

Sex biased natal dispersal in a closed, saturated population of Seychelles warblers *Acrocephalus sechellensis*

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The distances that individuals disperse, from their natal site to the site of first breeding and between breeding sites, have important consequences for the dynamics and genetic structure of a population. Nearly all previous studies on dispersal have the problem that, because the study area encompassed only a part of the population, emigration may have been confounded with mortality. As a result long-distance dispersers may have been overlooked and dispersal data biased towards short distances. By studying a virtually closed population of Seychelles warblers *Acrocephalus sechellensis* we obtained almost unbiased results on several aspects of dispersal. As in the majority of other avian species, natal dispersal distance was female biased in the Seychelles warbler. Female offspring also forayed further from the natal territory in search of breeding vacancies than male offspring. The sex bias in natal dispersal distance did, however, depend on local breeding density. In males, dispersal distance decreased as the number of territories bordering the natal territory increased, while in females, dispersal distance did not vary with local density. Dispersal by breeders was rare and, unlike in most species, distances did not differ between the sexes. We argue that our results favour the idea that the sex bias in natal dispersal distance in the Seychelles warbler is due to inbreeding avoidance and not resource competition or intrasexual competition for mates.

The distances between natal sites and the sites of first breeding (natal dispersal distance), and between breeding sites (breeding dispersal distance), have important consequences for the dynamics and genetic structure of a population (Greenwood and Harvey 1982, Horn 1984, Rockwell and Barrowclough 1987, Hanski 2001). Two general patterns have emerged from the plethora of studies undertaken on dispersal distance: the frequency distribution of dispersal distances decreases with increasing distance to the previous territory, and natal dispersal distances are greater than breeding dispersal distances (Paradis et al. 1998). Because of the latter pattern, natal dispersal contributes most to the dynamics and structure of a population. A host of factors has been put forward to explain individual variation in natal dispersal distance. First, many studies have focussed on gender-related differences in dispersal, which have been argued to result from factors such as inbreeding avoidance, resource competition and intra-sexual competition for mates (Greenwood 1980). Second, intrasexual differences in natal dispersal distances have been shown to result from differences in social and environmental circumstances such as breeding density (Pyle 2001, Forero et al. 2002), food availability (Adriaensen et al. 1998, Byholm et al. 2003), hatching rank (Forero et al. 2002), or brood size (Tinbergen 2005). Furthermore, natal dispersal distance may have a heritable component

(Keppie 1980, Dingemanse et al. 2003) or be dependent on the age at which individuals disperse (Pasinelli et al. 2004).

Because study areas are usually finite and the resulting dispersal data subsequently biased (i.e. long-distance dispersers may erroneously be assumed dead), what is known about dispersal may be less accurate than the literature suggests (Baker et al. 1995, Koenig et al. 2000, Lahaye et al. 2001). For example, a lack of data on long-distance dispersers will bias dispersal distributions towards philopatry. Field methods such as radio-tracking or surveying alternative study sites may help to correct for systematic bias (Paradis et al. 1998, Koenig et al. 2000). However, to obtain completely unbiased data on dispersal behaviour, a population without emigration or immigration must be studied. The Seychelles warbler *Acrocephalus sechellensis*, a small passerine endemic to four islands in the Seychelles, lives in populations that are virtually closed; in 20 years of study only two of 1,924 individually colour-ringed birds (0.1%) have been observed to disperse between islands (Komdeur et al. 2004). One female dispersed naturally from Cousin to Cousine island (1.6 km) in 1996, and one male that was translocated from Cousin to Cousine in 1990 returned to Cousin in 1991 (Komdeur et al. 2004). From 1995 onwards nearly all (>95%) individuals in the Cousin population have been ringed and monitored and considerable effort has been put in ringing and monitoring warblers

in the new populations ever since the translocations in 1988 to Aride island and in 1990 to Cousine island (Komdeur et al. 2004, unpubl. data). It is therefore unlikely that we have failed to observe any additional inter-island dispersers during the period that the warblers had the opportunity to disperse between populations.

