

1 Increased fecundity associates with earlier offspring dispersal and son-bias in cooperative  
2 breeding Seychelles warblers

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## Abstract

In cooperative breeding systems, sexually mature subordinate individuals limit reproduction to help dominants breed. Subordinate individuals are often offspring that delay dispersal, to help rear siblings, and sometimes co-breed themselves. Helper individuals share reproductive costs, elevating the fecundity of breeding individuals. However, the evolution of increased fecundity in cooperative breeders is potentially limited by resource-conflict costs because offspring delay dispersal from the territory of the breed group. We investigate life-history traits associated with increasing fecundity in cooperative breeding Seychelles warblers. We find breed groups are more fecund when more helping subordinates are present and that more subordinates are present when more food is available. Offspring born to breed groups of higher fecundity disperse earlier and are son-biased. We discuss how these behaviours may have evolved as counter-adaptations to reduce short term food competition costs of delayed offspring dispersal, whilst enabling breeders to reap long-term benefits of increasing fecundity in cooperative breeders. Our findings provoke consideration of co-evolutionary processes that occur to overcome changing selective forces in the evolution of cooperative breed groups.

*Keywords:* Fecundity, offspring sex-ratio, dispersal, cooperative breeding, Seychelles warbler



27 Cooperative breeding challenges traditional evolutionary theory because offspring often delay  
28 dispersal, becoming subordinates that limit reproduction to help dominants monopolize  
29 reproduction. In birds, non-random phylogenetic distributions of cooperative breeding suggest  
30 life-history traits predispose certain species to evolving cooperative breeding (1,2). A popular  
31 explanation of cooperative breeding evolution is that it occurs in lineages where costs of  
32 reproductive activities are high, making helpers necessary to share these costs in order to  
33 reproduce (3). Offspring delay dispersal to become helper subordinates because attempting to  
34 reproduce alone is potentially costly if food, mates and territories are limited or if acquisition of  
35 experience is necessary and because there are kin-selected benefits to helping rear siblings or  
36 half-siblings (4). There is good evidence that cooperative breeding may be a useful tool to  
37 alleviate high reproductive costs in birds because it occurs more frequently in altricial rather than  
38 precocial lineages (3,4) and in species with limited or unpredictable food availability (17), where  
39 lack of helping behaviour may result in failure to reproduce. Helpers lightening the reproductive  
40 load of breeders can improve body condition, interbirth intervals, clutch or litter size and  
41 breeding frequency of breeding females, increasing the fecundity of cooperative breeders (5).  
42 Increasing fecundity in turn, has been suggested to drive cooperative breeding by limiting  
43 positions available for dominant breeding and increasing the need for helpers to maintain high  
44 fecundity levels (6–9). Within cooperatively breeding birds, an association of more helpers and  
45 increased maternal fecundity has been reported in apostlebirds (*Struthidea cinerea*) (10) and red-  
46 winged fairy wrens (*Malurus elegans*) (11). However, according to theory, increased fecundity  
47 in cooperative breeders should be constrained by resource conflicts within limited territory space  
48 from prolonged parent-offspring association (12). Individuals that increase fecundity in  
49 cooperative breeding systems risk impairing future ability to reproduce due to resource conflicts

from overcrowding generating selective pressures for co-evolved mechanisms to overcome this constraint on reproductive success.

The Seychelles warbler (*Acrocephalus sechellensis*) is an excellent study system to investigate feedback mechanisms in the co-evolution of increased fecundity and cooperative breeding. There is considerable variation in the amount of social breeding (13–15) and variation in the number of offspring produced per breeding season both within and between individuals (16,17). In the Cousin Island population, 96% of all individuals have been monitored for conservation efforts since 1986, including genetic pedigree data from 1996 onwards (14). Relative to related warbler species (18), Seychelles warblers live long at ~5.5 years old (13), with dominants claiming and defending a territory for a lifetime even after a partner dies (15). Offspring delay dispersal, becoming temporary helping or non-helping subordinates in the natal territory (19), with females becoming subordinates more than males (88% n=217, 68%, n=63, (14,20)). Subordinate males do not breed (97.5%, n=990 (21)) whereas co-breeding is common for female subordinates after 2 years (14,22). Breed groups are therefore challenged for resources by offspring co-residing with social parents in limited territory space during subsequent years and daughters that co-breed in the natal territory threaten exponential increases in group size.

