Do mating opportunities influence within-season dispersal in Penduline Tits?

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Abstract To find better mating opportunities may be one of the reasons why birds disperse from one population to another, although evidence is scarce to prove this proposition. Penduline Tit is a highly suitable model species to clarify this question, since both males and females may have several mates during a single breeding season. We followed the dispersal of Penduline Tits in a system consisting of six populations. Our study provided evidence for short distance within-season breeding dispersal in Penduline Tit between our study sites. Both the rate of immigration and emigration showed a strong seasonal pattern, which may be related to the fluctuation in mating opportunities. The number of immigrating males increases with the number of unmated females in the population, i.e. mating opportunities of males. Furthermore, the number of unmated males (mating opportunities of females) in the population increased with the number of immigrating males. Our results thus indicate a relationship between dispersal behaviour and mating opportunities in Penduline Tits. Further studies are needed to distinguish between cause and effect.

Keywords: dispersal, *Remiz pendulinus*, mating system, mating opportunities

Összefoglalás A szaporodási időszakon belüli diszperzió egyik lehetséges oka, hogy az egyedek az optimális szaporodási feltételek érdekében vándorolnak át az egyik populációból a másikba, bár kevés bizonyíték támasztja alá ezt a feltételezést. A függőcinege különösen alkalmas a fenti kérdés tisztázására, mivel egy egyednek több egymást követő párja is lehet egy költési időszakon belül. Vizsgálatunkban egy hat populációból álló rendszerben követtük nyomon a függőcinegék diszperzióját. Eredményeink bizonyították szaporodási időszakon belüli diszperzió meglétét a vizsgált populációk között. Mind a bevándorlás, mind a kivándorlás mértéke jelentős szezonális mintázatot mutatott, amely összefüggésben lehet a párosodási esélyek változásával. A bevándorló hímek száma nőtt a populációban lévő párnélküli tojók számával. Ugyanakkor a párnélküli hímek száma (tojók párbaállási esélyei) is nőtt a populációba történő hím bevándorlással. Eredményeink szerint a függőcinegénél összefüggés lehet a diszperziós viselkedés és a pártalálási esélyek között. Az ok-okozati összefüggések megállapításához azonban további vizsgálatokra van szükség.

Kulcsszavak: diszperzió, *Remiz pendulinus*, szaporodási rendszer, párosodási esélyek

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1. Introduction

Dispersal is one of the most fundamental and a well studied population functions. During natal dispersal, young individuals move from their birth place to their breeding site, while during breeding dispersal they move between successive breeding sites (Greenwood 1980). Dispersal plays an important role in source-sink dynamics (Clobert *et al*. 2001), in gene-flow between populations (Neigel & Avise 1993), in adaptation to changing environmental conditions (Ronce 2007) and in the population regulation of many bird and mammal species (Greenwood 1980). It may enhance sur-

vival chances of small population (Brown & Kodric 1977), for example by decreasing inbreeding depression (Greenwood & Harvey 1982) or by reducing the effect of environmental stochasticity on population dynamics. In Indigo Bunting (*Passerina cyanea*) for instance, dispersal can affect effective population size (Payne & Payne 1993). However, in some circumstances high levels of dispersal may increase the risk of global extinction (Molofsky & Ferdy 2005). Most studies focused on natal dispersal and showed that it is more extensive than breeding dispersal (Greenwood & Harvey 1982). Many fewer studies have addressed breeding dispersal; nevertheless, several factors have been shown to influence it. For instance breeding dispersal between years is more extensive among females than among males in birds, and this pattern may be explained by their mating system (Greenwood 1980, Greenwood & Harvey 1982, Liu & Zhang 2008). In the resource-defence mating system of most birds, where males invest more energy in competing for resources in order to attract females, males are less likely to disperse than females. Paradis *et al.* (1998) showed that migrant species disperse further than resident ones, and species living in wet habitats disperse further than those living in dry habitats, which could be explained by the greater patchiness of wet habitats in space and/or time.

