



Breeding Site Fidelity in Urban Common Redstarts *Phoenicurus phoenicurus*

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Breeding site fidelity in urban Common Redstarts

Phoenicurus phoenicurus

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We investigated breeding patch fidelity and between-year territory movements in relation to breeding success and habitat characteristics in a colour-ringed urban population of the Common Redstart *Phoenicurus phoenicurus*. In 1996–2004, 111 marked adults (59 males and 52 females) produced 60 recapture events (41 in males and 19 in females) from 39 individuals (29 males and 10 females). Redstarts showed moderate between-year breeding patch fidelity of 46.3% males and 31.1% females returning. However, 56.1% of males and 47.4% of females shifted territory within the study area between consecutive seasons. Most of the Redstart males moved to an adjoining territory, whereas females on average moved further (197 vs. 331 m). We suggest that local experience is important for territory choice in males, whereas females use other cues, such as quality of nest cavities and mates, for dispersal decisions. We found no effect of breeding success (nest failure and number of fledglings) in the previous season on the probability of between-year territory shifts. However, Redstarts showed a tendency to switch territories towards areas with a higher proportion of tree cover and the latter could probably provide some advantage, e.g. supply of food and nest cavities, lower competition and predation rates.

Key words: *Phoenicurus phoenicurus*, site tenacity, territory movements, habitat selection, breeding success, patchy environment

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INTRODUCTION

Migratory bird species often show a tendency to return to breeding sites used during the previous season (Greenwood & Harvey 1982, Paradis *et al.* 1998). Familiarity with the breeding site brings many advantages, and also reduces the risk of not finding a (better) new territory (Pärt 1995). Many studies of site tenacity and breeding dispersal in birds addressed factors that may influence individual decisions to remain faithful to a previous terri-

tory or move to a new location (Greenwood and Harvey 1982, Switzer 1993, 1997, Paradis *et al.* 1998). An important identifier for nest-site fidelity is breeding success in the previous season. The *reproductive performance hypothesis* predicts that birds use past reproductive success at a territory to assess its future quality (Newton 2001, Sergio & Newton 2003, Pasinelli *et al.* 2007). Complete nest failure caused by predation often leads to between-year territory shifts (Haas 1998; Forero *et al.* 1999; Pasinelli *et al.* 2007). Similarly, the probability of

dispersion increases with lower previous-season fecundity (Bensch & Hasselquist 1991, Sedgwick 2004).

The *habitat choice hypothesis* states that individuals move to a new breeding site to improve the quality of resources within the territory (Bollmann *et al.* 1997, Switzer 1997, Sergio & Newton 2003). Nest site quality can directly increase reproductive success via lowered predation risk. Quality of foraging habitat and high prey abundance may increase foraging efficiency, positively influencing individual fitness through quality and number of fledglings. High foraging efficiency also allows individuals to allocate more energy and time to territory and nest defence against intruders or predators (Newton 1989, Sutherland 1996, Sergio & Newton 2003).

Individuals are often faithful to the same patch of habitat but shift territory between consecutive breeding seasons (Bensch & Hasselquist 1991, Hansson *et al.* 2002, Pasinelli *et al.* 2007). This behaviour could be explained by the *public information hypothesis*, which proposes that individuals should use not only their own reproductive success but the success of all individuals within a patch to assess its quality (Doligez *et al.* 2002, 2004, Pärt & Doligez 2003, Ward & Weatherhead 2005). Factors related to habitat quality can cause short-distance breeding dispersal within the preferred patch.

There is a good support for the reproductive performance hypothesis in many bird populations (Switzer 1997, Haas 1998, Newton 2001, Hansson *et al.* 2002, Sedgwick 2004, Pasinelli *et al.* 2007). Relatively few studies considered differences in habitat quality to explain site fidelity and territory shifts. Switzer (1993) developed a general model which proposes that individuals should change territories only in such environments where spatial and temporal variation in territory quality is expected. This prerequisite is often measured as territory attractiveness (Sergio & Newton 2003), but environmental predictors could be difficult to quantify in many cases due to habitat homogeneity such as in reedbeds (Bensch & Hasselquist 1991), grasslands (Bollmann *et al.* 1997) or woodlands (Andreu & Barba 2006).

