



RESEARCH ARTICLE

Ecological and social correlates of natal dispersal in female and male Thorn-tailed Rayadito (*Aphrastura spinicauda*) in a naturally isolated and fragmented habitat

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ABSTRACT

Sex-biased natal dispersal is predicted to be a consequence of differences in the costs and benefits of dispersal perceived by each sex. Although female-biased dispersal has been described for numerous birds in heterogeneous landscapes, studies documenting sex-related differences in the causes and consequences of natal dispersal in fragmented habitats are comparatively scarce. We used capture–mark–recapture data and genetic analyses in a population of Thorn-tailed Rayadito (*Aphrastura spinicauda*) from north-central Chile in order to investigate how the possible causes and consequences of dispersal are linked to sex-specific dispersal behavior in a naturally isolated and fragmented forest habitat. We analyzed 36 recaptured post-fledging birds to test whether female-biased dispersal reflected differential responses between sexes to potentially long-term acting selective pressures related to habitat fragmentation and high population densities. In this population, females disperse long distances (median distance: 780 m), whereas males are mostly philopatric (median distance: 85 m). Results suggest that female dispersal is possibly a response to the local density of breeding birds and mate availability, and comes without apparent reproductive costs. Inbreeding avoidance was not evident, but females may already be decreasing the probability of mating with relatives by moving away from their natal neighborhood where male kin usually remain. Our findings also indicate that male dispersal, while reduced in relation to females, can result from a tradeoff between the social benefits of settling near the natal territory and the associated costs of high breeding densities and kin competition. An increase of paternity loss was evident for males moving long distances. Follow-up studies should assess the differences in the costs and benefits of within- and between-fragment dispersal in this population.

Keywords: dispersal strategies, Fray Jorge National Park, inbreeding avoidance, kin competition, population density, reproductive consequences

Correlatos ecológicos y sociales de la dispersión natal en hembras y machos del Rayadito (*Aphrastura spinicauda*) en un hábitat naturalmente aislado y fragmentado

RESUMEN

La dispersión sesgada al sexo resulta de diferencias en los costos y beneficios de la dispersión para cada sexo. Aunque la dispersión sesgada hacia las hembras ha sido descrita para varias especies de aves en paisajes heterogéneos, son escasos los estudios que documenten la variación ínter-sexual en las causas y consecuencias de la dispersión natal en hábitats fragmentados. Usamos datos de captura–marcaje–recaptura y análisis genéticos en una población de Rayadito (*Aphrastura spinicauda*) en el norte-centro de Chile para investigar cómo se relaciona la dispersión de cada sexo y sus posibles causas y consecuencias en un ambiente boscoso aislado y naturalmente fragmentado. Analizamos 36 individuos recapturados para probar si la dispersión sesgada hacia las hembras refleja respuestas diferenciales entre sexos a potenciales presiones selectivas asociadas con la fragmentación gradual del hábitat y altas densidades poblacionales. En esta población, las hembras dispersan largas distancias (mediana: 780 m), mientras los machos son filopátricos

(mediana: 85 m). Los resultados sugieren que las hembras dispersarían en respuesta a la densidad local de individuos reproductores y la disponibilidad de parejas sin ningún costo reproductivo aparente. No evidenciamos evasión de endogamia, aunque es posible que las hembras disminuyan la posibilidad de aparearse con individuos emparentados al alejarse de su vecindario natal donde los machos parientes suelen permanecer. Nuestros resultados también indican que la dispersión de los machos, aunque más reducida que en las hembras, resultaría de un compromiso entre los beneficios sociales de permanecer cerca de su lugar natal y el costo asociado a las altas densidades de individuos reproductivos y la competencia entre parientes. Evidenciamos un aumento en la pérdida de paternidad en machos que dispersaron largas distancias. Próximos estudios en esta población deberán investigar las diferencias en los costos y beneficios de la dispersión dentro y entre fragmentos de bosque.

Palabras clave: Estrategias de dispersión, Parque Nacional Fray Jorge, densidad poblacional, evasión de endogamia, competencia entre parientes, densidad poblacional, consecuencias reproductivas

INTRODUCTION

Natal dispersal, the movement of individuals from birthplace to first breeding site, is often viewed as a strategy to reduce mating between closely related individuals, or simply to avoid competition among kin (i.e. inbreeding avoidance and kin competition avoidance, respectively; see Greenwood 1980, Greenwood and Harvey 1982, Pusey 1987, Perrin and Mazalov 1999). Natal dispersal can also be caused by a decrease in the quality of the natal habitat due to environmental fluctuations or to density-dependent factors, such as increased competition for food and breeding opportunities (Greenwood 1980, Dobson and Jones 1985, Newton 2003). But despite its potential benefits, dispersal is a costly behavior, as movement across unfamiliar habitat and selection of a potential nesting site may not only be time- and energetically demanding, but could also increase the risks of starvation and predation (Bonte et al. 2012). Even after successful transfer, individuals settling in a socially and ecologically unfamiliar territory might incur additional costs, including decreased survival, limited mating opportunities, and reduced breeding success (Greenwood 1980, Bonte et al. 2012).

The evolution of natal dispersal patterns in natural populations is driven by the tradeoffs between the costs and benefits of dispersal (Clobert et al. 2004). Hence, individual differences in life-history traits will partly determine the relative costs and benefits of dispersal (Bowler and Benton 2005). Because females and males can be differentially affected by the factors promoting/hindering dispersal (Greenwood 1980, Pusey 1987, Arlt and Pärt 2008), sex biases in dispersal frequency and/or distance are frequent among birds (Clarke et al. 1997, Paradis et al. 1998, Newton 2003). Although both sexes may disperse, sex-biased dispersal can arise when there are asymmetric competitive roles for defending a breeding territory (Greenwood 1980). For instance, many passerine birds have a resource-defense mating system in which males must establish a territory in order to attract females, and therefore female-biased dispersal would result due to the higher benefits of philopatry perceived by males relative to females (Greenwood 1980, Greenwood and Harvey 1982). Some studies, however,

have shown that sex-specific differences in natal dispersal can vary among populations within species (Matthysen et al. 1995, 2001), and that the perceived costs and benefits of dispersal are context-dependent, resulting from the interaction between phenotypic traits and local environmental conditions (Tarwater and Beissinger 2012).