Within-season breeding dispersal is the least known form of dispersal, although its role could be very similar to between-season dispersal. One reason for the lack of studies of within-season dispersal is that it is not extensive in most species (Greenwood & Harvey 1982). Jackson (1989) examined three hypotheses in Prairie Warblers (*Dendroica discolor*) to explain within season dispersal: avoidance of predation, avoidance

of depleted resources and the possibility of fast renesting. He found that predation is the most likely explanation, because moving to new territories before renesting can reduce the probability of nesting failure caused by predators. In line with this explanation Greig-Smith (1982) showed that pairs of Stonechats (*Saxicola torquata*) moved further if they renested after predation. Supporting a role for avoidance of depleted resources Greig-Smith (1982) found that pairs that raised large broods moved greater distances than did pairs whose broods were small.

The Penduline Tit (*Remiz pendulinus*) is a small passerine bird (body mass 9-10g) is one of the handful species in which within-season breeding dispersal is common. The appearance and disappearance of adult individuals in a population can be observed all over the breeding season from early April to early August (I. Szentirmai, R.E. van Dijk, T. Székely, unpublished data). In Penduline Tits either the male or the female deserts the clutch during the egg-laying phase, and parental care is provided by a single parent. Additionally, 30-40% of clutches is deserted by both parents and doomed to failure (Persson & Öhrström 1989, Szentirmai 2007). After desertion, males and females search for new partners and may remate up to six times during a breeding season and produce multiple broods.

Dispersal may play an important role in the breeding system of Penduline Tits. Emigration of deserting individuals may decrease the number of available partners in one subpopulation, but these individuals could provide a source of new partners in the subpopulations to which they immigrate. Through mating opportunities dispersal may influence the payoffs of desertion and eventually parental care strategies (Székely *et al.* 2000).

Through operational sex ratio, dispersal can also affect the viability of populations. If there are not enough unmated individuals in the population due to the lack of dispersal, deserters will have a lower chance of finding a new mate and this can reduce the reproductive success of these individuals. The objective of this study was to collect evidence for the existence of breeding dispersal in Penduline Tits between our study populations and to investigate the relationship between mating opportunities and dispersal behaviour. We hypothesised first that disappearing Penduline Tits continue breeding in a different population and that new-coming individuals come from other populations. Second, we assumed that attractive males have better mating opportunities and therefore are less likely to emigrate. Third, we hypothesised that emigration will be high when mating opportunities are low, and low when mating opportunities are high. Finally, we predicted that immigration will influence the operational sex ratio of the population, and through this breeding system.

2. Methods

2.1. Data collection

We studied Penduline Tits at Fehértó, southern Hungary (46°19'N, 20°5'E), between 2002 and 2004 to examine causes and consequences of dispersal. Fehértó is an extensive fishpond system (1321ha) where approximately 90 males and 50 females breed each year on dykes separating fishpond units. Five other sites within 50 km of Fehértó (Fig. 1) were also investigated in 2006 and 2007 to detect the movements of Penduline Tits.

Szegedi Fertő (500 ha) and Csaj-tó (958 ha) are also fishpond systems, very similar habitat to Fehértó. Fertő is very close to Fehértó, but we treated them as distinct populations, since they were separated by a main road and we did not observe regular movements of Penduline Tits between them. Population of Penduline Tit consists of 20 pairs in Fertő and 15 pairs in Csaj-tó. Maty-ér is 3 km long rowing course and fishing area where 25 pairs breed regularly. Madarász-tó is a small fishpond system (200 ha) with extensive reedbeds and willow trees, but it supports only two pairs of Penduline Tits. Kisszéksós-tó is a lake (30 ha) almost completely covered with reed where five pairs of Penduline Tits breed. The exact population size was known, beacuse we estimated all Penduline Tits in our study population by regular counts throughout the breeding season.

At each study site males were caught using mist-nets and using song playback at their first nest, and were individually colour-ringed. Females were caught either together with their mate or during incubation in the nest, using a purpose-designed net. We measured their wing length and took pictures of the masks of males. The area of the mask was measured from photographs (see details in Kingma *et al.* 2008). During the study we examined 563 nests at Fehértó, and 142 nests in the other sites. We followed 172 colour ringed males and 105 females in Fehértó throughout the breeding seasons (April-August) in 2002-2004, and a total of 47 males and 20 females in the other study sites. We checked their nests in Fehértó (2002-2004) and Maty-ér (2006-2007) at least every other day, and once a week in the other locations (2006). The exact nest initiation date was determined if the nest was found in an early building stage, or estimated based on its stage if found later (see details in Szentirmai *et al*. 2005). We defined the date of pair formation as the date

Figure 1. Map of study sites

when the pair was first seen copulating near their nest or building the nest together. Date of desertion was defined when one or both of the parents was not seen at the nest for at least 15 minutes for at least two consecutive nest checks (van Dijk et al. 2007).

