Should I stay or should I go?
Eikenaar, Cas

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2008

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
An investigation of inbreeding avoidance mechanisms in a contained population of the Seychelles warbler

Cas Eikenaar
Jan Komdeur
David S. Richardson

Accepted for Journal of Evolutionary Biology
Abstract

In this study we investigate whether mechanisms exist that prevent inbreeding in a small isolated population of the cooperatively breeding Seychelles warbler. Specifically we test whether patterns of territory inheritance, social mate choice, and sex-biased natal dispersal act as inbreeding avoidance mechanisms in this species. First we test if territory inheritance depends on relatedness between the potential within group inheritor and the surviving opposite sex breeder using both natural and experimental data. Then we assess if dispersers avoid settling with related individuals. Finally, we determine whether the female-bias in natal dispersal distance observed in this species is associated with the distribution of related individuals around the dispersers’ natal territories. Our results show that Seychelles warblers do not reduce the likelihood of inbreeding by avoiding related individuals as mates; territory inheritance did not depend on whether the remaining breeder was a parent or an unrelated breeder that had replaced a parent, and dispersers were no less related to their eventual mates than expected given the pool of candidate mates. We suggest that the lack of inbreeding avoidance through mate choice is the result of the severe constrained availability of breeder positions in this small, isolated and saturated population. Intriguingly the female-bias in natal dispersal distance does not appear to facilitate inbreeding avoidance because, contrary to our prediction, there was no sex-difference in the clustering of related opposite-sex breeders around the natal territories of dispersers. As a result, the chance of females mating with close relatives was not reduced by their greater dispersal distance compared to that of males. We discuss why other main evolutionary models for sex-biased dispersal (sexual asymmetries in local mate and resource competition and local resource enhancement) also seem inappropriate explanations for the female-biased natal dispersal observed in the Seychelles warbler and suggest that the bias may be a phylogenetic relic, which seems at present of no adaptive significance.
Introduction

Dispersal of individuals from their natal group in order to reproduce is common in most vertebrate taxa and generally the rate or distance of such natal dispersal is sex-biased (Greenwood 1980; Clarke et al. 1997). Inbreeding avoidance has frequently been hypothesized to have contributed to the evolution of natal dispersal (e.g. Packer 1979; Greenwood 1980; Pusey 1987). By leaving the natal area young may reduce the chance of eventually mating with a parent, while a sex-bias in the rate or distance of dispersal is thought to result in the spatial separation of siblings. Although alternative processes, such as intra-sexual competition for mates (Dobson 1982; Moore & Ali 1984) may also play a role (Johnson & Gaines 1990; Handley & Perrin 2007), several field studies do suggest that natal dispersal is indeed an adaptation to inbreeding avoidance (Packer 1979; Balcombe 1989; Koenig et al. 1998).

There are, however, costs associated with dispersal, both in terms of survival (Johnson & Gaines 1990) and reproduction. For example, the probability of an individual gaining a breeder position decreases with increasing dispersal distance from the natal territory (Stamps 1987; Beletsky & Orians 1993). Furthermore, territory inheritance does not necessarily lead to inbreeding, e.g. an opposite-sex parent may be replaced by an unrelated individual at the time of territory inheritance (Woolfenden & Fitzpatrick 1986; Koenig et al. 1998). Therefore, if natal dispersal has evolved to avoid inbreeding then selection should also be expected to favour individuals that recognize when to disperse and when to stay; i.e. when a natal area breeder vacancy involves a closely related individual that they should avoid as a mate as opposed to an unrelated individual that they can mate with. Although many mate choice experiments have shown that individuals avoid mating with litter- or nestmates and siblings (reviewed in Pusey & Wolf 1996), few field-studies have provided evidence for inbreeding avoidance through mate choice within the natal territory. In the Florida scrub-jay (Aphelocoma coerulescens), territory inheritance was observed more often when the surviving breeder was a stepparent of the non-breeder heir rather than its natural parent, (Woolfenden & Fitzpatrick 1986; Balcombe 1989). Moreover, we are unaware of field studies that have experimentally investigated whether young are more likely to inherit a territory with a stepparent than with a parent. If natal dispersal has evolved to avoid inbreeding then selection should also be expected to favour unrelated individuals as mates. However, in many species individuals that disperse from the natal site to breed often do not seem to reduce inbreeding through active mate choice (Keller & Arcese 1998; Daniels & Walters 2000; Richardson et al. 2004; Van de Casteele & Matthysen 2006; Hansson et al. 2007, but see Wheelright & Mauck 1998; Wheelright et al. 2006).

