Title

Sex-specific covariation between exploratory behavior and natal dispersal strategies in a wild cooperative breeding passerine

Running title

Dispersal and animal personalities in Seychelles Warblers

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Sex-specific covariation between exploratory behavior and natal dispersal strategies in a natural cooperative breeding passerine population

Abstract

Natal dispersal is a major life-history strategy that has pervasive consequences on the spatial and genetic structure of populations. Between-individual variation in personality traits is increasingly recognized as an important determinant of natal dispersal via ‘personality-dependent dispersal’. However, few studies have investigated the importance of personalities in the context of delayed natal dispersal, in part due to the difficulty of monitoring the movements of individuals in open populations and over long periods of time. Here, we assessed personality-dependent natal dispersal strategies in an island population of cooperatively-breeding Seychelles warblers *Acrocephalus sechellensis,* where individuals have the option to delay dispersal in favor of remaining at their natal site. Specifically, we tested the effect of novel environment and novel object exploration on whether an individual delayed natal dispersal following sexual maturity, as well as the age of dispersal and the distance dispersed. We found males, but not females, with higher novel environment exploration scores were more likely to delay natal dispersal. In contrast, females that were more exploratory in a novel environment dispersed further, but this was not the case for males. The sex-specific nature of the relationship between exploration and natal dispersal in this system highlights the importance of considering sexual dimorphism in life-history strategies when investigating personality-dependent dispersal. Future studies should continue to assess the implications of animal personality on delayed natal dispersal, particularly in cooperatively breeding systems where the timing of dispersal has important implications on reproduction and fitness.

Keywords: cooperative breeding, delayed natal dispersal, exploration, personality-dependent dispersal, birds

Introduction

Natal dispersal, the movement of an individual from their birthplace to a site of first breeding, is a fundamental life-history strategy that plays a crucial role in many ecological and evolutionary processes (Clobert et al. 2001; Clobert et al. 2004). Natal dispersal has important implications on the persistence of spatially structured populations (Pulliam 1988), gene flow (Bohonak 1999) and ecological invasions (Sakai et al. 2001). Within-species variation in dispersal strategies can be contingent on many extrinsic (e.g. competition, food availability; Komdeur 1992) and intrinsic (e.g. age, sex; Bowler and Benton 2005) factors. However, due to its complexity the precise mechanisms contributing to between-individual variation in natal dispersal remain unclear.

Animal personalities, a phenomenon where individuals consistently vary between one another in behavioral traits, have been proposed to play a functional role in facilitating dispersal (Réale et al. 2007; Cote et al. 2010). As both departure from a natal territory and settlement at a new site is often associated with cost to the disperser (Bonte et al. 2012), individuals who possess more ‘reactive’ or ‘riskier’ behavioral traits, are expected to show a greater dispersal tendency. For example, bolder individuals should be less fearful of potential predators encountered during movement (Fraser et al. 2001), aggressive individuals are more likely to win in territorial disputes with conspecifics (Duckworth and Badyaev 2007) and highly active dispersers are more likely to travel further and encounter suitable habitats while prospecting (Debeffe et al. 2014). This has been documented in a variety of taxa, including birds (Dunn et al., 2011; Duckworth & Badyaev, 2007), mammals (Myers and Krebs 1971; Krackow 2003; Hoset et al. 2011; Debeffe et al. 2012), fish (Cote et al. 2013; Edelsparre et al. 2013) and insects (Bonte et al. 2004; Gyuris et al. 2011).

Exploration, the measure of an individual’s response to novelty (Verbeek et al. 1994), has been found to play an important role in personality-dependent dispersal (Cote et al., 2010; Wey et al., 2015). Slow explores, who are more avoidant of novelty compared to fast exploring counterparts, are predicted to be deterred by novel environments and situations encountered during movement to a new site, and subsequently forgo immigration into a new population (Guillette et al. 2009; Rodríguez-Prieto et al. 2011). In comparison, fast explorers are more likely to foray away from their natal site and encounter breeding vacancies due to the superficial nature of their movement. Fast explorers not only show a greater tendency to disperse away from their natal populations, but often travel longer distances when doing so. For example, Trinidad killfish *Rivulus hartii*, that readily explored a novel environment, were shown to disperse longer distances in a mark-recapture study (Fraser et al. 2001). Further, this association can be sex-specific, where the strength, direction or presence of personality-dependent dispersal can vary relative to the costs of dispersal in males and females (Gros et al. 2008; Immonen et al. 2018). This has been demonstrated in two separate wild populations of great tits *Parus major*, where post-fledging movements were greatest for fast exploring females but showed no relationship with exploration in males (Dingemanse et al. 2003; van Overveld et al. 2014).

