Site fidelity of Great and Blue Tits in the Pilis-Visegrád Mountains

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Abstract. We present an analysis of natal and breeding site fidelity of the Blue and the Great Tit (*Parus caeruleus, P. maior*) based on the data collected between 1982-1995 in the Pilis-Visegrád Mountains. Site fidelity depended in both species on age: natal site fidelity (500 m, 1000 m) is much weaker than breeding site fidelity (median distance within year 39 m, 55 m; between years about 80 m in both species). Natal dispersal among Great Tits and between years breeding site fidelity among Blue Tits depended on sex (males had shorter dispersal distances). There was no difference in the spatial distribution within plots between yearling birds immigrated to or resident in the area. Proportion of birds changing nest box within one season if they reared no young from the first brood was higher comparing to pairs with successful first breeding especially in Great Tits, but also in Blue Tits. There was no difference in the distance moved to the site of replacement clutch by birds whose nest was failed before or after hatching. After the total failure, Great Tits with predated first brood moved further than birds lost their brood by other reasons (i.e. interspecific competition). Neither the failure of the first, nor of the replacement and second clutch affected site fidelity between years.

Passerines known to be resident rarely remain on the same territory throughout their life. However, they do return to a restricted area, which behaviour is called as site fidelity, and the distance moved is the dispersal distance. Site fidelity can be measured to natal, breeding, feeding, wintering or roosting areas. After the familiarity hypotheses, the benefit of site fidelity is the knowledge of the area (as birds are familiar with resources, competitors and dangers). Birds on a familiar area may have higher fitness than birds living on formerly unknown area (SLAGSVOLD & LIFJELD, 1990). Site fidelity decreases (dispersal distance increases) if birds are living among spatially or temporally heterogeneous, thus unpredictable environmental variables (JÄRVINEN, 1989); or if an area was proved to be unfavourable (e.g. individuals had bad reproduction).

Site fidelity may affect local survival estimations (BARROWCLOUGH, 1978). Natal and breeding site fidelity should be investigated in evolutionary and population biology and behavioral ecology studies because it usually affects the demographic parameters (LIDICKER, 1975; BREITWISCH, 1989), and also affects genetic variance (WRIGHT, 1946; ERHLICH & RAVEN, 1969; SHIELDS, 1983; PERRINS, 1990).

In this study we analysed some possible causes and consequences of natal and breeding site fidelity of two common tit species, the blue and the Great Tit. The main questions addressed were whether there are site fidelity differences between sexes, age groups, birds with different previous experiences (e.g. birds living on known or unknown area, MCCLEERY & CLOBERT, 1990; birds with failed or successful former breeding attempt, birds with surviving recruits, birds with clutch lost by predation or by other kind of disturbance, NUR, 1988; PÄRT & GUSTAFSSON, 1989; SLAGSVOLD & LIFJELD,1990;

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SHIELDS, 1984; NEWTON & MARQUISS, 1982; review in GAVIN & BOLLINGER, 1988). We also asked whether recruitment rate is affected by site fidelity.

Study area, species and methods

Study area lays in the eastern part of the Pilis-Visegrád Mountains, 50 km from Budapest to NW, in an oak-hornbeam forest managed by the Pilis Park Forestry. Average age of forest is between 60-70 years. More detailed descriptions and maps about the area, and the long-term population biology and behavioral ecology studies on the nine artificial nest-box plots may be found in TÖRÖK & TÓTH (1988a, 1988b), TÓTH (1985) and KÖNCZEY (1990). Human disturbance is significant in some plots owing to the paths and roads crossing them. Nest predation rate on average is 0.1 (fluctuating between 0-0.3 between plots and years). Most frequent nest predator is the dormouse, but woodpeckers, grass-snakes, mustelids (weasel, marten), cats are also observed or potential predators on the plots. Nest predation results in total failure in about 85% of cases. Other important causes of nesting failure are inter- or intraspecific competition for boxes, human disturbance (e.g. tits are highly intolerant to disturbance at nest during egg-laying and incubation; KANIA, 1989).

