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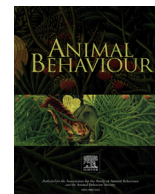
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## Implications of adult sex ratios for natal dispersal in a cooperative breeder

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In cooperatively breeding species, sexually mature individuals may delay natal dispersal and become subordinates, helping a dominant pair raise offspring. To understand how cooperative breeding evolved, it is important to determine the mechanisms leading to delayed dispersal. Adult sex ratio (ASR) variation may affect dispersal by limiting breeding vacancies available to the more abundant sex, and cooperative breeders often have a more biased ASR than noncooperative breeders. However, no studies of cooperative breeders have related ASR at both the local and population level with dispersal. Using the long-term Seychelles warbler, *Acrocephalus sechellensis*, data set, we tested the influence of population-wide and local ASR, and density, on natal dispersal of yearlings. Our ASR - density hypothesis predicts that the probability of natal dispersal is lower when the ASR is biased towards the sex of the focal individual, but only when the population density is high. Dispersal was associated with population density and population-wide ASR in males, but not in females; males were more likely to delay dispersal when ASR was male biased and density was high. Our findings illustrate a complex association between demographic factors and cooperative breeding and suggest that individuals alter their dispersal behaviour in response to the demographic composition of the population.

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Many social animals live and reproduce in stable groups. Cooperative breeding, although once considered a rare phenomenon (Brown 1987; Emlen, 1982), is commonly observed across taxa (Choe and Crespi 1997; Cockburn, 2006; Lukas & Clutton-Brock, 2012; Solomon & French, 1997; Taborsky, 1994). It is often characterized by a dominant breeding pair being assisted by nonbreeding, sexually mature subordinates that provide offspring care (Cockburn, 1998). Delayed dispersal, whereby offspring remain in the natal territory after they reach sexual maturity is a common route to cooperative breeding (Ekman et al., 2004; Griesser et al., 2017; Kingma et al., 2021; Koenig et al., 1992). A central question in the study of cooperative breeding is which circumstances drive such philopatric

individuals to delay dispersal instead of leaving to breed independently (Ekman et al., 2004; García-Ruiz et al., 2022; Hatchwell, 2009; Koenig et al., 1992; Wiley & Rabenold, 1984).

The adult sex ratio (ASR, the proportion of adults that are male) is a major potential determinant of the costs and benefits of dispersal, since the scarcity of one sex directly influences the availability of potential mates for the other sex (Brown 1987; Hatchwell & Komdeur, 2000). ASR can strongly influence life history trajectories and vice versa (Székely et al., 2014). A meta-analysis found that ASRs are more biased in cooperatively breeding species compared to noncooperatively breeding species, and that within cooperatively breeding species ASR is positively associated with helper sex ratio (Komdeur et al. 2017b). If dispersal is associated with higher mortality than helping, sex-biased dispersal and helping behaviour could result in consistent biases in ASR. Alternatively, population ASR may influence dispersal

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propensity and can lead to an increase in group formation and be a pathway to cooperative breeding behaviour, although the direction of causality is unclear. For instance, if the ASR is male biased, males will have more difficulty finding independent breeding vacancies, and therefore may benefit by staying in the natal territory. This effect can act both on the local social neighbourhood and at the population level within species. At the population level, ASR may affect direct costs and benefits of dispersal, whereas at the local level, ASR could provide a proxy of direct social information on the number of adult males and females that individuals have access to when deciding whether to disperse from their natal territory. Additionally, ASR is an important demographic driver of interspecific and intraspecific behavioural variability across the sexes (Jennoins & Kokko, 2010; Liker et al., 2013; McNamara et al., 2000; Rosa et al., 2017; Zheng et al., 2021). Dispersing individuals are often, but not always, changing their status from subordinate to dominant breeder (Groenewoud et al., 2018; Jungwirth et al., 2023; Kutsukake & Clutton-Brock, 2007; Nelson-Flower et al., 2011), meaning availability of mates often dictates the opportunities for successful dispersal. Males are less likely to search for additional female mates and increase parental care when the ASR is male biased compared to when it is female biased (Eberhart-Phillips et al., 2018; Fromhage & Jennions, 2016). This suggests that ASR may also be an important driver of social behaviours that could lead to cooperative breeding. The effect of ASR on cooperative breeding has mainly been observed in between-species comparisons, whereas within species different mechanisms may be at play (Komdeur et al. 2017b; but see Curry & Grant, 1989; Pruett-Jones & Lewis, 1990). One study, which explored cooperative breeding and manipulated local ASR in brown-headed nuthatches, *Sitta pusilla*, found that males postpone breeding because of a shortage of available mates (Cox et al., 2019; Kingma & Székely, 2019).

Most studies do not account for an accurate assessment of ASR and density for entire populations, usually because of a combination of migration and difficulty in tracking individuals. Consequently, it is difficult to assess the impact of demographic effects such as ASRs in wild populations. Moreover, studies often assume biases in ASR to be a consequence of sex differences in dispersal (i.e. a sex bias in dispersal costs driving a bias in ASR), rather than as a driving mechanism of dispersal (i.e. ASR bias limits breeding opportunities leading to different dispersal decisions in the two sexes; Pen & Weissing, 2000; Leturque & Rousset, 2004; Wild & Taylor, 2004; Gros et al., 2008). Therefore, to assess whether and to what extent ASR drives sex-biased dispersal, it is of key importance to measure ASR just prior to dispersal and to monitor its effect on dispersal propensity, instead of measuring ASR during or after dispersal.

Population density can also influence the strength of evolutionary drivers of cooperative breeding, for example through the degree of habitat saturation and number of sexual partners in a population (Brown 1987; Pen & Weissing, 2000). ASR often covaries with population density (Donald, 2007; Kokko & Rankin, 2006), and population density can potentially alter the ASR-dependent change in natal dispersal propensity. For example, the direction and magnitude of the effect of ASR on dispersal costs and benefits may vary over different population densities, as this indicates the potential availability of breeding partners as well as the level of competition for breeding vacancies (Kokko & Rankin, 2006). This makes it important to include both parameters when studying the demographic drivers of cooperative breeding. However, we are not aware of previous studies on cooperatively breeding species that have investigated the combined effects of density and ASR on dispersal.