One element of personality-dependent dispersal that has been studied comparatively less but is equally important for individual fitness and population dynamics, is the timing of natal dispersal. Deciding to delay dispersal in favour of remaining at the natal site is an important as it not only influences timing of reproduction, but is also associated with dispersal-related mortality risks (Koenig et al. 1992; Cockburn 1998). In accordance with current literature, individuals who possess risk-taking traits, such as exploration, are expected to favour immediate, rather than delayed natal dispersal as they are less deterred by the potential costs associated with movement to a new site (Cote et al. 2010). This has been demonstrated to a certain extent in captivity, where more active round gobies *Neogobius melanostomous*, and exploratory male house mice *Mus musculus musculus*, had shorter dispersal latency than risk-averse individuals (Krackow 2003; Thorlacius et al. 2015). However, empirical evidence is limited, particularly in cooperatively breeding systems where adults can delay natal dispersal (and breeding) in favor of helping to raise young produced by other group members (Cockburn 1998). This is a least partly due to the difficulty of monitoring the movement of individuals in open populations, as long-distance dispersal can often not be distinguished from death (Tesson and Edelaar 2013). Further, quantifying elements of dispersal can often be challenging in populations where natal and breeding sites overlap imperfectly, or if there are no clear territorial or range boundaries (Spiegel et al. 2017).

Here, we investigate whether individuals with differing exploratory personality traits demonstrated varied natal dispersal strategies in a wild population of the facultatively cooperatively-breeding Seychelles warbler *Acrocephalus sechellensis*, on Cousin Island. This system provides an excellent opportunity to study personality-dependent dispersal for multiple reasons. First, Seychelles warblers can adopt a variety of life-history strategies, including either immediate or delayed natal dispersal following sexual maturity (Komdeur et al. 2016). Second, they do not perform inter-island dispersal (Komdeur et al. 2004); virtually the whole population is colour ringed and annual resighting rates are high (Brouwer et al. 2010; Hammers et al. 2015), thus individuals that disappear can be accurately assumed to have died rather than dispersed long distance (Koenig et al. 1996; Komdeur et al. 2004). Third, all birds are individually marked and monitored from birth to death, meaning we can obtain high resolution data on age at dispersal, as well as distance travelled – something that is hard to obtain in wild populations (Koenig et al. 1996). Fourth, alternative drivers of dispersal have been explored in Seychelles warblers, and so can be accounted for in analyses, including sex (Eikenaar et al. 2008; Kingma et al. 2017; Groenewoud et al. 2018), natal group size (Eikenaar et al. 2007), island-wide population (Eikenaar et al. 2007; Eikenaar et al. 2009) and island-wide food availability (Groenewoud et al. 2018).

Cousin Island has reached carrying capacity (Komdeur et al. 2016), and competition for breeding vacancies is high, thus we expect more exploratory Seychelles warblers to be more likely to disperse from their natal territory, disperse at a younger age, and be more likely to travel longer distances compared to their slow-exploring counter-parts. As male and female Seychelles warblers adopt different life-history strategies, where females have the opportunity to reproduce as subordinates, but males must first obtain a dominant breeding position (Komdeur 1994), we also tested these hypotheses separately in each sex. Specifically, we predict that whilst the covariance between exploration and natal dispersal strategies to be similar in both sexes, that exploration will play a stronger functional role in males.

Methods

Study system

The Seychelles warbler is a facultatively cooperatively breeding passerine endemic to the Seychelles archipelago (Richardson et al. 2002). On Cousin Island (0.29 km^2; 4°20′S, 55°40′E), this species has been studied since 1985, and have reached a carrying capacity of ca. 320 individuals across ca. 115 territories (Komdeur 1991; Komdeur and Pels 2005; Hammers et al. 2015)). In this population, offspring do not disperse before reaching sexual maturity at 6 months of age (Komdeur 1996), and often remain on their natal territory as subordinates (ca. 50% of territories support 1–5 subordinates: Richardson et al., 2002; Hammers et al., 2019). Subordinates of either sex may become helpers under specific circumstances (approx. 20% of males and 42% of females; Hammers *et al.*, 2019), who assist in caring for the dominant breeding pair's offspring to differing extent (Komdeur 1991; Richardson et al. 2003b).