The evolution of sex-biased dispersal has received as much attention as dispersal itself, with many studies linking a sex-bias in natal dispersal distance (NDD) to inbreeding avoidance (Greenwood 1980; Pusey 1987; Biek et al. 2006; Vignieri 2007). Although one sex may disperse further than the other there is normally considerable
overlap in NDD between the sexes (e.g. Woolfenden & Fitzpatrick 1984; Koenig et al. 2000). This implies that the separation of closely related opposite-sex individuals through sex-biased dispersal is far from complete. Therefore, to determine if sex-biased natal dispersal functions to avoid inbreeding we need to know if the difference in NDD between the sexes is sufficient to reduce the chance of mating between close relatives. This is a major challenge, because it requires unbiased dispersal data and accurate knowledge of the spatial distribution of related individuals within the dispersal range (Van de Casteele & Matthysen 2006).

The population of Seychelles warbler (Acrocephalus sechellensis) on Cousin Island provides a unique opportunity to investigate the role of dispersal patterns in inbreeding avoidance for two reasons. Firstly, the intense long term monitoring of this small isolated population means that the natal dispersal histories of almost all individuals is known for many cohorts of individuals (Eikenaar et al. 2008). Secondly, but perhaps more importantly, as off-island dispersal is virtually absent (Komdeur et al. 2004a) the patterns of dispersal observed are not biased by a lack of data on individuals that disperse outside the area of observation. In this species NDD is female-biased, but distances overlap between the sexes (median NDD: males = 2 and females = 4 territory widths, Eikenaar et al. 2008). Furthermore, there is evidence that close inbreeding occurs in this population (Richardson et al. 2004; Brouwer et al. 2007), which may have fitness effects. Finally, because the entire population has been genotyped using a suite of 28 previously isolated microsatellite loci (Richardson et al. 2000; unpublished results) relatedness values between dispersers and breeders can be estimated.

The aims of the current study are three fold. First we assess if territory inheritance in the Seychelles warbler depends on the degree of relatedness between the potential heir and the surviving breeder. This is done using both natural correlative data and a removal experiment in which non-breeders were given the opportunity to inherit a breeder position by pairing up with either a parent or a stepparent. We predict territory inheritance to occur only with unrelated breeders.

Secondly, we assess if individuals that do disperse from their natal territory avoid related individuals as mates. A previous study on the Seychelles warblers that compared the relatedness of existing pairs with all potential random pairs across the entire population found no evidence for inbreeding avoidance through social or extra-pair mate choice (Richardson et al. 2004). However, since most dispersers in this population settle relatively close to the natal territory (Eikenaar et al. 2008) including all opposite sex breeders as candidate mates may not be realistic. In the current study, we limit the pool of candidate mates to those that were present within the distance that included 95% of observed natal dispersal distances. We also assess whether there is a relation between the distance an individual disperses and the number and pattern of closely related opposite sex breeders in adjacent territories. If natal dispersal is a direct facultative response to avoid inbreeding we expect individuals to disperse further when the natal territory is surrounded by individuals to which they are related.

Thirdly, we assess whether the female-bias in NDD contributes to inbreeding
avoidance; specifically whether this dispersal bias is associated with a difference in the distribution of related individuals around the natal territories for each sex. For females, we expect clustering of closely related opposite sex breeders around their natal territories because their male siblings will previously have dispersed over short distances (Eikenaar et al. 2008). For males, we expect little or no clustering of closely related opposite sex breeders around their natal territories because their female siblings will previously have dispersed over relatively long distances (Eikenaar et al. 2008). If inbreeding is reduced by the greater female NDD, we expect that the chance of females mating with a close relative will be lower at the median female NDD than at the median male NDD. For males we expect no difference between the median female and male NDD.