In small and isolated populations where the risk of inbreeding is high, sex-biased dispersal is primarily viewed as an inbreeding avoidance mechanism, as it allows spatial separation of closely related individuals (Paris et al. 2016). Nonetheless, the direction of dispersal biases is an ultimate consequence of the differences in the costs perceived by each sex (Pärt 1994, Pärt 1995, Weelwright and Mauck 1998, Awade et al. 2017), and, as such, it cannot be predicted by inbreeding avoidance alone (Perrin and Mazalov 1999). Although female-biased dispersal has been described for numerous songbird species in fragmented landscapes (e.g., Matthysen et al. 1995, 2001, Verhulst et al. 1997, Awade et al. 2017), studies documenting sex-related differences in the causes and consequences of natal dispersal in fragmented habitats are comparatively scarce and primarily focused on island populations (e.g., Pärt 1994, 1995, 1996, Weelwright and Mauck 1998, Paris et al. 2016). Whether or not sex-specific costs and benefits of dispersal in naturally fragmented landscapes resemble those observed in “true” islands needs to be further investigated, but to the extent of our knowledge, there is little information regarding the correlates of natal dispersal in continental bird populations inhabiting vegetation patches surrounded by a non-habitable matrix (but see Tarwater and Beissinger 2012). Understanding this is now crucial within the context of rapid global change, especially for forest birds threatened by habitat loss and fragmentation.

Here, we investigated the potential causes and consequences of natal dispersal in a forest passerine occupying a naturally isolated and fragmented forest habitat in Fray Jorge National Park (30.63°S, 71.66°W), north-central Chile. We studied the Thorn-tailed Rayadito (*Aphrastura spinicauda*), a secondary cavity-nesting bird with limited dispersal that is negatively affected by forest fragmentation at the local scale (Vergara and Marquet 2007, Vergara et al. 2010). At Fray Jorge, rayaditos breed inside forest relict

fragments and make locally restricted movements, seldom crossing open areas requiring flights >50 m (Vergara and Marquet 2007). Fray Jorge contains an isolated population of rayaditos at the northern limit of the species' distributional range (Gonzalez and Wink 2010, Yáñez 2013), which has experienced long-term isolation and fragmentation processes since the end of the Tertiary as a consequence of historical climatic changes (Villagrán et al. 2004). In addition, density of breeding adults is nearly 3 times that of other populations (Botero-Delgadillo et al. 2017; see Methods) and baseline corticosterone levels are also higher (Quirici et al. 2014, 2016), pointing to Fray Jorge as a stressful and competitive environment.

A previous study has shown that female-biased natal dispersal is the dominant pattern at Fray Jorge, where settlement of pre-reproductive females follows a random pattern throughout the landscape, while males tend to settle near their natal site and seldom leave the forest fragment where they fledged (Botero-Delgadillo et al. 2017). In this population, a dispersal bias could be reflecting differential responses between sexes to long-term acting selective pressures related to gradual habitat fragmentation and high population density. In this study, we used capture-mark-recapture (CMR) data and genetic analyses to explore whether female-biased dispersal in this locality corresponds to sex-related differences in the

potential ecological and social causes of natal dispersal and the associated reproductive consequences. Specifically, we addressed the following questions: (1) Are female and male natal dispersal differentially affected by local breeding bird density and the likelihood of inbreeding/kin competition? and (2) Is variation in natal dispersal related to individual variation in breeding success, and does this relationship differ between the sexes?

METHODS

Study Area and Population

This study was carried out during 2008–2016 in Fray Jorge National Park, located in the Coquimbo Region, north-central Chile (Figure 1). Although the entire region is dominated by a semi-arid steppe, Valdivian temperate rainforest relicts occur at sea-facing slopes atop the coastal mountain range at ~600 masl, where a fog-induced humid microclimate is maintained throughout the year (Villagrán et al. 2004, Luebert and Plischoff 2006). The landscape at Fray Jorge consists of several forest fragments (0.5–22.5 ha) surrounded by an extensive shrub-dominated matrix (Cornelius et al. 2000; see Figure 1). These forest relicts became restricted to the coastal mountain range during the Quaternary (Villagrán et al. 2004), and there is still an ongoing gradual fragmentation process (Gutiérrez et al.