In the current study we aim to contribute to the understanding of dispersal by presenting virtually unbiased dispersal data gathered in the Seychelles warbler population of Cousin island. We determine the natal and breeding dispersal distributions of males and females. To investigate whether natal dispersal is random with respect to distance, we calculate an expected natal dispersal distance, based on the available dispersal destinations, and compare this with the observed distance for each disperser. Furthermore, we assess whether our observations of young Seychelles warblers prospecting for a territory match the observed natal dispersal pattern. Finally, we determine how environmental and social factors affect natal dispersal distance. Because familiarity with a site may be an important factor in acquiring a breeder position in a territory (e.g. Stamps 1987, Jacquot and Solomon 2004), we expect natal dispersal to be shorter than the average distances to all potential destinations available. Because the frequency of extra-group paternity is high (40%) in the Cousin population and extra-group males are normally from nearby territories (number of territories away from natal territory where 0 = adjacent territory: mean 1.86 ± 2.22 , median = 1, Richardson et al. 2001), females that disperse a short distance have a higher chance of dispersing into the territory that holds their genetic father than females dispersing further from the natal territory. In contrast, as territory switching is rare (Komdeur 1996; this study) and egg dumping does not exist in the Seychelles warbler (Richardson et al. 2001), males that disperse a short distance have an equally low chance of dispersing into the territory that holds their genetic mother as do males dispersing further. Because in the Seychelles warbler there is evidence for inbreeding depression (Richardson et al. 2004), we expect females to disperse further from the natal territory than males.

Methods

Study species and population

The Seychelles warbler is a facultative cooperative breeder. They live either in pairs, or in groups consisting of the primary pair and one or more offspring that have delayed dispersal and remained in the natal territory as subordinates (Komdeur 1992, 1994). The primary male and female were defined as the dominant, pair-bonded male and female in the territory. All other birds, old enough to disperse (> six months old), resident in the territory were defined as subordinates. Some subordinates become helpers and assist parents in raising non-descendent kin (Komdeur 1992, Richardson et al. 2003, 2004). Each pair or group defends an all-purpose territory year-round (Komdeur 1991) and normally produces only a single egg each breeding season, but 20% of nests contain two or three eggs (Richardson et al. 2001).

The current study was carried out on Cousin Island (29 ha) in the Seychelles. Since 1982 the resident Seychelles warbler population has been stable with between 105–120 territories (Komdeur 2003). Except for a barren rocky outcrop in the centre of the island, all habitat is occupied. The presented data on natal dispersal are based on individuals that were colour-ringed on their natal territory between 1985 to 2004. These are offspring that were either ringed in the nest or that were caught on the natal territory as dependent young up to six months after fledging (on Cousin, young warblers never dispersed when younger than six months, Komdeur 1996). Blood samples (ca. 15 μ l) were collected by brachial venipuncture and stored in 100% ethanol at room temperature. Molecular sexing using the polymerase chain reaction (PCR) method devised by Griffiths et al. (1998) was used to confirm the sex of each ringed individual. In all years of study all territories were mapped in detail. The territory was defined as the area that a pair or group defended against non-group members. Territories are always occupied, normally by at least two birds, but if one of the breeders dies, leaving a breeder vacancy, there may temporarily be only one bird in a territory. This widowed breeder usually remains in the territory and the breeder vacancy is normally filled within a few days by a subordinate from another territory (Komdeur 1992). Territory boundaries were determined using observations of and fights between colour-ringed birds and mapped with the help of a 50 \times 50m grid of permanent marker poles. The position of the nest in the territory was not used to define territory boundaries. For all individuals the status (primary or subordinate) and territory of residence were determined in each year during the peak breeding season (June–August) and in some years also during the minor breeding peak (December–February). During the breeding seasons, all territories were monitored at least once every two weeks. As inter-island dispersal is extremely rare (Komdeur et al. 2004), warblers that were missing from their territory and not found on other territories can safely be considered dead. From 1995 onwards, most individuals in the population have been individually colour-ringed (90–97%). However, between 1985 and 1994 the fraction of birds ringed was considerably less (20–40% of all individuals, unpubl. data). Therefore, data collected in this period were only used in the construction of the frequency distribution of natal dispersal distances (NDD) and in the analyses of factors affecting natal dispersal distance.