In this study, we used longitudinal data from the cooperative breeding Seychelles warbler system to investigate life-history traits associated with increased fecundity. We investigated environmental factors associated with increased offspring production and then tested two hypotheses for how breed group size may be regulated in subsequent years despite greater offspring production. The first hypothesis posits increased offspring dispersal regulates the number of individuals within the territory in subsequent years. We predicted that as the number

of offspring born in a breed group in a given breeding season increases, those offspring disperse earlier. The second hypothesis posits that when producing more offspring, food competition intensifies which favors son production as daughters, but not sons can reproduce on the natal territory. We predicted that mothers producing more offspring should male-bias offspring sex ratios to limit offspring reproduction on the natal territory.

## Materials and methods

### Study system

The Seychelles warbler is an insectivorous, facultatively cooperative breeding passerine endemic to the Seychelles archipelago. Monitoring of the Cousin Island (29 ha, 04°20'S, 55°40'E) population started in 1981 to track the then critically low population. Dominant breeding pairs forage exclusively on their respective territories, defending them for life (mean=5.5 years, max=19 years) (23), making territories temporally stable. 30%-50% of dominant breeding pairs have reproductively mature, subordinate individuals that limit their own reproduction and can help dominants produce offspring (13–15,19). Female subordinates often reproduce (44%, n= 43, 47% (22), n=157 (14) whereas males rarely reproduce (0%, n=3 (22), 15%, n=20 (14). Helping individuals tend to be female (24,25), and female helpers provide more efficient help (26) than counterpart male helpers. As there is no (0.1%) migration between islands (27), this represents an enclosed population enabling the lifetimes of all individuals to be tracked for a wealth of life-history parameters, across changing climates.

### Data collection

We used data collected from field trips sampling every major breeding season and eighteen minor seasons between 1996-2018. Data included in this study used sex, pedigree (identity of genetic parents), status (according to one of chick, subordinate non-helper, subordinate helper or dominant breeder) and territory quality. Territories were monitored and the number of individuals recorded. Each individual was identified by a unique colour ring combination and a

BTO metal ring. Ringless individuals were caught using mist nests and given a unique ring combination. Blood samples were used for molecularly sexing (28) and relatedness was calculated based on genotype data for 30 microsatellites (29,30). Offspring that could be assigned genetic parentage with at least 50% confidence (mean  $\pm$  SE confidence of parentage =  $0.98 \pm 0.002$ ,  $n = 1140$ ) were included. Assigning dominance status to one of dominant or subordinate and helping status of subordinates was based on close observation of behavioural interactions between individuals in the territory. Territory quality was calculated by combining mean annual territory size and monthly food availability, proxied by multiplying insect abundance with foliage cover (31) as Seychelles warblers take 98% of insect food from leaves (16). Territory quality estimates were standardized across territories by log-transforming and then mean centering and dividing by two standard deviations (32) following van Boheemen et al. (33).

