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Research

Exploratory behavior, but not aggressiveness, is correlated with breeding dispersal propensity in the highly philopatric thorn-tailed rayadito

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Studies on the relationship between behavioral traits and dispersal are necessary to understand the evolution of dispersal syndromes. Empirical studies have mainly focused on natal dispersal, even though behavioral differences between dispersers and philopatric individuals are suspected to hold through the whole life cycle, potentially affecting breeding dispersal propensity. Using capture–mark–recapture data and behavioral trials in a forest passerine, the thorn-tailed rayadito *Aphrastura spinicauda*, we describe inter-individual differences in exploratory behavior and aggressiveness, and investigate the relationship between those traits and breeding dispersal. Our study took place in Fray Jorge National Park, north-central Chile, where a relatively isolated population of rayaditos inhabits a naturally fragmented environment. We found that scores for behavioral traits were consistent between years. Exploratory behavior was similar between sexes, while males showed higher levels of aggression towards a conspecific male intruder. Only exploratory behavior was related to breeding dispersal propensity, with fast-exploring rayaditos being more likely to have dispersed between seasons. This finding provides indirect evidence for the existence of a dispersal strategy that could reduce dispersal costs in the fragmented landscape of Fray Jorge. To our knowledge, this is the first study documenting an association between breeding dispersal and exploratory behavior in a wild bird population. A longitudinal individual-based study will help determining whether this association constitutes a behavioral syndrome.

Keywords: behavioral traits, breeding dispersal, Chile, dispersal syndromes, Furnariidae



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Introduction

The association of dispersal with physiological, morphological, behavioral and/or life-history traits have been documented in several species (Cote and Clobert 2012, Ronce and Clobert 2012). Recent evidence suggests that dispersal phenotypes may be functionally and genetically integrated with behavioral traits such as aggressiveness or boldness – i.e. dispersal syndromes (Duckworth 2012, Korsten et al. 2013, Duckworth et al. 2015). In fact, consistent inter-individual differences in behavior – i.e. personality – appear to be linked with the propensity to disperse: in many species, dispersers tend to be faster explorers, bolder, more active, more aggressive and less social than philopatric individuals, although opposite trends have also been reported (Clobert et al. 2009, Cote et al. 2010).

Different behavioral traits can influence the decisions that individuals take during different stages of their lives, e.g. more exploratory individuals being more prone to leave a territory (Cote et al. 2010). However, it could be argued that individual decisions during natal dispersal – i.e. the movement from the natal site to the first breeding site – are more likely to be affected by genetic and maternal effects than during breeding dispersal – i.e. the movement between breeding sites during consecutive reproductive seasons –, given that adults have accumulated more experience and information on the distribution of resources, which may affect future dispersal decisions (Bowler and Benton 2005, Pakanen et al. 2011). In fact, studies on several avian systems have revealed that the proximate causes of natal dispersal differ from those of breeding dispersal, whereby the latter is mainly predicted by habitat quality, pairing status and past reproductive success (Greenwood and Harvey 1982, Clarke et al. 1997, Newton 2003). Perhaps for these reasons, studies of dispersal syndromes have mainly focused on natal dispersal (Dingemanse et al. 2003, Duckworth and Badyaev 2007, Duckworth 2008, 2009, Korsten et al. 2013).

The behavioral differences between dispersers and philopatric individuals are suspected to hold through the whole life cycle (Cote et al. 2010; but see Hoset et al. 2011). Therefore, individual variation in exploratory behavior, aggressiveness and/or boldness could partially explain differences in breeding dispersal propensity (Valcu and Kempenaers 2008), but this remains to be tested. Here, we investigate whether breeding dispersal is related to variation in behavioral traits in the thorn-tailed rayadito *Aphrastura spinicauda*, a small cavity nesting bird that breeds in temperate forests along an extensive latitudinal gradient throughout Chile and western Argentina (30°S–55°S; Remsen 2003). We studied a population close to the northern limit of the species distribution, in Fray Jorge National Park, north-central Chile, where a research project on its breeding biology has been carried out since 2007 using nestboxes. This is a relatively isolated population of rayaditos that breeds in a naturally fragmented forest surrounded by an extensive semiarid matrix (González and Wink 2010, Yáñez 2013, Quirici et al. 2014), where local breeding dispersal is

restricted and adult philopatry is common among female and male birds (Botero-Delgadillo et al. 2017a). Because of the long-term fragmentation process that has been taking place in this location (see below), dispersal phenotypes might have locally evolved as a response to an enduring heterogeneous landscape configuration, making this population of interest to investigate the correlation between dispersal and behavioral traits.

In this study, we first describe between-year and sex-related differences in exploratory behavior and aggressiveness in rayaditos based on data from behavioral trials. Subsequently, we assess the relationship between these traits and the occurrence of breeding dispersal by using capture–mark–recapture (CMR) data collected during three consecutive reproductive seasons. Because current evidence suggests that faster explorers and/or more aggressive individuals are typically more prone to disperse (reviewed in Cote et al. 2010), we predicted that individuals with higher scores in behavioral trials assessing exploratory behavior or aggressiveness would exhibit an increased tendency to disperse between reproductive seasons.