Natal and breeding dispersal distances

In the calculation of dispersal distances only individuals that settled as a primary breeder were used and the two cases of inter-island dispersal were excluded. Observed natal and breeding dispersal distances were calculated as the minimal number of territories an individual must have traversed to reach its (new) breeding territory. Territories are rather small (roughly 0.2 ha) which means a warbler will need only about 50m to traverse a territory. The maximum possible dispersal distance on Cousin was 13 territory widths. To determine whether natal dispersal was skewed towards short or long distances, we calculated an expected natal dispersal

distance and compared this with the observed distance for each disperser. This expected distance was defined as the median distance (in territories widths) from the resident territory to all the same-sex breeder vacancies that became available between the year the focal subordinate was born and the year it first occupied a primary breeder position. Territories which were newly established during this period were included as vacancies. We could not calculate an expected distance for floaters-birds that are rarely present on any particular territory (Komdeur and Edelaar 2001), nor for birds born between 1985–1994 (not all vacancies were known, because of relatively many unrunng breeders). Therefore these were excluded from the comparison.

In our calculation of expected distances, we used all vacancies throughout a bird's pre-dispersal life. Such a measure assumes that both an individual's motivation and ability are constant throughout the individual's pre-dispersal life. The large majority (89.4%, $n=104$) of individuals for which we could calculate an expected distance settled within two years after fledging. We therefore would argue that the assumption of constant motivation to disperse is met. Because some birds dispersed as yearlings and others as two-year olds, the ability to disperse could have been different between these two age groups. We thus wished to know if the birds that dispersed two years after birth did so, because they were constrained in their ability to disperse in their first year of life. In the Seychelles warbler, the majority of males and females obtain a breeder position (and mate) through the occupation of a vacancy that is left after a breeder dies (Komdeur and Edelaar 2001). This suggests that for this species, the number and distribution of breeder vacancies around the natal territory are very important determinants of an individual's ability to disperse. These factors did not seem to have constrained the ability of two-year olds to disperse earlier; for birds that dispersed two years after birth, the median distance between the natal territory and breeder vacancies did not differ between the first and second year of life (Wilcoxon signed ranks, $Z = -1.78$, $P = 0.08$, $n = 40$). Nor was the number of breeder vacancies different between the first and second year of life (Wilcoxon signed ranks, $Z = -0.93$, $P = 0.35$, $n = 40$). We therefore would argue that the assumption of constant ability to disperse is also met and feel that calculating expected distances by using all vacancies throughout a bird's pre-dispersal life is biologically meaningful.

Foraging behaviour of subordinates

Prospecting (by means of extra-territory forays) data consisting of catches or observations of colour-ringed subordinates outside their resident territory were gathered between 1995 and 2004. Because subordinates of both sexes behave surreptitiously during forays (C. Eikenaar pers. obs.) and are therefore difficult to observe, most foray data came from catches (62.8% for males and 71.9% for females) and fewer data from observations (37.2% for males and 28.1% for females). Catches or observations of floaters were not included. Subordinate males appear never to sire extra-group offspring (Richardson et al. 2001) and if subordinate females search for extra-pair copulations outside the natal

territories, they probably would only do so during the very short period of peak fertility. We therefore assume that forays are undertaken to get information about (future) breeding vacancies and to a lesser extent to gain access to extra-pair mates or food. The distance (in territory widths) between the territory in which a prospecting bird was observed and that bird's territory of residence was calculated for males and females. This was done using two datasets. First, including all data (full data set) and, second, including only prospecting events two territories or further from the resident territory (restricted data set). This restriction was made to exclude the possibility that the birds may have merely been attracted into an adjacent territory by the play-back song (which is different from the neighbours' songs) that is sometimes used when catching or searching for warblers. Because the distance distributions of catches did not differ from the distance distribution of observations (Kolmogorov-Smirnov, $Z = 0.82$, $P = 0.52$), we combined data from both sources.