#### Statistical analyses

We used generalized linear mixed models (GLMMs) assuming either poisson error structure for total offspring produced or binomial error structure for offspring sex-ratio and offspring dispersal status. GLMMs were fitted with the package *lme4* version 1.1-12 (34) in R version 3.6.2 (35). First, we used GLMMs to determine the impact of both the abiotic (territory quality) and biotic (number of adult subordinates) environment on the number of offspring produced by breed groups ( $n=863$ ) and also on the number of offspring produced by mothers ( $n=977$ ) for a total of 1177 offspring. We always controlled for the territory and field period identity as random effects as inland, sheltered territories may consistently produce more offspring and some field periods may sample more productive seasons. We always controlled for the length of the field period in



125 which sampling took place as a random effect in these models as mothers can lay nests  
126 sequentially. For breed groups, we controlled for identity of the dominant male and female. For  
127 mothers, we included the effect of being a dominant or subordinate on the number of offspring  
128 produced. Second, we used a GLMM to investigate the impact of territory quality on the number  
129 of adults in territories, including identity of the territory, field period, dominant male and  
130 dominant female as random effects as these may consistently influence the number of adults in  
131 the territory. Third, we used a GLMM to investigate predictors of offspring dispersal from the  
132 natal breed group up to three subsequent years as most offspring (this study: 92.1%, n=508)  
133 disperse by then. We included offspring sex, natal territory quality, number of adult subordinates  
134 present at birth and the number of offspring co-born in the breed group, years since birth and the  
135 interaction between number of offspring co-born in the breed group and years since birth. The  
136 interaction was included because as offspring disperse through time, the influence of the number  
137 of offspring co-born in the breed group diminishes. To control for offspring born in the same  
138 breed group, territory and season and those born to the same mother and father, the identities of  
139 the natal breed group, natal territory, natal field period, genetic mother and genetic father were  
140 included as random effects. Fourth, we used a GLMM to investigate the impact of sex, natal  
141 territory quality, the number of offspring co-born in the territory and the number of adults in the  
142 natal territory, on whether offspring established dominance in subsequent years. We included  
143 identities of the natal territory, natal field period, genetic mother and genetic father as random  
144 effects. Finally, we used a GLMM to investigate the effect the number of offspring produced,  
145 territory quality, number of subordinates and dominance on offspring sex-ratio of mothers,  
146 controlling for natal territory, natal field period and mother identity as random effects.

## Results

### Offspring production

Most mothers have singleton clutches per breeding season, though 14.7% (144/977) produce multiple offspring, up to four per breeding season (mean  $\pm$  SE=  $1.17 \pm 0.014$ ). As 13.7% (128/931) of mothers are co-breeding subordinates, this produces variation in the number of offspring produced by breed groups, with an upper limit of seven per breeding season (mean  $\pm$  SE=  $1.68 \pm 0.031$ ). Breed groups with more helping subordinates, but not non-helping subordinates produce more offspring (figure 1), with no impact of territory quality or field period length in which sampling took place (table 1). Breed groups in better quality territories sustain more adult individuals (estimate= 0.179, SE= 0.080,  $p= 0.025$ , figure 2). Per mother, the number of offspring produced is not influenced by territory quality (estimate= 0.039, SE= 0.068,  $p= 0.566$ ), by the number of helping subordinates (estimate= 0.0610, SE= 0.068,  $p= 0.566$ ), or by non-helping subordinates in the breed group (estimate= 0.003, SE= 0.035,  $p= 0.938$ ), whether she is dominant or subordinate (estimate= 0.032, SE= 0.102,  $p= 0.756$ ), or the field period length in which sampling took place (estimate<0.001, SE= 0.002,  $p= 0.893$ ).

### Offspring dispersal and dominance

53.2% (453/851) of offspring disperse after one year, 85.9% (556/647) after two years and 92.1% (468/508) after three years. Rates of offspring dispersal from the natal territory increases when offspring natal territory quality is higher and when more offspring are born in the breed group (table 2, Fig. 2). There is also a significant negative interaction between the number of offspring co-born in the breed group and the number of years after birth on offspring dispersal. There is no effect of sex or the number of adult subordinates in the breed group on offspring

170 dispersal. Sons become dominants more than daughters in each year (estimate= 0.301, SE= 0.101  
 171  $p= 0.003$ ) with 89.6% (241/269) of sons becoming dominant and 82.8% (198/239) of daughters  
 172 becoming dominant three years later. There is no impact of natal territory quality (estimate= 0.  
 173 252, SE= 0.150,  $p= 0.093$ ), the number of offspring co-born in the natal territory (estimate= -  
 174 0.042, SE= 0.059,  $p= 0.476$ ) or the number of adult subordinates in the natal territory (estimate=  
 175 -0.061, SE= 0.069,  $p= 0.380$ ) on whether offspring established dominancy in subsequent years.