Here we examine breeding patch fidelity and between-year territory movements in relation to breeding success and habitat types in a small population of the Common Redstart *Phoenicurus phoenicurus* breeding in urban green areas. The Redstart is a long-distance migrant exhibiting high breeding site fidelity (Ruiter 1941). It occupies open woods of the western Palearctic and also inhabits parks and gardens in human settlements (Fuchs *et al.* 2002). Thanks to the spatial heterogeneity of urban environments, particular territories differ in characteristics referring to foraging habitat quality (Sedláček *et al.* 2004). We consider two (not mutually exclusive) hypotheses for the occurrence of breeding site fidelity and territory shifts. The breeding performance hypothesis (Pasinelli *et al.* 2007) predicts that previous breeding success of Redstarts will be responsible for territory tenacity. The site choice hypothesis (Pasinelli *et al.* 2007) predicts that some patches in a mosaic of habitats are more attractive than others, and this will influence individual decisions to remain faithful or to switch the territory to a habitat of higher quality.

METHODS

The study was conducted in the small town of Břežnice (3600 inhabitants, 1.2 km²) in Central Bohemia (Czech Republic, 13°56'E, 49°34'N, 460 m a.s.l.). Our Redstarts occupy urban green areas dominated by deciduous trees, i.e. three small and two larger parks (covering 0.4 km² in total), tree-lined streets, gardens and sport fields. Woodlands within a circle of 25 km from the study area (called breeding patch for Redstart in the text) are spruce *Picea abies* monocultures, which are not suitable for breeding by Redstarts. In consequence, the towns and villages with, mostly broad-leaved, urban tree growth represent well-defined patches of breeding habitat for the Redstart within the study region (Sedláček, unpubl. data). The population in Břežnice has been partially supported by nest-boxes, placed in established territories of Redstarts (in 2001) to avoid population density

manipulation. Nest-boxes enabled us to check for the breeding success of particular pairs. Boxes were repaired and cleaned after each breeding season to avoid accumulation of ectoparasites and other negative effects that could affect the re-use of a nest hole (Stanback & Rockwell 2003).

Data were collected from 1996 to 2004 mainly for pairs breeding in nest-boxes. The number of territorial Redstarts in Březnice varied between 21 (1996) and 26 (2002–04) singing males during the study period and the population was stable or slightly increasing. The Redstarts arrive during the last decade of April. The arrival peak is very short and shifts among seasons depending mainly on the local weather during the second half of April. About 60% of pairs breed in nest-boxes in the study area. Nest failure is about 36% at the study locality ($n = 45$). Mean clutch size is 6.3 ($n = 29$), and mean number of fledgling per successful nest 5.7 ($n = 35$). Only about 5% of the pairs produce two broods per season.

We captured adult birds within established territories from late April to late June, but mainly during the nestling period. We marked the birds with unique combinations of National Museum Prague aluminium bands and coloured plastic bands. Ages were scored as 1 year or older (2K and +2K in the Euring system) (Svensson 1992). Thirteen of the 225 ringed nestlings, which returned as 2K to the place of their birth, were captured and colour-ringed as well. We confirmed resightings during intensive field surveys of the study area throughout the breeding seasons.

We used the minimum convex polygon method (Ford & Myers 1981) to map the territories based on singing locations of males. In females, we used territories of their mates for the analysis. We measured habitat variables in territories referring to foraging habitat quality - proportion cover of buildings, bare ground, sparse herb layer, short and dense herb layer, tall and dense herb layer, shrubs, tree cover (tree canopy projection on the ground), and presence of water in each territory. Because we did not find any significant differences in habitat composition of territories between the two age groups (Mann-Whitney U-test, $P > 0.10$ for all

habitat variables), the data were pooled for further analyses.

