

Sex biased natal dispersal is not a fixed trait in a stable population of Seychelles warblers

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Summary

We observed a change in the sex-specific rate of delayed natal dispersal in a stable population of Seychelles warblers over a period of 20 years. At first, females were more likely to delay dispersal in their first year of life than were males, whereas later there was no sex bias in the rate of delayed natal dispersal. Similarly, the female-bias in helping-at-the-nest and the male-bias in floating have also weakened over time. These changes may have resulted from the decrease in variation in territory quality observed in the population over the study period. Our findings strengthen the view that natal dispersal is a highly plastic response to local ecological and social circumstances, and clearly show that rates of sex-biased dispersal cannot be considered a species or population constant. Our study also highlights the importance of collecting long-term datasets to understand complex behaviour such as natal dispersal.

Keywords: natal dispersal, sex bias, territory quality, habitat change, sex ratio, *Acrocephalus sechellensis*, delayed dispersal.

Introduction

Group living occurs in a wide range of taxa and often results from delayed dispersal of independent offspring (Emlen, 1995). Although both sexes may

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delay their dispersal, one of the sexes generally is more prone to disperse or to disperse earlier in life than the other sex (reviewed in Greenwood, 1980; Clarke et al., 1997). This sex bias in dispersal rate has been related to processes such as inbreeding avoidance, local resource and local mate competition (Greenwood, 1980; Dobson, 1982; Pusey, 1987), and local kin cooperation (Perrin & Lehmann, 2001; Le Galliard et al., 2006). Numerous studies have investigated natal dispersal in many different species and many of those report sex-biased dispersal. This seems to suggest that a sex bias in delayed natal dispersal is a species or population constant. However, delayed natal dispersal may probably best be viewed as a plastic response to local ecological and social conditions (Clobert et al., 2001, 2004; Baglione et al., 2006; Handley & Perrin, 2007). When changes in the local environment elicit different responses from the sexes, such changes could alter the strength or even the direction of sex biased natal dispersal. Therefore, it is not unlikely that, for some species, the direction of sex biased delayed natal dispersal in a population varies over time.

Several field experiments support the idea that whether or not offspring delay their dispersal depends on local ecological and social conditions. For example, after transfer of carrion crow (*Corvus corone corone*) eggs from a non-cooperative colony in which offspring do not delay dispersal to a cooperative colony, most juveniles that hatched from the transplanted eggs delayed dispersal (Baglione et al., 2002). Similarly, in two newly founded populations of Seychelles warblers (*Acrocephalus sechellensis*) the length of time by which dispersal was delayed increased with increasing population size (Komdeur, 1992; Komdeur et al., 1995). There now also are suggestions that, in a stable population of Seychelles warblers, the initially observed sex-bias in delayed dispersal has disappeared, possibly because the sexes have responded differently to changes in the local environment. Using data collected in the Cousin Island population from 1985 to 1994, Komdeur (1996) showed that the higher the quality (in terms of food availability) of the natal territory, the longer independent offspring delayed dispersal. Because females were usually born on higher quality territories than males (Komdeur et al., 1997), females delayed dispersal longer than males (Komdeur, 1996). However, a study in the same population between 1995 and 2005 revealed that during this period males were just as likely to delay dispersal in their first year of life as were females (Eikenaar et al., 2007). Furthermore, the

quality of the natal territory no longer affected dispersal decisions of yearlings (Eikenaar et al., 2007). Natural succession of the vegetation and the continued effort of Nature Seychelles staff to restore the original vegetation seem to have caused a redistributed of food resources over the population (J. Komdeur, pers. obs.), which may be the link to the different findings of the two dispersal studies. We here investigate this potential redistribution of food resources as an explanation for the change in dispersal behaviour. We focus on the redistribution of food resources rather than possible changes in average territory quality because the number of birds and territories has been relatively stable since the start of the study (Komdeur, 2003; Brouwer et al., 2006, 2009), suggesting that the average food availability per territory has not changed.