Most frequent breeding species (with descending frequency) on the plots are: Collared Flycatcher (*Ficedula albicollis*), Great Tit, Blue Tit, Nuthatch (*Sitta europaea*). The outcome of competition for boxes is strongly affected by body mass of birds and the time period of competition (see e.g. SLAGSVOLD, 1975; GUSTAFSSON, 1988). Both tit species are territorial and resident. Males take up territories in autumn (DRENT, 1983), and both sexes and species form flocks during winter. Breeding starts between end of March and middle of April. Egg-laying is synchronised with the peak period of caterpillars, the main food of tits during breeding (VAN BALEN, 1973; TÖRÖK & TÓTH, 1988b.). Incubation period is 2 weeks, the young fledge at day 18-20 after hatching. Breeding failure is usually followed by a repeated clutch. After fledging the first clutch, a second clutch can be laid in late May. Size of second clutch, as well as repeated clutch, and the success of second breeding is smaller than those of the first breeding.

We measured site fidelity by the distance in meters of the two boxes occupied by the same individual in consecutive breeding attempts within or between years (GREIG-SMITH, 1982; SHIELDS, 1984). Data of (young or breeding) birds dispersing from the closed plots were omitted. Reliability of distance measures is 1 m, of bearing is 5. Maps were digitalized to get the coordinates of boxes. When a box was moved to a nearby tree (e.g. after natural fell of a dead trunk) the new coordinates of it were determined.

Boxes were checked 1-3 times per week from the beginning of breeding season. The following breeding phenological data of tits were used in this study: place of breeding, onset of breeding (considering the date of first egg laid in the population as day 1), ring number of parents and young, age of parents (2Y=yearling, or older), adult survival to the next breeding season, number of eggs, hatched, fledged and recruited young (recaptured the next spring or later), factor determined as reason for nest failure. More than 80% of females, and more than 90% of young were ringed. Males captured only since 1987, and only in 40% of tit nests (mainly because failure during incubation makes males impossible to catch and identify). We used standardised breeding parameters to decrease year-to-year and site-to-site variances.

Site fidelity of tits were tested using Mann-Whitney U-test, Chi-square test and Spearman rank correlation (SPSS/PC+ software were used in all analyses, SPSS Inc. 1984-1985). Probabilities are two-tailed.

Results

Natal site fidelity

Yearling Great Tits showed sex-dependent site fidelity towards their natal site (male median = 899 m, n = 15, female median = 1144 m, n = 13; Mann-Whitney U-test, Z = -2.19, $p < 0.05$). In Blue Tit the difference was not significant (male median = 418 m, n = 10, female median = 555 m, n = 8; Z = -1.07, NS).

On plots smaller than 6 hectares tits prefer the marginal boxes (KÖNCZEY, 1990), and recruitment rate of young fledged from these boxes are better than those of fledged from "inside" boxes (our unpublished data). According to the familiarity hypothesis birds remaining on their natal area, thus knowing better their environment (resources, competitors, predators) are in favour comparing to birds immigrating to the area. As a consequence, more resident yearlings are expected to breed in the preferred marginal boxws. We examined the proportion of resident and immigrant 2Y tits breeding in marginal and inside boxes regarding the two species and both sexes. Individuals born on or immigrated onto their first breeding area occupied the two types of boxes with the same probability (^{2} in all cases < 1.74, df = 1).

Mate fidelity

Mate fidelity in tits could be analysed only in the very few cases where both parents were captured, and 1.) both were recaptured and formed a breeding pair again, or 2.) one of them was recaptured in the next breeding period and had different partner, or 3.) both were recaptured in different boxes in the next breeding period. The members of 5 Great Tit and 4 Blue Tit pairs of replacement or second broods remained the same as in the first brood, i.e. mate fidelity was characteristic to them within season. Recruitment rate of tits is considerably low, thus it was not surprising that 14 Great Tit females and 10 males ("widow" birds) recaptured in two consecutive years with different or unringed partner and only one with the same partner (faithful), and one with a male captured with another female in previous year ("divorced"). Among Blue Tits, two pairs were faithful, one pair divorced, and 5 females and 7 males were determined as widows. Faithful birds in every cases bred closer to their previous nest than divorced ones, although because of the small sample sizes we did not prove it by statistics.

