Lifetime fitness benefits of short-distance dispersal and low costs of inbreeding drive inbreeding tolerance in an avian cooperative breeder

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Title: Lifetime fitness benefits of short-distance dispersal and low costs of inbreeding permit inbreeding tolerance in an avian cooperative breeder

Abstract

Inbreeding, or breeding with close relatives, often decreases individual fitness, but mate choice can increase inbreeding risk in some species. Inbreeding is more likely in species with limited dispersal, such as cooperative breeders, where offspring frequently breed close to home. We leverage 32 years of data from a population of Florida Scrub-Jays (*Aphelocoma coerulescens*), an avian cooperative breeder, to investigate whether mate choice, and its lifetime fitness outcomes, affects inbreeding tolerance. We find that both sexes show shorter dispersal distances than expected under random mating. While female-biased natal dispersal mitigates inbreeding risk to some extent, limited movement away from the breeding territory by both sexes for later pairings (following mate death or divorce) results in higher relatedness between mates than expected under random mating. Males paired with close relatives and females who move longer distances experience equivalently reduced lifetime reproductive success (LRS). Moreover, breeders who move farther for first pairings experience reduced survival likelihood and consequently reduced LRS. Fitness benefits of short-distance dispersal and relatively low fitness costs of inbreeding thus permit inbreeding tolerance in Florida Scrub-Jays. Understanding how and why mate choice contributes to inbreeding is crucial for informed conservation of endangered species like the Florida Scrub-Jay.

Keywords: Mate choice, inbreeding tolerance, site fidelity, lifetime fitness outcomes, Florida Scrub-Jay

Main Text

Introduction

Matings among relatives, or inbreeding, can have severe negative fitness consequences such as increased susceptibility to parasites [1], lower birth rates and offspring survival [2,3], and increased risk of mortality during severe weather events [4]. In wild populations, inbreeding can be the result of two non-exclusive factors. First, in populations that are small and isolated, mating with relatives might be inevitable even when mating is random [5]. Second, mate choice may be driven by factors that increase fitness despite the risk of inbreeding, such as phenotype matching or limited dispersal [6]. In the latter case, while inbreeding tolerance may persist without severe population-level impacts in large, well-connected populations, it may exacerbate inbreeding depression in isolated population fragments [7]. Understanding how mate choice may result in increased instances of inbreeding in species of conservation concern is thus vital for informed conservation action.

Moving away from their natal area—*i.e.*, natal dispersal—is the primary mechanism by which animals avoid mating with kin [8,9]. However, natal dispersal may be limited in some species, such that when individuals become breeders, they often choose mates that are geographically close [8,10]. While limited natal dispersal can lead to fitness benefits such as better access to resources [11], higher survival [12], and nepotism [13], it can also increase kin competition [14] and the likelihood of mating with a close relative [15–17]. Similarly, once individuals establish a breeding territory, any subsequent dispersal also may be geographically limited even when pairing with a new mate [8]. Such site fidelity may have fitness benefits due to familiarity and reduced competitive interactions [18–20], but can also increase inbreeding risk in spatially structured populations where limited dispersal results in the formation of kin neighborhoods [21]. Nevertheless, if the fitness benefits of limited dispersal outweigh the costs of inbreeding at the individual level, the risk of inbreeding may be tolerated [6,22]. Conversely, additional behaviors such as kin avoidance—where individuals can recognize and avoid mating with kin—and sex-biased dispersal—where one sex disperses farther than the other—may prevent inbreeding even in species with limited dispersal [6].

Previous studies investigated whether species with limited dispersal exhibit inbreeding tolerance or avoidance behaviors [7,23–28] and quantified the fitness tradeoffs between dispersal distance and kinship in mate choice [23]. However, few such studies have incorporated measures of lifetime fitness. This matters because reproductive strategies over an individual's lifetime, especially in long-lived species such as many cooperative breeders [29,30], may compensate for any short-term fitness costs associated with inbreeding or dispersal. Thus, we must examine lifetime fitness to obtain a comprehensive understanding of the individual fitness outcomes underlying mate choice that may increase inbreeding risk. Additionally, the importance of dispersal distance in mate choice may differ based on whether an individual is breeding for the first time ("first pairing") versus an experienced breeder pairing with a new mate ("later pairing") [8]. Because most studies only examine mate choice during first pairing, mechanisms such as site fidelity that may limit dispersal or increase inbreeding risk at later life stages [8] tend to be ignored. Here, we leverage 32 years of individual-level data on dispersal, mating, reproductive success, and survival from a continuously monitored population of an avian cooperative breeder, the Florida Scrub-Jay (*Aphelocoma coerulescens*), to investigate whether inbreeding risk is elevated due to mate choice throughout an individual's lifetime, and the resulting lifetime fitness outcomes.

Fewer than 6,000 individuals of the Federally Threatened Florida Scrub-Jay remain, located in numerous isolated populations and restricted to fire-maintained, xeric oak scrub habitats of the Florida peninsula [31]. Their preferred habitat is usually saturated with year-round territories, each occupied by a socially monogamous dominant breeding pair, accompanied often by subordinate non-breeders of both sexes [32]. Subordinates are primarily offspring from previous broods that delay dispersal and remain in their natal territory for one or more years, despite being physiologically capable of breeding at one year of age [32].

Most individuals become breeders by dispersing to replace dead breeders on existing territories, though direct inheritance or "budding" of natal territories sometimes occurs [32]. Females disperse farther than males, though neither sex typically disperses very far [33,34]. Once they become breeders, Florida Scrub-Jays remain breeders until their death, pairing with a new mate after their current mate dies [32], or in rare cases when the mate is still alive ("divorce") [35]. Though Florida Scrub-Jays are not known to be able to recognize kin, breeding pairs of close relatives, such as parent-offspring and sibling pairs, are rare, likely due to social group members avoiding pairing with each other [31], though such pairings are more common in fragmented habitats with increased geographical isolation and fewer choices of non-kin mates [36]. Here, we focus on a population of Florida Scrub-Jays that has been intensively studied at Archbold Biological Station in central Florida (27.10°N, 81.21°W) since 1969 [32]. Immigration into the Archbold population from neighboring populations has declined since 1995, leading to a corresponding increase in inbreeding and some associated fitness costs [3].

To investigate how mate choice impacts inbreeding risk, we first examined how the relatedness of Florida Scrub-Jays to potential mates varied with distance from both their natal and any subsequent breeding territories. Given fine-scale genetic isolation-by-distance in this population [34], we predicted that potential mates closer to both their natal and breeding territories would be relatively closely related for both sexes, and more so for females since males are the more philopatric sex [33]. Second, we examined the extent to which dispersal distance, relatedness, or both, correspond with mate choice. Previous work in this study population found individuals that dispersed shorter distances had higher fitness [37], and inbred individuals have lower fitness [3]. Thus, we predicted that both dispersal distance and relatedness of mates would deviate from expectations under a random mating scenario, with average dispersal distance shorter, and relatedness of mates lower (owing to inbreeding avoidance), than expected under a random mating scenario.

