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RESEARCH ARTICLE

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Subordinate females in the cooperatively breeding Seychelles warbler obtain direct benefits by joining unrelated groups

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Abstract

1. In many cooperatively breeding animals, a combination of ecological constraints and benefits of philopatry favours offspring taking a subordinate position on the natal territory instead of dispersing to breed independently. However, in many species individuals disperse to a subordinate position in a non-natal group ("subordinate between-group" dispersal), despite losing the kin-selected and nepotistic benefits of remaining in the natal group. It is unclear which social, genetic and ecological factors drive between-group dispersal.
2. We aim to elucidate the adaptive significance of subordinate between-group dispersal by examining which factors promote such dispersal, whether subordinates gain improved ecological and social conditions by joining a non-natal group, and whether between-group dispersal results in increased lifetime reproductive success and survival.
3. Using a long-term dataset on the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*), we investigated how a suite of proximate factors (food availability, group composition, age and sex of focal individuals, population density) promote subordinate between-group dispersal by comparing such dispersers with subordinates that dispersed to a dominant position or became floaters. We then analysed whether subordinates that moved to a dominant or non-natal subordinate position, or became floaters, gained improved conditions relative to the natal territory and compared fitness components between the three dispersal strategies.
4. We show that individuals that joined another group as non-natal subordinates were mainly female and that, similar to floating, between-group dispersal was associated with social and demographic factors that constrained dispersal to an independent breeding position. Between-group dispersal was not driven by improved ecological or social conditions in the new territory and did not result in higher survival. Instead, between-group dispersing females often became co-breeders, obtaining maternity in the new territory, and were likely to inherit the territory in the future, leading to higher lifetime reproductive success compared to females that floated. Males never reproduced as subordinates, which may be one explanation why subordinate between-group dispersal by males is rare.

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5. Our results suggest that subordinate between-group dispersal is used by females to obtain reproductive benefits when options to disperse to an independent breeding position are limited. This provides important insight into the additional strategies that individuals can use to obtain reproductive benefits.

KEYWORDS
benefits of philopatry, communal breeding, cooperative breeding, joint nesting, natal dispersal, subordinate between-group dispersal

1 | INTRODUCTION

In many cooperatively breeding species, ecological conditions and low breeder turnover limit the possibilities of independent breeding, leading to intense competition for breeding vacancies ("ecological constraints hypothesis"; Emlen, 1982; Hatchwell & Komdeur, 2000). In addition, the benefits that individuals obtain by being in a group as subordinates can outweigh the benefits of leaving and breeding independently, even if breeding vacancies are available ("benefits of philopatry hypothesis"; Stacey & Ligon, 1991; Komdeur, 1992). Subordinates therefore often delay dispersal and help with raising the offspring of the breeding pair in the natal territory during future breeding attempts, until they can disperse to an independent breeding position (Hatchwell, 2009; Koenig & Dickinson, 2016; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992).

Subordinates may obtain important benefits by remaining in their natal territory and should only disperse when the benefits of dispersal outweigh the benefits of philopatry (Komdeur, 1992; Stacey & Ligon, 1991) and the costs associated with dispersal (Bonte et al., 2012; Heg, Bachar, Brouwer, & Taborsky, 2004; Johnson, Fryxell, Thompson, & Baker, 2009; Kingma, Komdeur, Hammers, & Richardson, 2016). Subordinates often benefit through access to food resources and protection from predators, thereby increasing survival or body condition (Heg et al., 2004; Ridley, Raihani, & Nelson-Flower, 2008). These effects can be further augmented by nepotistic benefits, where parents preferentially allocate protection or resources towards offspring (Dickinson, Euaparadorn, Greenwald, Mitra, & Shizuka, 2009; Ekman, Bylin, & Tegelström, 2000; Nelson-Flower & Ridley, 2016). Subordinates can also obtain indirect benefits by helping to rear related offspring (Briga, Pen, & Wright, 2012; Hamilton, 1964; Richardson, Komdeur, & Burke 2003), or direct reproductive benefits by gaining parentage within the territory (Richardson, Burke, & Komdeur, 2002). A high likelihood of inheriting the territory (Pen & Weissing, 2000), or "shifting" to a nearby vacancy (Kingma, Bebbington, Hammers, Richardson, & Komdeur, 2016; Kokko & Ekman, 2002) in the future might also select for philopatry.

Despite the benefits that can be obtained through natal philopatry, in many species subordinates disperse and accept a subordinate position in other, often unrelated, groups (henceforth: "subordinate between-group dispersal"; Reyer, 1982; James & Oliphant, 1986; Martín-Vivaldi, Martínez, Palomino, & Soler, 2002; Seddon et al., 2005; see also Riehl, 2013). As nepotism and kin-selected benefits are absent or minimal, investigating why subordinates move to non-natal groups can reveal important information about the social and environmental factors that drive both philopatry and dispersal. Subordinate between-group dispersal may be a best-of-a-bad-job strategy for subordinates forced, such as by eviction, to disperse from their natal territory. Eviction is common in cooperatively breeding systems and typically occurs when there are conflicting fitness interests between dominants and subordinates (Cant, Hodge, Bell, Gilchrist, & Nichols, 2010; Fischer, Zöttl, Groenewoud, & Taborsky, 2014). Subordinates who cannot control the timing of dispersal are likely to disperse under suboptimal conditions, and may become floaters (i.e., roaming through the population without association with any territory). Floaters lack access to group-defended resources and protection from predators, which can reduce survival and reproduction (Berg, 2005; Kingma, Bebbington, et al., 2016; Ridley et al., 2008). Joining an unrelated group as a subordinate could function to avoid such costs (e.g., Reyer, 1980; Ridley et al., 2008; Riehl, 2013). On the other hand, irrespective of the possibility of remaining in the natal territory, between-group dispersal could function to increase an individual's fitness prospects. For instance, the fitness prospects of subordinates may increase if between-group dispersal leads to increased access to food, breeding opportunities, or a shorter queue to inherit a territory (e.g., Nelson-Flower, Wiley, Flower, & Ridley, 2018).

