



Original Article

Investigating social and environmental predictors of natal dispersal in a cooperative breeding bird

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Natal dispersal is a crucial life-history trait that affects both individual fitness and population structure, yet drivers of variation in dispersal probability and distance are difficult to study in wild populations. In cooperatively breeding species, individuals typically delay dispersal beyond their first breeding season and remain on the natal territory as nonbreeders, which prolongs social dynamics that can affect dispersal decisions. Using a 35-year data set covering almost 600 dispersal events in the cooperatively breeding Florida scrub-jay (*Aphelocoma coerulescens*), we examined the environmental and social parameters that predict dispersal probability over time and distance. In both sexes, dispersal probability increased with age, which, in turn, was negatively correlated with dispersal distance. In males, individuals occupying low-quality natal territories and living with a stepfather had an increased probability of dispersal. Older and more dominant males were more likely to inherit their natal territory. In females, which generally disperse earlier and farther than males, socially subordinate jays dispersed farther than dominant ones. Overall, jays that delayed dispersal the longest were more likely to attain breeding status near their natal territory, which was previously found to be associated with increased survival and lifetime fitness. Our results suggest that social dynamics and environmental factors on the natal territory affect delayed dispersal patterns differently for the two sexes in this cooperative breeder.

Key words: *Aphelocoma coerulescens*, cooperative breeding, delayed dispersal, discrete-time logistic regression, natal dispersal, social dynamics.

INTRODUCTION

Natal dispersal, defined as permanent movement from natal to breeding territory, is a fundamental life-history event, which affects individual fitness, population structure, and gene flow (Greenwood and Harvey 1982; Clobert et al. 2001; Bonte and Dahirel 2017). Dispersal is a nonrandom process that depends on an individual's social and physical environment, along with its phenotype, and many such factors shape the cost–benefit balance of dispersal patterns in natural populations (Clobert et al. 2009; Matthysen 2012). Studying dispersal in wild populations is challenging because of geographical limits of study sites and difficulties of disentangling the effects of individual ecological drivers for a particular system

(Koenig et al. 1996; Nathan 2001; Bonte et al. 2012; Scandolaro et al. 2014). Consequently, dispersal distance has also received little attention in empirical studies on wild populations (Ferrer 1993; Hansson et al. 2004; Selonen et al. 2012) as research has mostly been limited to metapopulation dynamics in fragmented landscapes (Bonte et al. 2010). Here, we use long-term data collected on an intensively monitored, unfragmented population of Florida scrub-jays, *Aphelocoma coerulescens*, to investigate which environmental and social aspects of early life explain variation in dispersal age and distance in these cooperatively breeding birds.

Dispersal decisions in cooperative breeders are particularly complex as sexually mature offspring typically delay dispersal and independent reproduction and contribute to raising offspring of breeders (Emlen et al. 1983; Koenig et al. 1992; Koenig and Dickinson 2016). Despite apparent disadvantages of delayed

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reproduction among cooperative breeders (Covas and Griesser 2007), philopatric individuals can gain direct fitness benefits by remaining on the natal territory (Ekman et al. 1999; Sparkman et al. 2011; Tanaka et al. 2016). Such benefits of philopatry include parental nepotism (Ekman et al. 2001; Nelson-Flower and Ridley 2016; Mayer et al. 2017), increased chances of territorial inheritance (Woollenden and Fitzpatrick 1978), direct reproduction with unrelated breeders (Cockburn et al. 2008; Groenewoud et al. 2018), or access to favorable breeding opportunities nearby (Zack and Stutchbury 1992; Kokko and Ekman 2002; van de Pol et al. 2007; Kingma et al. 2016). Conversely, local competition for resources such as food or breeding position may reduce the benefits of philopatry (Wiley and Rabenold 1984; Kokko and Ekman 2002). For example, offspring may shorten their tenure on the natal territory if they are subordinate to their siblings that outcompete them for resources and breeding opportunities (Eden 1987; Strickland 1991; Ekman et al. 2002; Pasinelli et al. 2002; Nelson-Flower et al. 2018). Additionally, when a stepparent replaces a biological parent, offspring may either disperse earlier because of diminished indirect benefits (Heg et al. 2011) or, if perceived to be a competitor, because of aggression by the same-sex stepparent (Goldstein et al. 1998; Eikenaar et al. 2007; Mayer et al. 2017). Although many studies have investigated the effects of social drivers on the presence or timing of delayed dispersal, it remains unclear what factors, if any, explain variation in dispersal distance.

Despite their strong implications for gene flow, metapopulation dynamics, and range expansion, the drivers of dispersal distance in cooperative breeders are poorly understood (but see Pasinelli et al. 2004; Green and Hatchwell 2018). Costs of dispersal, mediated by energetic constraints and predation risk, generally increase with distance traveled (Murrell et al. 2002; Rousset and Gandon 2002; Bonte et al. 2012). Therefore, dispersers are only expected to move long distances if the benefits outweigh these costs. For example, variation in natal territory quality can drive density-dependent dispersal (Bitume et al. 2013; Scandolara et al. 2014; Maag et al. 2018; Puzin et al. 2019) because individuals are more likely to disperse from territories of low quality when local competition for resources is high (Komdeur 1992; Matthysen 2012). If resource availability and territory quality are spatially autocorrelated, individuals may also need to travel longer distances in search of better breeding territories (Trenham et al. 2001; Bonte et al. 2010; Valcu and Kempenaers 2010). Furthermore, environmental factors may interact with individual attributes to influence dispersal decisions (Ims and Hjermann 2001; Clobert et al. 2009). For example, birds hatched earlier in the year tend to be in better condition than late-hatching individuals (Saino et al. 2012), which may result in higher capacity for longer dispersal distances (Ferrer 1993) or may enable dispersers to be more selective about breeding opportunities (Nilsson 1989; Stamps 2006; Warner and Shine 2008). Thus, environmental factors may mediate dispersal decisions both directly and indirectly by altering the costs and benefits of dispersal distances.

We examined which social, environmental, and phenotypic factors are associated with the age-dependent probability and distance of dispersal in a wild population of cooperatively breeding Florida scrub-jays. In this species, nonbreeders typically delay dispersal for 1–2 years and form distinct within-group dominance hierarchies. The delay in dispersal is thought to arise from an overarching ecological constraint of limited breeding opportunities within sharply defined habitat boundaries (Woollenden and Fitzpatrick 1977, 1984; Fitzpatrick and Bowman 2016). In this system, extra-pair paternity is essentially absent, so nonbreeders that delay dispersal

gain neither direct reproductive benefits nor any appreciable indirect benefits from helping as opposed to independent breeding (Townsend et al. 2011; Fitzpatrick and Bowman 2016). Rather, delayed dispersal allows nonbreeders to compete for breeding vacancies without leaving the natal territory, thereby receiving group-living benefits such as a coordinated sentinel system and cooperative territory defense (Fitzpatrick and Bowman 2016). Previous work also showed that shorter-distance dispersal is associated with higher lifetime reproductive success due to higher survival during the first 1–2 years as a breeder (Fitzpatrick et al. 1999; Coulon et al. 2010; Fitzpatrick and Bowman 2016). Within this framework, we investigated how social and environmental factors in early life shape 1) the decision to delay dispersal and 2) dispersal distances of Florida scrub-jays within a large and contiguous population.