Initially, natal dispersal data were collected while Komdeur was continuously present on the island, whereas from 1990 onwards data were collected during (bi-)yearly fieldwork periods. The aim of this study is to (i) statistically determine whether the initially observed female-bias in delayed natal dispersal has disappeared over the course of the study period by using the same time unit (yes/no dispersal within a year of birth), (ii) determine which sex has altered its dispersal behaviour and (iii) examine if indeed the variation in territory quality has changed in the Cousin population over time, and discuss whether this could be the cause of the change in dispersal behaviour.

Methods

Study population

Seychelles warblers live in pairs or groups that defend an all-purpose territory year-round (Komdeur, 1991). A group usually consists of a dominant pair and one or more offspring that have delayed dispersal and remained in the natal territory as subordinates (Komdeur, 1992). Some subordinates become helpers and assist the dominant birds in raising non-descendant kin (Komdeur, 1992; Richardson et al., 2003).

The present study (1985–2006) was carried out on Cousin Island (29 ha) in the Seychelles. The vegetation on Cousin is dominated by *Pisonia grandis* trees and, except for a barren rocky outcrop in the centre of the island, all habitat is occupied by warblers. The annual number of territories in the population has been relatively stable from 1985 to 2006 (average \pm SE =

112.3 \pm 1.2; Brouwer et al., 2006). In all years all territories were mapped in detail, except for the years 1991–1994 when only a part of the population was monitored (68% of territories). Territory boundaries were based on the outcome of inter-group disputes and on observations of colour-ringed birds. For all individuals the status (dominant or subordinate) and territory of residence were determined in each year during the peak of breeding from June to September (dry season), and in the years 1985–1990, 1998, 1999 and 2003–2005 this was also done during the minor breeding period from January to March (wet season). During the breeding seasons, all territories were checked for the presence of warblers at least once every two weeks. As inter-island dispersal is extremely rare (0.1%, $N = 1924$, Komdeur et al., 2004) warblers that were missing from their territory and not found on other territories can safely be assumed dead. Dispersal data was based on individuals that were colour-ringed on their natal territory from 1985 to 2005. As instances of territory inheritance have been very rare over the entire period of study (3.7%, $N = 219$, Eikenaar et al., 2008), the patterns of delayed dispersal that we present reflect patterns of natal dispersal.

Territory quality gradient

Seychelles warblers take 98% of their food from the underside of leaves, foraging mainly on the three dominant tree species of Cousin Island: *Pisonia grandis*, *Morinda citrifolia* and *Ficus* sp. (Komdeur, 1991, 1994). Consequently, to get an estimate of food abundance for each territory on Cousin, estimates of insect density per dm² leaf area, vegetation abundance scores and territory sizes were used to calculate an index of territory quality following Komdeur (1992). Insects were counted on the underside of 50 leaves of each of the three main tree species in 14 sites on Cousin Island. The division into 14 regions was chosen to incorporate those territories that had comparable vegetation and that were subject to similar amounts of wind driven salt spray (Komdeur, 1991). Salt spray probably has a considerable impact on the density of insects, because it causes defoliation. In the most central territory of each region, the number of insects on 50 leaves of each plant species present in the region was counted. Counts in the central territory of a given region were used in the calculations of quality of all territories within that region. Leaf area was assessed by measuring the size of 250 leaves at 50 random sites on the island (five leaves per species per site). The amount

of foliage was scored in each territory separately, by determining the presence or absence of each plant species (more or less than 50% cover as seen through a circular tube) at 20 random points in the territory in the following height bands: 0–0.75 m, 0.75–2 m, 2–4 m, and at 2-m intervals thereafter. Territory size was inferred from territory maps.

