Lifetime fitness benefits of short-distance dispersal are associated with inbreeding tolerance despite multiple inbreeding avoidance mechanisms

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Abstract

Breeding with relatives often decreases individual fitness but can be mitigated via inbreeding avoidance mechanisms such as dispersal, mate-switching, and kin avoidance. Disentangling the effects of multiple mechanisms is challenging without detailed individual-level data and incomplete without considering all life stages. We leveraged 32 years of data from a population of Florida Scrub-Jays (*Aphelocoma coerulescens*) to investigate how dispersal and mate choice contribute to inbreeding risk across individuals' lifetimes and quantify the associated fitness outcomes. We find that when mating is random, inbreeding is two-fold higher when dispersal is limited, but adding sex-biased dispersal significantly reduces inbreeding risk. Limited movement away from the breeding territory for later pairings (site fidelity) contributes more to higher-than-expected levels of inbreeding than limited natal dispersal. Within observed dispersal constraints, however, inbreeding is lower than expected under random mating, suggesting Florida Scrub-Jays actively avoid mating with relatives, especially first-order kin. Finally, males paired with close relatives and females who move farther for later pairings experience equivalently lower lifetime reproductive success. Breeders who move farther for first pairings have lower survival. Overall, our results show how variation in fitness tradeoffs and mate choice behavior across life stages affects inbreeding in a long-lived, social species.

Keywords: dispersal**,** mate choice, inbreeding tolerance, inbreeding avoidance, site fidelity, lifetime fitness, Florida Scrub-Jay

Main Text

Introduction

Matings among relatives, or inbreeding, have been shown to sometimes have negative fitness consequences in both experimental and observational studies (Jiménez et al., 1994; Keller et al., 1994; Coltman et al., 1999; Chen et al., 2016; Szulkin et al., 2007; C. W. Fox et al., 2008). Consequently, it is commonly assumed that inbreeding depression will lead to the evolution of reproductive strategies for inbreeding avoidance such as dispersal, mate switching (*i.e.*, "divorce"), and kin avoidance via mechanisms of kin recognition (Pusey & Wolf, 1996). However, evidence for such strategies is mixed (de Boer et al., 2021), in part because disentangling inbreeding avoidance strategies operating at different stages of mate choice is challenging (Szulkin et al., 2013).

In most species, moving away from the natal area (*i.e.*, natal dispersal) is a passive mechanism that adequately facilitates inbreeding avoidance (Perrin & Goudet, 2001). However, natal dispersal may be limited in some species, such that individuals are unable or disinclined to move far from their place of birth (Hamilton, 1964), often due to fitness benefits such as better access to resources (Pärt, 1994), higher survival (Griesser et al., 2006), and nepotism (Thünken et al., 2007). In such species, when individuals become breeders, they often choose mates that are geographically close (Greenwood & Harvey, 1982; Clutton-Brock & Lukas, 2012), though inbreeding risk can be mitigated if one sex disperses farther than the other (*i.e.*, sex-biased dispersal) (Greenwood & Harvey, 1982; Li & Kokko, 2019; Lawson Handley & Perrin, 2007). If natal dispersal is limited to some extent in both sexes, as is the case in many social species, active inbreeding avoidance mechanisms via mate choice, such as kin recognition and divorce, may additionally mitigate inbreeding risk (Cockburn et al., 2003; Nichols, 2017; Galezo et al., 2022; Leedale et al., 2024). Kin recognition for inbreeding avoidance in such cases could be largely based on early-life association via either geographic proximity or group membership (Riehl & Stern, 2015). However, active inbreeding avoidance behavior can also be costly if individuals have to forego breeding or spend more energy and incur higher fitness costs to find unrelated mates (Bengtsson, 1978; Kokko & Ots, 2006). Theory

suggests that if the fitness costs of inbreeding avoidance strategies outweigh the fitness costs of inbreeding, inbreeding may instead be tolerated (Kokko & Ots, 2006; Nichols, 2017).

Inbreeding avoidance strategies may vary at different life stages. For example, moving away from the breeding territory for any subsequent pairings may carry an increased mortality risk (Daniels & Walters, 2000a), whereas site fidelity (*i.e.*, remaining at or close to the same territory across breeding seasons) can lead to fitness benefits due to familiarity and reduced competitive interactions (Schmidt, 2014; Beck et al., 2020; Byrne et al., 2022). In a kin-structured population, with short natal dispersal distances, such site fidelity for later pairings can also increase inbreeding risk (Nelson-Flower et al., 2012; van Dijk et al., 2015), but if the fitness benefits of site fidelity outweigh the costs of inbreeding during later pairings, inbreeding tolerance may be higher for individuals at later life stages. Further, since distance moved for first pairing tends to be longer than distance moved for later pairings (Paradis et al., 1998), mate choice at later life stages could potentially contribute more to inbreeding. Disentangling inbreeding avoidance strategies thus requires examining events across an individual's lifetime, not just at the natal dispersal and first mate choice stage.

A rigorous test of inbreeding tolerance or avoidance requires five key components: (i) a study system with sufficient variation in relatedness between potential mates, the ability to identify both (ii) actual and (iii) potential mates, (iv) accurate measures of relatedness, and (v) an accounting of mate choice events occurring throughout different stages of an individual's lifetime (Szulkin et al., 2013). Though previous studies of inbreeding have incorporated one or several of these components, to date no single study meets all the requirements (Gibbs & Grant, 1989; Wheelwright & Mauck, 1998; Daniels & Walters, 2000b; Foerster et al., 2006; Frommen & Bakker, 2006; Szulkin et al., 2009; Billing et al., 2012; Galezo et al., 2022). Additionally, most studies lack measures of lifetime fitness. Reproductive strategies over an individual's lifetime, especially in long-lived species, may compensate for any short-term fitness costs associated with inbreeding or inbreeding avoidance strategies (Van de Casteele et al., 2003). Thus, we need more studies that explicitly consider dispersal and mate choice decisions throughout an individual's lifetime

and lifetime fitness consequences of different strategies to better understand how dispersal and mate choice decisions contribute to inbreeding risk in natural populations.