Because all distance distributions were positively skewed, tests on differences between the sexes in foraging distances, and tests between observed and expected dispersal distances were non-parametric. All dispersal distances in the results section are presented as the median \pm inter-quartile range.

Analyses of environmental and social effects

The effects of sex of the subordinate, year of fledging, period of fledging, local and population breeding density, age when dispersing, expected dispersal distance and quality of the natal territory on natal dispersal distance were analyzed using multi-level mixed modelling procedure in MlwiN (Rasbash et al. 2004). As some birds that fledged in different years came from the same territory, territory was included as the level two unit of variation and subordinate as the level one unit of variation. Model selection was based on both backward and forward method, in which non-significant terms ($P > 0.05$) were removed from the model in order of least significance. Estimates of variables are presented as in the step in which the variable was removed from the model or, when it had a significant effect on NDD, as in the final model. In the two instances that two dispersers originated from the same nest, one was randomly excluded. Prior to analyses, dispersal distances (response variable) were $\log(x + 0.5)$ transformed which resulted in a normal distribution of error terms. Since the error terms are the only random ones in the model, then the assumptions also apply to observations of the response variable (Quinn and Keough 2002, p. 92). Because the sexes may react differently to environmental and social circumstances, we also studied interactions between sex and all other variables.

The year of fledging was entered into the model as a continuous variable, because population density varied over the course of the study and we are testing whether this variation has an impact on dispersal behaviour. The period of fledging was entered as a fixed factor. On Cousin island Seychelles warblers may breed during two periods each year. The main period (June-August) falls in the dry season and almost all groups attempt to breed, whereas during the minor period in the wet season (December-February), only a fraction of the groups attempt breeding (Komdeur and

Daan 2005). The effect of density was tested by entering both local and population level parameters of breeding density into the model as continuous variables. For each disperser, local density was expressed as the number of territories adjacent to the natal territory in the year of birth, while population density was the total number of territories in the population in that year. Dispersers were divided into two fixed age groups: individuals that dispersed as yearlings and individuals that dispersed later in life. Territory quality (TQ), in terms of insect prey availability, was measured as described by Komdeur (1991, 1994), and entered as a continuous variable. The components of TQ are insect density per dm² leaf area, vegetation abundance scores and territory size. TQ was measured in the dry season of 1986, 1987, 1999, 2003 and 2004. Because the quality of a territory varied among years, we could not use averaged values of TQ and extrapolate these to years in which TQ was not measured. Instead, to determine whether TQ affected dispersal distance, we only included individuals that were born in one of the main breeding (dry) seasons during which TQ was measured. Instead of the absolute TQ, the TQ relative to that of other territories may be a better predictor of dispersal behaviour (Koenig et al. 1992). Therefore, TQ was calculated as the TQ of a territory minus the median TQ in the population that year.

Territories in the centre of the island have more adjacent territories and lower possible maximum dispersal distance than territories at the edge of the island. This could on itself result in a relation between dispersal distance and local density. To check for this relation, we entered the expected dispersal distance (calculated as described above) into the model. Entering the expected distance takes into account the fact that, depending on the position on the island of the natal territory, breeder vacancies were at different distances for each disperser. It furthermore takes into account the fact that not all dispersers had an equal number of vacancies available (this number varies between the sexes and among years). Because expected distances could only be calculated for birds born after 1994 that did not become a floater, we first ran one model excluding expected distance (thus using data from all years in the study period). Then a second model (with smaller sample size) was run which included expected distance (thus including only data from 1995 onwards and excluding data on floaters). The reference categories were the same in both models: for disperser sex the reference category was male, for age it was one year olds, and for period it was the main breeding season. Entering TQ in the model resulted in a severe loss of sample size. Therefore, to test for an effect of TQ on NDD, we entered TQ into the final model of the first trial (the model using data from all years in the study period).