Material and methods

Study area and species

This study was part of a long-term nestbox monitoring program carried out in Fray Jorge National Park, Coquimbo Region, northern Chile. Fray Jorge is a semiarid landscape dominated by matorral steppe (Luebert and Plissock 2006), where a fog-supported fragmented relict of Valdivian temperate forest occurs at the top of the coastal mountain range (del-Val et al. 2006). It has been estimated that the forest relict at Fray Jorge became isolated and restricted to the mountain range during the Quaternary as a result of climatic changes (Villagrán et al. 2004). Forest habitat in this area has been, and still is, subjected to a long and slow natural fragmentation process that is caused by a complex dynamic of tree regeneration (del-Val et al. 2006, Kelt et al. 2016). The total forest area in Fray Jorge extends to ~2.4 km² and it is comprised by several forest fragments (0.5–22.5 ha) that are distributed from north to south (Vergara and Marquet 2007, Botero-Delgadillo et al. 2017a). A total of 101–157 nestboxes were installed between 2006 and 2015 in forest patches, being regularly distributed (25–35 m) and geo-referenced with 2 m measurement error. Details on nestbox installation and spatial distribution are given elsewhere (Vergara and Marquet 2007).

The thorn-tailed rayadito is a socially monogamous bird without obvious sexual dimorphism that exhibits biparental care (Moreno et al. 2005, 2007). Age at first breeding in the Fray Jorge population ranges from one to three years, and adult survival is relatively high for both sexes (68%; Botero-Delgadillo et al. 2017a), with some individuals still being recorded as breeders after nine years since first capture (Botero-Delgadillo, unpubl.). Breeding pairs establish and defend nesting territories during the

reproductive season (Ippi et al. 2017), after which territoriality is no longer evident and individuals form conspecific or mixed-species flocks (Ippi and Trejo 2003, Vergara and Marquet 2007). As a forest-dwelling species, daily movements of rayaditos depend on habitat availability and connectivity, and thus are affected by forest fragmentation (Vergara and Marquet 2007, Vergara et al. 2010). In fragmented landscapes, rayaditos have been observed traveling up to 930 m through open habitat, but they seldom cross distances larger than 300 m (Vergara et al. 2010). In Fray Jorge, movements appear to be more limited, with traveling distances across the scrub matrix being frequently shorter than 50 m (Vergara and Marquet 2007). Recent studies showed that rayaditos are highly philopatric and that both natal and breeding dispersal might be restricted by landscape heterogeneity (Botero-Delgado et al. 2017a, 2019a). Breeding dispersal in this population is not frequent (~30%) and usually involves both members of the breeding pair (Botero-Delgado 2017), whose movements are commonly < 100 m – i.e. movements between adjacent nestboxes – and mostly occur within forest patches (Botero-Delgado et al. 2017a).

Breeding monitoring and capture procedure

Each year (2007–2015), we monitored occupied nestboxes to record laying, hatching date and fledging date (see Moreno et al. 2005 for details). We captured breeding adults using nestbox traps when nestlings were 12–14 d old, and subsequently marked them with a numbered aluminum band (Moreno et al. 2005, Quirici et al. 2014) and a unique combination of plastic colored bands for subsequent identification during behavioral trials (see below). Each bird was measured (tarsus length, wing chord and tail length, ± 0.05 mm) and weighed (body mass, ± 0.1 g), and a blood sample (ca 20 μ l) was taken by puncturing the brachial vein with a sterile needle (Quirici et al. 2014). Blood samples were stored on FTA™ Classic Cards (Whatman™) for molecular sexing.

Molecular sexing

A detailed protocol for DNA extraction and molecular sexing is described by Botero-Delgado et al. (2017a). In brief, we used a sex-specific length polymorphism in the CHD gene that can be PCR amplified with primers P2 and P8 (Griffiths et al. 1998). One primer (P8) was fluorescently labeled with 6-FAM™ (Thermo Fisher Scientific). The PCR products were mixed with formamide and a size standard (GeneScan™ 500 LIZ), heat denatured and resolved in POP4 polymer on an ABI™ 3130 Genetic Analyzer (Thermo Fisher Scientific, Darmstadt, Germany). The size of fragments was determined with the GeneMapper 4.0 software (Applied Biosystems). Heterogametic females (ZW) show the 382 bp W-chromosomal fragment CHD-W together with one of the Z-chromosomal fragments (CDH-Z1: 357 bp or CDH-Z2: 358 bp). Homogametic males (ZZ) can be homo- or heterozygous at the CHD-Z locus.

Behavioral trials

Behavioral tests were carried out in 2013–2014 during the nestling phase between 06:00 and 13:00 h. Two behavioral traits were scored: exploratory behavior and aggressiveness.