Here, we leverage 32 years of individual-level data on dispersal, mating, survival, and reproductive success from a continuously monitored population of Florida Scrub-Jays (*Aphelocoma coerulescens*) to test for contributions of dispersal and mate choice across an individual's lifetime to inbreeding risk and quantify the associated lifetime fitness outcomes. Florida Scrub-Jays are avian cooperative breeders that defend year-round territories in a social group comprising a dominant breeding pair and non-breeding subordinates, the majority being first-order kin, that remain as helpers for one or more years before dispersing to breed (Woolfenden & Fitzpatrick, 1984). Though females disperse farther than males, neither sex typically disperses more than 2.5 km away (or the equivalent of five territories) (Suh et al., 2020), such that the relatedness of potential mates within a population range from parents/full-siblings to unrelated immigrants (Aguillon et al., 2017). Florida Scrub-Jays pair with a new mate after their current mate dies (Woolfenden & Fitzpatrick, 1984), or in rare cases when the mate is still alive (*i.e.*, divorce) (Marzluff et al., 1996). Here, we focus on a population of Florida Scrub-Jays that has been intensively studied at Archbold Biological Station in central Florida since 1969 (Woolfenden & Fitzpatrick, 1984). Detailed monitoring data from this population provides the unique ability to identify all actual and potential mates, calculate accurate relatedness measures using a single, extensive pedigree, incorporate mate choice events throughout individuals' lifetimes, and quantify lifetime fitness in terms of reproductive success and survival (Fitzpatrick & Bowman, 2016). Moreover, previous work has found evidence of inbreeding depression in Florida Scrub-Jays, suggesting that inbreeding avoidance strategies may be adaptive in this species (Chen et al., 2016), though long-distance dispersal may also have associated fitness costs (Fitzpatrick et al., 1999).

We performed a series of analyses to quantify the effects of dispersal and mate choice decisions on inbreeding risk across sexes and life stages. First, we compared the observed distance moved for pairing and levels of inbreeding (relatedness to mate) to simulated means generated under three random mating scenarios: (i) no constraints on dispersal distance, (ii) limited dispersal distance with existing sex bias included, and (iii) limited dispersal distance with any sex bias removed. As limited dispersal is expected to

increase inbreeding risk, we predicted that observed inbreeding will be higher than expected under the unconstrained model (scenario i). Further, we predicted that if, when dispersal is limited, sex-biased dispersal helps reduce inbreeding risk, simulated relatedness to mates will be lower in the model with sex-biased dispersal (scenario ii) than in the model without (scenario ii). In fact, if sex-biased dispersal is sufficient to overcome increased inbreeding risk due to limited dispersal, simulated relatedness to mates should be equivalent between the sex-biased, limited dispersal model and unconstrained dispersal model. Finally, we predicted that in addition to passive mechanisms, if Florida Scrub-Jays actively avoid mating with kin, observed inbreeding should be lower than expected under the limited, sex-biased dispersal model. If such kin avoidance is facilitated by kin recognition based on familiarity of individuals within the natal social group, the observed proportion of first-order kin mates should be lower than that expected under the limited, sex-biased dispersal model. Additionally, we tested whether divorce is another mate choice strategy to mitigate inbreeding risk. We predicted that pairs with more closely related mates will be more likely to dissolve because of divorce than death of a mate.

Finally, to investigate the relative fitness costs and benefits associated with inbreeding and inbreeding avoidance strategies, we quantified the impact of distance moved and inbreeding on breeder survival and lifetime reproductive success (LRS). We predicted that, for both sexes, both inbreeding and longer dispersal distances at all life stages would result in lower LRS and survival. Further, we predicted that if we found no evidence of active inbreeding avoidance, the fitness cost of inbreeding will be lower than the cost of long-distance dispersal. Conversely, if individuals are actively avoiding inbreeding, the fitness costs of inbreeding will be higher than or equivalent to the cost of long-distance dispersal. Ultimately, we delineate passive and active mechanisms of inbreeding avoidance, and quantify the associated fitness outcomes, to provide the first complete picture of how dispersal patterns and mate choice contribute to—or mitigate—inbreeding risk in a natural population experiencing inbreeding depression.

Methods

Data collection

126 Florida Scrub-Jays at Archbold Biological Station (27.10°N, 81.21°W) have been continuously monitored
127 since 1969, with the study tract expanded to its current size (mean ± sd = 914.04 ± 143.44 ha) by 1990
128 (Woolfenden & Fitzpatrick, 1984). All birds are banded with unique combinations of color bands.
129 Throughout the breeding season (early March to early June), all nests are located and monitored for fledging
130 or failure. All territories are mapped in April, with territory boundaries assigned at locations of territorial
131 disputes between neighboring groups. In addition to nest monitoring, the population is censused each
132 month, resulting in detailed data on dispersal and survival of both fledglings and adults. Pairs are socially
133 monogamous, with very low rates of extra pair-paternity (<1%) (Townsend et al., 2011), allowing accurate
134 parentage inference from field observations alone. Furthermore, previous work verified genetic parentage
135 of offspring born between ~1989-1991, 1994-1995, and 1999-2013 (Chen et al., 2016). Using these detailed
136 data, we have accumulated a 15-generation pedigree of known-age, known-parentage individuals with
137 precise measurements of lifespan and reproductive success. For this study, we used data from 1990-2021,
138 which included on average (± SD) 71.4 (± 14.7) territories (area mean ± sd =13.24 ± 6.37 ha) per year.
139 Fieldwork was approved by the Institutional Animal Care and Use Committees at Cornell University
140 (IACUC 2010-0015) and Archbold Biological Station (AUP-006-R) under permits from the US Fish and
141 Wildlife Service (TE824723-8, TE-117769), the US Geological Survey (banding permits 07732, 23098),
142 and the Florida Fish and Wildlife Conservation Commission (LSSC-10-00205).
143
144 *Observed mates*
145 Our dataset of actual mates included all new breeding pairs formed between 1990 and 2021 (N = 1077).
146 New breeding pairs include pairs formed by two first-time breeders, one first-time and one experienced
147 breeder, or two experienced breeders. For first-time breeders, we called the event a "first pairing" and for
148 experienced breeders, a "later pairing". The first pairing for one mate is thus not always the first pairing for
149 the other mate (*e.g.*, an experienced male could repair with a female who is a first-time breeder, and vice
150 versa). New pairs might occupy a new territory, which may be inherited by one of the two breeders or
151 formed as an extension of their natal territory in a process called "budding" (Woolfenden & Fitzpatrick,

1984; Fitzpatrick & Bowman, 2016). Alternatively, a new pair might form on a non-natal territory already occupied by one of the two breeders, where a breeding vacancy is typically formed due to the death of a breeder, but occasionally via divorce ” (Woolfenden & Fitzpatrick, 1984; Fitzpatrick & Bowman, 2016). Thus, both first and later pairings can occur without any movement away from the currently occupied territory by at least one of the two breeders.