We defined immigrants as individuals that arrived from other populations and emigrants as individuals that left the population to reproduce in other population. Therefore only individuals that arrived after the date of first emigration from the population were considered as immigrants. Individuals that arrived earlier are likely to come from the wintering grounds and were defined as indigenous. Similarly, emigrants were defined as individuals that left the population before the date of the last immigration to the population. Individuals that left later are likely to leave for the wintering grounds and were defined as residents. These definitions were based on the assumption that emigration from and immigration to different populations are more or less synchronised. Immigration date of males was defined as the date when they started to build their first nest. Immigration date of females was defined as the date of their first mating, because until this time unmated females could not be detected and we supposed that they were not present in the population before the day of their mating. The date of emigration was defined as the date when a male or a female left his/her last nest and was not seen in the population afterwards.

2.2. Data processing and statistical analyses

The proportion of immigrants (n = 159 males and 72 females) and emigrants (n = 52 males and 38 females) in the population was calculated for both males and females and compared between years and sexes by chi-square test. We divided the breeding season into decades (10-day periods) from 1 April. The number of immigrating and emigrating individuals were calculated for each day of the breeding season and then summed for each decade to analyse seasonal trends in the rate of dispersal. Since there was no difference between years (see below) the mean values across years were used in the analyses. We used quadratic regression to analyse seasonal changes in immigration and linear regression to analyse emigration.

Mating opportunity of males was defined as the number of unmated females in the population, and mating opportunity of females as the number of unmated males. The number of unmated males and females was calculated for each day and summed for decades. The influence of mating opportunities on dispersal was investigated by relating the number of immigrating and emigrating males to the number of unmated females in the population, and the number of immigrating and emigrating females to the number of unmated males in the population. The influence of dispersal on mating opportunities was investigated by relating the number of unmated males in the population to the number of immigrating and emigrating males, and the number of unmated females to the number of immigrating and emigrating females. Decades were the units of the latter analyses. Statistical analyses were performed using SPSS 11.0 for Windows.

3. Results

3.1. Evidence for within-season breeding dispersal in Penduline Tits

Our study provided the first evidence for within-season breeding dispersal between study
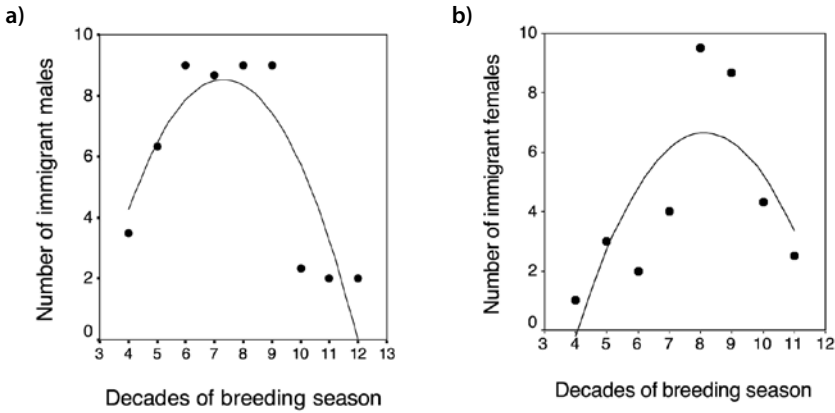
Figure 2. Seasonal changes in the number of immigrant male (a) and female (b) Penduline Tits in Fehértó
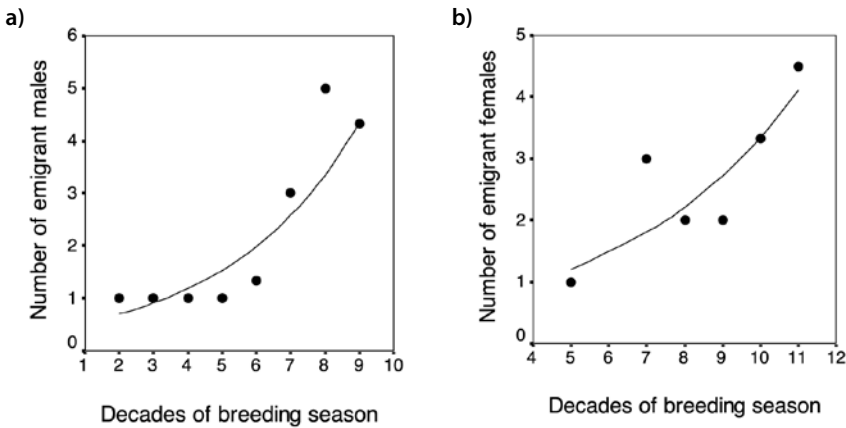