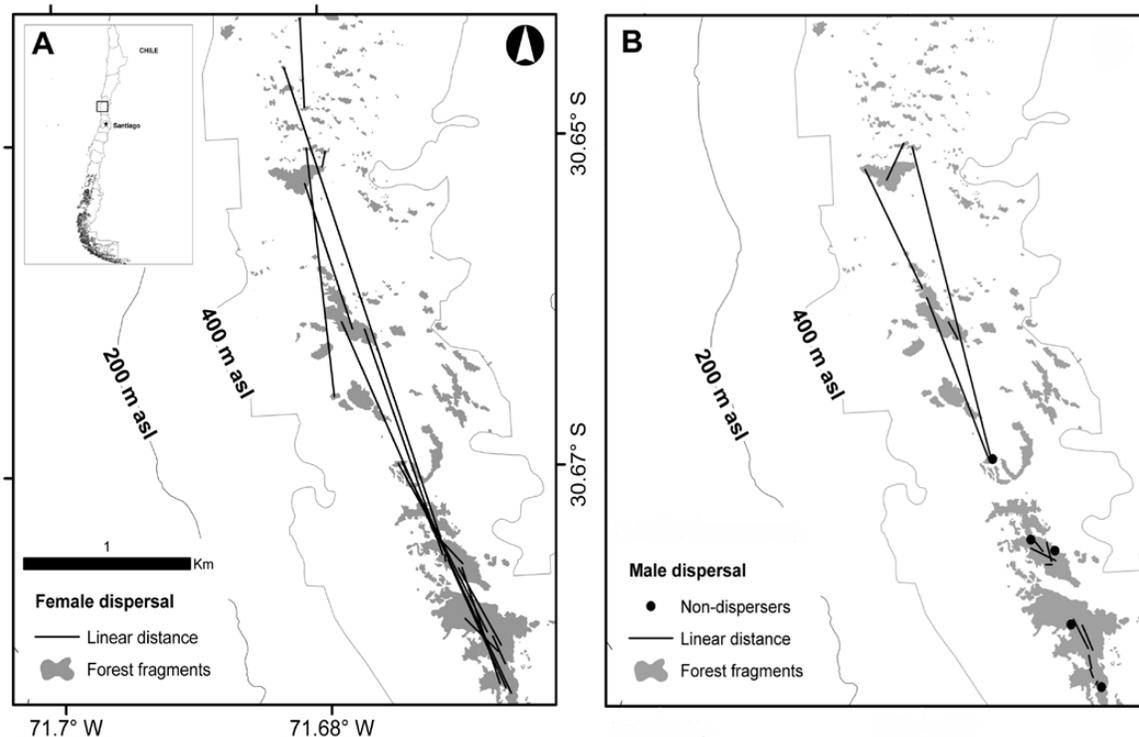


FIGURE 1. Natal dispersal of Thorn-tailed Rayadito in Fray Jorge National Park, north-central Chile. Dispersal distances and directions for (A) females (median distance: 780 m; range: 40–2,734 m) and (B) males (median distance: 85 m; range: 0–1,831 m) recaptured during the study period.

2008). The closest known population of rayaditos is 170 km south from our study site, where they also breed in a forest remnant at the top of Cerro Santa Inés (see, e.g., Ippi et al. 2011).

The study plot at Fray Jorge is ~ 5.3 km², of which ~ 2.4 km² is covered by forest fragments (Botero-Delgadillo et al. 2017). As part of a long-term study on the breeding biology of rayaditos, 101–157 nests boxes (georeferenced with a 2 m measurement error) have been offered since 2008 in this locality (Appendix Figure 4). Nest boxes were regularly distributed within forest fragments at an average distance of 21 ± 2.6 m (mean \pm SD), taking into account previous estimates of breeding bird density from this population (8.2 pairs ha⁻¹; Vergara and Marquet 2007). Nest box occupation rates during the study period were ~ 30 – 40% , and $<5\%$ of all adult birds that were captured/sighted in the nest box plots during each year were breeding in natural cavities.

Field Methods and Genetic Analysis

Nest boxes were monitored annually during the whole breeding season, from September through December (see Quirici et al. 2014). Methods regarding bird capture, marking, measuring and weighing are described in detail elsewhere (see Moreno et al. 2005, 2007, Quirici et al. 2014, 2016, Botero-Delgadillo et al. 2017, Espíndola-Hernández et al. 2017). Briefly, all birds using nest boxes were captured and marked with individual aluminum bands when nestlings were 12–14 d old. During mid-September, nest boxes were checked every 3–5 d until occupied by rayaditos, after which the nest-check frequency was increased in order to document breeding phenology. Measures of breeding success (e.g., clutch size and egg volume, brood size, hatching and fledging success) were recorded for every nest box, including replacement clutches. Rayaditos in Fray Jorge have no second breeding attempts.

After capture, adults and nestlings were blood sampled (~ 15 μ L) by puncturing the brachial vein with a sterile needle. Blood samples were stored on filter paper (FTA Classic Cards, Whatman, Buckinghamshire, UK) and later used for molecular sexing and genotyping. A detailed description of DNA extraction methods and microsatellite amplification analyses is given elsewhere in Botero-Delgadillo et al. (2017). Briefly, individuals were molecularly sexed using a sex-chromosome-linked marker (P2/P8; Griffiths et al. 1998) and genotyped at 13 autosomal, polymorphic microsatellite loci, using 8 species-specific markers (see Yáñez et al. 2015), and 5 cross-species amplifying markers. Twelve microsatellite markers showed no significant deviation from Hardy-Weinberg equilibrium (HWE; all $P > 0.1$) and had null allele frequencies <0.05 . These markers were used to estimate genetic relatedness and for parentage analysis (see below).

Documenting Natal Dispersal

Events of natal dispersal were documented based on CMR data obtained during 2008–2016. Natal dispersal was defined as the distance between the natal nest box and the first recorded breeding nest box. We measured natal dispersal as the linear distance (m) between natal and breeding site (Figure 1A, B), although a corrected estimate was later used in subsequent analyses (see below). Individuals whose first breeding attempt was recorded in their natal nest box were considered as “non-dispersers” (see Figure 1B). Both dispersers and non-dispersers were included in all analyses.

Dispersal analyses were based on 36 recaptures from a total of 562 marked nestlings, giving a raw recapture rate of 6.4%, similar to reported values in other studies (see Newton 2003 for a review). Although seemingly low, estimates of juvenile mortality for 2008–2015 ($\sim 77\%$) suggest that our sample size comprises $\sim 28\%$ of all surviving fledglings in Fray Jorge during the study period (Botero-Delgadillo et al. 2017). Although we might have missed some marked birds that went overlooked while breeding in natural cavities, we carried out intensive weekly searches inside the study plots during each breeding season to increase the probability of recapturing/resighting such individuals. Other birds might have been missed as they delayed their first breeding attempt, which seems to occur to some extent in the Fray Jorge population (see Botero-Delgadillo et al. 2017).

In order to generate a measure of dispersal distance that was independent of the yearly variation of breeding densities, we transformed linear distances into territory units following the method described in Botero-Delgadillo et al. (2017). In brief, we estimated the “number of territories dispersed” by each individual by dividing the linear dispersal distance into the mean territory diameter calculated for each breeding season. Breeding territories were modeled and estimated using Dirichlet tiles (Valcu and Kempenaers 2008).

Ecological and Social Correlates of Natal Dispersal

Variables used to assess the potential causes of natal dispersal were measured for 17 female and 19 male birds either during the natal or settlement (i.e. breeding) years (see Nilsson 1989, Pärt 1990). We focused on the effects that density-dependent processes, kin competition avoidance, and inbreeding avoidance might have on dispersal behavior. As a proxy of density-dependent effects, we included (1) the local density of adult neighbors at the natal site during the settlement year (both in nest boxes or natural cavities), measured as the mean distance to the first-order neighboring breeding pairs around the natal nest box. First-order neighbors (from 3 to 5) were defined according to the Dirichlet tiles. To assess kin competition

avoidance, we calculated (2) the genetic relatedness with adult neighbors of the same sex at the natal site during the settlement year (Weelwright and Mauck 1998). Finally, as a proxy of inbreeding avoidance we used (3) the genetic relatedness with adult neighbors of the opposite sex at the natal site during the settlement year (Arcese 1989, Payne 1991). The last 2 variables were measured relative to the settlement year because birds will likely need previous exposure to their kin in order to be able to recognize them later, and thus the decision to stay or leave around the natal site could take place during the onset of the following breeding season depending on the presence of “familiar” birds settling nearby.