Redstart territories in the study area have about a 100 m radius (Sedláček *et al.* 2004) and mean nearest neighbour distances are 109 ± 27 m ($n = 26$, breeding season 2004) Thus, we assumed that a bird changed territory if (1) it moved more than 100 m and (2) overlap of territories in consecutive seasons was smaller than 25%. The linear distance between consecutive territories was measured from the geometric centre of the territory polygon. Successful nests were those which produced at least one fledgling. We used the number of fledglings produced per successful breeding attempt as a second measure of reproductive performance.

We included all recaptures in the analyses including pseudoreplications, i. e. all resightings of the same individual in consecutive years (Fig. 1). Yates' correction was applied in Chi-square tests

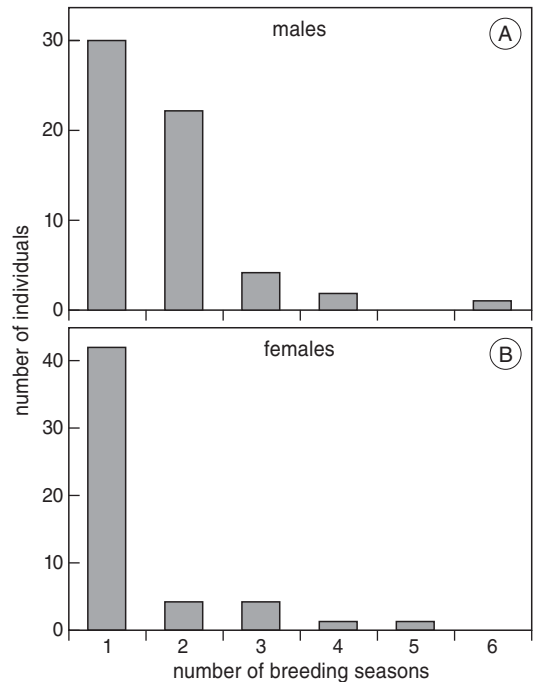


Figure 1. Residence periods of colour-ringed Redstarts in the study area in 1996–2004.

when necessary (Everitt 1977). We used non-parametric tests to compare proportions of habitats in territories. For habitat comparisons, we included only individuals which returned to the same breeding patch (town) between seasons. In the first step, we compared habitat composition in territories of individuals that remained faithful to their territory occupied in previous season (re-occupied territories) vs. territories of those individuals that shifted territory within the study area between consecutive seasons (abandoned territories). In the second step, we consider only individuals that shifted territory between seasons and compared habitat composition of their abandoned territories from previous breeding season and newly established territories. Values are reported as means \pm SD.

RESULTS

During the study period, we captured 111 adults (59 males, 52 females) and recorded 60 recapture events (41 in males, 19 in females) from 39 individuals (29 males, 10 females). The average between-year fidelity of ringed individuals to the breeding patch was $46.3 \pm 8.3\%$ in males and $31.1 \pm 13.0\%$ in females (Table 1), and the differ-

ence between sexes was significant ($\chi^2 = 4.19$, $P = 0.04$). We found no effect of age on fidelity to the breeding patch (males: $\chi^2 \sim 0$, $P = 0.95$; females: Yates' corrected $\chi^2 = 1.56$, $P = 0.21$). Males usually returned only once or twice to the study area; repeated breeding in consecutive years was relatively rare in both sexes. Maximum confirmed residence was 6 breeding seasons in a male and 5 breeding seasons in a female (Fig. 1).

Males returned in 18 cases (43.9%) to the same territory as in the previous year, whereas 23 males (56.1%) moved to a new territory within the study area. Females remained faithful to the same territory in 10 cases (52.6%), and 9 times (47.4%) shifted their territory within the study area. The difference in dispersion probability between sexes was not significant ($\chi^2 = 0.45$, $P = 0.53$); we also did not find an effect of age ($\chi^2 = 0.43$, $P = 0.51$).