Methods

Study species and population
The Seychelles warbler is a passerine endemic to four small islands in the Seychelles. It is a facultative cooperative-breeding species that lives either in pairs, or in groups which normally consist of a primary breeding pair and one or more offspring that have delayed dispersal and remained in the natal territory as subordinates (Komdeur 1992; 1994). Occasionally subordinates may also be previously dominant females that have been deposed (Richardson et al. 2007). Some subordinates become helpers and assist in raising non-descendent kin, whereas other subordinates stay on the natal territory without engaging in helping behaviour (Komdeur 1992, Richardson et al. 2002, Richardson et al. 2003b). They defend all-purpose territories year-round (Komdeur 1992) and breeder positions are generally acquired through the occupation of a vacancy that resulted from the death of a breeder, although about 20% of males become breeders by creating a new territory among the existing ones (Komdeur 1992). Each group normally produces only a single egg every breeding season, but 20% of nests contain two or three eggs (Richardson et al. 2001).

The present study was carried out on Cousin Island (29 ha.) in the Seychelles. This population has been monitored intensively since 1985. Many of the birds have been caught (> 96% of birds since 1997; Richardson et al. 2001) and individually colour-ringed using a unique combination of three colour rings and a British Trust for Ornithology metal ring. Blood samples (ca 25 µl) were taken from captured birds 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 individual.

The Cousin Island population has been relatively stable since 1982 with 105–120 territories (containing a total of 300-350 individuals) and, except for a barren rocky outcrop in the centre of the island, all habitat is occupied. Each territory borders, on average, five other territories. In most years since 1985 all territories were mapped in
For every colour-ringed individual the status (primary or subordinate) and territory of residence were determined in each year during the peak breeding season (June–September), and in some years also during the minor breeding peak (December–January). The primary male and female were defined as the dominant, pair-bonded male and female in the territory. All other birds that were old enough to disperse (> six months old) but were still resident in the territory were defined as subordinates. During fieldwork periods all territories were checked at least once every two weeks. As inter-island dispersal is extremely rare (0.1 %, \( n = 1924 \), Komdeur et al. 2004a) warblers that were missing from their territory and not found on other territories were assumed to have died.

**Calculation of relatedness**

We used the software program KINSHIP (Goodknight & Queller 1999) to calculate individual pairwise relatedness estimates (\( r \)) based on genotypic similarity at 28 microsatellite loci (Richardson et al. 2000; unpublished data). Pairwise relatedness, which ranges from –1 to +1, is a measure of the extent to which two individuals have alleles that are identical by descent relative to allele frequencies in the entire population. A positive value signifies that two individuals are related, whereas values of zero or below indicate non-relatives. A previous study on the Cousin population (using just 14 microsatellites) revealed that mother-offspring \( r \) for assigned offspring was normally distributed around a mean of 0.46 ± 0.17 SD (Richardson et al. 2004). We have now increased the number of microsatellite loci used to 28. However, considering the large spread around the mean observed in the previous study, we used conservative definitions of relatedness and termed individuals to be closely related when their \( r \geq 0.35 \) and moderately related when \( 0.10 < r < 0.35 \).

**Territory inheritance**

Since 1985, eight (five males and three females) of the 219 warblers (3.7%) for which the complete natal dispersal history is known inherited their natal territory. For these eight individuals we estimated the degree of relatedness between them and their social mate in the newly inherited territory. We used genealogies and where possible also calculated the \( r \) between the individuals of the pairs that formed after territory inheritance.

