

Breeding-season dispersal of male and female Penduline Tits (*Remiz pendulinus*) in south-western Poland

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Dispersal during the breeding season is common among multiple-brooding bird species, such as the Penduline Tit *Remiz pendulinus*, in which both sexes are sequentially polygamous and one or both parents may abandon the clutch. Penduline Tits were studied at a large fishpond system in south-western Poland over six breeding seasons (2004–2008 and 2011). Breeding dispersal of 97 males and 44 females were recorded. Females dispersed longer distances than males, and dispersal distances of both males and females did not vary significantly between years. Mating success at the previous nest did not influence the dispersal distance of males. Females who found new mates after a successful breeding attempt settled closer than those who had abandoned their previous nest. The distances of females remating after nest failure were similar to those of abandoning females. These results corroborate the general pattern of dispersal in birds, in which females commonly disperse further than males. This bias can be explained by a sex-dependent difference in breeding-site availability. Male Penduline Tits attract females to their nests and can choose from all vacant sites to settle, whereas females are restricted by males' dispersion and may be forced to go further.



1. Introduction

Dispersal within a breeding season is common to many multiple-brooding birds as well as to those attempting to re-nest. Movements between two breeding sites within one season may be up to several hundred kilometres in the Common Redpoll *Carduelis flammea* (Antikainen *et al.* 1980) and the Eurasian Dotterel *Charadrius morinellus* (Whitfield 2001). Within-season dispersal over

shorter distances is quoted in, e.g., Siskin *Carduelis spinus*, Bullfinch *Pyrrhula pyrrhula* (Newton 2000), Tengmalm Owl *Aegolius funereus* (Korpimäki *et al.* 2011) and Penduline Tit *Remiz pendulinus* (Franz *et al.* 1987, Franz 1988). Factors affecting dispersal may be variable, including depletion of food resources (Greig-Smith 1982), parasite avoidance (Stanback & Dervan 2001) or predation (Darley *et al.* 1971, Harvey *et al.* 1979, Greenwood & Harvey 1982). A general pattern of

bird dispersal is that both natal and breeding dispersal is usually female biased (Greenwood 1980, Greenwood & Harvey 1982, Clarke *et al.* 1997). This bias is thought to be the result of the territoriality and resource defence by males (Greenwood 1980), inbreeding avoidance (Wolff & Plissner 1998) or difference in breeding-site availability between males and females (Arlt & Pärt 2008).

In the present study, the within-breeding-season dispersal of the Penduline Tit, a small passerine bird with a complex breeding system, was studied. Both males and females may have up to six partners during one breeding season, and parental care is uni-parental, i.e., brood care is provided by either the male or the female (Persson & rstr 1989). Nest building is initiated by the male, and the female may join him at any stage (for detailed information on nest-building, see Czyż *et al.* 2009). Males may remain unmated for several weeks, after which they abandon the incomplete nest and start to build a new one (Cramp *et al.* 1993).

In the population studied here, 38% ($N = 478$) of nests were such that the male did not succeed in attracting females (B. Czyż, unpublished data). Females lay eggs in unfinished nests, and during egg laying the male or the female usually abandons the clutch. About 30–40% of clutches are abandoned by both parents and are therefore doomed to failure (Persson & Öhrström 1989, van Dijk *et al.* 2007). Apart from possible differences between males and females in breeding-season dispersal, the impact of the fate of previous nests on dispersal was examined.

2. Material and methods

The study was carried out at Milicz fish ponds in south-western Poland. The study area (1,200ha) covered 28 out of 31 ponds in Stawno system (51°3' N, 17°1' E). Most of the ponds support extensive reed beds, and dykes are vegetated with deciduous trees, mostly oak *Quercus* sp., willow *Salix* sp., birch *Betula pendula* and poplar *Populus* sp. Penduline Tits build their nests predominately on the latter three species.