Figure 3. Seasonal changes in the number of emigrant male (a) and female (b) Penduline Tits in Fehértó

sites. We found two males that dispersed from one population to another. One of the males started breeding at Fehértó, where he had one nest, and then moved to breed 5 km away in Fertő, where he had another three nests. Another male moved from Maty-ér to Fertő (15 km) and had one nest at both sites.

3.2. The pattern of breeding dispersal in Fehértó

Immigration to Fehértó was male biased (χ^2 test: $\chi^2_2 = 5.292$, $p = 0.021$). Contrastingly, emigration was more widespread among females than among males ($\chi^2_2 = 5.753$, $p = 0.016$). The proportion of immigrants did not significantly differ between years either in males or in females (males: $\chi^2_2 = 5.663$, $p = 0.059$; females: $\chi^2_2 = 0.581$, $p = 0.748$). Similarly, year had no effect on emigration rates of females ($\chi^2_2 = 0.882$, $p = 0.643$). For males immigration was higher in 2002 than in 2003 and 2004 ($\chi^2_2 = 7.513$, $p = 0.023$).

Both immigration and emigration had a remarkable seasonal pattern. More birds immigrated into the population in the middle of
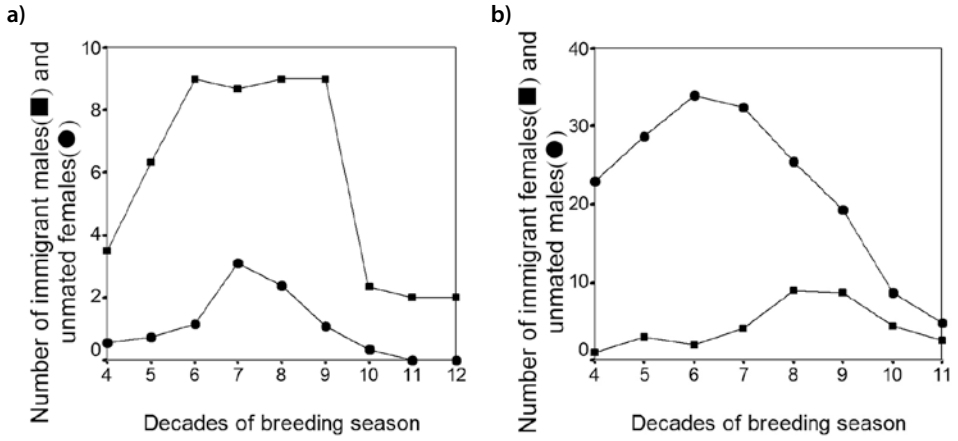
a)

b)

Figure 4. Seasonal changes (a) in the number of immigrant male and unmated female, and (b) in the number of immigrant female and unmated male Penduline Tits at Fehértó
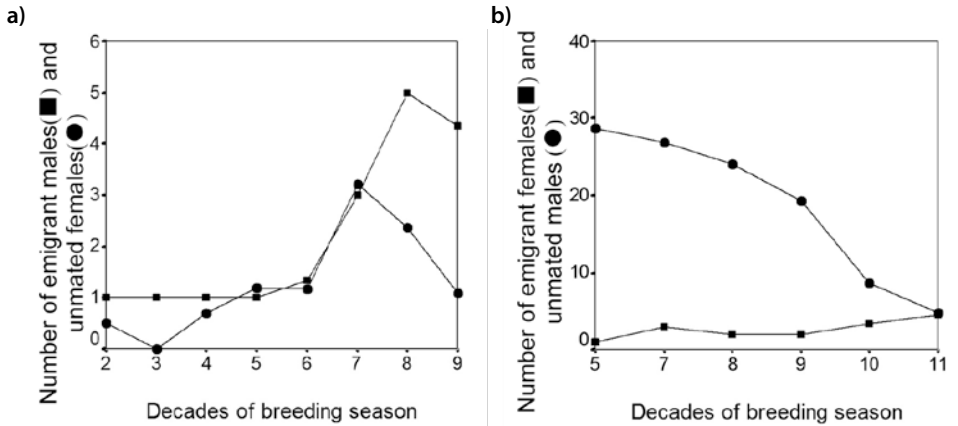
a)