Results

Foraging behaviour, natal and breeding dispersal distances

Using the full foraging data set, females were not caught or observed further from their resident territory than males (Mann-Whitney U, $Z = -1.23$, 42 males, 32 females, $P = 0.22$). However, when data on territories adjacent to the

resident territory were excluded, females did foray further from their resident territory than males (Mann-Whitney U, $Z = -3.27$, 27 males, 19 females, $P < 0.01$).

The median natal dispersal distances were 4.0 ± 4.0 territories for females and 2.0 ± 2.0 territories for males (Fig. 1). Both sexes dispersed shorter distances than expected on the basis of random dispersal to available same-sex vacancies (expected versus observed distances: females: 5.57 ± 1.51 versus 3.0 ± 3.75 , $n = 48$, Wilcoxon signed ranks, $Z = -3.99$, $P < 0.01$; males: 5.69 ± 1.70 versus 2.0 ± 3.0 , $n = 56$, Wilcoxon signed ranks, $Z = -5.40$, $P < 0.01$; Fig. 2a, b). Breeding dispersal was not common in the Cousin population; of 263 breeder vacancies that became available between 1995 and 2004, 10 were taken by male and 15 by female primary breeders, which accounts for on average 1.3% of breeders dispersing each year. Most dispersing breeders travelled short distances and distances did not differ between the sexes (males: 1.50 ± 2.25 , $n = 10$; females: 2.0 ± 2.0 , $n = 15$; Mann-Whitney U, $Z = -0.33$, $P = 0.77$). For females, breeding dispersal distances were shorter than natal dispersal distances (Mann-Whitney U, $Z = -2.31$, $P = 0.02$). For males, natal and breeding dispersal distances were not different (Mann-Whitney U, $Z = -0.88$, $P = 0.38$).

Factors influencing natal dispersal distance

Forward and backward stepwise methods resulted in the same factors affecting NDD (Table 1). Beside sex of the disperser, local breeding density also affected NDD. The significant interaction between local density and sex indicated that this effect was different for males and females. For males dispersal distance decreased with an increasing local density, while for females dispersal distance was not affected by local density (Table 1, Fig. 3). For both sexes, local density was positively related to: i) the yearly average number of breeder vacancies becoming available in adjacent territories, and ii) the yearly average number of adjacent competitors (same-sex subordinates) present in adjacent territories (Spearman's correlation, all $P < 0.05$). Averages were single mean values based on the years from birth until settlement as a breeder. Population breeding density, age when dispersing and period of fledging did not

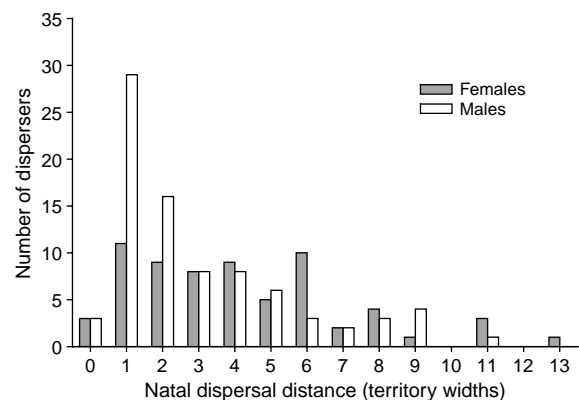


Fig. 1. Frequency distribution of the natal dispersal distances of male and female Seychelles warblers on Cousin island between 1985 and 2005. Males $n = 86$ and females $n = 69$.