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#### 177 Offspring sex-ratios

178 Dominant mothers male-bias offspring sex ratios when increasing the number of offspring  
 179 produced, despite even mean offspring sex-ratios (0.48) (table 3, Fig. 3a). There is no  
 180 relationship between number of offspring produced and offspring sex-ratio in subordinate  
 181 mothers, maintaining a male-biased mean offspring sex-ratio of 0.62 (78/126, two-tailed  
 182 binomial test= 0.009) (table 3, Fig. 3b). There is no influence of territory quality or the number  
 183 of adult subordinates in the territory on offspring sex-ratios.

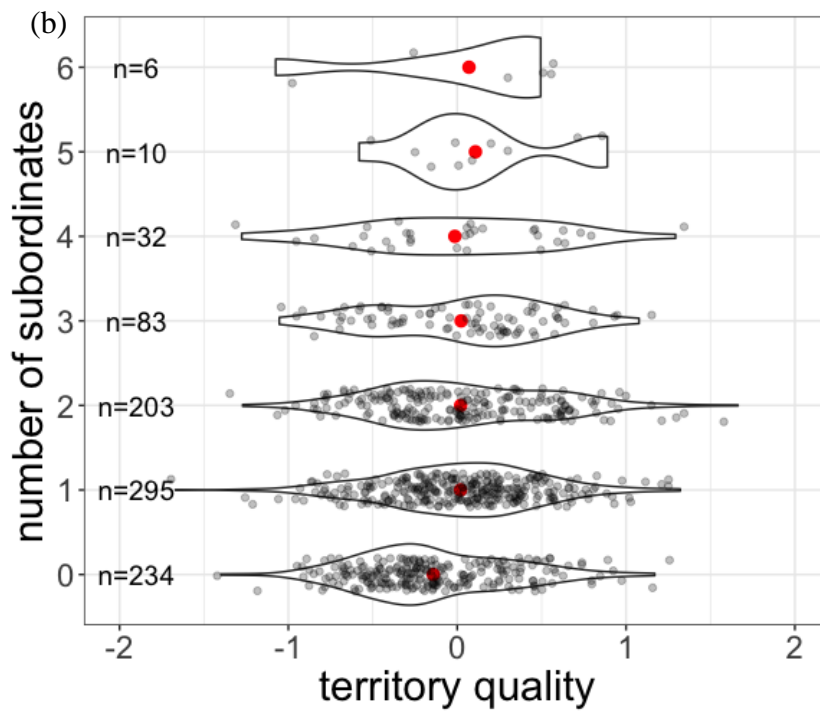
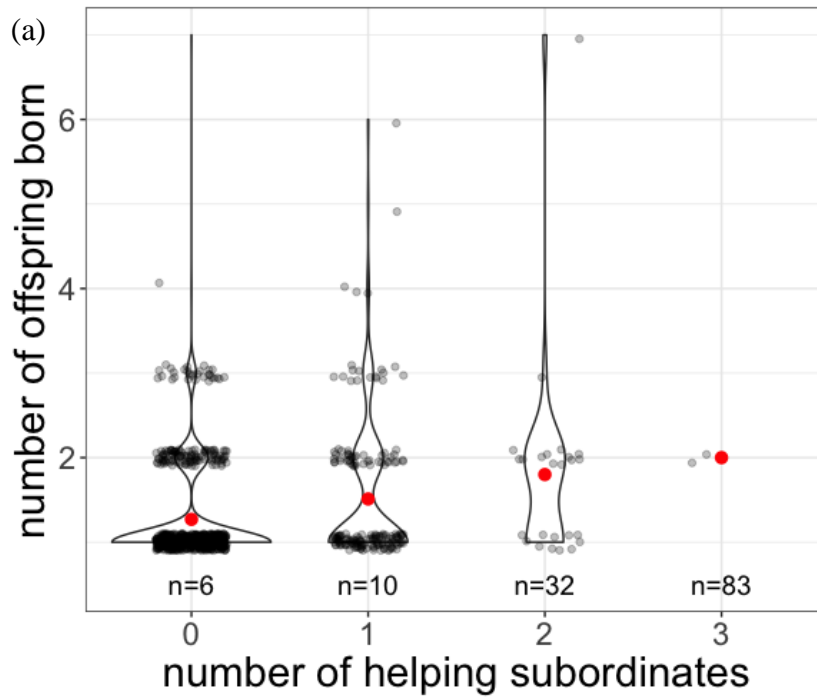