First, we investigated how social and environmental factors on the natal territory influenced age-specific probability of dispersal. Previous work on a different study population showed that first-year jays delayed dispersal when biological parents were alive and when potential mates in the surrounding landscape existed at intermediate densities (Breininger et al. 2010). However, overall variation in dispersal age remained unexplored and it is unclear why some jays remain on the natal territory for up to 6 years (Fitzpatrick and Bowman 2016). Based on the benefits of philopatry hypothesis, we predicted that dominant nonbreeders in high-quality territories would delay dispersal longer than lower-ranked jays in poor-quality territories. We also predicted that jays in lower-quality territories would be more likely to disperse early because of higher within-family competition for local resources. In addition, we revisited the positive effect of stepparents on dispersal probability of same-sex offspring, which was observed in a previous study by Goldstein et al. (1998). We also examined which proximate factors best explain instances of direct territory inheritance among nonbreeding males.

Second, we investigated correlates of dispersal distance. Fitzpatrick et al. (1999) suggested that early dispersers move farther than later dispersers but did not detect any additional effects of the social environment, such as family size, family composition, or neighborhood density. We addressed this question using a much larger data set and by considering environmental and phenotypic traits, in addition to social ones. We included age as a phenotypic trait and predicted a negative relationship with dispersal distance: young jays at the bottom of the social hierarchy, lacking full access to benefits of philopatry (e.g., inheritance opportunities and nearby breeding opportunities), should move farther to escape local competition (Pasinelli et al. 2002) despite costs of extended dispersal periods (Bonte et al. 2012). We also predicted that, within groups, jays that hatched later in the year would disperse farther than early hatched dispersers because they are less competitive for nearby breeding opportunities (Spear et al. 1998; Scandolara et al. 2014). Jays on territories with more same-sex nonbreeders also may experience higher competition for resources and should, thus, disperse farther to avoid competition (Bebbington et al. 2017). We predicted that jays hatched on low-quality territories would disperse farther than those from high-quality territories, especially, if there is spatial autocorrelation in territory quality as might be expected for a fire-prone ecosystem in which fire swaths encompass many territories.

Lastly, we explicitly tested how within-brood dominance affects differences in dispersal patterns of same-age, same-sex brood mates, which allowed us to control for confounding factors of the natal territory, such as genetic and maternal effects. Because routes to breeding in Florida scrub-jays are sex specific

(Woolfenden and Fitzpatrick 1978, 1984), we conducted separate analyses for each sex.

METHODS

Study species and system

The Florida scrub-jay is a resident habitat specialist restricted to fire-maintained oak scrub habitats of the Florida peninsula. Optimal habitat includes large patches of recently burned scrub (Breininger and Oddy 2004; Fitzpatrick and Bowman 2016). This habitat is usually saturated with territorial groups and most offspring delay dispersal from the natal territory, spending at least one breeding season as nonbreeding helpers that assist in territory defense, sentinel behavior, and rearing of young (McGowan and Woolfenden 1989; Mumme 1992). Florida scrub-jays form strict social hierarchies within family groups: breeders dominate helpers, males dominate females, and older birds dominate younger ones (Woolfenden and Fitzpatrick 1977; Tringali and Bowman 2012).

Most individuals of both sexes acquire breeding positions by replacing dead breeders on existing territories. However, males can inherit their natal territory or bud a portion of the natal territory to form a new territory, whereas females typically disperse from the natal territory (Woolfenden and Fitzpatrick 1978). The asymmetries in routes to breeding between males, which can inherit or bud territories, and females, which are limited to replacing lost breeders or pairing with a budding male, suggest that different ecological and social factors may drive their respective dispersal decisions.

We study a color-banded population of Florida scrub-jays at Archbold Biological Station in central Florida (27.10°N, 81.21°W), where intensive monitoring across a large spatial scale has been ongoing for five decades. Throughout each breeding season, all nests were located and monitored until fledging or failure (Woolfenden and Fitzpatrick 1984). Data for this study include successful natal dispersal events for birds hatched between 1980 and 2014. We included only successful dispersers that acquired a breeding position for at least one breeding season and laid or sired at least one egg (Townsend et al. 2011). Toward the end of the breeding season, we conducted surveys of suitable habitat up to 40 km from our study site. Dispersal beyond 25 km is exceedingly rare in this species (Coulon et al. 2010), so our off-site surveys enabled us to document a number of long-distance dispersal events beyond our study plot.

Early in each breeding season, all territories were mapped by assigning boundaries wherever territorial disputes occurred between neighboring groups (Woolfenden and Fitzpatrick 1984). Maps were digitized using ArcGIS (ESRI, Redlands, CA) and we assigned an annual estimate of habitat quality to each territory based on area of oak scrub habitat within each territory (Abrahamson et al. 1984; Supplementary Material 1).

To capture social dynamics in the natal territory, we assigned within-group dominance hierarchies for each sex first by age, with older birds being dominant to younger birds (Woolfenden and Fitzpatrick 1977), and within-brood dominance using relative body mass at 11 days posthatching. We assumed that relative body mass as nestlings drives within-brood dominance because this relationship has been observed in other avian species (Safriel 1981; Nathan et al. 2001). In Florida scrub-jays, relative mass among brood mates is mostly determined by hatching order and tends to remain consistent over time (Mumme et al. 2015). We designated social position using a categorical ranking system in which nonbreeders within the group were ranked as dominant if oldest or, in the absence of

older nonbreeders, heaviest within the same brood. Nonbreeders other than the dominant individual were ranked as subordinate and nonbreeders without same-sex nonbreeders were designated as singletons. We defined stepparents as breeders that replaced a biological parent and recorded their date of arrival or acquisition of breeder position.

Statistical analyses

Dispersal probability

We inferred dispersal parameters from the monthly census data and defined date of departure as the last census date an individual was observed in its natal territory. Because Florida scrub-jays in our population exhibit bimodal dispersal timing across the year (Figure 1), we defined age at dispersal as the number of semesters (i.e., potential dispersal windows) spent as a nonbreeding helper on the natal territory. The first semester spans the period from the hatch date to the December census of the same year. Subsequent semesters ranged from the January to June census, then the July to December census.