Our aim was to elucidate the proximate drivers of subordinate between-group dispersal and its fitness consequences. We do this by comparing subordinate between-group dispersal with two other common dispersal strategies (floating, and direct dispersal to a dominant position) in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). Where previous studies on this species have emphasized the ecological and social correlates of philopatry *vs*. dispersal (Eikenaar, Richardson, Brouwer, & Komdeur, 2007; Kingma, Bebbington, et al., 2016), here we focus specifically on dispersing individuals. The majority of subordinate Seychelles warblers disperse from the natal territory at some point, even if they initially delay dispersal (Eikenaar et al., 2007; Kingma, Bebbington, et al., 2016). We thus provide a cross-sectional overview of the conditions under which dispersal occurs. Individuals should prefer to disperse to a dominant position over becoming a floater, because floating is costly in this species (Kingma, Komdeur, Burke, & Richardson, 2017). However, the proximate drivers and the fitness consequences of subordinate between-group dispersal relative to these strategies are unclear. First, we assess which social (group size, breeder replacement and population density), ecological (territory quality) and individual (sex and age) factors are associated with subordinate between-group dispersal. Second, we test whether subordinate between-group dispersers eventually inhabit a better territory than their own natal territory and better than individuals that floated or dispersed to a dominant position. Food availability, competition for breeding positions and the possibility of direct benefits are all important for survival and reproductive success in the Seychelles warbler (Brouwer, Richardson, Eikenaar, & Komdeur, 2006; Komdeur, 1992; Richardson et al., 2002) and should therefore affect dispersal decisions. Lastly, we test whether subordinate between-group dispersal ultimately leads to reproductive and survival benefits compared to dispersing to a dominant position, or floating. Together, our study provides valuable insights into the benefits of subordinate between-group dispersal that are independent of natal philopatry and kin-selected benefits and therefore contributes to understanding the drivers of sociality, dispersal and cooperation.

2 | MATERIALS AND METHODS

2.1 | Study species

The Seychelles warbler is a small insectivorous passerine endemic to the Seychelles archipelago in the Indian Ocean (Hammers et al., 2015; Komdeur, Dugdale, Burke, & Richardson, 2016). Data were collected on Cousin Island (29 ha, 04°20′S, 55°40′E) from 2002 to 2015. The Cousin Island population of Seychelles warbler fluctuates around 320 adult birds on 110–115 territories. Since 1997, ca. 96% of the adult population has been ringed in any given year, with each individual having a unique colour and metal ring combination (Hadfield, Richardson, & Burke, 2006; Hammers et al., 2015). Seychelles warblers are socially monogamous, but on Cousin, *ca* 50% of territories contain one to four subordinates (mean ± *SE* = 0.7 ± 0.02; 55% of subordinates are female) that are usually, but not always, retained offspring from previous breeding attempts (Kingma, Bebbington, et al., 2016). Territories are stable between years and territory boundaries are identified based on spacing behaviour and conflicts with intruding conspecifics (Komdeur, 1991). Two distinct breeding seasons occur: one major breeding season (June–September) and one minor breeding season (January–March; Komdeur & Daan, 2005). Clutches typically contain a single egg (91% of clutches) and many nests fail during incubation due to nest predation (Komdeur & Kats, 1999). We performed regular censuses throughout the breeding season to determine (1) group membership, based on where birds are consistently seen foraging and involved in nonantagonistic interactions with other resident birds, and (2) status in the group (dominant breeder or subordinate) based on mate guarding, courtship feeding and other affiliative behaviours (Kingma, Komdeur, et al., 2016; Richardson et al., 2002). Resighting probabilities are extremely high in our study population (92%–98%; Brouwer et al., 2010), so individuals that are not observed over two seasons can be confidently assumed dead. Birds are caught using mist nets and unringed individuals are subsequently ringed. Blood samples (25 μl) are taken by brachial venipuncture and used for sexing and parentage analyses (see below).

Seychelles warblers take most of their arthropod prey from the underside of leaves (Komdeur, 1991). Therefore, territory quality can be accurately estimated in terms of arthropod abundance (see Komdeur, 1992 and Brouwer et al., 2009 for a detailed description). In brief, arthropod abundance was estimated at 14 locations each month during the breeding season by counting the number of arthropods on the underside of 50 leaves for the most abundant plant species (mostly trees). For each territory, in each breeding season, we determined the vegetation cover of each of the plant species and the size of the territory. Territory quality was calculated by multiplying the mean number of arthropods per plant species and the relative cover of that plant species, summed over all plant species. These values were then multiplied by territory size and log-transformed. For our analyses, territory quality was mean-centred within breeding seasons by estimating the best linear unbiased predictors (BLUPs; Robinson, 1991) from a random regression model to account for between-year differences due to variation in the timing and frequency of sampling. For a subset of territories (28%) for which no estimate of territory quality was available at the time of dispersal (e.g., territory quality was not always measured in winter seasons), we used the BLUPs for that territory across all seasons for which a measurement was available, which is the best approximation of territory quality in any given season (Hammers, Richardson, Burke, & Komdeur, 2012; Groenewoud et al. in prep).

2.2 | Dispersal strategies

Dispersal to dominant or non-natal subordinate positions was defined as individuals permanently leaving their natal territory and settling in a different territory for at least one season as a dominant or subordinate. Individuals that dispersed to a dominant position usually filled a vacancy after the original dominant individual had died or dispersed or they, less commonly, deposed the dominant (Richardson, Burke, & Komdeur, 2007). In some cases, subordinates founded a new territory, for example, by budding off part of their resident territory (Komdeur & Edelaar, 2001). Individuals were assigned as floaters when they permanently left their natal territory and were recorded in at least three territories during the breeding season, without associating with any specific group (Kingma, Bebbington, et al., 2016). All individuals were of known sex, which was determined using molecular techniques (Richardson, Jury, Blaakmeer, Komdeur, & Burke, 2001).

We defined the age at which an individual dispersed using the mean date between when it was last seen in its natal territory and when first seen in its new territory. Most birds (410/461) dispersed between fieldwork periods, in which case we used the mean date between these fieldwork periods (mean ± *SE* number of days between fieldwork periods = 117.6 ± 50.7 days). Dispersal distance was determined as metres between the geometric centres of the natal territory and the territory to which the individual dispersed.