Figure 1. Violin plots showing kernel probability density of the data at different values overlaid on scatter plots of the relationship between (a) the number of helping subordinates and number of offspring born per breed group and (b) territory quality and the number of adults per breed group. Each jittered black dot is a breed group in a breeding season. Red dots represent mean values.

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193 *Table 1. The impact of field period length, territory quality and the number of subordinates on*  
 194 *offspring production per breeding season.*

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| Fixed effect                                 | Estimate            | SE                  | p                   |
|--|---------------------|---------------------|---------------------|
| Field period length                          | <-0.001             | 0.001               | 0.860               |
| Territory quality                            | 0.087               | 0.062               | 0.161               |
| Number of non-helping subordinates           | 0.030               | 0.033               | 0.361               |
| <b><i>Number of helping subordinates</i></b> | <b><i>0.164</i></b> | <b><i>0.053</i></b> | <b><i>0.002</i></b> |

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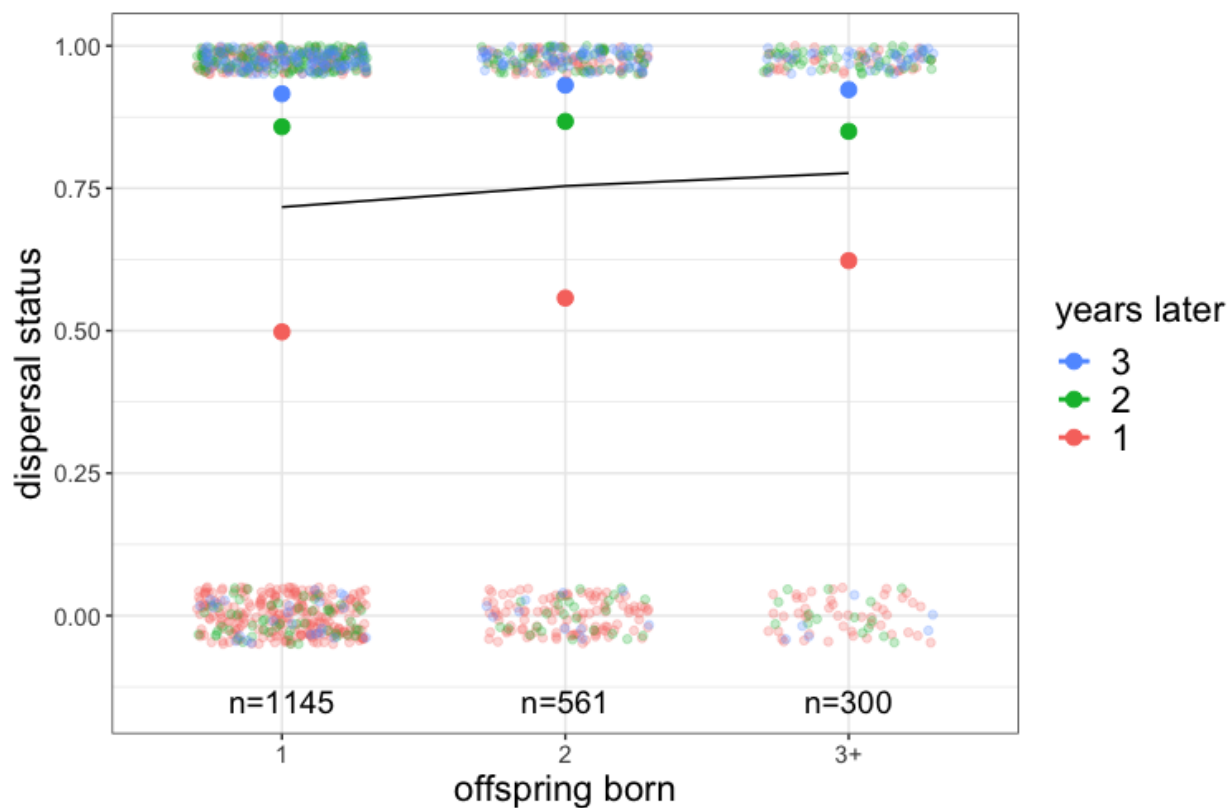