Here, we investigated the importance of local and population-wide ASR, and how these interact with density, for dispersal in a

species with facultatively cooperative breeding. We determined which parameters influence the dispersal probability of juveniles (see Table 1 for details) in the Seychelles warbler, *Acrocephalus sechellensis*. This system provides an excellent model for this question since the species is a facultative cooperative breeder, meaning breeders are not fully dependent on always having helping subordinates in their territory. Dominant Seychelles warblers increase their reproductive output when helpers are present (Komdeur, 1994), while subordinates gain survival benefits from staying in the natal territory as well as direct (Richardson et al., 2002) and indirect (Komdeur, 1992) reproductive benefits. Most dispersals happen within the first 2 years of life (Eikenaar et al., 2008). The Cousin Island study population is contained, and dispersal off the island is extremely rare (ca. 0.1%, Komdeur et al., 2004), almost all individuals (>96%) are individually colour ringed (Hammers et al., 2019; Komdeur, 1992) and resighting rates are high (Brouwer et al., 2009); thus, dispersal and mortality are not confounded in this species. The whole population has been continuously monitored since 1985, with data being most complete from 1995 onwards, and we have accurate measures of population ASR and density for 25 years. Moreover, the data set includes individual life histories, individual environmental and social conditions and biannual assessment of dispersal of all individuals. The population is largely saturated, meaning competition for breeding vacancies is high (Komdeur & Pels, 2005). Although a negative association between dispersal probability and population density has been reported in the Seychelles warbler (Eikenaar et al., 2007), how ASR affects natal dispersal and whether density affects the slope and direction of this relationship have not yet been investigated. Here, we focused on ASR rather than OSR (operational sex ratio, proportion of sexually active individuals that are male), since we were specifically interested in the potential frequency-dependent aspects of sexual selection and intrasexual competition on individual behaviour. ASR is a product of demographic processes (therefore includes nonreproducing subordinates) whereas OSR is influenced by reproductive decisions of individuals (Székely et al., 2014). Moreover, ASR strongly predicts mating systems (Székely et al., 2014), parental investment (Fromhage & Jennions, 2016) and sex roles (Gonzalez-Voyer et al., 2022; Kokko & Jennions, 2008; Liker et al., 2013). Therefore, OSR bias emerges as a consequence of sex-biased behaviour (e.g. dispersal to independent breeding) rather than being a driver of sex-biased behaviour (Komdeur et al. 2017b; Long et al., 2022; Székely et al., 2014). In socially monogamous mating systems, OSR is expected to emerge from ASR through monogamous pair bonds, whereas for polygamous species OSR is largely dependent on the rate of mate monopolization and parental care that can be sex biased (Carmona-Isonza et al., 2017; Székely et al., 2014). Seychelles warblers often pair for life, meaning there is hardly any mate acquisition during breeding (Edwards et al., 2018; Komdeur, 1991). Thus, the cooperatively breeding and socially monogamous Seychelles warbler provides an excellent opportunity to assess the interplay between ASR variation and dispersal propensity. We assessed the effect of ASR during the breeding season before potential dispersal because this can provide insights into whether variation in ASR predicts subsequent individual dispersal decisions. As inheriting a natal territory is extremely rare in the Seychelles warbler (8% of individuals), acquiring a dominant breeding position happens primarily through dispersal (Kingma et al. 2016a). Thereby, dispersal propensity is likely to be strongly driven by intrasexual competition for breeding vacancies. Since we expected yearling males and females to explore their local neighbourhood more intensively than the entire population and might use this as a proxy for demographic information on the population (Eikenaar et al., 2008), we assessed the effects of ASR on dispersal at both a local (neighbouring territory level) and population level. Our

ASR - density hypothesis predicts an interacting effect of ASR and density on natal dispersal: specifically, with an ASR that is biased towards the focal individuals' own sex and with high population density, the focal individual is predicted to delay dispersal, since under these conditions we expect competition for residency and breeding positions in territories to be very high, thereby increasing costs of dispersal. Likewise, when the focal individual is a member of the rarer sex but the density is high, we expect dispersal propensity to be higher as there will be more breeding opportunities elsewhere. We expect this effect will decrease or disappear when ASR is less biased and/or the density is low, since the competition for residency will be lower. The effect of ASR and density on dispersal is predicted to be less pronounced in subordinate females than in subordinate males, since subordinate females often produce offspring within their territory through co-breeding with the dominant female when they delay dispersal, whereas subordinate males rarely gain parentage as a subordinate (Groenewoud et al., 2018; Richardson et al., 2001, 2002). This study provides novel insights on the combined effects of ASR and population density on natal dispersal in cooperative breeders.

## METHODS

### Study Population and Data Collection

The Seychelles warbler is a small insectivorous passerine endemic to the Seychelles archipelago. The population on Cousin island (29 ha, 04°20'S, 55°40'E) consists of ca. 320 birds in ca. 110 territories, which are maintained year round (Brouwer et al., 2009; Hammers et al., 2019; Komdeur, 1992). In each year as many Seychelles warblers as possible are caught/recaught using mist nets to ring birds and take morphometric measures (including tarsus length  $\pm 0.5$  mm as a measure of skeletal size) and collect DNA (using ca. 25  $\mu$ l blood taken from the brachial vein) to determine sex using up to three sexing markers (following Richardson et al., 2001). We used data from 1995 to 2019, since >96% of the population had been ringed with a unique metal and colour ring during this period (Hammers et al., 2019; Komdeur, 1992). Breeding occurs during the main breeding season (May–September) in the period when food availability is highest (breeding occurs in 94% of territories in this period), although individuals in 18% of territories breed during a minor breeding season (January–March; Komdeur