2.3 | Genetic relatedness and reproductive success

Pairwise genetic relatedness (*R*) was estimated based on 30 microsatellite loci (Richardson et al., 2001; Spurgin et al., 2014) using the Queller and Goodnight (1989) estimation implemented in the R-package "RELATED" v0.8 (Pew, Muir, Wang, & Frasier, 2015). A previous study using these microsatellite loci in the Seychelles warbler has confirmed that relatedness for known parent–offspring pairs does not differ from $R = 0.5$ (Richardson, Komdeur, & Burke, 2004). To determine whether dispersers that joined another territory as non-natal subordinates ($n = 3$ males, $n = 20$ females) obtained parentage as subordinates, we assigned parentage for all offspring that were produced in that territory during a focal subordinate's tenure using MASTERBAYES 2.52 (Hadfield et al., 2006; Dugdale et al. in prep.).

Lifetime reproductive success was estimated by assigning all offspring produced per breeding female, excluding those that did not survive to subadulthood (>5 months of age). Individuals are caught at different points after hatching, including as nestlings, fledglings or juveniles but almost all individuals are caught before reaching subadulthood. Furthermore, mortality is highest prior to subadulthood (Brouwer et al., 2010), and individuals never breed before this age (Komdeur, 1995). Using this criterion therefore more accurately reflects recruitment than using all offspring produced. Lifetime reproductive success was determined only for females because almost all non-natal subordinates were female (20/23). Only females for which we had documented all lifetime reproductive events, that is, that died before the end of our study ($n = 123$, $n = 18$, $n = 8$ for females moving to a dominant, non-natal subordinate or floating position, respectively; mean age at death was 4.6 years and did not differ between different strategies), were included. Furthermore, we excluded all individuals that were translocated to another island (2004 and 2011; Wright, Spurgin, Collar, & Komdeur, 2014) within a year after they dispersed for the analysis of survival, and all individuals that were translocated for the analysis of lifetime reproductive success.

2.4 | Statistical analyses

2.4.1 | Proximate drivers of between-group dispersal

To identify the proximate factors that determine individual dispersal strategies, we applied a multinomial logistic regression analysis using the R-package "BRMS" v1.5.1 (Bürkner, 2017) which fits models through a Hamiltonian Monte Carlo (HMC) algorithm in STAN (Hoffman & Gelman, 2014; Stan Development Team 2015). Multinomial logistic regression generalizes the logistic regression to allow for the fitting of more than two possible discrete outcomes. We fitted the three alternative dispersal strategies: dispersal to (1) a dominant position (reference category; $n = 406$), (2) a non-natal subordinate position ($n = 23$) or (3) floating ($n = 32$) as a response variable. We added individual (age at dispersal, sex), social (whether breeder replacement had occurred, group size, population density) and ecological (territory quality) factors in the natal territory as predictors. Group size was expressed as the number of subordinates (i.e., older than three months) present in the territory. Population density (i.e., the total number of birds >6 months on the island at the start of the breeding season) was included as a proxy for the overall degree of competition for dominant positions. Individuals younger than 6 months seldom disperse (Komdeur, 1996; Eikenaar et al., 2007; this study) and therefore rarely compete for breeding positions. We included "field season" as a random effect. We used weakly regularizing normal priors on all beta coefficients and half-Cauchy priors on variance components (McElreath, 2015). Model convergence and assumptions ($\hat{R}$ (Gelman & Rubin, 1992) and posterior predictive checks) were inspected using the package "SHINYSTAN" v2.0.0 (Chang, Cheng, Allaire, Xie, & McPherson, 2017; Gabry, 2015). All parameter estimates are reported as means with 95% Bayesian credible intervals.

2.4.2 | Dispersal to improve conditions

We investigated whether subordinates improved their conditions by dispersing, and whether such improvements differed between dispersal strategies, using predictions derived from a benefits-of-philopatry framework. We tested whether subordinates with different dispersal strategies experienced a change (compared to their natal territory) in (1) territory quality, (2) group size and (3) reproductive competition (i.e., whether there was a same-sex subordinate in the group) by fitting separate (generalized) linear mixed effects models with varying intercepts for individuals ($n = 461$). Specifically, we fitted (1) territory quality as a response variable with a Gaussian error and included "natal vs. dispersal territory" (i.e., a dummy variable (0/1) which expresses the difference, or slope, between the natal and dispersal territory in the response), dispersal strategy, sex and the three-way interaction between "natal vs. dispersal territory," dispersal strategy and sex as predictors. To estimate changes in group size, (2) we fitted group size as a response variable assuming a Poisson error. We included "natal vs. dispersal territory," dispersal strategy and the interaction between "natal vs. dispersal territory" and dispersal strategy as predictors. To assess whether individuals experienced a change in reproductive competition, (3) we fitted the presence/absence of a same-sex subordinate in the group as a response variable assuming a binomial error distribution. We included "natal vs. dispersal territory," dispersal strategy and the interaction between "natal vs. dispersal territory" and dispersal strategy as predictors. We fitted different changes between males and females only for the analysis of territory quality; a lack of variation in the response prohibited accurate estimation of sex effects in the other two models, and males and females were therefore analysed together.

Subordinates may increase their chances of territory inheritance by joining a territory where the same-sex breeder is older than the same-sex breeder in their natal territory and thus is more likely to die in the near future (Hammers et al., 2015). To test this prediction, we compared the age of the same-sex dominant breeder in the natal and dispersal territories at the time of dispersal by fitting the ages of the same-sex dominant breeders as a response variable in a linear mixed model with varying intercepts (i.e., random effects) for different birds (subordinate between-group dispersers only; $n = 21$ and 23, for natal and dispersal territories, respectively). We included "natal vs. dispersal territory" as a predictor. Furthermore, we assessed subordinate-breeder relatedness in the natal and non-natal territory to test whether individuals that dispersed to non-natal subordinate positions did so to territories with related breeders where they could gain indirect genetic benefits. We fitted pairwise relatedness (*R*; see above) as a response variable assuming a Gaussian error distribution and fitted "natal vs. dispersal territory," "dominant sex" and its interaction as predictor variables. We distinguished between female and male dominants in this analysis, because (due to extra-pair paternity) relatedness to the dominant female is higher than relatedness to the dominant male, and the former is therefore a more reliable indicator of the indirect benefits to be gained (Komdeur, Richardson, & Burke, 2004; Richardson et al., 2003). Only subordinate between-group dispersers were included in this analysis (*n* = 23).