Komdeur estimated an index of territory quality in the dry (main breeding) seasons of 1986, 1987 and the wet (minor breeding) season of 1988. For each territory, Komdeur (1996) averaged these three territory quality estimates to describe the relation between the quality of a territory and the time young born in that territory delay dispersal. Here we used these averages to construct the frequency distribution of territory quality in the population in the period 1986–1988. During the later years of the study all the components to estimate territory quality were measured in the dry seasons of 1999, 2003 and 2004, and in the wet seasons of 1999 and 2005. To construct the frequency distribution of territory quality in the second period (1995–2006), we used the averages of territory quality estimates of the 2003 and 2004 dry and the 2005 wet season because these are consecutive in the same fashion as the 1986–87–88 seasons.

To investigate which component of the territory quality gradient may have changed we also calculated variation in foliage cover and insect numbers separately. Similar to territory quality, averages of measurements from the years 1986, 1987 and 1988, and the years 2003, 2004 and 2005 were used to construct the frequency distributions of foliage cover and insect numbers in the population in the two periods.

Measurements in the period 1986–1988 revealed that coastal territories (approx. one-third of all territories) were always of low quality (Komdeur, 1992), probably because wind driven salt spray causes defoliation and reduces insect densities. Due to the succession of the vegetation at the coast (J. Komdeur, pers. obs.) the quality of the coastal territories may have increased. Because we were interested in a potential redistribution of food resources over the territories, in both study periods, we compared the territory quality scores, foliage cover and insect numbers between coastal and inland territories. Coastal territories were defined to have part of their boundary set by the shoreline. A region was defined to be coastal when the territory in which insects were counted was a coastal territory. Of the 14 regions, seven were coastal and seven were inland.

Data analysis

We analysed natal dispersal with a binary logistic regression (an individual could either disperse or delay dispersal in its first year of life) using MLwiN 2.0 (Rasbash et al., 2004). Sex of the individual was entered into the model as a categorical variable and the individual's year of birth was entered as a linear covariate. The interaction between sex and year is the term of interest for this study, as a significant interaction is indicative of a change in sex-biased delayed natal dispersal over time. As data points from the same year may not be independent, we also entered year of birth as a random effect.

We used a Levene's test of homogeneity of variance to determine if the distributions of territory quality (parameters) were different between the two periods in which territory quality was estimated. The Levene's test is robust in the face of departures from normality. Differences in territory quality (parameters) were assessed using parametric tests unless data were not normally distributed. Probabilities are two-tailed in all tests.

Results

Natal dispersal

Figure 1 shows the proportion of male and female Seychelles warblers that dispersed from the natal territory within their first year of life. The figure indicates that in the early stages of the study, females were far more likely to delay their dispersal than were males, whereas in later years this difference in dispersal rate was absent (note that not all years are presented due to lack of sufficient data). The statistical analysis (which included all dispersal data) confirmed this trend (Table 1); there was a significant interaction between sex and year. Figure 1 also indicates that the disappearance of the sex bias in delayed natal dispersal was primarily the result of a change in female dispersal behaviour, with yearling females more prone to disperse in later years of the study.

Territory quality gradient

Figure 2 depicts the frequency distributions of territory quality scores, insect numbers and foliage cover in the Cousin Island population in the periods 1986–1988 and 2003–2005. The variance in quality among territories was