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Figure 5. Seasonal changes (a) in the number of emigrant males and unmated females, and (b) in the number of emigrant females and unmated males during the breeding season
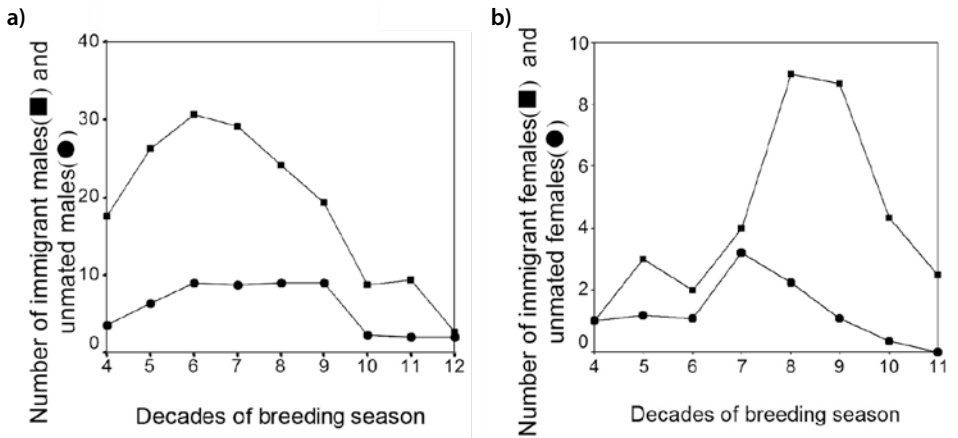
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Figure 6. Seasonal change (a) in the number of immigrant males and unmated males, and (b) in the number of immigrant females and unmated females during breeding season

breeding season (June) than in the beginning or the end of it (Fig. 2). While this relationship between immigration and season was significant in males (quadratic regression, ANOVA: $F_{2,6} = 8.687$, $R^2 = 0.658$, $p = 0.017$), it was non-significant in females ($F_{2,5} = 3.384$, $R^2 = 0.405$, $p = 0.118$). The numbers of emigrating males and females increased over the breeding season (linear regression, males: $F_{1,6} = 24.891$, $R^2 = 0.773$, $p = 0.003$; females: $F_{1,4} = 9.700$, $R^2 = 0.635$, $p = 0.036$; Fig. 3).

3.3. Relationship between dispersal and individual traits

None of the investigated morphological traits were different between immigrant and indigenous or emigrant and resident individuals either in males or females (Table 1). Although males with longer wings appeared at Fehértó later in the breeding season, none of the other investigated traits was related to the date of immigration or emigration in either males or females (Table 2).

3.4. Dispersal and mating opportunities

The number of immigrating males increased with the number of unmated females in the population (Pearson correlation: $r = 0.610$, $n = 22$, $p = 0.003$; Fig. 4a). The number of immigrating females however, was unrelated to the number of unmated males ($r = 0.176$, $n = 14$, $p = 0.546$; Fig. 4b). The number of emi-

Table 1. Relationships between immigration rates and individual traits in Penduline Tits.

	Wing length			Mask size		
	F	*df*	*p*	*F*	*df*	*p*
Immigrants versus indigenous						
Males	1.349	1,158	0.247	0.069	1,76	0.054
Females	3.802	1,96	0.793			
Emigrants versus residents						
Males	0.477	1,157	0.505	0.658	1,76	0.420
Females	1.838	1,96	0.178			

Table 2. Relationships between immigration dates and individual traits in Penduline Tits.