& Daan, 2005). The number of yearlings assessed for dispersal ranged between one and 28 individuals per breeding season. Seychelles warblers are facultative cooperative breeders, with approximately 50% of breeding pairs being accompanied by up to four subordinates (average  $\pm$  SE =  $0.7 \pm 0.02$ ) of either sex, which are often retained offspring from previous breeding attempts (Kingma et al. 2016a). Remaining subordinates of either sex can become helpers, but most helpers are female (88%; Komdeur, 1996, p. 68%; Richardson et al., 2002). Dispersal likelihood is not sex biased (although females disperse further than males), nor is likelihood of becoming a dominant breeder after dispersal (Groenewoud et al., 2018). However, females are much more likely to become non-natal subordinates whereas males are more likely to become floaters (dispersing individuals that are not part of a group). Breeding attempts usually consist of a single egg (91%; Richardson et al., 2002). After hatching, fledglings are fed for up to 3 months until independence (Komdeur, 1994). Postfledging survival in the first year is  $0.61 \pm 0.09$  SE, and increases to  $0.81 \pm 0.04$  in adulthood (i.e. 1 year of age; Brouwer et al., 2006). There is no sex difference in annual survival likelihood of adults (Brouwer et al., 2006). Adults that acquire a dominant breeding position usually defend their territory and remain with the same partner until death (Richardson et al., 2007). Therefore, territory boundaries are relatively stable between years (Komdeur, 1991).

In each breeding season, every territory was monitored regularly throughout the breeding season to determine group membership and social status by assessing an individual's presence for 15 min and antagonistic and affiliative interactions with conspecifics (Kingma et al. 2016b; Richardson et al., 2002). Dominant breeders were identified mainly via pair and courtship behaviour and mate guarding. Sexually mature individuals within a breeding group that were not dominant breeders were classified as subordinates. In territories with nests, 1 h watches were performed to verify residency and social status of individuals by assessing their incubation and feeding behaviour (Van de Crommenacker et al., 2011). Since interisland dispersal is extremely rare (<0.1%; Komdeur et al., 2004) and annual resighting probabilities are extremely high in the study population (Brouwer et al., 2010), individuals that are not resighted in two consecutive breeding seasons could be assumed to be dead. As Seychelles warblers mainly feed on insects on leaves and lack natural predators, an index of territory quality was calculated using insect prey abundance. Every

**Table 1**

Parameters of interest, the predictions on their relationship with dispersal probability of yearling Seychelles warblers, and whether these predictions were met in the present study

Parameter	Predicted effect on dispersal probability	Prediction met?
Population ASR	Stronger population sex bias leads to decreased dispersal by the more abundant sex, due to lack of breeding opportunities	Males: yes (Table 2, Fig. 1a) Females: no
Local ASR	Stronger local sex bias leads to decreased dispersal by the more abundant sex, due to apparent lack of breeding opportunities	No
Population density	A more pronounced effect of population ASR when population is close to saturation, due to more pronounced lack of breeding opportunities	Males: yes (Table 2, Fig. 1a) Females: no
Local density	A more pronounced effect of local ASR when local group is (close to) being saturated, due to more pronounced lack of breeding opportunities	No
Territory quality	A higher natal territory quality will reduce dispersal probability	No
Natal territory composition	If same-sex (and for females similar aged) subordinates are present, dispersal probability increases due to local competition	No
Body size (tarsus length)	Increase in dispersal probability, since larger individuals can afford the costs of dispersal better	No

ASR: adult sex ratio.



breeding season, the numbers of insects on the underside of leaves (where Seychelles warblers forage) were counted, and foliage cover and species abundance measured. Next, mean monthly insect density was calculated per territory, corrected for the plant species present (for a detailed description of the territory quality calculations, see Brouwer et al., 2009; Komdeur, 1992). We excluded two field seasons in 2004 and 2011 because 58 and 59 birds, respectively, were translocated to another island just before the breeding season as part of a conservation programme (Richardson et al., 2006; Wright et al., 2014).

#### ASR and Density

ASR and density were measured at the population level and at the local level. 'Population ASR' was calculated as the proportion of adult individuals sighted in the population during a field season that were male, with 0.5 indicating an equal number of adult males and females. Population size was used as a measure of 'population density', since the number of territories was almost constant over time. 'Local ASR' and 'local density' were assessed using all resident individuals from territories located within two territory borders away from the home territory of the focal individual in all directions during a field season. We defined local groups as such since males disperse up to two territories away from their home territory more often than females which typically disperse further from their natal territory (56% and 33%, respectively; Eikenaar et al., 2008). Additionally, most extragroup fathers (59% of paternities) are resident dominant males within two territories of the focal offspring's territory (Richardson et al., 2001), meaning that short- and long-distance dispersal likely have different costs and benefits associated with them (Kingma et al., 2017). Since there is nearly no migration off the island (Komdeur et al., 2004), ASR and density are dependent on recruitment and death of adult individuals. We expected the variability in ASR and density to be small on fine temporal scales, meaning seasonal demographic measurements of the breeding season prior to dispersal will capture a close estimate of the measures during the moment individuals decide whether to disperse. We classified natal dispersal as establishment (i.e. consistently seen in the territory during weekly checks throughout the breeding season) in a territory other than the natal territory. Individuals rarely visit other territories, as they are attacked by the territory owners when doing so (Kingma et al. 2016b). Natal dispersal was determined for yearlings only (dispersal until 1 year of age) to exclude potential influences from previous potential dispersal events (i.e. if individuals 'choose' not to disperse before, they might be more/less likely to do so later) and age-dependent effects on dispersal. Only including yearlings also eliminates pseudoreplication due to the same individual being included repeatedly. Since most Seychelles warblers disperse from their natal territory as yearlings (Groenewoud et al., 2018), most natal dispersal events are still captured by our analyses. As we could not determine whether juveniles that did not survive to 1 year of age had attempted to disperse from their natal territory, we cannot directly infer the mortality of dispersing and thus the direct cost of dispersing per se.