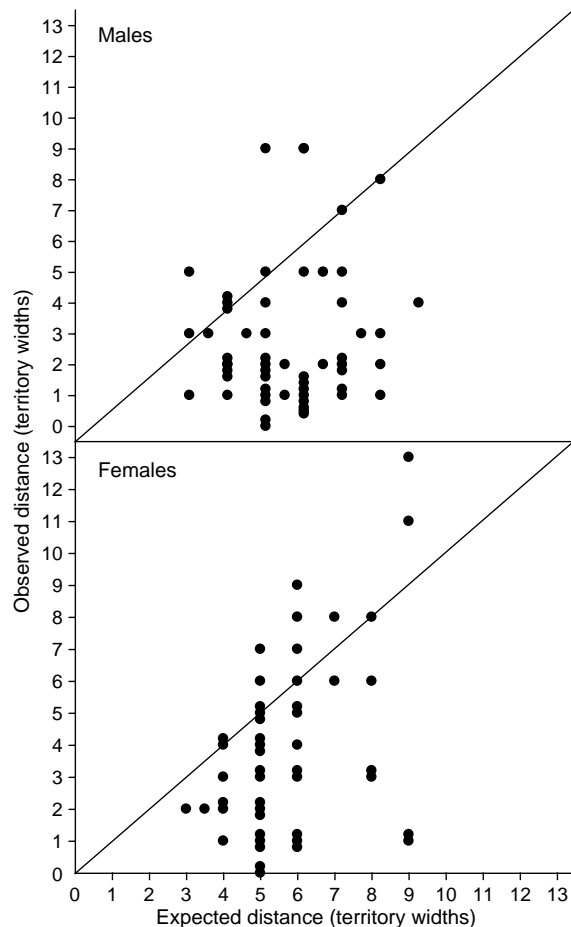


Fig. 2. Observed and expected natal dispersal distances of male and female Seychelles warblers on Cousin between 1995 and 2005. Males $n = 56$ and females $n = 48$. The expected distance is the median distance of the resident territory to all same-sex vacancies that became available between the year the disperser was born and the year it first occupied a primary breeding position. A point below the diagonal line represents an individual that dispersed closer than expected, and a point above the line an individual that dispersed further than expected.

have a significant effect on NDD, and none of the other interactions were significant. In the final model's variance decomposition, territory did not explain any variance in NDD between individuals ($\sigma^2 \pm SE = 0.00 \pm 0.00$), possibly because the number of repeats was very low, compared to a residual variance of $\sigma^2 \pm SE = 0.084 \pm 0.01$. The quality of the natal territory did not affect NDD ($n = 57$, $\beta \pm SE = 0.02 \pm 0.02$, $\chi^2 = 1.22$ and $P = 0.27$).

When the expected distance was included in the model as an explanatory variable (thus excluding data gathered before 1995 and data on floaters), the effects of sex ($\beta \pm SE = 0.09 \pm 0.06$, $\chi^2 = 2.24$ and $P = 0.13$, $n = 104$) and of the interaction between sex and local density ($\beta \pm SE = 0.07 \pm 0.05$, $\chi^2 = 2.10$ and $P = 0.15$, $n = 104$) on NDD were no longer significant. The direction of the effects of sex and the interaction between sex and local density on NDD was the same as in the analysis including all data; females tended to disperse farther than males and local density tended to affect NDD in males only. This suggests that the loss of significance resulted from the severe decrease in

Table 1. Model summaries examining natal dispersal distance of subordinate Seychelles warblers ($n = 155$) in relation to ecological and social factors. Summaries derived from the mixed-modelling procedure in MLwiN. The final model is in bold text.

Explanatory variables	$\beta \pm SE$	χ^2	df	P
Constant	1.07 ± 0.14			
Disperser sex	-0.48 ± 0.20	5.63	1	0.02
Local density	-0.12 ± 0.03	21.13	1	<0.01
Age when dispersing	-0.08 ± 0.05	3.05	1	0.08
Year of fledging	-0.002 ± 0.006	0.16	1	0.69
Period of fledging	0.02 ± 0.06	0.20	1	0.65
Population density	0.001 ± 0.004	0.11	1	0.74
Local density \times disperser sex	0.12 ± 0.04	9.49	1	<0.01

Reference categories: sex = male, age = one year olds, and period = main season.

sample size in this analysis. Note that the direction (positive or negative) and size of the betas of 'sex' and 'local density' can not be compared directly between the two analyses, because in one analysis the interaction remained in the model, whereas in the other it was removed from the model. Local density did still have a significant effect on NDD ($\beta \pm SE = 0.07 \pm 0.02$, $\chi^2 = 7.59$ and $P < 0.01$). Expected distance did not affect NDD ($\beta \pm SE = 0.02 \pm 0.02$, $\chi^2 = 0.99$ and $P = 0.32$), nor did any of the other variables or interactions.

