A path analysis disentangling determinants of natal dispersal in a cooperatively breeding bird

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Abstract

Delayed offspring dispersal is an important aspect of the evolution of cooperative breeding. Applying a path-analysis approach to the long-term Seychelles warbler (*Acrocephalus sechellensis*) dataset, we studied whether and how delayed dispersal is affected by territory quality, the presence of helpers and non-helping subordinates, maternal breeding status and fecundity, and offspring sex ratio. We found that offspring are more likely to disperse when their genetic mothers are co-breeders, helpers are absent and territory quality is high. In contrast to earlier findings, our analysis does not support the idea that offspring sex ratio is affected by territory quality and helper presence. Our findings suggest that a complex interplay of ecological and social factors shapes dispersal decisions. Our study underscores the importance of considering proximate factors in understanding cooperative breeding dynamics, and it shows that path analyses offer valuable insights into dissecting the intricate relationships influencing dispersal in wild populations.

Introduction

Theories on the evolution of group living and cooperative breeding rest on assumptions as to why offspring remain philopatric rather than dispersing to seek mating opportunities elsewhere (García-Ruiz *et al.* 2022; Hatchwell 2009; Ligon & Stacey 1989). Numerous hypotheses have been proposed to address this question, primarily framed within cost-benefit analyses of remaining on the natal territory versus dispersal. Potential benefits of philopatry include access to resources within the natal territory, thereby enhancing offspring survival (e.g. Ekman & Griesser 2002; Kingma *et al.* 2016; Robles *et al.* 2022; Suh *et al.* 2020). Moreover, social dynamics within the natal territory can influence dispersal probabilities. For instance, dispersal may increase when relatedness between parents and offspring is low, such as when parental mortality leads to new step-parents assuming breeding dominance (Suh *et al.* 2020), as this reduces the inclusive fitness benefits for parents of offspring staying. Conversely, high relatedness between parents and offspring may drive dispersal, as an evolved response to mitigate kin competition (Hamilton 1967). The presence of conspecifics of similar (dominance) status and sex within the social group may also influence dispersal tendencies by altering territory inheritance probabilities (Pasinelli & Walters 2002), and larger groups could decrease per capita food availability (Dietz *et al.* 2022).

External factors further complicate the cost-benefit analysis of natal dispersal. Territory and mate availability outside of the natal habitat, influenced by factors like population density and sex ratios, can sway dispersal tendencies (Emlen 1982; Maag *et al.* 2018; Nelson-Flower *et al.* 2018; Speelman *et al.* 2024). Additionally, the costs and benefits of offspring dispersal might differ between parents and offspring, potentially leading to conflict (Port *et al.* 2020). Therefore, it is important to consider who decides whether offspring disperses (Quiñones *et al.* 2016) and whether parents and offspring attempt to manipulate each other to influence the dispersal outcome. For instance, male white-fronted bee-eaters (*Merops bullockoides*) actively try to disrupt the independent breeding attempts of their sons (Emlen & Wrege 1992), to persuade them to return as helpers. Parents could also influence the (social)

environment of offspring by changing brood size, and thus sibling competition, which could influence the dispersal tendency of the offspring (Pasinelli & Walters 2002). Further, parents could alter the offspring sex ratio towards or away from the helping sex. For example, in ants (*Formica exsecta*) both parents and workers try to change the offspring sex ratio to their benefit (Chapuisat *et al.* 1997; Sundström *et al.* 1996).

Before understanding of the evolution of group living and cooperative breeding can be improved, more research on proximate factors influencing dispersal tendencies of offspring is necessary. Experiments on this topic in the field are challenging, as manipulations can often also influence other potential factors that may affect offspring dispersal. Hence, many natural population studies on this topic are correlational. Yet, disentangling the complex web of factors causally influencing dispersal in wild populations can be confounded by intercorrelations among predictor variables. Path analyses and structural equation models offer valuable tools to help tease apart these relationships (e.g. Busana 2021). Structural equation models (SEMs) are a class of models which include a hypothesised causal framework, which allows examination of more complicated relations among variables. Path analyses are a subset of structural equation models that also include such a causal framework. The advantage of path analyses and SEMs is that they quantify the size of direct effects and of total effects of predictors on a dependent variable. In other words, by correcting for correlations between predictor variables, the estimates of direct effects on the dependent variable in question can be estimated without inflating these estimates through indirect effects. More complex structural equation models can also include latent variables (unobserved variables) and can take measurement errors into account. Hence, these complicated structural equation models are beneficial when only proxies of variables can be measured, or when predictions about measurement error exist.

In this study, we employ a path analysis framework to investigate potential factors underpinning delayed dispersal in the Seychelles warbler (*Acrocephalus sechellensis*). This species is a facultative

cooperative breeder, where subordinates may delay dispersal and can assist dominant breeding pairs raise offspring (Komdeur 1994). While having helpers can be beneficial for both parents and offspring (Hammers *et al.* 2019; Komdeur 1994), it is not a necessity to raise offspring in facultative cooperative breeders. Roughly half of the territories harbour additional sexually mature subordinates (1-5 subordinates per territory, median = 1), some of which (20% of males and 40% of females) engage in alloparental care (Borger *et al.* 2023; Hammers *et al.* 2019). Female helpers provide more help than male helpers (higher provisioning rate, and only female helpers incubate; Richardson *et al.* 2003), and some subordinate females may also engage in reproduction, which we call co-breeding (~10% of young are from co-breeders; Raj Pant *et al.* 2019; Richardson *et al.* 2001). This raises the possibility that the costs and benefits of staying or leaving are different for offspring from dominant or subordinate females, since the relatedness of the young to the dominant territory owners differs and helping is mostly directed towards the dominant female. Moreover, the probability of having female helpers increased with age of the dominant breeding female (Hammers *et al.* 2019). Additionally, Seychelles warblers have been found to produce different offspring sex ratios depending on the environment (Komdeur *et al.* 1997). This was hypothesised to be adaptive, as mostly daughters were produced when an extra helper would be beneficial (when territory quality is high and no helpers are yet present) and sons when extra help would not be beneficial (when territory quality is low or when helpers are already present). Also, it was previously found that males dispersed at a younger age than females (Komdeur 1992), though in later years this difference had disappeared (Eikenaar *et al.* 2010; Speelman *et al.* 2024). Moreover, offspring were more likely to disperse when one or both of their social parents had died, or had been replaced (Eikenaar *et al.* 2007). Lastly, male offspring were more likely to delay dispersal when they had higher novel environment exploration scores (Cox *et al.* 2023).