#### Statistical Analysis

We separately assessed the natal dispersal probability of male ( $N = 145$ ) and female ( $N = 132$ ) yearlings, since we expected that ASR would affect male and female dispersal propensities in opposite directions. The data set included the following fixed effects: population and local ASR during the breeding season before potential yearling dispersal is tracked (between fledging and reaching 1 year of age), population density and local density, tarsus length,

(natal) territory quality, number of female subordinates (split into  $<2$  years and  $\geq 2$  years old, see below) and number of male subordinates on the natal territory (Table 1). Individuals can disperse when they are 3 months old, but the exact timing of dispersal could not be determined since the populations are only monitored in the breeding seasons. Thus, we assumed the ASR and density at time of dispersal to be that when individuals reached 1 year of age. Female subordinates were categorized as  $<2$  and  $\geq 2$  years old, since subordinates older than 2 were never observed to prospect away from their resident territory (Kingma et al. 2016a). Since male subordinates  $>2$  years old were very rare ( $N = 8$ , 3% of all natal territories) all male subordinates were pooled in the analysis. Tarsus length might affect dispersal probability (see Camacho et al., 2013) as it describes overall body size and serves as a proxy for physiological condition (e.g. telomere length; Bebbington et al., 2017; Spurgin et al., 2018; Brown et al., 2022) and might be correlated with social dominance (Vedder et al., 2010). Natal territory quality might affect dispersal probability, since yearlings can benefit more from staying in a high-quality territory than in a low-quality territory (Komdeur, 1992). Finally, territory group composition potentially affects dispersal; for example, more subordinates in the territory increases competition, especially if they are of the same sex as the focal individual, thereby increasing dispersal likelihood (Groenewoud et al., 2018). To account for pseudoreplication, we included the breeding season and breeding group (i.e. all individuals in a territory in a given field period) as random effects, since two yearlings can come from the same breeding group ( $N = 21$  individuals born in the same group in the same breeding season).

We used a model averaging approach in R (4.2.2; R Core Team, 2020), using global generalized mixed-effect models (GLMMs) containing all fixed effects. Global GLMMs were built with binomial error structure and a logit link function using the lme4 (1.1–23) package (Bates et al., 2015), with the 'Bobyqa' nonlinear optimization (Powell, 2009) to aid model convergence. Territory quality measures were log transformed to correct for the right skew in these data. All continuous variables were z-transformed (mean centred and scaled by one SD) over the entire observation period to facilitate interpretation and comparison of model coefficients. To assess whether there was an overall sex difference in ASR-dependent dispersal probability, we built a separate global GLMM including two three-way interactions between (1) sex, population ASR and population density and between (2) sex, local ASR and local density. However, we may not have sufficient power to model three-way interactions with the sample size of this study, especially for dispersal, a complex behaviour that may be driven by multiple factors that explain variance. Therefore, we tested the effect of population ASR and population density and local ASR and local density separately for each sex. The global model included interaction effects between population density and population ASR, as well as between local density and local ASR. Using the variance inflation factor (VIF) we found no substantial collinearity between fixed effects (all  $VIF \leq 3$ ). There was no correlation between population ASR and population density (Pearson correlation:  $r = 0.137$ ,  $t_{31} = 0.771$ ,  $P = 0.45$ ) and local ASR and local density (Pearson correlation:  $r = -0.006$ ,  $t_{252} = -0.087$ ,  $P = 0.93$ ), which allowed them to be included in the same model. From each global model, we built competing models based on all possible combinations of fixed effects and ranked these models by Akaike's information criterion corrected for small sample size (AICc) score (MuMIn package, 1.43.17; Bartoń, 2020). All models with  $\Delta AICc \leq 7$  were included in the top model set (Burnham et al., 2011). We reanalysed our top model set with a more conservative cutoff of  $\Delta AICc = 2$  and found our results to be consistent. We calculated conditional averaged estimates for each variable containing the natural

averages, i.e. model-weighted predictions for the variable of interest at the mean of all other parameters. We used natural averages rather than full averaged models since we were specifically interested in the effects of ASR and density on dispersal, and these could otherwise be masked by other covariates on the models (Grueber et al., 2011).

### Ethical Note

The research adhered to the ASAB/ABS Guidelines for ethical treatment of nonhuman animals in research. Fieldwork was conducted with the permission of the Seychelles Bureau of Standards and the Seychelles Ministry of Environment, Energy and Climate Change, and adhered with all local ethical guidelines and regulations. Nature Seychelles provided permission to work on Cousin Island.

## RESULTS

Over the 33 (main and minor) breeding seasons monitored in our study, the population density ranged between 267 and 369 individuals (mean  $\pm$  SD = 338  $\pm$  37; Fig. A1). Of all territories with fledglings that survived to 1 year of age for which we had access to all fixed-effect data ( $N_{\text{fledglings}} = 277$ ; Table 1), 57% contained subordinates (range 25–68% per year,  $N_{\text{territories}} = 146$ ), with one to four subordinates per territory. Population ASR was on average female biased (range 0.44–0.54; mean  $\pm$  SD = 0.48  $\pm$  0.03; Fig. A1) and deviated significantly from 0.5 (one-sample  $t$  test:  $t = -4.096$ ,  $N_{\text{seasons}} = 33$ ,  $P < 0.001$ ). Local ASR varied more widely but was still on average female biased (range 0.35–0.68; mean  $\pm$  SD = 0.48  $\pm$  0.05) and deviated significantly from 0.5 (one-sample  $t$  test:  $t = -5.450$ ,  $N_{\text{territories}} = 256$ ,  $P < 0.001$ ). Of all yearling warblers, 40% ( $N = 79$ ) of males and 41% ( $N = 73$ ) of females dispersed.

Natal dispersal of juvenile males was best described by an interaction between population ASR and population density (Table 2, Fig. 1a). This interaction indicates that in years with moderate to high population density male dispersal probability increased when the population ASR was more female biased, whereas in years with a lower population density (i.e. below the long term saturation level of the population) there was no effect of ASR on dispersal propensity (95% confidence interval, CI of the

mean ASR effect for the 33% lowest population densities overlaps zero). All other variables tested, including population ASR and population density separately, had 95% CIs overlapping zero, meaning they were not associated with male natal dispersal.

The probability of female juvenile natal dispersal was not associated with any of the variables in the model (Table A1, Fig. 1b, d). Finally, the top model set of natal dispersal probability for both sexes found no interaction between sex, ASR and density (neither at the local nor at the population level; Table A2). None of the models in the model set that included the interaction between sex, ASR and density showed a significant interaction, indicating that neither overall ASR nor density differed significantly in how they influence the dispersal propensity of either sex.