To investigate predictors of dispersal probability, we constructed discrete-time logistic regression models, a type of survival analysis that models the probability of events as a function of covariates that vary over time (Allison 1982, 2010; Willett and Singer 1993; Maul 1994). This conservative analysis accounts for the fact that social dynamics change over the early years of Florida scrub-jays: as they age, nonbreeders rise in hierarchical rank within the group and become more likely to obtain a stepparent (Supplementary Material 2). The probability of dispersal at discrete-time events, measured here as semesters, was modeled as a binomial process (1 = disperse, 0 = remain on territory) as a function of time-varying covariates: age in semesters, arrival of a stepparent, social rank within group, and territory quality (Table 1). We considered dispersal events for 311 males and 284 females over a total of 2002 jay-semester observations (males $n = 1109$; females $n = 893$).

Territorial inheritance

To investigate drivers of variation in direct inheritance among males, we constructed a discrete-time logistic regression model with a binomial error distribution for inheritance ($\text{inherit} = 1$,

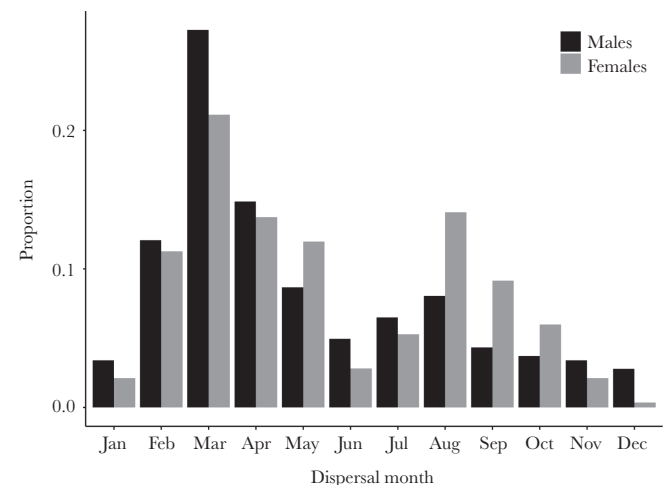


Figure 1

Timing of dispersal by Florida scrub-jays. Proportion of males and female birds that disperse each month (males: $n = 311$; females: $n = 284$). The two peaks coincide with the start (March) and end (August) of breeding season.

disperse = 0) with the same fixed effects as the dispersal probability model (Table 1). We only investigated territory inheritance in males because females almost never directly inherit the parental territory (<1% of dispersal fates; Woolfenden and Fitzpatrick 1984; Fitzpatrick and Bowman 2016). We considered 291 males (total of 1109 jay semesters), out of which just 20 inherited their full natal territory.

Dispersal distance

For dispersal events entirely within the study area, we measured dispersal distance as the distance between natal and breeding territory centroids using ArcGIS. For dispersals beyond the boundaries of Archbold Biological Station, we measured the distance between the natal territory centroid to the survey point at which the disperser was first detected. For dispersers detected on off-site surveys, we assumed they had acquired their first breeding position in their observed location (Coulon et al. 2010).

To investigate which early life factors affected dispersal distance, we constructed separate linear mixed models (LMMs) for each sex that included age at dispersal in semesters, territory quality, within-group rank, number of same-sex helpers, and hatch date as fixed effects (Table 2). Here, we excluded the 20 males that inherited their natal territory and, therefore, considered dispersal events for 268 male and 234 female jays.

Same-sex brood mates

To test whether within-brood dominance affects dispersal, we compared dispersal among same-sex brood mates, which allowed us to

control for maternal and territory effects. From data on known-origin natal dispersers, we compiled dispersal information for a subset that had same-sex brood mates that were alive when the successful disperser left the natal territory. We conducted *t*-tests to test for differences in dispersal age and distance in relation to within-brood rank among sibling pairs. We assigned within-brood rank as a binary category with the heaviest bird considered dominant and the others as subordinates. In rare cases with more than two same-sex brood mates, we randomly selected one as the subordinate for the comparison (Pasinelli et al. 2002). We considered 172 pairs of brood mates (males $n = 66$ pairs; females $n = 96$ pairs). Because males dominate females within families, we did not compare siblings of different sexes.

We conducted all statistical analyses in R v 3.5.0 (R Core Team 2019). We used the package “lme4” (Bates et al. 2015) to construct LMMs and discrete-time logistic regression models with logit links (Allison 1982, 2010). Exploratory analyses revealed that the random effect “nest year,” a term encompassing group identity and year which could control for unaccounted differences among territories or family lineages, did not explain any variation (i.e., parameter estimate ~ 0). We, thus, did not include the term in the models but we did include year of dispersal as a random effect in all models. To facilitate interpretation, we standardized area of scrub habitat, number of same-sex helpers, and hatch date in our models by centering the parameters on 0 and scaling the values by dividing them by their standard deviations. Furthermore, we log-transformed dispersal distances in LMMs to conform to model assumptions about residual distributions. Therefore, we present standardized parameter estimates

Table 1

Parameters used to investigate probability of dispersal and inheritance and dispersal distance in Florida scrub-jays.

Response	Predictor	Description	Prediction	Support
a) Dispersal probability	Age	Semesters spent on natal territory	Older jays disperse	Yes
	Natal scrub area	Area of oak scrub habitat (m^2) in the natal territory	Jays on high-quality territories delay dispersal	Yes, for males
	Rank	A categorical rank of the social dominance within same-sex helpers (dominant, subordinate, and singleton)	High-ranking and singleton jays delay dispersal	No
	Stepmother	Presence of unrelated breeding female at the time of dispersal	Presence of stepmother induces earlier dispersal for females	No
b) Inheritance probability (males)	Stepfather	Presence of unrelated breeding male at the time of dispersal	Presence of stepfather induces earlier dispersal for males	Yes, for males
	Age	Semesters spent on natal territory	Older males inherit	Yes
	Natal scrub area	Area of oak scrub habitat in the natal territory (m^2)	Jays on high-quality territories delay dispersal	No
	Rank	A categorical rank of the social dominance within same-sex helpers (dominant, subordinate, and singleton)	High-ranking and singleton jays inherit	Trend
c) Dispersal distance	Stepmother	Presence of unrelated breeding female at the time of dispersal	Males inherit in presence of stepmother	No
	Stepfather	Presence of unrelated breeding male at the time of dispersal	Males do not inherit in presence of stepmother	Yes
	Age	Semesters spent on natal territory	Younger jays disperse farther	Yes
	Natal scrub area	Area of oak scrub habitat in the natal territory (m^2)	Jays on low-quality territories disperse farther	No
	Rank	A categorical rank of the social dominance within same-sex helpers (dominant, subordinate, and singleton)	High-ranking and singleton jays disperse closer	Yes, for females
	Helpers	Number of same-sex helpers on the natal territory that year	More helpers result in farther dispersal	No
	Hatch date	Ordinal date of hatching	Jays hatched later in the year disperse farther	No

Table 2**Summary statistics of age at dispersal and dispersal distance by sex**

	Male Mean \pm SE (<i>n</i>)	Female Mean \pm SE (<i>n</i>)
Age at dispersal (years)	2.7 \pm 0.1 (322)	2.5 \pm 0.1 (285)
Dispersal distance (m)	822.9 \pm 72.8 (318)	2511.0 \pm 264.2 (273)

β (\pm standard error [SE]), as well as associated z - and P -values. To explicitly test for model fit, we used the package “DHARMA” to investigate model residuals (Hartig 2019; Supplementary Material 3). We checked for multicollinearity by investigating variable inflation factors (VIFs) and confirmed this to be of no concern in all our models (all VIF < 4.0 ; Supplementary Material 4). To provide descriptive comparisons of sex differences in dispersal age and distance, we conducted t -tests. We produced all visualizations with the package “ggplot2” (Wickham 2016). For survival plots, we used the package “survminer” (Kassambara et al. 2019).