Each year during the minor (January–February) and major (June–September) breeding seasons, we catch as many individuals as possible using mist nets. Individuals caught for the first time are given a unique ring combination (a British Trust for Ornithology metal ring and 3 colour rings). Since 1997, virtually all (≥96%) individuals have been ringed (Hammers et al. 2015). Where available, lay, hatch or fledge dates are used to age individuals (Richardson et al. 2003a). Otherwise, eye colour at first capture indicates whether an individual is either a fledgling (grey eyes; 1–5 months), subadult (light brown eyes; 6–12 months) or adults (dark brown eyes; >12 months) (Komdeur 1992). All birds are blood sampled using brachial venipuncture for molecular sexing and parentage assignment (Richardson et al. 2001; Sparks et al. 2021) and their morphometric measurements recorded (Richardson et al. 2001). During the breeding seasons, island censuses are performed regularly (at least weekly for each territory) to determine each individuals' resident territory and breeding status (mean ± SD number of dominance vacancies between consecutive major breeding seasons: males = 29.9 ± 7.2, females = 29.8 ± 6.9, see Figure S1). Territories are usually stable between years and territory boundaries are identified based on spacing behavior and conflicts with intruding conspecifics (Komdeur 1991). Migration to or from the island is virtually absent (<0.1%, N = 1924, Komdeur *et al.*, 2004) and re-sighting probabilities between years are very high: 0.98 ± 0.01 SE for birds over two years of age and 0.92 ± 0.02 SE for younger individuals (Brouwer et al. 2010). This means accurate hatch and death dates are recorded, and death is not confounded with migration.

Previous work has identified multiple extrinsic drives that affect dispersal in the Seychelles warbler. To account for them, we included in analyses the natal group size (Eikenaar et al. 2007), the island-wide population size (Eikenaar et al. 2007; Eikenaar et al. 2009) and island-wide insect abundance (Groenewoud et al. 2018), all from the individual's first year of life (excluding individuals <6 months old in population and group size estimates). Seychelles warblers are insectivorous and obtain most of their arthropod prey from gleaning the undersides of leaves (Komdeur 1991). In each month of the major breeding season, we count the number of arthropods on the underside of 50 leaves for the most abundant plant species in 14 locations (Komdeur 1992). Vegetation cover is surveyed at 20 random locations within each territory once during the breeding season, where the presence (>50% cover) or absence of vegetation was scored at height intervals of 0–0.75 m, 0.75–2 m and nine 2 m intervals thereafter. A territory's insect density was calculated as $\mu_{x=1}(c_x, i_x)$, where c_x is the relative cover for species x and i_x is the mean arthropod abundance per unit leaf area for species x (Spurgin et al. 2018). As insect availability fluctuates with inter-annual variation in precipitation (Komdeur and Daan 2005), and surveys are conducted under varying weather conditions within a season, we calculated the mean number of insects per unit leaf area over all surveys within a season.

Personality assays

We assayed two behaviors following methodology developed by Edwards et al., (2017) (based on: Verbeek et al. 1994). Novel environment exploration was assayed during both major and minor breeding seasons 2012–2015, 2019 and 2021, as well as the minor breeding season in 2020 and 2022. Novel object exploration assays were conducted during all of these seasons apart from the major and minor seasons in 2012. In each assay an individual was introduced to a novel environment (Oxygen 4 tent) containing three artificial trees, and the total number of hops, flights and unique trees visited (hereafter, "exploration score") were recorded over 5 minutes. After the novel environment assay, individuals remained in the tent for 2 minutes before the novel object assay (see acclimatization tests: Edwards et al. 2015; Edwards et al. 2017), where a pink toy was introduced and exploration score recorded. Over the sampling period, tent colour (blue/green) and branch orientation (diagonal/parallel) varied, and had a significant effect on exploration score (Cox et al. 2022). Both novel environment and object exploration are repeatable (0.23, 95% credible interval [CrI] = 0.08–0.36, and 0.37, 95% CrI = 0.04–0.59, respectively) and novel environment exploration is heritable (0.17, 95% CrI = 3e-4–0.33; Edwards et al., 2017).

Natal dispersal

We focused on three aspects: whether an individual delayed dispersal (i.e. >12 months) (yes/no), age at natal dispersal (months) and dispersal distance (meters). We define natal dispersal as an individual departing their natal territory and occupying a dominant breeding position in a new territory for at least one field season (Clobert et al. 2001). This excluded 36 individuals who performed natal dispersal to a subordinate position and 21 individuals that inherited a dominant breeding position in their natal territory, as both tactics are considered separate natal dispersal strategies (Eikenaar et al. 2009). Dispersal date was estimated as the mid-point between when an individual was last seen in their natal territory and first seen in their new territory (Groenewoud et al., 2018). Age at dispersal was the number of months from hatch to departure date. Following Eikenaar et al., (2007) we defined delayed dispersal as dispersal after 12 months old (Figure S2) (mean ± SD age at dispersal = 15.4 ± 7.9 months). Most birds (243/285) dispersed between breeding seasons, so we used the midpoint between breeding seasons (mean ± SD number of days between fieldwork periods included in this study = 183 ± 77 days). As fieldwork did not occur during summer 2021 due to Covid restrictions, this created an interval between winter 2021 and winter 2022 of ca. 9 months, and so natal dispersal events that occurred during this period were excluded to prevent error in interval calculations. Using ArcGIS 10.6 (ESRI 2021), we measured dispersal distance in meters between the geometric centers of the natal and non-natal breeding territory. Previous research has shown mean age at natal dispersal (± SE) to a dominant breeding position of 1.34 ± 0.05 years for males and 1.23 ± 0.04 years for females (female vs. male: 0.10 ± 0.06, $F = 2.59$, $p = 0.11$; Groenewoud et al. 2018). In comparison, mean dispersal distance (± SE) was 109 ± 8.39 meters for males and 232 ± 8.99 meters for females (female vs. male: −1.21 ± 0.12, $F= 103.2$, $p < 0.001$; Groenewoud et al. 2018)

