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Meszaros, AL; Kajdocsi, S; Szentirmai, [No Value]; Komdeur, J; Szekely, T; Mészáros, Anna Lída; Szentirmai, István

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Anna Lília Mészáros · Szabolcs Kajdócsi ·
István Szentirmai · Jan Komdeur · Tamás Székely

Breeding site fidelity in penduline tit *Remiz pendulinus* in Southern Hungary

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Abstract Birds move between breeding locations to gain a better territory, avoid competition or reduce the deleterious effect of inbreeding. We investigated breeding site fidelity in a small European passerine, the penduline tit (*Remiz pendulinus*). This species has an exceptionally diverse breeding system, in which both males and females may have up to 5–7 mates in a single breeding season, and the eggs are incubated by a single parent: either the male or the female. We investigated the movements of males and females within three breeding seasons in Southern Hungary (2002–2004). Males moved for shorter distances between breeding sites (116 m, 63–333 m; median, lower quartile–upper quartile) than females (942 m, 415–2,382 m). Movements of males and females were consistent between years, and they were repeatable between subsequent nests of males, but not of females. Taken together, our results suggest that adult male penduline tits are more site-faithful than adult

females. We suggest that this difference has an implication on their breeding ecology since male parental behaviour (desert/care) is expected to be influenced by local mating opportunities, whilst female parental behaviour is likely to depend on the mating opportunities in a large area around their breeding site.

Keywords Breeding site fidelity · Breeding territory · Mating system · *Remiz pendulinus*

Introduction

Movements between habitat patches (i.e. dispersal) may influence the structure and viability of populations. First, dispersal between populations or subpopulations may increase effective population sizes and genetic diversity of populations, thereby enhancing their viability (Gilpin, 1991). Second, dispersal within populations, the subject of this work, may change local population densities, the local sex ratio and the distribution of individuals of different quality in the population (Clobert et al., 2001). Thus, dispersal within and between populations may alter the local ratios of sexually receptive males and females and thereby influence mating systems (Székely et al., 2000; Pilastro et al., 2001). For example, local mating opportunities were suggested to influence clutch desertion and mating system in European penduline tit *Remiz pendulinus* (Persson and Öhrström, 1989).

Penduline tits have an unusually variable breeding system, in which sequential polygamy by both sexes occurs in the same population (Persson and Öhrström, 1989; Szentirmai and Székely, personal communication). Incubation and brood care are strictly uniparental either by the male or the female. Males desert 50–70% of clutches, whereas females desert 5–20% of clutches. In addition, 30–40% of clutches are deserted by both parents, so that these offspring are doomed to failure (Franz and Theiss, 1983; Persson and Öhrström, 1989). Both sexes may have up to 5–7 mates within a single breeding season at different locations (Cramp and Simmons, 1983). Unmated males build a sophisticated

A. L. Mészáros (✉)
Department of Medical Biology,
University of Szeged,
Szeged, 6720, Somogyi Béla 4,
Hungary, UK
e-mail: stupello@yahoo.de

S. Kajdócsi
Department of Ecology,
University of Szeged,
Szeged, 6721, Egyetem 2,
Hungary, UK

I. Szentirmai
Department of Ethology,
Eötvös Lóránd University,
1117, Budapest, Pázmány P. sétány 1/C,
Hungary, UK

J. Komdeur
Animal Ecology Group, Centre for Ecological and
Evolutionary Studies, University of Groningen,
PO Box 14, 9750 AA Haren, The Netherlands

T. Székely
Department of Biology and Biochemistry,
University of Bath,
Bath, BA2 7AY, UK

nest to attract females (Szentirmai et al., personal communication). If he is successful in attracting a female, he may start building a new nest whilst his mate is laying her eggs. Furthermore, egg-laying females visit the nests of prospective new mates. Thus, each clutch ends up with male-only care, female-only care or no care (McNamara et al., 2000).

Here we investigate breeding site fidelity of male and female penduline tits. Specifically, we compare breeding site fidelity of adult males and females within a breeding season. We also investigate whether site-fidelity of individual males and females is repeatable between breeding attempts.

Methods

We studied the penduline tits at Fehértó, Southern Hungary (46° 19' N, 20° 5' E), between April and August of the years 2002–2004. Fehértó is an extensive fishpond (1,320 ha), and the penduline tits breed on the dykes separating the

Fig. 1 The distribution of median breeding distance of male (a) and female (b) penduline tits ($n=94$ males and 19 females)

Fig. 2 Box-plot of breeding distances randomly chosen for each male and female penduline tits ($n=94$ males and 19 females, Mann–Whitney U test, $U=1313$, $p<0.001$). The boxes represent median, lower quartile–upper quartile, and the whiskers stand for minimum and maximum

fishpond units. The entire study area was searched for nests nearly every day, so it is likely that we found all nests (see below). Nest coordinates were recorded using global positioning system (GPS). Seventy-one per cent of males and 48% of breeding females were caught and ringed with an individual combination of one metal and three plastic colour rings. We made a consistent attempt to follow marked individuals whilst they stayed in our study area by checking the study site nearly everyday (see details in Bleeker et al., 2005; Szentirmai et al., personal communication). Most nests were found in early stages of nest-building; thus, we believe that we encountered virtually all nests (Bleeker et al., 2005).