## DISCUSSION

Demographic composition may play a key role in explaining some of the considerable interspecific and intraspecific variation in dispersal behaviour observed in cooperative breeders. Our study revealed that population ASR and population density predicted the natal dispersal probability of male, but not female, yearlings in the Seychelles warbler. We found no evidence for a three-way interaction between ASR, density and sex in an analysis with both sexes combined, indicating that there is no significant sex difference in dispersal in relation to ASR and density. However, an analysis performed for both sexes separately showed that there was evidence for a density-dependent effect of ASR on dispersal in males, but not in females. The effect of ASR on male natal dispersal probability varied with population density, that is, the propensity of male yearlings to disperse in response to biases in ASR changed with respect to density. Specifically, males were more likely to disperse from their natal territory when the population ASR was female biased and the population density was moderate to high, but this effect disappeared when the population density became lower.

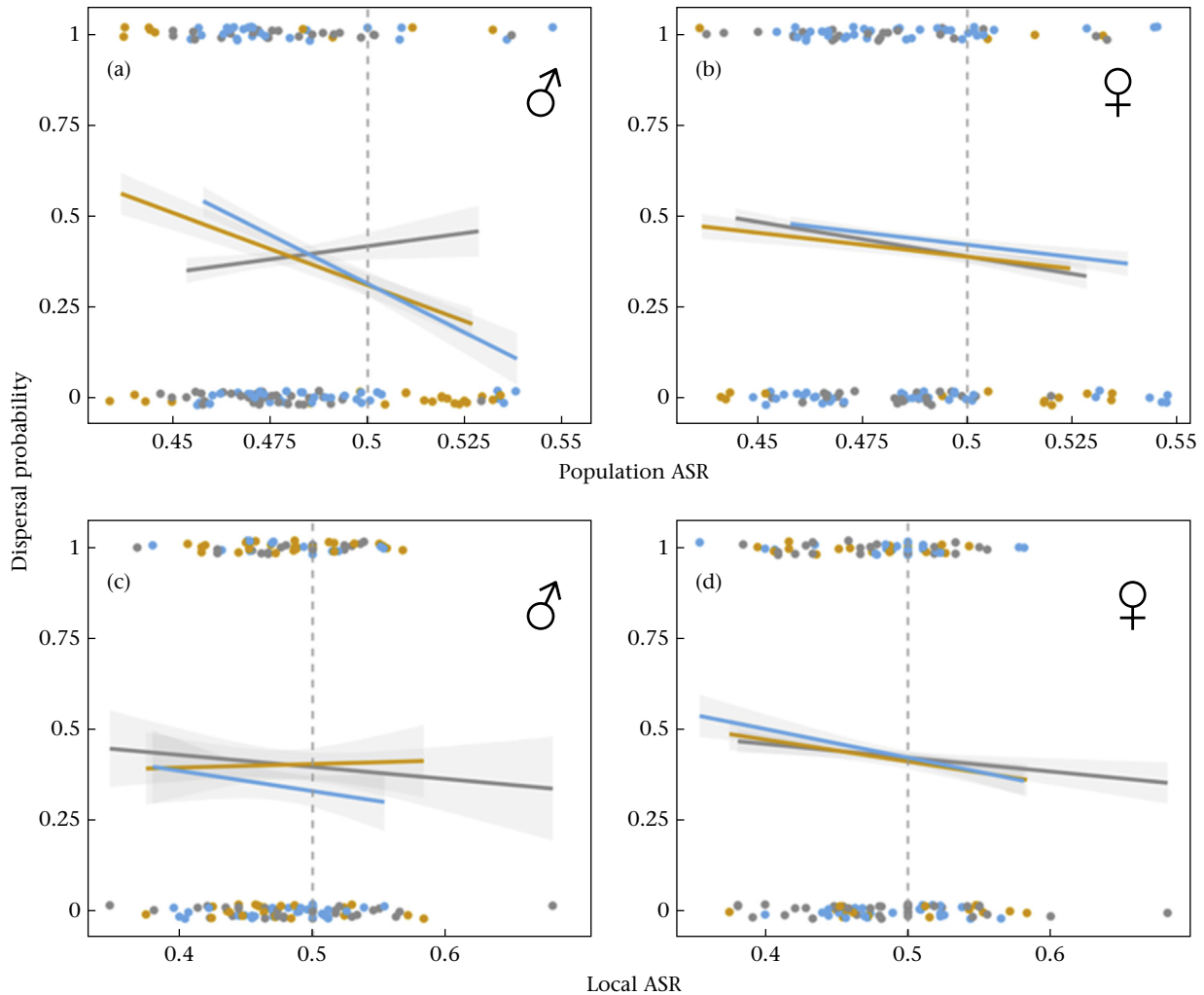
When there are more males in a population, the competition for a breeding vacancy for males will likely increase, independent of the mating system. Indeed, when ASR is male biased and population density is high, there is a high absolute number of males in the population, which may cause high dispersal costs in terms of increased competition among males for residency in a territory and

**Table 2**

Model-averaged parameters: the effect of socioecological predictors on the probability of dispersal in male Seychelles warblers until the age of 1 year

	$\beta$	SE	$z$	95% CI
<b>Fixed</b>				
(Intercept)	-0.48	0.24	1.97	-0.96, -0.001
Population ASR	-0.45	0.25	1.77	-0.94, 0.05
Local group density	-0.36	0.24	1.47	-0.84, 0.12
Population density	0.08	0.22	0.34	-0.36, 0.51
<b>Population ASR*Population density</b>	<b>-0.74</b>	<b>0.34</b>	<b>2.16</b>	<b>-1.41, -0.07</b>
Territory quality	0.29	0.22	1.29	-0.15, 0.72
Local ASR	0.28	0.24	1.14	-0.20, 0.76
Male subordinates	-0.21	0.23	0.87	-0.68, 0.26
Young female subordinates	-0.08	0.20	0.40	-0.48, 0.32
Old female subordinates	-0.06	0.20	0.27	-0.46, 0.35
Tarsus length	-0.01	0.24	0.06	-0.49, 0.46
Local ASR*Local group density	0.29	0.33	0.86	-0.37, 0.95
<b>Random</b>	$\sigma^2$	$N$		
Field period*Breeding group	0.687	139		
Field period	0	30		
<b>Response: juvenile male dispersal likelihood (<math>N = 145</math>)</b>				
Candidate models: 800. Top set models: 332				

ASR: adult sex ratio. Conditional model-averaged estimates ( $\beta$ ), standard errors (SE),  $z$  values, and 95% confidence intervals (CIs) are shown for all predictors featuring the top model set ( $\Delta\text{AICc} \leq 7$ ). Random effect variances ( $\sigma^2$ ) and number of levels ( $N$ ) in the best model are also shown. Significant predictors whose CIs do not overlap with zero are given in bold.