2.4.3 | Fitness consequences of subordinate between-group dispersal

We investigated the fitness benefits of becoming a subordinate on a non-natal territory by assessing (1) whether they obtained a dominant position through inheritance or "staging" (dispersing again after remaining in the non-natal territory for at least one season; Cockburn, Osmond, Mulder, Green, & Double, 2003) and (2) whether they gained parentage (Richardson et al., 2002). Furthermore, we (3) compared lifetime reproductive success (number of independent offspring; see 2.3 "Genetic relatedness and reproductive success") of females that dispersed to non-natal subordinate or dominant positions, or that became floaters. Many females in our dataset never successfully reproduced (58/149); therefore, total lifetime reproductive output was fitted as the response variable in a zero-inflated Poisson regression model. Dispersal strategy was added as a predictor and Bayes factors were calculated to assess the differences between these strategies.

Dispersal strategies might have different costs (Kingma, Bebbington, et al., 2016, Kingma et al., 2017). We compared survival to the next season in the first year after an individual had left its natal territory for individuals that dispersed to non-natal subordinate or dominant positions, or that became floaters, in a generalized linear model with a binomial error structure. We included age at dispersal (in years) as a covariate in the model. We fitted separate models for males and females, because the low occurrence of male between-group dispersal prevented accurate estimation of the "sex x dispersal strategy" interaction.

All frequentist models were fitted with package "LME4" v1.1-12 (Bates, Mächler, Bolker, & Walker, 2015) and checked for model assumptions such as overdispersion, homogeneity of variance and normality. We used an information theoretic model selection approach using AICc (Akaike, 1973; Hurvich & Tsai, 1989). We fitted full models and removed variables from the model if this resulted in a lower AICc value. Parameter estimation was based on the model with the lowest AICc value, and previously dropped variables were re-entered sequentially to be estimated. Parameter significance was estimated on the basis of likelihood ratio tests between nested models assuming a χ^{2-} distribution or F-distribution. Similar "intermediate" model selection approaches have been advocated in Zuur, Ieno, Walker, Saveliev, and Smith (2009). All higher-order interactions were dropped for the estimation of main effects, and model predictions were made using the package "AICCMODAVG" v2.1-1 (Mazerolle, 2017). We used to the package "MULTCOMP" v1.4-6 (Hothorn, Bretz, & Westfall, 2008) and "PHIA" v0.2-1 (De Rosario-Martinez, 2015) to obtain linear contrasts between different factor levels and interactions. All analyses were performed in R version 3.3.1 (R Core Team, 2016).

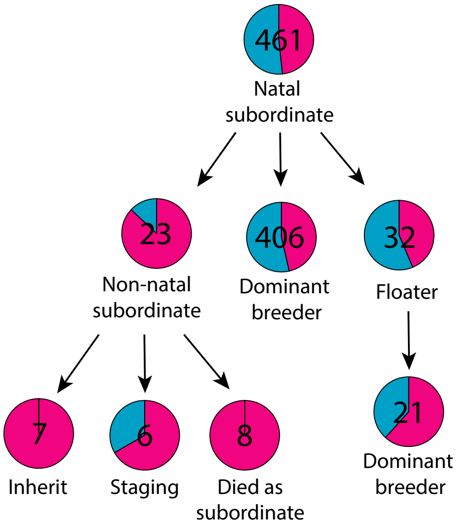

FIGURE 1 The fate of 461 subordinate Seychelles warblers that followed different dispersal trajectories from their original natal territory, with proportions of males (blue) and females (pink) in each category. When numbers are not carried through to the next category, this means that these individuals were seen last in that earlier position

3 | RESULTS

3.1 | Subordinate dispersal strategies

We identified dispersal events for 461 subordinates (*n* = 223 females, *n* = 238 males; Figure 1, Table 1). Dispersal to a dominant position was most common (*n* = 406, 88%), while 23 individuals (5%) dispersed to a subordinate position in a non-natal territory and 32 individuals (7%) became floaters. Of the individuals that moved to a subordinate position, six acted as stagers, moving again to either a dominant (three females and two males) or another subordinate position (one female) after staying in the territory for only a short time (mean ± *SE* = 0.75 ± 0.88 years; seven inherited the dominant position after a mean of 2.54 ± 0.82 years (all females), and eight remained as subordinates in their new territory until they died (tenure as subordinate: mean ± *SE* = 2.77 ± 0.76 years; all females).

3.2 | Proximate drivers of between-group dispersal

Several proximate factors were associated with the likelihood that individuals dispersed to a non-natal subordinate position,

TABLE 1 Differences in age at dispersal and dispersal distances for subordinates in the Seychelles warbler with different dispersal strategies using linear models with sex, dispersal strategy and the interaction "sex × dispersal strategy". Contrasts that differed significantly are displayed in bold