Next, to investigate the relative fitness costs and benefits involved in mate choice patterns, we quantified the impact of distance moved and relatedness between mates on lifetime reproductive success and breeder survival. We predicted that for both sexes, longer dispersal distances for both first and later pairings would result in lower lifetime reproductive success and survival [37]. Further, we predicted that if we found no evidence of kin avoidance in our mate choice analysis, the fitness cost of relatedness between mates would be equivalent to or lower than the cost of long-distance movement (suggesting inbreeding tolerance). Finally, we examined whether Florida Scrub-Jays employ other reproductive strategies, such as divorce, to minimize the costs of inbreeding. Since lifetime reproductive success is directly proportional to the number of breeding attempts [31], Florida Scrub-Jays may favor early breeding with a close relative over not breeding at all, but then may switch to less related mates when an opportunity arises. Thus, we predicted that pairs with more closely related mates would be more likely to dissolve because of divorce than death of a mate. Ultimately, by linking the effect of distance and kinship on mate choice with individual lifetime fitness outcomes, we investigated how mate choice that increases inbreeding risk can persist in a population.

Methods

Data collection

Florida Scrub-Jays at Archbold Biological Station have been continuously monitored since 1969, with the study tract expanded to its current size (mean ± sd = 914.04 ± 143.44 ha) by 1990 [31]. All birds are banded with unique combinations of color bands. Throughout the breeding season (early March to early June), all nests are located and monitored for fledging or failure [31]. All territories are mapped in April, with territory boundaries assigned at locations of territorial disputes between neighboring groups [31]. In addition to nest monitoring, the population is censused each month, resulting in detailed data on dispersal and survival of both fledglings and adults. Pairs are socially monogamous, with very low rates of extra pair-paternity (<1%) [38], allowing accurate parentage inference from field observations alone. Furthermore, previous work verified genetic parentage of offspring born between ~1989-1991, 1994-1995, and 1999-2013 [3]. Using

these detailed data, we have accumulated a 15-generation pedigree of known-age, known-parentage individuals with precise measurements of lifespan and reproductive success. For this study, we used data from 1990-2021, which included on average (± SD) 71.4 (± 14.7) territories (area mean ± sd =13.24 ± 6.37 ha) per year. All analyses were conducted using R version 4.2.2 [39]. Fieldwork was approved by the Institutional Animal Care and Use Committees at Cornell University (IACUC 2010-0015) and Archbold Biological Station (AUP-006-R) under permits from the US Fish and Wildlife Service (TE824723-8, TE-117769), the US Geological Survey (banding permits 07732, 23098), and the Florida Fish and Wildlife Conservation Commission (LSSC-10-00205).

We first measured observed dispersal distances and calculated relatedness to mate for both male and female breeders in all new breeding pairs formed between 1990 and 2021. New breeding pairs include pairs formed by two first-time breeders, one first-time and one experienced breeder, or two experienced breeders. For first-time breeders, we called the event a "first pairing" and for experienced breeders, a "later pairing". The first pairing for one mate is thus not always the first pairing for the other mate (*e.g.*, an experienced male could repair with a female who is a first-time breeder, and *vice versa*). New pairs might occupy a new territory, which may be inherited by one of the two breeders or formed as an extension of their natal territory in a process called "budding" [31]. 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 [31]. 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. 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.

The previous territory—*i.e.*, territory of origin—for any movement associated with a new pairing was identified as the territory where the individual was seen or caught the previous year between March to June (breeding season), and, if the bird was not seen within that time duration, between July to December (post-breeding season) since dispersal peaks at the start and end of the breeding season [33]. However, when two experienced breeders formed a new breeding pair, their breeding territories in the previous breeding season were assigned as their previous territories. Additionally, to account for territory vacancies being filled throughout the year, when a first-time breeder formed a new pair with an experienced breeder who retained its breeding territory, the previous territory for the first-time breeder was identified as the territory in which it was seen or caught in the month preceding the last month that its new mate's previous mate was seen in the breeding territory. 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 [40]). For staging individuals that eventually became breeders, we used movement from their staging to breeding territory to calculate dispersal distance for their first pairing. However, using distance from natal to breeding territory as distance moved for first pairing did not change our results (see *SI*).

In accordance with previous work in this system, we used the observed number of territories crossed as the most biologically relevant measure of distance moved [37]. The number of territories crossed was highly correlated with distance moved in meters (Pearson's $r = 0.91$; [37]). To calculate the number of territories crossed by a jay for a new pairing, we drew a straight-line movement trajectory from the centroid of its previous territory to the centroid of its new breeding territory. We then used the *st_intersects* function from the R package *sf* [41] to calculate the number of territories (*i.e.*, polygons) that each line intersected. For cases where the function returned a distance ≥ 1 territory away, but the territory name did not change from its natal or previous breeding territory, we manually corrected distances using territory maps (see *SI*). This occurred in 88 out of 1669 [5%] of movement events due to minor inconsistencies in territory naming conventions, where territories were named based on the dominant male breeder rather than territory location, and stochastic drift in territory boundaries. To examine sex-bias in distance moved for first and later pairings, we ran generalized linear mixed models (GLMMs) with distance moved as the dependent

variable, sex as the fixed effect, and a random effect of year. A random effect of individual ID was also included in the model for distance moved for later pairings to account for individuals who re-paired multiple times in their lifetime. The models had a negative binomial error distribution and were run separately by pairing type using the function *glmer.nb* in the R package *MASS* [42].

We calculated the kinship coefficient between mates for all new breeding pairs using the population pedigree with the *kinship* function in the R package *kinship2* [10]. 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; 0.125 is the average kinship coefficient between half-siblings, grandparents-grandchildren, and aunt/uncle-niece/nephew pairs; and 0.0625 is the average kinship coefficient between first cousins [43]. Pedigree-based inbreeding estimates are correlated with genomic-based estimates in our study population [3].
talk about this in Discussion

Data analysis

First, to examine how relatedness to potential mates varies with distance, we constructed a dataset of all possible mate pairings for each year and each sex separately. We only included breeders who formed new breeding pairs in a given year (*i.e.*, individuals that were both available as potential mates *and* successful at finding new mates), which comprised both first-time and experienced breeders. We paired all available females with each available male and *vice versa* (*N*: Male, First pairing = 426; Male, Later pairing = 241; Female, First pairing = 395; Female, Later pairing = 251 individuals). We calculated the potential distance that each focal individual would have to travel to realize this pairing as the distance between the individual's previous territory to the potential mate's territory in the current year. For simplicity, we assumed that the potential mate would retain its territory. We calculated the kinship coefficient for all potential pairings as described above, and classified potential mates to whom the kinship coefficient of the focal individual was ≥ 0.0625 (at least as related as first cousins, Fig. S2) as close relatives. We then fit GLMMs with whether the potential mate was a close relative (1 = yes, 0 = no) as the dependent variable, a binomial error structure, distance to mate as a fixed effect, and year and focal individual ID as random effects. We fit separate models for each sex and pairing type (*N*: Male, First pairing = 12,111; Male, Later pairing = 11,121; Female, First pairing = 10,800; Female, Later pairing = 10,464 possible pairings).

Second, we investigated the effects of distance to mate and relatedness on mate choice. As in previous studies that investigate mate choice [7,23,26], we quantified deviations of distance moved and average relatedness of mates from expectations under random mating. To simulate a random mating scenario, we randomly permuted all available mates of the opposite sex among all available mates of the focal sex for each year 1000 times. We then calculated the distance and kinship coefficient to mate using the same methods as above for each randomly generated pair. We calculated the mean distance and kinship coefficient to mate for each iteration for each focal sex and pairing type. We then compared these expected distributions of mean distances and kinship coefficients to observed means by calculating empirical p-values [44]. Specifically, we quantified the proportion of simulations that had a mean distance to mate that was lower than or equal to the observed mean (S_{low}), and the proportion of simulations that had a mean kinship coefficient to mate that was both lower than or equal to (to test for kin avoidance; S_{low}) and higher than or equal to (to test for inbreeding tolerance or kin preference; S_{high}) the observed mean. Empirical p-values were calculated as $(S_{high/low}+1)/(N+1)$, where N was the total number of simulations (*i.e.*, 1000).