Discussion

Natal and breeding dispersal

We found that, in the Seychelles warbler, females dispersed further from their natal territories than did males and that this sex bias depended on local breeding density. Our study also showed that both sexes dispersed shorter distances than expected on the basis of random dispersal to available same-sex vacancies. We furthermore found that both sexes made forays but that females forayed further from the natal territory than males, which corresponds to the female biased dispersal. In contrast to natal dispersal distances, breeding

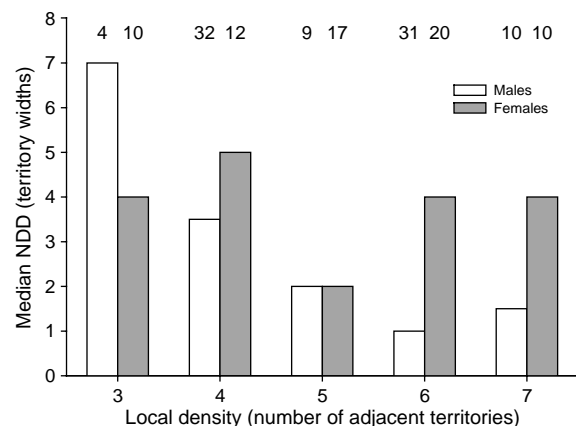


Fig. 3. Median natal dispersal distances (NDD) at different local breeding densities of male and female Seychelles warblers on Cousin between 1985–2005. Local breeding density is the number of territories adjacent to the natal territory in the year of birth. Numbers above bars represent sample sizes.

dispersal distances did not differ between the sexes. It is remarkable that even in our tiny enclosed study population where the maximum dispersal distances are extremely limited it is possible to find evidence of sex biased natal dispersal patterns. This contrasts with findings in other small island populations, in which no sex bias in natal dispersal distance was observed (e.g. song sparrow *Melospiza melodia*; Arcese 1989, and Savannah sparrow *Passerculus sandwichensis*; Wheelright and Mauck 1998). An explanation for this discrepancy may be that these two species differ from the warblers in how they compete over food and mates in the following aspect. Unlike the warblers, individuals (and especially juveniles) of both sparrow species spend much of their time foraging off territory in undefended common areas such as the intertidal zone. In these areas, females may be able to select among available mates and therefore do not have to disperse greater distances than males (Wheelright and Mauck 1998).

Several previous studies have presented data on natal dispersal distances that also must have come close to the true, unbiased dispersal distribution. Paradis et al. (1998) extracted average dispersal distances of 75 British bird species from the bird ringing data of the British Trust for Ornithology. They estimated natal dispersal using birds ringed in the year of birth and recovered dead at breeding age. Using resampling method with four species, they showed that their estimates of dispersal distance were unbiased. Unfortunately, because most birds were not sexed when ringed or recaptured they were unable to study sex-specific natal dispersal. Large-scale studies on red-cockaded woodpeckers *Picoides borealis* (Walters 1990), and Florida scrub-jays *Aphelocoma coerulescens* (Stith et al. 1996) did present data on sex biased natal dispersal. In these species, most offspring disperse relatively short distances, but long distance dispersal events also occur. Because the sites studied in these cases were extraordinarily large, most long distance dispersers were probably located. In agreement with these and most other avian dispersal studies (Clarke et al. 1997, Greenwood 1980), we found that females dispersed farther from their natal territory than males.

Although females seemed to foray over larger distances, we found that both male and female subordinates engaged in forays and that both sexes dispersed. Similarly, in acorn woodpeckers both sexes foray and disperse (Hooge 1995), whereas in brown jays *Cyanocorax morio*, and Florida scrub-jays, both foray activity and dispersal primarily occur in only one of the sexes (Woolfenden and Fitzpatrick 1984, Williams and Rabenold 2005). The observation that the sex that engages in forays is also the sex that disperses strongly suggests that forays are a means of reconnoitring for available breeder vacancies (Woolfenden and Fitzpatrick 1984).