Exploratory behavior was assessed once for 84 birds (42 from each sex; from these, only 16 could be assessed during both 2013 and 2014) using a novel environment test (Réale et al. 2007), following the methodology described in van Dongen et al. (2010). Trials were carried out immediately after bird capture (nestling age: 12–14 d, see above), prior to marking and measuring. Each bird was first put in a holding cage (30 cm length \times 25 cm width \times 39 cm height) covered with a cloth. This cage was placed in a larger field-portable aviary (270 \times 150 \times 150 cm) installed 30–60 m from a focal nestbox. Aviaries were made of PVC poles covered with semi-transparent black shading cloth and contained four wooden perches diagonally arranged at distances of 60–70 cm along the long axis. After a 5 min of acclimatization, we removed the cloth of the holding cage and opened the door. For 10 min, we recorded the behavior of the focal bird with a Sony™ DCR-68⁺ high definition camera placed at 5–7 m from the aviary. Later, we recorded the number of movements (flights and hops) during each trial, and the position of the bird (14 possible areas could be visited, including the four perches and 10 additional surfaces, i.e. floor, walls and roof) was defined as in van Dongen et al. (2010). All videos were analyzed using JWatcher 1.0 (Blumstein et al. 2010). Individual exploratory behavior was quantified using two variables: 1) exploration speed, measured as the movement rate during the trial (number of movements per minute), and 2) exploration diversity (van Dongen et al. 2010), quantified by the Brillouin's diversity index – appropriate when the probability of a visit to any particular area is not equal; see Krebs (1989). To calculate this index, we used the frequency of visits in each of the 14 areas and the exact time spent there by each bird. The correlation between exploration speed and diversity was rather small and statistically inconclusive (Pearson's $r = 0.21$, $p = 0.11$, $n = 84$). Birds that were subjected to novel environment experiments were gently captured with a butterfly net after the test, subsequently processed (mark and blood sample) in 3–5 min, and then released nearby their nestbox. Subsequent visits to the nestboxes allowed us to confirm that captured adults resumed their parental duties and that fledging success was not compromised.

Aggressiveness was measured once for 74 individuals (37 from each sex; from these, only 15 could be assessed during both 2013 and 2014) using a simulated territory intrusion by a conspecific male (STI; Wingfield et al. 1987). We tested each breeding pair three days after exploration experiments when nestlings were 15–16 d old. We placed a stuffed mount of a male rayadito at 3–5 m from the nestbox, and played back tape-recorded songs of a male (see details in Ippi et al. 2011, 2013) during 10 min. A hidden observer at 10–15 m from the nestbox recorded all behaviors on a Sony™ ICD-BX700⁺ digital voice recorder. The same mount was used for all birds assayed and all experiments

involved the same observer. Recordings were analysed with JWatcher to extract two variables: 1) alarm activity, measured as the total number of movements during the trial (Ippi et al. 2013), and 2) the total number of aggressive interactions with the intruder, including pecking the intruder, flying over the intruder or hovering close to it. There was a moderate, positive correlation between the number of aggressive interactions and alarm activity (Pearson's $r = 0.42$, $p = 0.08$, $n = 74$). We estimated variance inflation factors to assess whether collinearity represented a problem in those models where these two variables were included.

Definition of breeding dispersal

We used capture–mark–recapture data obtained during 2012–2014 to track bird movements between consecutive reproductive seasons. We defined dispersal both as a continuous – i.e. linear distance – and as a categorical variable – i.e. dispersal status – based on the distance between nestboxes used by each individual in consecutive years. Linear distances were transformed into territory units in order to control for the potential effect of yearly differences in breeding densities on dispersal behavior (Botero-Delgado et al. 2017a, 2019a). For dispersal status, we considered any recaptured bird that moved further than the upper limit of the 95% confidence interval (CI) of the annual mean territory diameter as ‘dispersed’, whereas individuals retaining the same nestbox or moving to adjacent nestboxes were ‘non-dispersed’ (sensu Valcu and Kempenaers 2008). We modelled breeding territories separately for each breeding season using Dirichlet tessellation (Adams 2001), and calculated annual mean territory diameters (95% CI for 2013: 20–36 m, 2014: 16–45 m). Spatial analyses were performed in ArcGIS 9.3 (ESRI 2008).

From all individuals that were assessed for exploratory behavior, 57 birds were recaptured during consecutive years and thus had known dispersal status (‘dispersed’: 11 females and 10 males; ‘non-dispersed’: 18 from each sex). For aggressiveness, we had data on 49 recaptured adults (‘dispersed’: 10 from each sex; ‘non-dispersed’: 15 females and 14 males). Most sampled individuals were paired with each other during 2012–2014 (29 pairs in total).

Data analysis

Sample size and composition varied between behavioral variables (Supplementary material Appendix 1 Table A1) due to adult mortality and/or nest failure, and hence, we analyzed exploratory behavior and aggressiveness separately. For those birds that were subjected to behavioral trials during both 2013 and 2014 (see above), we only considered data from first captures in our analyses. We recognize that repeated measurements are essential to assess repeatability and behavioral plasticity (Cote et al. 2010, Dingemanse et al. 2010), but performing behavioral assays to confidently estimate repeatability for these two traits – at least five times/trial/bird – was logistically not

feasible and would have meant subjecting breeding birds to a highly invasive sampling protocol. The repercussions of using one-time responses for each individual are discussed below (see Discussion).

We first tested for differences in measurements of behavioral traits between reproductive seasons – i.e. between-year differences – and sexes. For exploratory behavior, we used a multivariate linear model (Quinn and Keough 2002) that included both exploration speed and exploration diversity as a composite response variable. Conversely, measurements of aggressiveness were modeled independently due to differences in their distribution of errors: we fitted a linear model for alarm activity and a negative-binomial regression for the number of aggressive interactions (a Poisson regression showed overdispersion and fitted the data poorly: log-likelihood ratio test comparing between full models with the different error distributions: $\chi^2 = 65.94$, $df = 2$, $p < 0.001$). In all models we included year, sex and their interaction as predictors.