Third, to examine how distance and relatedness to mate impacts lifetime fitness of Florida Scrub-Jays, 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 [32,45–47]. Since the mean growth rate of our study population is close to 1 (0.998) [48], we deemed LRS an appropriate metric of individual fitness [49]. For

this analysis, 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 [50,51]. The final dataset for all fitness analyses included individuals born between 1988-2006 and in 2009 (*N*: Males =197, Females =120).

We then 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 kinship coefficient to mates, and breeding lifespan as fixed effects (*N*: Males = 197, Females = 120). Fixed effects were not correlated (Table S1). We calculated the weighted kinship coefficient by multiplying the relatedness 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. We defined breeding lifespan as the number of years from becoming a breeder to death. 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 [31]. The effect of distance moved on breeder survival, and thus breeding lifespan, was examined separately as described below. We included natal year as a random effect to account for variation between birth cohorts. Further, 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*: Male = 91, Female = 50). All GLMMs were fit using the function *glmer.nb* in the R package *MASS* [42].

Next, 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 [52]. 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*, Fig. S7-S8) [52]. We used the *Surv* and *coxph* function from the R package *survival* [53] to fit separate models by sex of breeder, and incorporated natal year as a random effect (*N*: Male = 197, Female = 120). For the subset of individuals who switched mates at least once in their lifetime (*N*: Male = 91, Female = 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, $P = 0.61$).

Finally, 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 [54]. We fit separate GLMMs by sex and pairing type using the function *glmer* in the R package *lme4* (*N*: Male, First pairing = 194; Male, Later pairing = 187; Female, First pairing = 163; Female, Later pairing = 169 pairings) [55]. Fixed effects for all models were standardized using *z* scores [56], and the variance inflation factor was < 2 for all fixed effects in all GLMMs [57].

Results

The number of available mates ranged from 15-40 females and 14-43 males across our study period with an average (± SD) of 25.8 (± 7.33) males and 25.0 (± 6.88) females available as mates per year. These available mates accounted for, on average, 36% of all breeders per year. Of the individuals included in our lifetime fitness analysis, 42% of females (50 out of 120) and 46% of males (91 out of 197) switched mates at least once in their lifetime (mean ± SD number of mate switching instances per lifetime: Males = 0.83 ± 1.19, range: 0-6; Females = 0.74 ± 1.06, range: 0-4). 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. Females, on average, moved farther than males, though for the effect size was greater for first pairings (Male = 1.05 ± 1.53, Female = 1.90 ± 2.50 territories crossed; $Z = 5.86$, $P < 0.001$); [33]) than later pairings (Male = 0.30 ± 0.78, Female = 0.56 ± 1.17territories crossed; $Z = 3.64$, $P < 0.001$). 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. Furthermore, we found that out of all mate switching events observed, ~18% (*N*: Males = 64 of 381, Females = 64 of 332 events) were due to divorce, not mate death, a similar proportion to that found previously [32].

The kinship coefficient to mate ranged from 0 (unrelated) to 0.25 (*i.e.,* either full siblings or parent-offspring). Across all years, only 43 out of 1077 (4%) of observed 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 (0.01%) of observed breeding pairs comprised first-order relatives (7 mother-son, 3 father-daughter, and 3 full sibling pairs; Fig. S4). As predicted, we found that both sexes were more closely related to available opposite-sex breeders at shorter geographical distances on both their natal and breeding territories, with the greatest effect size for females on their natal territories (Males, Natal: $Z = -11.37$, $P < 0.001$; Females, Natal: $Z = -14.53$, $P < 0.001$; Males, Breeding: $Z = -8.10$, $P < 0.001$; Females, Breeding: $Z = -10.07$, $P < 0.001$; Fig. 1).

We found that dispersal distance, more than relatedness to mate, impacted mate choice decisions in Florida Scrub-Jays. When compared to a random mating scenario, both sexes moved significantly shorter distances within the study tract than expected under random mating for both first and later pairings (empirical p-value ≤ 0.05 for both), even though females moved farther than males in the first pairing stage (Fig. 3A). We found no evidence of kin avoidance: the mean kinship coefficient to mates for both sexes was never lower than predicted by the random mating model ($P > 0.05$ across all categories). Instead, we found evidence of inbreeding tolerance. For first pairings, mates were more closely related than expected by chance for females ($P = 0.05$; Fig. 3B), and the pattern approached statistical significance for males ($P = 0.07$; Fig. 3B). Mates in later pairings were more closely related than expected by chance for both sexes (Males: $P = 0.001$; Females: $P = 0.003$; Fig. 3B). The proportion of random mating iterations with mean relatedness to the mate equal to or higher than the observed mean—*i.e.*, the likelihood of the observed degree of relatedness to mate being recapitulated by random chance—was over an order of magnitude higher for first pairings (Males: 6.6%, Females: 4.6%) than later pairings (Males: 0.0%, Females: 0.2%).

Next, we quantified the lifetime fitness consequences of different mate choice decisions. We found that a higher weighted kinship coefficient to mates over an individual's lifetime resulted in 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. 3B, D; Table 1), but not females (all breeding females: $Z = 0.31$, $P = 0.76$; only females that switched mates at least once: $Z = -0.09$, $P = 0.97$; Fig. 3B, D; Table 1). The few males who bred with closely related females for the majority of their lifetime had LRS close to zero (Fig. 3B, D), but we did not observe the same pattern in females. —. Females, but not males, who moved farther distances for later pairings had significantly fewer offspring who survived to adulthood (Females: $Z = -2.62$, $P = 0.01$, Males: $Z = -0.64$, $P = 0.52$; Fig. 3C, Table 1), with a similar trend for

dispersal distance at first pairing, though the effect was not significant (Females: $Z = -1.43$, $P = 0.15$, Males: $Z = -0.29$, $P = 0.77$; Fig. 3A, Table 1). Moreover, as we predicted, breeding lifetime—*i.e.*, the number of years an individual spends as a breeder—had the largest effect on LRS for both sexes: longer breeding lifetimes resulted in more total offspring surviving to adulthood (Table 1).

For both sexes, breeding lifespan was affected by natal dispersal distance. We found that distance moved for first pairing was associated with higher mortality in the first four years after breeding onset (Male: $Z = 2.16$, $P = 0.03$; Female: $Z = 3.36$, $P = 0.001$), but the relationship was reversed in subsequent years (Male: $Z = -2.07$, $P = 0.04$; Female: $Z = -2.02$, $P = 0.04$). 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*; upper quartile of breeding lifespan: Males = 6, Females = 7 years, Fig. S9). However, dispersal away from an established breeding territory in the event of mate switching did not impact breeder survival for either sex (Male: $Z = -0.37$, $P = 0.71$; Female: $Z = 0.76$, $P = 0.45$).