Statistical analyses

We performed analyses using R v.4.0.2 (RStudio Team 2022) and the package MCMCglmm v 4.2.1 (Hadfield 2010). We ran all analyses using bivariate generalized linear mixed models in a Bayesian framework, thus avoiding the “stats on stats” approach associated with using best linear unbiased predictors (Houslay and Wilson 2017). Personality score (novel environment/object exploration) was included as a response variable alongside a second response variable of either delayed natal dispersal (yes/no), age at dispersal (months) or distance (meters). As sex mediates personality-dependent dependent dispersal in other species (Dingemanse et al. 2003; Krackow 2003; van Overveld and Matthysen 2010), and sexual dimorphism in life-history strategies occurs in this system (Komdeur et al. 2016), all models were run separately for males and females. As fewer individuals were tested for novel object exploration ($N = 192$) compared to novel environment exploration (*N* = 285; see Table S1–2), models were ran using novel environment and object exploration separately. Poisson error distributions were fit for all response variables apart from delayed natal dispersal (yes/no), which was fit using a threshold distribution (Figure S3–4).

Methodological fixed effects previously shown to affect exploration score in this species were fitted, including assay number (to control for habituation), and age (years) as both linear and quadratic terms (Cox et al. 2022). Tent colour (blue/green) for novel environment exploration and branch orientation (diagonal/parallel) for novel object exploration were also included as fixed effects (Cox et al. 2022). Fixed effects known to influence warbler dispersal were fitted in all models, including: natal group size (Eikenaar et al. 2007), natal island-wide population (where individuals <6 months old were excluded for group size and island-wide population counts) (Eikenaar et al. 2007; Eikenaar et al. 2009) and island-wide insect density during the major breeding season (as explained earlier) (Groenewoud et al. 2018). All continuous fixed effects were standardized by subtracting the mean and dividing by two standard deviations in arm v.1.13-2. We also checked there was no collinearity between fixed effects by ensuring Variance Inflation Factors (VIFs) were <3. Random effects included observer ID for exploration, dispersal year (Table S3) for dispersal distance and bird ID for both exploration and all measures of dispersal.

Following Houslay & Wilson (2017), correlation coefficients were calculated at the between-individual level (r_i) using the posterior mode and corresponding 95% credible intervals. In brief, we divided the focal between-individual covariance by the square-root of focal between-individual variance of both traits multiplied together (O'Dea et al. 2021). All models used an uninformative Inverse-Wishart prior (V = diag(n) + 0.002, nu = n + 0.002; where n is the number of response variables) for both the residual and random effects structure. As multiple repeats were obtained for exploration score, compared to the single values for the life-history traits, we used 'covu = TRUE' in the primary residual structure specified in the prior to allow covariance between the individual-level random effect for the exploratory trait and the residual variance of the life-history trait (see supplementary material of Thomson et al., 2017). Posterior distributions were sampled every 550 iterations, with a burn-in of 200,000 and a run of 4,200,000 iterations. We visually checked time-series plots of model parameters and assessed multiple convergence diagnostics, including autocorrelation (<0.1) values, effect sizes (≥1,000), Geweke tests and Heidel diagnostics.

Ethical statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. We received approval from Nature Seychelles to conduct fieldwork on Cousin Island Nature Reserve. The Seychelles Department of Environment and the Seychelles Bureau of Standards authorized fieldwork and sampling.

Results

Delayed natal dispersal was more common than early dispersal in both males (N = 110, 69%) and females (N = 74, 59%) (Figure S2), with the mean (± SD) age at dispersal being 15.9 ± 8.2 months for males and 14.9 ± 7.6 for females. The mean (± SD) distance travelled between the natal site and site of first breeding was 126 ± 117.5 meters for males and 252.8 ± 158.3 meters for females.

We found males, but not females, with higher novel environment exploration scores were more likely to delay natal dispersal (Figure 1, Tables S4). However, we found no association for either sex between exploration and age at dispersal in months (Figure 1, Table S4). In contrast, females that were more exploratory in a novel environment dispersed further, but this was not the case for males (Figure 1, Table S4) (see Tables S5–7 for variance components of random effects for all models).

