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Differential dispersal costs explain sex-biased dispersal distance in a cooperatively breeding bird

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LAY SUMMARY

Why does the distance that young animals disperse between their natal- and breeding territory usually differ between males and females? We show that in cooperatively breeding Seychelles warblers, males are reluctant to disperse and disperse less far than females because for males dispersal is more costly due to attacks by conspecifics. We did not find evidence for regularly-invoked hypotheses for sex-biased dispersal (e.g. sex differences in territory defense and sex-biased dispersal as inbreeding avoidance mechanism).

ABSTRACT

In most bird species, dispersal distance from the natal territory to a breeding territory is greater for females than males. Sex-biased dispersal may have important implications for population dynamics and sexual reproduction because it can affect social recognition, genetic population structure, inbreeding and kin selection. Two main hypotheses have been proposed to explain sex-biased dispersal distance: 1) it serves as an inbreeding-avoidance mechanism or 2) it is linked to a sex difference in resource-holding potential. Additionally, in species where individuals delay dispersal and become subordinates in a natal territory, differences in benefits of philopatry (e.g. territory inheritance, opportunities for reproduction) may also affect sex-biased dispersal. We show that in the group-living Seychelles warbler, *Acrocephalus sechellensis*, females disperse further to obtain a breeding position than do males. However, female-biased dispersal distance is not explained by the above-mentioned hypotheses: further dispersal does not lead to less-related partners, both sexes defend the territory, both sexes can inherit a territory, and subordinate females are more likely to obtain some reproduction than subordinate males. Instead, we provide evidence for a little-explored hypothesis based on a sex difference in dispersal costs: extra-territorial forays to search for limited vacancies are more costly, in terms of increased mortality, for males. In line with such differential dispersal costs, males foray less far than females and often wait for local dispersal opportunities, ultimately resulting in a shorter average dispersal distance than in females. This explanation may help future studies in explaining sex-biased dispersal in social and perhaps also non-social species.

Key-words: cooperative breeding, delayed dispersal, habitat saturation, inbreeding, sex-biased dispersal

INTRODUCTION

In animals, the distance of dispersal from the natal territory or site to a place for independent breeding is often sex-biased (Greenwood 1980; Pusey 1987; Clarke, Sæther and Roskaft 1997). Sex-biased dispersal can have important implications for the dynamics and the genetic structure of populations (Aars and Ims 2000; Prugnolle and De Meeus 2002). Understanding its causes and consequences is therefore important to understanding how processes like kin cooperation and competition, resource defence and inbreeding avoidance can affect mating systems and population dynamics.

Two main non-exclusive hypotheses have been invoked to explain sex-biased dispersal (Greenwood 1980; Greenwood and Harvey 1982; Pusey 1987). First, the *inbreeding-avoidance* hypothesis predicts that the risk of mating with closely related individuals is reduced if dispersal distance is different between the sexes (Pusey and Wolf 1996; Perrin and Mazalov 2000; Perrin and Goudet 2001). This mechanism may especially be important in species with high levels of extra-pair mating, where dispersing females run the risk of mating with their own fathers (who sired the female in an extra-pair fertilisation), whereas dispersing males cannot mate with their mother, as their mothers are always from within the natal territory. Second, the *resource-holding potential* hypothesis predicts that dispersal asymmetry between the sexes is a consequence of bias in the degree of advantage gained from familiarity with the area during intra-specific competition for resources towards the sex that defends those resources (Greenwood 1980; Pusey 1987). Although both hypotheses have obtained some degree of support (Johnson and Gaines 1990; Bowler and Benton 2005; Lawson Handley and Perrin 2007), their respective importance remains unclear.

In species where opportunities for independent breeding are limited, such as family-living and cooperatively breeding species, subordinate individuals either have to wait in a resident territory for a breeding vacancy to arise nearby or to search for a vacancy in the population (Cockburn 1998). Waiting in a resident territory may yield benefits to subordinate individuals (Stacey and Ligon 1991; Koenig & Dickinson 2004) and, if such 'benefits of philopatry' differ between males and females, this may lead to sex bias in motivation to search for an independent breeding vacancy, resulting in differences in the ultimate dispersal distance (Brown 1987; Cockburn 1998; Kingma et al. 2016a,b). As such, differences in the '*reproductive benefits of philopatry*' (i.e., the likelihood of obtaining a share in reproduction in the resident territory, and/or inheriting the breeding position; e.g. Cockburn 1998; Kokko and Ekman 2002; Richardson et al. 2002) might explain sex-biased dispersal. Sex differences in the probability of territory inheritance may arise when the more competitive sex does not accept a related individual as a partner and could expel either an inheriting offspring or the remaining related breeder from the territory (e.g., Koenig and Stacey 1990; Nelson-Flower et al. 2012). Alternatively, or additionally, individuals who delay dispersal and remain in a resident territory may gain '*energetic benefits of philopatry*', such as access to food. It is not immediately clear if and how such benefits differ between the sexes. However, the role that any such benefits play in explaining delayed dispersal would also depend on the costs of leaving, which may well be sex-specific (Perrin and Mazalov 2000; Gros et al. 2008).