**Figure 1.** Dispersal probability of yearlings in relation to adult sex ratio (ASR) and density in the Seychelles warbler. (a, b) The interaction between population ASR and population density for (a) male and (b) female yearlings. (c, d) The interaction between local ASR and local density for (c) male and (d) female yearlings. For the sake of visualization, population ( $N = 33$ ) and local density ( $N = 256$ ) are categorized in even sample sizes as low (in grey, lowest 33%), middle (in orange, middle 33%) and high (in blue, highest 33%) but are used as continuous variables in the analyses. Lines depict the model-averaged predictions (see main text), with the 95% confidence interval (shaded area). Each point refers to one individual ( $N = 145$  males,  $N = 132$  females). The dashed line depicts an equal ASR. See Table 2 for statistical results.

for breeding positions. Therefore, a better strategy for male Seychelles warbler yearlings may be to delay dispersal and remain in a territory either to inherit it (although this is very rare; Kingma et al. 2016a), bud off a part of the natal territory as their own breeding territory (Komdeur & Edelaar, 2001) or to wait for breeding vacancies as they become available in nearby territories (Kingma et al. 2016a). An alternative to staying is to disperse as a floater: roaming through the population without association with any territory (Groenewoud et al., 2018). However, this is a highly costly strategy as they cannot enjoy group-living benefits generally experienced by cooperative breeders (Koenig et al., 1992; Ridley et al., 2008). The survival of floaters is very low in Seychelles warblers, with only 9% of floaters surviving to the next breeding season compared to 67% of subordinates that are resident in a territory (Kingma et al. 2016a). Still, in scenarios with extremely high competition for breeding vacancies, floating might be a valuable strategy as floaters are more likely to detect potential breeding vacancies as they move freely through the population (Kokko & Sutherland, 1998). In breeding seasons with low population density, there is likely to be reduced overall competition, which makes dispersal less costly, independent of ASRs. Competition among males is likely to be lower even when ASR is still male biased, since

the population is not saturated, and males may be better able to find residency and perhaps even become a dominant breeder. Even in years with low population densities and a male-biased ASR, all breeding vacancies for the rarer sex (here, females) are usually filled. As this species is socially monogamous, this implies there is no shortage of potential partners per se, but rather a shortage of available territories. This result is congruent with recent findings indicating the relationship between dispersal and cooperation need not be straightforward, and dispersal in cooperative breeders is likely to be strongly influenced by intrasexual competition (Jungwirth et al., 2023). Dispersal propensity of cooperatively breeding species displays strong intrasexual variation (Trochet et al., 2016), which may be strongly dictated by demographic composition.

Contrary to our expectation, the relationship between population-wide ASR and density and male dispersal was not found for local ASR and density. One possible explanation may be that, due to the low frequency and stochastic nature at which breeding vacancies become available on the island, local ASR and density may be less informative for the availability of dispersal opportunities than population-wide ASR and density. Furthermore, population-wide rather than local effects of ASR and density on dispersal might

occur when dispersers have more opportunities to occupy breeding vacancies at the edge of the population than at the more central areas (e.g. due to lower breeder survival in these edge territories; Komdeur, 1992), although this possibility remains to be investigated. The finding that male dispersal was associated with population-wide ASR and density suggests that males may have access to information on the availability of breeding vacancies in the entire population. Most males disperse further than their neighbouring territory to a breeding position (57.2%, Kingma et al., 2017), and males prospect between three and six territories from their natal territory before dispersing during the breeding season (Kingma et al., 2017). Outside the breeding season, when warblers are likely to be more relaxed in terms of territory defence and antagonistic interactions, some males survey a considerable part of the population (Komdeur, 1991; Komdeur & Edelaar, 2001). Moreover, since individuals can face high fitness costs by being attacked by conspecifics during prospecting trips (Kingma et al. 2016a), they are often very inconspicuous to avoid antagonistic interactions (Komdeur, 1991), making it harder to detect them in the field which may lead to a bias in observing short-distance prospecting trips. Finally, selectively prospecting certain territories may increase the likelihood of successful dispersal even when prospecting is directed to territories further away, as was found in cooperatively breeding fish *Neolamprologus pulcher* (Jungwirth et al., 2015), although individuals in this species also prospect nearby territories (Bergmüller et al., 2005). When competition for breeding vacancies is expected to be high, prospecting larger areas (here, population rather than local neighbourhood) may provide strong benefits in likelihood of acquiring a breeding position, especially in highly saturated populations. Therefore, population-wide rather than local effects of demographics might be more informative when assessing dispersal in male Seychelles warblers.

We found no association between any tested variable and natal dispersal probability in females, which was expected since females are less dependent on becoming a dominant breeder to produce offspring since they can also become a co-breeder. However, we found no significant difference in the effect of ASR and density on dispersal propensity between males and females. This is consistent with previous work indicating there is no sex bias in natal dispersal in the Seychelles warbler (Groenewoud et al., 2018). Still, we suggest that the lack of an effect may be due to our limited sample size. The variance in population ASR is relatively small and mostly female biased. Therefore, it might not be possible to find a significant effect of ASR and density on female dispersal probability, as the effect in females is in any case expected to be small due to co-breeding opportunities, and we would mostly expect an effect in years with a male-biased ASR. Thus, finding a significant three-way interaction between sex, ASR and density would probably require more power; also, we expect other factors to have an influence on dispersal (variance that could be considered noise in our model). We expect our results on male dispersal to be important, but they should be considered with care, and we hope future research can consider this question as well for comparison.