Finally, the kinship coefficient to their mate had no effect on the likelihood of divorce in any scenario (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: $Z = 0.22$, $P = 083$; Females, First pairing: No instances of divorce when paired with a first-order relative; Females, Later pairing: $Z = 0.52$, $P = 0.60$).

Discussion

In many animals, the costs of inbreeding avoidance, such as traversing a long distance to find an unrelated mate, might outweigh the benefits of behaviors that can increase the likelihood of inbreeding, such as limited dispersal [22]. Some limited risk and amount of inbreeding may be tolerated, even while behaviors such as sex-biased dispersal and kin recognition may have evolved to prevent it [6,58,59]. In cooperatively breeding species, where offspring often delay dispersal from their natal territory for one or more years and frequently breed near home, fitness benefits of familiarity with the surrounding area, nepotism, or both, can lead to extremely limited dispersal [8]. Additionally, since cooperative breeding typically arises in habitats saturated with territories, breeders may show extreme site fidelity when pairing with a new mate [8]. Thus, especially among long-lived species, both sexes may exhibit little propensity for movement far away from their natal and breeding territories, thereby increasing the likelihood of pairing with closely related mates. Here, we investigated the impact of dispersal distance and relatedness on mate choice in an avian cooperative breeder, the Florida Scrub-Jay. This species exhibits limited dispersal for both first and subsequent pairings. We found that fidelity to their breeding territory, more so than limited movement for the first pairing, resulted in higher relatedness between mates than expected by random chance. Moreover, we found that both pairing with close relatives and moving a greater distance from breeding territory were negatively correlated with LRS, although the effects varied by sex. However, LRS did not vary with distance moved for first pairing when controlling for breeding lifespan. As breeding lifespan is strongly correlated with LRS, it is possible that natal dispersal distance indirectly affected LRS of both sexes via decreased breeding lifespan. Moving away from the breeding territory, however, did not affect breeder survival. Overall, our results suggest that while sex-biased natal dispersal mediates inbreeding avoidance to some extent in Florida Scrub-Jays, the fitness benefits short-distance dispersal may outweigh the costs of breeding with close relatives, resulting in inbreeding tolerance.

As expected for a highly philopatric species, we found that Florida Scrub-Jays are more closely related to geographically closer potential mates on both their natal and breeding territories. Previous work has shown that when pairing for the first time, Florida Scrub-Jay females move farther distances than males [32,33,34]. This sex-bias in distance moved for first pairing is reflected in our finding that females are more closely

related to potential mates (*i.e.*, males) closer to their natal territory than males are to potential mates (*i.e.*, females). Further, even around the breeding territory, both sexes were more closely related to potential mates at closer geographical distances. Thus, in agreement with previous work examining genetic isolation-by-distance in this species [34], and similar to other communal or cooperatively breeding species [60,61], Florida Scrub-Jays exhibit a viscous population structure such that inbreeding risk is elevated at shorter dispersal distances.

Surprisingly, we found that despite elevated inbreeding risk at shorter dispersal distances and evidence of inbreeding depression in our study population [3], mate choice was affected primarily by distance to mate. We compared observed means of distance moved and kinship coefficient to mate to those expected under a random mating scenario using a similar approach as previous studies of breeding populations of territorial birds where most, if not all, individuals were uniquely marked [7,23,26]. However, contrary to previous studies, we differentiated between instances of first and later pairings. We found that neither sex at either pairing stage exhibited significantly lower than expected kinship coefficient to mates, indicating no evidence of inbreeding avoidance. We found that the distances moved for first and later pairings are both lower than expected under a random mating scenario for both sexes. Though female bias in distance moved for first pairing somewhat mitigates inbreeding risk, females still show considerable philopatry, only dispersing on average ~2 territories away for first pairings, and are thus still likely to encounter related potential mates. Nevertheless, for both sexes, the likelihood that the observed higher degree of relatedness to mate for first pairings occurs by random chance is more than an order of magnitude higher than that for later pairings. We found a weaker sex bias in distance moved for later pairings, which likely leads to the greater deviation of observed relatedness to mate than expected under a random mating scenario for later pairings. Thus, our results suggest that fidelity to the breeding territory, more so than limited natal dispersal, is a more frequent cause of inbreeding in Florida Scrub-Jays. To our knowledge, this is the first study to examine the role of breeding site fidelity on inbreeding risk. The factors influencing mate choice for later pairings might be drastically different from mate choice for first pairings [8]. Future studies on mate choice and inbreeding patterns in this and other species would do well to take later life stages into account.

Significant philopatry, which has been found in both social and asocial species, can be driven by various factors such as better access to resources and protection from predators due to prior local experience [11] or higher habitat quality [33], lower competition due to nepotism [62,63], and high physiological costs of dispersal [64]. Although we expected to find a pattern of kin avoidance given that inbred Florida Scrub-Jay offspring have a lower probability of survival [3], theoretical work suggests that if the frequency and/or cost of inbreeding is low, inbreeding avoidance mechanisms—such as kin recognition—may not evolve [22]. Inbreeding—especially with close relatives—is relatively rare in our study population, with only 3% of all breeding pairs resulting in consanguineous matings and only 0.01% resulting in matings between first-order relatives. Further, the cost threshold for the evolution of inbreeding avoidance can be fairly high, especially in the absence of numerous viable mates [22]. Since our results suggest that geographical distance might constrain the pool of viable mates in our study population, kin discrimination and avoidance may lead to further loss of breeding opportunities and thus may not be adaptive. Finally, breeders may employ reproductive strategies that minimize the fitness costs of inbreeding over their lifetime in more nuanced ways not yet detected in our study.

Next, we investigated how lifetime fitness varies with dispersal distance and relatedness to mates in Florida Scrub-Jays. As predicted, we found a negative effect of both dispersal distance and relatedness on LRS and breeder survival. The number of offspring that survived to adulthood was lower for males that mated with closely related females for longer proportions of their breeding lifetime. On the other hand, relatedness to mate did not significantly predict female LRS. Instead, females that moved longer distances for their later pairings had lower lifetime fitness. This finding is contrary to other studies on avian species where breeding dispersal increases LRS, generally because dispersers settle on territories of higher quality than their previous territory [65–68]. Most of those studies are on species that migrate seasonally, which could

decrease the cost of acquiring a new territory at the start of the breeding season. However, Canada Jays (*Perisoreus canadensis*), which, similar to Florida Scrub-Jays, defend year-round territories and cache food—which could lead to higher costs of acquiring new territories and a greater benefit of site fidelity to a familiar territory—have been found to have higher lifetime fitness when they engage in breeding dispersal [68]. But unlike our much more stable study population [48], the study population for the Canada Jay study is declining, which may lead to more breeding vacancies and increased fitness as a result of breeding dispersal [68]. We further found that breeder survival decreased with farther distance moved for first pairings, though this effect was limited to the first few years post breeding onset. Coupled with the finding that breeding lifespan has the strongest positive effect on LRS, longer natal dispersal distance can thus negatively affect LRS by reducing the breeding lifespan of both sexes, as has been shown previously in this study population [37]. For individuals with a breeding lifespan of >4 years (>35% of breeders of both sexes), survival was higher 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 [33].Moreover, contrary to the same previous study [37], we found that distance moved for first pairing did not affect LRS for either sex. However, after accounting for the effect of breeding lifespan, we found that distance moved for first pairing had no additional effect on LRS for either sex, suggesting no further effect of dispersal distance on fitness beyond reducing breeding lifespan. Surprisingly, we did not find an effect of the loss of the breeding territory on breeder survival in either sex.