Distribution of dispersal distances was highly skewed, with birds being distributed in two groups that closely matched the two categories defined for dispersal status (Supplementary material Appendix 1 Fig. A1). Hence, we only used dispersal status (‘dispersed’/‘non-dispersed’) as the response variable to test whether breeding dispersal was related to variation in behavioral traits. To that end, we fitted generalized linear models with a binomial error distribution and a log-link function (Quinn and Keough 2002). As explained above, exploratory behavior and aggressiveness were analyzed separately, and only recaptured individuals with known dispersal status were considered. Behavioral traits in interaction with sex were introduced as predictors. As we did not find between-year differences in the scored values for any of the behaviors measured (see Results), we did not enter year as a co-factor in these models. Although pairing status is an important predictor of breeding dispersal probability in birds (Blakesley et al. 2006, Calabuig et al. 2008, Valcu and Kempenaers 2008), including rayaditos (Botero-Delgado 2017), we did not include this variable, given the limited number of widowed or divorced adults for which behavioral information was available (exploratory behavior: two females; aggressiveness: five females, three males). This meant that our analyses only included birds that paired again with their previous partner. Past reproductive success – i.e. number of fledglings produced – was not considered in the models as it showed very low variation during 2013 and 2014 (Botero-Delgado et al. 2017b).

It is known that members of a social pair can coordinate their behavior – e.g. during territorial defense; see Hall and Peters (2008), Schuppe et al. (2016) –, and thus, mated females and males could influence each other's response to behavioral trials – e.g. STIs. Because breeding pairs comprised the majority of our sample, we performed intra-pair correlation analyses for exploratory behavior and aggressiveness to detect a potential influence. In addition, we used mixed-effects models (Zuur et al. 2009) to perform the same analyses mentioned above while including breeding pair identity as

a random effect, in order to control for non-independence in dispersal status between members of the same pair. For testing between-year and sex-related differences in exploratory behavior, we fitted a multivariate multilevel linear model (Snijders and Bosker 2012) that included exploration speed and exploration diversity as a composite response variable. Consequently, we partitioned the data into two sub-sets, one for each response variable, and included partition and pair identity as random effects.

All statistical tests were performed in R version 3.4.0 (R Development Core Team). Fixed- and mixed-effects models were fitted using the packages lme4 (Bates et al. 2015) and MASS (Venables and Ripley 2002), while the nlme package (Pinheiro et al. 2018) was used for the multivariate multilevel analysis. Continuous p-values were reported as measure of compatibility between the null hypothesis and our data (Amrhein et al. 2019, Greenland 2019, Wasserstein et al. 2019).

Results

Intra-pair correlation coefficients were small and statistically inconclusive for exploration speed (Pearson's $r=0.15$, $p=0.28$, $n=54$ dyads) and exploration diversity ($r=-0.02$, $p=0.92$, $n=54$). The same was observed for alarm activity ($r=0.10$, $p=0.50$, $n=47$) and the number of aggressive interactions ($r=0.17$, $p=0.26$, $n=47$) during STIs. Given the low correlation between members of breeding pairs and the fact that results did not differ when controlling for breeding-pair identity (see results from mixed-effects models in Supplementary material Appendix 1 Table A2, A3), here we only present results from the fixed-effects models.

Between-year and sex-related differences in behavioral traits

Mean values (with standard deviation) for the four behavioral traits measured are summarized for each sex in Supplementary material Appendix 1 Table A1.

None of the analyses provided evidence for between-year differences in the observed values for behavioral traits (Table 1, Fig. 1). Differences between sexes were not always conclusive, depending on the trait examined. The multivariate linear model showed that exploratory behavior did not vary between sexes (Table 1, Fig. 1a). Although alarm activity during STIs tended to be higher in females relative to males (Fig. 1b), there was some degree of overlapping between sexes and the difference was inconclusive (Table 1). However, the number of aggressive interactions directed at the conspecific intruder was higher in male rayaditos compared to females (Table 1, Fig. 1b).

We calculated pairwise correlation coefficients amongst all behavioral variables based on those individuals for which we had data for both exploration and aggressiveness ($n=59$). The resulting correlation matrix showed that, at the individual level, variables aiming to measure the same or different behavioral traits were weakly correlated with each other (Supplementary material Appendix 1 Fig. A2).

Behavioral correlates of breeding dispersal

The binomial model for exploratory behavior showed that regardless of sex, the probability of breeding dispersal was predicted by exploration speed but not by exploration diversity (Table 2). We observed that slow-exploring rayaditos (< 20 movements min^{-1} , corresponding to the 20th percentile)

Table 1. Fixed-effects models for testing between-year and sex-related differences in behavioral traits in a population of thorn-tailed rayadito in Fray Jorge National Park. Behavioral data were collected during two reproductive seasons in 2013–2014.