Random mating models

To delineate passive and active mechanisms of inbreeding avoidance, we constructed three random mating scenarios with (i) no constraints on dispersal distance, (ii) limited dispersal distance with existing sex bias included, and (iii) limited dispersal distance without sex bias (Figs. S1-S2). For the unconstrained model, we defined potential mates for all individuals of one sex in a given year as all individuals of the opposite sex from our dataset of observed mates (*i.e.*, individuals that were both available as potential mates and successful at finding new mates) (*N* focal individuals: mean ± SD = 25.4 ± 7.06; *N* available mates per individual: mean ± SD = 25.5 ± 7.01; see *SI* for more details). For the limited dispersal with sex-biased dispersal model, we limited available mates to opposite sex individuals at the observed dispersal distance of each individual (*N* available mates per individual: mean ± SD = 1.37 ± 0.63). Finally, for the limited dispersal but no sex bias model, we randomly shuffled observed dispersal distances values across sexes, but within life stages (*i.e.*, first or later pairing). We then limited available mates for each focal individual to opposite sex individuals at the assigned dispersal distance (*N* available mates per individual: mean ± SD = 1.39 ± 0.68). For each focal individual we then randomly assigned an available mate for each year. These random assignments were permuted 1000 times. In dispersal constrained models, individuals that did not move away from their territory but paired with a new mate in a given year were assigned the dispersal distance value of their new mate. While both mates may move territories to form a new breeding pair (107 out of 1077 [10%] observations), our simulations are sex-specific and assume that only the focal individual moved to the territory occupied by the potential mate.

Distance moved for pairing

We measured the distance moved for pairing as the number of territories crossed, which is the most biologically relevant measure of distance moved (Fitzpatrick et al., 1999; Greenwood & Harvey, 1982). The number of territories crossed was highly correlated with distance moved in meters (Pearson's $r = 0.91$; (Fitzpatrick et al., 1999)). We drew a straight-line movement trajectory from the centroid of an individual's previous territory to the centroid of its new breeding territory. We then used the *st_intersects* function from the R package *sf* (Pebesma, 2018) to calculate the number of territories (i.e., polygons) that each line intersected (see *SI* for more details). When the focal individual remained on its natal territory and became a breeder, formed a territory by budding, or remained on its non-natal breeding territory, we quantified distance moved as 0 m.

To obtain accurate measures of distance moved, we excluded any pairings that involved movement that started or ended outside of the study tract. We also excluded any movement that did not end with the individual attaining a breeding position (*i.e.*, staging, a strategy adopted by about 28% of yearlings (Suh et al., 2022)). For staging individuals that eventually became breeders, we used movement from their staging to breeding territory to calculate distance moved for first pairing. However, using distance from natal to breeding territory as distance moved for first pairing did not change our results (see *SI*, Fig. S3, Table S1).

Relatedness to mate

To quantify levels of inbreeding, we calculated the kinship coefficient between mates for all observed and simulated breeding pairs using the population pedigree with the kinship function in the R package *kinship2* (Sinnwell et al., 2014). With no inbreeding, the kinship coefficient ranges from 0 to 0.5, such that 0.5 is an individual's kinship coefficient with itself; 0.25 is the average kinship coefficient between siblings and between parents and offspring (first-order kin); 0.125 is the average kinship coefficient between half-siblings, grandparents-grandchildren, and aunt/uncle-niece/nephew pairs (second-order kin); and 0.0625 is the average kinship coefficient between first cousins (third-order kin) (Malécot, 1948). Pedigree-based inbreeding estimates are correlated with genomic-based estimates in our study population, confirming that

our pedigree is complete enough to provide accurate measures of inbreeding and relatedness (Chen et al., 2016).

Lifetime fitness metrics

We assessed breeder survival using monthly census and capture records and calculated breeding lifespan as the number of years from becoming a breeder to death. We calculated lifetime reproductive success (LRS) for all breeders as the total number of offspring produced over an individual's lifetime that survived to adulthood, *i.e.*, age 1 year, the stage at which Florida Scrub-Jays become physiologically capable of breeding (McGowan & Woolfenden, 1990; Mumme et al., 2015; Schoech et al., 1996; Woolfenden & Fitzpatrick, 1984). Since the mean growth rate of our study population is close to 1 (0.998) (Summers et al., 2024), we deemed LRS an appropriate metric of individual fitness (Brommer et al., 2002). For all fitness analyses, we restricted our dataset to individuals from cohorts from which all members born within the study tract were last observed before 2021 to eliminate bias towards short-lived individuals (Barve et al., 2021; Shah & Rubenstein, 2022). The final dataset for all fitness analyses included individuals born between 1988-2006 and in 2009 (*N*: Males = 197, Females = 120).

Data analysis

All analyses were conducted using R version 4.2.2 (R Core Team, 2022). Fixed effects for all models were standardized using z scores (Schielzeth, 2010), and the variance inflation factor was < 2 for all fixed effects in all GLMMs (J. Fox & Monette, 1992).

Effects of dispersal and mate choice on inbreeding: To quantify the contributions of dispersal and mate choice behavior to levels of inbreeding, we compared observed population means of inbreeding (measured as kinship coefficient to mates), aggregated across years, to the expected distributions generated by our random mating simulations using empirical *p*-values (Davison & Hinkley, 1997). Specifically, we quantified the proportion of simulations that had a mean value lesser than or equal (S_{low}) or greater than or

equal (S_{high}) to the observed mean. Empirical *p*-values were then calculated as ($S_{high/low}$+1)/(N+1), where N was the total number of simulations (*i.e.,* 1000). For all random mating scenarios, we tested whether the observed kinship coefficient and proportion of first-order kin pairs was greater or less than expected by random chance across sexes and pairing types. We also compared the simulated kinship coefficients between the limited dispersal models with and without sex-bias using *t*-tests, with Bonferroni corrections to *p*-values to account for multiple testing.

Divorce as an inbreeding avoidance strategy: To investigate whether Florida Scrub-Jays compensated for the impact of inbreeding on reproductive success via divorce, we fit GLMMs with the cause of pair dissolution (1 = divorce, 0 = mate death) as the dependent variable, the kinship coefficient to mate as a fixed effect, year and individual ID as random effects, and a binomial error structure. We also fit models with a categorical fixed effect of kinship between mates (1 = first-order relative, 0 = not a first-order relative) to account for cases where opposite-sex offspring might inherit dominant breeding positions, resulting in mother-son or father-daughter pairings that may be more likely to end in divorce (Cockburn et al., 2003). We fit separate GLMMs by sex and pairing type using the function *glmer* in the R package *lme4* (N: Males, First pairing = 194; Males, Later pairing = 187; Females, First pairing = 163; Females, Later pairing = 169 pairings) (Bates et al., 2015).