	Wing length			Mask size		
	r	*n*	*p*	*r*	*n*	*p*
Date of immigration						
Males	0.178	125	0.047	-0.060	55	0.662
Females	0.078	65	0.535			
Date of emigration						
Males	0.049	124	0.592	0.077	55	0.575
Females	0.047	65	0.708			

grating males and females was not related to their mating opportunities (males: $r = 0.440$, $n = 15$, $p = 0.101$; females: $r = -0.329$, $n = 14$, $p = 0.251$; Fig. 5). The number of unmated males in the population increased with the number of immigrating males ($r = 0.726$, $n = 22$, $p < 0.001$, Fig. 6a). Contrastingly, there was no significant relationship between the number of unmated females in the population and the number of immigrating females ($r = 0.396$, $n = 14$, $p = 0.161$; Fig. 6b).

4. Discussion

4.1. Evidences of breeding dispersal

Our study confirmed the existence of short distance breeding dispersal in Penduline Tits between our study sites. Some previous studies showed that breeding Penduline Tits disappeared from populations and some individuals appeared during the breeding season (Szentirmai 2005), and Franz *et al.* (1987) found that a certain female bred in two populations within the same breeding season. The movement of breeding birds between populations was observed twice in 2006.

The proportion of emigrants found to settle in other populations is surprisingly low: only two out of 102 individuals. We suspect two possible reasons for the low number of resighted birds. Firstly, our study could not cover all the potential breeding areas around Fehértó. For example there are many artificial ditches around Fehértó which were not involved in our study (see Fig. 1), and two large lakes in Serbia. However, the largest potential breeding sites of Penduline Tits in South Hungary are the floodplain forests along River Tisza and River Maros. Although we have no data on the popula-

tions of the latter two areas, Barbácsy Z. found one nest per 700 m along the Rába, a smaller river in West Hungary (Haraszty *et al*. 1984). Secondly, the dispersal distances might be larger than the distance between Fehértó and our other study sites. Species living in wet habitats disperse further than those living in dry habitats (Paradis *et al.* 1998). Possibly, dispersal distance of Penduline Tits was greater than we expected, because of their spatially scattered breeding habitats. A study in Germany showed that a female Penduline Tit moved more than 200 km between two consecutive breeding sites (Franz *et al.* 1987). In South Hungary the Tisza may be an ecological corridor between populations along which Penduline Tits can move large distances in a favourable habitat.

We believe that individuals that disappeared from the population of Fehértó are very likely emigrants, because we never observed them there again in the same breeding season. Although some dispersers might have died, this is unlikely to influence our results, since predation of Penduline Tits is low during the breeding season (Persson & Öhrström 1989).

4.2. Patterns of dispersal

A higher proportion of immigrants among males than among females may explain the male-biased sex ratio of the population. The same number of males and females (5-10 individuals) arrive in Fehértó at the beginning of the breeding season, whereas the maximum population size is approximately 90 for males and only 50 for females (Szentirmai 2005). This population size is reached over the breeding season through the immigration of twice as many males than females. Furthermore, Persson and Öhrström (1989)

observed that sex-ratio shifted toward males during the breeding season in a Swedish population of Penduline Tits.

In contrast to our expectation, emigration was more intensive among females than among males. We expected the opposite result, since mating opportunities of females are much better than mating opportunities of males, so females should have less motivation to leave the population in the search for new mates (Szentirmai 2005). Our result is however, consistent with the overall trend in birds, i.e., females disperse more frequently, because they invest less energy into maintaining their territory (Greenwoood 1980, Greenwoood 1982). Mészáros *et al*. (2006) also showed that female Penduline Tits move further than males between their consecutive nests within a population (males: 116 m, females: 942 m). This difference may be due to the fact that males chose their nest-sites, and familiarity with the area may be advantageous (Szentirmai *et al.* 2005). Females however, chose males and they invest more energy in finding a good quality mate, which may mean that they have to cover large distances (Johnston et al. 1996).

The immigration of both sexes was most intensive in the middle of the breeding season (June), and continuously declined thereafter. This pattern may be explained by the pattern of desertion frequencies, since most individuals immigrate after they have deserted their offspring in a different population. The number of deserting males and females is highest during the middle of the breeding season in all populations investigated so far (Persson & Öhrström 1989, Szentirmai 2005, O. Kiss unpublished data).