Position after dispersal	*n*		Age at dispersal (years) (mean ± *SE*)			Dispersal distance (m) (mean ± *SE*)		
	Female	Male	Female	Male		Female	Male	
Dominant	189	217	1.23 ± 0.05	1.34 ± 0.04	Dom vs. Sub: 0.27 ± 0.14, $t = -1.96$, $p = 0.12$	231.58 ± 8.99	109.25 ± 8.39	Dom vs. Sub: 0.31 ± 0.27, $t = 1.15$, $p = 0.47$
Non-natal subordinate	20	3	1.05 ± 0.14	0.52 ± 0.36	Sub vs. Float: 0.03 ± 0.18, $t = 0.18$, $p = 0.98$	204.35 ± 27.65	46.77 ± 71.39	**Sub vs. Float: −1.48 ± 0.37, $t = -3.94$, $p < 0.001$**
Floater	14	18	0.9 ± 0.17	1.07 ± 0.15	**Float vs. Dom: −0.30 ± 0.12, $t = 2.58$, $p = 0.03$**	325.03 ± 34.29	262.35 ± 43.72	**Float vs. Dom: 1.17 ± 0.28, $t = 4.20$, $p < 0.001$**
Total	223	238	Female vs. Male: 0.10 ± 0.06, $F = 2.59$, $p = 0.11$			**Female vs. Male: −1.21 ± 0.12, $F = 103.2$, $p < 0.001$**		

became a floater, or dispersed to a dominant position directly (Figure 2). Subordinate between-group dispersers were most often female (87%), dispersed during periods of high population density, came from smaller groups, and were both younger (see also Table 1) and more likely to have experienced dominant male turnover in their natal territory than individuals that dispersed to a dominant position directly (Figure 2). Individuals that became floaters were younger than those that moved to a dominant position directly, but they were not more likely to be female (Figure 2; 44% of floaters are female) and the likelihood of becoming a floater was not related to population density. Similar to individuals that moved to a subordinate position, floaters often left their natal territory after replacement of the dominant male (dominant males were replaced for 9/32 (28%) floaters, 6/23 (26%) of subordinate between-group dispersers and 46/406 (11%) of individuals that dispersed to a dominant position). Replacement of the dominant female in the natal territory did not affect dispersal strategy (Figure 2).

3.3 | Dispersal to improve conditions

There was no difference in the quality of the natal and dispersal territory for subordinate between-group dispersing females ($\chi^2_1 < 0.01$, $p = 0.97$; Figure 3a). Females ($\chi^2_1 = 5.28$, $p = 0.04$) and males ($\chi^2_1 = 6.85$, $p = 0.04$) that moved to a dominant breeding position had significantly lower territory quality in their new territory (Figure 3a). For females that obtained a dominant position after floating, territory quality was also lower in the new territory than in the natal territory ($\chi^2_1 = 6.24$, $p = 0.04$). Males that obtained a dominant position after floating experienced no significant change in territory quality ($\chi^2_1 = 0.03$, $p = 0.97$). Subordinate between-group dispersers ($\chi^2_1 = 0.79$, $p = 0.56$) and individuals that obtained a position after floating ($\chi^2_1 = 0.06$, $p = 0.81$) did not move to groups of different size than their natal territory (Figure 3b). However, subordinates that dispersed directly to a dominant breeding position moved to groups that contained fewer subordinates than their natal territory ($\chi^2_1 = 30.94$, $p < 0.001$; Figure 3b). Subordinates dispersing directly to a dominant breeding position also moved to smaller groups relative to subordinate between-group dispersers ($df = 1$, $z = 2.21$, $p = 0.03$; Figure 3b). The probability of having a same-sex subordinate in the natal and new territory was similar for subordinate between-group dispersers ($\chi^2_1 < 0.001$, $p = 0.99$; Figure 3c), and there were no differences between dispersal strategies (interaction "natal vs. dispersal territory × dispersal strategy": $\chi^2_3 = 4.55$, $p = 0.21$). Overall, the probability of having a same-sex subordinate was lower in the new territory than in the natal territory ($\chi^2_1 = 19.74$, $p < 0.001$). Subordinate between-group dispersers did not move to territories with an older same-sex breeder dominant ($\chi^2_1 = 0.25$, $p = 0.61$; Figure 3d), and this did not differ between subordinate sexes ($\chi^2_1 = 0.06$, $p = 0.79$).

Subordinates were highly related to the dominants in their natal group ($R_{\text{natal male}}$: mean ± $SE = 0.29 \pm 0.04$, $z = 6.61$, $p < 0.001$; $R_{\text{natal female}}$: mean ± $SE = 0.39 \pm 0.05$, $z = 8.72$, $p < 0.001$), but not to the dominants in the territory that they joined as subordinates after dispersing ($R_{\text{dispersal male}}$: mean ± $SE = -0.02 \pm 0.04$, $z = -0.44$, $p = 0.99$; $R_{\text{dispersal female}}$: mean ± $SE = 0.03 \pm 0.04$, $z = 0.778$, $p = 0.89$). Subordinates were consequently less related to the dominants in the territories they joined as subordinates than they were to the dominants in their natal territory, and this decrease was similar between subordinates and the dominant female and male (change in R: mean ± $SE = -0.33 \pm 0.04$, $\chi^2_1 = 48.78$, $p < 0.001$). Subordinate-breeder relatedness between the natal and dispersal territory showed a similar decrease when we included only between-group dispersing subordinate females ($n = 20$; change in R: mean ± $SE = -0.36 \pm 0.04$, $\chi^2_1 = 47.12$, $p < 0.001$).