Maximum likelihood coefficients of pairwise genetic relatedness (r) between all adult birds sampled during the study period ($n = 138$) were calculated using ML-Relate software (Kalinowski et al. 2006), and then a mean relatedness coefficient was computed between each focal bird and the first-order female–male neighbors around its natal site, using the linear distances between them as relative weights.

Natal Dispersal and Breeding Success

Three additional variables were measured for the recaptured individuals to assess the potential reproductive consequences of natal dispersal. All these variables were measured during the settlement year. We calculated (1) the breeding performance for both female and male birds, as the proportion of the clutch that successfully fledged (Pärt 1990). For females, we also calculated (2) clutch volume as the sum of the egg volumes for the entire clutch (see Moreno et al. 2005). In addition, we estimated (3) paternity loss in the social brood for males, measured as the proportion of extrapair young in the nest. Clutch size (mode = 3 eggs (86%), range: 1–3, $n = 36$) and brood size (mode = 3 nestlings (83%), range: 1–3, $n = 36$) were not considered in this study as they showed little variation in the sampled birds.

Estimates of paternity loss were obtained for each male based on parentage analysis, including all breeding adults that were captured and genotyped during the study period ($n = 138$) and their offspring ($n = 232$). We first performed parentage analysis as implemented in CERVUS 3.0.7 (Kalinowski et al. 2007) based on 12 microsatellite loci (combined probability of exclusion in both populations, $P > 0.999$), using the logarithm of odds (LOD score) and critical Delta values for assigning paternity. Results from this analysis were subsequently checked to confirm or exclude paternity. Assignment was confirmed whenever the most likely parent showed no mismatches with the putative offspring and there was a 95% confidence level around the assignment based on LOD or Delta scores (i.e. strict confidence; Kalinowski et al. 2007). If the social

father was the most likely candidate and showed no or one (3 cases) mismatch, and no other male showed zero mismatches, assignment was still confirmed regardless of the confidence level.

Data Analysis

We used an information-theoretic approach to analyze the association of natal dispersal with variables related to the ecological/social correlates and measurements of breeding success (Burnham and Anderson 2002). All analyses were performed in R 3.4.0 (R Core Team 2017).

Dispersal distance was used either as a response variable or as a predictor, depending on whether we were analyzing the ecological and social correlates of dispersal (i.e. the potential causes) or the association of dispersal and breeding success (i.e. the potential reproductive consequences). The “number of territories dispersed” (log-transformed) was included as the measure of dispersal distance in the analyses described below. We used log-transformed values in order to reduce the influence of rare long-dispersal events (Winkler et al. 2005) and to approximate the variable to a normal distribution (Arcese 1989). Additionally, all analyses were replicated using a measure of dispersal that controlled for the effect that the size of the natal fragment might have on dispersal behavior. Given that the size of the fragment can have either a positive or negative effect on dispersal distance (Baguette et al. 2012, Dytham and Travis 2012), we regressed the number of territories dispersed (log) on the area of the natal fragment (log) and used the residuals as a corrected measure of dispersal. We fitted both a linear and a quadratic model, but only used the first as it performed better according to values of the second-order AIC_c corrected for small samples (linear model: $df = 3$, $AIC_c = 64.89$; quadratic: $df = 4$, $AIC_c = 67.45$; see also Appendix Figure 5).

For the ecological and social correlates of dispersal distance, we fitted 2 separate linear models aiming to test the main effects of (1) the density of adult neighbors at the natal site, and (2) the genetic relatedness with female/male neighbors during the settlement year. In both models sex was entered as an interacting factor. While fitting one model for all variables combined would have been ideal, over-parameterization and high uncertainty around the estimated coefficients was a likely outcome due to our reduced sample size (Forstmeier and Schielzeth 2011). The 2 models were fitted sequentially, using the standardized residuals from the first model (i.e. dispersal distance regressed against neighbor density) as the response variable in the second model. This allowed us to assess the potential effects of genetic relatedness with female/male neighbors on dispersal distance while controlling for the density of adult neighbors. Both

models described above were compared against an intercept-only model by means of a log-likelihood ratio test so as to determine whether the observed effects were likely to arise by sampling variation alone (Forstmeier and Schielzeth 2011).

The potential reproductive consequences of natal dispersal were assessed using 3 separate models, which included the aforementioned measurements of breeding success as response variables. Because “breeding performance” and “within-pair siring success” were strongly bimodal, they were transformed into binary variables for subsequent analyses: for the first variable, individuals were assigned to categories of “high performance” (all eggs in the clutch successfully fledged) and “reduced performance” (partial clutch mortality); for the second variable, males were grouped into 2 classes, those that did lose paternity in their brood and those that did not. We fitted a linear model to assess the relationship between dispersal distance and female clutch volume. Generalized linear models (GLM; Zuur et al. 2007) with binomial structure and logit link were employed to analyze the relationship between dispersal and breeding performance (with sex as interacting factor) and between dispersal and male paternity loss. Log-likelihood ratio tests were used to compare the fitted models against intercept-only models.

RESULTS

The size of the natal fragment had no effect on the number of territories dispersed by rayaditos (95% confidence interval for the estimated effect = $-0.53-0.22$); despite that, there was a minor reduction in dispersal distance as the area of the natal fragment increased (Appendix Figure 5). The analyses using the number of territories dispersed and the corrected dispersal distance provided similar results,

and therefore we only present those based on the corrected variable (see below).