Data were collected from April to August in 2004–2008 and in 2011. New nests were sought

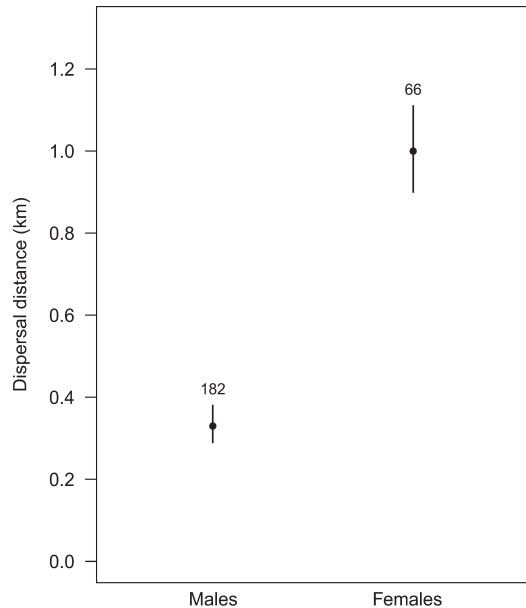


Fig. 1. Dispersal distances for male and female Penduline Tits. Mean value with standard error, and sample size are given.

nearly every day, and the inspection of the whole area took about 2–3 days. Birds were captured during nest-building time using mist nets with the aid of song playback, and were then individually marked with three colour rings and one metal ring. Some individuals were caught and ringed during incubation phase. Marked birds were followed during the breeding season. During the nest-building and egg-laying periods, nests were visited at least every 2–3 days. During these visits, colour rings of birds at nests were always recorded to confirm the identity of the observed individuals. If one of the parents started incubation, the nest was visited twice a week until the nest fledged or failed. The position of nests was recorded with GPS receiver.

The distance between nests was calculated using odlegloc 1.1 software (<http://www.zadorski.loonar.pl/gps/index.htm#odlegloc>) and approximated to the nearest 10 m.

The data were subjected to a General Linear Mixed Model (GLMM). Distance measures between consecutive nests were root transformed to normalize the residuals. Sexes were examined separately, but a general model was first built, with sex as an independent fixed variable and year and

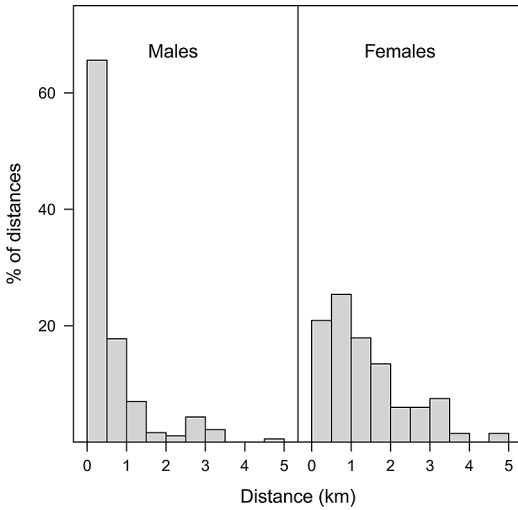


Fig. 2. Distribution of within-breeding-season dispersal distances of female ($n = 66$) and male ($n = 182$) Penduline Tits.

individual identity as random factors. Because different individuals had been sampled in different years, identity was nested within year. Apart from distance, the model for females included the fate of the previous nest (abandoned, failed or successful) as a fixed variable, while that for males had mating success (successful vs unsuccessful) at previous nest as a fixed variable. In both models, year and identity were random factors, with identity being nested within year.

Statistical analyses were performed using R 2.13.1 with nlme package (R Development Core Team 2011).

