,5 | 28.018*** | 26.074** | 16.472** | 18.514** |
| Pair ID × sex | 7,5 | 0.937 | 0.910 | 1.943 | 2.045 |
| Pair ID × season | 7,5 | 3.577 | 3.564 | 3.448 | 9.162* |
| R ² (adj) | | 0.92 | 0.89 | 0.85 | 0.89 |

Home-range overlap of 1-ha patches between mates, seasons and years

Fifteen owls surveyed in adjacent summer and winter seasons expressed an almost complete inter-seasonal overlap (Fig. 4) and nine owls surveyed in different summers expressed a mean inter-annual overlap of 85%. In both seasons, the mean overlap between mates was significantly lower than expected by chance and tended to be lower in winter (56%) than in summer (82%, paired t -test: $t_5 = -2.114$, $P = 0.09$).

Home-range overlap between neighbours

The pairs shared on average 9% of their range with each of the neighbouring pairs, measured as overlap of 1-ha squares (Fig. 4). This corresponded to a mean overlap of 95%-kernels at 7% (95% CI = 3–11%) throughout the year. There were no significant seasonal differences in neighbour overlap of 95%-kernels, except in females that appeared to overlap less in winter than in summer (Table 3). Likewise, neighbouring males did not differ from females in intra-sexual neighbour overlap, nor did the neighbour overlap between individuals of the same or opposite sex differ significantly from each other. Overall, the two sexes did therefore appear to be equally exclusive against neighbouring owls, irrespective of their sex.

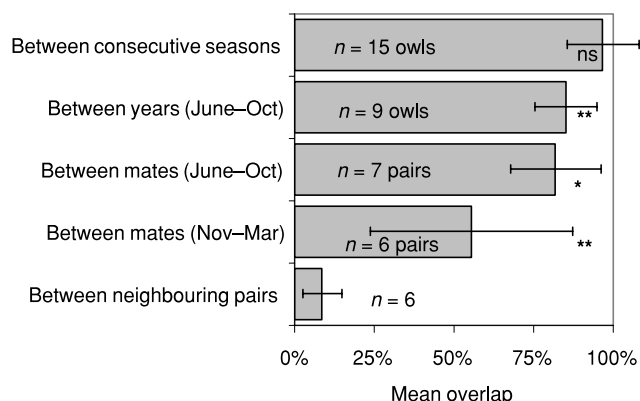


Fig. 4. Mean (95% confidence zones) overlap of 1-ha squares of paired samples of telemetry fixes from non-breeding owls (see text for methods). The upper-most bar depicts the proportional overlap between individual owls surveyed at adjacent summer (June–October) and winter (November–March) periods. The next bar shows the overlap between owls surveyed during the summer season in 2 different years. The two following bars show the overlap between mates during June–October and November–March, respectively. The lower-most bar shows the overlap between neighbouring pairs with all four birds being radio tagged. In the four within-owl or between-mate pair comparisons, the deviations of the mean from a 100% overlap expectation are tested with one-tailed t -tests (*, $P < 0.05$; **, $P < 0.01$).

Table 3. Summary of Wilcoxon's signed rank tests for matched pairs for differences in overlap of 95%-kernels (see text for methods) between neighbouring males (MM), neighbouring females (FF), neighbouring owls of opposite sex (MF/FM), neighbouring owls of the same sex (MM/FF), neighbouring owls of any sex (individuals) and pairs (shared home range of mates). All data originates from non-breeding owls divided on adjacent 'summer' (June–October) and 'winter' (November–March) periods. The neighbour relation between pairs are used as an observation unit, so in those cases that both adjacent owls of the same (i.e. overlap between male A + male B and female A + female B) or opposite sex (overlap between male A + female B and female A + male B) are known, the mean of the two measures are used. The same principle applies to the overlap between individuals of any sex (i.e. male A + female B, male A + male B, male B + female A, female A + female B). *n* indicates the number of tested pairs, divided on positive ranks, negative ranks and ties. The test statistic, *T*, is the minimum sum of ranks. A single significant test result ($P < 0.05$) is marked as "*", all other test results were not significant (NS)