In 2004 birds were caught on Cousin and transferred to Denis Island as part of the long-term conservation effort to save the Seychelles warblers. We used this opportunity to perform a breeder removal experiment to test if territory inheritance depends on the degree of relatedness between the potentially inheriting subordinates and the remaining breeders. In 10 territories we removed the primary breeder (five males and five females) that was the same sex as the subordinate(s) living in that territory. Each of the five territories in which the breeder female was removed contained a single female subordinate. Three territories in which the breeder male was removed contained a single male subordinate while two territories held two male subordinates each, one
of which was randomly excluded in the analysis. All subordinates were all old enough to breed and could potentially inherit the breeder position in the territory by mating with the ‘widowed’ breeder. Genealogies indicated that in five territories the remaining breeder was a (social) parent of the subordinate while in five territories it was a (unrelated) breeder that had replaced a parent. Calculations of $r$ between breeders and potential inheritors matched genealogies in all but one occasion. Excluding this exception, the mean $r$ was $0.41 \pm 0.12$ when genealogy indicated a parent and $0.03 \pm 0.08$ when genealogy indicated a replacement. The exception was a ‘widowed’ breeder male whose ‘daughter’ was the result of extra-pair paternity, which is frequent in this species (40%, Richardson et al. 2001). We assigned this male to the parent group because social, not genetic, parentage represents the offspring’s perception of who their parents are (Richardson et al. 2003a,b, Komdeur et al. 2004b). Therefore, five subordinates had the opportunity to mate with a (perceived) parent and five had the opportunity to mate with an apparently unrelated replacement

**Mate choice of dispersers**

All dispersal data is based on individuals that were caught and ringed for the first time while still living on their natal territory. These individuals were either ringed in the nest or caught within six months of fledging while still reliant on their parents (on Cousin young never disperse before six months of age, Komdeur 1996; Eikenaar, unpublished work). NDD was defined as the minimal number of territories an individual traversed from its natal territory to reach its breeding territory, measured in a straight line.

For individuals that fledged between 1997–1999 - three years for which we had exceptionally accurate data on the reproductive output of all individuals in all territories (Richardson et al. 2002) - and had a known natal dispersal history, we assessed whether they were less related to their chosen mates than could be expected from random mating. We expressed expected values in two ways; a) as the average $r$ between dispersers and all their candidate mates, and b) as the proportions of closely or moderately related pairs that would have resulted from all pairings between dispersers and their candidate mates. We defined the pool of candidate mates as all opposite sex primary breeders that were present outside the natal territory but within the distance that included 95% of observed natal dispersal distances. This was estimated as seven territory widths for males and eight territory widths for females. The two dispersers that paired with an unringed breeder were excluded from the analyses.

**Structuring of relatedness across the landscape**

We calculated $r$ between each disperser (fledged between 1997–1999) and all the opposite sex primary breeders present in the population in the year the disperser settled as a primary breeder. These values were used to construct the relatedness landscape that individuals faced in the year they dispersed. We expressed this relatedness landscape in two different ways. First, we expressed it as the averages of the $r$ between
each disperser and all the opposite sex primary breeders at each potential NDD, i.e. average $r$ of all opposite sex primary breeders in territories adjacent to the natal territory, two territories distant from the natal territory, etc. Second, we expressed it as the proportions of opposite sex primary breeders that were closely ($r \geq 0.35$) or moderately ($0.10 < r < 0.35$) related to the disperser at each potential NDD. Relatedness landscapes were calculated separately for male and female dispersers. Some birds dispersed from the centre of the population and, consequently, had a lower maximum potential NDD than birds that dispersed from the periphery of the population. To avoid bias due to decreasing sample sizes at the higher end of potential NDDs, calculations for the relatedness landscapes were limited to the smallest maximum potential NDD in the dataset, which was seven territory widths. In the rare instances that more than one same-sex disperser originated from the same territory and settled in the same year, only one randomly selected individual was included in the calculation of relatedness landscapes.

Data analyses
Transformations and nonparametric tests were used where appropriate. Proportional data were arcsine square root transformed prior to analyses. All tests were performed using SPSS 14.0 (SPSS inc. 1999) and were two-tailed. Statistical significance was set at $P < 0.05$. Because the sample was small we used Fisher’s exact test to assess if experimental territory inheritance depended on the degree of relatedness between the potential inheritor and the surviving breeder.