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 inbreeding tolerance in accordance with theoretical expectations [22]. 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 [69]. Additionally, 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 [70,71]. Our results are similar to those found in a range of other animal taxa—including insects such as the field cricket (*Teleogryllus commodus*) [72] and the parasitoid wasp *Venturia canescens* [73]; birds such as the Eurasian blue tit (*Cyanistes caeruleus*) [24], great tit (*Parus major*) [27], medium ground finch (*Geospiza fortis*) [26], collared flycatcher (*Ficedula albicollis*) [15], and red-cockaded woodpecker (*Leuconotopicus borealis*) [23]; and mammals such as reindeer (*Rangifer tarandus*) [74], grey wolf (*Canis lupus*) [75], and arctic fox (*Vulpes lagopus*) [75]—where higher than expected levels of inbreeding are tolerated despite some level of inbreeding depression. Interestingly, we found no evidence that Florida Scrub-Jays are more likely to divorce closely related or even first-order mates, suggesting that breeding with close relatives is not simply a response to lack of mate availability [17]. Further, since reproductive success increases with pair experience in Florida Scrub-Jays [32], mate switching due to divorce may prove costly. While we did not find evidence of preference for closely related mates, breeding with kin is also thought to confer kin selection benefits that may additionally contribute to inbreeding tolerance in some species [22,76].

In summary, we show that a mate choice behavior that maximizes individual lifetime fitness—*i.e.*, short-distance dispersal—contributes to some inbreeding in an avian cooperative breeder. Importantly, we show that it is site fidelity at the later pairing stage, not just limited dispersal away from the natal territory, that can lead to higher inbreeding than expected under random mating. Despite documented inbreeding depression, we find no evidence of inbreeding avoidance. Instead, we find that individual lifetime fitness costs of inbreeding are low enough for inbreeding tolerance and the persistence of limited dispersal. On a population level, inbreeding tolerance in mate choice might exacerbate inbreeding depression due to increasing population isolation. Our study underscores the importance of examining the costs and benefits underlying mate choice at all life stages to better understand the drivers of inbreeding in species of conservation concern. From a conservation standpoint, since large populations tend to be less inbred, our findings also underscore the profound importance of protecting large, contiguous populations in which

successful long-distance dispersal is possible, thereby reducing levels of inbreeding to tolerable levels over the long term.

References

1. Coltman DW, Smith JA, Bancroft DR, Pilkington J, MacColl ADC, Clutton-Brock TH, Pemberton JM. 1999 Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *Am. Nat.* **154**, 730–746. (doi:10.1086/303274)

2. Szulkin M, Garant D, Mccleery RH, Sheldon BC. 2007 Inbreeding depression along a life-history continuum in the great tit. *Journal of Evolutionary Biology* **20**, 1531–1543. (doi:10.1111/j.1420-9101.2007.01325.x)

3. Chen N, Cosgrove EJ, Bowman R, Fitzpatrick JW, Clark AG. 2016 Genomic consequences of population decline in the endangered Florida scrub-jay. *Curr. Biol.* **26**, 2974–2979. (doi:10.1016/j.cub.2016.08.062)

4. Keller L, Reeve HK. 1994 Partitioning of reproduction in animal societies. *Trends Ecol. Evol.* **9**, 98–102. (doi:10.1016/0169-5347(94)90204-6)

5. Keller LF, Waller DM. 2002 Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**, 230–241. (doi:10.1016/S0169-5347(02)02489-8)

6. Nichols HJ. 2017 The causes and consequences of inbreeding avoidance and tolerance in cooperatively breeding vertebrates. *J. Zool.* **303**, 1–14. (doi:10.1111/jzo.12466)

7. Billing AM *et al.* 2012 Evidence of inbreeding depression but not inbreeding avoidance in a natural house sparrow population. *Molecular Ecology* **21**, 1487–1499. (doi:10.1111/j.1365-294X.2012.05490.x)

8. Greenwood PJ, Harvey PH. 1982 The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **13**, 1–21. (doi:10.1146/annurev.es.13.110182.000245)

9. Szulkin M, Stopher KV, Pemberton JM, Reid JM. 2013 Inbreeding avoidance, tolerance, or preference in animals? *Trends Ecol. Evol.* **28**, 205–211. (doi:10.1016/j.tree.2012.10.016)

10. Clutton-Brock TH, Lukas D. 2012 The evolution of social philopatry and dispersal in female mammals. *Mol. Ecol.* **21**, 472–492. (doi:10.1111/j.1365-294X.2011.05232.x)

11. Pärt T. 1994 Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. *Animal Behaviour* **48**, 401–409. (doi:10.1006/anbe.1994.1254)

12. Griesser M, Nystrand M, Ekman J. 2006 Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1881–1886. (doi:10.1098/rspb.2006.3527)

13. Thünken T, Bakker TCM, Baldauf SA, Kullmann H. 2007 Active inbreeding in a cichlid fish and its adaptive significance. *Current Biology* **17**, 225–229. (doi:10.1016/j.cub.2006.11.053)

14. West SA, Pen I, Griffin AS. 2002 Cooperation and competition between relatives. *Science* **296**, 72–75. (doi:10.1126/science.1065507)

15. Pärt T. 1996 Problems with testing inbreeding avoidance: the case of the collared flycatcher. *Evolution* **50**, 1625–1630. (doi:10.1111/j.1558-5646.1996.tb03934.x)

16. Daniels SJ. 1997 Female dispersal and inbreeding in the red-cockaded woodpecker. Virginia Polytechnic Institute and State University.

17. Szulkin M, Sheldon BC. 2008 Dispersal as a means of inbreeding avoidance in a wild bird population. *Proc. R. Soc. B.* **275**, 703–711. (doi:10.1098/rspb.2007.0989)

18. Beck KB, Loretto M-C, Bugnyar T. 2020 Effects of site fidelity, group size and age on food-caching behaviour of common ravens, *Corvus corax*. *Animal Behaviour* **164**, 51–64. (doi:10.1016/j.anbehav.2020.03.015)

19. Schmidt KA. 2014 Site fidelity curbs sequential search and territory choice: a game theoretical approach. *Funct. Ecol.* **28**, 1494–1503. (doi:10.1111/1365-2435.12291)

20. Byrne ME, Cohen BS, Collier BA, Chamberlain MJ. 2022 Nest site fidelity and nesting success of female wild turkeys. *Wildlife Society Bulletin* **46**, e1279. (doi:10.1002/wsb.1279)

21. Hamilton WD. 1964 The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4)

22. Kokko H, Ots I. 2006 When not to avoid inbreeding. *Evol.* **60**, 467–475. (doi:10.1111/j.0014-3820.2006.tb01128.x)

23. Daniels SJ, Walters JR. 2000 Inbreeding depression and its effects on natal dispersal in red-cockaded woodpeckers. *The Condor* **102**, 482–491. (doi:10.1093/condor/102.3.482)

24. Foerster K, Valcu M, Johnsen A, Kempenaers B. 2006 A spatial genetic structure and effects of relatedness on mate choice in a wild bird population. *Molecular Ecology* **15**, 4555–4567. (doi:10.1111/j.1365-294X.2006.03091.x)

25. Frommen JG, Bakker TCM. 2006 Inbreeding avoidance through non-random mating in sticklebacks. *Biology Letters* **2**, 232–235. (doi:10.1098/rsbl.2005.0432)

26. Gibbs HL, Grant PR. 1989 Inbreeding in Darwin's medium ground finches (Geospiza fortis). *Evolution* **43**, 1273–1284. (doi:10.1111/j.1558-5646.1989.tb02574.x)

27. Szulkin M, Zelazowski P, Nicholson G, Sheldon BC. 2009 Inbreeding avoidance under different null models of random mating in the great tit. *Journal of Animal Ecology* **78**, 778–788.