Behavioral trait	Variable measured	Models					
Exploratory behavior	Composite variable*	Multivariate linear model					
			Roy's largest root	F value	p		
		Intercept	30.57				
		Exploration~Year	0.008	$F_{2,79}=0.31$	0.73		
		Exploration~Sex	0.005	$F_{2,79}=0.19$	0.82		
Aggressiveness	Alarm activity	Exploration~Year:Sex	0.0003	$F_{2,79}=0.01$	0.97		
		Linear model					
			Estimate	SE	t value	p	
		Intercept	63.65	7.10			
		Year [^]	5.06	10.47	$t_{70}=0.483$	0.63	
	Sex [^]	-17.65	10.04	$t_{70}=-1.758$	0.08		
	Year:Sex [^]	-9.94	14.81	$t_{70}=-0.671$	0.50		
	No. of aggressions	Negative-binomial model		Estimate	SE	z value	p
			Intercept	-0.9163	0.4788		
			Year [^]	0.1625	0.6906	$z=0.235$	0.81
Sex [^]			1.7707	0.5957	$z=2.973$	0.002	
Year:Sex [^]			-0.2392	0.8673	$z=-0.276$	0.78	

* Composite variable consisted of exploration speed and exploration diversity.

[^] Parameter estimates and standard errors (SE) were estimated relative to '2013' level in variable 'Year', and 'Female' level in variable 'Sex'.

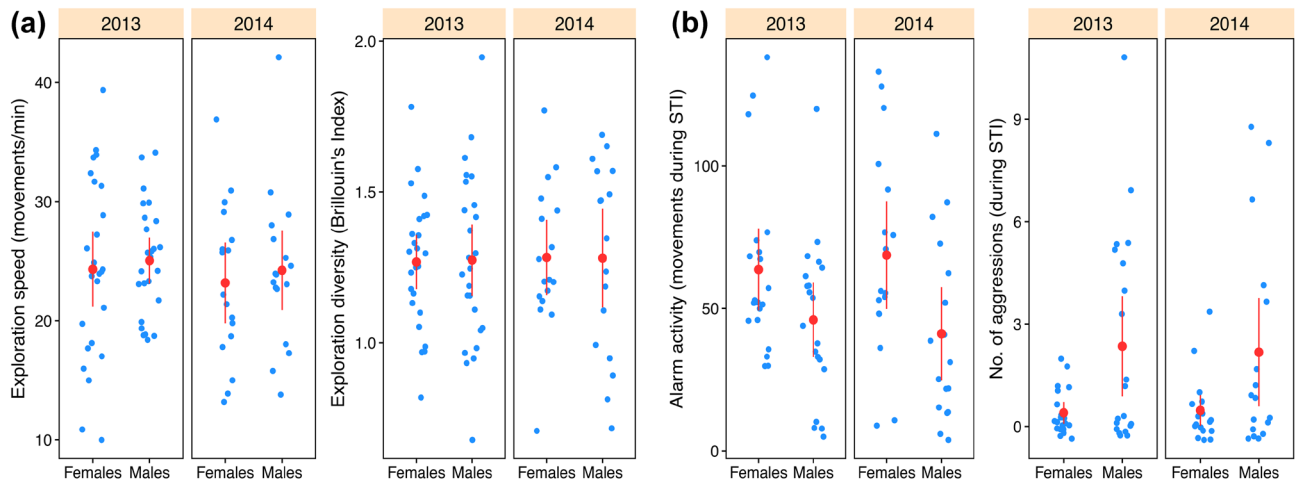


Figure 1. Mean values for behavioral traits measured for female and male thorn-tailed rayaditos in Fray Jorge National Park during 2013–2014. (a) Exploratory behavior was assessed by measuring exploration speed (left) and exploration diversity (right) using a novel environment test. (b) Aggressiveness was assessed by means of a simulated territorial intrusion (STI) to measure alarm activity (left) and the number of aggressive interactions with a conspecific intruder (right). Bars represent 95% confidence intervals.

were more likely to have remained philopatric before being recaptured during the breeding season, while faster explorers (> 30 movements min^{-1} , corresponding to the 80th percentile) had a higher probability of having dispersed (Fig. 2a). Even though superficial explorers (exploration diversity scores < 1 ; 20th percentile) tended to be ‘non-dispersed’ birds (Fig. 2b), the relationship between exploration diversity and dispersal predicted by our data was still compatible with the null hypothesis (Table 2).

We did not find evidence for an effect of aggressiveness on breeding dispersal probability, neither an interaction with sex (Table 2). Variation in alarm activity during STIs showed no clear relationship with dispersal behavior, as passive and active birds were equally likely to either have remained philopatric or dispersed (Fig. 3a). Likewise, the likelihood of breeding dispersal was not related with the number of aggressive interactions with the intruder (Fig. 3b).

Discussion

Intercorrelation among behavioral traits

Based on one-time behavioral responses recorded in the field, we have shown that measures of behavioral traits in a natural population of thorn-tailed rayadito exhibited large inter-individual variation, and this was consistent over two years. The fact that we found weak correlations among the four measured behavioral traits (i.e. exploration speed, exploration diversity, alarm activity during the intrusion of a conspecific male, and the number of aggressive interactions with the intruder) was unexpected, particularly considering that behavioral responses to distinct stimuli are often moderately to strongly intercorrelated in a number of avian models (Groothuis and Carere 2005, Réale et al. 2007; but also see Dingemanse and Réale 2005).