In view of this earlier work on the Seychelles warbler, we predict that offspring dispersal will be influenced by the natal territory quality, composition and size of the natal group, maternal social status (dominant vs. co-breeder), and offspring sex ratio. We assumed that population level effects (i.e. adult

125 sex ratio, population density), as well the effect of survival of social parents only affected the residuals
126 of dispersal, and thus did not affect the estimated coefficients of the causal network. Therefore, we
127 did not incorporate them in our causal network. Other variables (i.e. female breeder age, offspring
128 personality) were excluded from the model as well, as we had no clear hypotheses on how these would
129 affect all variables in the causal network. We anticipate that offspring opt to remain in high-quality
130 territories and that parents allow them to stay in these territories, as resources are abundant. Group
131 size might affect the per capita resource availability and therefore dispersal. Moreover, the status of
132 these other individuals within the territory might be of importance for dispersal tendencies. For
133 instance, when no helper is present on a high-quality territory, offspring might stay to become helper,
134 even when non-helping subordinates are present. Furthermore, we explore the potential effects of the
135 status of the mother on offspring dispersal, considering the different costs and benefits associated
136 with staying versus leaving for both categories. For example, offspring of dominant parents might have
137 more incentive to become helpers, or dominant parents might prefer to enhance the survival of their
138 own young versus those of co-breeders by letting their own offspring stay and making the offspring of
139 co-breeders disperse. However, there is no evidence that birds can differentiate between genetic
140 versus non-genetic offspring (Kempenaers & Sheldon 1996; Lattore *et al.* 2019), including in the
141 Seychelles warbler (Richardson *et al.* 2003b), so a potential difference in dispersal between these
142 categories does not have a strong proximate basis. Finally, we examine the impact of offspring sex
143 ratio on dispersal, positing that a female-biased sex ratio may promote philopatry due to their higher
144 probability of becoming a helper.
145
146 **Material and Methods**
147 Study system
148 The Seychelles warbler is an insectivorous, facultatively cooperative breeding passerine endemic to
149 the Seychelles archipelago. Monitoring of the contained Cousin Island (29 ha, 04°20'S, 55°40'E)
150 population, which consists of about 300 adult individuals on ~115 territories, commenced in 1985.

151 Seychelles warblers have a major breeding season (June-September), in which most individuals breed,
152 and a minor breeding season (February-March), in which a fraction of individuals reproduce (Komdeur
153 1996; Raj Pant *et al.* 2022). Dispersal off the island is rare (<0.1%; Komdeur *et al.* 2004) and resighting
154 rates are high (~92%, Brouwer *et al.* 2006), minimising potentially confounding effects of off-island
155 dispersal on survival. Territories are temporally relatively stable as Seychelles warblers have a long
156 lifespan (mean = 5.5 years for fledglings; Raj Pant *et al.* 2020) and generally stay in a territory for the
157 remainder of their lives after obtaining it. Females typically (~80% of all cases, Richardson *et al.* 2001)
158 lay a single egg per clutch. Natal dispersal predominantly occurs within the first two years of their lives
159 (~90%; Eikenaar *et al.* 2008), and inheriting a natal territory is rare (8% of individuals; Kingma *et al.*
160 2016; Komdeur & Edelaar 2001).
161
162 Hypothetical causal network
163 Our path analysis model is based on a directed acyclic graph (DAG) that represents all expected causal
164 relationships between factors that are considered "reasonable", see Fig. 1. All arrows in Fig. 1 are
165 expected causal relationships, and for each potential relationship we formulated multiple hypotheses
166 on how factors could influence or (partially) cause the other factors. Our data is analysed on the
167 mother-level, i.e. if a mother would produce multiple offspring within one season, this would be one
168 datapoint. First, we expect territory quality to have a positive effect on the number of helpers and
169 non-helpers in a territory, as territories of higher quality are expected to support more individuals.
170 Second, the number of offspring might be affected by territory quality, helper presence, the number
171 of subordinate non-helpers, the number of mothers on a territory, and the status of a mother
172 (dominant or subordinate). Territory quality indicates resource availability, helper presence should
173 reflect how many of these resources could be obtained by offspring, and helpers and non-helpers could
174 deplete the resources available for offspring. The presence of a co-breeder could increase competition
175 among offspring, and the social status of the mother might affect how many offspring the mother can
176 produce in one season, if, for example, co-breeders are limited in their reproductive output by

177 dominant breeders. Third, the offspring sex ratio produced by the focal mother may be affected by
178 territory quality, helper presence, number of non-helpers, the number of offspring of a mother, the
179 number of mothers on a territory and the status of the mother. Territory quality and helper presence
180 could affect the need for a helper, and therefore the offspring sex ratio. The status of the mother could
181 influence the offspring sex ratio as well, as mothers of different status might obtain different benefits
182 from helpers, e.g. dominant breeders might have more certainty about breeding in the same territory
183 in the future than co-breeders and might therefore benefit more from producing helpers.
184
185 Data Collection
186 Our analyses are based on data collected in 37 field seasons between 1996-2018, including all major
187 breeding seasons and fourteen minor breeding seasons (n = 719 data points from 339 mothers, who
188 produced 808 offspring). Birds were caught using mist nets, and ringed with a unique combination of
189 three colour rings and a metal ring from the British Trust for Ornithology. Most of the population
190 (>95%) has been ringed since 1997 (Hammers *et al.* 2019; Richardson *et al.* 2002) . Blood samples (~25
191 µl) were obtained via brachial venipuncture. DNA from these samples was used for molecular sexing
192 and parentage analysis (Sparks *et al.* 2022). Based on observations during each breeding season,
193 territory boundaries, group membership and social status (dominant breeder, helper, non-helping
194 subordinate, or offspring) were determined. Co-breeding females were later determined after genetic
195 parentage analysis (Sparks *et al.* 2022). Dominant breeders were identified by contact calls, pair
196 interactions, mate guarding and intensive breeding effort. Helpers were identified as subordinate
197 individuals that incubate or feed offspring, and non-helping subordinates were all other subordinates
198 on the territory. Only offspring that were blood sampled were included in our analysis, since DNA
199 samples were necessary for sexing and to determine parentage. While some offspring were sampled
200 as nestlings, many offspring were sampled after fledging. This therefore excludes any offspring that
201 had died before the point of capture, or that were never sampled. Territory quality was estimated by
202 combining territory size, leaf coverage and monthly insect abundance (Spurgin *et al.* 2018). These

territory quality estimates showed a strong right-sided skew, and therefore were standardised by log transformation, mean centering and dividing by the standard deviation.