Breeding site fidelity

Breeding site fidelity of birds between years was much stronger than natal site fidelity of young (Mann-Whitney U-tests, Great Tit female Z = -5.60, $p < 0.0001$, male Z = -3.85, $p = 0.0001$; Blue Tit female Z = -2.84, $p < 0.005$, male Z = -3.19, $p < 0.005$). On the base of site fidelity of females recaptured within season (within year site fidelity is the distance moved from the box of the first breeding to the second or repeated breeding), we can state that both species held their territories during a breeding season: median of distance between sites of first and replacement nests in Great Tit was 55 m, in Blue Tit was 42 m, while median of distance between sites of first and second nests was 52 m in Great Tit, and zero in Blue Tit (Great Tit Z = -2.0, $p < 0.05$; Blue Tit Z = -0.94, NS). We analysed the independence of shifting between boxes or holding a box vs. having a successful or failed first breeding. Significantly more birds laid the second clutch in the box of the first clutch after a successful breeding (8 Great Tit pairs of the 35, and 5 Blue Tit pairs of the 9) than after an unsuccessful one (0 Great Tit pairs of 59, and 3 Blue Tit pairs of 17; Great Tit $^2 = 14.74$, df = 1, $p < 0.0005$, Blue Tit $^2 = 3.97$, df = 1, $p < 0.05$).

Within year and between years breeding site fidelity of females differed in both species (Great Tit female: $Z = -2.76$, $p < 0.01$, male: $Z = -1.61$, $p = 0.107$; Blue Tit female: $Z = -4.13$, $p < 0.0001$, male: $Z = -1.89$, $p = 0.059$, *Fig. 1*): namely within year site fidelity was stronger than between year site fidelity. The difference in between years site fidelity of male and female Great Tits was found to be not significant ($Z = -0.69$, NS, *Fig. 1*). Site fidelity of male Blue Tits was stronger than that of the females ($Z = -2.16$, $p < 0.05$, *Fig. 1*).

The effect of females' age and breeding success on site fidelity were analysed in detail. We found no difference in within year site fidelity among 2Y and older birds of both Great and Blue Tits (Great Tit: older median = 54m, n = 59, 2Y median = 55m, n = 47; $Z = -0.71$, NS; Blue Tit: older median = 40m, n = 11, 2Y median = 33m, n = 11; $Z = -0.20$, NS). However between years breeding site fidelity of 2Y Great Tit males was found to be stronger than that of the older males (Table 1). No similar age effect was documented in Great Tit females and in any sexes of Blue Tits (Table 1). Omitting birds with unsuccessful breeding attempt in the first investigated season the similar analyses was carried out, and no age dependent differences were found in their site fidelity.

The date when first clutch failed (i.e. failed before or after hatching) did not affect the site fidelity, the distance between boxes of the unsuccessful first and the repeated clutch (Great Tit: clutch failed before hatching, median = 56 m, n = 44; clutch failed after hatching, median = 55 m, n = 14, $Z = -0.14$, NS; Blue Tit: clutch failed before hatching, median = 38 m, n = 16, the pair with the only clutch failed after hatching occupied a box 45 m far from the first for repeated clutch, $Z = -0.20$, NS). In Great Tit failures caused by nest predation resulted in greater avoidance (median of distances between first and repeated clutches = 87 m, n = 5), than those failed for another reason (e.g. competition for nestbox, human disturbance, median = 49 m, n = 25, $Z = -2.48$, $p < 0.05$). No similar effect was found in Blue Tits (predated: median = 79 m, n = 7, non predated: median = 53 m, n = 3, $Z = -0.57$, NS).