Lifetime fitness outcomes: First, we examined the effect of distance moved on breeder survival. We found that fitting Cox proportional hazard models with distance moved for first pairing as a fixed effect violated the proportional hazards assumption for both sexes (Males: $\chi^2 = 4.33$, df = 1, $P = 0.04$; Females: $\chi^2 = 4.21$, df = 1, $P = 0.04$), suggesting that the effect of distance moved for first pairing on the hazard rate varies over time. To account for this time-varying effect, we fit stratified Cox proportional hazards models with two time intervals: ≤ 4 years and > 4 years from the start of breeding (Zhang et al., 2018). We tested varying thresholds for splitting the analysis time into intervals and chose a cut time of 4 years based on visual assessment of variation in the hazard ratio over time (see *SI*, Table S2, Fig. S4) (Zhang et al., 2018). We

used the *Surv* and *coxph* function from the R package *survival* (Therneau, 2022) to fit separate models by sex of breeder, and incorporated natal year as a random effect (*N*: Males = 197, Females = 120). For the subset of individuals who switched mates at least once in their lifetime (*N*: Males = 91, Females = 50), we also examined the effect of territory loss (*i.e.*, total distance moved for later pairings ≥ 1 territory away) on breeder survival. We fit Cox proportional hazards models with loss of territory (1 = territory lost, 0 = territory retained) as a fixed effect and natal year as a random effect. The proportional hazards assumption was met for these models (Males: $\chi^2 = 1.17$, df = 1, $P = 0.28$; Females: $\chi^2 = 0.27$, df = 1, $P = 0.61$).

Next, to examine how distance moved for pairing and inbreeding impacts lifetime fitness of Florida Scrub-Jays, we fit two separate GLMMs by sex with negative binomial error distributions (to account for overdispersion), LRS as the dependent variable, and distance moved for first pairing, weighted relatedness to mates, and breeding lifespan as fixed effects (*N*: Males = 197, Females = 120). We calculated weighted kinship coefficient to mates for all breeders across their lifetimes by multiplying the kinship coefficient of the focal individual to each of their mates by the number of years they were paired with that mate and summing the resulting values. Breeding lifespan was included in the model to account for the fact that the more breeding seasons a breeder experiences, the more chances it has at successful reproduction (Fitzpatrick & Bowman, 2016). We also included natal year as a random effect to account for variation between birth cohorts.

Finally, to specifically examine the effect of moving away from the breeding territory, we also fit two additional GLMMs with the same error structure, dependent variable, and random effects, with total distance moved for later pairings, weighted kinship coefficient to mates, and breeding lifespan as fixed effects using a truncated dataset that only included individuals that had switched mates in their lifetimes (*N*: Males = 91, Females = 50). All GLMMs were fit using the function glmer.nb in the R package MASS (Venables & Ripley, 2002). Model fits were checked using quantile-quantile plots of residuals (Fig. S5). Fixed effects were not correlated (Table S3).

Results

Observed dispersal and mate choice patterns

The annual number of new breeding pairs ranged from 17-47 pairs with an average (± SD) of 29.2 (± 8.03) new pairs per year (including both first and later pairings). Of the individuals included in our lifetime fitness analysis, 42% of females (50 out of 120) and 46% of males (91 out of 197) had later pairings at least once in their lifetime. Surprisingly, only about half of all mates in later pairings were naïve breeders for both sexes (Males: 218 out of 427 [51%], Females: 213 out of 421 [51%] instances). Thus, not all later pairings were a result of subordinates moving in to fill a breeding vacancy—nearly half of such cases were a result of the mate also re-pairing because of death of, or divorce from, their previous mate. However, for breeders that retained their breeding territory for later pairings, ≥ 90% of new mates were from ≤ 2 territories away (Fig. S6). Furthermore, we found that out of all later pairing events observed, 18% were due to divorce, not mate death (Males = 33 out of 187; Females = 31 out of 169 pairings).

Females, on average, moved farther than males, though the effect size was greater for first pairings than later pairings (see *SI*, Fig. S1). In 197 out of 848 (23%) instances of later pairings the focal individual (62% of whom were females) moved one or more territories away from its established breeding territory. The kinship coefficient (*i.e.*, relatedness) to mate ranged from 0 (unrelated) to 0.25 (*i.e.*, either full siblings or parent-offspring) (Fig. S2). Across all years, only 43 out of 1077 (4%) of observed new breeding pairs were comprised of individuals who were at least as closely related as first cousins (*i.e.*, had a kinship coefficient ≥ 0.0625) and only 13 out of 1077 (1.2%) of observed breeding pairs comprised first-order relatives (7 mother-son, 3 father-daughter, and 3 full sibling pairs; Fig. S7). Relatedness to potential mates was significantly higher at closer geographical distances (see *SI*, Fig. S8).

Passive and active mechanisms of inbreeding and inbreeding avoidance

We found that limited dispersal is an important component of the mating pattern increasing inbreeding risk in Florida Scrub-Jays. Under a model of random mating with limited but not sex-biased dispersal, mean

305 relatedness to mates was two-fold or more higher for both sexes for all life stages than expected under a
306 model of random mating with unconstrained dispersal (Males, First Pairings: $t_{637757} = 68.12$, $P < 0.001$;
307 Females, First pairings: $t_{565627} = 72.94$, $P < 0.001$; Males, Later pairings: $t_{472441} = 82.40$, $P < 0.001$, Females,
308 Later pairings: $t_{503923} = 77.13$, $P < 0.001$; Fig. 1A-D). Sex-biased dispersal does help mitigate inbreeding
309 risk: the expected level of inbreeding across both sexes was significantly lower (by ≥ 50%) when we added
310 sex-biased dispersal for both sexes for first pairings (Males: $t_{527991} = -44.39$, $P < 0.001$; Females: $t_{520491} = -$
311 46.64, $P < 0.001$, Fig. 1A-B) and for females for later pairings ($t_{597723} = -13.39$, $P < 0.001$, Fig.1C), but the
312 pattern was reversed for males for later pairings ($t_{585009} = 34.9$, $P < 0.001$, Fig. 1D).

313 As predicted, we found that, compared to an unconstrained random mating scenario, both sexes
314 moved significantly shorter distances within the study tract ($P \leq 0.05$ for both, Fig. S9). Observed
315 relatedness to mates was higher than expected by chance under unconstrained random mating for both sexes
316 at all life stages, except males for first pairings where the difference approached significance (Males, First
317 pairings: $P = 0.07$; Females, First pairings: $P = 0.05$; Males, Later pairings: $P = 0.001$; Females, Later
318 pairings: $P = 0.003$; Fig. 1A-D). However, observed mean relatedness to mates remained significantly lower
319 across all sexes and life stages than expected under the limited, sex-biased dispersal scenario (Males, First
320 pairings: $P = 0.005$; Females, First pairings: $P < 0.001$; Males, Later pairings: $P = 0.03$; Females, Later
321 pairings: $P = 0.04$; Fig. 1A-D), indicating additional active inbreeding avoidance behavior.