Sex biased natal dispersal and inbreeding avoidance

In the model that included data gathered in all years of study, the sex bias in NDD depended on local breeding density. With increasing density the natal dispersal distances of males decreased, whereas density did not affect dispersal distances in females. It seems unlikely that differences in

resource competition or intrasexual competition for mates (Greenwood 1980) caused the sex biased dispersal in our study population. First, the number of individuals competing over breeder positions is similar for the sexes; the population sex-ratio of young is not biased towards one sex (Komdeur et al. 1997) and survival probabilities do not differ between the sexes (Brouwer et al. 2006). Second, the route to gaining a primary breeder position is similar for both sexes; the majority of males and females obtain a position (and mate) through the occupation of a vacancy that is left after a breeder dies (Komdeur and Edelaar 2001). Similarly, because the Seychelles warbler do not have a resource-defence mating system (both sexes defend their all-purpose territory), resource competition probably did not cause females to disperse further than males. It seems more plausible to suggest that the sex biased dispersal resulted from inbreeding avoidance (Greenwood 1980), or more specifically incest avoidance. The level of extra-group paternity is high (40%) in the Cousin population, and extra-group males are normally from nearby territories (Richardson et al. 2001). Therefore, the genetic father of any given female disperser is likely to be resident in a territory near to the female's natal territory. In order to avoid incestuous matings, females should, therefore, disperse far from the natal territory, no matter what local breeding density. As egg dumping is non-existent in this population (Richardson et al. 2001) and territory switching rare (Komdeur 1996, this study), the genetic mother of any male is from his natal territory, and so dispersing males do not have to avoid nearby territories to avoid mating with their mothers. Short distance dispersal may, however, be costly when the chance of finding a vacancy is very low due to a low local breeding density. We indeed showed that with lower local breeder densities, fewer vacancies were available in territories adjacent to the natal territory. However, with lower local breeder densities, also fewer competitors were present in adjacent territories, suggesting that the strength of competition over breeding vacancies may not change with local breeding density. Even though competition may not change with density, quite often there were no vacancies opening in adjacent territories for males in low density areas. For 7 of 22 subordinate males (32%) born in low local densities (3 or 4 adjacent territories) not a single vacancy opened in the years they lived on their natal territories, whereas this happened to only 2 of 29 subordinate males (7%) born in high local densities (6 or 7 adjacent territories). This was not a result of earlier dispersal of males born in high local breeding densities. Consequently, at low local breeding densities, subordinate males may be forced to expand their search area, and as a result, disperse further than at high local densities. The idea that inbreeding avoidance causes the sex biased dispersal seen in our study population is supported by the evidence which shows that, unlike natal dispersal distances, breeding dispersal distances were equal and short in both sexes. Primary females can disperse short distances without a high risk of incestuous matings, because they have already dispersed and therefore already are at a distance from their relatives.

A previous study of the Seychelles warblers concluded that primary females did not avoid inbreeding through social mate choice (Richardson et al. 2004) based on the

observation that relatedness between females and their social mates was not smaller than their relatedness to random males in the entire population. However, constraints on social mate choice may act in natural populations through, for example, dispersal distance. Because both male and female natal dispersal distances in the Seychelles warbler are shorter than the maximum distance they could disperse, the pool of males that the females could choose from may, in reality, be very much smaller than all males in the population. Moreover, because short dispersal distances may result in the spatial clustering of close relatives (Daniels and Walters 2000), the mean pairwise relatedness between females and the restricted pool of potential mates, may actually be higher than the values used previously. The occurrence of extra-group fathers close to the natal territories of female subordinates will contribute to the spatial clustering of relatives. Further work creating a genetic landscape in which the relatedness between dispersers and all other individuals in the population are calculated may provide more conclusive results on the role of inbreeding avoidance in sex biased dispersal.

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