In species both with and without delayed dispersal, searching for an independent breeding position involves extra-territorial forays through unfamiliar or unfavourable habitat (Reed et al. 1999). In a number of species it has been shown that such forays are associated with reductions in survival and body condition due to harassment by predators and conspecifics, and such costs have been invoked as explanation for delayed dispersal (e.g., Yaber and Rabenold 2002; Griesser et al. 2006; Ridley, Raihani & Nelson-Flower 2008; Ridley 2012; Kingma et al. 2016a). If such costs are different between both sexes, for example because of differences in conspicuousness to predators or because attacks by conspecifics may be more frequently directed at the sex that threatens the reproduction of the resident individuals more, they may well explain sex-biased dispersal distance. Whether this *dispersal-cost hypothesis* is supported is unclear, however, partly because extra-territorial forays have received relatively little empirical attention (Reed et al. 1999) and because studies of sex-biased dispersal intrinsically focus on proximate and ultimate factors underlying dispersal, rather than the actual movement *per se* (Lawson Handley and Perrin 2007). Together, these hypotheses, in addition to the more conventional hypotheses of inbreeding avoidance and sex bias in resource-holding potential, provide an interesting avenue to determine the importance of various social and ecological factors for the evolution of sex-biased dispersal.

Here we tested all the above-mentioned hypotheses for female-biased dispersal distance (see Table 1 and below) in the cooperatively breeding Seychelles warbler, *Acrocephalus sechellensis*. This system is very suitable for testing these hypotheses for several reasons. First, females on average disperse further from their natal territory than males (Eikenaar et al. 2008a). Second, distinguishing dispersal from mortality is generally difficult (Koenig et al. 1996), but the Seychelles warblers exist on a contained island with virtually no emigration between islands, so individuals that have disappeared from the study-population almost certainly died (Komdeur et al. 2004). Third, in this long-term study population nearly all individuals are individually marked and followed throughout their life, so that their natal territory, dispersal behavior, relatedness to other individuals, and dates of birth and death are known. Fourth, habitat saturation inhibits independent breeding of subordinate individuals, but individuals can improve the likelihood of obtaining an independent breeding position by extra-territorial forays to find a position (Eikenaar et al. 2008a,b; Kingma et al. 2016a,b). Although such behaviors may be difficult to assess in general (Reed et al. 1999), our detailed monitoring allows us to make inferences about prospecting and floating.

We used a framework based on the above-mentioned hypotheses (see Table 1) to develop and test predictions of how different proximate and ultimate factors may explain female-biased dispersal distance in Seychelles warbler. Specifically, we assessed (1) whether dispersal over greater distance leads to the acquisition of a less-related partner, and whether this is especially the case for females who may mate with their extra-pair sire *(inbreeding-avoidance),* (2) whether males and females differ in territory defence (*resource-holding-potential*), (3) whether the probability of obtaining parentage as a subordinate and territory inheritance rates differ between male and female subordinates (*reproductive-benefits-of-*

philopatry), and (4) whether the costs of finding an independent breeding territory differ between males and females in Seychelles warblers (*costly-dispersal*).

METHODS

Study system

We studied a population of ca. 320 individually colour-ringed Seychelles warblers on Cousin Island, Seychelles (29 ha; 04°20′S, 55°40′E) during the main breeding seasons (June-September) from 2003 until 2014. Each of the ca. 110 territories are occupied year-round by a dominant breeding pair, of which approximately half are accompanied by 1 to 4 independent subordinates. Dominant individuals rarely disperse and usually remain present in their territory until death (Hammers et al. 2015). Intruding conspecifics are physically attacked (Kingma *et al.* 2016a,b). Because of this, territory boundaries are easily determined based on border disputes between groups. Breeding vacancies are limited because all suitable habitat is occupied (Komdeur 1992) and Seychelles warblers are relatively long lived (average 5.5 years; Hammers et al. 2015). Individuals can improve their likelihood of finding a breeding vacancy by either temporarily (prospecting) or permanently (floating) leaving their territory to foray and search for vacancies across the island (Kingma *et al.* 2016b).

In each season we performed regular censuses (at least weekly per territory) to identify for each individual the resident territory (i.e., where birds were consistently observed foraging, performing reproductive tasks and/or involved in non-antagonistic interactions with other resident individuals) and breeding status (*dominant*: based on affiliative behavior between the pair members; *subordinate*: reproductively mature individuals but not involved in direct pair behaviors or initiation of breeding activities, or independent *juvenile*: 3-5 months old). Birds were captured using mist nets and each bird was given a unique combination of three colour rings and a numbered metal ring (if not already ringed). Body mass (± 0.1 g) and tarsus length (± 0.1 mm) were measured, and a small blood sample was taken to determine sex (following the protocol in Griffiths et al. 1998) and for genotyping (see below).