RESULTS

Dispersal probability

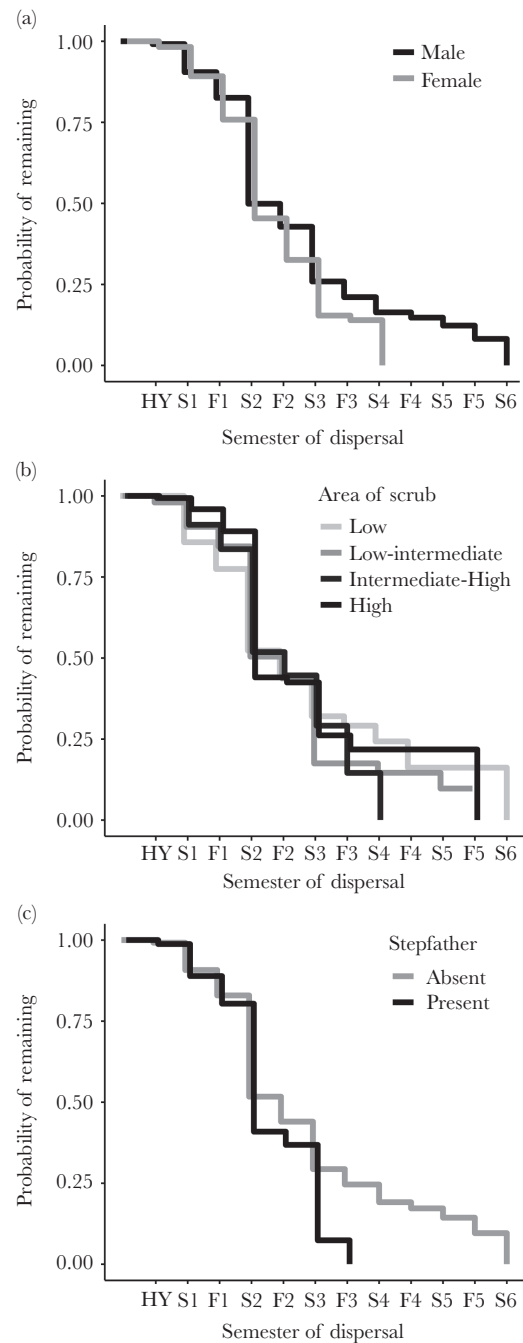
Males dispersed later than females (Table 2; Figure 2a; t -test degrees of freedom [df] = 601, $t = -2.15$, $P = 0.03$). For both sexes, the probability of dispersal increased with age, as measured in semesters (males: $\beta = 0.59 \pm 0.06$ (\pm SE), $z = 10.1$, $P < 0.001$; females: $\beta = 0.77 \pm 0.08$, $z = 9.87$, $P < 0.001$; Tables 3 and 4; Figure 2b). Males from high-quality natal territories were less likely to disperse ($\beta = -0.17 \pm 0.08$, $z = -2.08$, $P = 0.04$; Table 3) and males with stepfathers were more likely to disperse ($\beta = 0.57 \pm 0.21$, $z = 2.75$, $P = 0.006$; Figure 2c). Probability of dispersal did not change with presence of a stepmother or the dispersing individual's within-group rank (Table 3). For females, singletons tended to be more likely to disperse than dominant individuals ($\beta = 0.39 \pm 0.22$, $z = 1.76$, $P = 0.08$; Table 4). Dispersal probability among females did not change with presence of a stepmother, stepfather, area of scrub, or the dispersing individual's within-group rank (Table 3).

Territorial inheritance

Older males were more likely to inherit territories ($\beta = 0.39 \pm 0.12$, $z = 3.41$, $P < 0.001$; Table 5), as were dominant males compared with singleton ($\beta = -0.95 \pm 0.52$, $z = -1.81$, $P = 0.07$) or subordinate males ($\beta = -1.40 \pm 0.82$, $z = -1.72$, $P = 0.09$). Presence of stepparents or area of scrub did not affect probability of territorial inheritance (Table 5).

Dispersal distance

Females dispersed farther than males (Table 2; Figure 3; t -test df = 313, $t = 6.16$, $P < 0.001$). Age at dispersal was the only significant predictor of dispersal distance for both male and female dispersers (Tables 6 and 7). Younger dispersers bred farther from their natal territories than older dispersers (males: $\beta_{\text{age}} = -0.16 \pm 0.03$, $z = -5.1$, $P < 0.001$; females: $\beta_{\text{age}} = -0.18 \pm 0.05$, $z = -3.79$, $P = 0.0002$; Figure 4). Territory quality, within-group rank, the number of helpers, and hatch date did not explain variation in dispersal distance for males (Table 6). However, within-group

**Figure 2**

Correlates of dispersal probability in Florida scrub-jays. Survival plots per age group by (a) sex and, for males, by (b) territory quality and (c) presence of stepfather. For semester of dispersal, S denotes spring (first semester of a year) and F denotes fall (second semester of a year). Territory quality (b) is categorized into four quantiles for illustrative purposes (low-, low-intermediate-, intermediate-high-, and high-quality territory) but was a continuous predictor in our analyses.

rank correlated with dispersal distance in females with subordinates moving farther ($\beta = 0.42 \pm 0.19$, $z = 2.19$, $P = 0.03$, Table 7) than dominant females. Territory quality, number of helpers, and hatch date were not significantly correlated with female dispersal distances (Table 7).