Males tested for novel environment exploration were more likely to delay natal dispersal and disperse at an older age when they experienced poor island-wide food availability during their first year of life (Tables 1–2), as well as disperse at an older age if their natal group size was small (Table 2). Females who spent their early-life in a larger natal group were also more likely to delay natal dispersal and disperse at an older age (Tables 1–2). Whereas none of these estimates affected dispersal distance (Table 3).

Discussion

In this study, we analyzed the association between novel environment exploration and novel object exploration with natal dispersal separately in males and females. While all models displayed a positive relationship between increased exploration and delayed natal dispersal, as well as age at dispersal, only male novel environment exploration scores were a significant predictor of delayed natal dispersal. Further, female, but not male, novel environment exploration was positively associated with distance travelled between the natal and breeding territory.

That delayed natal dispersal was positively correlated with male novel environment exploration conflicts with the hypothesis that risk-averse individuals are deterred by the costs associated with dispersal. In our population, less exploratory male Seychelles warblers were more likely to depart from their natal territory as yearlings rather than delay departure. While the causality of this relationship cannot be resolved based on correlational data alone, there are several possible explanations for this apparently contradictory result. First, exploratory behavior may constrain an individual’s ability to disperse from their natal territory as a yearling. In Seychelles warblers, dominant breeding pairs will often engage in fights when defending their territory against non-resident conspecifics (Komdeur 1992; Kingma et al. 2016a) and prospecting individuals often suffer costs to body condition (Kingma et al. 2017). If the superficial nature of exploratory movement increases the likelihood of encountering conspecifics, then prospecting behavior may be more costly for fast-exploring individuals. Such negative effects may be exacerbated in males, which are more likely to be attacked by conspecifics when intruding into non-natal territories (Kingma et al. 2017). Indeed, male Seychelles warbler floaters – individuals that prolong the transience stage of dispersal – have lower levels of survival compared to dispersers who obtain a dominant breeding position immediately following departure from their natal site. In comparison, females suffer similar mortality regardless of whether they float or disperse immediately (Kingma et al. 2016b; Kingma et al. 2017; Groenewoud et al. 2018). These sex-specific costs suggest that exploratory movement could be disproportionately costly for males, thus resulting in more exploratory individuals being more likely to delay natal dispersal.

Alternatively, exploratory behavior may provide a competitive advantage to individuals who wish to access the benefits of philopatry (Stacey and Ligon 1991; Komdeur 1992). Across many taxa, exploratory traits have been shown to covary with agonistic behaviors, such as aggression, boldness and asociality, to form behavioral syndromes (Sih et al. 2004; Garamszegi et al. 2013). In group-living species, aggressive individuals have been shown to drive away less aggressive counter parts (Rudin and Briffa 2012; Kaiser et al. 2019). This was demonstrated in a study on western mosquitofish *Gambusia affinis*, where individuals were more likely to disperse from populations containing bolder or more asocial individuals (Cote et al. 2011). Personality of kin can also affect other dimensions of dispersal, as shown in male Western bluebirds *Sialia Mexicana*, where individuals with aggressive kin are more likely to disperse longer distances (Aguillon and Duckworth 2015). If such behavioral syndromes and social dynamics exist within our Seychelles warbler population, then less exploratory male subordinates may be encouraged to depart earlier from their natal territory, allowing more exploratory males to gain the benefits of residing in a smaller group.

Another competitive advantage of exploratory behavior may be related to an individual's ability to 'pay-to-stay' in their natal territory (Gaston 1978). While it is usual for breeding pairs of

Seychelles warblers to rear offspring and contribute to territory defense, not all subordinates will necessarily help with these activities (Komdeur and Edelaar 2001; Richardson et al. 2002; Richardson et al. 2003b). It is possible that exploratory males may be better able to pay-to-stay by helping the breeding pair, thus resulting in delayed dispersal. Whilst empirical studies investigating behavioral syndromes between helping and exploration are limited, research on the cooperatively breeding Lake Tanganyika cichlid fish *Neolamprologus pulcher*, showed that risk-taking traits, such as high aggression and activity, co-varied with helping, particularly in riskier roles such as territory defense (Bergmüller and Taborsky 2007; Le Vin et al. 2011). Further, multiple avian studies have highlighted that fast explorers elicit stronger defensive responses to a territorial threat (Amy et al. 2010; Snijders et al. 2014). Therefore, if exploratory individuals display a greater propensity to help at their natal site, they may be of greater value to the breeding pair and be allowed to stay. As male Seychelles warblers are less likely to help than females (Richardson et al. 2002; Richardson et al. 2003b), as well as disproportionately contribute to nest guarding as they do not assist with incubation (Komdeur and Kats 1999; Veen et al. 2000), the pay-to-stay effect may be more pronounced in males, resulting in males demonstrating a significant relationship between increased exploration and delayed natal dispersal.