The effects of group size on the dispersal probability of offspring were studied per sub-group (helpers, non-helping subordinates and young offspring) because their presence might influence dispersal probabilities differently. The number of non-helpers was classified into three categories (0,1, or >1 non-helpers), as more than two non-helpers rarely occurred in the used dataset (0.7% of territories with non-helpers had >2 non-helpers). The number of helpers was classified as helper absence or helper presence (0 or ≥1 helpers), again because there was little variance in the number of helpers in our dataset (3.8% of territories had more than 1 helper).

<u>Statistical analyses</u>

We fitted fully Bayesian path models based on the DAG in Fig. 1. With the exception of territory quality (TQ) and the Status of the mother (Sm), all nodes (circles) represent endogenous response variables, i.e., they have at least one directed edge ("arrow") entering them. For each such response variable, every directly "upstream" node was entered as an additive predictor variable (at the logit scale) in a regression model. Since all response variables are discrete and many breeding females had been observed multiple times, we used generalised linear mixed models, with maternal ID as varying ("random" in frequentist terminology) multivariate normal intercepts that were correlated across response variables. Specifically, we implemented the following multivariate response model:

logit(pH) = 1+TQ+(1|m|ID)	Bernoulli: H in {0,1}
logit(pNH) = 1+TQ+(1|m|ID)	Ordinal cumulative: NH in{0,1,>1}
logit(pO) = 1+TQ+H+NH+Sm+(1|m|ID)	Bernoulli: O in {1,>1}
logit(pS) = 1+TQ+H+NH+O+Sm+(1|m|ID)	Binomial: S in {0,1,…,4}
logit(pD) = 1+TQ+ H+NH+O+Sm+SR+(1|m|ID)	Binomial: D in {0,1,2,3}

228 On the far right are the assumed conditional probability distributions of the response variables. For all
229 response variables, logistic models were used for the probability p of observing a particular outcome,
230 hence logit link functions (logit(p)=log(p/(1-p)) were applied in all cases. Each response has a mean
231 intercept indicated by the "1" directly to the right of the equality sign, and each response has a
232 maternal ID-specific Gaussian deviation from the mean intercept, denoted by (1|m|ID). The shared
233 "m" in this notation indicates that a full covariance matrix was estimated for the maternal deviations,
234 containing the variances of maternal deviations within traits, as well as covariances of maternal
235 deviations between traits.
236
237 H is a binary variable that indicates helper presence at the focal female's territory, with H = 0 encoding
238 an absence of helpers and H = 1 the presence of at least one helper. The notation pH = Pr(H = 1)
239 represents the probability of observing H = 1. NH is an ordinal variable indicating an absence of non-
240 helpers (NH = 0), the presence of a single non-helper (NH = 1), or the presence of multiple non-helpers
241 (NH > 1). The binary variable O represents the number of offspring of the focal female, indicating a
242 single offspring (O = 1) or multiple offspring (O > 1). S and D are binomial response variables indicating
243 the number of sons out of all offspring, and the number of dispersing offspring out of all offspring of
244 the focal female produced within a season, respectively.
245
246 Note that H, NH and O occur both as response and predictor variables. Additional predictor variables
247 include the ordinal variable Sm the status of the mother, indicating that the focal female is a dominant
248 breeder without co-breeders on the territory (Sm = 1), a dominant breeder with co-breeders on the
249 territory (Sm = 2), or a co-breeder (in a group with a dominant breeder, Sm = 3). Finally, SR is a
250 continuous predictor, quantifying the proportion of sons among the focal female's offspring (usually 0
251 or 1, as often only 1 offspring is produced).
252

All statistical analyses were conducted using R version 4.3.1 (R Core Team 2021) with RStudio version 2023.06.0 (RStudio Team 2020). Bayesian models were fitted using the R package brms version 2.19.0 (Bürkner 2017), which interfaces the MCMC sampler called by the R package cmdstanr version 2.32.0 (Gabry *et al.* 2023). We used "weakly informative" Gaussian priors (Lemoine 2019) for population-level effects ("fixed" effects in frequentist terminology), i.e. normal densities with mean zero and unit standard deviation. For the covariance matrix of the varying intercepts, we used the default priors of brms, i.e. half-t(3) densities for standard deviations and lkj(1) densities for correlation coefficients (Bürkner 2017).

For each model we ran 4 chains of 4000 iterations, including 1000 "warm-up" iterations. Hence 12000 samples from the posterior were stored for analyses. Proper mixing of chains was monitored using trace plots and convergence of chains was verified by inspecting R-hat values, which were all close to 1.000 (one was 1.001, the rest 1.000; monte-carlo SE were all <0.005). Goodness-of-fit was inspected using the pp_check function of brms.

To test hypotheses, we used two approaches. First, for each model parameter we calculated the probability of direction (the pd-value), i.e. the posterior probability that the sign of a focal model parameter equals the sign of the marginal posterior distribution's median value for that parameter. A pd-value can range from 0.5 (half of the posterior distribution is on the same side of 0 as the median) to 1.0 (the whole distribution is on the same side as the median). To allow our readers to interpret the results themselves, we have shown all results with a pd>0.9. In old-fashioned frequentist terms, a pd-value above 0.975 would be considered "statistically significant" (≈ a p-value of 0.05). Yet, for interpretation of the results we encourage readers to look at both the pd-values and the effect sizes, as in our opinion this is a more transparent way of reporting science than clear cut-offs for significance. Second, for each directed arrow of the DAG, we compared the full model to a model without that arrow using the leave-one-out (LOO) information criterion, with the brms function loo_compare

(Vehtari *et al.* 2016). There were no colliders in the DAG (Cinelli *et al.* 2022), allowing for estimation of all direct effects from the same model. In our results and discussion we use the terminology 'affected by' to indicate all associations with a pd>0.9. However, we do not claim to have shown causal relationships between these variables. Moreover, we think that the discussion about what true causation is, is to be held in a different place than this manuscript.