Ecological and Social Correlates of Natal Dispersal

The log-likelihood ratio tests showed that models for both density of adult neighbors ($\chi^2 = 24.71$, $df = 2$, $P < 0.001$) and genetic relatedness with females/males at the natal site ($\chi^2 = 15.62$, $df = 4$, $P = 0.008$) explained variation in the response variable better than random chance alone. Overall, both models indicated that the density of adult neighbors and the genetic relatedness between the studied birds with their male neighbors at the natal site had a sex-dependent effect on natal dispersal distance (Table 1). Neighbor density was positively related to dispersal distance in both sexes, as birds moved longer distances when the natal patch was more densely occupied by breeding adults during the settlement year (Figure 2A). Still, females seemed to respond more strongly to local breeding density than males (Figure 2A, Table 1). On the other hand, genetic relatedness was correlated only to male dispersal behavior, in the sense that they moved farther away from their natal site as relatedness with established male neighbors increased (Figure 2B). Genetic relatedness with female neighbors on the natal patch had no effect on dispersal distance (Table 1).

Natal Dispersal and Breeding Success

According to log-likelihood ratio tests, the model for the relationship between dispersal distance and male paternity loss differed from the intercept-only model ($\chi^2 = 11.51$, $df = 1$, $P < 0.001$), whereas models for breeding performance ($\chi^2 = 2.48$, $df = 2$, $P = 0.29$) and female clutch volume ($\chi^2 = 0.61$, $df = 1$, $P = 0.44$) did not. We observed no difference in dispersal distance between “high performance” (all eggs fledged) and “reduced performance” (partial mortality) birds (Table 2A), and female clutch volume showed no relationship with natal dispersal distance (Table 2B;

TABLE 1. Linear models showing the effects of ecological and social factors on natal dispersal distance of Thorn-tailed Rayadito in Fray Jorge National Park. Models were fitted to assess the effect of (A) the density of adult neighbors, and (B) the genetic relatedness with neighbors (either females or males) at the natal site during the settlement year. SE = standard error; L/U 95% CI = lower/upper 95% confidence interval for the estimate. Bold numbers indicate intervals that did not touch zero.

	Estimate	SE	L 95% CI	U 95% CI
A. Density of adult neighbors				
Intercept	-0.78	0.36	-2.16	0.04
Density of adult neighbors	0.50	0.15	0.19	0.81
Sex* density of adult neighbors ^a	-0.26	0.07	-0.40	-0.11
B. Genetic relatedness with neighbors				
Intercept	-0.10	0.19	-0.49	0.28
Genetic relatedness with females	0.03	0.91	-1.83	1.89
Genetic relatedness with males	0.89	0.91	-0.96	2.74
Sex* genetic relatedness with females ^a	0.71	1.68	-2.73	4.15
Sex* genetic relatedness with males ^a	2.46	1.06	0.32	5.24

^a Parameter estimates and SE (standard errors) for interaction terms were estimated relative to “female” level in variable “Sex.”

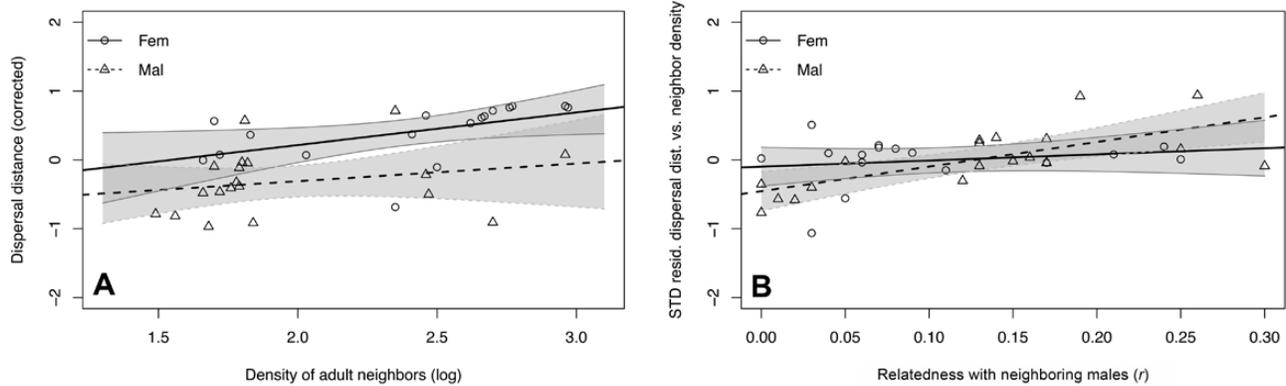


FIGURE 2. Potential social and ecological correlates of natal dispersal for Thorn-tailed Rayadito in Fray Jorge National Park, north-central Chile. **(A)** Sex-specific relationships between natal dispersal distances (corrected by fragment size) and density of adult neighbors at the natal site during the settlement year. **(B)** Sex-specific relationships between dispersal (standardized residual values regressed against neighbor density) and genetic relatedness with male territorial neighbors at the natal site during the settlement year. Shown are the model estimates (bold lines) and the corresponding 95% confidence intervals (in gray).

TABLE 2. Models showing the potential reproductive consequences of natal dispersal for Thorn-tailed Rayadito in Fray Jorge National Park. Models were fitted to assess the effect of dispersal distance on **(A)** breeding performance (all eggs fledged vs. partial clutch mortality), **(B)** female clutch volume, and **(C)** male paternity loss (lost paternity: yes/no). SE = standard error; L/U 95% CI = lower/upper 95% confidence interval for the estimate. Bold numbers indicate intervals that did not touch zero. Models **(A)** and **(C)** were fitted using a generalized linear model with binomial structure and logit link; model **(B)** was fitted using a linear model.

	Estimate	SE	L 95% CI	U 95% CI
A. Effect on breeding performance				
Intercept	-0.21	0.46	-1.18	0.66
Natal dispersal distance	1.62	1.13	-0.47	4.08
Sex*natal dispersal distance ^a	-2.43	1.69	-6.05	0.73
B. Effect on female clutch volume				
Intercept	2.55	0.03	2.48	2.63
Natal dispersal distance	-0.05	0.06	-0.18	0.09
C. Effect on male paternity loss				
Intercept	1.52	1.06	-0.21	4.15
Natal dispersal distance	6.20	2.98	1.91	13.96

^a Parameter estimates and SE (standard errors) for interaction terms were estimated relative to “female” level in variable “Sex.”

Appendix Figure 6). There was, however, a negative effect of dispersal distance on male within-pair siring success (Table 2C). Males that dispersed farther from their natal site were more likely to lose paternity in their own brood (Figure 3A). This pattern held even after performing the same analysis without 1 (95% confidence interval for the estimated effect = 1.75–13.96; Appendix Figure 7B) or 2 of the most extreme data values (95% confidence interval for the estimated effect = 1.47–13.94; Appendix Figure 7C). The difference in dispersal distance between males with or without paternity loss was also evident when comparing the number of territories dispersed (uncorrected distance; Figure 3B).