322 We also found that observed proportions of pairing between first-order kin were not significantly
323 different from those expected under the unconstrained model (Males: $P = 0.43$, Females: $P = 0.32$, Fig.
324 1E-F) but were significantly lower than those expected under the limited, sex-biased dispersal model in
325 both sexes for first pairings (Males: $P < 0.001$, Females: $P = 0.008$, Fig. 1E-F). Conversely, for later
326 pairings, the observed proportions of first-order kin were significantly higher than expected under the
327 unconstrained model (Males: $P = 0.05$; Females: $P = 0.04$, Fig. 1G-H), and, for males, not significantly
328 different from expectations under the limited, sex-biased dispersal model (Males: $P = 0.28$, Females: $P =$
329 0.008, Fig. 1G-H). For second- and third-order kin mates, patterns were more variable across sexes and
330 dispersal types (Fig. S10). Overall, both sexes exhibited higher proportions of non-kin mates than expected

under the limited, sex-biased dispersal model for first pairings, but not for later pairings (Males, First pairings: P = 0.009, Females, First pairings: P = 0.04, Males, Later pairings: P = 0.10, Females, Later pairings: P = 0.17; Fig. S10).

Divorce as an inbreeding avoidance strategy

Relatedness to their mate had no effect on likelihood of divorce for either sex at either life stage (Males, First pairing: Z = 0.42, P = 0.68; Males, Later pairing: Z = 0.42, P = 0.68; Females, First pairing: Z = -0.84, P = 0.40; Females, Later pairing: Z = 0.76, P = 0.45), nor was divorce more likely in cases of pairing with first-order relatives (Males, First pairing: Z = 1.87, P = 0.06; Males, Later pairing: Z = 0.22, P = 0.83; Females, First pairing: No instances of divorce when paired with a first-order relative; Females, Later pairing: Z = 0.52, P = 0.60).

Lifetime fitness outcomes

For both sexes, breeding lifespan was affected by distance moved for first pairing: longer distance moved was associated with higher mortality in the first four years after breeding onset (Males: Z = 2.16, P = 0.03; Females: Z = 3.36, P = 0.001), but the relationship was reversed in subsequent years (Males: Z = -2.07, P = 0.04; Females: Z = -2.02, P = 0.04) (Fig. S11). Though the median breeding lifespan for both sexes was 4 years, 37% of individuals lived past their fourth year as a breeder (Males: 73 out of 197, Females: 45 out of 120 individuals). We obtained qualitatively similar results when we varied the interval split times between 5-7 years post breeding (see *SI,* Table S2; upper quartile of breeding lifespan: Males = 6, Females = 7 years, Fig. S12). However, dispersal away from an established breeding territory in the event of later pairing did not impact breeder survival for either sex (Males: Z = -0.37, P = 0.71; Females: Z = 0.76, P = 0.45).

We found that a higher weighted kinship coefficient to mates over an individual's lifetime was associated with significantly fewer offspring that survived to adulthood for males (all breeding males: Z = -2.83, P = 0.005; only males that switched mates at least once: Z = -0.28, P = 0.09; Fig. 2B, D; Table 1),

357 but not females (all breeding females: $Z = 0.31$, $P = 0.76$; only females that switched mates at least once:
358 $Z = -0.09$, $P = 0.97$; Fig. 2B, D; Table 1). The few males who bred with closely related females for the
359 majority of their lifetime had LRS close to zero (Fig. 2B, D), but we did not observe the same pattern in
360 females. Females, but not males, who moved farther distances for later pairings had significantly fewer
361 offspring who survived to adulthood (Males: $Z = -0.64$, $P = 0.52$, Females: $Z = -2.62$, $P = 0.01$; Fig. 2C,
362 Table 1). After controlling for the significant negative effect of breeding lifespan—which is lower for
363 individuals that move longer distances for first pairings—on lifetime reproductive success (Males: $Z = 0.93$,
364 $P < 0.001$, Females: $Z = 0.86$, $P < 0.001$; Table 1), we did not find an additional effect of distance moved
365 for first pairing on lifetime reproductive success for either sex (Males: $Z = -0.29$, $P = 0.77$, Females: $Z = -$
366 0.29, $P = 0.77$; Fig. 2A, Table 1).
367

368 **Discussion**

369 Testing for inbreeding avoidance using observational datasets can be difficult since the underlying
370 mechanisms can operate at different stages of mate choice (Szulkin et al., 2013) and their relative strength
371 can vary at different life stages (Nelson-Flower et al., 2012). Here, we leverage data on pedigree
372 relationships, dispersal, mate pairings, and fitness from a long-term, continuously monitored population of
373 Florida Scrub-Jays to disentangle the contribution of passive and active inbreeding avoidance strategies to
374 inbreeding risk across different life stages and quantify the associated lifetime fitness outcomes. First, using
375 random mating simulations with varying dispersal constraints, parametrized with empirical data, we show
376 that limited dispersal is expected to increase inbreeding by at least two-fold, and that sex-biased dispersal
377 plays an important role in mitigating this risk, especially at the first pairing stage. Though theoretical models
378 have shown this effect of sex-biased dispersal, to our knowledge this is one of the first empirical
379 demonstrations (see Blyton et al., 2015). Second, we find that observed inbreeding levels are higher than
380 expected under an unconstrained random mating model. Within the observed, sex-biased dispersal
381 limitations, however, observed relatedness to mates is lower than expected by chance for both sexes across
382 both life stages, suggesting that though Florida Scrub-Jays are not more likely to divorce when paired with

383 close relatives, they actively avoid pairing with them in the first place. This pattern can be largely explained
384 by avoidance of first-order kin during first pairings for both sexes and life stages, except males during later
385 pairings. The nearly two-fold higher propensity of males to remain on their breeding territory, compared to
386 females, for later pairings likely increases inbreeding risk. Finally, we find that dispersing farther, at both
387 life stages, and pairing with close relatives is associated with lower fitness, suggesting that Florida Scrub-
388 Jays balance the tradeoffs of dispersal and inbreeding such that some level of inbreeding is tolerated, in
389 accordance with theoretical expectations (Kokko & Ots, 2006). Overall, our results show how variation in
390 fitness tradeoffs and mate choice behavior across life stages affects inbreeding risk in a long-lived, social
391 species.