| Group | Matched pairs between | <i>n</i> | | | <i>T</i> | Sig. |
|-------------|-----------------------|----------|---|---|----------|------|
| | | + | – | 0 | | |
| MMs | Summer–winter | 2 | 4 | 2 | 7 | NS |
| FFs | Summer–winter | 1 | 6 | 3 | 2 | * |
| MF/FM | Summer–winter | 3 | 6 | 5 | 14 | NS |
| Individuals | Summer–winter | 4 | 6 | 4 | 19 | NS |
| Pairs | Summer–winter | 3 | 3 | 0 | 10 | NS |
| Summer | MM–FF | 4 | 1 | 1 | 4 | NS |
| Summer | MM/FF–MF/FM | 5 | 5 | 4 | 24 | NS |
| Summer | Individuals–pairs | 4 | 1 | 1 | 5 | NS |
| Winter | MM–FF | 1 | 4 | 1 | 4 | NS |
| Winter | MM/FF–MF/FM | 6 | 2 | 4 | 10 | NS |
| Winter | Individuals–pairs | 4 | 2 | 0 | 6 | NS |

Within-home-range association of mates

The mean inter-mate distance was 367 m (SD = 103, $n = 8$) in summer and 409 m (SD = 145, $n = 6$) in winter (paired *t*-test: $t_5 = -2.037$, $P = 0.097$). A two-way ANOVA using $\ln[\text{expected mean distance}/\text{observed mean distance}]$ as response variable, rendered that the average distance between mates were 2.7% shorter than expected from random ($F_{1,12} = 5.847$, $P = 0.032$), independent of season ($F_{1,12} = 0.080$, $P = 0.8$). Overall, there was no evidence for any of the four inter-mate distance categories differing from random (Fig. 5).

Vocalization rates

The owls were more inclined to vocalize in the periphery than in the centre of their home range (Friedman tests, $\chi^2_2 = 6.73$, $n = 12$ pairs, $P = 0.034$). This pattern appeared to be the same for both sexes (nine males and 10 females; within-subject comparisons from repeated-measure ANOVA: territory zone: $F_{2,12} = 8.913$, $P = 0.004$; zone \times pair: $F_{20,12} = 1.579$, $P = 0.21$; zone \times sex: $F_{2,12} = 0.523$, $P = 0.61$).

On a temporal scale, the vocalization rate varied significantly among years and months and appeared to be lower for parents with dependent young than for