DISCUSSION

Previous studies have shown that a variety of ecological conditions can promote natal dispersal in birds and

determine its potential consequences, and for many species studied to date, females and males are differentially affected (Greenwood and Harvey 1982, Newton 2003). Despite relatively low sample sizes, our results indicate that female-biased dispersal in this isolated population of rayaditos could be explained, at least partially, by sex-related differences in the ecological and social factors driving natal dispersal, and perhaps by the associated reproductive consequences. Of course, there may be other factors that affect natal dispersal which we did not measure in this study, such as hatching asynchrony or hatching rank in the brood, and laying date (see Byholm et al. 2003).

Given the estimated proportion of marked nestlings that were recaptured during this study (~28%), dispersal distances analyzed here could be assumed as underestimated values. More data will be needed to test whether the distances used here were biased or not, yet observational

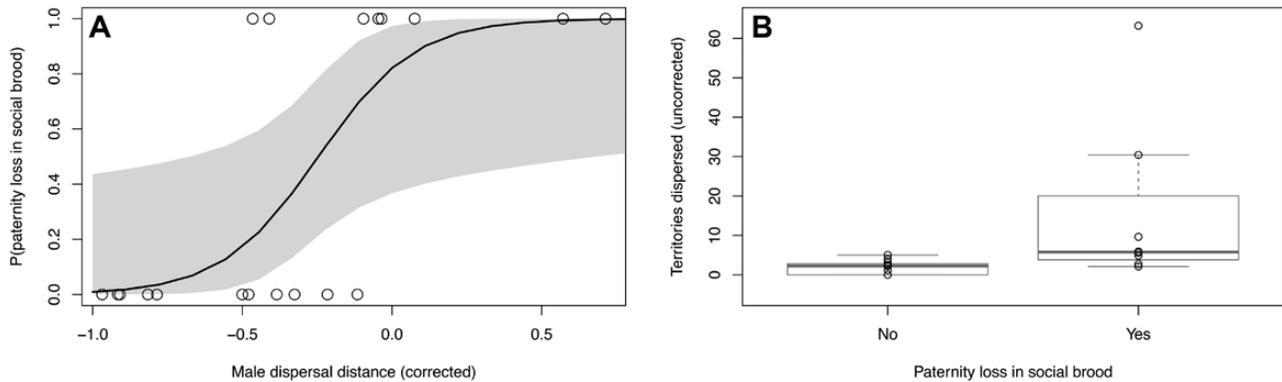


FIGURE 3. Relationship between natal dispersal distance and breeding success in male Thorn-tailed Rayadito in Fray Jorge National Park, north-central Chile. **(A)** Predicted probability of paternity loss in the social brood as a function of natal dispersal distance (corrected by fragment size). Shown are the model estimates (bold line) and the corresponding 95% confidence intervals (in gray). **(B)** A comparison of the number of territories dispersed (uncorrected) by males with and without paternity loss.

studies of dispersal behavior of rayaditos in fragmented landscapes have shown that they rarely move distances exceeding 900 m (Vergara et al. 2010), which is similar to the median distance dispersed by females in Fray Jorge (i.e. 740 m; Botero-Delgadillo et al. 2017), and is far below the maximum distance that we recorded for female and male birds (see Figure 1). Thus, although we might have missed a relevant proportion of dispersing individuals (see Methods for details), we think the potential bias in the variation of dispersal distances in our sample could be rather low.

Are the Sexes Differentially Affected by Density and Kin Interactions?

Density-dependent processes can be particularly important for individual dispersal decisions in heterogeneous or isolated habitats (Bowler and Benton 2005, Clobert et al. 2009, Benton and Bowler 2012, Matthysen 2012). If, for instance, low emigration rates due to isolation cause a steady increase in population density and competition for breeding sites, positive density-dependent dispersal could be observed in both sexes (see, e.g., Arcese 1989, Paris et al. 2016). This is what we actually found in our study site, where both sexes dispersed farther away from densely populated natal patches. It is then possible that the density of breeding pairs is used as a cue about the availability of vacant sites and potential mates by male and female rayaditos, respectively (i.e. informed dispersal; see Clobert et al. 2009).

It is worth mentioning, however, that females seemed to respond more intensely to local breeding density than males. This apparent difference could stem from the existence of sex-specific roles in the establishment of a breeding site. While sexual roles in territory acquisition are not yet clear in the case of rayaditos, males seem to be more involved in the defense of the nesting site (see Ippi et al. 2017), as in many other socially monogamous birds with

resource-defense mating systems (Greenwood 1980). In these species, breeding site accessibility for females is usually constrained by the availability of males owning a territory, and thus female dispersal can be a result of intra-sexual competition for locating a potentially available mate (Arlt and Pärt 2008). Given the high breeding bird density in Fray Jorge and the fragmented nature of the landscape, some females could ultimately be forced to move large distances towards less occupied patches. Despite a lack of direct evidence of female–female competition for breeding opportunities, the documented settlement patterns of post-fledging females in this population indicate this might be the case, as they gradually move away from their natal site until the first available male or vacant site is found (Botero-Delgadillo et al. 2017).

Our results showed that, after controlling for the effect of breeding bird density, kin competition avoidance also explained variability in male dispersal distances. If males were more related to the territorial males around their natal site, they dispersed farther to establish their first breeding territory. But why would males respond to both overall bird density and the abundance of kin? Even in the case that male rayaditos are capable of using the local density of breeding pairs as an indicator of nesting site availability, they might remain philopatric if the costs of dispersal exceed the costs of settling in a densely occupied neighborhood. In Fray Jorge, post-fledging males tend to establish in proximity to male kin (Botero-Delgadillo et al. 2017), probably because the likelihood of acquiring a territory is higher in a socially familiar environment (Greenwood 1980, Greenwood and Harvey 1982, Payne and Payne 1993). In such a case, this social benefit could only be overridden by the costs of intense local competition, and as a consequence, males would also respond to variations in the abundance of close kin. This explanation implies the existence of kin recognition mechanisms in

rayaditos, something that deserves further investigation. Nonetheless, this is likely in our study population, where the frequent and perhaps intense social interactions due to long-term isolation and habitat reduction may have facilitated the evolution of such mechanisms.