28. Wheelwright NT, Mauck RA. 1998 Philopatry, natal dispersal, and inbreeding avoidance in an island population of savannah sparrows. *Ecology* **79**, 755–767. (doi:10.1890/0012-9658(1998)079%5B0755:PNDAIA%5D2.0.CO;2)

29. Beauchamp G. 2014 Do avian cooperative breeders live longer? *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140844. (doi:10.1098/rspb.2014.0844)

30. Arnold KE, Owens IPF. 1998 Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proc. R. Soc. Lond. B* **265**, 739–745. (doi:10.1098/rspb.1998.0355)

31. Fitzpatrick JW, Bowman R. 2016 Florida scrub-jays: Oversized territories and group defense in a fire-maintained habitat. In *Cooperative Breeding in Vertebrates* (eds WD Koenig, JL Dickinson), pp. 77–96. Cambridge University Press. (doi:10.1017/CBO9781107338357.006)

32. Woolfenden GE, Fitzpatrick JW. 1984 *The Florida Scrub Jay: Demography of a Cooperative-breeding Bird*. Princeton University Press.

33. Suh YH, Pesendorfer MB, Tringali A, Bowman R, Fitzpatrick JW. 2020 Investigating social and environmental predictors of natal dispersal in a cooperative breeding bird. *Behav. Ecol.* **31**, 692–701. (doi:10.1093/beheco/araa007)

34. Aguillon SM, Fitzpatrick JW, Bowman R, Schoech SJ, Clark AG, Coop G, Chen N. 2017 Deconstructing isolation-by-distance: The genomic consequences of limited dispersal. *PLoS Genet.* **13**, e1006911. (doi:10.1371/journal.pgen.1006911)

35. Marzluff JM, Woolfenden GE, Fitzpatrick John W, Balda RP. 1996 Breeding partnerships of two New World jays. In *Partnerships in Birds: The Study of Monogamy* (eds JM Black, M Hulme), p. 0. Oxford University Press. (doi:10.1093/oso/9780198548614.003.0007)

36. Roberts KA, Valine A, Tringali A, Dent M, Bowman R. 2023 Comparing the frequency of incest between siblings in two populations of florida scrub-jays (Aphelocoma coerulescens). **51**, 16–22.

37. Fitzpatrick JW, Woolfenden GE, Bowman R. 1999 Dispersal distance and its demographic consequences in the Florida Scrub-jay. In *Proceedings of the International Ornithological Congress*,

38. Townsend AK, Bowman R, Fitzpatrick JW, Dent M, Lovette IJ. 2011 Genetic monogamy across variable demographic landscapes in cooperatively breeding Florida scrub-jays. *Behavioral Ecology* **22**, 464–470. (doi:10.1093/beheco/arq227)

39. R Core Team. 2022 R: A Language and Environment for Statistical Computing.

40. Suh YH, Bowman R, Fitzpatrick JW. 2022 Staging to join non-kin groups in a classical cooperative breeder, the Florida scrub-jay. *J. Anim. Ecol.* **91**, 970–982. (doi:10.1111/1365-2656.13669)

41. Pebesma E. 2018 Simple features for R: Standardized support for spatial vector data. *The R Journal* **10**, 439. (doi:10.32614/RJ-2018-009)

42. Venables W, Ripley B. 2002 *Modern Applied Statistics with S*. 4th edn. New York: Springer. See https://www.stats.ox.ac.uk/pub/MASS4/.

43. Malécot G. 1948 *Les mathématiques de l'hérédité*. Paris: Masson.

44. Davison AC, Hinkley DV. 1997 *Bootstrap Methods and Their Application*. Cambridge University Press.

45. 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. (doi:10.1642/AUK-14-258.1)

46. McGowan KJ, Woolfenden GE. 1990 Contributions to fledgling feeding in the Florida Scrub-Jay. *Journal of Animal Ecology* **59**, 691–707. (doi:10.2307/4889)

47. Schoech SJ, Mumme RL, Wingfield JC. 1996 Delayed breeding in the cooperatively breeding Florida scrub-jay (Aphelocoma coerulescens): inhibition or the absence of stimulation? *Behav Ecol Sociobiol* **39**, 77–90. (doi:10.1007/s002650050269)

48. Summers J, Cosgrove EJ, Bowman R, Fitzpatrick JW, Chen N. 2024 Density dependence maintains long-term stability despite increased isolation and inbreeding in the Florida Scrub-Jay. *Ecology Letters* **27**, e14483. (doi:10.1111/ele.14483)

49. Brommer JE, Merilä J, Kokko H. 2002 Reproductive timing and individual fitness. *Ecology Letters* **5**, 802–810. (doi:10.1046/j.1461-0248.2002.00369.x)

50. Barve S, Riehl C, Walters EL, Haydock J, Dugdale HL, Koenig WD. 2021 Lifetime reproductive benefits of cooperative polygamy vary for males and females in the acorn woodpecker (Melanerpes formicivorus). *Proceedings of the Royal Society B: Biological Sciences* **288**, 20210579. (doi:10.1098/rspb.2021.0579)

51. Shah SS, Rubenstein DR. 2022 Prenatal environmental conditions underlie alternative reproductive tactics that drive the formation of a mixed-kin cooperative society. *Sci. Adv.* **8**, eabk2220. (doi:10.1126/sciadv.abk2220)

52. Therneau T. 2022 A Package for Survival Analysis in R.

53. Therneau T. 2022 coxme: Mixed Effects Cox Models. R package.

54. Cockburn A, Osmond HL, Mulder RA, Green DJ, Double MC. 2003 Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus* . *J. Anim. Ecol.* **72**, 189–202. (doi:10.1046/j.1365-2656.2003.00694.x)

55. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)

56. Schielzeth H. 2010 Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**, 103–113. (doi:10.1111/j.2041-210X.2010.00012.x)

57. Fox J, Monette G. 1992 Generalized Collinearity Diagnostics. *Journal of the American Statistical Association* **87**, 178–183.

58. Pusey A, Wolf M. 1996 Inbreeding avoidance in animals. *Trends Ecol. Evol.* **11**, 201–206. (doi:10.1016/0169-5347(96)10028-8)

59. Leedale AE, Simeoni M, Sharp SP, Green JP, Slate J, Lachlan RF, Robinson EJH, Hatchwell BJ. 2020 Cost, risk, and avoidance of inbreeding in a cooperatively breeding bird. *Proceedings of the National Academy of Sciences* **117**, 15724–15730. (doi:10.1073/pnas.1918726117)

60. Double MC, Peakall R, Beck NR, Cockburn A. 2005 Dispersal, philopatry, and infidelity: dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). *Evol.* **59**, 625–635.