Results

Fig. 2 shows the posterior distributions of all estimated effects, and Fig. 3 summarises these results in a DAG. Table 1 shows a summary of all results. Fig. 4 shows the effects of all variables with a pd > 0.9, and below we will discuss these effects.

<u>Dispersal</u>

Offspring of co-breeders had a higher probability of dispersing than those of dominant breeders, whether those dominants had co-breeders or not (Fig. 2; Fig. 4h; Table 1). On territories where helpers were present, offspring had a lower probability of dispersing (Fig. 2; Fig. 4g; Table 1). Lastly, offspring dispersal probability increased with increasing territory quality (Fig 2; Fig 4c; Table 1).

<u>Offspring sex ratio</u>

Dominant females with co-breeders and co-breeders both produced more sons than dominant females without co-breeders (Fig 2; Fig 4f; Table 1). Additionally, when more than one non-helper was present on a territory, the offspring sex ratio was more male-biased (Fig 2; Fig 4e; Table 1).

<u>Number of offspring</u>

The probability to produce more than one offspring increased with increasing territory quality (Fig 2; Fig4b; Table 1), and was higher when helpers were present than when helpers were absent (Fig. 2; Fig.

4d; Table 1). Additionally, dominant breeding mothers with a co-breeder produced more offspring than dominant breeding mothers without a co-breeder (Fig. 2; Fig. 4d; Table 1).

Helper presence and number of non-helpers

Helper presence was not affected by territory quality, but fewer non-helping subordinates were found with increasing territory quality (Fig. 2; Fig 4a; Table 1).

Discussion

In this study, we found that Seychelles warbler offspring were more likely to disperse when their mothers were co-breeders, territory quality was higher and helpers were absent. The offspring sex ratio of the focal mother was more male-biased when more than 1 non-helper was present on the territory, and when the mother was a dominant breeding female with a co-breeder. More offspring were born per mother when territory quality was higher and when helpers were present. Dominant breeding mothers produced more offspring when a co-breeder was present compared to when a co-breeder was absent. The number of non-helping subordinates on a territory decreased with increasing territory quality. All other effects had a lower pd (<0.9) and thus no evidence was found for these associations.

The differential dispersal tendencies of offspring from co-breeding and dominant mothers suggest a potential parental influence on dispersal tendencies. This is an intriguing result, as so far no clear evidence exists that birds can recognise genetic kin (Kempenaers & Sheldon 1996; Lattore *et al.* 2019). Since there is a clear difference in dispersal probability, somehow a difference between these offspring must exist. Possible explanations for this result include temporal differences in breeding activity between dominant breeders and co-breeders, leading to competitive disparities among offspring, which then could lead to weaker individuals being forced out of the territory. Co-breeders might lay their egg in the same clutch, but consistently after the dominant breeder, resulting in offspring of

330 dominant breeders having a competitive advantage. Alternatively, co-breeders might lay their egg at
331 a different moment in the breeding season, which could also lead to a competitive disparity between
332 dominant and co-breeder offspring. However, the precise mechanisms underlying these differences
333 warrant further investigation. A previous finding in the Seychelles warbler also suggests that dominant
334 breeders have some control on who is residing on the territory. Eikenaar *et al.* (2007) showed that
335 offspring were more likely to disperse when one or both of the dominant breeders had died or had
336 been replaced. However, in that study the difference in dispersal tendency can also be explained by a
337 difference in familiarity and is not necessarily caused by kin recognition. Alternatively, the difference
338 in dispersal tendency could be explained by a difference in the willingness of offspring to stay when
339 they have a low relatedness to the dominant breeding female. A decrease in willingness to become a
340 helper is expected from a kin-selection perspective, yet it is also possible for individuals to stay and
341 not help. If delaying dispersal is a way to increase condition (as discussed below), then there is no
342 apparent reason for offspring of co-breeders to decrease their willingness to stay. Hence, more
343 research on differences between offspring from dominant and co-breeding females is necessary.
344 Higher dispersal tendencies when there is low relatedness with dominant breeders is also found in
345 Florida scrub-jays (*Aphelocoma coerulescens*; Goldstein *et al.* 1998; Suh *et al.* 2020), Siberian jays
346 (*Perisoreus infaustus*; Ekman & Griesser 2002), and southern pied babblers (*Turdoides bicolor*; Nelson-
347 Flower & Ridley 2016).
348
349 Contrary to our expectations, offspring exhibited higher dispersal probabilities when hatched on high-
350 quality territories. We hypothesise that delaying dispersal could serve as a strategy to enhance
351 individual condition, if dominants tolerate offspring on their territory (Ekman & Griesser 2002). This
352 might be less necessary for offspring born on high-quality territories, as they might reach a good
353 condition faster, and hence can successfully compete for a position elsewhere. Similar results were
354 found in red kites (*Milvus milvus*), which dispersed earlier in life when food availability was artificially
355 increased (Scherler *et al.* 2023). Yet, opposite patterns have also been found in the Florida scrub-jay