We found no evidence that the risk of inbreeding affected natal dispersal decisions in either sex. Given the settlement patterns of rayaditos in this locality, it could be expected that inbreeding avoidance partially explains the longer dispersal distances of females, because the tendency of males to remain close to their natal site might increase the risk of inbreeding (see Daniels and Walters 2000). Although we did not find evidence for inbreeding avoidance (as in e.g., Weelwright and Mauck 1998, Hansson et al. 2007, Eikenaar et al. 2008), females may already decrease the probability of mating with relatives simply by moving away from their natal sites where male offspring usually remain. Indeed, several studies have shown that demographic processes and random dispersal may suffice to account for low levels of inbreeding in bird populations (Arcese 1989, Gibbs and Grant 1989, Lebigre et al. 2010), also implying that active avoidance mechanisms may be hard to detect or be absent (see Szulkin and Sheldon 2008).

Are there Sex-Specific Reproductive Consequences of Natal Dispersal?

The “mating system” model of Greenwood (1980) predicts higher dispersal costs for male birds compared with females, a pattern already reported in several species (e.g., Bensch et al. 1998, Germain et al. 2017). Our results suggest this might also be the case for rayaditos in Fray Jorge. For instance, we found that males had a higher probability of losing paternity in their brood (lower within-pair siring success) as dispersal distance increased. By contrast, we did not detect any negative effect of dispersal on females.

The mechanisms behind the difference between the sexes in the relationship between breeding success and dispersal are possibly manifold, but the costs experienced by male rayaditos dispersing longer distances could result from the lack of familiarity with the new breeding site in combination with their lack of reproductive experience or low phenotypic quality (Pärt 1994, Pärt 1995, Brown et al. 2008, Germain et al. 2017). Previous studies in a semi-isolated population of Great Reed Warbler (*Achrocephalus arundinaceus*) found that philopatric males had higher mating success compared with dispersing males, and that the larger song repertoires of the first was positively correlated with their probability of obtaining extrapair fertilizations (Hasselquist et al. 1996, Bensch et al. 1998). If dominant male rayaditos remain closer to their natal site and subordinate individuals are forced to move farther (social dominance hypothesis; Arcese 1989), the lack of prior knowledge about the new patch and/or the difference

in intrinsic quality may be causing the observed effects. For instance, paternity loss could result from females compensating for the perceived low quality of their social mate by engaging in extrapair copulations or lower condition males might be worse at mate guarding. Male dominance is perhaps mediated by body size, or even by personality traits such as boldness and aggressiveness (Botero-Delgadillo 2017), which should be explored in the future.

It was not possible for us to compare the reproductive consequences of dispersal that involved movements within and between forest fragments. It has been shown that within- and between-fragment movements entail different costs for dispersing individuals in fragmented landscapes (Tarwater and Beissinger 2012), and hence, this could also be happening in Fray Jorge. Unfortunately, our dataset was not suitable for testing this, as females mostly engaged in between-fragment dispersal (13 out of 17 recaptured birds), whereas males moved almost exclusively within forest patches (17 out of 19 individuals). This is an interesting topic that should be addressed in the future as soon as more information becomes available from CMR data.

The risk of mortality is another aspect that will need further attention, as we currently lack enough data to estimate apparent survival rates for post-fledging birds (see Botero-Delgadillo et al. 2017). Post-fledging males dispersing large distances might pay high mortality costs during both transfer and settlement, and this could be a major cause of female-biased natal dispersal in Fray Jorge. There is evidence that transfer and settlement in unfamiliar habitats increases the mortality rates of dispersing birds (see Yoder et al. 2004, Brown et al. 2008), and that this effect can differ between sexes (Germain et al. 2017). In patchy environments, these differences can be caused by sex-specific responses to habitat loss and fragmentation. Recently, Awade et al. (2017) showed that in a population of White-backed Fire-eyes (*Pyriglena leucoptera*) inhabiting a fragmented landscape, predation risk increases as birds travel longer distances between patches, especially for males. The authors showed that in spite of males having higher flight capability, they were more risk-prone when moving throughout the matrix; conversely, females exhibited greater navigation ability when crossing large gaps of non-habitat.

Preliminary research on dispersal syndromes in the Fray Jorge population suggest that dispersing males are more risk-prone than philopatric individuals (Botero-Delgadillo 2017), and thus may suffer higher mortality. Follow-up studies using translocation experiments (e.g., Awade et al. 2017, Cornelius et al. 2017) will determine if differences in navigation abilities and risk-taking behavior also explain female-biased dispersal in this locality.

Concluding Remarks

Opportunities for territory establishment and breeding for rayaditos might be limiting in Fray Jorge National

Park, possibly due to a prolonged reduction of their breeding habitat. Increased competition and social interactions may affect each sex differently, with sex-biased dispersal as the likely outcome. Our data support the idea that density-dependent processes could be the main driver of female natal dispersal in this population (see Botero-Delgadillo et al. 2017). Although mortality costs associated with dispersal were not considered, we found no negative effects on reproductive success for females that moved longer distances, while natal dispersal seemed costly for males. Variability in male dispersal distances can result from a tradeoff between the social benefits of settling near the natal site (e.g., lower aggression and no paternity loss) and the associated costs of higher competition with kin.