Males that changed their territory between consecutive breeding seasons moved an average distance of 197.4 ± 198.2 m, and females 330.7 ± 146.1 m (Fig. 2). This difference between sexes is marginally non-significant (t -test, $n_m = 23$, $n_f = 9$, t -value = 1.77, $P = 0.086$).

In 50 recapture events (32 in males, 18 in females), we were able to test the effect of breeding success in the previous year on the probability

Table 1. Number of Redstart adults ringed and resighted within the same breeding patch (town of Březnice, Czech Republic) in subsequent years.

	Males		Females	
	No. ringed ^a	% Breeding patch fidelity (<i>n</i>)	No. ringed ^a	% Breeding patch fidelity (<i>n</i>)
1996–1997	4 (4/-)	50.0 (2)	3 (3/-)	33.3 (1)
1997–1998	6 (4/2)	50.0 (3)	8 (7/1)	25.0 (2)
1998–1999	12 (9/3)	50.0 (6)	11 (9/2)	18.2 (2)
1999–2000	11 (5/6)	36.4 (4)	5 (3/2)	20.0 (1)
2000–2001	7 (3/4)	57.1 (4)	2 (1/1)	50.0 (1)
2001–2002	15 (11/4)	53.3 (8)	10 (9/1)	40.0 (4)
2002–2003	19 (11/8)	36.8 (7)	11 (7/4)	45.5 (5)
2003–2004	19 (12/7)	36.8 (7)	18 (13/5)	16.7 (3)
average \pm SD		46.3 ± 8.3		31.1 ± 13.0

^a Between brackets: for first time ringed / ringed in a previous year.

of territory abandonment. We found no significant effect of nest failure on individual decisions to shift territory between seasons (males: Yates' corrected $\chi^2 = 0.95$, $P = 0.33$; females: Yates' corrected $\chi^2 = 0.34$, $P = 0.56$). Almost half of the birds which bred successfully during the previous season moved territory (12 shifted vs. 15 re-occupied territories in males, 7 shifted vs. 9 re-occupied in females). There were also unsuccessful breeders which remained faithful to the same territory during the next season (4 shifted vs. 1 re-occupied territory in males, 1 shifted vs. 1 re-occupied territory in females). Nest failure did not have a significant effect on dispersal probability in both age groups (1-year old birds: Yates' corrected $\chi^2 = 0.30$, $P = 0.58$; older birds: Yates' corrected $\chi^2 = 0.08$, $P = 0.44$). We were able to identify the number of fledglings produced per successful breeding attempt for 28 Redstart individuals which showed breeding patch fidelity. On average, males

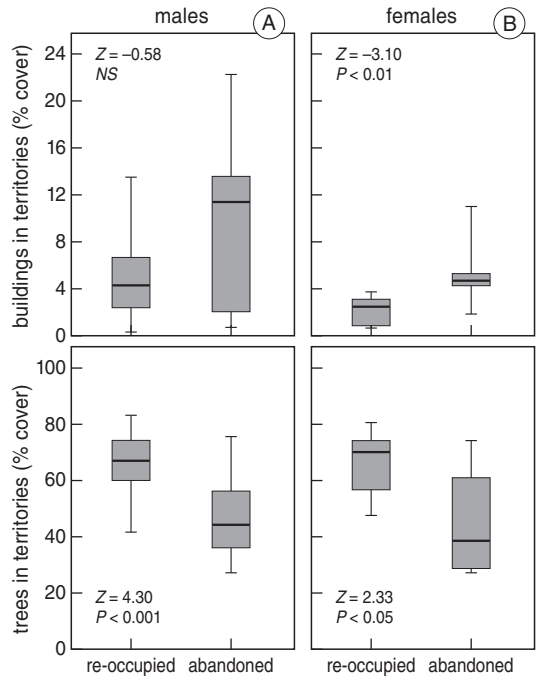


Figure 3. Percentage cover of buildings and trees in territories of all resighted Redstarts: territories re-occupied by the same individuals between seasons vs. territories abandoned by individuals which shifted to a new territory. Medians, 25% and 75% percentiles and variance are given. Mann-Whitney U-test statistics are indicated.