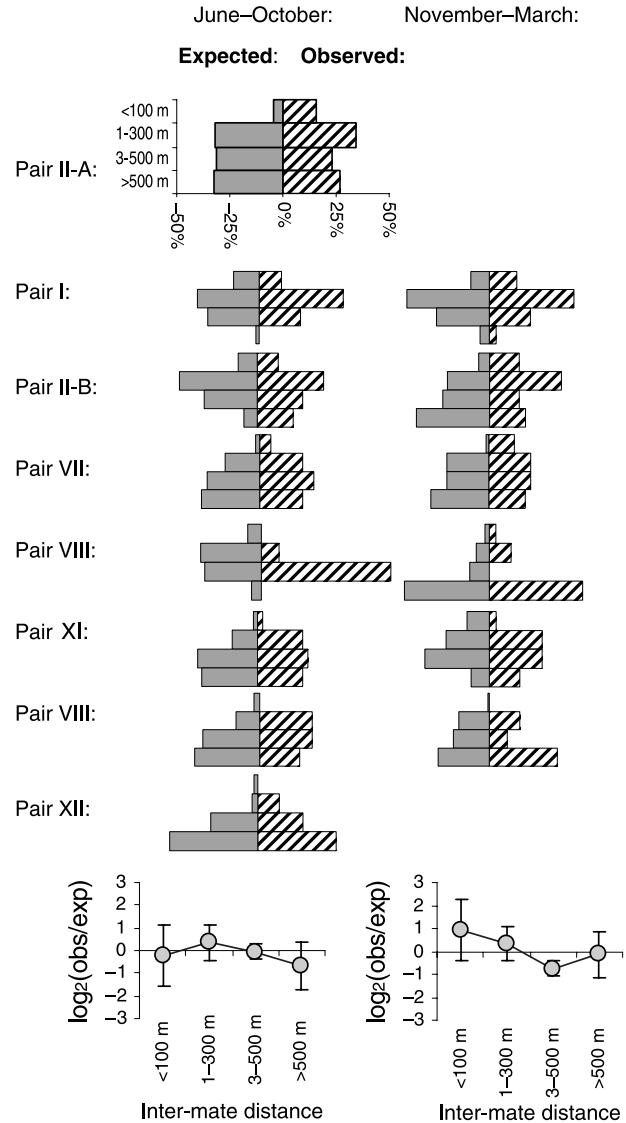


Fig. 5. Frequency distributions of observed inter-mate distances as opposed to the distances expected if the mates were randomly associated. Figures are given for non-breeding birds during the summer and winter season. The graphs in the bottom of the columns show the mean preference values (95% error bars) for each of the four distance categories, measured as $\log_2(\text{observed frequency}/\text{expected frequency})$. A mean preference value of 0 indicates no difference between observed and expected frequency; a value of 1 that the observed frequency was two times higher than the expected frequency, a value of two, a fourfold preference, etc. Overall, the observed and expected distributions did not differ for any of the seasons (compositional analyses; summer: Wilk's $\lambda = 0.53$, $F_{3,5} = 1.50$, $P = 0.32$; winter: Wilk's $\lambda = 0.36$, $F_{3,3} = 1.78$, $P = 0.33$) or overall (intercept: Wilk's $\lambda = 0.53$, $F_{3,10} = 2.960$, $P = 0.084$; interaction with seasons: Wilk's $\lambda = 0.80$, $F_{3,10} = 0.86$, $P = 0.5$).

non-breeders, but was independent of sex (log-likelihood test: $\chi^2_1 = 0.041$, $P > 0.8$), territory ID or territory size (Fig. 6, Table 4).