Results

Territory inheritance
Of the eight instances of natural territory inheritance, five subordinates mated with a (social) parent and three mated with a breeder that had replaced a parent. Relatedness values could be calculated for three of the five parent-offspring pairs and were 0.47, 0.43 and –0.06. This last $r$ was low, because although the breeder male mated with his apparent ‘daughter’, this ‘daughter’ was actually the result of extra-pair paternity. Relatedness values could be calculated for two of the three instances of inheritance with a replacement breeder and were 0.05 and –0.06. This suggests that there was no inbreeding avoidance through mate choice within the natal territory.

The territory inheritance experiment confirmed the absence of inbreeding avoidance through differential territory inheritance; inheritance did not occur more often with a stepparent than with a parent (Fisher’s exact test: $P = 0.52$, $n = 10$). Of the five subordinates that had the opportunity to inherit the territory and mate with a replacement breeder only one did so while three of the five subordinates that had the opportunity to inherit the territory and mate with a parent did so.
Mate choice of dispersers
Dispersing subordinates did not seem to avoid inbreeding through mate choice. The relatedness of dispersers to their chosen mates actually was higher than the average relatedness to candidate mates (paired samples $T$ test: $t_{67} = 2.72, P = 0.01$). Similarly, the proportion of mates that was closely related to the dispersers was higher for chosen than for candidate mates (Chi-square test: $\chi^2_{1} = 4.68, P = 0.03, n = 68$). The proportion of mates that was moderately related to the dispersers was not different between chosen and candidate mates (Chi-square test: $\chi^2_{1} = 0.57, P = 0.45, n = 68$). The distance that subordinates dispersed was not correlated with the proportion of related opposite sex breeders present in territories adjacent to the natal one (Fig. 3.1, Spearman rank correlation: closely related: $\rho = 0.09, P = 0.47, n = 70$; moderately related: $\rho = -0.04, P = 0.74, n = 70$). Furthermore, whether or not subordinates dispersed beyond adjacent territories did not depend on the proportion of related opposite sex breeders present in territories adjacent to the natal one (Mann-Whitney $U$ test: closely related: $Z = -0.85, P = 0.39, n = 70$; moderately related: $Z = -0.01, P = 0.99, n = 70$). These results on dispersal distance were similar when tested separately for the sexes.

Dispersal and relatedness landscape
There was little apparent clustering of related opposite sex breeders around the natal territories of dispersers (Figs 3.2 and 3.3), except for a slight elevation in the proportion of closely related opposite sex breeders in territories very close to the natal territories of dispersers. This elevation seemed most pronounced for female dispersers (Fig. 3.2A). However, the proportion of closely related opposite sex breeders in adja-

![Figure 3.1](image-url). The relationship between observed natal dispersal distances and the proportion of opposite sex breeders in adjacent territories that were A) closely and B) moderately related to the disperser ($n = 70$).
cent territories was not different between the sexes (Mann Whitney U test, $Z = -1.29$, $P = 0.20$, $n = 70$). Furthermore, the average proportion of closely related opposite sex breeders in territories within the median male NDD (two territory widths) was not different between the sexes (Mann Whitney U test, $Z = -1.02$, $P = 0.31$, $n = 70$). Therefore, when dispersing to territories very close to the natal territory, females do not have a higher chance of pairing with a closely related individual than males.

For female dispersers there was no difference in the proportion of related male breeders that would be encountered at the median female NDD (four territory widths) and median male NDD (closely related, Wilcoxon signed ranks test: $Z = -0.41$, $P = 0.68$, $n = 37$; moderately related, Paired samples $T$ test: $t_{36} = 1.54$, $P = 0.13$). Nor was there a difference in the mean level of $r$ between female dispersers and all male breeders at the median male and median female NDD (Paired samples $T$ test: $t_{36} = 0.67$, $P = 0.50$). For male dispersers there was no difference in the proportion of related primary female breeders at the median male and median female NDD.
Our results indicate that Seychelles warblers do not appear to reduce inbreeding either through differential territory inheritance, mate choice or sex-biased dispersal. This suggests that in this species, in its current environment, natal dispersal does not facilitate inbreeding avoidance. First, the occurrence of territory inheritance did not depend on whether or not the opposite sex breeder that the heir would have to pair closely related, Wilcoxon signed ranks test: $Z = -0.77, P = 0.44, n = 33$; moderately related, Paired samples $T$ test: $t_{32} = -0.56, P = 0.58$). Nor was there a difference in the mean level of $r$ between male dispersers and all primary female breeders (Paired samples $T$ test: $t_{32} = -0.12, P = 0.91$).