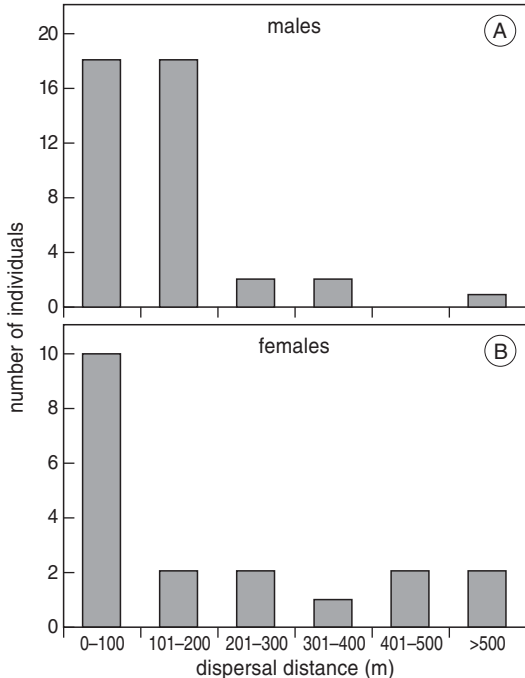


Figure 2. Between-year dispersal distances of Redstart males and females.

that shifted their territory produced a slightly lower number of fledglings (5.14 ± 1.35) than males that remained faithful to the territory between consecutive seasons (6.13 ± 0.83). However, this difference was not significant (t -test; $t = -1.73$, $n_1 = 7$, $n_2 = 8$, $P = 0.11$). The average number of fledglings produced per breeding attempt did not significantly differ between the two groups in females (shifted territory: 5.83 ± 0.98 , re-occupied territory: 5.29 ± 1.70 ; t -test, $t = 0.69$, $n_1 = 6$, $n_2 = 7$, $P = 0.50$).

For habitat comparisons, we included only individuals which returned to the same breeding patch (town) between seasons. Territories that were abandoned by both males and females between seasons had a significantly lower proportion cover of trees than those re-occupied by the same

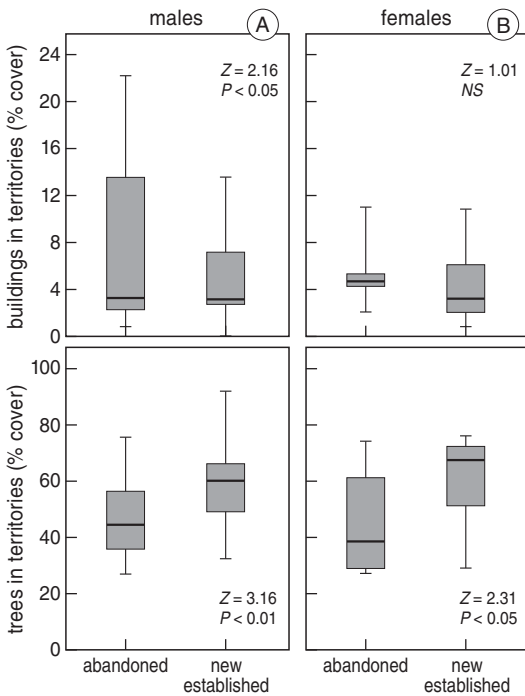


Figure 4. Percentage cover of buildings and trees in territories of resighted Redstarts which shifted their territories within the study area between two consecutive breeding seasons: abandoned vs. newly established territories. Medians, 25% and 75% percentiles and variance are given. Wilcoxon matched pairs test statistics are indicated.

individuals during the consecutive season. In females, abandoned territories had a significantly larger proportion cover of buildings (Fig. 3). The abandoned and re-occupied territories did not significantly differ in other habitat characteristics (Mann-Whitney U-tests, $P > 0.05$).