392 We find that Florida Scrub-Jays exhibit a degree of inbreeding tolerance due to limited dispersal at
393 all life stages. Although elevated risk of inbreeding and associated inbreeding depression should select for
394 longer dispersal distances, limited dispersal is found in both social and asocial species. Individuals that do
395 not disperse far may gain better access to resources and protection from predators due to prior local
396 experience (Pärt, 1994) or higher habitat quality (Suh et al., 2020), face lower competition due to nepotism
397 (Green & Hatchwell, 2018; Kokko & Ekman, 2002), and not incur the high physiological costs of dispersal
398 (Maag et al., 2019). As such, limited dispersal has been shown to increase levels of inbreeding in various
399 taxa (Keller et al., 1994; Costantini et al., 2007; Lubin et al., 2009; Lloyd et al., 2018; De Ro et al., 2021;
400 Ceresa et al., 2024). Similarly, our results suggest that limited natal dispersal in Florida Scrub-Jays results
401 in higher levels of inbreeding than expected under a model of unconstrained dispersal. We also considered
402 instances of all subsequent pairings with new mates at later life stages. We found that high site fidelity, *i.e.*
403 limited movement away from the breeding territory for later pairings, also results in higher levels of
404 inbreeding than expected under a scenario of unconstrained dispersal. In fact, for both sexes, the difference
405 between observed relatedness to mates and its expected distribution under random mating with
406 unconstrained dispersal is an order of magnitude higher for later pairings than first pairings. While studies
407 have rarely examined the contribution of dispersal patterns in later life stages to inbreeding, site fidelity to
408 lekking areas in red deer (*Cervus elaphus*) lead to inbreeding by increasing the chances of males mating

with females of the same matriline (Stopher et al., 2012). Thus, neglecting later stages of life excludes demographic processes that can significantly contribute to inbreeding, especially in long-lived species.

Sex-biased dispersal is a passive mechanism that can mitigate inbreeding risk. The difference in expected relatedness to mate under a limited dispersal scenario with and without sex-bias provides clear evidence of the importance of sex-biased dispersal in lowering inbreeding risk in our study population during the first pairing stage. However, Florida Scrub-Jay females still show considerable philopatry at this stage, only dispersing on average ~2 territories away for first pairings. The likelihood of encountering a closely related potential mate is thus still significantly higher within the average dispersal distance of both sexes. These results add to a growing body of literature showing that sex-biased dispersal in social vertebrates is not enough to mitigate inbreeding risk due to the opposing fitness benefits of remaining in the same social group as, or close to, kin (Daniels & Walters, 2000b; Riehl & Stern, 2015; Kingma et al., 2017; Morrison et al., 2023).

The sex-bias in distance moved for later pairings was less pronounced, but males were still twice as likely as females to remain on their breeding territory for later pairings. A similar pattern of sex bias in breeding territory fidelity is found in other avian taxa, though the underlying causes and fitness consequences may differ (Harvey et al., 1979; Clarke et al., 1997). In Florida Scrub-Jays, females may be more likely to lose their breeding territory when they switch mates (later pairing) as a result of social dominance dynamics or avoidance of inbreeding with first-order kin if their son is more likely to inherit the territory than daughters are for male breeders (Woolfenden & Fitzpatrick, 1984). Thus, site fidelity in males may face stronger selective pressures resulting in reduced variation. Moreover, contrary to our predictions, removing the sex bias in distance moved for later pairings, *i.e.*, relaxing the strong skew in males towards site fidelity, decreased, rather than increased, inbreeding risk in males by 50% (though this decrease is countered by a 17% increase in mean inbreeding for females). This result suggests that fitness tradeoffs may shift over time in long-lived species, influencing dispersal patterns and inbreeding risk. Future studies should investigate dispersal dynamics during later life stages in more detail in this and other cooperative breeding, non-migratory species.

While passive mechanisms of inbreeding avoidance do not entirely mitigate inbreeding risk in Florida Scrub-Jays, we found evidence of active kin avoidance given observed dispersal limitations. For both sexes during first pairings, the proportion of observed first-order kin mates—*i.e.*, parent-offspring or sibling—was significantly lower than expected under the limited dispersal, sex-biased model and was not significantly different from expectations under the unconstrained model. These results suggest that active inbreeding avoidance in Florida Scrub-Jays during first pairing might be based on strong avoidance of close relatives based on familiarity. Florida Scrub-Jays live in cooperative breeding groups where the majority of helpers are offspring from previous broods that delay dispersal for one or more years to act as helpers (Woolfenden & Fitzpatrick, 1984). Thus, first-order kin have ample opportunity to build familiarity. Additionally, in a cooperatively breeding species like the Florida Scrub-Jays, kin recognition may be more likely to evolve, since it could serve an additional purpose in facilitating behaviors that result in indirect fitness benefits from helping kin (Nichols, 2017). Similar patterns of kin avoidance have been shown in some social species such as yellow baboons (*Papio cynocephalus*) (Galezo et al., 2022), mountain gorillas (*Gorilla beringei beringei*) (Morrison et al., 2023), acorn woodpeckers (*Melanerpes formicivorus*) (Haydock et al., 2001), long-tailed tits (*Aegithalos caudatus*) (Hatchwell et al., 2000; Leedale et al., 2020), and superb fairy-wrens (*Malurus cyaneus*) (Cockburn et al., 2003).

Interestingly, we found that the pattern of kin avoidance was weaker for later pairings, with the observed proportion of first-order kin mates being significantly higher than expected under the unconstrained model for both sexes, and not significantly different from the limited, sex-biased dispersal model for males. This result further suggests that, with a shift in fitness tradeoffs, inbreeding tolerance may increase for Florida Scrub-Jays at later life stages. Future research into the mechanisms underlying sexual selection and mate choice at all life stages in Florida Scrub-Jays, which still remain unknown, would help clarify mechanisms of inbreeding avoidance while accounting for other factors underlying mate choice.

Finally, though divorce is a common active inbreeding avoidance strategy in birds (Hatchwell et al., 2000; Cockburn et al., 2003; Hidalgo Aranzamendi et al., 2016), we did not find a similar pattern in Florida Scrub-Jays. However, pairs of close relatives are relatively rare in our study population, with only

4% of all breeding pairs resulting in consanguineous matings and only 1.2% resulting in matings between first-order relatives. Active kin avoidance may reduce the likelihood of first-order kin pairs forming in the first place. Further, since reproductive success increases with pair experience in Florida Scrub-Jays (Woolfenden & Fitzpatrick, 1984), mate switching due to divorce may prove costly.

Finally, we found that Florida Scrub-Jays experience fitness costs with longer distances moved at all life stages. We found that breeder survival decreased with farther natal dispersal distances, though this effect was limited to the first few years post breeding onset. For individuals with a breeding lifespan of >4 years, survival was greater for breeders that had moved farther for their first pairing, potentially because individuals of both sexes that disperse from their natal territory at a younger age generally disperse farther (Suh et al., 2020). We found that distance moved for first pairing did not affect LRS for either sex after accounting for breeding lifespan, suggesting no further effect of dispersal distance on fitness beyond reducing breeding lifespan. These results are consistent with previous work in this species and underscore the importance of breeders survival on the lifetime fitness and contribution to population growth in Florida Scrub-Jays (Fitzpatrick et al., 1999; Summers et al., 2024). Similarly, in long-lived species across different taxa, breeder survivorship, rather than fecundity, has been shown to have a greater effect on individual fitness and population growth (Brommer, 2000; Sæther & Bakke, 2000; McAdam et al., 2007).