Inheritance, dispersal, prospecting and floating

We determined whether each subordinate observed in a season was present by the beginning of the next season as a subordinate on the same territory, obtained a breeding position, or had died. For individuals that obtained a breeding position, we determined whether this was achieved through inheritance of the natal territory or dispersal from that territory. We determined dispersal distance as the minimum number of territories that an individual had to cross between its natal territory and the territory where it obtained its breeding position (following Eikenaar et al. 2008b). A small number of individuals (n = 3 of 215 males and 5 of 218 females) settled as subordinates in a non-natal territory before obtaining a breeding position elsewhere, but we assess here the dispersal distance between the original natal territory and a breeding position only. The maximal possible distance that individuals could disperse over the island ranged from 9 to 16 territories (median = 12), and this did not differ between males (median: 12, n = 215) and females (median: 12, n = 218; generalized linear mixed model with maximum possible dispersal distance as a response variable, sex as an independent variable and 'natal-territory-identity' as a random variable: $\beta = -0.004 \pm 0.028$, $z = -0.13$, $P = 0.90$). Some individuals were observed or caught while prospecting (defined as individuals observed >2 territories away from their resident territories and returned after prospecting to that territory) or floating (individuals only observed on non-resident territories multiple times throughout the season; see Kingma et al. 2016a,b for details). For each prospector we determined the maximum number of territories it was seen away from its resident territory, similarly as for determining dispersal distance.

Statistical analyses

For the statistical analyses, models were fitted in R 3.2.0. (R development core-team, 2016) using the 'lme4' and 'lmerTest' packages (for linear mixed models and generalized linear mixed models; Bates et al. 2015; Kuznetsova et al. 2016), unless stated otherwise. Non-significant variables (*P* > 0.05) were sequentially excluded from the model, starting with the least significant variable, until the model only contained significant variables. Values for non-significant variables were obtained by re-including them in turn in the final model to confirm that the order of exclusion did not change the results. Mean values and model estimates (β) are reported ± standard error (SE).

Sex-biased dispersal distance and prospecting behavior

We first confirmed findings from an earlier study (Eikenaar et al. 2008a), by testing whether dispersal distances between natal and subsequent breeding territory were different for males and females (n = 215 and 218, respectively) using a generalized linear mixed model with Poisson error, including 'natal-territory-identity' as random variable.

We also tested whether the maximum distance that individuals prospected from the natal territory was different between males and females, using a generalized linear model with Poisson error.

Inbreeding avoidance

We tested whether dispersal distance and sex of the focal individual predicted the relatedness between that bird and its new partner (response variable) using a general linear mixed model with ‘natal-territory-identity’ as a random effect (excluding seven pairs for which relatedness could not be determined due to an unsampled breeder). To test whether the effect of dispersal distance differed between males and females, we added the interaction between sex and distance. We excluded 41 individuals that inherited their natal territory from the analysis. Relatedness of dispersing individuals to their (first) dominant partner (R) was calculated using GenAlEx 6.5 (Peakall and Smouse 2012), using Queller and Goodnight (1989) estimation. We used genotypes of all individuals involved in included breeding pairs, as determined using 30 microsatellite markers (see for details: Richardson et al. 2000; Spurgin et al. 2014).

To assess whether females are likely to end up in an incestuous relationship with their extra-group father, we used two approaches. First, we tested whether pair-relatedness was different between females that obtained a partner after short-distance dispersal (1 or 2 territories from their natal territory) and those that dispersed further, using a linear mixed model with ‘natal-territory-identity’ as a random factor. Second, we tested whether pair-relatedness was different between short-distance dispersing males and females using a similar model. The distance of 1 or 2 territories for ‘short-distance dispersal that may lead to incestuous mating’ was chosen because two territories is the median distance between an extra-group offspring’s territory and its sire (62% of extra-group fathers lived within two territories distance; Richardson et al. 2001). Note however, that the results are similar if this distance would be chosen differently, because females who dispersed further did not pair with less related males (see Fig. 1b).

Resource-holding potential

We analysed two probable determinants of sex-differences in resource-holding potential. First, we assessed whether breeding males were larger and/or heavier than breeding females.

We compared tarsus length (averaged if an individual was measured more than once) of males and females using a t-test. Subsequently, using all catches of each individual, we tested in a linear mixed model whether body mass (as response variable) was different between the sexes and added 'individual-identity', year and 'resident-territory-identity' as random factors and time [morning (6:34-10:00), midday (10:00-14:00), afternoon (14:00-19:10)] of capture as an independent variable to account for temporal and spatial variation in body mass. Second, using 121 opportunistically observed antagonistic interactions (observed during weekly censuses in each territory) between (identified) resident individuals and intruders, we determined whether male residents were more likely to be involved in antagonistic interactions than female residents using a binomial test.

Reproductive benefits of philopatry (parentage acquisition and territory inheritance)

Previously, it was shown that parentage success was substantially higher for female than male subordinates (Richardson et al. 2002), so that we can exclude this factor as an explanation for female-biased dispersal.