We calculated one variable to describe the movements of penduline tits: breeding distance, i.e. the distance between consecutive nests of individual males and females. If a penduline tit bred in several years, only one randomly chosen year was included in the analyses. For each bird, only one randomly selected breeding distance was included in the analyses. Randomisation was carried out by MySQL Database System (Welling and Thomson, 2003). Breeding distance was non-normally distributed; thus, we used non-parametric statistical tests, except the analyses of repeatability between subsequent nests. Repeatability was counted according to the method of Harper (1994). We only included data from individually marked adults. Distances were calculated from the EOVS (Unified National Projection) coordinates of nests using the Pythagorean theorem. Statistical tests were performed by R Project for Statistical Computing software (R Development Core Team, 2004), and all tests were two-tailed.

Results

We recorded the breeding distances of 94 individually ringed males and 20 females. The median number of nests over the breeding season was two for males (range 1–8)

Fig. 3 Breeding distances between consecutive nests of male (a) and female (b) penduline tits. N2–N3 refers to the distance between the second and third nests, and similar logic applies for N3–N4, N4–N5, N5–N6 (n_{N2-N3} 52 males and 11 females; $N3-N4$ 24 males and 5 females; $N4-N5$ 13 males; $N5-N6$ 6 males)

and one for females (range 1–5). The number of nests correlated positively with the number of days spent on the study site (Spearman rank correlations—males: $r_s=0.697$, $n=142$, $p<0.001$; females: $r_s=0.620$, $n=92$, $p<0.001$). Breeding distances of males (116 m, 63–333 m; median, lower quartile–upper quartile) and females (942 m, 415–2382 m) were not different between years (Kruskal–Wallis tests— $\chi^2=1.098$, $n=94$ males, $p=0.578$; $\chi^2=3.370$, $n=19$ females, $p=0.186$). Therefore we chose randomly one year for each penduline tit breeding in the study area over more years.

Median breeding distances were skewed toward short distances (Fig. 1), and they were significantly smaller for males than that for females (Fig. 2, Mann–Whitney U test, $U=1313$, $n=113$, $p<0.001$). The breeding distances of males and females did not show a monotonous trend over the breeding season (Spearman rank correlations—males: $r_s=-0.40$, $n=91$, $p=0.704$; females: $r_s=0.112$, $n=18$, $p=0.653$).

Breeding distances were moderately repeatable for males (Fig. 3; $r=0.563$, $F_{3,91}=3.296$, $p=0.024$) and not repeatable for females ($r=-1.095$, $F_{1,14}=0.249$, $p=0.626$). This means that males tend to build his nests at consistent distances

from their previous nests, whereas movements of females were highly variable between their nests.

Discussion

We show here that both sexes of penduline tits move extensively between subsequent breeding sites; thus, penduline tits appear to have lower site fidelity than some of the closely related, highly territorial passerines (Greenwood and Harvey, 1982). For instance, male and female blue tits (*Parus caeruleus*) only move 40 and 75 m, respectively, between years (Winkel and Frantzen, 1991), and in savannah sparrow (*Passerculus sandwichensis*), breeding distances were negligible once they established a territory (median distance between nests within breeding seasons, 16.9 m, $n=227$ females; between breeding seasons, 31.8 m, $n=173$ females; Wheelwright and Mauck, 1998). The distances we reported for penduline tits within a breeding season were about ten times higher than the breeding distances of two closely related tit species that breed in Hungary: great tit (*Parus major*, median 52 m) and blue tit (median 0 m; Könczey et al., 1997). Nevertheless, some passerines show low nesting-site fidelity within a breeding season as do penduline tit, e.g. the grey wagtail (*Motacilla cinerea*) and the song sparrow (*Melospiza melodia*). The low site fidelity (in 57% of the cases, at least one member of the pair changed territory) of grey wagtails was interpreted as an adaptation to variable conditions at the breeding habitat, whereas the reason for leaving a territory (males 69%, females 87%) in song sparrows are low nesting success and territory quality (Weatherhead and Boak, 1986; Klemp, 2003).

We suggest three reasons for the low breeding-site fidelity in penduline tits, and we fully acknowledge that these arguments need further tests. First, territory quality may be more variable over the breeding season in penduline tits than in great tits and blue tits. This means, for example, that at the beginning of a breeding season, a breeding spot may have abundant nest materials and plenty of food, although later in the breeding season, the same spot may not have as much nest material and prey availability. This hypothesis predicts that males choose the best territory at a given date in the breeding season. Second, the mating success or the quality of the local mates may vary over time. We argue that this may well be the case since arrival (or departure) of one sex from a specific location should influence mating opportunities. Third, nest sites may be more limited in great tits and blue tits, so that they may be forced to keep their territory in order to breed successfully. In contrast, penduline tits are relatively flexible in choosing nest sites, as long as there are plenty of nest materials and prey around their prospective nest.

We showed that females are less faithful to the nest site than males in penduline tits. This is consistent with the typical avian pattern (Cramp and Simmons, 1983). Breeding distance of male penduline tits may be influenced by the distance between trees with good nesting-site opportunities. This in turn may influence breeding distances of females

since they visit the nest of unmated males. Females may move further than males in order to find a new male perhaps to fully explore which male would be the best choice or to reduce the chance of mating with a relative to avoid inbreeding depression (Hatchwell et al., 2000).

Taken together, our study showed that male penduline tits move further away than females. Both sexes, however, appear to move to larger distances than in closely related tits *Paridae*. We call for further works to investigate the factors that influence the breeding behaviour of tits both within and between species. Do local food supply and availability of nest material differ between or within years? Does the distribution of males influence female settlement? If it does, does this feed back to the movements of males? We anticipate that pursuing these objectives will lead to a better understanding of movement patterns and breeding systems.

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