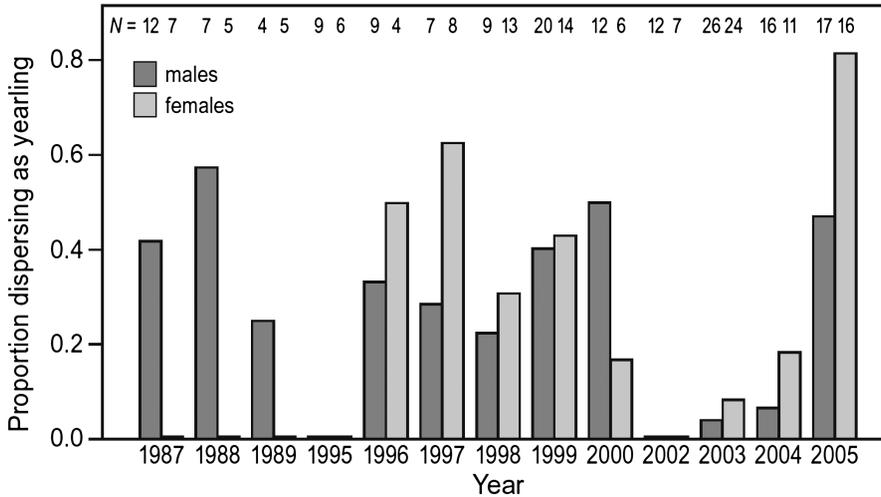


Figure 1. The yearly proportion of Seychelles warbler males and females that dispersed from their natal territory within a year of birth. Only years from which the dispersal history of at least four males and four females were known are included in the figure. Numbers above bars are sample sizes.

Table 1. Model summaries examining natal dispersal decisions (yes/no dispersal) of yearling Seychelles warblers ($N = 304$) in relation to sex of the yearling and year of birth.

Explanatory variable	$\beta \pm SE$	χ^2	df	p
Sex	2.33 ± 0.76	9.41	1	0.002
Year of birth	0.03 ± 0.05	0.44	1	0.51
Sex \times year of birth	-0.16 ± 0.05	11.92	1	<0.001

not equal in the two periods (Levene statistic = 57.2, $p < 0.001$, $N = 228$) and has become much smaller over time (median \pm inter-quartile range: 1986–1988: 1.37 ± 2.0 ; 2003–2005: 2.07 ± 1.1). The number of territories in the higher part of the territory quality range has decreased considerably over time as did the number of territories in the lowest score (Figure 2A). The median territory quality was statistically higher in the 2003–2005 period than in the 1986–1988 period (Mann–Whitney test: $Z = -3.27$, $p < 0.01$, $N = 228$). Among region variation in the total number of insects was not equal in the two periods (median \pm inter-quartile range: 1986–1988: 74.6 ± 125.6 ; 2003–2005: 80.6 ± 27.5 , Levene statistic = 18.4, $p < 0.001$, $N = 14$,

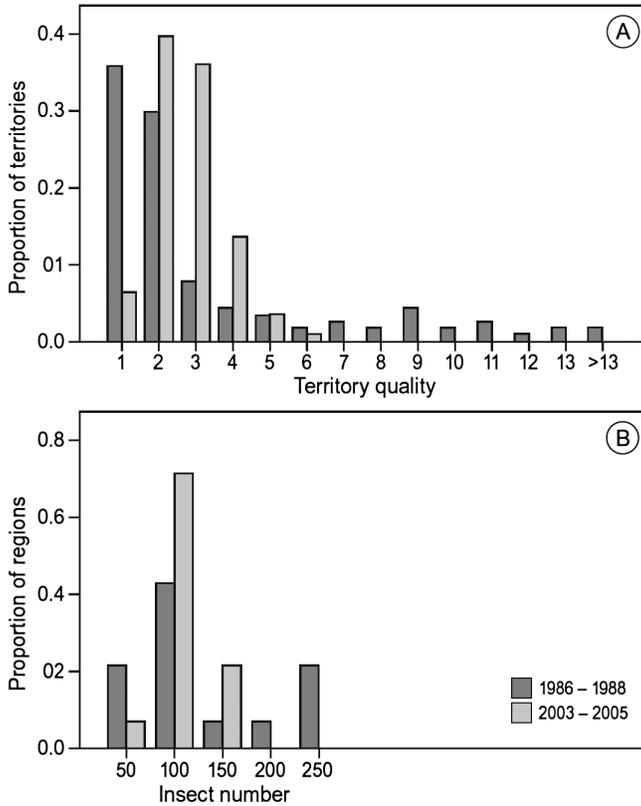


Figure 2. Frequency distributions of (A) territory quality index, (B) total insect numbers and (c) foliage cover in the Cousin Island population for the periods 1986–1988 and 2003–2005. Each score, number and cover is the average of the three measurements taken across each period. Territory quality estimates are on a ratio scale and values between 0 and 1 were grouped in score 1, values between 1 and 2 in score 2, etc. Insect numbers and foliage cover are presented as absolute numbers. Insect numbers from 0 to 50 were grouped in score 50, from 50 to 100 in score 100, etc. Foliage cover from 0 to 10 was grouped in score 10, from 10 to 20 in score 20, etc. Sample sizes of both territory quality scores and foliage cover were 117 for the 1986–1988 period and 111 for the 2003–2005 period. Sample sizes of insect numbers were 14 in both periods.