In the second step, we considered only individuals that shifted territory between seasons. Newly established territories of such individuals had a significantly higher proportion cover of trees and – for males only – a significantly lower proportion cover of buildings than in territories that had been abandoned (Fig. 4). The abandoned and newly established territories did not significantly differ in other habitat characteristics (Wilcoxon matched pairs tests, $P > 0.05$).

DISCUSSION

Our study of colour-ringed Redstarts revealed that this long-distance migratory species shows moderate between-year fidelity. Pronounced site fidelity is typical for species with a patchy distribution of the breeding habitat (Weatherhead & Forbes 1994, Travis & Dytham 1999, Hansson *et al.* 2002). Breeding in patchy environments is characteristic for many synanthropic species, such as Lesser Kestrel *Falco naumanni* (Negro *et al.* 1997), Black Redstart *Phoenicurus ochrurus* (Wegglar 2000), Barn Swallow *Hirundo rustica* and House Martin *Delichon urbica* (Shields 1984, Paradis *et al.* 1998). Moreover, populations of woodland birds living in cities, such as Blackbird *Turdus merula*, show increased sedentariness in comparison with rural populations (Partecke & Gwinner 2007). The limited exchange of individuals between urban and rural populations, typically in areas where the native habitat beyond towns is absent, may contribute to changes in behaviour, physiology, life history traits and genetic divergence of populations living in close proximity of humans (Diamond 1986, Partecke *et al.* 2004, 2005, 2006a,b, Partecke & Gwinner 2007). Redstarts commonly breed in urban environments in the Czech Republic (Fuchs *et al.* 2002, Štátný *et al.* 2006). Moreover, parks and gardens in towns represent an important habitat in areas covered by woodlands (spruce monocultures) unsuitable for breeding by Redstarts. We suggest that in such areas moderate fidelity to breeding patches could contribute to adaptation of urban populations to the close proximity of humans.

We showed that about 46% of marked males compared to about 31% of females returned to breed within the same breeding patch as in the previous season. This is in congruence with the general pattern of a female-biased dispersal in birds, which is assumed to be related to lower costs of dispersal in females (Clarke *et al.* 1997). However, based on our data we are not able to distinguish whether females dispersed from the study area to another patch of habitat, or that the difference in recapture rate between sexes is caused by

sex-biased mortality with higher rates in females (Donald 2007). We suggest that greater parental investment could cause higher mortality in Redstart females either during the breeding season, or during migration and on wintering grounds.

Almost half of the males and females that returned to breed again in the study area shifted their territory within the town. Numerous studies on birds showed that lower reproductive success during the previous season influences breeding dispersal decisions (Bensch & Hasselquist 1991, Haas 1998, Newton 2001, Hansson *et al.* 2002, Wesołowski 2006, Pasinelli *et al.* 2007). In our study we were able to assess the reproductive success in only a small proportion of the population. However, almost half of the males and females which bred successfully during the previous season decided to shift territory but, on the other hand, there were also some individuals that remained faithful to the same site in spite of a nest failure. We also found no effect of the number of fledglings produced during the previous season on the probability of dispersal. Although our data on breeding success are sparse, it seems that the reproductive performance hypothesis received rather weak support in the case of our urban Redstarts.