3. Results

During the five breeding seasons, 182 dispersal movements of 97 males and 66 movements of 44 females were observed. Mean distance between consecutive nests of females was greater than

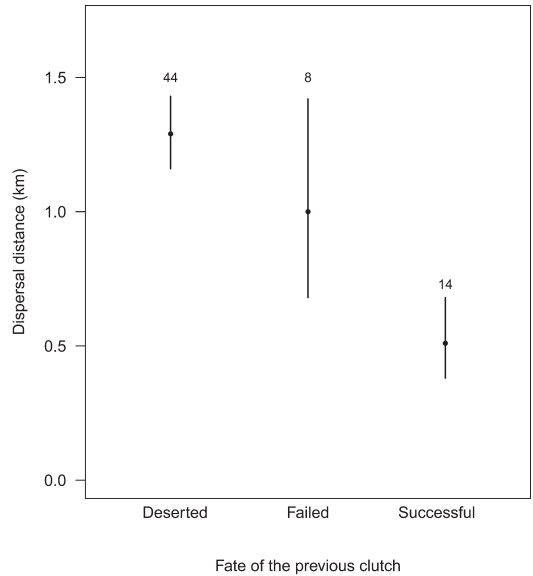


Fig. 3. Dispersal distances of female Penduline Tits in relation to the fate of their previous nest. Mean value with standard error, and sample size are given.

those of males (1.00 km vs 0.33 km; $t_{134} = 6.43, p < 0.001$; Fig. 1). Males were thus more stationary, most of them moving less than 0.5 km between consecutive nests and distances over 1 km were rare (Fig. 2). Females frequently moved 0.5–1.5 km (almost 50% of cases) and distances >1.5 km were common (>30% of cases; Fig. 2). There was no significant difference between years for males or females (likelihood ratio test; $p > 0.4$).

Males who had not managed to attract a female to the nest did not move further than males who abandoned the clutch (0.29 km vs 0.35 km; $t_{84} = 0.88, p = 0.38$). Females who found a new mate after successfully rearing offspring settled significantly closer than those who deserted (0.54 km vs 1.23 km), but no significant differences were found between dispersal distances of abandoning and remating after a nest loss females (1.0 km; Fig. 3, Table 1).

Table 1. GLMM for the dispersal distance of female Penduline Tits.

Variable	Estimate	SE	df	<i>t</i>	<i>p</i>
Intercept	1.030	0.035	38	29.74	<0.001
Fate of the nest [lost]	-0.026	0.065	20	-0.36	0.72
Fate of the nest [successful]	-0.16	0.051	20	-3.12	0.005

4. Discussion

The results confirm that female Penduline Tits disperse further than males within a breeding season. This is consistent with the common pattern in birds that females disperse further than males in natal dispersal as well as in breeding dispersal (Greenwood & Harvey 1982). A similar pattern for the Penduline Tit has earlier been observed in southern Hungary, but the median distances were shorter (116 and 942 m for males and females, respectively; Mészáros *et al.* 2006). Franz (1988) observed considerably greater breeding-dispersal distances in Germany and Austria, where the mean distances were 7.1 km for males and 13.7 km for females, but only distances >500 m were considered in that study. The difference may also be caused by variation in study-area characteristics, as Franz (1988) conducted the study in a river valley where distances between nests may be greater due to often linearly-arranged territories.

Dispersal during the breeding season is well known in bird species which breed more than once per season or reneest after nest loss (Powell & Frasch 2000). Distances between consecutive nests may depend on many factors, such as depletion of local food resources (Greig-Smith 1982), sex ratio (Marzluff & Balda 1989), territory quality (Switzer 1993) or predation (Jackson *et al.* 1989). Mészáros *et al.* (2006) suggested possible reasons for the common breeding dispersal in the Penduline Tit: (i) territory quality during breeding season for the focal species may vary more than for other similar species; (ii) suitable nest sites may be less limited; and (iii) mating success and mate quality may change, which force the individual to disperse. It seems probable that the dispersal of male Penduline Tits could be determined by the availability of suitable nest sites, and in turn female dispersal could be influenced by the dispersion and quality of males. This hypothesis explains the difference in breeding dispersal between male and female Penduline Tits. Arlt and Pärt (2008) considered sex-biased dispersal in birds as being a result of differences in the availability of breeding options, which may be higher for males. If males establish territories before females arrive, they may choose from all available sites, whereas females are restricted to the sites chosen by males. In the Penduline Tit, the nest site is first chosen by the

male, and female may or may not join him later on. Thus, the difference in dispersal distances between males and females are in line with the hypothesis of Arlt and Pärt (2008).