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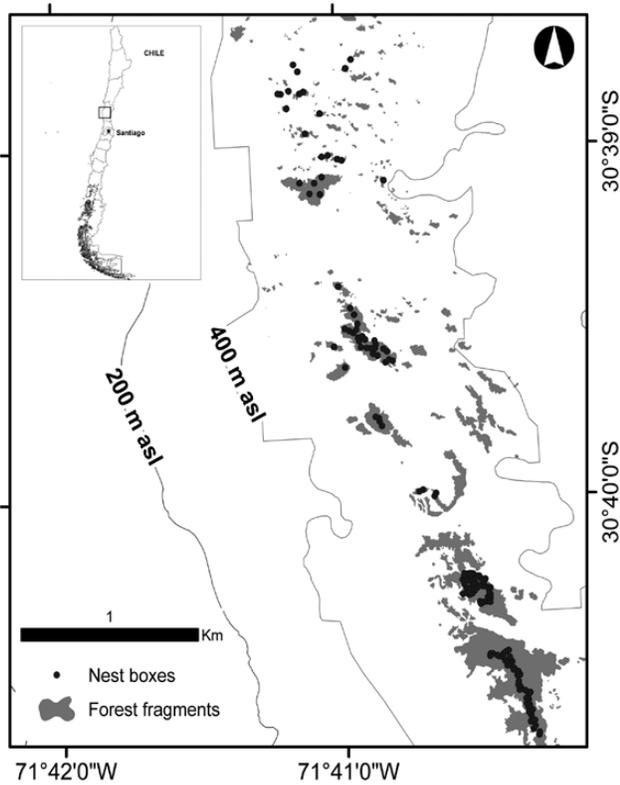
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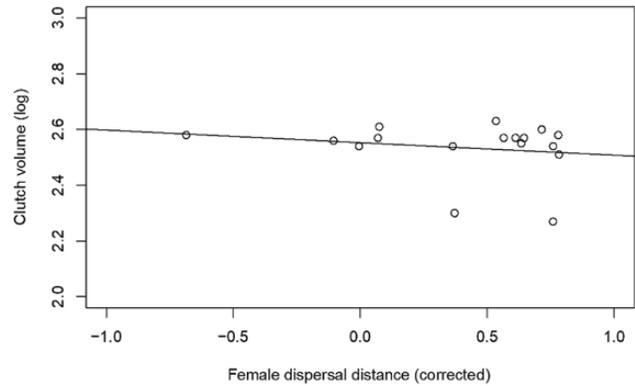
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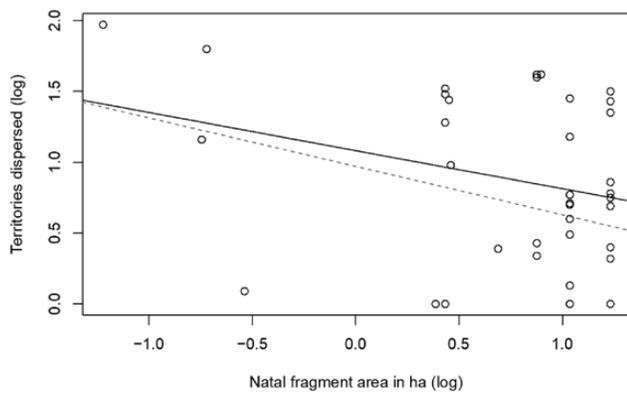
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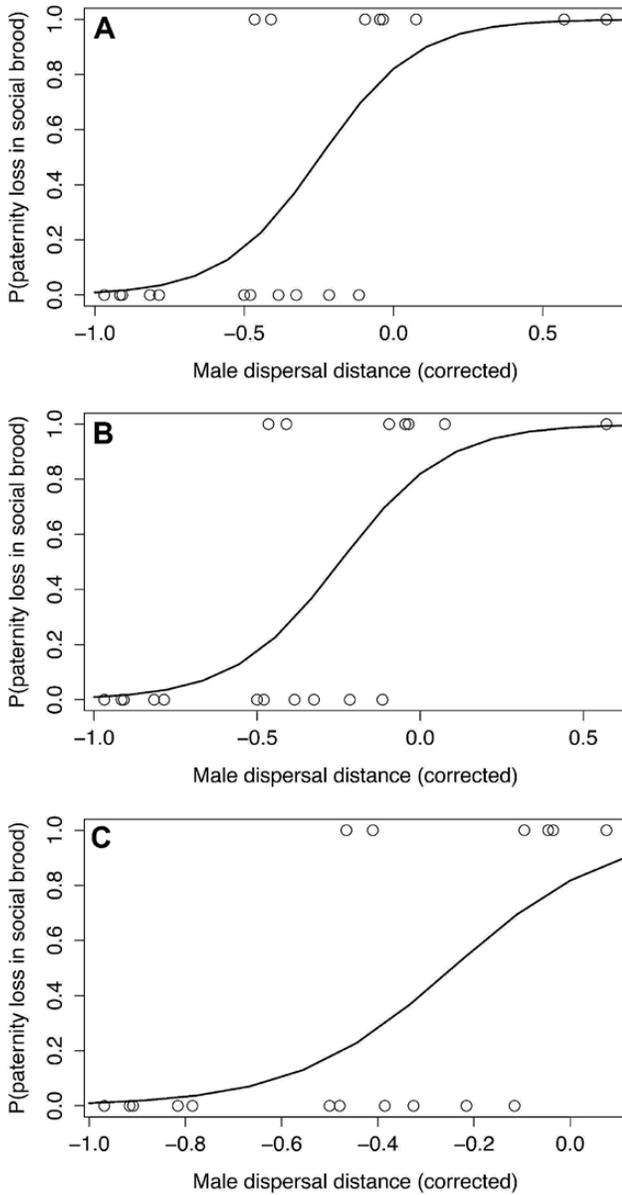
APPENDIX FIGURE 4. Spatial distribution of nest boxes installed since 2008 in Fray Jorge National Park, north-central Chile, to study the breeding biology of Thorn-tailed Rayadito. Nest boxes were distributed within forest fragments.



APPENDIX FIGURE 6 Linear model fitted to assess the relationship between natal dispersal distance (corrected; see main text for details) and clutch volume (log) for female Thorn-tailed Rayaditos in Fray Jorge National Park, north-central Chile.



APPENDIX FIGURE 5. Linear (solid, black line) and quadratic (dashed, grey line) models fitted to assess the relationship between size of the natal forest fragment (log) and number of territories dispersed (log) by Thorn-tailed Rayaditos in Fray Jorge National Park, north-central Chile. Despite the decreasing trend, the estimated effects were not different from zero (see main text for details).



APPENDIX FIGURE 7. Binomial model predicting the probability of paternity loss as a function of dispersal distance (corrected; see main text for details) for male Thorn-tailed Rayaditos in Fray Jorge National Park, south central Chile. **(A)** Model fitted with all recaptured males ($n = 19$; also showed in the main text). **(B)** Model fitted without the most extreme observation ($n = 18$). **(C)** Model fitted without the two most extreme observations ($n = 17$).