Table 2. Binomial fixed-effects models testing the relationship between breeding dispersal and behavioral traits in a population of thorn-tailed rayadito in Fray Jorge National Park. Models used individual dispersal status (‘dispersed’/‘non-dispersed’) as the response variable. Capture–mark–recapture data to identify dispersal status were collected during three reproductive seasons in 2012–2014.

Behavioral trait	Models by factors	Estimate	SE	z value	p
Exploratory behavior	Intercept	−9.86	3.80		
	Exploration speed (ES)*	0.19	0.08	$z=2.10$	0.03
	Exploration diversity (ED)*	3.34	2.30	$z=1.45$	0.15
	Sex [^]	4.32	5.08	$z=0.85$	0.39
	ES:Sex [^]	−0.17	0.12	$z=−1.36$	0.17
	ED:Sex [^]	−0.19	2.98	$z=−0.06$	0.94
Aggressiveness	Intercept	0.86	1.13		
	Alarm activity (AA)*	−0.02	0.02	$z=−1.19$	0.23
	No. of aggressions (NA)*	−0.13	0.61	$z=−0.21$	0.84
	Sex [^]	−1.96	1.38	$z=−1.42$	0.15
	AA:Sex [^]	0.01	0.02	$z=−0.64$	0.52
	NA:Sex [^]	0.49	0.64	$z=0.77$	0.44

* Variance inflation factors of each independent variable: ES=1.98; ED=1.79; AA=1.08; NA=2.04.

[^] Parameter estimates and standard errors (SE) were estimated relative to ‘female’ level in variable ‘sex’.

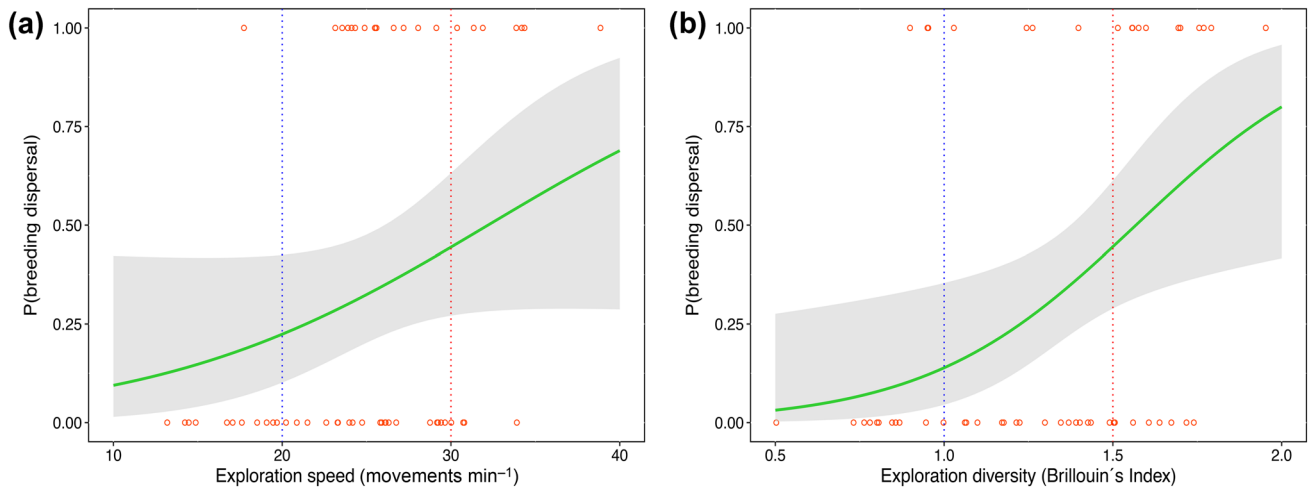


Figure 2. Predicted probability of breeding dispersal during consecutive reproductive seasons in thorn-tailed rayaditos in relation to exploratory behavior. (a) Plot showing breeding dispersal as a function of exploration speed, highlighting slow (blue dotted line; 20th percentile) and fast (red dotted line; 80th percentile) explorers. (b) Plot showing breeding dispersal and exploration diversity, highlighting superficial (blue dotted line; 20th percentile) and thorough (red dotted line; 80th percentile) explorers. Shown are the model estimates (green line) and the corresponding 95% confidence intervals (in grey).

The rather small correlation between measured behaviors in this population has important implications for three aspects relevant to the study of behavioral syndromes. First, it could imply that the extent of within-individual variation differs between traits, thus obscuring a potential link between different aspects of behavior. Second, it can also suggest that distinct variables measured from a single assay may represent different behavioral traits. And third, it indicates that exploratory behavior and aggressiveness are not necessarily functionally integrated (Dingemanse and de Goede 2004, Araya-Ajoy and Dingemanse 2014), despite the evidence of such correlation in other species (Verbeek et al. 1996,

Carere et al. 2003, Martins et al. 2007). This is plausible given that the covariation among exploration and aggressiveness depends on the local conditions and the ecological context (Bergmüller 2010).

We must acknowledge that given the lack of repeatability estimates, it is not possible to conclude that our behavioral measurements reflect consistent inter-individual differences – i.e. personality traits –, and hence our results should be interpreted with caution. Nonetheless, a recent study on a population in southern Chile showed that behavioral traits in rayaditos are not only repeatable (95% CI $R = 0.29-0.69$), but also heritable (95% CI $h^2 = 0.22-0.45$; Poblete 2018).