356 (*Aphelocoma coerulescens*; Suh *et al.* 2020). However, this correlation might differ on the within-
357 territory level compared to the between-territory level. Within territories, offspring of lowest quality
358 might be outcompeted by siblings and thus forced to leave (Dietz *et al.* 2022), while at a between-
359 territory level, higher quality offspring might disperse more as they can outcompete others for a
360 position elsewhere. If delaying dispersal is a way of improving condition, it could also explain why fewer
361 non-helpers were found with increasing territory quality. Furthermore, offspring were less likely to
362 disperse when helpers were present. This result is puzzling, especially as it cannot be caused by an
363 indirect territory quality effect.
364
365 Interestingly, we were unable to reproduce the results of Komdeur *et al.* (1997), and did not find an
366 effect of territory quality and helper presence on the offspring sex ratio. However, we did not test
367 whether our and Komdeur's results significantly differed from each other, which is not possible,
368 because not all data necessary for our model is available for the years used in Komdeur's study (1993-
369 1995; e.g. genetic verification of number of offspring and co-breeder status). These different results
370 could be caused by differences in territory quality between then and now. Since the island was
371 restored in 1986 the natural vegetation has been improving in quality and volume. As all territories
372 have improved in quality and variance in territory quality has reduced over the years, it is possible that
373 sex ratio strategies have changed over time. Since many years were included in our analysis, the effect
374 of territory quality on offspring sex ratio could have changed, or weakened, resulting in no 'significant'
375 effect of territory quality on offspring sex ratios. In our dataset, the territory quality measure did not
376 seem to improve over years, but in Komdeur *et al.* (2016) an increase in territory quality was found
377 over time, where years were divided into blocks, while we used every year separately. We also ran our
378 model on subsets of the data to check for a temporal disappearance or weakening of this trend (1996-
379 2000, 2001-2005, 2006-2010, 2011-2015; see supplementary materials for results) and found no effect
380 of helper presence on the sex ratio in any of these subsets. Territory quality showed a weak association
381 with the offspring sex ratio between 2001-2005. However, this effect was not found in any of the other

subsets, and so a disappearance or weakening of this effect cannot be concluded. Alternatively, the difference in timing of measurement of the offspring sex ratio between Komdeur *et al.* (1997) and our study could cause the different results, as we only included chicks that are part of the pedigree and therefore generally at least have survived until fledging. In contrast, Komdeur *et al.* (1997) looked at nestlings. Hence any effect could have disappeared due to sex-specific mortality in early development, though this is impossible to study in new data, as most nests are not reachable (currently most nests are over 8 metres high in extremely soft wood trees). Moreover, Komdeur *et al.* (1997) did not distinguish between helpers and co-breeders, as parentage analysis was started later, and there was less information about the helping behaviour of individuals, which could have made a distinction between helpers and non-helping subordinates more difficult. In conclusion, more research is necessary to fully understand offspring sex ratio trends in the Seychelles warbler.

We also found that mothers were more likely to produce >1 young when territory quality was higher, which agrees with previous findings (Komdeur 1994). This also agrees with Both & Visser (2000), who experimentally increased territory quality of great tit (*Parus major*) territories and found a higher offspring production. Additionally, we found that dominant mothers produced more offspring when helpers were present, again in accordance with previous findings (Komdeur 1994). Such a correlation has also been found in cichlids (*Neolamprologus obscurus*; Tanaka *et al.* 2018) and meerkats (*Suricata suricatta*; Russell *et al.* 2003). Lastly, we found that dominant breeding mothers produced more offspring when a co-breeder was present. This could indicate that co-breeders are more effective helpers than non-breeding helpers, thereby increasing the production and/or survival of offspring from the dominant breeding female.

One important note that we like to reiterate is that some of the results mentioned above have a relatively small effect size, and that we encourage the reader to make their own judgement about our

findings based on effect sizes and pd-values. Hence, one should be careful not to read too much into the effects with small effect sizes and low pd-values.

Understanding which factors are associated with dispersal decisions when only observational data can be collected should be done using path analyses or structural equation models when it is expected that these factors could also be causally linked among each other (Busana 2021; Streiner 2005; Wright 1934), or at least a DAG-based justification should be provided about the factors that are included or excluded in the model (Cinelli *et al.* 2022; McElreath 2020). These methods can disentangle direct and indirect effects of each factor, and can separate correlated factors. Thus, they provide more insight than 'normal' (generalised) linear mixed models. Additionally, they can reach interesting insights as disentangled direct effects might show different patterns than total effects. Therefore, clear hypotheses (preferably with accompanying hypothetical networks) can improve knowledge on dispersal decisions and the evolution of cooperation. Additionally, DAGs could improve our understanding of the differences and similarities between different cooperative breeding study systems, and enhance our general understanding of the evolution of cooperative breeding and sociality. Last, it is important to note that our results indicate proximate effects on dispersal, while in the discussion we hypothesise ultimate reasons why these proximate factors might affect dispersal in Seychelles warblers.

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584 **Table 1**: The complete model output. Per sub model and per variable the median of the posterior
585 distribution is given as well as the 95% credible interval and the probability of direction (pd).
586 Additionally, we also used the leave-one-out (LOO) criterion to see if it would improve the model when
587 an arrow is left out. Here we indicate whether the complete model wins in this comparison, what the
588 difference is and what the standard error of that difference is.

Variable	Posterior median	Credible interval	pd	Complete model wins	Difference	SE of difference
Effects on helper presence						
Territory quality	0.03	-0.13 : 0.02	0.66	No	-0.7	0.5
Effects on number of non-helpers						
Territory quality	-0.17	-0.33 : 0.01	0.98	Yes	-1.7	2.1
Effects on number of offspring						
Territory quality	0.27	0.03 : 0.51	0.99	Yes	-1.4	2.3
Helper presence	0.52	-0.01 : 1.08	0.97	Yes	-1.0	1.9
1 non-helper (with respect to 0 helpers)	0.04	-0.56 : 0.63	0.56	No	-1.1	0.5
2 or more non-helpers (with respect to 0 helpers)	0.29	-0.69 : 1.15	0.73			
Dominant breeder with co-breeder (compared to	0.50	-0.15 : 1.09	0.94	No	-0.8	1.5

dominant breeder without co-breeder)						
Co-breeders (compared to dominant breeders without co-breeder)	0.18	-0.53 : 0.86	0.70			
Effects on offspring sex ratio						
Territory quality	0.02	-0.13 : 0.16	0.59	No	-0.9	0.3
Helper presence	0.02	-0.33 : 0.35	0.54	No	-1.0	0.3
1 non-helper (with respect to 0 helpers)	-0.13	-0.49 : 0.21	0.78	Yes	-0.8	2.2
2 non-helpers (with respect to 0 helpers)	0.58	-0.02 : 1.21	0.97			
More than 1 offspring (compared to 1 offspring)	-0.07	-0.46 : 0.32	0.63	No	-0.7	0.4
Dominant breeder with co-breeder (compared to dominant breeder without co-breeder)	0.36	-0.04 : 0.78	0.96	Yes	-0.5	2.0
Co-breeders (compared to dominant breeders without co-breeder)	0.29	-0.15 : 0.74	0.89			