To assess whether the chances of territory inheritance are different for males and females, we used a number of approaches. First, for 96 territory vacancies where a subordinate was resident in a natal territory at the time a vacancy arose, we tested directly whether inheritance occurred more for female vacancies than for male vacancies using a χ^2-test. Second, we used a generalized linear mixed model to test whether individuals were more related to the opposite-sex breeder (response variable) if they inherited than if they dispersed, and tested whether this effect was different between the sexes (included as independent variables and their interaction), including 'natal-territory-identity' of the focal individual as a random effect (excluding seven pairs for which relatedness could not be determined due to an unsampled breeder). Third, if males can expel females, we would expect that males are more likely than females to inherit the territory if the opposite-sex is related because males may expel their mothers, but females not their fathers. Therefore, we tested whether the likelihood that subordinates filled a vacancy in their territory (response variable) was dependent on the interaction between the sex of the subordinate and whether the opposite-sex breeder was related or not (social parent or not; based on social pedigree data). We removed one individual for which it was unknown whether the remaining breeder was related and 18 cases where more than one same-sex subordinate was present, as the presence of a same-sex subordinate reduces the chance that an individual would inherit the territory. Fourth, to determine whether the probability of staying as breeder after inheriting a position with a related partner was different between sexes, we determined whether females in incestuous pairs were more likely to divorce and leave than males.

Costly dispersal

In order to make inferences about sex-biased costs of dispersal, we tested whether male and female prospectors / floaters differed in the probability that before the next breeding season they (1) died (Fisher exact test) and (2) obtained a breeding position (χ^2 test; including individuals who died). As individuals only prospect or float before they are two years of age (see Kingma et al. 2016b), we restricted the analyses to birds younger than two years. In each season we determined whether individuals prospected or floated (see Kingma et al. 2016b for details), and each individual was included in only one season, as only one female was observed prospecting for two years in a row (for which only the first season was included).

On occasion, foraying birds were caught opportunistically together with resident territory owners while they were involved in intraspecific chases (Kingma et al. 2016a). Therefore, to make inferences about whether foraying males were more often attacked by territory owners than foraying females, we tested whether foraying (prospecting and floating combined) males were more often caught with resident territory owners than foraying female (using all catches). We fitted a GLMM with 'bird-identity' as a random factor to account for multiple inclusions of individuals, whether or not an individual was caught with a resident individual as a response variable, and whether individuals prospected or floated, and sex (and their interaction), as independent variables.

Ethical note

All protocols conformed to legal requirements for use of animals in research and were approved by Seychelles Department of Environment and Seychelles Bureau of Standards (permit: A0157).

RESULTS

Sex-biased dispersal distance and prospecting behavior

To test for sex bias in dispersal distance and prospecting behavior we compared these two measures between males and females. Females dispersed further from their natal territory than males (Fig. 1a). Females (median = 5 territories distance; range = 3-12) were also observed prospecting further than males (median = 3; range = 3-6; $\beta = 0.460 \pm 0.156$, $z = 2.95$, $P = 0.003$). We have shown elsewhere that females prospect more often than males (annually 19% of 175 females and 9% of 162 males; Kingma et al. 2016b).

Inbreeding avoidance

Inbreeding avoidance is generally hypothesized to underlie sex-biased dispersal distance. However, dispersal distance (excluding inheriting individuals) did not affect the relatedness of the resulting breeding pair and this was similar for male and female dispersers (Table 2a; Fig. 1b).

If females disperse further to avoid the risk of mating incestuously with an extra-group father (nearby males), then we would expect to find that short-distance dispersal by females would be more likely to result in incestuous pairs. However, short-distance dispersing females were not more related to their new partner (R = 0.030 ± 0.036, n = 48) than further-dispersing females (R = 0.004 ± 0.018, n = 143, Table 2c) or short-distance dispersing males (R = 0.035 ± 0.018, n = 128; Table 2d).

Resource-holding potential

Tarsus length and body mass were used as measures of competitive ability and resource-holding potential. On average, males (25.9 ± 0.04 mm, n = 309) had a 6.3% longer tarsus length than females (24.4 ± 0.03 mm, n = 274; t = -29.96, P < 0.001). Similarly, males (mean mass = 16.5 ± 0.03 g, n = 784 catches) were on average 9.6% heavier than females (15.0 ± 0.04 g; n = 576; β = -1.425 ± 0.060, t = -23.95, P < 0.001; correcting for time of capture (relative to morning): midday: β = 0.053 ± 0.056, t = 0.948, P = 0.34, afternoon: β = 0.255 ± 0.055, t = 4.65, P < 0.001).

Despite the asymmetry in size, however, both sexes were equally represented in agonistic interactions with intruders (62 of 121 attacks (51%) were performed by females and 59 (49%) by males; binomial exact test: P = 0.86). This included attacks by 19 subordinates (10 females, 9 males), but excluding these did not change the result (P = 0.92).