Females, but not males, with high novel environment exploration scores travelled longer distances to their new territory compared to their less exploratory counterparts. This aligns with current literature, which suggests exploratory individuals are less risk adverse (Groothuis and Carere 2005), making them more likely to prospect over large ranges and identify breeding vacancies further away from their natal site (Cote et al. 2010; Réale et al. 2010). The sex-specific nature of this relationship has also been shown in great tits, where exploratory females, but not males, dispersed longer distances (Dingemanse et al. 2003; van Overveld et al. 2014). However, more studies are required to understand the mechanistic link driving sex-specific covariation between personality and dispersal distance. In the Seychelles warbler, subordinate females show higher rates of prospecting compared to subordinate males (Kingma et al. 2016a), which could potentially facilitate dispersal of longer distances compared to males, and thus increase the likelihood of a syndrome developing between exploration and dispersal distance. Further research into the functional role of exploration on dispersal is required to fully understand the sex-specific nature of personality-dependent natal dispersal in this system.

Interestingly, we found that while novel environment exploration scores covaried with natal dispersal strategies, novel object exploration did not, despite the two traits forming a behavioral syndrome in previous studies (Edwards et al. 2017; Cox et al. 2022). One explanation is that each trait plays a distinct functional role, whereby exploration of a novel environment has greater ecological relevance to territory prospecting behavior in the wild and therefore more likely to be linked with dispersal strategies (Carter et al. 2012; Takola et al. 2021). However, whilst not significant, the direction of the relationships between novel object exploration and dispersal tactics paralleled those shown for novel environment exploration. Therefore, it is possible that as relatively less individuals were tested for novel object exploration, the absence of a significant relationship may have resulted from a lack of power to detect an effect.

Summary

In summary, we have shown exploratory traits affect natal dispersal strategies in the Seychelles warbler in a sex-specific manner. Contrary to our prediction, males, but not females, with high novel environment exploration scores were more likely to delay natal dispersal to a dominant position, which suggests individuals with riskier traits do not always adopt fast life-history strategies. We also show that fast exploring females, but not males, are likely to disperse longer distances. The mixed nature of our results suggests the functional role of exploratory traits on natal dispersal can be sex-specific, where the strength, direction and presence of an association vary depending on ecological context of the study system. Future studies should continue explore the effect of animal personalities on delayed natal dispersal, whilst being careful to consider the importance of species- and sex-specific ecology prior to making predictions.

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Figure legends

Figure 1. Correlation estimates between either **a**) novel environment exploration (*N*=160 and 125 males and females, respectively) or **b**) novel object exploration (*N*=112 and 80 males and females, respectively) and either delayed natal dispersal (yes/no), age at natal dispersal (months) or dispersal distance (meters) in the Seychelles warbler. Correlations were estimated as the mode of the posterior distribution with 95% higher probability density credible intervals (CrIs) from bivariate Bayesian mixed-effects models. Lack of statistical significance indicated by 95% CrIs overlapping zero.

Tables and table legends

Table 1. Bivariate MCMC model results investigating the covariation between either novel environment exploration or novel object exploration and delayed natal dispersal (yes/no) as response variables in the Seychelles warbler. Reported are the posterior modes and their 95% credible intervals of all fixed effects in the model. Fixed effects for exploration include: age at exploration test (years) (quadratic and linear terms), assay number, and tent colour (contrast level=blue) for novel environment exploration, or branch orientation (contrast level=parallel) for novel object exploration. For delayed natal dispersal, fixed effects include natal group size, island-wide population during hatch field period and island-wide food availability during hatch field period. Statistical significance of fixed effects is indicated by 95% credible intervals not overlapping zero and these are denoted in bold.

	(a) Novel environment exploration		**(b) Novel object exploration**	
	Male	Female	Male	Female
Exploration : Age	**1.693 [0.676, 2.676]**	**1.903 [0.616, 3.191]**	0.699 [-0.641, 1.991]	**5.007 [2.422, 7.500]**
Exploration : Age^2	**-1.001 [-1.88, -0.087]**	**-1.199 [-2.298, -0.082]**	-0.106 [-1.207, 1.046]	**-3.751 [-6.003, -1.656]**
Exploration : Assay number	**0.296 [0.147, 0.453]**	**0.720 [0.491, 0.970]**	**0.597 [0.219, 1.007]**	**0.859 [0.308, 1.387]**
Exploration : Tent colour (green)	**-0.405 [-0.786, -0.018]**	-0.222 [-0.699, 0.277]		
Exploration : Branch orientation (parallel)			-0.351 [-0.867, 0.134]	-0.262 [-0.973, 0.470]
Delayed dispersal : Natal group size	0.694 [-0.155, 1.490]	**2.186 [1.095, 3.225]**	0.829 [-0.082, 1.781]	**1.594 [0.448, 2.778]**
Delayed dispersal : Island-wide population	-2.308 [-5.656, 0.834]	-0.272 [-3.861, 3.463]	-2.296 [-4.976, 0.390]	0.076 [-3.290, 3.230]
Delayed dispersal : Island-wide food	**-0.698 [-1.323, -0.099]**	0.695 [-0.078, 1.454]	-0.471 [-1.065, 0.154]	0.402 [-0.388, 1.196]