Effects on offspring dispersal probability						
Territory quality	0.13	-0.03 : 0.28	0.95	Yes	-0.6	1.7
Helper presence	-0.51	-0.86 :-0.15	1.00	Yes	-3.8	2.9
1 non-helper (with respect to 0 helpers)	-0.19	-0.56 : 0.16	0.85	No	-1.2	1.2
2 non-helpers (with respect to 0 helpers)	0.05	-0.57 : 0.70	0.57			
More than 1 offspring (compared to 1 offspring)	0.13	-0.27 : 0.54	0.74	No	-0.5	0.7
Dominant breeder with co-breeder (compared to dominant breeder without co-breeder)	0.10	-0.31 : 0.50	0.68	Yes	-5.4	3.6
Co-breeders (compared to dominant breeders without co-breeder)	0.89	0.40 : 1.40	1.00			
Offspring sex ratio	-0.10	-0.42 : 0.21	0.74	No	-0.4	0.6

589

590

591 **Figure Legends**

592 **Figure 1: Directed acyclic graph (DAG) representing the hypothetical causal network underlying**
593 **offspring dispersal.** We expected Dispersal (D) to be associated with Territory Quality (TQ), Helper
594 presence (H), number of Non-Helpers (NH), number of Offspring (O), Status of the mother (Sm) and
595 the offspring Sex Ratio (SR). However, these variables were also expected to be associated with each
596 other. Each arrow in the figure indicates such an expected association, see methods for the reasoning
597 behind the arrows. Note that all factors in this DAG are measured on the territory or maternal level.

598

599 **Figure 2: Posterior distributions of all estimated associations.** The y-axis shows the associations from
600 which the regression coefficient is estimated. The coloured density plots show the 95% credible
601 interval of this distribution, the error bars show the 50% credible intervals of the distribution and the
602 black points show the median. Number of non-helpers and the status of the mother are variables with
603 three categories, and hence the distributions show the difference between the first category and the
604 other two categories (e.g. Sm[2] compares between category 1 (breeding female without co-breeder)
605 and 2 (breeding female with co-breeder) of status of the mother). For abbreviations on the y-axis see
606 Figure 1.

607

608 **Figure 3: Directed acyclic graph (DAG) of the hypothetical causal network, showing all results with**
609 **pd ≥ 0.9.** All direct effects with a pd<0.9 are indicated with dashed lines, while all direct effects with a
610 pd ≥ 0.9 are indicated with a solid line, including a positive or negative sign for the direction of the
611 effect.

612

613 **Figure 4: All effects of the causal network with a pd>0.9. (a)** The probability to produce more than
614 one offspring increases with increasing territory quality. **(b)** The probability of a mother to produce
615 more than 1 offspring increases when helpers are present compared to when helpers are absent. **(c)**
616 The probability that a mother produces more than one offspring is higher when she is a dominant

breeder with a co-breeder compared to when she is a dominant breeder without a co-breeder. **(d)** The probability of 0 non-helpers (0 NH), 1 non-helper (1 NH) or more than 1 non-helper (>1 NH) is affected by territory quality. **(e)** The proportion of sons a mother produces is affected by the number of non-helping subordinates. **(f)** The proportion of sons a mother produces is affected by the status of the mother. **(g)** the probability that offspring disperses increases with increasing territory quality. **(h)** The dispersal probability of offspring decreases when helpers are present compared to when these are absent. **(i)** The probability that offspring disperse is affected by the status of the mother. The shadows in (a),(d) and (g) indicate the 95% credible intervals. In the other graphs the median values of the distributions are indicated with the dot, and the error bars indicate the 95% credible intervals. In (c), (f) and (i) the status of the mother is indicated by numbers, 1 indicates a dominant breeding female without co-breeders, 2 indicates a dominant breeding female with co-breeders, and 3 indicates co-breeders.