Table 3

Correlates of dispersal probability in males. Standardized parameter estimates (β), associated SEs, z - and P -values for discrete-time logistic regression model results for 311 (1109 jay semesters) nonbreeding Florida scrub-jay males dispersing from their natal territory. Year of dispersal was included as a random effect. Bold values indicate $P < 0.05$

Parameter	B	SE	z	P
Intercept	-3.003	0.277	-10.838	<0.001
Age at dispersal	0.591	0.059	10.095	<0.001
Rank (singleton)	0.184	0.192	0.957	0.339
Rank (subordinate)	0.001	0.218	0.005	0.996
Stepmother	0.149	0.200	0.742	0.458
Stepfather	0.572	0.208	2.751	0.006
Area of scrub	-0.166	0.080	-2.079	0.038

Table 4

Correlates of dispersal probability in females. Standardized parameter estimates (β), associated SEs, z - and P -values for discrete-time logistic regression model results for 284 (893 jay semesters) nonbreeding Florida scrub-jay females dispersing from their natal territory. Year of dispersal was included as a random effect. Bold values indicate $P < 0.05$; italics indicate $P < 0.1$

Parameter	B	SE	z	P
Intercept	-3.219	0.310	-10.396	<0.001
Age at dispersal	0.768	0.078	9.870	<0.001
Rank (Singleton)	<i>0.387</i>	<i>0.219</i>	<i>1.764</i>	<i>0.078</i>
Rank (Subordinate)	0.163	0.237	0.686	0.493
Stepmother	-0.093	0.225	-0.415	0.678
Stepfather	-0.091	0.240	-0.377	0.706
Area of scrub	-0.113	0.094	-1.199	0.231

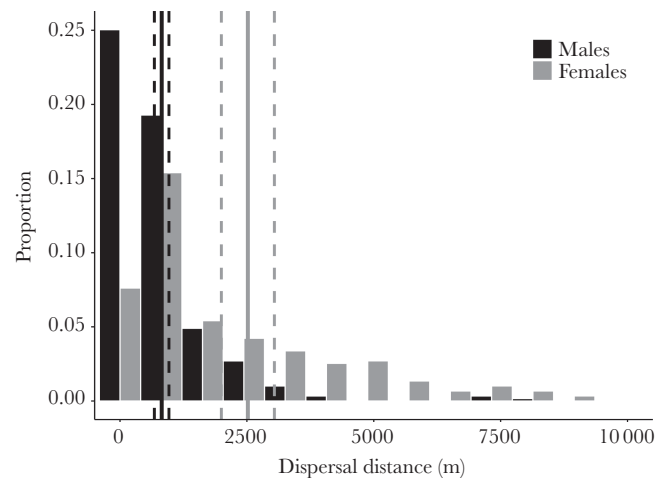
Table 5

Correlates of inheritance probability in males. Standardized parameter estimates (β), associated SEs, z - and P -values for discrete-time logistic regression model results for 291 (1109 jay semesters) nonbreeding Florida scrub-jay males, out of which 20 inherited their natal territory. Year of dispersal was included as a random effect. Bold values indicate $P < 0.05$; italics indicate $P < 0.1$

Parameter	B	SE	z	P
Intercept	-4.878	0.718	-6.797	<0.001
Age at dispersal	0.392	0.115	3.410	<0.001
Rank (singleton)	<i>-0.945</i>	<i>0.522</i>	<i>-1.810</i>	<i>0.070</i>
Rank (subordinate)	<i>-1.402</i>	<i>0.817</i>	<i>-1.716</i>	<i>0.086</i>
Stepmother	0.443	0.548	0.810	0.418
Stepfather	-1.461	1.089	-1.342	0.180
Area of scrub	-0.395	0.254	-1.551	0.121

Dispersal among same-sex brood mates

Within-brood dominance, approximated by relative nestling weight, was not significantly linked to dispersal age in either sex (Table 8; t -test, males: $df = 36$, $t = -1.40$, $P = 0.17$; females: $df = 37$, $t = 0.37$, $P = 0.71$). In addition, within-brood dominance was not significantly correlated with dispersal distance (Table 8; males: $df = 34$, $t = 1.18$, $P = 0.25$; females: $df = 34$, $t = -1.62$, $P = 0.11$).

**Figure 3**

Natal dispersal distances of Florida scrub-jays. Data for birds hatched during the years 1980–2014 at Archbold Biological Station (males: $n = 288$; females: $n = 234$). We excluded four females and one male whose dispersal distance exceeded 10 km. Solid lines indicate mean and dashed lines indicate 95% confidence intervals (black—male, gray—females).

Table 6

Correlates of dispersal distance in males. Standardized parameter estimates (β), associated SEs, z - and P -values for LMM of log-transformed dispersal distance for 268 nonbreeding Florida scrub-jay males. Year of dispersal was included as a random effect. Bold values indicate $P < 0.05$

Parameter	β	S.E.	z	P
Intercept	6.978	0.162	43.048	<0.001
Age at dispersal	-0.158	0.031	-5.148	<0.001
Rank (singleton)	-0.005	0.161	-0.031	0.975
Rank (subordinate)	-0.105	0.133	-0.787	0.432
Same-sex helpers	0.074	0.080	0.920	0.358
Area of scrub	0.059	0.047	1.244	0.215
Hatch date	0.067	0.049	1.358	0.176

Table 7

Correlates of dispersal distance in females. Standardized parameter estimates (β), associated SEs, z - and P -values for LMM of log-transformed dispersal distances for 234 nonbreeding Florida scrub-jay females. Year of dispersal was included as a random effect. Bold values indicate $P < 0.05$

Parameter	β	SE	z	P
Intercept	7.937	0.236	33.701	<0.001
Age at dispersal	-0.180	0.048	-3.794	<0.001
Rank (singleton)	-0.343	0.220	-1.554	0.122
Rank (subordinate)	0.419	0.191	2.188	0.030
Same-sex helpers	-0.110	0.116	-0.952	0.342
Area of scrub	-0.059	0.069	-0.849	0.397
Hatch date	0.077	0.061	1.255	0.211

DISCUSSION

Dispersal strategies in Florida scrub-jays vary with social dynamics and habitat quality of the natal territory. In both sexes, the

probability of dispersal increased with age and early dispersers were more likely to disperse greater distances. In males, the probability of inheriting the natal territory also increased with age, confirming a direct benefit of delayed dispersal. Among females, lower-ranking individuals were more likely to disperse farther than dominant ones. However, we found no effects of within-brood dominance on the timing or distance of dispersal. In cooperative breeding species where multiple cohorts overlap, the effect of within-brood dominance is likely masked by within-group social dynamics. Overall, our results show that both environmental and social dynamics affect dispersal timing and distance, both of which have strong fitness consequences (Fitzpatrick and Bowman 2016). Therefore, our findings support the findings of Nelson-Flower et al. (2018) that no single category of predictors affects dispersal decisions in cooperative breeders.

Who delays dispersal?