The pattern of emigration rate is slightly different, the number of emigrants gradually increases during breeding season. The seasonal increase in number of emigrants may be explained by increasing number of birds that finished breeding or it may simply be the result of increasing population size over the breeding season and thus increasing emigration potential (Szentirmai 2005).

4.3. Dispersal and mating opportunities

In agreement with our expectations more males immigrated to the population when the number of unmated females was higher. This result may indicate that dispersal behaviour of males is influenced by their mating opportunities, i.e. they tend to immigrate to a population where mating opportunities are high. This result is in line with the idea that one of the possible causes of dispersal is that settlement pattern can maximize fitness (Holt & Bartfield 2001). In Penduline Tits reproductive success of both sexes strongly depends on the number of mates they can acquire (Szentirmai *et al.* 2007). Therefore selection may favour those individuals that emigrate from population with low mating opportunities to other populations with higher mating opportunities. An alternative explanation for the relationship between dispersal and mating opportunities may be that both are related to the breeding season and thus there is no causal relationship between the two variables. In contrast to males, there was no apparent relationship between the number of immigrating females and the number of unmated males in the population. However, it could be observed that the peak in female immigration follows the peak in the number of unmated males.

We found no clear relationship between emigration and mating opportunities. However, Fig. 5 shows that the peak of male emigration coincided with a steep decline in the number of unmated females in the population. Similarly, female emigration started

to rise when the number of unmated males decreased most steeply. Our data thus show that although there may be a relationship between mating opportunities and emigration rates, it is not a linear relationship. This is surprising, because recent studies proved that mating opportunities influence the reproductive success of Penduline Tits (Szentirmai *et al*. 2007). Perhaps, our tests were not sufficiently sensitive to demonstrate these effects. Some other reasons can explain our findings. Results may reflect seasonal effect, or other factors like individual qualities conceal the connections between mating opportunities and emigration. For example, individuals with better qualities can find a mate when mating opportunities are low, and they do not disperse. Another possible reason is that the effect of competition or inadequate food supply are more important than are mating-opportunities in determining dispersal rates. Stonechats (*Saxicola torquata*) disperse further after predation and human disturbance than after low reproductive success or various other reasons (Greig-Smith 1982). Gregoire *et al*. (2007) found that within-season breeding dispersal can be a predation avoidance strategy. The seasonal changes in seed supplies drive within-season breeding dispersal in Cardueline Finches (*Carduelis sp.*) (Newton 2000). Another possible explanation is that when mating opportunities are unfavourable in Fehértó, they are even worse in other populations. This seems to be a convenient explanation, because Fehértó has a more dense Penduline Tit population than other examined populations (Haraszthy et al. 1994, Kiss O. unpublished data). The predation rate is just 4 % (Persson & Öhrström 1989), because nest-structure and location of protect them against predators. Predation rate probably does not notably influences emigration.

Not only mating opportunities may influence dispersal, but dispersal may influence mating opportunities as well. As expected the number of unmated males in the population increased with male immigration. This is an important finding, because we know that mating opportunities play a major role in the determination of the frequency of care types in populations in other bird species (Emlen & Oring 1977, Bennet & Owens 2002). In our case, increasing male immigration enhances the mating opportunities of females in the population and thus may shift the breeding system towards female desertion and male care. It is thus possible that high male immigration rates in the middle of the breeding season may play a role in the high frequencies of female desertion and the appearance of male-only care in the population at the same time (Persson & Öhrström 1989, Szentirmai 2005).

There was no relationship between the dispersal of females and mating opportunities of males. Probably, desertion is a more important factor than immigration, in the case of females, but this assumption needs examination. Mating opportunities for males were mainly influenced by other process in the population. Since we could not detect all immigrant females, it is important to remember that the data about females are less accurate.

Conclusions

Our study suggests that within-season breeding dispersal may play an important role in the complex breeding system of Penduline Tits. Dispersal may at least partly be driven by mating opportunities and males tend to immigrate to the population when the number of available females is highest. In

turn dispersal will influence mating opportunities in the population. Our results may however, be confounded by seasonal effects, and to establish causal relationships between dispersal and mating opportunities further, especially experimental studies are needed.

Acknowledgements

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