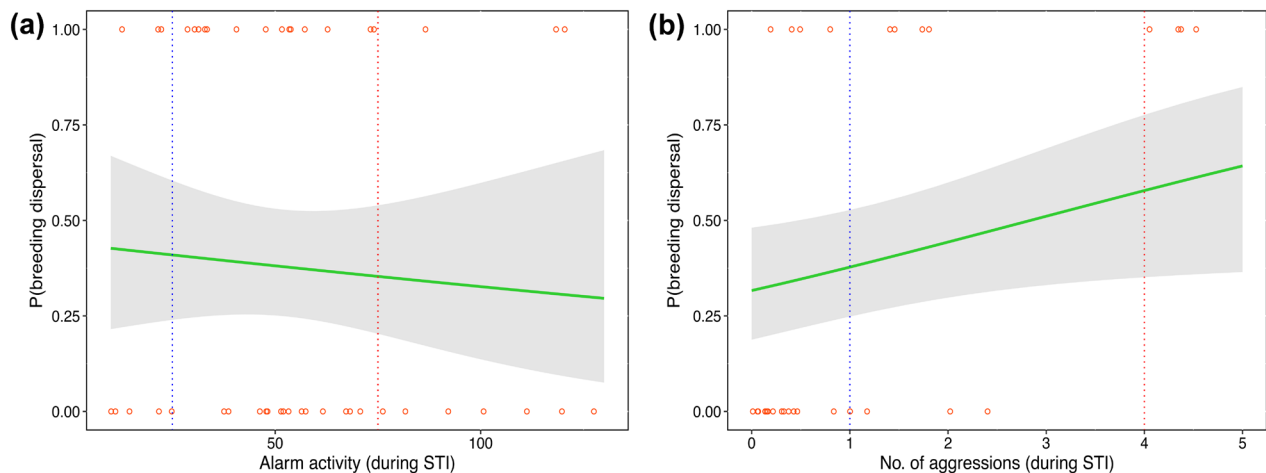


Figure 3. Predicted probability of breeding dispersal during consecutive reproductive seasons in thorn-tailed rayaditos in relation to aggressiveness (measured by a simulated territorial intrusion STI). (a) Plot showing breeding dispersal as a function of alarm activity, highlighting passive (blue dotted line; 20th percentile) and active (red dotted line; 80th percentile) individuals. (b) Plot showing breeding dispersal and the number of aggressive interactions with the intruder during STIs, highlighting submissive (blue dotted line; one aggression or less) and aggressive (red dotted line; four or more aggressions) individuals. Shown are the model estimates (green line) and the corresponding 95% confidence intervals (in grey).

And similar to us, the author found no support for a correlation between exploratory behavior and aggressiveness. It is therefore reasonable to believe that these two traits are repeatable in Fray Jorge. The long-term reproductive monitoring of this population will allow us to increase our capture–mark–recapture dataset and hence the number of individuals with repeated behavioral measures across years. A forthcoming study will use these data in order to determine the presence of personalities in this population.

Sex-related differences in behavioral traits

Unlike what has been described by others (Wischoff et al. 2018), we found no evidence of a ‘breeding-pair’ effect on individual measurements of exploratory behavior and aggressiveness, as revealed by both intra-pair behavioral correlations and mixed-effects models. This is important given that the majority of individuals included in our study were sampled as part of a social pair.

Exploratory behavior varied largely between individuals, but not between sexes. This is not surprising considering that exploration is essential to gather information from the immediate surroundings, and thereby being linked to key aspects of the life history of both sexes such as foraging behavior (Verbeek et al. 1994), risk-taking behavior (van Oers et al. 2003) and stress responses (Cockrem 2007). This is in line with other studies on exploratory behavior in birds, where sex differences have rarely been reported (but see Carere et al. 2005).

Levels of aggressiveness differed between sexes, showing consistent patterns during 2013 and 2014. Although alarm activity during simulated territorial intrusions (STIs) was higher in females than males, differences were not statistically conclusive. Nevertheless, males showed higher aggression scores than females when considering the number of aggressive interactions with the intruder during STIs. A previous study already showed that male rayaditos engage more in physical aggression towards a conspecific male intruder, while the intensity of non-physical aggressive interactions – i.e. alarm activity – is similar between sexes (Ippi et al. 2017). In general, higher aggression levels in males during territorial defense are common in passerine birds, especially towards conspecific males (Fedy and Stutchbury 2005). Moreover, male rayaditos exhibit higher aggression levels than females in other contexts, for instance, during nest defense against predators (Ippi et al. 2013). This overall difference in aggressiveness could be related to stronger intra-sexual selection on males (Ippi et al. 2017), such that more aggressive individuals would be more successful at competing for access to mates and breeding territories. This remains to be investigated.

As in other socially monogamous species with biparental care (Fedy and Stutchbury 2005), female rayaditos also play an active role during territorial defense. In fact, joint territorial defense has been documented in other populations across the distributional range of thorn-tailed rayadito, as evidenced by a positive correlation in nest defense behavior among members of breeding pairs (Ippi et al. 2017). Our data also showed

that females actively participate in nesting-site defense, but the low degree of intra-pair behavioral correlation does not support the idea that individuals could adjust their defense strategy in response to the levels of aggression showed by their social mate. This requires more detailed study.