Florida scrub-jay males were more likely to disperse in the presence of a stepfather or when they hatched on low-quality territories with limited oak scrub habitat. Dominant males that delayed dispersal had a higher chance of inheriting their fathers' territory, suggesting that waiting for inheritance opportunities contributed to the evolution of delayed dispersal in this species (Woollenden and Fitzpatrick

1978; Zack 1990; Fitzpatrick and Bowman 2016). In this system, indirect fitness benefits associated with helping behavior are limited and cannot account for the evolution of delayed dispersal on their own (Woollenden and Fitzpatrick 1984; Fitzpatrick and Bowman 2016). As vacant habitat is essentially absent in this saturated social landscape, offspring are less likely to disperse from high-quality natal territories or when they may benefit from paternal nepotism. These benefits of philopatry resemble those reported from other cooperative breeding systems (e.g., Pärt 1991; Stacey and Ligon 1991; Ekman and Griesser 2002).

Overall, delayed dispersal in Florida scrub-jays follows the predictions of the recently conceptualized “dual benefits” framework (Shen et al. 2017). Resource defense benefits accrue from group defense of critical resources, whereas collective action benefits simultaneously accrue from social coordination, such as shared sentinel and provisioning behaviors (Shen et al. 2017). We found that dispersal decisions by male Florida scrub-jays were affected by territory quality—the more resources in the territory, the less likely a nonbreeder was to disperse. Mumme et al. (2015) found that natal territory size and group size both increased offspring survival but, in large groups occupying small territories containing limited oak scrub, juveniles were smaller and experienced decreased survival. Combined, these findings suggest that resource defense benefits are not absolute but themselves can be limited by the social environment. Biological fathers tolerating their sons can be seen as a collective action benefit as groups with helpers tend to expand their territories (Woollenden and Fitzpatrick 1984). These results align well with the “dual benefits” framework: for cooperative breeders that delay dispersal, resource defense is a primary fitness benefit, whereas collective action, such as provisioning and sharing sentinel duties by additional group members, contributes to survival and group productivity.

Our results support the previous observation that arrival of a same-sex stepparent leads to a more rapid departure from the natal territory (Goldstein et al. 1998), a pattern also observed in other study systems (Ekman and Griesser 2002; Nelson-Flower and Ridley 2016). Same-sex stepparents, specifically stepfathers, may perceive unrelated nonbreeding males as competitors and evict stepsons, causing them to disperse earlier. Alternatively, without the benefit of paternal nepotism, nonkin helpers may choose to disperse. These results demonstrate how genetic relationships between the breeding pair and nonbreeders, and potentially the effect of nepotism, affect dispersal delays.

Who disperses farther?

We found that long-distance dispersers are younger at the time of dispersal, consistent with earlier findings (Fitzpatrick et al. 1999). Additionally, among females, subordinates dispersed farther than

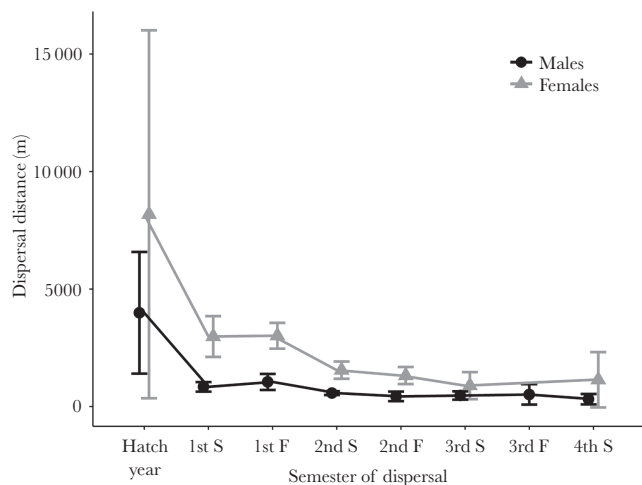


Figure 4
The effect of dispersal age on dispersal distance in Florida scrub-jays. Mean (\pm SE) dispersal distance (meters) for each dispersal semester (males: $n = 288$; females: $n = 234$). S denotes spring (first semester of a year) and F denotes fall (second semester of a year). Jays that disperse in their hatch year have been removed for visualization purposes but are kept in the models.

Table 8
Summary of dispersal patterns of within-brood siblings by sex. Values indicate mean \pm SE; t - and P -values obtained from paired t -tests

	Males				Females			
	Dominant	Subordinate	t	P	Dominant	Subordinate	t	P
Age (days)	614.2 \pm 45.4	689.2 \pm 46.0	−1.397	0.171	607.5 \pm 47.2	588.2 \pm 33.8	0.369	0.714
Distance (m)	937.1 \pm 149.3	749.6 \pm 112.8	1.182	0.246	2459.4 \pm 431.2	3250.3 \pm 425.73	−1.619	0.115

dominants, suggesting that intragroup competition affects dispersal distance. In Florida scrub-jays, fitness benefits of short-distance dispersal may arise due to retained familiarity with surroundings, which can have a strong effect in this long-lived species that reaches ages up to 15 years in the wild (Fitzpatrick and Bowman 2016). The effect of familiarity may have stronger fitness consequences than energetic or internal condition-dependent costs of the movement itself. Regardless, the negative correlation between dispersal age and distance supports the idea that short-distance dispersal and delayed breeding are coupled through potential benefits by remaining on the territory (Zack 1990). This finding is further supported by the fact that jays in inherited territories typically have the highest adult survival, which correlates strongly with lifetime reproductive success (Fitzpatrick and Bowman 2016).

Our results may explain why long-distance dispersers are less successful and, therefore, contribute less to gene flow in fragmented landscapes at the landscape scale (Coulon et al. 2010). Specifically, long-distance dispersers tend to be younger, subordinate individuals that dispersed early because they lacked either capacity or opportunity to compete for high-quality breeding opportunities in their natal neighborhood. Early dispersers may be making the best of a bad situation by leaving their natal territories to search for breeding opportunities elsewhere. As Florida oak scrub is a fire-prone and fire-maintained ecosystem, this bimodal dispersal strategy may be adaptive: frequent fires, especially large ones, open up new colonization opportunities in early successional scrub, where reproductive success is highest (Breininger and Oddy 2004; Fitzpatrick and Bowman 2016).

CONCLUSIONS

In summary, our results show that both social and environmental factors influence dispersal decisions and help to explain the evolution of delayed dispersal in cooperatively breeding species (Clobert et al. 2001; Kokko and Ekman 2002; Matthysen 2012; Shen et al. 2017). For individuals in poor habitat or subordinate social positions, early and long-distance dispersal creates opportunities to locate breeding vacancies elsewhere, including the possibility of colonizing a recently burned habitat. In Florida scrub-jays, delayed dispersal appears to be an especially adaptive strategy for dominant offspring that have access to preferred, short-distance dispersal opportunities with high fitness payoffs (Ekman et al. 2002; Kokko and Ekman 2002; Cockburn et al. 2008; Fitzpatrick and Bowman 2016).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Young Ha Suh (2020).