Females can reproduce as a subordinate (natal and non-natal) by becoming a co-breeder, whereas males almost never gain paternity as a subordinate (Richardson et al., 2002). Co-breeding occurs frequently: ca. 30–40% of the subordinate females produce offspring in a given year (Richardson et al., 2001, 2002, 2003), totalling 11% of offspring being produced by subordinate females (Raj Pant et al., 2019). Subordinate reproduction is common among cooperatively breeding species but there is large intersex and interspecies variation in reproduction rates (Komdeur et al. 2017a), which may in turn affect how strongly ASR dictates intrasexual competition and dispersal propensity among different species. Dominant females also gain benefits from subordinate females in

their breeding territory: helping by female subordinates is associated with increased life span and delayed senescence of the dominants (Hammers et al., 2019). Finally, females can gain substantial inclusive fitness benefits through helping in their natal territory when the dominant breeders are their parents. Helper presence increases the reproductive success of their parents (Komdeur, 1994), and dominant females gain inclusive fitness benefits by allowing subordinates to breed; they increase their own reproductive success and gain indirect benefits from related subordinates producing offspring (Richardson et al., 2002). When parents are replaced by unrelated step-parents, subordinates are more likely to disperse from their natal territory, presumably since future indirect fitness benefits decrease (Eikenaar et al., 2007).

Individuals that disperse and become subordinates in non-natal groups are predominantly female (87%; Groenewoud et al., 2018). Female intruders are attacked less than males by conspecifics when venturing to new territories (Kingma et al., 2017), and therefore may be more likely to be accepted as a non-natal subordinate. Additionally, females may also gain parentage by co-breeding as a non-natal subordinate (Groenewoud et al., 2018; Richardson et al., 2002). Thus, females can still breed and disperse when dominant breeder vacancies are not readily available. Conversely, males rarely settle as non-natal subordinates (Groenewoud et al., 2018), and only very rarely gain paternity as a subordinate (Richardson et al., 2001, 2002; Sparks et al., 2021). Therefore, males are more limited in their options and highly dependent on the available breeding vacancies.

Since delayed dispersal is a route to cooperative breeding and group living (Ekman et al., 2004; Griesser et al., 2017; Kingma et al., 2021; Koenig et al., 1992), the association between dispersal probability, population density and adult sex bias has important implications. In a recent theoretical framework, García-Ruiz et al. (2022) showed that delayed dispersal as a pathway to cooperative breeding can be solely explained by group-living benefits, and the possibility of gaining a breeding position in the natal territory by queuing as a subordinate. However, in the Seychelles warbler, territory inheritance as a subordinate is rare (Kingma et al. 2016a), and intrasexual competition is likely to be a predominant mechanism behind delayed dispersal in this highly saturated population. Additionally, group size is negatively associated with adult survival in this species (Brouwer et al., 2006), suggesting that the main benefits of group living in this species are mostly driven by direct and indirect reproductive benefits (Komdeur, 2021). Our study therefore provides a rare empirical link between demographic drivers and routes to cooperative breeding. To our knowledge, this is the first study on dispersal in which ASR and density are considered on both a local and population level, since accurate measures of population density and ASR are extremely rare in the wild. Our study highlights the importance of taking sex-specific effects into account when studying the evolution of group living. We suggest including all adult individuals in the population in future studies assessing sex ratio effects (i.e. ASR) in socially monogamous species. By only including the sexually active individuals (operational sex ratio; OSR), it is impossible to isolate sex ratio as an external factor that predicts dispersal decisions since it may be both a cause and a consequence of dispersal. We assessed ASR and density seasonally, rather than individually at maturation, meaning there is some variability in the temporal distance between assessment of demographics and potential dispersal among individuals. A closer temporal proximity to the focal yearling's decision to disperse would allow for a more accurate assessment of the effect of ASR and density. However, ASR does not vary greatly among breeding seasons, meaning the noise introduced by the temporal variability is expected to be minimal. Additionally, since we cannot assess exactly when an individual decides to disperse in



response to the demographic composition, it is impossible to determine the precise moment ASR and density should be assessed. To elucidate the causal relationships between demographic factors and dispersal in cooperative breeders and identify the timeframe of information used for dispersing, it is necessary to experimentally manipulate population ASR and density. For example, dispersal propensity can be experimentally tested in response to temporarily removing individuals from a breeding territory, as was done by Heg et al. (2008). Future studies may experimentally manipulate population ASR and density to investigate the causal relationships between these factors and dispersal in cooperative breeders. We hope our analyses stimulate researchers to unravel how variation in ASR affects the fitness costs and benefits of dispersal.

### Author Contributions

**Speelman, F.J.D.:** Conceptualization, Formal analysis, Methodology, Writing – Original draft. **Borger, M.J.:** Conceptualization, Methodology, Writing – Review & editing, Investigation. **Hammers, M.:** Writing – Review & editing, Methodology, Investigation. **Van Eerden, A.O.K.:** Formal analysis, Investigation. **Richardson, D.S.:** Writing – Review & editing, Investigation, Project administration. **Burke, T.:** Methodology, Project administration. **Dugdale, H.L.:** Writing – Review & editing, Project administration. **Komdeur, J.:** Conceptualization, Supervision, Writing – Review & editing, Project administration.

### Data Availability

Data are available on the University of Groningen dryad, via the following link: <https://doi.org/10.34894/OXQ2PW>.

### Declaration of Interest

All authors declare no conflict of interest.