There was no difference in the between years site fidelity between birds with successful or unsuccessful breeding (Table 2, Mann-Whitney U-test NS for both species, for both sexes). We could not analyse the effect of total failure on the site fidelity of different age groups because unsuccessful yearlings were almost no recaptured after their unsuccessful breeding. Recruitment rate of 2Y Blue Tit females was lower for unsuccessful ones than for females rearing at least one fledgling in their first breeding season ($^2 = 5.52$, df = 1, $p < 0.01$). Expected and observed local survival of 2Y Great Tits, 2Y male Blue Tits and all old tits were not different (^{2} in all cases < 0.95, df = 1).

Only a small fraction of fledged young survived to the first breeding season (recruitment rates were 0.5% and 0.8% for Blue and Great Tits respectively). Considering the 0.5-6 km distance of our study plots from each other, the above reported 1 km (Great Tits), or half km (Blue Tits) extent of natal site fidelity means the correct sampling of the population as well. We examined whether the site fidelity of parents having at least one, or have no survived offspring was the same. Although both species and sexes having no recaptured offspring showed weaker site fidelity, these differences were not significant (Z in all cases < -1.5). Sample sizes were extremely low in these analyses.

Table 1. Between years breeding site fidelity of yearling and older tits

Species	Sex	Yearling median (n)	Older median (n)	Z	p
Great Tit	female	85 m (36)	62 m (39)	−0.69	NS
	male	65 m (8)	120 m (10)	−2.05	< 0.05
Blue Tit	female	105 m (16)	95 m (23)	−0.63	NS
	male	75 m (8)	71 m (8)	−0.05	NS

Table 2. Between years breeding site fidelity of Great and Blue Tits with unsuccessful or successful breeding attempt

Species	Sex	Seaso started		Season finished	
		unsuccessfully	successfully	unsuccessfully	successfully
		median (n)	median (n)	median (n)	median (n)
Great Tit	female	43 m (3)	71 m (37)	91 m (12)	65 m (62)
	male	22 m (3)	86 m (12)	38 m (3)	94 m (14)
Blue Tit	female	126 m (4)	104 m (31)	119 m (5)	100 m (32)
	male	86 m (2)	76 m (13)	86 m (2)	72 m (14)

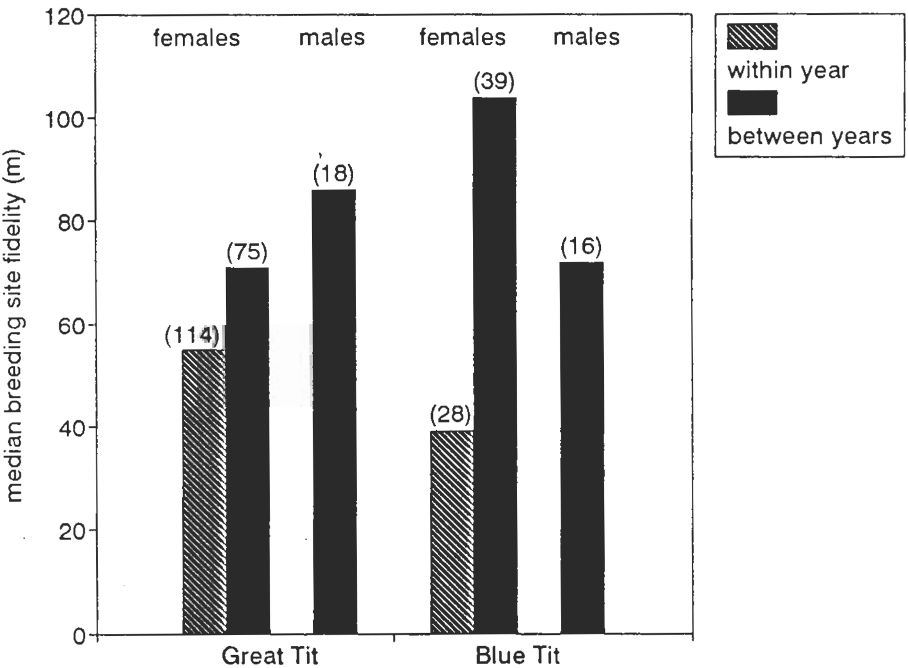

Fig. 1. Within and between years site fidelity of Great and Blue Tits. (Sample sizes are in parentheses)