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REFERENCES

- Abrahamson WG, Johnson AF, Layne JN, Peroni PA. 1984. Vegetation of the Archbold Biological Station, Florida: an example for the southern Lake Wales Ridge. *Florida Sci.* 47:209–250.
- Allison PD. 1982. Discrete-time methods for the analysis of event histories. *Sociol Methodol.* 13:61–98.
- Allison PD. 2010. Survival analysis using SAS: a practical guide. 2nd ed. Cary (NC): SAS Institute Inc.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67:1–48.
- Bebbington K, Kingma SA, Fairfield EA, Spurgin LG, Komdeur J, Richardson DS. 2017. Consequences of sibling rivalry vary across life in a passerine bird. *Behav Ecol.* 28:407–418.
- Bitume EV, Bonte D, Ronce O, Bach F, Flaven E, Olivieri I, Nieberding CM. 2013. Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecol Lett.* 16:430–437.
- Bonte D, Dähirel M. 2017. Dispersal: a central and independent trait in life history. *Oikos.* 126:472–479.
- Bonte D, Hovestadt T, Poethke H-J. 2010. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos.* 119:560–566.
- Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehoucq V, Matthysen E, Mustin K, Saastamoinen M, et al. 2012. Costs of dispersal. *Biol Rev.* 87:290–312.
- Breininger DR, Oddy DM. 2004. Do habitat potential, population density, and fires influence Scrub-Jay source-sink dynamics? *Ecol Appl.* 14:1079–1089.
- Breininger DR, Stolen ED, Carter GM, Oddy DM, Hunt DK. 2010. A model-selection approach to predicting whether Florida scrub-jays delay breeding. *Condor.* 112:378–389.
- Clobert J, Danchin E, Dhondt AA, Nichols JD. 2001. Dispersal. New York: Oxford University Press.
- Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett.* 12:197–209.
- Cockburn A, Osmond HL, Mulder RA, Double MC, Green DJ. 2008. Demography of male reproductive queues in cooperatively breeding superb fairy-wrens *Malurus cyaneus*. *J Anim Ecol.* 77:297–304.
- Coulon A, Fitzpatrick JW, Bowman R, Lovette IJ. 2010. Effects of habitat fragmentation on effective dispersal of Florida scrub-jays. *Conserv Biol.* 24:1080–1088.
- Covas R, Griesser M. 2007. Life history and the evolution of family living in birds. *Proc Biol Sci.* 274:1349–1357.
- Eden SF. 1987. Dispersal and competitive ability in the magpie: an experimental study. *Anim Behav.* 35:764–772.
- Eikenaar C, Richardson DS, Brouwer L, Komdeur J. 2007. Parent presence, delayed dispersal, and territory acquisition in the Seychelles warbler. *Behav Ecol.* 18:874–879.
- Ekman J, Baglione V, Egger S, Griesser M. 2001. Delayed dispersal: living under the reign of nepotistic parents. *Auk.* 118:1–10.
- Ekman J, Bylin A, Tegelström H. 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proc R Soc B Biol Sci.* 266:911–915.
- Ekman J, Eggers S, Griesser M. 2002. Fighting to stay: the role of sibling rivalry for delayed dispersal. *Anim Behav.* 64:453–459.
- Ekman J, Griesser M. 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proc Biol Sci.* 269:1709–1713.
- Emlen ST, Vehrencamp SL, Ligon JD, Rowley I. 1983. Cooperative breeding strategies among birds. In: Brush AH, Clark GAJ, editors.