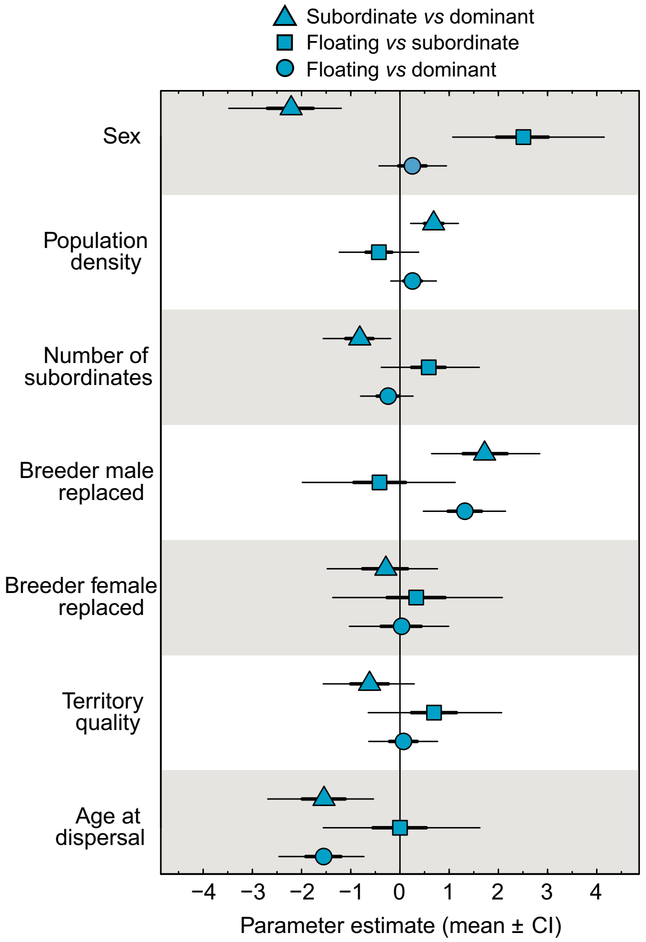

FIGURE 2 Parameter estimates with 50% (thick error bars) and 95% (thin error bars) credible intervals of the proximate factors that may drive the dispersal strategies of 461 subordinate Seychelles warblers. Symbols represent the mean effect (log odds ratios) that individuals will disperse to a non-natal subordinate position relative to a dominant position (triangles), become floaters relative to moving to a non-natal subordinate position (squares) or become floaters relative to the probability of moving to a dominant position (circles). The reference category for sex is "female"

3.4 | Fitness consequences of subordinate between-group dispersal

About 38% (8/21) of between-group dispersing subordinate females gained parentage in their non-natal territory. Subordinate between-territory dispersing females had a moderate likelihood of inheriting their non-natal territory (33%; 7/21), and 57% (4/7) of these inheriting subordinates gained parentage as a subordinate in their non-natal territory. Similarly, among the between-group dispersing females that died as a subordinate in their non-natal territory, 50% (4/8) reproduced as a subordinate. Stagers (n = 6/21 between-group dispersers) never obtained parentage (Table 2). Subordinate females produced 52% (15/29) of all offspring produced in their non-natal territories during their tenure.

Almost all floater females (93%; 13/14), but only 44% (8/18) of floater males, obtained a dominant position after floating (male vs. female floaters obtaining a dominant position after floating (Pearson's χ^2-test with MCMC simulated p-values, n = 2,000): χ^2 = 8.18, p = 0.005). This difference is explained by male floaters having a lower probability of survival to the next breeding season than males that dispersed directly to a dominant position (41% vs. 91% survival; $\beta_{\text{floater-dominant}}$: mean ± SE = −2.54 ± 0.54, χ^2 = −2.52, p < 0.001; Figure 4a). Females showed no significant differences in survival between dispersal strategies (χ^2 = 0.05, p = 0.97; Figure 4a).

Female subordinates that dispersed to a non-natal subordinate position had similar lifetime reproductive success to females that moved directly to dominant position ($\beta_{\text{subordinate-dominant}}$: mean (95% CI) = 0.21 (−0.16, 0.57); Figure 4b), and both had higher lifetime reproductive success than female floaters ($\beta_{\text{subordinate-floater}}$: mean (95% CI) = 0.97 (0.19, 1.84); $\beta_{\text{floater-dominant}}$: mean (95% CI) = −0.76 (−1.58, −0.04); Figure 4b).

4 | DISCUSSION

In cooperatively breeding species, subordinates are expected to disperse when the fitness benefits of doing so outweigh those of natal philopatry (Stacey & Ligon, 1991). In many species, individuals leave their natal territory to settle as a subordinate elsewhere, despite the lack of nepotism and kin-selected benefits on non-natal territories. Why they do so has been largely unexplored (but see Riehl, 2013). Our analyses reveal that dispersal to a non-natal subordinate position and floating are associated with reduced nepotism (i.e., higher likelihood of dominant male replacement) and constraints on dispersal (i.e., higher population density). However, subordinate females can escape the costs of floating by becoming a cobreeder in an unrelated group. We discuss our results below and explain how they allow inferences about the importance of the benefits of philopatry and ecological constraints hypotheses in explaining sociality in this cooperatively breeding species.

4.1 | Proximate factors promoting between-group dispersal

Nepotism and parental tolerance can affect dispersal decisions and fitness (Eikenaar et al., 2007; Ekman & Griesser, 2002; Nelson-Flower & Ridley, 2016). Our analyses show that the replacement of the dominant male, but not the female, in the natal territory is associated with subordinates joining an unrelated group or becoming a floater (Figure 2). This result indicates that nepotism (tolerance by a related dominant male) plays a role in explaining philopatry in this species. Due to high rates of extra-pair paternity (ca. 40% of offspring; Richardson et al., 2001), philopatric subordinates are on average more related to the breeding female than to the breeding male (Richardson et al., 2002). If kin-selected benefits drove philopatry, we would expect higher dispersal propensity when the breeding female, rather than the breeding male, is replaced. Thus, our results are consistent with reduced nepotistic benefits and potential eviction, but not reduced indirect benefits, driving dispersal. That eviction is