Discussion

Although yearling tits choose breeding area much farther from their natal site than adults from their previous breeding site, even this distance is comparable with the sizes of territories (SHIELDS, 1982). Benefit of the weaker natal site fidelity is that it indirectly decreases inbreeding both among sisters and brothers (if natal dispersal is different for sexes) and moreover both among parents and offspring. Natal dispersal can be influenced by the time of fledging (PAYNE, 1991; DHONDT & HUBLÉ, 1978), brood size (PÄRT, 1990), density at the time of fledging (DRENT, 1983; NILSSON, 1989), sex (reviewed in GREENWOOD & HARVEY, 1982) and condition of fledglings, their dominance status (DHONDT, 1979), the quality of natal area (NEWTON & MARQUISS, 1983).

Studies provided evidences that breeding site fidelity can be affected by sex, age (PÄRT & GUSTAFSSON, 1989; HARVEY et al., 1984), previous breeding performance (VON HAARTMAN, 1949; FREER, 1979; PÄRT & GUSTAFSSON, 1989), wintering and migration, breeding density (PÄRT, 1990), parents condition which is affected by the food supply of the habitat (SHAW, 1990) and genetic factors (reviewed in GREENWOOD & HARVEY, 1982; SHIELDS, 1984).

Correspondingly to GREENWOOD et al. (1979) young Great Tit males in the Pilis-Visegrád Mountains chose breeding ground closer to their natal site than females. Natal site fidelity of Blue Tits was unrelated to sex. The extent of the observed natal dispersal distance in our area is in accordance with the data of other European population (Great Tit male: ranging from 354 m to 1017 m, female: ranging from 543 m to 1269 m, in GREENWOOD et al., 1979). Tits were faithful to their breeding area as it was shown by the median of between years site fidelity (less than 100 m, which data corresponds to the studied British population, HARVEY et al., 1979). GREENWOOD (1980) found that females have weaker site fidelity than males in species where males defend territory, while in species where males defend females, the pattern is opposite. Our results on Great Tits, of which male defends not only the territory, but guards the female as well, correspond to this theory because site fidelity of sexes is similar. However we found sex-dependent breeding site fidelity in Blue Tits where males had stronger site fidelity than females.

Mate fidelity is characteristic within season. Mate fidelity between years (of which benefit is considered to be the higher breeding success, which benefit could make reasonable the strong site fidelity, SCHIECK & HANNON, 1989) was extremely rare in these populations, where the survival rate is also very low. The higher between years mate fidelity found in Great Britain (HARVEY et al., 1979) can be partially owned to the mild winter climate: birds stay for almost whole year on the breeding ground, while in the Pilis-Visegrád Mountains the winter flocks move greater distances and spend more time in valleys to utilize the better feeding possibilities. In the above British population mate fidelity is more frequent than divorce, and divorced Great Tit females bred farther from their previous year box than faithful ones. Owing to the low data size we could not prove statistically that site fidelity of widow and divorced birds is weaker than of faith birds.

Birds were born on the area where they started to breed were not in favour comparing to yearling birds immigrated to the breeding ground.

Total failure increased the chance of finding a new box for replacement brood within season in both Great and Blue Tits. Brood status (before or after hatching) in the time of nest failure did not affected the distance moved to the site of replacement brood. After a total failure, Great Tit pairs with predated first brood moved further than birds lost their brood by other reasons. Neither the failure of the first, nor of the replacement or second clutch affected site fidelity between years, although fewer unsuccessful 2Y Blue Tit females returned to the breeding ground than expected. These result about the effect of breeding success on site fidelity only partly correspond with NUR (1988) who found stronger site fidelity after successful season. Although both species and sexes having no recruit showed weaker site fidelity than individuals with at least on survived offrspring, these differences were not significant.

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