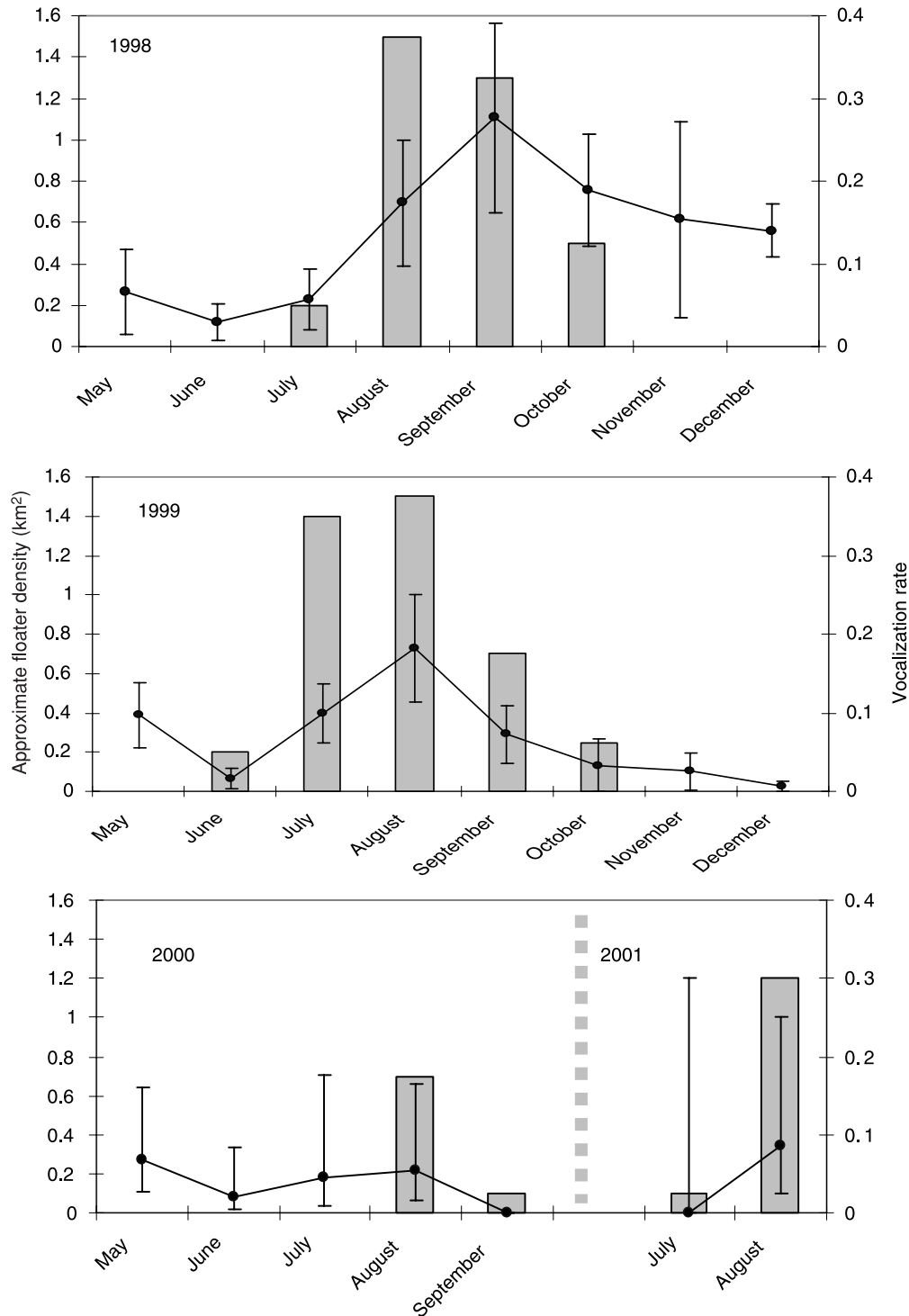


Fig. 6. Vocalization rate per month (lines, $\pm 95\%$ CI of monthly means) compared with the approximate density of juvenile floaters in the study area (bars; number of radio-tagged, independent juveniles in the study area, divided with the proportion they comprised of the total number of chicks fledged from the study area that year).

When the effect of floater density was entered in the final step of the analysis, the between-year effect and the difference between breeders and non-breeders were no longer significant and the amount of variation explained by month was halved. The parameters of the final model showed that the vocalization rate increased with floater

density and from June to September after an early peak in May (Table 4). The apparent differences in timing and intensity of the vocalization activity among years were therefore mainly due to variation in number and time of emergence of independent juveniles in different years.

Table 4. Results of generalized linear models of factors influencing the vocalization rate during May–September 1998–2001. In each step, a set of explanatory variables is entered and the least significant terms successively removed until only the significant ($P < 0.01$) effects are included in the final model. Significance is evaluated from χ^2 -statistics based on change in scaled deviance (ΔD) on entering a new factor in the model (Type I analysis. ΔR^2 is the additional variation explained by a new factor) or removing it from the final model (Type III analysis). In step I, the variation in vocalization rate is tested against month, year, Pair ID, breeding status (dependent offspring or non-breeding) and territory size (80%-kernel). In step II, the effect of floater density is tested upon the three factors found to be significant in step I. ^aModel parameters: $V/R = \exp(Z)/[1 + \exp(Z)]$, $Z = -2.158 + 0.647$ (in May) $- 0.976$ (in June) $+ 0.0545$ (in July) $+ 0.388$ (in August) $+ 0$ (in September) $+ 0.507$ (in 1998) $+ 0$ (in 1999) $- 0.967$ (in 2000) $- 0.395$ (in 2001) $- 0.993$ (in owls with fledglings). ^bModel parameters: $V/R = \exp(Z)/[1 + \exp(Z)]$, $Z = -3.195 + 1.319 \times$ Floater density (km^{-2}) $+ 0.806$ (in May) $- 0.827$ (in June) $- 0.680$ (in July) $- 0.343$ (in August) $+ 0$ (in September)

Model I (floater density not included)

| | | Type I | | | | | Type III | |
|----------------------------------|--------------------------------|----------|------------|--------------|-------|------------|------------|-------|
| | | Deviance | ΔD | ΔR^2 | d.f. | P | ΔD | P |
| Included in model ^a : | Intercept: | 126.540 | | | 0,62 | | | |
| | Month | 92.785 | 28,485 | 23% | 5,62 | < 0.0001 | 13.861 | 0.008 |
| | Year | 81.185 | 9.789 | 8% | 2,62 | 0.020 | 14.487 | 0.002 |
| | Breeding status | 73.188 | 6.748 | 5% | 1,62 | 0.009 | 6.748 | 0.009 |
| Not significant: | Month \times year | 59.316 | 11.706 | 9% | 9,53 | 0.23 | | |
| | Month \times breeding status | 72.881 | 0.259 | 0% | 2,60 | 0.88 | | |
| | Year \times breeding status | 71.033 | 1.818 | 1% | 2,60 | 0.40 | | |
| | Pair ID | 63.289 | 8.354 | 7% | 11,51 | 0.68 | | |
| | Territory size | 71.657 | 1.303 | 1% | 1,61 | 0.25 | | |