Reproductive benefits of philopatry (parentage acquisition and territory inheritance)

If the reproductive benefits of philopatry (parentage acquisition and territory inheritance) are different between the sexes, then this might lead to sex-biased dispersal distance. As we could exclude differential parentage acquisition by subordinates as mechanism based on previous research (female subordinates are more likely to reproduce than male subordinates;

Richardson et al. 2002), we tested subsequently whether females were more likely to inherit the territory than males. This was, however, not the case. First, the chances of territory inheritance are equal for males and females: overall, 41 of the 433 breeding vacancies (9.5%) were filled by inheritance (Fig. 1a), and if the respective-sex subordinate was present then inheritance was equally likely for female (23 of 56 cases; 41.1%) and male vacancies (17 of 40 cases, 42.5%; $\chi^2_1 < 0.01$, $P = 1.00$). Second, as expected given that most subordinates are retained offspring, inheriting individuals ($R = 0.221 \pm 0.039$, $n = 41$) were more related to their partner than dispersing individuals ($R = 0.020 \pm 0.011$, $n = 385$) but this effect was not different between males and females (Table 2b, Fig. 1b). Third, the likelihood of filling a vacancy in the resident territory tended to be higher when subordinates were unrelated to the opposite-sex breeder (12 of 23, 52.2%) than when the remaining breeder was a social parent (16 of 54, 29.6%; $\beta = -0.952 \pm 0.513$, $t = -1.86$, $P = 0.063$), but this effect did not depend on the sex of the subordinate (interaction: $\beta = 1.708 \pm 1.082$, $z = 1.58$, $P = 0.11$). Social fathers were equally likely to accept their daughter as a partner (in 8 of 31 cases; 25.8%) as social mothers were to accept their son (in 8 of 23 cases; 34.8%; $\chi^2_1 = 0.171$, $P = 0.68$). Fourth, although the small sample of divorcing incestuous pairs did not permit adequate statistical testing, only 1 of 8 father–daughter pairings and 3 of 8 mother–son pairings ended by divorce, where in two cases the female left (daughter and mother) and in two cases the son left.

Costly dispersal

By assessing sex differences in mortality and intraspecific interactions of floaters and prospectors, we studied the potential sex-biased costs of dispersal. Male floaters were significantly more likely to die than female floaters before the beginning of the next season (Fig. 2), and male floaters tended to be less likely to obtain a breeding position before the beginning of the next season (47% of 15 individuals) than female floaters (79% of 19) (although this result was not significant; $\chi^2_1 = 2.51$, $P = 0.11$). Males and females that engaged in temporary prospecting trips (before returning to their natal territory) were equally likely to die (Fig. 2) and to obtain a breeding position before the beginning of the next season (62% of 13 males and 54% of 39 females obtained a position; $\chi^2_1 = 0.01$, $P = 0.94$). Male forayers (prospectors and floaters combined) were nearly twice as often caught with a resident individual (29% of 24 catches) than female forayers (15% of 39 catches) but this effect was not statistically significant, either alone ($\beta = 0.804 \pm 0.658$, $z = 1.22$, $P = 0.22$) or in interaction with whether individuals prospected or floated ($\beta = -2.465 \pm 1.665$, $z = -1.48$, $P = 0.14$). The likelihood of being caught with a resident individual, did not differ between prospectors (20% of 35 individuals) and floaters (21% of 28; $\beta = 0.206 \pm 0.744$, $z = -0.28$, $P = 0.78$).

DISCUSSION

Sex-biased dispersal distance in Seychelles warblers

In line with many studies (see Greenwood 1980) and with previous work on Seychelles warblers (Eikenaar et al. 2008a), we show that female subordinate Seychelles warblers disperse further from their natal territory to obtain a breeding position than males. This effect was not the result of females floating more often (i.e. permanently leaving a natal territory to search for a vacancy, likely occurring because of eviction by breeders; Eikenaar et al. 2007, Kingma et al. 2016b). However, female Seychelles warblers engage in temporary prospecting trips more often than males (19% vs 9%; Kingma et al. 2016b) and they prospect over larger distances than males (this study; see also Eikenaar et al. 2008a). This suggests that males generally remain as subordinates within a territory and explains why males often shift to a nearby vacancy when the opportunity arises (Fig. 1a), whereas females more often actively search for such vacancies, resulting in a breeding position further afield. There are several potential explanations for sex-biased dispersal (Table 1), and below we discuss whether these can explain sex-biased dispersal distance in Seychelles warblers.

Benefits of philopatry, incest and inbreeding avoidance, and resource-holding potential

We tested the predictions of several hypotheses for sex-biased dispersal (Table 1), but the results indicate that we can reject most of these hypotheses to explain female-biased dispersal distance in Seychelles warblers.

Sex-biased dispersal in species where subordinate individuals delay dispersal is hypothesized to be based on differences in reproductive benefits-of-philopatry (i.e., in reproduction as subordinate, territory inheritance or differences in competitive ability and resource holding potential; Greenwood 1980; Zack and Rabenold 1989; Richardson et al. 2002). We can rule out sex differences in reproductive benefits gained by subordinates as an explanation for female-biased dispersal distance in Seychelles warblers: subordinate females are more likely to gain parentage than subordinate males (Richardson et al. 2001; Richardson et al. 2002), and territory inheritance is rare (9.5% of positions) and achieved equally by males and females. Furthermore, although incest avoidance inhibits territory inheritance to some extent (whether or not the opposite-sex breeder was a social parent tended to predict (P = 0.06) whether subordinates inherited), incestuous pairs are formed in ca. 30% of the cases and this was not more likely for female subordinates than for males. Moreover, although the sample size was small, incestuous pairs between mothers and sons did not always end in divorce (only in 3 of 8 cases) and, importantly, were not more likely to end in a female leaving than a male. This suggests that males are not necessarily dominant over females and that this cannot explain female-biased dispersal distance in this species. Similarly, although males are larger and heavier, males did not appear to be more engaged in territory defence than females (as is, for example, the case in some migratory species where males arrive earlier at the breeding ground to establish territories; Arlt and Pärt 2008), leaving the ‘resource-holding potential hypothesis’ unlikely as a direct explanation for our results. The latter is also confirmed by observations that, after the disappearance of a breeding male, females are capable of holding the territory until she pairs with a new male (median duration until the male vacancy was filled in an experimental removal of breeding males was 2 days; Eikenaar et al. 2009). Thus, overall, these results suggest that differences in reproductive benefits for philopatric individuals and resource-holding potential cannot explain sex-biased dispersal distance in Seychelles warblers.