**Discussion**

**Inbreeding avoidance through mate choice**

Our results indicate that Seychelles warblers do not appear to reduce inbreeding either through differential territory inheritance, mate choice or sex-biased dispersal. This suggests that in this species, in its current environment, natal dispersal does not facilitate inbreeding avoidance. First, the occurrence of territory inheritance did not depend on whether or not the opposite sex breeder that the heir would have to pair

![Figure 3.3. Box plots of the proportion of A) closely ($r \geq 0.35$) and B) moderately ($0.1 < r < 0.35$) related females around the natal territories of dispersing Seychelles warbler males, categorized by the number of territories away from the natal territory ($n = 33$). Outliers are indicated by solid circles. Median dispersal distances were two territory widths for males and four territory widths for females.](image-url)
up with was a parent or an unrelated replacement. This contrasts with findings in other cooperative breeders in which dispersal has been shown to be associated with inbreeding avoidance. In the Florida scrub-jay, territory inheritance was observed more often when the surviving breeder was a stepparent of the non-breeder heir rather than its natural parent, (Woolfenden & Fitzpatrick 1986; Balcombe 1989). In the acorn woodpecker (Melanerpes formicivorus), young were more likely to disperse following the death of a breeder of the same sex, rather than the opposite sex (Koenig et al. 1998). Similarly, non-cooperative breeding savannah sparrows (Passerculus sandwichensis) tend to shift to distinct parts of the population to breed if the parent of the opposite sex still occupies the territory where they had hatched, whereas dispersal was not affected by presence of same-sex parents (Wheelright & Mauck 1998). Second, in the Seychelles warbler the chosen mates of individuals that did disperse were more, instead of less, related to them than the average relatedness to all candidate mates. This may have resulted from the combination of our definition of the pool of candidate mates and the slight elevation in the proportion of closely related opposite sex breeders in territories very close to the natal territories of dispersers (Figs 2 and 3). Many dispersers settle very close to the natal territory (median NDD is two territory widths for males and four territory widths for females, Eikenaar et al. 2008), where the chances of mating with a close relative seem to be highest. The pool of candidate mates, however, was set to include all opposite sex primary breeders present within the distance that included 95% of observed natal dispersal distances, which was seven territory widths for males and eight territory widths for females. Alternatively this observation could be the result of a preference of dispersers for related individuals as mates, however additional mate choice experiments are required to test this hypothesis. Likewise, in many other species individuals dispersing from the natal site to breed do not seem to be able to reduce inbreeding through active mate choice (Keller & Arcese 1998; Daniels & Walters 2000; Duarte et al. 2003; Van de Casteele & Matthysen 2006; Foerster et al. 2006; Hansson et al. 2007). One notable exception is savannah sparrows, in which incestuous pairings are almost absent and dispersers settle further from their siblings than expected by chance (Wheelright & Mauck 1998; Wheelright et al. 2006). Male savannah sparrows often sing immediately after feeding their fledglings. Possibly females learn and recognize their fathers’ song and if song characteristics are inherited, females may be able to avoid pairing with male siblings, even when raised in different years (Wheelright & Mauck 1998).