Model II (floater density included)

| | | Type I | | | | | Type III | |
|----------------------------------|--------------------------------|----------|------------|--------------|-------|------------|------------|------------|
| | | Deviance | ΔD | ΔR^2 | d.f. | P | ΔD | P |
| Included in model ^b : | Intercept: | 126.540 | | | 0,65 | | | |
| | Month | 92.785 | 29.573 | 23% | 4,65 | < 0.0001 | 16.676 | 0.002 |
| | Floater density | 74.129 | 16.345 | 13% | 1,65 | < 0.0001 | 16.345 | < 0.0001 |
| Not significant: | Month \times floater density | 64.424 | 8.503 | 7% | 3,62 | 0.037 | | |
| | Year | 63.315 | 0.971 | 1% | 4,59 | 0.81 | | |
| | Breeding status | 63.429 | 0.872 | 1% | 1,61 | 0.35 | | |
| | Pair ID | 53.270 | 9.772 | 8% | 11,51 | 0.55 | | |
| | Territory size | 63.128 | 1.135 | 1% | 1,61 | 0.29 | | |

Territorial disputes

The dispute rate (the proportion of primary fixes where the owls were involved in vocal or aerial display directed against an alien owl) between neighbouring pairs correlated positively with the overlap of their territories (Fig. 7; $r_s = 0.886$, $n = 6$, $P = 0.05$).

We registered 22 cases of vocal disputes between members of neighbouring pairs and 23 cases involving flight display (Fig. 8). Usually, territorial disputes involved either one individual from each pair or all four owls; disputes between one owl vs. two were strongly underrepresented (test for deviation from a 1:2:1 [1–1: 1–2: 2–2] expectation: vocal display: Pearson's $\chi^2 = 38.00$, $P < 0.001$; disputes involving flight display: $\chi^2 = 15.78$, $P < 0.001$). When only two birds were involved, vocal display predominated, whereas flight display prevailed when the contest involved all four pair members (Fishers exact test, $P = 0.015$). Typically, a dispute started between two individuals encountering each other, after which the mates joined in, if the dispute lasted long enough. In conflicts involving one member of each pair, males were more often involved in vocal contest with other males, than expected from a 1:2:1 (M–M:M–F:F–F) distribution ($\chi^2 = 7.33$, $P = 0.026$), whereas no such

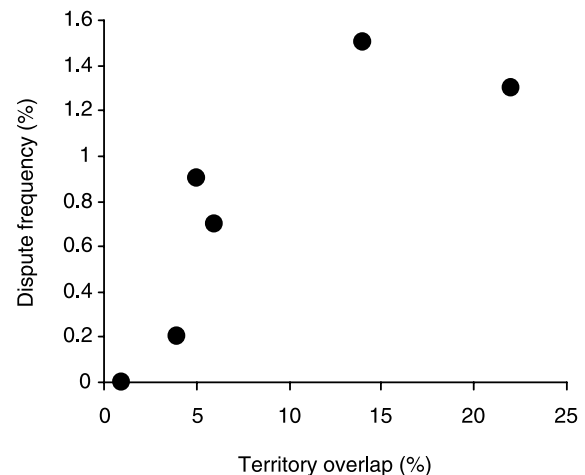
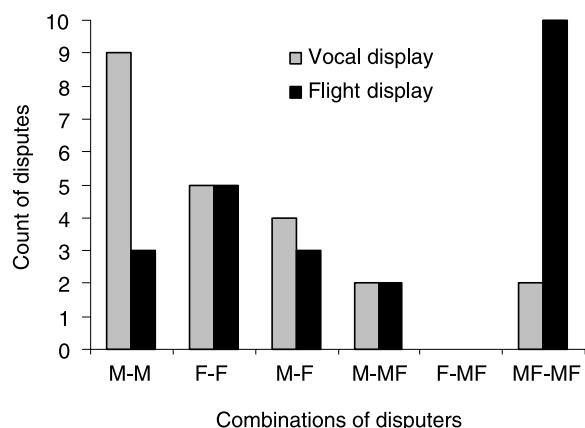


Fig. 7. Mean dispute rate (% of primary fixes) between neighbouring pairs with all four birds radio-tagged, plotted against their proportional overlap of 100-m squares.

difference existed for disputes involving aerial display ($\chi^2 = 3.00$, $P = 0.22$). The owls did not chase neighbours of their own sex more often than those of the opposite sex (sign test: $P = 0.23$).