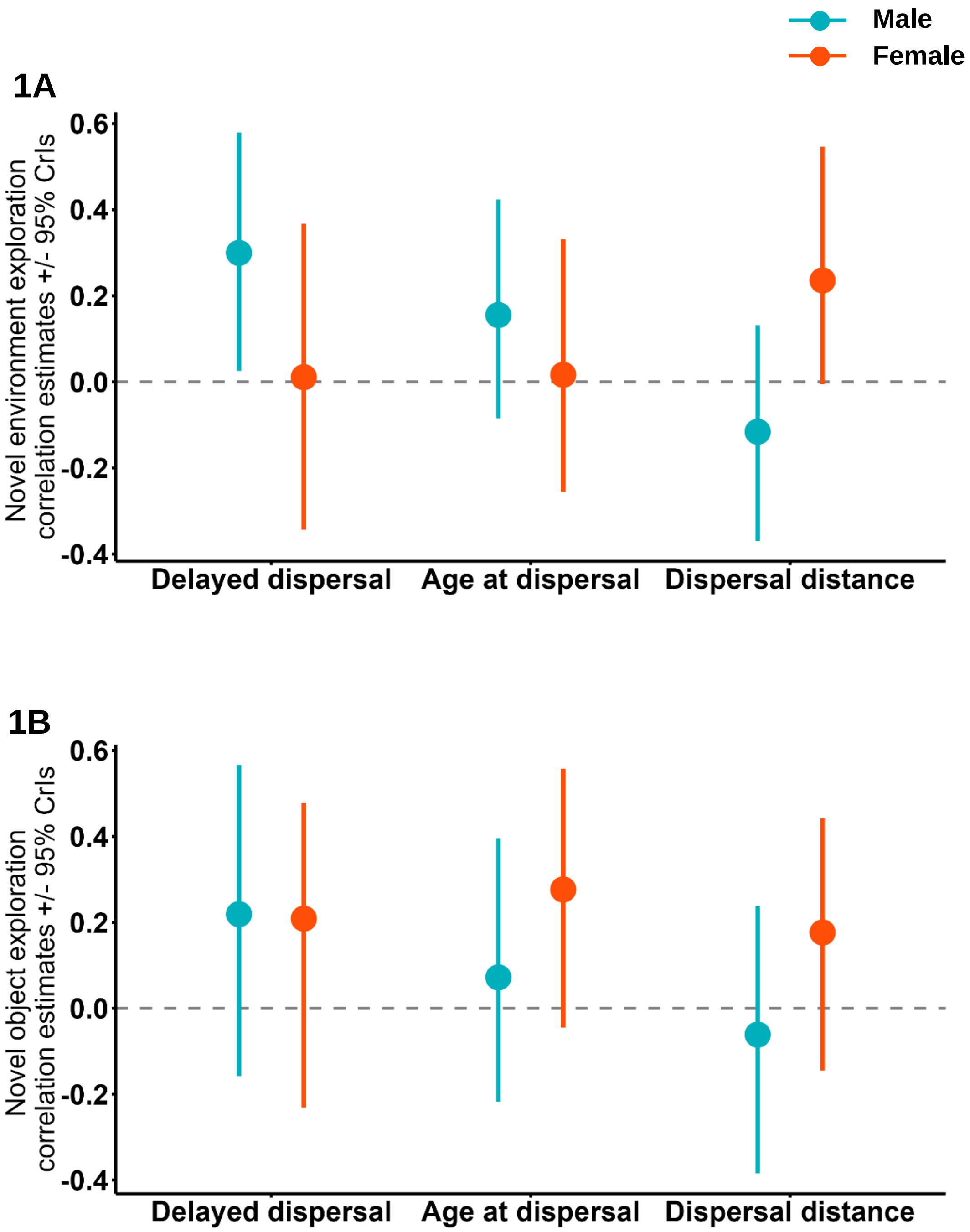
Table 2. Bivariate MCMC model results investigating the covariation between either novel environment exploration or novel object exploration and age at dispersal (months) as response variables in the Seychelles warbler. Reported are the posterior modes and their 95% credible intervals of all fixed effects in the model. Fixed effects for exploration include: age at exploration test (years) (quadratic and linear terms), assay number, and tent colour (contrast level=blue) for novel environment exploration, or branch orientation (contrast level=parallel) for novel object exploration. For age at dispersal, fixed effects include natal group size, island-wide population during hatch field period and island-wide food availability during hatch field period. Statistical significance of fixed effects is indicated by 95% credible intervals not overlapping zero and these are denoted in bold.