Figure 1

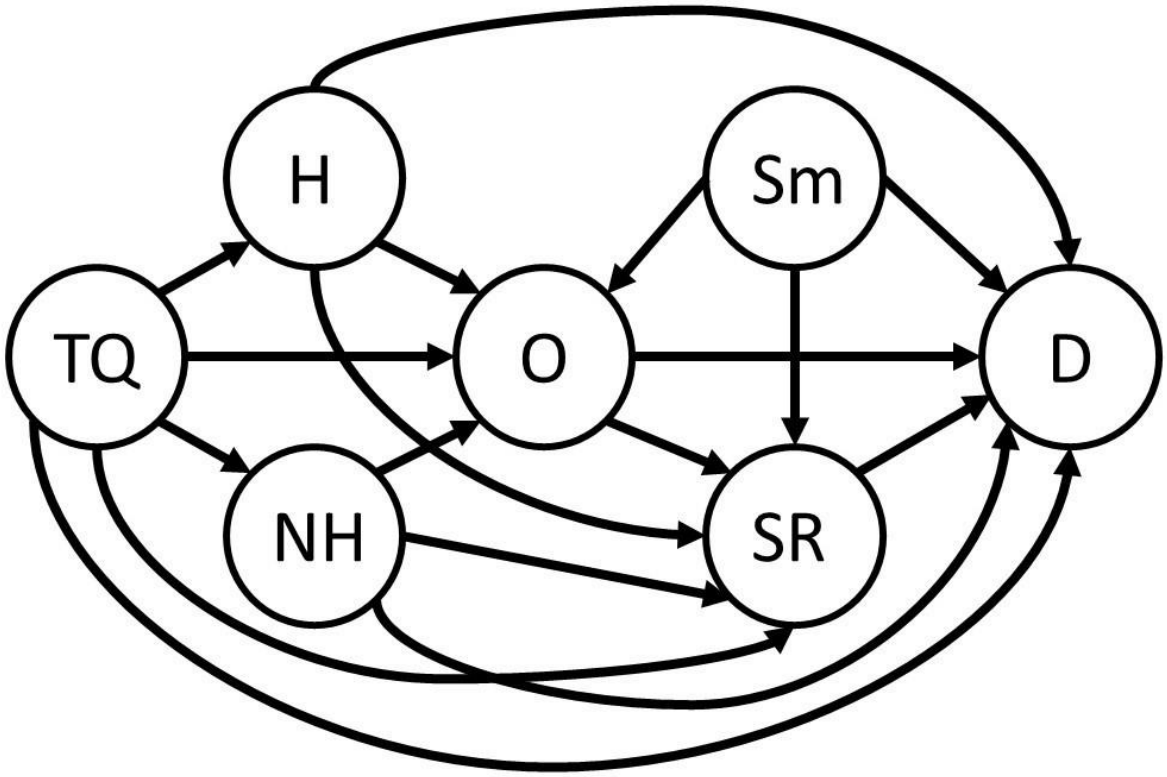
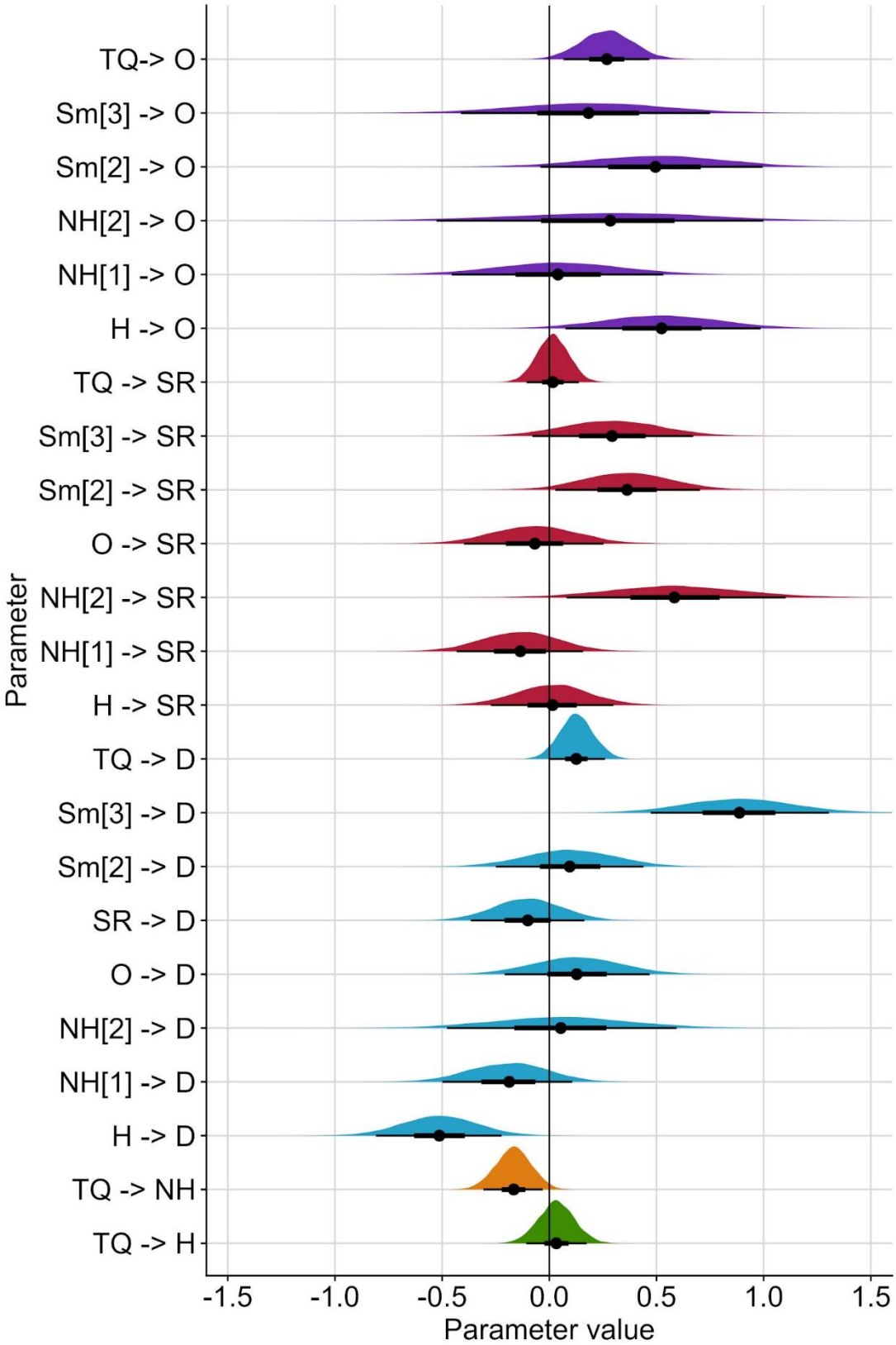
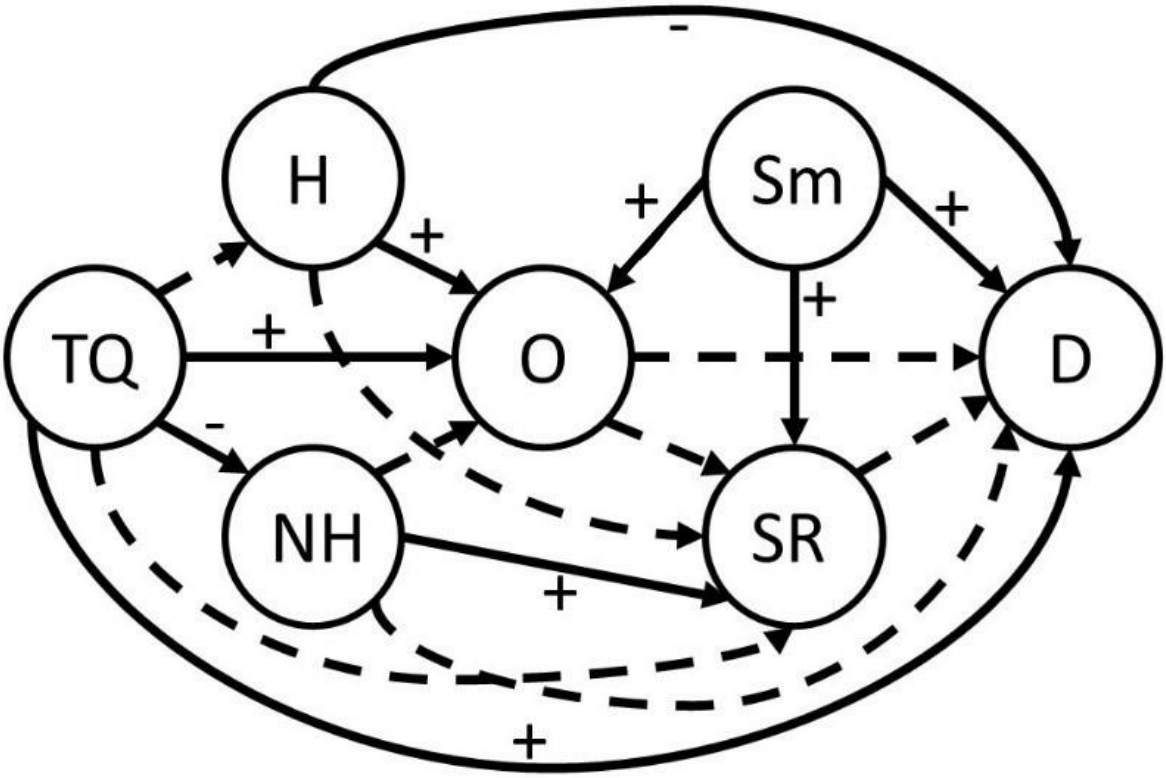