Table 5. Cases of disappearances of territory holders, subsequently replaced with newcomers. Dates of replacement indicate the date an untagged establishing tawny owl *Strix aluco* was caught and radio tagged. F, female; M, male

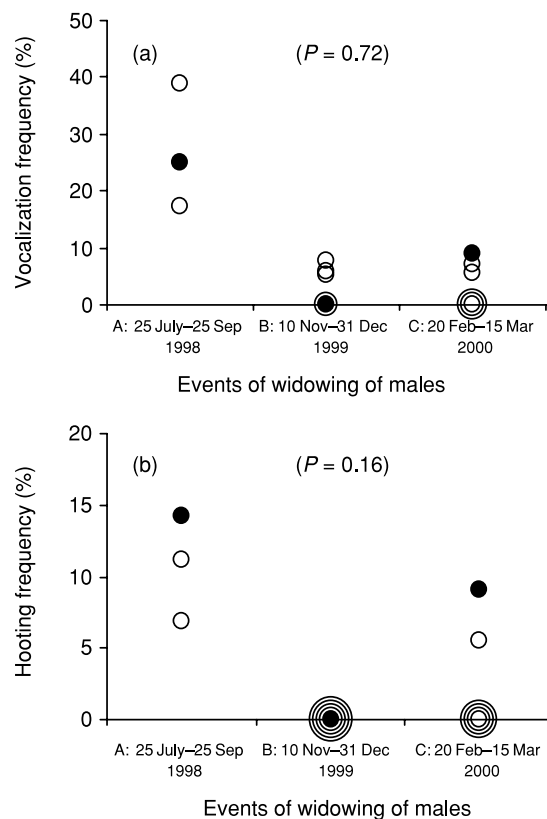
| Territory | Sex | Date of disappearance | Reason for disappearance of initial owl | Replaced | Days | Comments |
|-----------|-------|-----------------------|---|--------------|-------|--|
| I | F | 29 June 98 | Car collision | ≤ 1 Nov. 98 | ≤ 94 | The first month after being alone, the male was busy, feeding chicks |
| I | F | Nov. 98 | Evicted | Nov. 98 | 0 | Initial female only established for few weeks (see text) |
| II | M + F | Oct. 98 | Dead by disease after contest | Oct. 98 | 0 | (see text) |
| VIII | F | 10 Nov. 99 | Car collision | ≤ 9 Jan. 00 | ≤ 60 | |
| VI | F | 12 Jan. 00 | Killed by raptor | ≤ 1 April 00 | ≤ 80 | |
| V | M | June–July 99 | ? | Aug. 99 | 20–60 | Radio-tagged juvenile surveyed during settling. Initial male heard hooting last time around 1 June |

**Fig. 8.** The number of registered inter-pair contests between members of neighbouring, radio-tagged pairs, showing the various combinations of sexes involved (both sexes in each pair were tagged). Vocal display is when the neighbouring owls are hooting or crying to each other without further approach. Flight display is when the owls are fighting or chasing each other.

Turnover of territory holders

During the entire telemetry survey (30.1 transmitter years), seven territory holders died (Table 1: three killed by raptors, two by disease and two killed in traffic) corresponding to a total annual mortality of 21% (95% CI: 6–33%) or 15% (2–27%) due to natural causes. None of the radio-tagged owls switched territory, apart from a newly established female that was evicted (see below). Six cases of replacement of territory owners in the study area could be studied more or less in detail (Table 5), showing that a newcomer usually filled empty gaps within 1–2 months. Three widowed males did not vocalize significantly more when establishing a new mate than other radio-tagged males (Fig. 9).

We recorded two cases of owls being replaced due to territorial disputes. In the first case, a female recently established in territory I was evicted in November 1998, less than 2 weeks after being caught responding to playback with the residing male. In the second case, October 1998, an untagged pair (possibly invading from territory XI judging from the location of the initial

**Fig. 9.** Spontaneous vocalization frequency (a, all types of vocalization; b, hooting only) of three widowed males (black spots) compared to other radio-tagged males during the same period (open spots, embedded spots indicate the number of tied observations). The *P*-values indicate the two-tailed likelihood that widowed and non-widowed males differ in vocalization frequency, found by means of randomization tests. The widowing incidents are listed in Table 5.

disputes) challenged the established pair of territory II, registered as vocal and aerial displays from both pairs. After the residing male died (diseased) on 16 October, the widowed female displayed alone until also dying of disease on 27 October. Immediately thereafter, the intruding pair (caught and radio tagged the following week) took over the territory.