The lack of inbreeding avoidance through active mate choice implies that inbreeding must occur in the Cousin population of Seychelles warblers. Indeed, a previous study on the same population estimated that 5% of nestlings were the result of inbreeding between first order relatives (Richardson et al. 2004). It was suggested that part of such pairings resulted from subordinates females mating and reproducing with their father on their natal territories (Richardson et al. 2001; 2002; 2004). The current study revealed that inbreeding may also result from territory inheritance and from the failure of dispersers to select unrelated individuals as mates. The lack of
inbreeding avoidance also suggests that selection against inbreeding is, at least at present, not strong in the Seychelles warbler. Indeed previous studies on the Seychelles warbler showed that an individual’s survival was not correlated with its own heterozygosity (Richardson et al. 2004; Brouwer et al. 2007). Low maternal heterozygosity was, however, associated with reduced offspring survival (Richardson et al. 2004; Brouwer et al. 2007), but only in years with low survival probabilities (Brouwer et al. 2007). Since these ‘bad’ years occur only once every ten years and average lifespan of birds surviving the first year is four years (Brouwer et al. 2007), selection against deleterious alleles exposed through homozygosity must be relatively weak. Such selection may have been much stronger during the severe bottleneck from 1920-1968 when the population consisted of only c. 30 individuals (Crook 1960) and may have resulted in the purging of recessive deleterious alleles from the population (e.g. Crnocrak & Barrett 2002; Swindell & Bouzat 2006). This may explain why, in the saturated population that exists on Cousin today, selection against inbreeding is weak. Avoidance of pairing with a parent by young Florida scrub-jays and acorn woodpeckers suggests that selection against inbreeding is stronger in these species. Possibly the populations of Florida scrub-jays and acorn woodpeckers that were studied have not experienced a recent bottleneck. On the other hand, both are threatened species and the populations studied are small (MacRoberts & MacRoberts 1976; Woolfenden & Fitzpatrick 1984, 1986).

A lack of inbreeding avoidance through mate choice may also result from the fact that in wild populations there may be severe constraints on mate choice. On Cousin such constraints would result from restricted availability of breeder positions; the population is saturated and adult survival probabilities are high (Komdeur 1992; Brouwer et al. 2006). Consequently, forsaking a rare opportunity to occupy a breeder vacancy may be much more costly than inbreeding. In the red-cockaded woodpecker (*Picoides borealis*) where costs of inbreeding are high and breeder vacancies scarce, females do not change their dispersal behaviour in the presence of related males near their natal territory (Daniels & Walters 2000). This lead the authors to suggest that natal dispersal behaviour is a trade-off between the benefits of short-distance dispersal, e.g. an advantage in competing for scarce breeding vacancies, and the costs of inbreeding. In the Seychelles warbler the benefits of short-distance dispersal are apparent in both sexes; the closer a subordinate lives to a breeder vacancy, the higher its chances of occupying that vacancy (Chapter 4). Why then do Seychelles warbler females disperse further than males?

**Inbreeding avoidance through sex-biased dispersal**

Our results indicate that the female-bias in NDD observed in the Cousin population (Eikenaar et al. 2008) does not contribute to inbreeding avoidance. Contrary to our prediction, there was no difference between the sexes in the proportion of related opposite sex breeders at the median male and female NDD. Furthermore, the chance of mating with a close relative when dispersing within the median male NDD was not
higher for females than for males. This implies that in order to avoid inbreeding females would not need to disperse beyond the median male NDD. Inconsistencies between observed patterns of dispersal and the relatedness structure within a population have been observed before (e.g. Biek et al. 2006) and have been hypothesized to result from inconspicuous components of dispersal or mating behaviour (e.g. cryptic migration, extra-pair paternity and polyandry, Winters and Waser 2003; Vignieri 2007). The dispersal data in our study are virtually unbiased (due to the complete sampling of the population and the lack of migration) however the high levels of extra-pair paternity in the Cousin population (40% Richardson et al. 2001) will have reduced dramatically the degree of relatedness between siblings. Because males disperse shorter distances than females (Eikenaar et al. 2008) for female dispersers we expected stronger clustering of related opposite sex breeders around their natal territories than for male dispersers. The low degree of relatedness between siblings will have weakened this sex-difference. A further explanation for the absence of a clear sex-difference in clustering of related opposite sex breeders may be that for most dispersing individuals very few opposite sex siblings would have previously recruited into the breeding population. This is a consequence of high adult survival probabilities (84%, Brouwer et al. 2006) which means that few breeder vacancies open each year and only a small fraction of the young will be able to settle as a breeder.