Surprisingly, we did not find an effect of the loss of the breeding territory on breeder survival in either sex. Instead, females that moved longer distances for their later pairings had lower LRS. Though we did not find a similar pattern in males, this may be due to lower variation in their distance moved for later due to their high breeding site fidelity. We note that the relationship between distance moved for first and later pairings and lower survival and LRS may be a result of lower-quality individuals dispersing farther and losing breeding territories rather than a cost of dispersal itself (Fuirst et al., 2023; Hui et al., 2012). Additionally, since helpers contribute to nest success to some extent in Florida Scrub-Jays (Woolfenden & Fitzpatrick, 1984; Mumme, 1992), the observed decline in LRS could also be a result of variation in helper number with distance moved. Future studies should examine the intrinsic and extrinsic factors influencing variation in reproductive success with distance moved in more detail.

The lifetime fitness costs of engaging in inbreeding were evident only in males, who had fewer offspring that survived to adulthood when they mated with closely related females for higher proportions of their breeding lifetime. Overall, while effects differed by sex, our results suggest that in Florida Scrub-Jays the cost of inbreeding does not outweigh the fitness costs experienced with longer distances moved at all breeding stages, resulting in a degree of inbreeding tolerance in accordance with theoretical expectations (Kokko & Ots, 2006). Our results are similar to those found in a range of other animal taxa, including insects (Jennions et al., 2004; Collet et al., 2020); birds (Gibbs & Grant, 1989; Pärt, 1996; Daniels & Walters, 2000b; Foerster et al., 2006; Szulkin et al., 2009), and mammals (Holand et al., 2006; Geffen et al., 2011), where higher levels of inbreeding than expected under an unconstrained random mating scenario are tolerated despite some level of inbreeding depression. Interestingly, our results show that LRS only approached zero for the few males that bred with closely related females for the majority of their lifetimes. A similar pattern of sharply reduced hatch failure in closely related pairs was found in a previous study (Chen et al., 2016). Combined, these results suggest that inbreeding costs may be sharply elevated for close kin, but inbreeding with more distant relatives is not costly enough to outweigh the benefits of limited dispersal in Florida Scrub-Jays. We note that our analysis likely underestimates the cost of moving farther distances, since it does not include individuals who die in transit or otherwise fail to establish as breeders as well as dispersers out of the study tract (Bonte et al., 2012).

In summary, we use data from a long-term, continuously monitored population with detailed individual life history data to disentangle passive and active mechanisms of inbreeding avoidance and quantify their fitness outcomes across the lifetime of a long-lived, cooperatively breeding species. Our results corroborate predictions from theoretical models, demonstrating how sex-biased dispersal can mitigate inbreeding risk and how, at the same time, in social species with fitness benefits of limited dispersal, such passive mechanisms of inbreeding avoidance do not ensure complete mitigation of inbreeding risk. As in other social species, we find some evidence of active inbreeding avoidance through avoidance of first-order, likely familiar, kin. However, we also find empirical evidence to support predictions from theoretical studies that inbreeding tolerance can persist when the fitness costs of

513 inbreeding do not outweigh the costs of inbreeding avoidance. Interestingly, we find that the degree of
514 inbreeding avoidance differs across life stages. Our study underscores the importance of examining the
515 costs and benefits underlying mate choice at all life stages to better disentangle the mechanisms underlying
516 inbreeding in natural populations.
517

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Figures and Tables

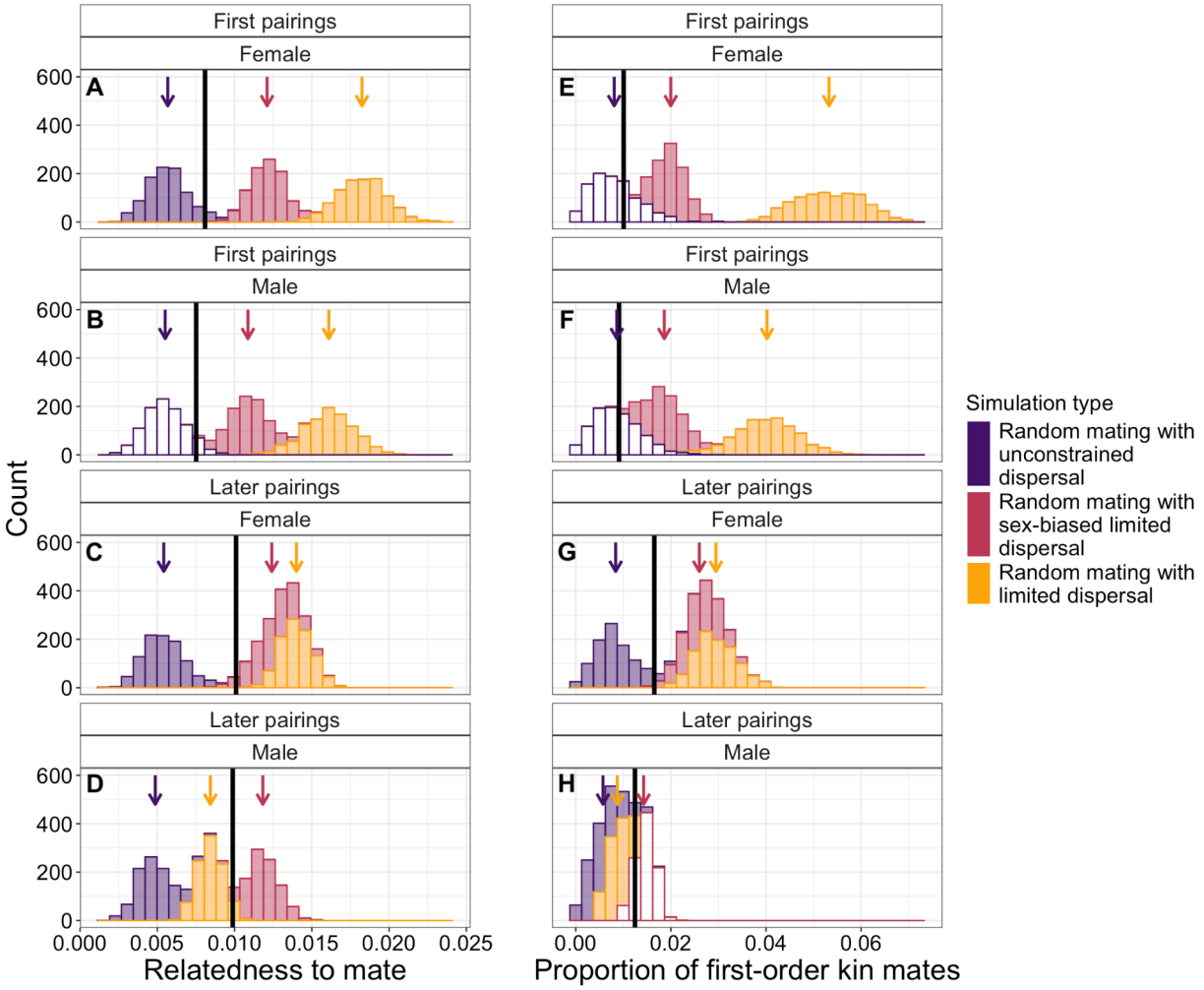

Figure 1. Relatedness to mate and proportion of first-order kin mates observed and expected under three different models of random mating in Florida Scrub-Jays at two life stages (first and later pairings) and for both sexes (male and female). The observed population means across all 32 years of our study period are indicated by black vertical lines. Histograms show the distributions of expected means under 1000 simulations of random mating in a scenario with unconstrained dispersal (purple), limited and sex-biased dispersal (red), and limited dispersal without sex-bias (yellow) (filled bars = distribution significantly different; unfilled bars = distribution not significantly different from the observed mean). Means of distributions are indicated by arrows.