Figure 2B). Similarly, among territory variation in foliage cover was not equal in the two periods (mean \pm SD: 1986–1988: 101.9 ± 29.6 ; 2003–2005: 72.9 ± 11.5 , Levene statistic = 65.1, $p < 0.001$, $N = 228$, Figure 2C).

Coastal territories were of lower quality than inland territories in the period 1986–1988 (Mann–Whitney test: $Z = -5.92$, $p < 0.01$, $N = 117$),

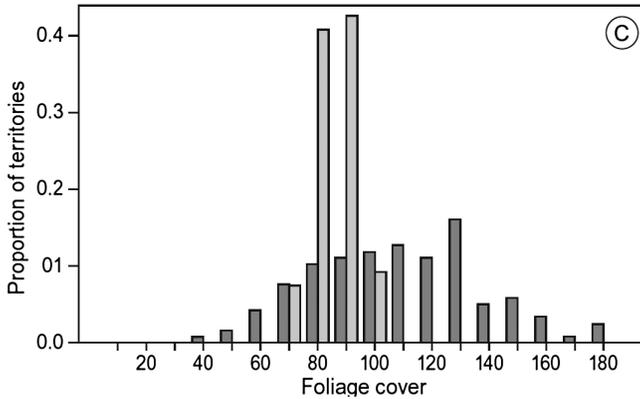


Figure 2. (Continued.)

whereas in the period 2003–2005 these territories did not differ in quality (t -test: $t_{110} = 1$, $p = 0.32$). Similarly, in the period 1986–1988, coastal regions contained fewer insects than inland regions (Mann–Whitney test: $Z = -2.49$, $p = 0.01$, $N = 14$), whereas in the 2003–2005 period there was no difference in insect numbers between these two regions (Mann–Whitney test: $Z = -0.96$, $p = 0.34$, $N = 14$). Foliage cover also was lower in coastal than in inland territories in the 1986–1998 period (t -test: $t_{116} = -2.64$, $p = 0.01$), whereas in the 2003–2005 period there was no difference (t -test: $t_{110} = -1.66$, $p = 0.1$).

Discussion

The female bias in delayed dispersal in the Cousin Island Seychelles warbler population observed in the early stages of the study was absent in later years. The change in dispersal coincided with a dramatic reduction in the extent of among territory variation in quality on Cousin (Figure 2A). This variation may have decreased because the differences in both foliage cover and insect numbers that existed between coastal (previously low quality) and inland territories in the early years of the study were absent in later years. Succession of the vegetation in coastal territories probably reduced the amount of salt spray that entered the territory, which may have resulted in the increased availability of insect prey in these territories. Natural succession of coastal vegetation was very likely sped up by the restorative actions of Nature Seychelles staff, who planted salt tolerant vegetation along the coastline. The ap-

parent decrease in quality of some inland territories may have been the result of freak storms that felled many of the largest trees that grew in the centre of the island (D.S. Richardson, pers. obs.). Nevertheless, although median territory quality was statistically higher in the later period of this study the number of birds and territories has been relatively stable (Komdeur, 2003; Brouwer et al., 2006, 2009). This suggests that an index rather than true territory quality is measured. Most likely, inclusion of estimates of foliage cover and territory size do not directly or proportionally translate into increased insect availability (Brouwer et al., 2009).