61. Leedale AE, Sharp SP, Simeoni M, Robinson EJH, Hatchwell BJ. 2018 Fine-scale genetic structure and helping decisions in a cooperatively breeding bird. *Mol. Ecol.* **27**, 1714–1726. (doi:10.1111/mec.14553)

62. Kokko H, Ekman J. 2002 Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *Am. Nat.* **160**, 468–484. (doi:10.1086/342074)

63. 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. U.S.A.* **115**, 12011–12016. (doi:10.1073/pnas.1815873115)

64. Maag N, Cozzi G, Bateman A, Heistermann M, Ganswindt A, Manser M, Clutton-Brock T, Ozgul A. 2019 Cost of dispersal in a social mammal: body mass loss and increased stress. *Proc. R. Soc. B.* **286**, 20190033. (doi:10.1098/rspb.2019.0033)

65. Payne RB, Payne LL. 1993 Breeding dispersal in indigo buntings: Circumstances and consequences for breeding success and population structure. *The Condor: Ornithological Applications* **95**, 1–24. (doi:10.2307/1369382)

66. Forero MG, Donázar JA, Blas J, Hiraldo F. 1999 Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology* **80**, 1298–1310. (doi:10.1890/0012-9658(1999)080%5B1298:CACOTC%5D2.0.CO;2)

67. Winkler DW, Wrege PH, Allen PE, Kast TL, Senesac P, Wasson MF, Llambías PE, Ferretti V, Sullivan PJ. 2004 Breeding dispersal and philopatry in the tree swallow. *The Condor: Ornithological Applications* **106**, 768–776. (doi:10.1093/condor/106.4.768)

68. Fuirst M, Strickland D, Norris DR. 2021 Breeding dispersal in a resident boreal passerine can lead to short- and long-term fitness benefits. *Ecosphere* **12**. (doi:10.1002/ecs2.3747)

69. Bonte D *et al.* 2012 Costs of dispersal. *Biol. Rev.* **87**, 290–312. (doi:10.1111/j.1469-185X.2011.00201.x)

70. Fuirst M, Strickland D, Freeman NE, Sutton AO, Ryan Norris D. 2023 Early-life sibling conflict in Canada jays has lifetime fitness consequences. *Proceedings of the Royal Society B: Biological Sciences* **290**, 20221863. (doi:10.1098/rspb.2022.1863)

71. Hui C, Roura-Pascual N, Brotons L, Robinson RA, Evans KL. 2012 Flexible dispersal strategies in native and non-native ranges: environmental quality and the 'good–stay, bad–disperse' rule. *Ecography* **35**, 1024–1032. (doi:10.1111/j.1600-0587.2012.07697.x)

72. Jennions MD, Hunt J, Graham R, Brooks R. 2004 No evidence for inbreeding avoidance through postcopulatory mechanisms in the black field cricket, teleogryllus commodus. *Evolution* **58**, 2472–2477. (doi:10.1111/j.0014-3820.2004.tb00876.x)

73. Collet M, Amat I, Sauzet S, Auguste A, Fauvergue X, Mouton L, Desouhant E. 2020 Insects and incest: Sib-mating tolerance in natural populations of a parasitoid wasp. *Molecular Ecology* **29**, 596–609. (doi:10.1111/mec.15340)

74. Holand Ø, Askim KR, Røed KH, Weladji RB, Gjøstein H, Nieminen M. 2006 No evidence of inbreeding avoidance in a polygynous ungulate: the reindeer (Rangifer tarandus). *Biology Letters* **3**, 36–39. (doi:10.1098/rsbl.2006.0575)

75. Geffen E *et al.* 2011 Kin encounter rate and inbreeding avoidance in canids. *Molecular Ecology* **20**, 5348–5358. (doi:10.1111/j.1365-294X.2011.05358.x)

76. Puurtinen M. 2011 Mate choice for optimal (k)inbreeding. *Evolution* **65**, 1501–1505. (doi:10.1111/j.1558-5646.2010.01217.x)

Figures and Tables

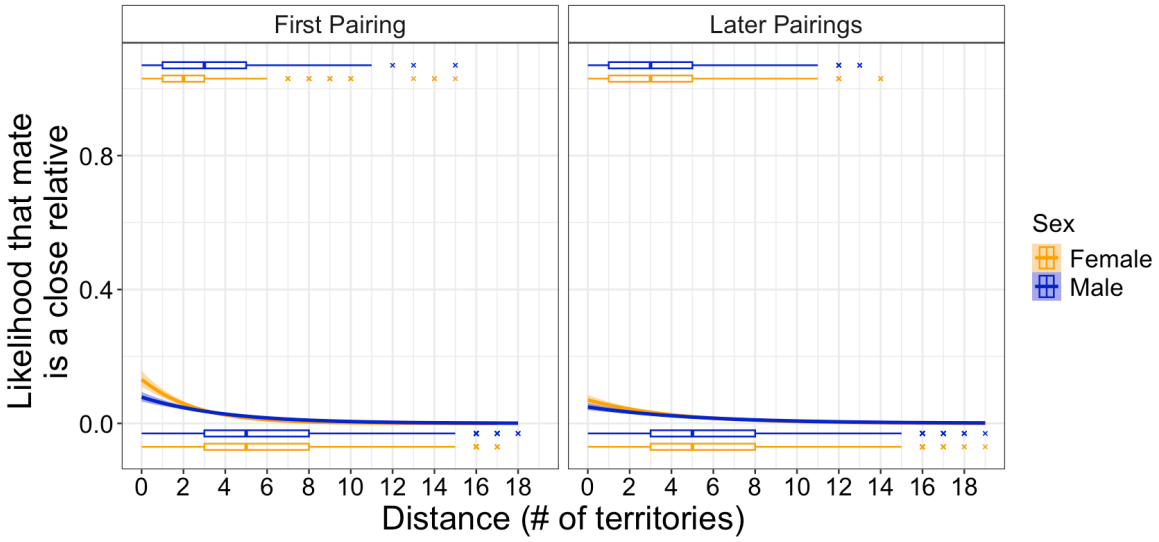

Figure 1. For both male (blue) and female (orange) Florida Scrub-Jays, mates at shorter distances from both their natal ("First Pairings") and breeding territories ("Later Pairings") are more likely to be close relatives. Lines indicate model fits, shaded areas 95% confidence intervals, and boxplots indicate distribution of raw data, with points indicating outliers. We defined close relatives as opposite sex individuals that are at least as closely related as first cousins to the focal individuals (1 = close relative, 0 = not close relative). We included all instances where individuals become breeders for the first time that year or switched mates (*N*: Male, First pairing = 12,111; Male, Later pairing =11,121 ; Female, First pairing = 10,800; Female, Later pairing = 10,464 possible pairings, with Male, First pairing = 426, Male, Later Pairing = 241, Female, First pairing = 395, and Female, Later pairing = 251 unique individuals).