- Perspectives in ornithology. Cambridge (UK): Cambridge University Press. p. 93–134.
- Ferrer M. 1993. Ontogeny of dispersal distances in young Spanish imperial eagles. *Behav Ecol Sociobiol.* 32:259–263.
- Fitzpatrick JW, Bowman R. 2016. Florida scrub-jays: oversized territories and group defense in a fire-maintained habitat. In: Koenig WD, Dickinson JL, editors. *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior*. Cambridge (UK): Cambridge University Press. p. 77–96.
- Fitzpatrick JW, Woolfenden GE, Bowman R. 1999. Dispersal distance and its demographic consequences in the Florida Scrub-Jay. In: Adams NJ, Slotow RH, editors. *International Ornithological Congress, Durban, Johannesburg: BirdLife South Africa*. p. 2465–2479.
- Goldstein JM, Woolfenden GE, Hailman JP. 1998. A same-sex stepparent shortens a prebreeder's duration on the natal territory: tests of two hypotheses in Florida scrub-jays. *Behav Ecol Sociobiol.* 44:15–22.
- Green JP, Hatchwell BJ. 2018. Inclusive fitness consequences of dispersal decisions in a cooperatively breeding bird, the long-tailed tit (*Aegithalos caudatus*). *Proc Natl Acad Sci USA.* 115:12011–12016.
- Greenwood PJ, Harvey PH. 1982. The natal and breeding dispersal of birds. *Annu Rev Ecol Syst.* 13:1–21.
- Groenewoud F, Kingma SA, Hammers M, Dugdale HL, Burke T, Richardson DS, Komdeur J. 2018. Subordinate females in the cooperatively breeding Seychelles warbler obtain direct benefits by joining unrelated groups. *J Anim Ecol.* 87:1251–1263.
- Hansson B, Bensch S, Hasselquist D. 2004. Lifetime fitness of short- and long-distance dispersing great reed warblers. *Evolution.* 58:2546–2557.
- Hartig F. 2019. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.6. <http://CRAN.R-project.org/package=DHARMA> (accessed December 2019).
- Heg D, Rothenberger S, Schürch R. 2011. Habitat saturation, benefits of philopatry, relatedness, and the extent of co-operative breeding in a cichlid. *Behav Ecol.* 22:82–92.
- Ims RA, Hjermann D. 2001. Condition-dependent dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p. 203–216.
- Kassambara A, Kosinski M, Biecek P. 2019. survminer: drawing survival curves using 'ggplot2'. R package version 0.4.6. <https://CRAN.R-project.org/package=survminer>.
- Kingma SA, Bebbington K, Hammers M, Richardson DS, Komdeur J. 2016. Delayed dispersal and the costs and benefits of different routes to independent breeding in a cooperatively breeding bird. *Evolution.* 70:2595–2610.
- Koenig WD, Dickinson JL. 2016. *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior*. Cambridge (UK): Cambridge University Press.
- Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT. 1992. The evolution of delayed dispersal in cooperative breeders. *Q Rev Biol.* 67:111–150.
- Koenig WD, Van Vuren D, Hooge PN. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol Evol.* 11:514–517.
- Kokko H, Ekman J. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *Am Nat.* 160:468–484.
- Komdeur J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature.* 358:493–495.
- Maag N, Cozzi G, Clutton-Brock T, Ozgul A. 2018. Density-dependent dispersal strategies in a cooperative breeder. *Ecology.* 99:1932–1941.
- Matthysen E. 2012. Multicausality of dispersal: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. *Dispersal ecology and evolution*. Oxford (UK): Oxford University Press. p. 3–18.
- Maul A. 1994. A discrete time logistic regression model for analyzing censored survival data. *Environmetrics.* 5:145–157.
- Mayer M, Zedrosser A, Rosell F. 2017. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. *Anim Behav.* 123:375–382.
- McGowan KJ, Woolfenden GE. 1989. A sentinel system in the Florida scrub jay. *Anim Behav.* 37:1000–1006.
- Mumme RL. 1992. Do helpers increase reproductive success—an experimental-analysis in the Florida scrub jay. *Behav Ecol Sociobiol.* 31:319–328.
- Mumme RL, Bowman R, Pruett MS, Fitzpatrick JW. 2015. Natal territory size, group size, and body mass affect lifetime fitness in the cooperatively breeding Florida Scrub-Jay. *Auk.* 132:634–646.
- Murrell DJ, Travis MJJ, Dytham C. 2002. The evolution of dispersal distance in spatially-structured populations. *Oikos.* 97:229–236.
- Nathan R. 2001. The challenges of studying dispersal. *Trends Ecol Evol.* 16:481–483.
- Nathan A, Legge S, Cockburn A. 2001. Nestling aggression in broods of a siblicidal kingfisher, the laughing kookaburra. *Behav Ecol.* 12:716–725.
- Nelson-Flower MJ, Ridley AR. 2016. Nepotism and subordinate tenure in a cooperative breeder. *Biol Lett.* 12:2016035. doi: 10.1098/rsbl.20160365.
- Nelson-Flower MJ, Wiley EM, Flower TP, Ridley AR. 2018. Individual dispersal delays in a cooperative breeder: ecological constraints, the benefits of philopatry and the social queue for dominance. *J Anim Ecol.* 87:1227–1238.
- Nilsson J-A. 1989. Causes and consequences of natal dispersal in the Marsh Tit, *Parus palustris*. *J Anim Ecol.* 58:619–636.
- Pärt T. 1991. Philopatry pays: a comparison between collared flycatcher sisters. *Am Nat.* 138:790–796.
- Pasinelli G, Schiegg K, Walters JR. 2004. Genetic and environmental influences on natal dispersal distance in a resident bird species. *Am Nat.* 164:660–669.
- Pasinelli G, Walters JR, Aug N, Walters R. 2002. Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. *Ecology.* 83:2229–2239.
- van de Pol M, Pen I, Heg D, Weissing FJ. 2007. Variation in habitat choice and delayed reproduction: adaptive queuing strategies or individual quality differences? *Am Nat.* 170:530–541.
- Puzin C, Bonte D, Pétillon J. 2019. Influence of individual density and habitat availability on long-distance dispersal in a salt-marsh spider. *Ethol Ecol Evol.* 31:28–37.
- R Core Team. 2019. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Rousset F, Gandon S. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *J Evol Biol.* 15:515–523.
- Safriel UN. 1981. Among siblings in broods social hierarchy of the oystercatcher *Haematopus ostralegus*. *Behav Ecol Sociobiol.* 9:59–63.
- Saino N, Romano M, Ambrosini R, Rubolini D, Boncoraglio G, Caprioli M, Romano A. 2012. Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching date and phenotypic quality. *J Anim Ecol.* 81:1004–1012.
- Scandolara C, Lardelli R, Sgarbi G, Caprioli M, Ambrosini R, Rubolini D, Saino N. 2014. Context-, phenotype-, and kin-dependent natal dispersal of barn swallows (*Hirundo rustica*). *Behav Ecol.* 25:180–190.
- Selonen V, Hanski IK, Mäkeläinen S. 2012. Predictors of long-distance dispersal in the Siberian flying squirrel. *Evol Ecol.* 26:1361–1369.
- Shen SF, Emlen ST, Koenig WD, Rubenstein DR. 2017. The ecology of cooperative breeding behaviour. *Ecol Lett.* 20:708–720.
- Sparkman AM, Adams JR, Steury TD, Waits LP, Murray DL. 2011. Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). *Behav Ecol.* 22:199–205.
- Spear LB, Pyle P, Nur N. 1998. Natal dispersal in the western gull: proximal factors and fitness consequences. *J Anim Ecol.* 67:165–179.
- Stacey PB, Ligon JD. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *Am Nat.* 137:831–846.
- Stamps JA. 2006. The silver spoon effect and habitat selection by natal dispersers. *Ecol Lett.* 9:1179–1185.
- Strickland D. 1991. Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. *Can J Zool.* 69:2935–2945.
- Suh Y, Pesendorfer MB, Tringali A, Bowman R, Fitzpatrick JW. 2020. Data from: Investigating social and environmental predictors of natal dispersal in a cooperative breeding bird. *Behav Ecol.* doi: 10.5061/dryad.stqjq2c0f
- Tanaka H, Frommen JG, Takahashi T, Kohda M. 2016. Predation risk promotes delayed dispersal in the cooperatively breeding cichlid *Neolamprologus obscurus*. *Anim Behav.* 117:51–58.
- Townsend AK, Bowman R, Fitzpatrick JW, Dent M, Lovette IJ. 2011. Genetic monogamy across variable demographic landscapes in cooperatively breeding Florida scrub-jays. *Behav Ecol.* 22:464–470.
- Trenham PC, Koenig WD, Bradley Shaffer H. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. *Ecology.* 82:3519–3530.

- Tringali A, Bowman R. 2012. Plumage reflectance signals dominance in Florida scrub-jay, *Aphelocoma coerulescens*, juveniles. *Anim Behav*. 84:1517–1522.
- Valcu M, Kempenaers B. 2010. Spatial autocorrelation: an overlooked concept in behavioral ecology. *Behav Ecol*. 21:902–905.
- Warner DA, Shine R. 2008. Determinants of dispersal distance in free-ranging juvenile lizards. *Ethology*. 114:361–368.
- Wickham H. 2016. *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag New York.
- Wiley RH, Rabenold KN. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution*. 38:609–621.
- Willett JB, Singer JD. 1993. Investigating onset, cessation, relapse, and recovery: why you should, and how you can, use discrete-time survival analysis to examine event occurrence. *J Consult Clin Psychol*. 61:952–965.
- Woelfenden GE, Fitzpatrick JW. 1977. Dominance in the Florida Scrub Jay. *Condor*. 79:1–12.
- Woelfenden GE, Fitzpatrick JW. 1978. The inheritance of territory in group-breeding birds. *Bioscience*. 28:104–108.
- Woelfenden GE, Fitzpatrick JW. 1984. *The florida scrub jay: demography of a cooperative breeding bird, monographs in population biology*. Princeton (NJ): Princeton University Press.
- Zack S. 1990. Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology*. 86:265–286.
- Zack S, Stutchbury BJ. 1992. Delayed breeding in avian social systems: the role of territory quality and “floater” tactics. *Behaviour*. 123:194–219.