	(a) Novel environment exploration		**(b) Novel object exploration**	
	Male	Female	Male	Female
Exploration : Age	**1.706 [0.703, 2.694]**	**1.927 [0.672, 3.272]**	0.748 [-0.541, 2.080]	**5.271 [2.823, 7.934]**
Exploration : Age^2	**-1.035 [-1.913, -0.140]**	**-1.218 [-2.286, -0.061]**	-0.155 [-1.260, 0.963]	**-3.980 [-6.196, -1.848]**
Exploration : Assay number	**0.306 [0.150, 0.467]**	**0.718 [0.460, 0.944]**	**0.590 [0.203, 0.979]**	**0.846 [0.298, 1.380]**
Exploration : Tent colour (green)	**-1.035 [-1.913, -0.032]**	**-0.229 [-0.719, 0.253]**		
Exploration : Branch orientation (parallel)			-0.350 [-0.866, 0.143]	-0.300 [-1.019, 0.424]
Age at dispersal : Natal group size	**0.357 [0.071, 0.638]**	**0.766 [0.461, 1.060]**	0.337 [-0.009, 0.669]	**0.811 [0.375, 1.208]**
Age at dispersal : Island-wide population	-0.123 [-0.936, 0.796]	0.550 [-0.429, 1.559]	-0.193 [-1.114, 0.750]	0.644 [-0.606, 1.775]
Age at dispersal : Island-wide food	**-0.212 [-0.395, -0.028]**	0.072 [-0.137, 0.277]	-0.119 [-0.351, 0.092]	0.033 [-0.253, 0.314]

Table 3. Bivariate MCMC model results investigating the covariation between either novel environment exploration or novel object exploration and dispersal distance (metres) as response variables in the Seychelles warbler. Reported are the posterior modes and their 95% credible intervals of all fixed effects in the model. Fixed effects for exploration include: age at exploration test (years) (quadratic and linear terms), assay number, and tent colour (contrast level=blue) for novel environment exploration, or branch orientation (contrast level=parallel) for novel object exploration. For dispersal distance, fixed effects include natal group size, island-wide population during hatch field period and island-wide food availability during hatch field period. Statistical significance of fixed effects is indicated by 95% credible intervals not overlapping zero and these are denoted in bold.

	(a) Novel environment exploration		**(b) Novel object exploration**	
	Male	Female	Male	Female
Exploration : Age	**1.736 [0.674, 2.695]**	**1.975 [0.664, 3.258]**	0.812 [-0.490, 2.030]	**4.901 [2.436, 7.352]**
Exploration : Age^2	**-1.021 [-1.907, -0.122]**	**-1.258 [-2.328, -0.108]**	-0.227 [-1.324, 0.857]	**-3.623 [-5.682, -1.578]**
Exploration : Assay number	**0.299 [0.148, 0.455]**	**0.710 [0.471, 0.958]**	**0.554 [0.175, 0.934]**	**0.847 [0.279, 1.385]**
Exploration : Tent colour (green)	-0.373 [-0.771, 0.009]	-0.280 [-0.791, 0.190]		
Dispersal distance : Branch orientation (parallel)			-0.387 [-0.913, 0.081]	-0.198 [-0.943, 0.533]
Dispersal distance : Natal group size	-0.029 [-0.468, 0.442]	-0.275 [-0.838, 0.233]	0.213 [-0.294, 0.745]	-0.520 [-1.269, 0.169]
Dispersal distance : Island-wide population	-0.910 [-2.669, 0.752]	-0.160 [-2.327, 1.998]	-0.971 [-2.869, 0.858]	-0.435 [-2.828, 1.983]
Dispersal distance: Island-wide food	0.0628 [-0.308, 0.388]	-0.209 [-0.603, 0.165]	0.014 [-0.394, 0.419]	-0.213 [-0.707, 0.263]

Figures


Male
Female
1A
Novel environment exploration correlation estimates +/- 95% CrIs
0.6
0.4
0.2
0.0
-0.2
-0.4
Delayed dispersal
Age at dispersal
Dispersal distance
1B
Novel object exploration correlation estimates +/- 95% CrIs
0.6
0.4
0.2
0.0
-0.2
-0.4
Delayed dispersal
Age at dispersal
Dispersal distance