Females of some bird species have been found to disperse shorter distances after successful than unsuccessful breeding (Beletsky & Orians 1991, Wiklund 1996, Catlin *et al.* 2005). A similar pattern was reported here for the Penduline Tit: successful breeding affected the dispersal distance of females. Renesting after successful breeding is not a common strategy of female Penduline Tits, and only females who breed early in the season (and probably only those in good condition) are able to reneest after a successful brood (15% of females in the studied population; $n = 94$). Moreover, 71% of these females took care of this second brood as well, thus they might be more prone to settle near the previous nest due to good experiences (high food resources, low number of predators) or due to the lack of time or high energetic costs of searching a new partner, possibly over a long distance. It remains unclear, however, whether such females visit nests of multiple males before their mating decision, but some of the nest-abandoning females explore a large part of the present study area before remating (authors' personal observations).

Cases of females reneesting after a nest failure were not common, and they tended to disperse similar distances to those of abandoning females. Dispersal of female Penduline Tits is apparently greatly affected by the dispersion of males and their attractiveness (which is independent of territory quality).

In contrast to what has been found in the Ortolan Bunting *Emberiza hortulana*, where males moved further if they did not attract females (Dale *et al.* 2005), dispersal of male Penduline Tits within a breeding season did not differ between males that had abandoned their clutch after successful mating compared to males that did not manage to attract females. One explanation for this could be that unsuccessful males may be prone to reneest in the neighbourhood of the previous nest because habitat structure does not influence the mating success of a male (van Dijk *et al.* 2008). In this situation, changing a nest site would not increase the chances of a male to mate.

The present results showed that within-season dispersal distances of male Penduline Tits were

not affected by whether they had been unsuccessful in mating or the clutch had been abandoned in their previous nest, whereas females were found to settle closer after successful breeding. Further studies would be needed to better understand the dispersal patterns in the Penduline Tit, for instance using radio telemetry.

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Koiraiden ja naaraiden pesimäkauden dispersaali Lounais-Puolan pussitiaisilla

Pesimäaikainen dispersaali on tavallista usean pesyeen lintulajeilla, kuten pussitiaisella (*Remiz pendulinus*), jolla molemmat sukupuolet ovat moniavioisia ja jolla toinen tai molemmat pariskunnan osapuolet voivat hylätä pesyeen. Lajia tutkittiin kalankasvatusaltilaiden verkostossa Lounais-Puolassa kuutena pesimäkautena (2004–2008 ja 2011). Siirtymisiä rekisteröitiin 97 koiralle ja 44 naaralle. Naaraat liikkuvat pidempiä matkoja, eivätkä kummankaan sukupuolen siirtymismatkat juuri vaihdelleet vuosien välillä. Edellisen pesän pariutumismenestys ei vaikuttanut koiraan siirtymismatkaan. Ne naaraat, jotka löysivät uuden puolison onnistuneen pesinnän jälkeen liikkuvat lyhyemmän matkaa kuin ne, jotka olivat hylänneet edellisen pesän. Epäonnistuneen edellisen pesinnän jälkeen pariutuneet naaraat liikkuvat yhtä pitkää matkoja kuin ne, jotka olivat hylänneet edellisen pesän.

Tulokset tukevat yleistä dispersaaliin liitettyä ilmiötä, jonka mukaan pesimäkaudella naaraat yleisesti liikkuvat koiraita pidempiä matkoja. Tätä eroa voidaan selittää sukupuolten välisellä erolla sopivien pesimäpaikkojen saatavuudessa: koiraat voivat valita minkä tahansa vapaana olevan reviirin, kun taas kevätmuutolta myöhemmin saapuvia naaraita rajoittaa koiraiden levittäytyminen, mikä voi pakottaa ne siirtymään pidempiä matkoja.

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