Figure 2. Jittered scatter plot of the relationship between number of offspring co-born in the breed group and dispersal status after one (red), two (green) and three (blue) years averaged by the black trend line. Each faded point is a single offspring and full colour points represent mean values.

207 *Table 2. The impact of sex, number of subordinates, territory quality, number of offspring co-*  
 208 *born in territory and the interaction between number of offspring co-born in the territory and*  
 209 *years since birth on offspring dispersal.*

210 .

| Fixed effect   | Estimate      | SE           | p                |
|--|---------------|--------------|------------------|
| Sex  | 0.227         | 0.214        | 0.287            |
| Number of adults                                       | 0.153         | 0.107        | 0.152            |
| Territory quality                                      | 0.227         | 0.214        | 0.506            |
| <i>Number of offspring co-born</i>                     | <i>0.601</i>  | <i>0.241</i> | <i>0.013</i>     |
| <i>Years later</i>                                     | <i>2.872</i>  | <i>0.313</i> | <i>&lt;0.001</i> |
| <i>Years later: number of offspring in breed group</i> | <i>-0.380</i> | <i>0.124</i> | <i>0.0022</i>    |

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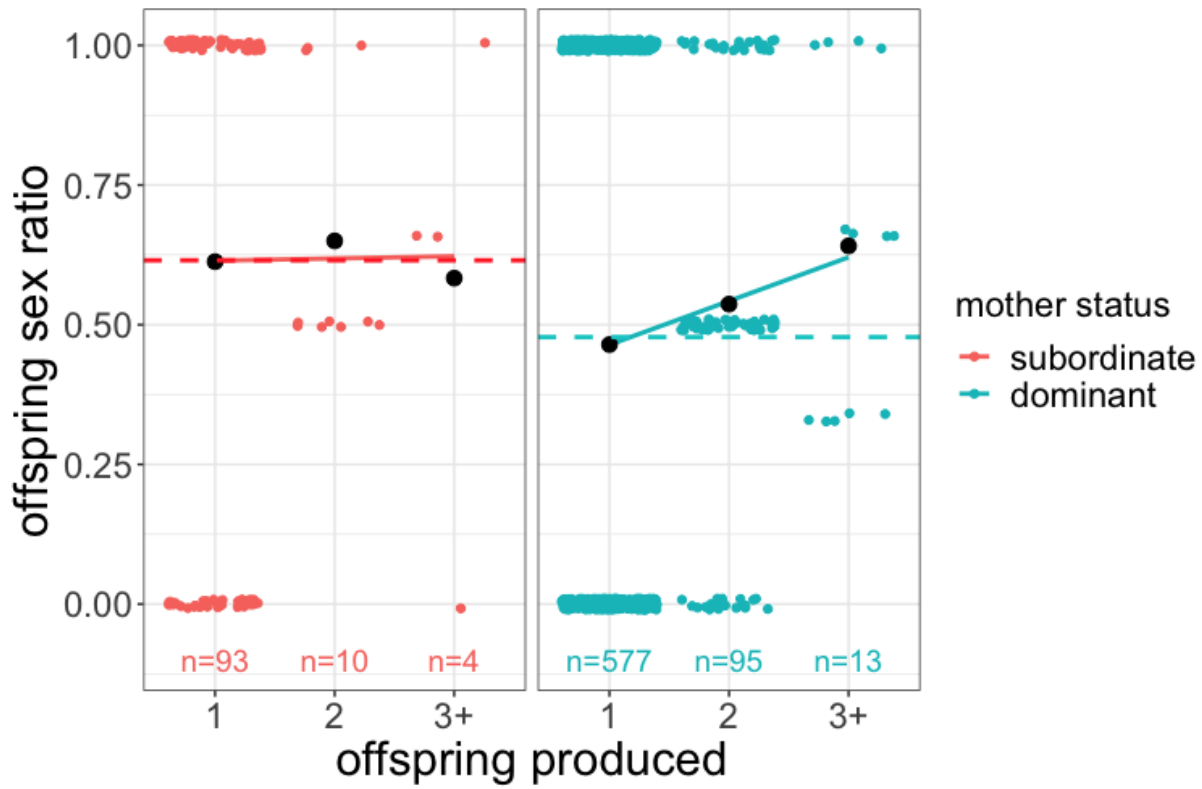


Figure 2. Jittered scatter plot of the relationship between number of offspring produced and offspring sex-ratio for subordinate (red,  $n=107$ ) and dominant (blue,  $n=685$ ) mothers. Dashed lines indicate total mean offspring sex ratios. Black dots are mean offspring sex ratios depending on number of offspring produced.

218 *Table 3. The impact of the number of offspring produced, dominance of mother, territory quality*  
 219 *and number of subordinates on a mother's offspring sex ratio in a breed season.*

220

| Fixed effect                               | Estimate             | SE                  | p                   |