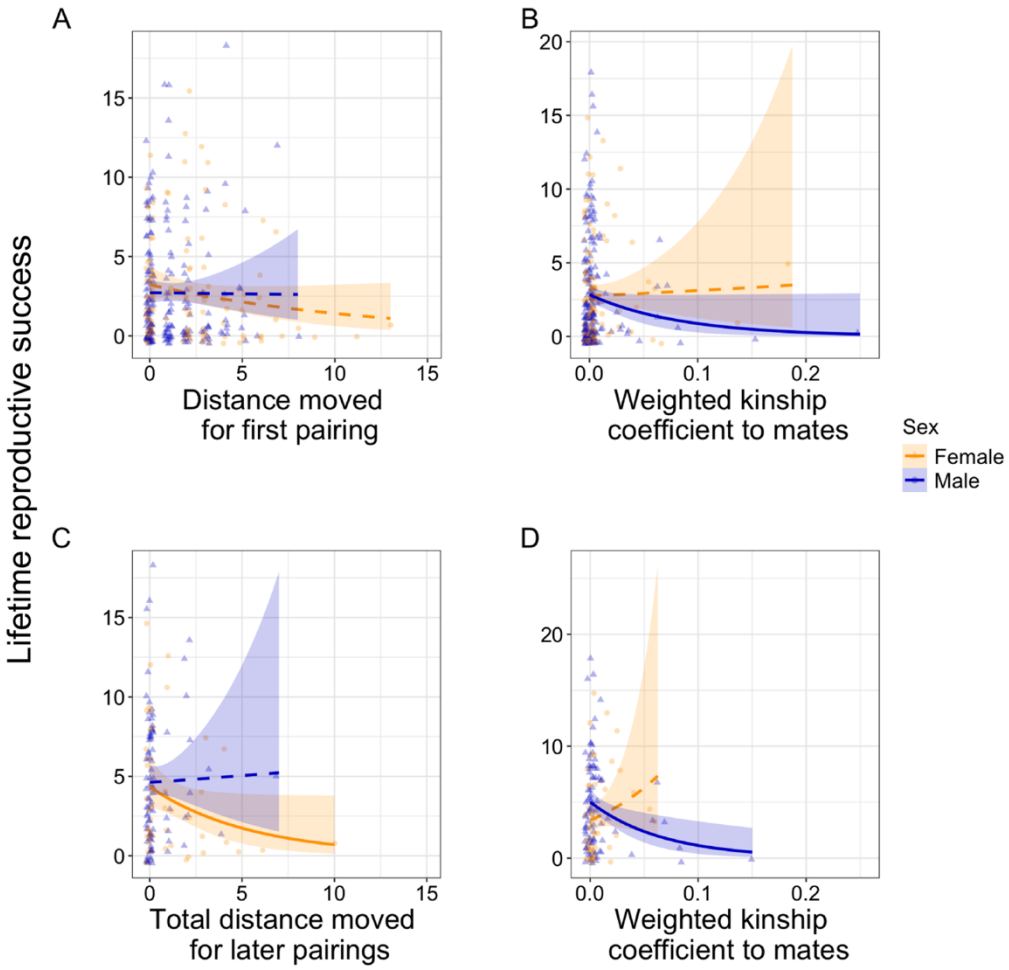

Figure 2. Predicted model fits investigating the effects (solid line = significant, dashed line = not significant; shaded area = 95% confidence interval) of (A) Distance moved for first pairing, and (B) Weighted kinship coefficients to mates on lifetime reproductive success (LRS) for Florida Scrub Jay male (blue, triangles) and female (orange, circles) breeders with lifetime data between 1990 and 2021 (*N*: Males = 197, Females = 120), and (C) Total distance moved for later pairings, and (D) Weighted kinship coefficients to mates for the subset of breeders that switched mates at least once in their lifetime (*N*: Male = 91, Female = 50). Females had lower LRS with greater total distance moved for later pairings, while males showed similarly lower LRS with higher kinship to mates over their lifetime. Points are jittered both horizontally and vertically for better visual discrimination.

806 **Table 1.** Results of generalized linear mixed models estimating the effect of distance moved for first
807 pairings, later pairings, relatedness to mate, and breeding lifespan on lifetime reproductive success (*i.e.*,
808 number of offspring surviving to adulthood) of Florida Scrub-Jays breeders. Significant effects are in bold.

Dataset	Sex	Fixed Effect	Estimate	Std Err	z-value	p-value
All breeders with lifetime data between 1990-2021	Male (*N*=197)	**Intercept**	0.47	0.08	5.86	**<0.001**
		Distance moved for first pairing	-0.09	0.09	-0.94	0.35
		Weighted kinship coefficient to mates	-0.34	0.12	-2.83	**0.005**
		Breeding Lifespan	0.93	0.07	13.75	**<0.001**
	Female (*N*=120)	**Intercept**	0.70	0.10	7.38	**<0.001**
		Distance moved for first pairing	-0.12	0.08	-1.43	0.15
		Weighted kinship coefficient to mates	0.03	0.08	0.31	0.76
		Breeding Lifespan	0.86	0.10	8.86	**<0.001**
Breeders with lifetime data between 1990-2021 that switched mates at least once	Male (*N*=91)	**Intercept**	1.25	0.08	14.90	**<0.001**
		Total distance moved for later pairings	-0.06	0.09	-0.64	0.52
		Weighted kinship coefficient to mates	-0.28	0.09	-3.05	**0.002**
		Breeding Lifespan	0.60	0.07	8.63	**<0.001**
	Female (*N*=50)	**Intercept**	1.21	0.10	12.15	**<0.001**
		Total distance moved for later pairings	-0.27	0.10	-2.62	**0.01**
		Weighted kinship coefficient to mates	-0.01	0.14	-0.04	0.97
		Breeding Lifespan	0.83	0.10	7.93	**<0.001**

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