Behavioral correlates of breeding dispersal

Here, we used post-dispersal behavioral measurements in order to investigate the relationship between exploration/aggressiveness and breeding dispersal. Although this approach has been commonly used in other studies – i.e. the use of post-dispersal behavioral measurements; see e.g. O’Riain et al. (1996), Dingemanse et al. (2003), Meylan et al. (2009) –, care should be taken due to the inherent difficulty to identify whether differences between dispersers and non-dispersers are a cause or a consequence of dispersal (Cote et al. 2010, Dubuc-Messier et al. 2018). Some authors have argued, however, that as long as differences in behavior arise before the onset of dispersal and are consistent, this should not be a major concern (Dingemanse et al. 2003, Cote et al. 2010). As stated earlier, measures of exploratory behavior and aggressiveness in rayaditos are repeatable – at least in other populations –, and moreover, individual differences in these traits seem to arise early in life (as tested in 12–14-d-old nestlings; Poblete 2018).

We found that among all behavioral traits measured in our study population, exploration speed predicted the probability of birds having dispersed between consecutive reproductive seasons. It has been demonstrated that individual dispersal behavior co-varies with exploration in a variety of taxa (Ronce and Clobert 2012). Interestingly enough, such findings come from studies entirely focused on the relationship between behavioral traits and natal dispersal, even though individual behavior is suspected to partially influence the decisions of adults in relation to whether or not to leave a previously established breeding territory (Valcu and Kempenaers 2008) or how far to disperse (Öst et al. 2011). Here we have presented evidence supporting this idea. This could mean that dispersal strategies within a population – or specific to a certain behavioral phenotype – not only can affect an individual propensity to engage in post-fledging dispersal (Dingemanse et al. 2003), but also later in life.

According to our results, fast-exploring rayaditos were more likely to have dispersed between breeding seasons. This is in line with the accumulating evidence showing that fast explorers are more prone to disperse than slow explorers (Cote et al. 2010), even though behavioral differences between dispersers and non-dispersers can vary ontogenetically (Hoset et al. 2011), or between populations according to the local conditions (Cooper et al. 2017). Because our sample consisted almost exclusively of remated breeding pairs, it could be argued that these findings reflect a relationship between behavior and dispersal at the pair level. Nonetheless, there are three reasons to believe that the observed results rather reflect variation at the individual level. First, behavioral traits showed low intra-pair correlation, suggesting no behavioral

coordination/adjustment between mates. Second, results did not change when using mixed-effects models that controlled for the identity of the breeding partner (Supplementary material Appendix 1 Table A3). And third, exploratory behavior was assessed separately for each bird. That being said, the data indicate that fast-exploring individuals – females or males – are more prone to disperse together with their social mate, if reunited, and dispersal would happen regardless of the exploratory tendency of their partner. It is unknown to what extent dispersal of remated birds comes from a decision taken collectively by both pair members, but our analyses support the idea of one individual being more influential. If this is the case, either the female or the male could have more influence depending on factors such as social dominance, experience, and/or personality. This means that both sexes might have an important role in territory establishment and/or nest-site selection, something already described in other furnariids (Remsen 2003). This requires further study in rayaditos.

Assuming that exploration and aggressiveness are also repeatable and heritable in the Fray Jorge population, the relationship between breeding dispersal and exploratory behavior found in our study provides indirect evidence for the existence of a dispersal strategy that could reduce dispersal costs (Ronce and Clobert 2012). Both natal and breeding dispersal appear to be costly in Fray Jorge (Botero-Delgado et al. 2019a), and consequently more exploratory habits could increase an individual's probability to procure territories of relative high quality after dispersal by acquiring knowledge about the distribution of key resources away from their natal/breeding area (Yasukawa 1979, van Overveld and Matthysen 2010). Alternatively, faster explorers would tend to disperse more frequently simply because they are more risk prone (Groothuis and Carere 2005), thus being more likely to leave a territory despite the related costs. While dispersing in a fragmented landscape might constitute a risky task for rayaditos (Vergara and Marquet 2007), it could prove beneficial in a densely populated environment such as Fray Jorge, where competition for nesting-sites and food availability during the reproductive season can be high (Botero-Delgado et al. 2017a) and vary strongly between years (Quirici et al. 2014).

Conclusions

Documenting the presence of behavioral correlates of dispersal is relevant to understand the ecological and social mechanisms affecting dispersal decisions, and ultimately, the trade-offs and constraints driving the evolution of distinct strategies within and across populations (Ronce and Clobert 2012). Here we showed that individual variation in behavioral traits is related to local breeding dispersal, with fast-exploring rayaditos being more prone to leave a former breeding territory. To our knowledge, this is the first study documenting an association between breeding dispersal propensity and exploratory behavior in a wild bird population.

A longitudinal individual-based study will be essential to determine if behavioral traits are repeatable and hence if personality-dependent dispersal is taking place in this species. This will help establishing whether the observed association constitutes a behavioral syndrome.

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.931zcrjtz>> (Botero-Delgado et al. 2019b).

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Author contributions – Project design: EB-D; experimental planning and data collection: EB-D, VQ, YP; research supervising: EP, BK, RAV; data collection and analysis: EB-D; data discussion: BK, RAV; manuscript writing: EB-D; manuscript editing: EP, BK, RAV.

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