A previous study suggested that inbreeding avoidance may underlie sex-biased natal dispersal in Seychelles warblers (Eikenaar et al. 2008). Based on considerable levels of extra-pair paternity in this species (~40% of offspring; Richardson et al. 2001), Eikenaar et al. (2008) hypothesized that females might generally disperse further than males because females who pair with local individuals risk pairing incestuously with their extra-pair father. Although females are indeed less likely to disperse to territories in the close vicinity (Fig. 1a), our investigation of relatedness of breeding pairs in relation to dispersal distance does not support this hypothesis. First, females pairing with a male within one or two territories of their natal territory were not more related to that partner than either subordinate males pairing with a female within a similar distance or females dispersing over a larger distances (Fig. 1b), as would be expected if females had a high likelihood of pairing with an extra-pair father. Second, although territory inheritance did frequently result in incestuous pairs (see above), the distance that females and males dispersed did not predict the relatedness of the resulting breeding pair, suggesting that inbreeding-avoidance does not underlie sex-biased dispersal distance in this species.

Costly dispersal

Our finding of lower mortality of female floaters compared to male floaters suggests that females may be more tolerated than males outside their resident territory. These differences in the costs of searching for an independent breeding territory may underlie the lower rate of prospecting by male subordinate Seychelles warblers than females, resulting in a shorter ultimate dispersal distance. The survival costs of prospecting did not differ between the sexes, but this may well be explained by prospecting individuals being able to return to their resident territory after an unsuccessful prospecting trip, thereby obtaining the benefits of philopatry like nepotistic benefits facilitating access to food (Kingma et al. 2016b). Nonetheless, several findings suggest that extra-territorial movement is more costly for male than for female Seychelles warbles. First, males experienced a higher mortality cost of floating than females (Fig. 2). Differential costs of floating are generally difficult to tease apart from variation in quality of individuals that leave (i.e. floaters may have been of poorer quality). However, that subordinate male Seychelles warblers search for vacancies (by means of prospecting) less often than females, is in line with males being reluctant to leave voluntarily because of relatively high costs. Second, Eikenaar et al. (2008a) found that males, but not females, in more densely-populated areas dispersed less far (independent of territory quality), which may suggest that dispersal by males in dense areas is more costly, perhaps because intruders are detected faster in denser areas resulting in an increasing number of attacks. Third, in line with reduced prospecting (and the resulting restriction to being able to only fill nearby vacancies), males were shown to obtain a breeding position on average at an older age than females (Eikenaar et al. 2009). While we can rule out predation (predation of adults is absent in this species), the exact mechanism for higher costs of dispersal for males is unknown so far. Although statistically not significant (perhaps due to limited sample size) our finding that foraying male subordinates were nearly twice as likely to be caught with an individual resident in the intruded territory may indicate that males are attacked more often than females. Perhaps males pose a greater threat to parentage of territory owners (e.g. due to extra-pair mating) but females are equally involved in territory defence and such sex-biased costs would only manifest during a brief period when individuals initiate breeding. Thus, the underlying mechanism for sex-biased dispersal costs, and also to what extent these costs apply in species where the habitat is not saturated, is an interesting topic for further investigation. Ultimately, however, our results suggest that the fact that males often disperse only one or two territories can be explained by the relatively high costs of extra-territorial movement driving males to wait for local opportunities to disperse. Thus, asymmetry in costs of dispersal may explain sex-biased dispersal distance in this, and possibly other species (see also Perrin and Mazalov 2000; Gros et al. 2008; Pakanen et al. 2016).

Conclusions

We conclude that sex-biased dispersal distance in Seychelles warblers is unlikely to support the currently often invoked hypotheses (see Table 1). Female-biased dispersal distance does not seem to be explained by inbreeding-avoidance and differences in reproductive benefits of philopatry and resource-holding potential. Instead, our data suggest that dispersal attempts are more costly for males than for females. This may explain why selection favours reduced male subordinate extra-territorial movement required to find a breeding vacancy, which in turn likely leads to reduced dispersal distances and later acquisition of a breeding position (Eikenaar et al. 2009). This additional mechanistic explanation may not only shed light on sex-biased dispersal in family-living and cooperatively breeding species, but costs associated with searching for an independent breeding position may potentially also play a role in dispersal strategies in non-social species.