DISCUSSION

Dispersion and stability of territories

As a whole, this telemetry study supported the general notion (Andersen, 1961; Southern, 1970; Hiron, 1985; Galeotti, 1990, 1994) that tawny owl home ranges are usually of constant size and shape in different seasons and over years, overlapping only marginally between neighbours. In accordance with Hiron's (1985) conclusions from Wytham (Oxford, U.K.), we also found the boundaries being almost identical with the mapping done by Andersen (1961) 40 years earlier. The robustness of the territory structure beyond generations was further demonstrated by the persistence in shape of territory II after the pair was replaced. The high annual survival rate and rareness of territory switching are also in line with previous studies on territorial dynamics (Southern, 1970; Hiron, 1985). Even though the population density (≈ 1.5 pairs km^{-2}) in this study is only one-third the density reported from deciduous woods in England, the social systems still seems similar, perhaps with the exception of no bigamous males being found. The limit of the species' range in central Norway where some females (no data on males) roamed large areas in the non-breeding season (Sunde *et al.*, 2001) appear therefore to be exceptional, and was possibly caused by environmental conditions in the north of the range.

Even though the telemetry data generally confirmed the conclusions from previous non-telemetric studies, the data also showed that inferences based on mapping of spontaneously vocalizing owls might produce biased estimates of the true activity distribution, as both sexes were more inclined to vocalize in the peripheries than in the centres of their range. The increased vocal effort in the peripheries of the range indicates that the entire home range was defended, thereby defining a territory (Davies, 1978). The increase in dispute rate with increasing territory overlap between neighbours was in accordance with theory (Stamps & Krishnan, 2001; Pereira, Bergman & Roughgarden, 2003) predicting extensive territorial overlaps to be costly in dispute effort.

Spatial interrelations of mates

We found evidence for a partial home-range partitioning of mates, as the mean overlap of 1-ha squares between mates was significantly lower than 100%. The tendency towards the overlap being least in winter was expected if the owls faced a trade-off between efficiency of territorial defence and foraging (Davies & Houston, 1984; see also Tobias, 1997). This is because food was scarce in winter but abundant in summer/autumn, whereas the investment in territorial effort was highest in summer/autumn.

Even though the mates were significantly positively associated, this association was so weak that it has no biological significance. Accordingly, no particular mate-distance zones were preferred compared to a random expectation.

Eviction risk, territorial efforts and the cooperation between mates

Two of the four cases of owls disappearing from territories due to natural causes were attributable to territorial disputes. This indicates that territory owners should take the risk of eviction seriously and allocate a considerable effort to territory defence, at least when the intruder pressure is high. In addition to the obvious advantages of land tenure, the defence effort might possibly also include the mate as well. Mate loss would not only decrease the breeding success of the remaining mate in the following season (Sasvári *et al.*, 2000), but might also increase that mate's own risk of eviction as indicated by the sudden death of the widowed female in territory II. There should therefore be a good adaptive basis for the mates to assist each other in resisting usurpers of the opposite sex (e.g. Mathews, 2002; but see also Ens, Safriel & Harris, 1993; Piper, Tischler & Klich, 2000). The owls appeared to adjust their territorial effort to the intruder pressure, as all variation in vocalization rate between years and about half of the variation between months, was attributable to variation in floater density. The real correlation between vocalization rate and floater density was possibly even higher, as our floater density estimate was likely to be increasingly underestimated during August–September as the proportion of radio-tagged juveniles in the local floater pool was gradually diluted by natal dispersal (Sunde, 2001). The model parameters predicting an increasing vocalization rate from June to September might reflect this. Alternatively, it might reveal an increasing intolerance to intruders as the autumn progressed.

The two sexes appeared to invest equally in territorial effort as they had similar vocalization and dispute rates as expected from above. This was also in general agreement with results from playback experiments (Galeotti & Pavan, 1993; Appleby *et al.*, 1999). However, contrary to the playback experiments, we did not find much evidence for territorial display being particularly directed against members of the same sex, apart from counter-singing males. Nor did we find any differences between intra- and inter-sexual overlap among neighbours, as might be expected if intra-sexual aggression predominated. In neighbour conflicts, it appeared as if the pairs attempted to keep the numerical balance so that the disputes either involved one bird from each pair or all four. The higher aggression level in disputes involving all four mates indicate that the mates backed each other up when vocal disputes escalated into chasing and fighting. We take that as an indication of a high degree of mutual defence effort.

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