|--|----------------------|---------------------|---------------------|
| <b><i>Number of offspring produced</i></b> | <b><i>0.322</i></b>  | <b><i>0.115</i></b> | <b><i>0.012</i></b> |
| <b><i>Dominance of mother</i></b>          | <b><i>-0.508</i></b> | <b><i>0.208</i></b> | <b><i>0.015</i></b> |
| Territory quality                          | 0.124                | 0.134               | 0.355               |
| Number of subordinates                     | 0.013                | 0.126               | 0.918               |

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## Discussion

Breed groups produce more offspring when there are more helping subordinates present (figure 1a) and more subordinates are present in breed groups in territories of better quality (figure 1b). In cooperative breeding Seychelles warblers, having more subordinates may be adaptive in converting increases in food availability into faster turnover of offspring production, increasing the proportion of descendants in the population. Territories with more food can sustain more subordinates to share the costs of activities associated with breeding such as, territory defence, nest building, egg incubation, and chick provisioning. Breeding costs are likely to be high and helpers can potentially drastically alter life-histories for breeders as evidenced by reduced telomere shortening in dominant Seychelles warblers that have helpers over conspecific breeders without helpers (36). Additionally, greater food availability may relax restriction on subordinate reproduction as food competition is less intense. As dominant breeders are often related to subordinates (17), there are potential kin-selected benefits when subordinates co-breed, at a reduced cost when food is abundant. Given conditions on Cousin Island are subject to extreme and short-lived monsoon winds or El Niño weather events, breed groups should face strong selection to adaptively increase offspring production by recruiting helpers when food is temporarily abundant.