Increasing evidence suggests that individuals shift between breeding sites in response to the quality of habitat (Bollmann *et al.* 1997, Switzer 1997, Sergio & Newton 2003, Pasinelli *et al.* 2007). In our study, Redstarts appeared to switch towards areas with a higher proportion of tree cover. The probability of territory abandonment increased in both males and females with a lower percentage of tree cover in territories and, at the same time, individuals that shifted their territory gained a new one with a higher proportion of trees. Although Redstarts forage mainly on the ground and relatively sparsely on trunks and foliage (Sedláček *et al.* 2004), general abundance and availability of invertebrates could increase with the proportion of tree cover. Hedblom & Söderström (2007) showed that Great Tits *Parus major* breed in higher densities in residential areas but their nestling condition is lower than in urban woods. This disproportion may suggest increased

competition for food in residential areas. We showed in a previous study that Redstarts may compete for resources with Black Redstarts, a larger and more dominant species (Sedláček *et al.* 2004, 2006, 2007). This could also be a reason for territory shifts of Redstarts towards sites with more trees, to avoid the build-up areas occupied by Black Redstarts. Furthermore, Lepczyk *et al.* (2003) found that there is a higher predation risk in residential areas than in suburban and rural areas due to the abundance of feral cats. Although we have no direct support for the adaptivity of between-year site movements, we suggest that a higher proportion of tree cover in territories of Redstarts could provide some advantage.

We showed that many male Redstarts shifted to a territory which adjoined the one occupied in the previous season. Birds often prospect the habitat in the vicinity of their territories and are able to assess its quality based on reproductive success of their conspecific neighbours. This could reflect in territory shifts during the next breeding season (Pärt 1995, Reed *et al.* 1999, Pärt & Doligez 2003). We have not investigated the consequences of dispersal. However, territory movements of males seem to be spatially non-random and this supports the public information hypothesis predicting that birds prefer to stay within the familiar area and that local experience is important for breeding site choice (Doligez *et al.* 2002, 2004). Females of Redstart on average dispersed over longer distances than males. This implies that their between-year movements could be influenced not only by habitat characteristics but also by the quality of nest cavities and/or mates, as has been shown for other cavity nesters (Pied Flycatcher *Ficedula hypoleuca*, Slagsvold 1986; Collared Flycatcher *F. albicollis*, Pärt 1991; Black-capped Chickadees *Poecile atricapillus*, Otter & Ratcliffe 1996; Black Redstart, Weggler 2000).

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SAMENVATTING

In het stadje Březnice in Centraal-Bohemen broeden Gekraagde Roodstaarten *Phoenicurus phoenicurus* in loofhoutrijke parken, straatbepantingen, tuinen en langs sportvelden. Rondom het stadje worden de bossen gedomineerd door monoculturen van fijnspar *Picea abies*. Deze bossen zijn ongeschikt als broedplaats, wat de loofhoutrijke dorpen tot aantrekkelijke broed-enclaves maakt. In dit onderzoek aan een nestkastbewonende en ge(kleur)ringde populatie is nagegaan of plaatstrouw en dispersie samenhangen met het broedsucces in het voorafgaande broedseizoen of met de kwaliteit van de broedplaatsen. Gemiddeld keerde 46% van de mannetjes en 31% van de vrouwtjes het volgende seizoen als broedvogel terug naar het stadje. Van de teruggekeerde mannetjes wisselde echter 56% van territorium; bij de vrouwtjes was dat 47%. Meestal betrof het een verplaatsing naar een naastgelegen territorium, waarbij de vrouwtjes zich gemiddeld verder verplaatsten dan de mannetjes (respectievelijk 331 en 197 m). Dispersie hield geen verband met het broedsucces in het voorafgaande seizoen, zoals gemeten aan de hand van nestmislukkingen en het aantal uitgevlogen jongen. Daarentegen tenderden de verplaatsingen naar territoria met een hoger aandeel bomen, wat vertaald zou kunnen worden in een groter aanbod van voedsel en nestholtes, minder competitie (in boomarme stadsdelen broeden Zwarte Roodstaarten *Phoenicurus ochruros*, die dominant zijn waar beide soorten naast elkaar voorkomen) en een geringere predatiedruk (vooral van Huiskatten *Felis catus*). (RGB)

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