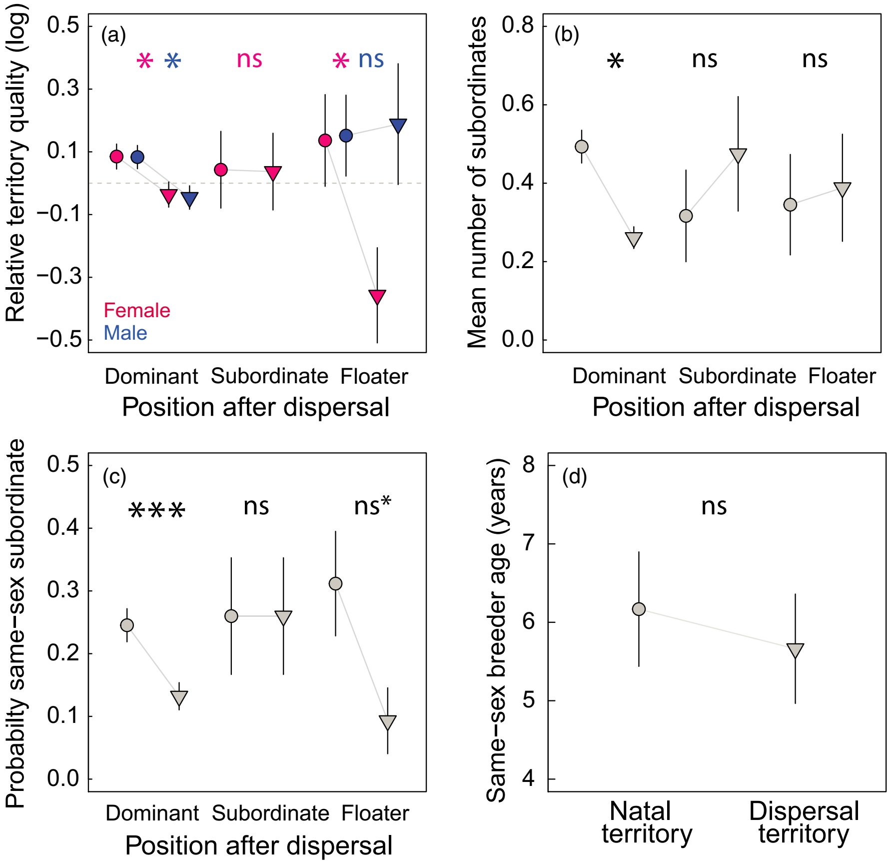

FIGURE 3 Changes in model predicted means (± *SE*) of (a) territory quality, (b) number of subordinates and (c) the probability of having a same-sex subordinate, between the natal (circles) and dispersal territory (triangles) for subordinates that moved to a dominant position ($n = 406$), a non-natal subordinate position ($n = 23$) or that obtained a territory after floating ($n = 21$). Similar to that, in (d), the age of the same-sex dominant breeder in the natal ($n = 21$) and dispersal ($n = 23$) territory are given. Asterisks indicate significance of slopes (ns, not significant, ns*$p < 0.10$, *$p < 0.05$, ***$p < 0.001$)

TABLE 2 Mean tenure duration, whether individuals help and gain reproductive success (number of individuals that gained parentage and number of offspring sired by subordinate vs. total offspring produced in the territory during subordinate tenure) of non-natal subordinate Seychelles warblers (while subordinate) with different eventual fates in the territory to which they dispersed. Most ($n = 20$) were females, but two males were observed staging

	Subordinate tenure duration (mean ± *SE* years)	Number of individuals		Offspring sired by subordinate (out of total number of offspring)
		Observed helping	Gained parentage	
Died ($n = 8$)	2.77 ± 0.76	7/8 (87.5%)	4/8 (50%)	11/17 (64.7%)
Inherit ($n = 7$)	2.54 ± 0.82	5/7 (71.4%)	4/7 (57.1%)	4/12 (33.3%)
Staging ($n = 6$)	0.75 ± 0.88	1/6 (16.7%)	0/6 (0%)	0/0 (0%)
Mean	2.11 ± 0.49	13/21 (61.9%)	8/21 (38.1%)	15/29 (51.7%)

responsible for subordinate dispersal to positions other than dominant ones, is further supported by between-group dispersers and floaters being younger at the time of dispersal and tending to disperse under higher population density than subordinates that dispersed to a dominant position (Figure 2, Table 1). These results are consistent with reduced parental tolerance for natal subordinates (Nelson-Flower & Ridley, 2016) and with increased competition for independent breeding positions after (forced) dispersal, such as proposed by the ecological constraint hypothesis (Emlen, 1982). Interestingly, our results suggest that reduced local competition (i.e., group size) increases the probability of between-group dispersal, but not floating, relative to dispersal to a dominant position (Figure 2). Previous studies in the Seychelles warbler suggest that this is not the result of dispersal due to increased competition (i.e., for food) in the group, because group size is not associated with the overall likelihood of dispersal (Eikenaar et al., 2007). One possibility is that small groups are an indication of poor group reproductive success and therefore of low predicted future benefits of cobreeding, which is one of the major benefits of female philopatry (Richardson et al., 2002).

4.2 | Between-group dispersal as a strategy

All floaters either died or gained a dominant position after floating, but none joined a group as a non-natal subordinate, which suggests that these individuals are using a different strategy. This is in contrast to pied babblers *Turdoides bicolor*, where floaters were more likely to regain a position as a subordinate than as dominant breeders

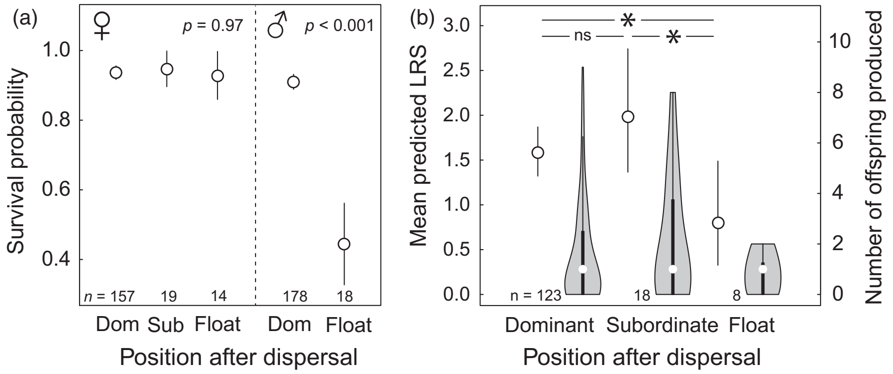

FIGURE 4 In (a), the model predicted mean probabilities (± *SE*) that dispersing subordinate females and males survive to the next breeding season depending on their position after dispersal (Dom = dominant, Sub = subordinate and Float = floater). Only two males joined another group as a non-natal subordinate, which was too small a sample size to analyse and was therefore excluded. In (b), the predicted mean lifetime reproduction (number of offspring produced that survived >5 months; open circles; left axis) (± 95% CI) and distribution of the raw data (median, interquartile range and density; right axis) of all females with complete reproductive histories. Asterisks indicate significant differences according to Bayes factors

(Ridley et al., 2008). That floating and becoming a non-natal subordinate are two different strategies in the Seychelles warbler is further supported by floaters dispersing further than subordinate between-group dispersers (Table 1). This suggests that between-group dispersers are unlikely to have floated before they join another territory as a subordinate. Females are also more likely than males to prospect as a subordinate (Kingma, Bebbington, et al., 2016), which might allow them to explore opportunities to join a territory as a non-natal subordinate in the future. Recent theoretical work has shown that, under intense competition for breeding vacancies, both strategies (i.e., obtaining a dominant position, or joining a non-natal group) can emerge and coexist in the same population (Port, Schülke, & Ostner, 2017).