Figure 2


TQ-> O
Sm[3] -> O
Sm[2] -> O
NH[2] -> O
NH[1] -> O
H -> O
TQ -> SR
Sm[3] -> SR
Sm[2] -> SR
O -> SR
NH[2] -> SR
NH[1] -> SR
H -> SR
TQ -> D
Sm[3] -> D
Sm[2] -> D
SR -> D
O -> D
NH[2] -> D
NH[1] -> D
H -> D
TQ -> NH
TQ -> H
Parameter
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Parameter value

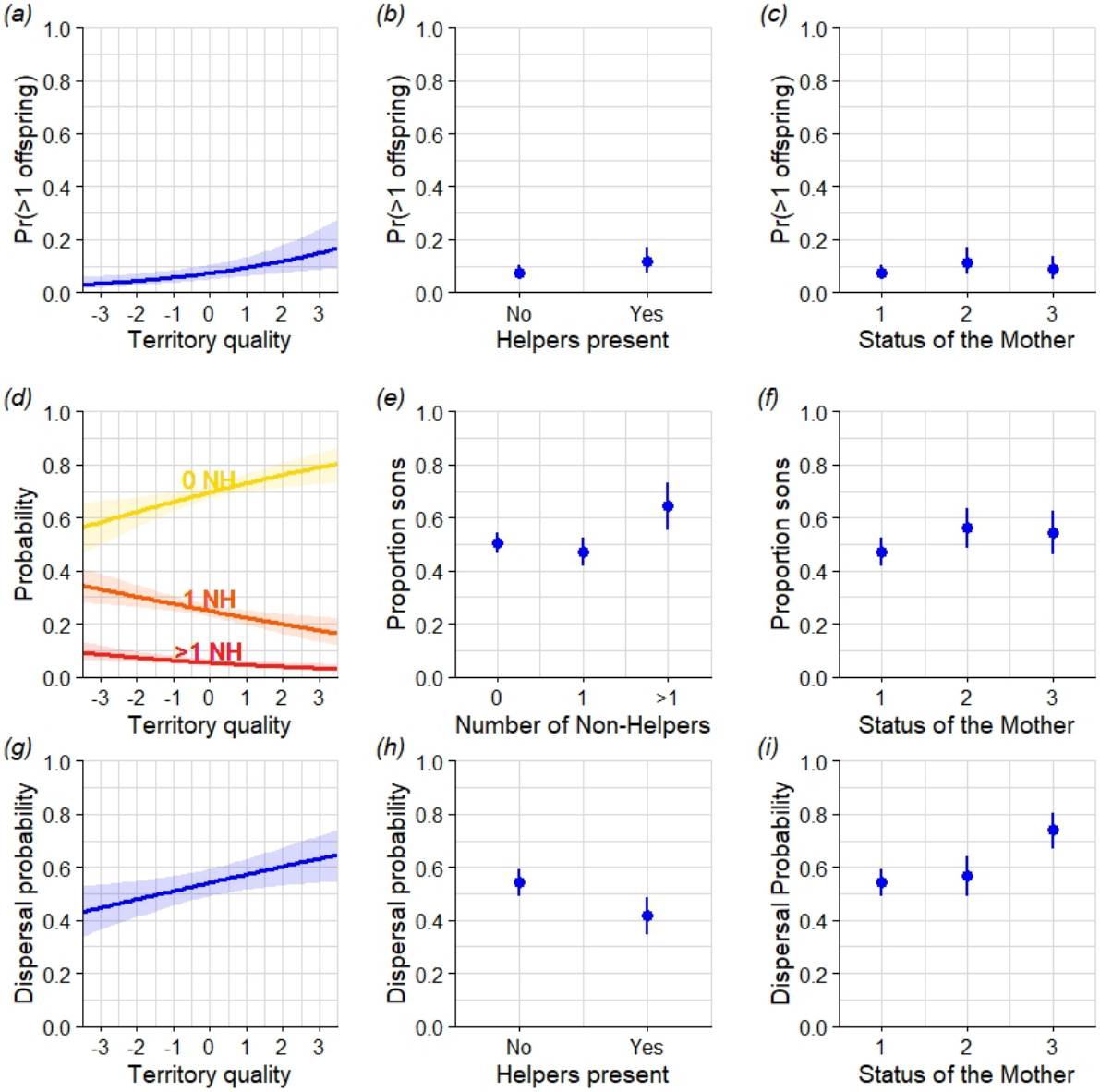
636 **Figure 3**



637

638

Figure 4


(a)
Pr(>1 offspring)
Territory quality
(b)
Pr(>1 offspring)
No
Yes
Helpers present
(c)
Pr(>1 offspring)
Status of the Mother
(d)
Probability
0 NH
1 NH
>1 NH
Territory quality
(e)
Proportion sons
Number of Non-Helpers
(f)
Proportion sons
Status of the Mother
(g)
Dispersal probability
Territory quality
(h)
Dispersal probability
No
Yes
Helpers present
(i)
Dispersal Probability
Status of the Mother