But why do Seychelles warbler females disperse further than males if it does not reduce inbreeding? As well as inbreeding avoidance, other evolutionary models for sex-biased natal dispersal invoke sexual asymmetries in local mate and resource competition (Greenwood 1980; Dobson 1982) and local resource enhancement (Perrin & Lehmann 2001; Le Galliard et al. 2006). None of these hypotheses seem appropriate explanations for the female-biased NDD in the Seychelles warbler. First, seeking to explain why in most mammals it is males that are more prone to disperse than females, Dobson (1982) argued that the sex in which competition for mates is most intense should disperse. In polygynous and promiscuous species such competition is most intense in males, because in these species the variation in reproductive output is usually greatest in males. Seychelles warblers are promiscuous (40% of young are extra pair, Richardson et al. 2001) and, although they are not polygynous, males sometimes reproduce with both the primary as well as the subordinate female in their territory (Richardson et al. 2001; 2002; 2004). Therefore, the variation in reproductive output and consequently the competition for mates is probably greatest in males. However, instead of being the more dispersive sex, males settle closer to their natal territories than females, a pattern which does not support theories based on local mate competition. Second, in many bird species there is a sexual asymmetry in local resource competition, because one of the sexes, usually males, acquire and defend a territory in order to attract a mate (Greenwood 1980). Because familiarity with the natal region increases the chance of settling in that region the sex that acquires and defends a territory disperses over short distances. In Seychelles warblers this sexual asymmetry is probably weak as both sexes usually acquire a territory by dispersing to join a widowed breeder.
on an existing territory (Komdeur & Edelaar 2001). Unlike females, male dispersers do sometimes (19.2%, n = 104) create novel territories instead of occupying a breeder vacancy (Chapter 4). However, the distance between the natal and novel territories of these males were not shorter than distances dispersed by males that occupied a breeder vacancy (median NDD = 2 territory widths for both groups; Mann-Whitney U: Z = –0.73, P = 0.47). Therefore, local resource competition cannot explain why females disperse further than males. Third, when kin cooperation, such as cooperative breeding or collective resource defence, benefits one sex more than the other local resource enhancement may induce philopatry in the sex that benefits most (Perrin & Lehmann 2001; Le Galliard et al. 2006). In Seychelles warblers, the benefits gained through kin cooperation (indirect fitness gains of helping parents to raise non-descendent kin and female subordinates gaining parentage on the natal territory) are significantly higher for females than males (Richardson et al. 2002). This does not support theories based on local resource enhancement, as rather than being the more philopatric sex, females disperse further than males.

Is it possible that the female-bias in NDD in the Seychelles warbler is merely a phylogenetic relic which is, at present, of no adaptive significance? In passerines, females generally disperse further than males (Greenwood 1980; Clarke et al. 1997). However, in the closely related great reed warbler (Acrocephalus arundinaceus) a capture-recapture study did not find a sex-bias in natal dispersal distance (Hansson et al. 2002). Unfortunately, with data on NDD in other Acrocephalus species lacking, the idea that the female-bias in NDD is a phylogenetic relic remains speculative. Nevertheless, if the female-biased NDD is indeed of no adaptive significance, selection against this bias can not be very strong.

**Conclusions**

Our results show that Seychelles warblers do not avoid inbreeding through active mate choice on the natal territory or when dispersing and that the female-bias in natal dispersal distance does not contribute to inbreeding avoidance. Other evolutionary theories also seem inappropriate to explain the female-biased natal dispersal distance observed in the Seychelles warbler. Our study therefore warrants further work to develop and test alternative hypotheses to explain sex-biased natal dispersal.

**Acknowledgements:** Nature Seychelles kindly allowed us to work on Cousin Island and provided accommodation and facilities during the stay. The Department of Environment and the Seychelles Bureau of Standards gave permission for fieldwork and sampling. We thank everyone that helped in the field since 1985, and K. Bouwman and two anonymous referees for constructive comments on the manuscript. This work was supported by a Marie Curie Fellowship (HPMF-CT-2000-01074) and a NERC postdoctoral fellowship (NER/I/S/2002/00712) awarded to David S. Richardson, by grants from the National Environmental Research Council to Terry Burke and Jan Komdeur (GR3/11154), the Large Australian Research Council (A19802459) and the Netherlands Organisation for Scientific Research (NWO-VICI, 86503003), both allocated to Jan Komdeur.