Our results show that subordinates did not join other groups to access a territory of higher quality, reduce competition for food (i.e., group size) or improve the chances of territory inheritance (Figure 2). However, subordinates that moved to a dominant position directly obtained lower quality territories than their natal territory (Figure 3a), which could be partly due to newly formed territories (e.g., by budding) being smaller than territories that have been able to expand over several years (Komdeur & Edelaar, 2001). Subordinates were, on average, related to the dominant male and female in their natal group, thus able to obtain indirect genetic benefits. Dominant-subordinate relatedness estimates were lower than predicted for parent–offspring dyads (R ≈ 0.5) and differed between breeding males and breeding females due to frequent extra-group paternity and subordinate cobreeding (Richardson et al., 2002). Between-group dispersers subsequently moved into unrelated groups, which excludes the possibility that subordinates accrue benefits through nepotism or relatedness by dispersing, but leaves the possibility that subordinate females are allowed to join and cobreed in these territories, because they are unrelated. However, previous work on the Seychelles warbler did not find any evidence for inbreeding avoidance when finding a mate (Eikenaar, Komdeur, & Richardson, 2008), and unrelated female subordinates are not more likely to reproduce, than related females (Richardson et al., 2002). In consequence, non-natal subordinates do not gain any of the social or ecological benefits that we have analysed here relative to their natal territories, but do gain other (reproductive) benefits, which we discuss next.

4.3 | Survival and reproductive benefits of between-group dispersal

For females, all dispersal strategies have the same high level of survival (Figure 4a). However, similar to what was found in Kingma, Bebbington, et al. (2016) and Kingma et al. (2017), male floaters suffer higher mortality when floating compared to male dispersers that obtain a dominant position directly. Differential survival for male and female floaters suggests that being associated with a territory has important survival benefits for males, but not for females. Male subordinates, however, seldom join non-natal territories as a subordinate and never reproduce when they do (Table 2). One explanation for this pattern is that females are tolerated in or around other territories much more than males. This is also supported by our previous finding that males are more likely to be attacked by conspecifics when intruding into territories than females (Kingma et al., 2017). This pattern of female acceptance vs. aggression towards males concurs with what we know of the Seychelles warbler, where there can be clear benefits of female cobreeding, but dominant males frequently lose paternity to males from other territories (Richardson et al., 2001).

Our results show that female subordinates were responsible for 52% of all offspring produced in their non-natal territories (Table 2), similar to the 47% gained by all female subordinates reported in another study (Richardson et al., 2002). However, non-natal subordinate females had a higher likelihood of inheriting their non-natal territory than was previously reported for natal subordinates (33% of non-natal subordinates inherited the territory vs. 2% of natal subordinates (Eikenaar, Richardson, Brouwer, Bristol, & Komdeur, 2008). As a result, females that dispersed to a non-natal subordinate position had higher lifetime reproductive success than females that floated first (Figure 4b; 1.98 vs. 0.79 offspring, respectively). We can speculate about several possible explanations: (1) females that join as subordinates move to higher quality territories than floaters (Figure 3a); (2) these females could potentially breed directly after dispersal as cobreeding subordinates (while floaters lost time in the process of floating). While the direct lifetime reproductive success of female between-group dispersers seems to be equal to that of females that disperse directly to a dominant position, we have not taken into account any potential indirect benefits that could be accrued by natal subordinates. Although indirect fitness benefits are relatively low in the Seychelles warbler (Richardson et al., 2002), they might give an advantage to natal philopatry over becoming a non-natal subordinate.

4.4 | Why do dominants accept non-natal subordinates?

An important finding of our study is that dispersal to a non-natal subordinate position is strongly female biased. A possible explanation for this could be the benefits that both the immigrant female and the original members of the new territory can obtain from another female joining the group. Incubation by subordinate females (males do not incubate) is common in the Seychelles warbler (Richardson et al., 2001) and reduces nest predation (Komdeur, 1994; Kingma et al., in prep). In addition, dominant males may sire additional offspring with cobreeding females (Richardson et al., 2001, 2002). In most species where subordinates join unrelated groups, immigrants tend to be males that seek copulations with resident females, or wait to inherit the breeding position in exchange for help (e.g., Reyer, 1982; Seddon et al., 2005; see also Riehl, 2013). In the Seychelles warbler, subordinate males provide only limited help and could potentially threaten the reproduction and position of the dominant male. Subordinate males may therefore be prevented from joining non-natal groups. Although our current framework did not set out to test the reasons why individuals were accepted in territories, future work should incorporate ecological and social factors that would increase the benefits groups could obtain from accepting additional group members. This could shed light on the question why we do not see more females disperse to non-natal subordinate positions.

5 | CONCLUSIONS

Our results shed light on the benefits of cooperative breeding under varying social and ecological conditions and show how these can be independent of benefits accrued through kin selection and nepotism. We suggest that becoming a floater can be considered a “last resort” strategy. Interestingly, both floating and dispersal to a non-natal subordinate position seem to be driven by constraints on the timing and destination of dispersal, such as increased competition for breeding positions and potential eviction from the natal territory. However, some dispersing females are able to join other territories and cobreed with the dominant pair, and many of these females inherit the territory. This results in dispersal to a non-natal subordinate position leading to higher lifetime reproductive success compared to floating and similar to subordinates that disperse to a dominant position.

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AUTHORS’ CONTRIBUTIONS

F.G., S.A.K. and J.K. conceived the study. F.G. analysed the data and wrote the first draft. J.K., D.S.R., H.L.D. and T.B. coordinated the long-term study and maintain the long-term dataset. All authors contributed critically to the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.30mc3h7 (Groenewoud et al., 2018).

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