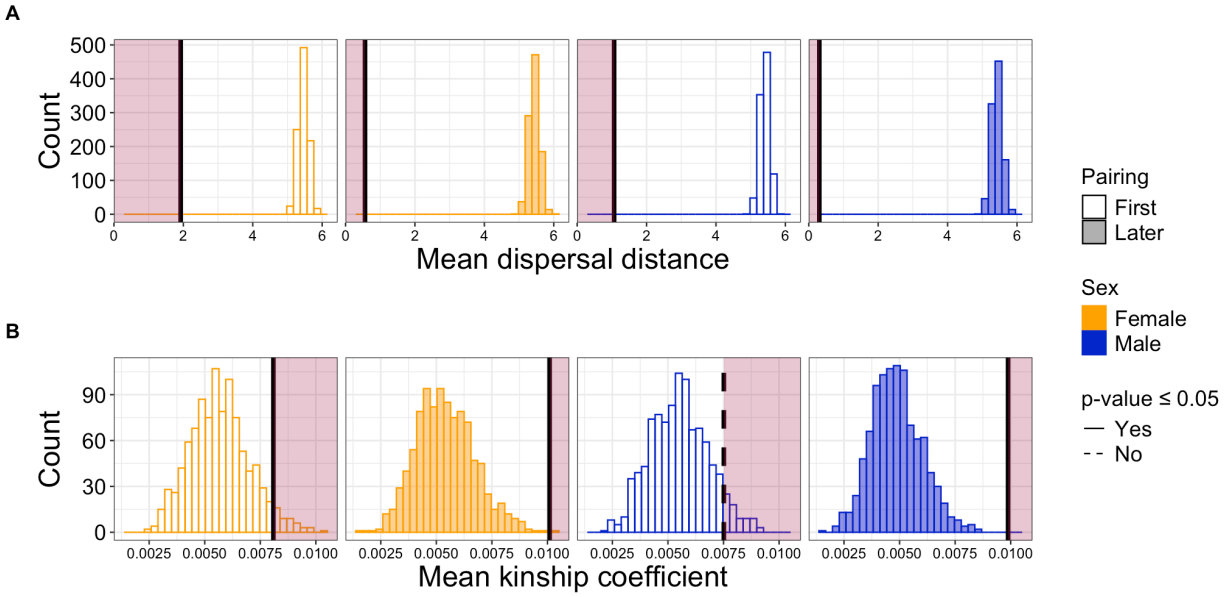

Figure 2. Observed and expected (under random mating) (A) dispersal distance and (B) relatedness to mate for male (blue) and female (orange) Florida Scrub-Jays at both the first (unfilled bars) and later (filled bars) pairing stages. Histograms show the distributions of expected means under 1000 simulations of random mating. The observed population means across all 32 years of our study period are indicated by vertical lines (solid = significant difference, dashed = no significant difference from expectations under a random mating scenario). Red shading denotes areas of the plot where data from simulated random mating scenarios would support the null hypotheses. Observed distances moved were significantly lower than expected for all four categories, while kinship coefficient to mate was higher than expected for both sexes at the later pairing stage, and females, but not males at the first pairing stage. However, the proportion of random mating iterations with mean relatedness to mate equal to or higher than observed mean (*i.e.*, within the red shading) was over an order of magnitude higher for first pairings (Males: 6.6%, Females: 4.6%) than later pairings (Males: 0.0%, Females: 0.2%).

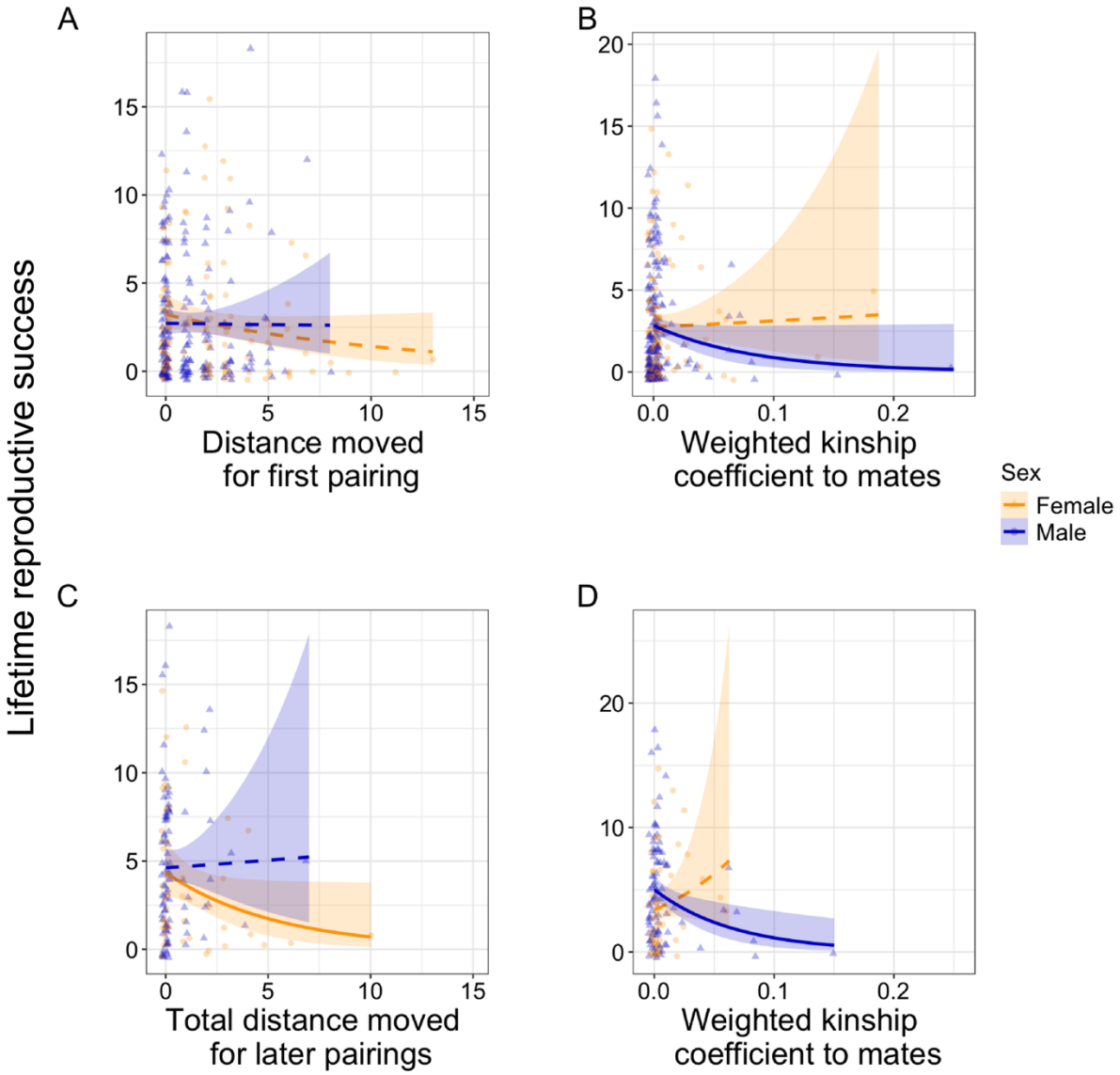

Figure 3. Predicted model fits investigating the effects (solid line = significant, dashed line = not significant; shaded area = 95% confidence interval) of (A) Distance moved for first pairing, and (B) Weighted kinship coefficients to mates on lifetime reproductive success (LRS) for Florida Scrub Jay 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). LRS is quantified as the number of offspring surviving to adulthood. Breeding lifespan (not shown) was also included as a fixed effect in the model, since the longer a breeder lives the more opportunities it has to accrue greater LRS. Females had reduced LRS with greater total distance moved for later pairings, while males showed a relatively similar reduction in LRS with higher kinship to mates over their lifetime. Points are jittered both horizontally and vertically for better visual discrimination.

Table 1. Results of generalized linear mixed models estimating the effect of distance moved for first pairings, later pairings, relatedness to mate, and breeding lifespan on lifetime reproductive success (*i.e.*, 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