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FIGURE LEGENDS

Figure 1. (a) Dispersal distance (minimum number of territories traversed between an individual's natal territory and the territory where they obtained a breeding position) of female (black bars) and male (grey bars) Seychelles warblers, and (b) the mean (±SE) relatedness of the ultimate breeding pairs in relation to the focal individual's dispersal distance. Numbers reflect number of individuals. Females dispersed on average further than males ($\beta = 0.604 \pm 0.061$, $z = 9.95$, $P < 0.001$). However, dispersal distance did not predict relatedness to the obtained partner for both females and males, other than that inheriting individuals (dispersal distance 0) obtained a more related partner than dispersing individuals.

Figure 2. The likelihood that prospecting and floating Seychelles warbler females (black bars) and males (grey bars) died before the subsequent season. Whereas there was no significant difference between prospecting males and females (Fisher exact test: $P = 1.00$), male floaters were more likely to die than female floaters (Fisher exact test: $P = 0.03$).

TABLES

Table 1. An overview of the concepts of the main hypotheses of sex-biased dispersal in cooperatively breeding birds. A set of predictions was developed to test whether these hypotheses explain female-biased natal dispersal distance in Seychelles warblers. Whether these predictions are met is stated in the final column.

Hypothesis	**Concept**	**Prediction in Seychelles warblers (female-biased dispersal)**	**Prediction met?**
Inbreeding avoidance	Dispersal leads to less related partner	Further dispersal leads to a less related partner	No (Fig. 1b)
		Females who disperse to nearby territories have a higher likelihood engage in an incestuous relationship (with extra-group father) than females who disperse further	No, locally dispersing females did not obtain a more related partner than far-distance dispersing females (Fig. 1b, Table 2c) No, relatedness between short-distance dispersers and their obtained partner was not different between males and females (Fig. 1b, Table 2d)
Resource-holding potential	Territory establishment and defence biased to one sex	Males are larger and heavier than females	Yes, males are 6% larger and 10% heavier
		Females defend less than males	No, females defend equally
Reproductive benefits of philopatry	Sex-biased dispersal driven by sex differences in ability to reproduce as subordinate	Subordinate males reproduce more than subordinate females	No, females reproduce more[1]
	Sex-biased dispersal driven by differences in chance of territory inheritance	Males are more likely to inherit the territory than females	No, equal likelihood (43 vs 41%), and only 9% of positions are inherited
		Inheritance improves chance of incest differently between males and females	No, although inheritance improves the chance of incestuous pairing, this was not different between males and females (Table 1b)
		Mothers accept sons as partner more than fathers accept daughters [2]	No, likelihood is equal (35% vs 26%)
		Males expel females after they inherit	No, only 4 of 16 incestuous pairs ended in divorce: in 2 of these the female left, and in 2 cases the male left
Costly dispersal	Costs of dispersal or floating are sex-specific	Sex-bias in reproductive threat of floaters for territory owners	Yes, extra-pair paternity occurs, but no egg-dumping, so that males are more of a threat[1]
		Males are attacked more in foreign territories than females	Maybe: male forayers are attacked twice as much but not significant (limited statistical power)
		Floating males are more likely to die than floating females	Yes, male floaters are 3.5 times as likely to die than female floaters (Fig. 2)

[1] 44% of subordinate females lay an egg, but only 1 of 55 young was sired by a subordinate male (Richardson et al. 2001). [2] In species with extra-group mating, the risk of engaging in an incestuous pair after territory inheritance is larger for males than for females, predicting male-biased dispersal. However, since dispersal distance was female-biased in Seychelles warblers, we did not include that hypothesis here.

Table 2. The effect of sex and/or dispersal distance on relatedness of Seychelles warbler pairs, when the focal subordinate (a) dispersed, (b) inherited or not, (c) dispersed long vs short distance (females only) and (d) dispersed a short distance.

		β	SE	*t*	*P*
a) Relatedness (non-inheriting pairs)	*Intercept*	0.020	0.011	1.82	0.07
(385 individuals, 118 territories)	Dispersal distance	0.0004	0.004	0.10	0.92
	Sex	0.020	0.022	0.90	0.37
	Dispersal distance * sex	0.001	0.009	0.17	0.87
b) Relatedness (inheritance vs. dispersal)	*Intercept*	0.020	0.011	1.81	0.07
(426 individuals, 120 territories)	Inherited	0.201	0.036	5.67	**< 0.001**
	Sex	0.019	0.021	0.91	0.36
	Inherited * sex	-0.001	0.072	-0.01	0.99
c) Relatedness (females only)	*Intercept*	0.002	0.019	0.11	0.91
(191 individuals, 86 territories)	Dispersal distance (short vs long)	0.027	0.037	0.72	0.47
d) Relatedness (only short distance)	*Intercept*	0.033	0.016	2.02	**0.045**
(176 individuals, 92 territories)	Sex	0.005	0.037	0.13	0.89

FIGURES

Figure 1.