Territory quality gradient and dispersal behaviour

When a population has a steep territory quality gradient, delaying dispersal may be a better option than dispersal for offspring born on high quality territories (Stacey & Ligon, 1987, 1991) while dispersal may be the better option for offspring born on low quality territories (Dobson et al., 1998). Seychelles warblers born on Cousin in the early years of the study entered a population with a steep territory quality gradient. Because at that time females were usually born on higher quality territories than males (Komdeur et al., 1997), these generally delayed dispersal for a longer period than males (Komdeur, 1996). The data from 2003–2005 revealed that the territory quality gradient across the population had become considerably less steep; there were no really high and few very low quality territories. This raises the possibility that there were fewer females delaying dispersal from high quality territories and fewer males dispersing early from poor quality territories. This may very well be the reason that the sex bias in delayed natal dispersal ceased to exist.

In the Seychelles warbler, the majority of male and female offspring remains in the natal territory and disperse only when they are able to claim a vacant dominant breeder position (Eikenaar et al., 2009). An alternative explanation for the change in dispersal observed in this study, therefore, could be that, over time, competition for dominant breeder positions weakened for females or became more intense for males. However, such changes do not seem to have occurred; survival probabilities of adults do not differ between the sexes and have not changed since 1985 (Brouwer et al., 2006), and the sex ratio of competitors for vacancies has not changed much over the years (see sample sizes in Figure 1). It also seems implausible that changes in demography contributed much to the observed change in dispersal behaviour;

since the start of the Seychelles warbler study on Cousin in 1985, the bird density and the number of territories and individuals have been relatively stable (Komdeur, 2003; Brouwer et al., 2006).

The change in delayed dispersal from female biased to unbiased has affected at least two other behaviours directly linked to natal dispersal. First, because the number of competitors per breeder vacancy did not change, in later years of the study more females left their natal territory without immediately claiming a dominant breeder vacancy. From 1985–1990 none of the female subordinates were observed as floaters (Komdeur, 1991), whereas from 1995–2005, 16% of female subordinates were seen floating at some stage before they settled as a dominant breeder (Eikenaar et al., 2009). Secondly, because delayed dispersal allows for offspring to help their parents (Ekman et al., 2004) the earlier dispersal of female offspring in later years meant that fewer were available to help their parents. The female bias in subordinates that help at the nest that was observed from 1986–1990 (88%; Komdeur, 1996) was in later years much weaker (68% in 1997–1999; Richardson et al., 2002).

Implications

In the Seychelles warbler (Komdeur, 1996) and several other species, both natal dispersal and offspring sex ratio have been shown to be biased in relation to certain environmental or social factors. For example, in Arctic foxes (*Alopex lagopus*) females are more often born in resource rich ranges and are less likely to disperse than males (Goltsman et al., 2005). Similarly, spider monkeys (*Ateles geoffroyi*) males are more philopatric than females and sex ratios were more male biased in good habitats than in less good habitats (Chapman et al., 1989). In Townsend's voles (*Microtus townsendii*) both the population sex ratio, as well as the amount of females that are philopatric, depends on vole density (Lambin, 1994). As in the Seychelles warbler, changes in the environment of these species could alter the interplay of environmental factors, offspring sex ratios and natal dispersal. For example, in the Arctic foxes group sizes were larger on resource rich ranges, because these ranges allowed for recruitment of daughters (Goltsman et al., 2005). Hypothetically, a local decrease in resource richness may force female offspring to disperse. Further experimental work on the Seychelles warbler and other species is now required to disentangle the interplay of environmental factors, offspring sex ratios and natal dispersal.

In a review on avian sex biases in both the rate and distance of dispersal, Clarke et al. (1997) already suggested that for many species it is inappropriate to consider a sex bias in dispersal to be a species constant. Our findings now show that even in stable populations, sex biased natal dispersal is not necessarily a fixed trait. This indicates that to explain natal dispersal patterns, local environmental factors, such as the distribution of resources over a population, have to be taken into consideration. Moreover, our study highlights the importance of collecting long-term datasets to understand complex behaviours such as natal dispersal.

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