As offspring often delay dispersal from the natal territory, increasing fecundity can be costly if conditions change and food becomes limited, as is often the case on their exposed equatorial island habitat. Intense food competition limiting group size in territories is well evidenced in Seychelles warblers. Removal experiments of subordinates in poor quality territories increases the number of young that successfully fledge (13). Survival decreases with increasing group sizes, most prominently in groups with more than five birds (37). Singleton

offspring are shown to have larger body mass and greater chances of survival to adulthood when compared with those born with a nest-mate (38). Therefore, the evolution of increasing facultative cooperative breeding to increase fecundity under favorable conditions in Seychelles warblers is likely to be constrained by resource availability in subsequent years. We find evidence for two hypotheses that consider how under favourable conditions, Seychelles warblers may increase the degree of cooperative breeding to increase fecundity, whilst offsetting future food competition from delayed offspring dispersal.

In the first hypothesis, offspring time dispersal according to the number of offspring born in the breed group because of food competition. We complement theoretical predictions (39) that cooperative breed groups producing more offspring, show earlier offspring dispersal (figure 2). Earlier offspring dispersal may be enforced by adults, or offspring may integrate social information such as the number of individuals in the breed group relative to food availability and choose to disperse earlier, finding territories with sufficient resources or those that have potential to take over as a dominant. Offspring dispersal correlates with the recentness of dominant turnover (40) and the population sex-ratio of the island (41) suggesting Seychelles warblers can integrate complex census information at local and island-wide scales when timing dispersal.

In the second hypothesis, cooperative breeders skew offspring sex-ratios to the sex yielding higher fitness benefits under higher fecundity. As offspring often delay dispersal for up to three years (figure 2), intense food competition following fecund seasons may select for a son-bias because daughters may reproduce at as young as three-years old within the natal territory (42), whereas sons only reproduce when dominant. Every daughter produced threatens exponential increases in group size, so fecund dominant mothers can prevent this by male-biasing offspring sex-ratios offspring (figure 3). When subordinate mothers co-breed, they

maintain 0.62 male-biased clutches (figure 3), because they add to the pool of offspring produced by dominants. Subordinate mothers may male-bias offspring sex-ratios no further than 0.62 because they are not fixed to their respective territories, weakening the subsequent competition costs they incur upon themselves when producing potentially productive daughters.

Under higher fecundity, son-biasing offspring may also be adaptive because studies have previously shown sons disperse earlier than daughters (20), reducing food competition within the territory. These studies suggest selection should be stronger on sons to disperse because male subordinates cannot co-breed, whereas female subordinates, including daughters can. Male subordinates also engage in less helping behaviour than daughters, so dominants benefit less from sons remaining in the natal territory. Furthermore, under higher fecundity, overproducing sons may play a role in reducing social conflict between individuals from adjacent territories via kin selection. As territory acquisition is correlated with proximity, offspring are more likely to take up territories as dominants in territories that surround their natal one (43). When individuals occupy territories adjacent to related males, but not related females, fights were less common, territory owners had more mass and their telomeres were longer (44). The authors suggest sex differences in territoriality results from higher relatedness between males in adjacent territories owing to males dispersing closer than females (45). Breed groups that overproduce sons when increasing offspring production may therefore buffer social conflict by kin-selection when they occupy nearby territories.

Studies that find association between fecundity and the degree cooperative breeding, rarely consider the mechanisms that make this possible despite ramifications to the size and composition of breed groups in subsequent years (10,11). In this study, we demonstrate in cooperative breeding Seychelles warblers, an association between cooperative breeding and

increased fecundity under higher food availability. When breed groups produce more offspring, we find an offspring sex-ratio skew to sons and increased offspring dispersal behaviour. These behaviours may have evolved as potential counteradaptations in cooperative breeders to buffer competition costs of excess philopatric offspring, whilst increasing the proportion of descendants in the next generation. These results suggest future research on the drivers of cooperative breeding evolution, such as increased fecundity, would benefit from investigating co-evolved changes to life-history traits, using data available from long-term studies on cooperative breeding systems.

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