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## Appendix

Table A1

Model-averaged parameters: the effect of socioecological predictors on the likelihood of dispersal in female Seychelles warblers until the age of 1 year

	B	SE	z	95% CI
<b>Fixed</b>				
(Intercept)	-0.30	0.22	1.38	-0.74, 0.13
Population ASR	-0.27	0.21	1.28	-0.68, 0.13
Old female subordinates	-0.21	0.20	1.05	-0.61, 0.19
Territory quality	-0.17	0.17	1.00	-0.52, 0.17
Young female subordinates	0.16	0.19	0.82	-0.22, 0.53
Local group size	0.18	0.22	0.79	-0.26, 0.62
Local ASR	-0.12	0.20	0.60	-0.53, 0.28
Population size	-0.11	0.20	0.55	-0.52, 0.29
Tarsus length	-0.03	0.23	0.14	-0.48, 0.41
Male subordinates	0.05	0.17	0.31	-0.29, 0.39
Population ASR*Population size	0.06	0.24	0.23	-0.41, 0.52
Local ASR*Local group size	-0.05	0.24	0.19	-0.51, 0.42
<b>Random</b>	$\sigma^2$	N		
Breeding season*Breeding group	0	127		
Breeding season	0.45	30		
<b>Response: juvenile female dispersal likelihood (N = 132)</b>				
Candidate models: 800. Top set models: 287				

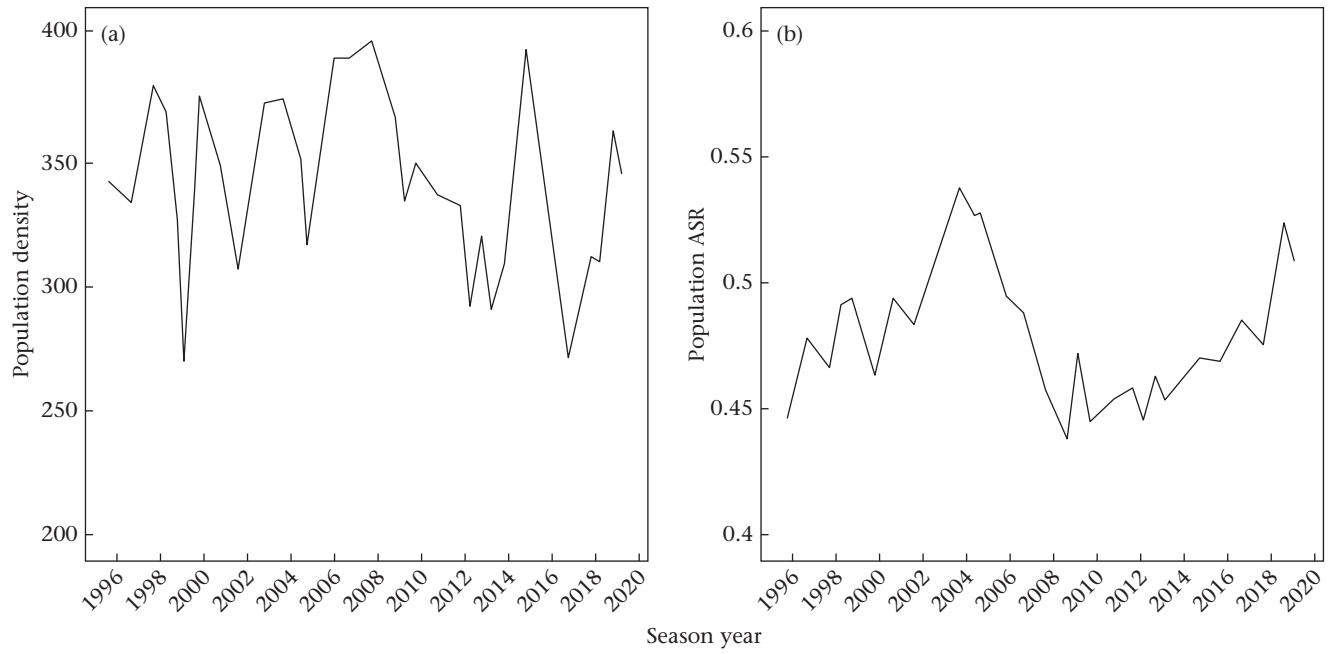
ASR: adult sex ratio. Conditional model-averaged estimates ( $\beta$ ), standard errors (SE), z values and 95% confidence intervals (CIs) are shown for all predictors featuring the top model set ( $\Delta AICc \leq 7$ ). Random effect variances ( $\sigma^2$ ) and number of observations (N) in the best model are also shown. All the predictors have a CI that overlaps with zero.

Table A2

Model-averaged parameters: the effect of socioecological predictors on the likelihood of dispersal in Seychelles warblers until the age of 1 year

	$\beta$	SE	z	95% CI
<b>Fixed</b>				
(Intercept)	-0.37	0.20	1.88	-0.76, 0.02
Population ASR	-0.29	0.17	1.69	-0.63, 0.05
Local group size	-0.06	0.24	0.23	-0.53, 0.42
Old female subordinates	-0.11	0.15	0.73	-0.40, 0.18
Local ASR	0.09	0.16	0.53	-0.24, 0.41
Sex (female)	-0.19	0.28	0.69	-0.73, 0.35
Tarsus length	-0.06	0.14	0.40	-0.33, 0.22
Young female subordinates	0.06	0.13	0.50	-0.18, 0.31
Population size	-0.01	0.17	0.06	-0.33, 0.31
Territory quality	0.01	0.13	0.09	-0.25, 0.28
Male subordinates	-0.01	0.13	0.04	-0.27, 0.25
Local group size*Sex (female)	-0.57	0.36	1.58	-1.27, 0.14
Population ASR*Population size	-0.19	0.20	0.98	-0.58, 0.20
Population ASR*Sex (female)	-0.09	0.28	0.31	-0.63, 0.46
Local ASR*Local group size	0.14	0.20	0.68	-0.26, 0.54
Local ASR*Sex (female)	0.24	0.27	0.89	-0.29, 0.76
Population size*Sex (female)	0.14	0.27	0.51	-0.39, 0.67
<b>Random</b>	$\sigma^2$	N		
Breeding season*Breeding group	0.32	133		
Breeding season	0.41	33		
<b>Response: juvenile dispersal likelihood (N = 277)</b>				
Candidate models: 7072. Top set models: 482				

ASR: adult sex ratio. Conditional model-averaged estimates ( $\beta$ ), standard errors (SE), z values and 95% confidence intervals (CIs) are shown for all predictors featuring the top model set ( $\Delta AICc \leq 7$ ). Random effect variances ( $\sigma^2$ ) and number of observations (N) in the best model are also shown. All the predictors have a CI that overlaps with zero.



**Figure A1.** Seasonal variability of (a) population density and (b) population adult sex ratio (ASR) of Seychelles warblers on Cousin Island between 1996 and 2020.