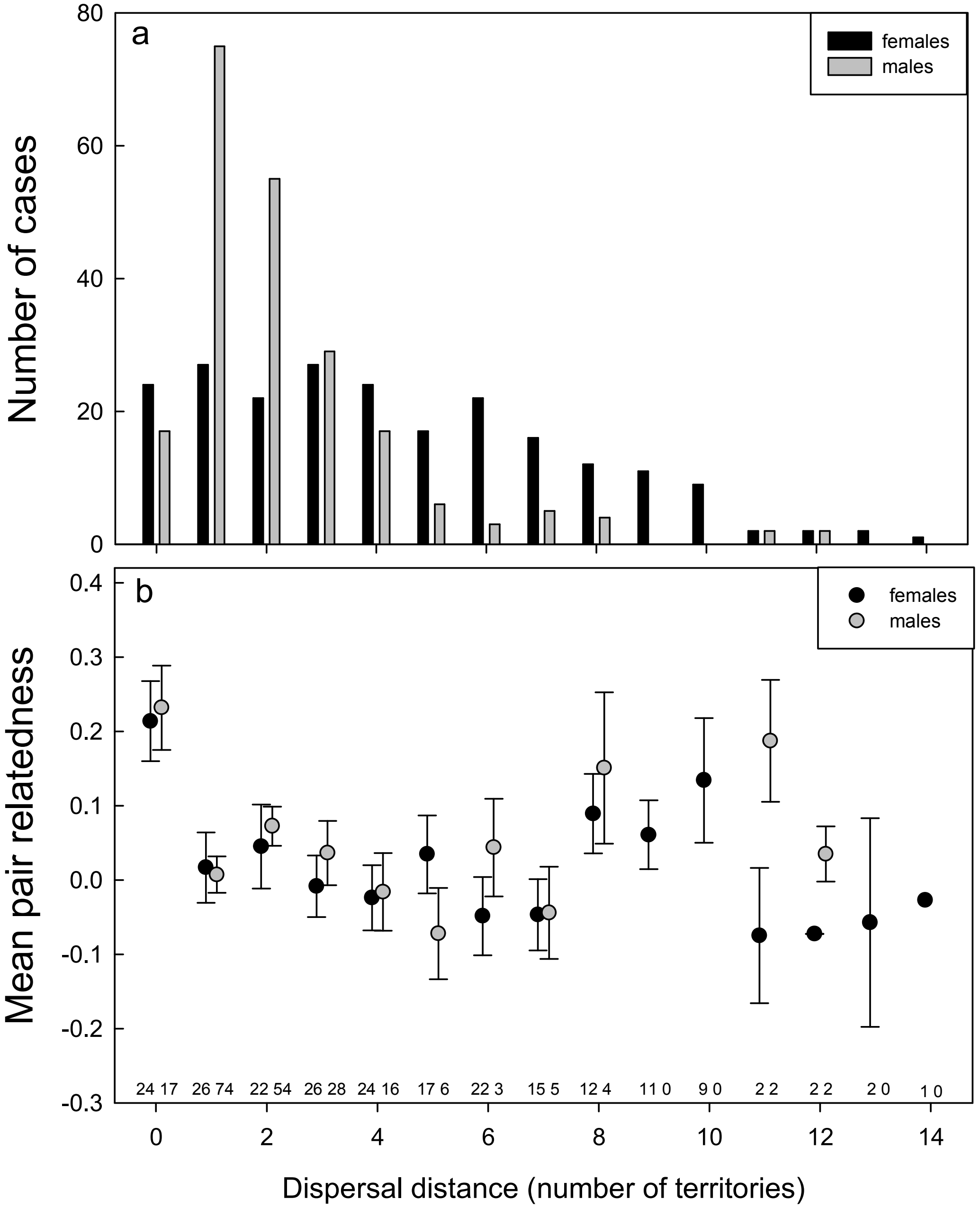
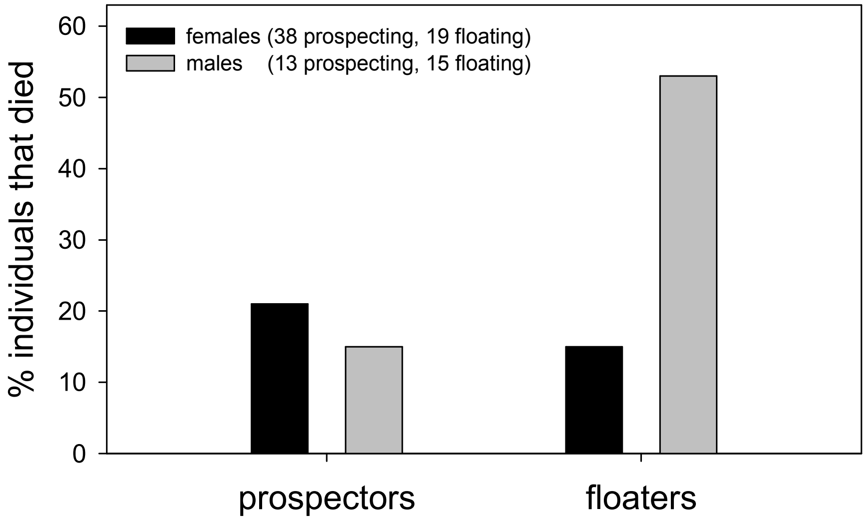


Figure 2.


60
50
40
30
20
10
0
% individuals that died
females (38 prospecting, 19 floating)
males (13 prospecting, 15 floating)
prospectors
floaters