Lifetime fitness benefits of breeding site fidelity and low costs of inbreeding permit inbreeding tolerance in an avian cooperative breeder

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Abstract

Inbreeding, or breeding with close relatives, often decreases individual fitness, but mate choice in many species can increase inbreeding risk. Inbreeding is more likely in species with limited dispersal, such as cooperative breeders where non-parental individuals—often offspring from previous broods—provide parental care and 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 a stronger preference for geographically closer rather than less related mates. While female-biased dispersal mitigates inbreeding risk when pairing for the first time, 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 that move longer distances experience equivalently reduced lifetime reproductive success. Fitness benefits of breeding site fidelity 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 action for endangered species like the Florida Scrub-Jay.

Keywords: Mate choice, inbreeding tolerance, site fidelity, cooperative breeding, 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.*, dispersal—is the primary mechanism by which animals avoid mating with kin [8,9]. However, 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 dispersal can lead to fitness benefits such as better access to resources [11], higher survival [12], and nepotism [13], it also can increase the likelihood of mating with a close relative [14–16]. 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 [17–19], but also may increase inbreeding risk in spatially structured populations where limited dispersal results in the formation of kin neighborhoods [20]. Nevertheless, if the fitness benefits of limited dispersal outweigh the costs of inbreeding at the individual level, inbreeding may be tolerated [6,21]. 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 have investigated whether species with limited dispersal exhibit inbreeding tolerance or avoidance behaviors [7,22–27], and even quantified the fitness tradeoffs between dispersal distance and kinship in mate choice [22]. 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 [28,29], may compensate for any 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] are 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, and the resulting fitness outcomes throughout an individual's lifetime.

Fewer than 6,000 individuals of the Federally Threatened Florida Scrub-Jay remain in numerous, widely isolated populations restricted to fire-maintained, xeric oak scrub habitats of the Florida peninsula [30]. 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 [31]. 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 [31].

Most individuals become breeders by dispersing to replace dead breeders on existing territories, though direct inheritance or "budding" of natal territories sometimes occurs [31]. Females disperse farther than males, though neither sex typically disperses very far [32,33]. Once they become breeders, Florida Scrub-Jays remain breeders until their death, pairing with a new mate if their current mate dies [31], or in rare cases when the mate is still alive ("divorce") [34]. 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 [31]. Immigration into the Archbold population from neighboring populations has declined since 1995, leading to a corresponding increase in inbreeding and associated fitness costs [3].

To investigate how mate choice affects 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 [33], 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 [32]. 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 [35], and inbred individuals have lower fitness [3]. Thus, we predicted that pairings with shorter dispersal distances and lower relatedness between mates would be more common, because these traits would be adaptively favored. Third, we tested whether dispersal distance and average relatedness of mates deviated from expectations under random mating. We predicted that average dispersal distance would be shorter than expected, and that the relatedness of mates would be lower than that expected under a random mating scenario (i.e., owing to inbreeding avoidance).

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 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 [35]. 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 increases with the number of annual breeding attempts [30], 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 sought evidence for 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 [30]. All birds are banded with unique combinations of color bands. Throughout the breeding season (mid-March to early June), all nests are located and monitored for fledging or failure [30]. All territories are mapped in April, with territory boundaries assigned at locations of territorial disputes between neighboring groups [30]. 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 [36], 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 =12.98 ± 6.94 ha) per year. All analyses were conducted using R version 4.2.2 [37]. 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 calculated observed dispersal distances and 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, as well as two experienced breeders. For first-time breeders, we called the event "first pairing" and for experienced breeders, "later pairing". 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" [30]. Alternatively, a new pair might form on a non-natal territory already occupied by one of the two breeders, where a breeding vacancy typically formed due to the death of a breeder, but occasionally via divorce [30]. 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. 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 [38]). For staging individuals that eventually became breeders, we considered it a first pairing event with movement from their staging to breeding territory.

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 [35]. The number of territories crossed was highly correlated with distance moved in meters (Pearson's $r = 0.91$; [35]). 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* [39] 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 (84 out of 1690 [5%] of movement events), we manually corrected distances using territory maps (see *SI*). We also 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 parent 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 [40]. Pedigree-based inbreeding estimates are correlated with genomic-based estimates in our study population [3].

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 that 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. For a given year, we paired all available females with each available male and vice versa (*N*: Male, First pairing = 421; Male, Later pairing = 249; Female, First pairing = 391; Female, Later pairing = 256 instances). We calculated the

potential distance that each focal individual would have to travel to realize this pairing as the distance between the individual's territory in the previous year to the potential mate's territory in the current year. For simplicity, we assumed that the potential mate would retain its territory. We also 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) as close relatives. We then fit generalized linear mixed models (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 = 12155; Male, Later pairing = 11837; Female, First pairing = 10938; Female, Later pairing = 11000 possible pairings).

Second, using the same dataset of all possible breeding pairs, we investigated the effect of distance to mate and relatedness on mate choice. We classified each potential pairing as "realized" (*i.e.*, observed that year) or "not realized" (*i.e.*, not observed that year). We then fit four separate GLMMs, one for each category, with whether a potential pairing was realized as the dependent variable and kinship coefficient and distance moved as fixed effects. We included year and focal individual ID as random effects and used a binomial error structure. We truncated the dataset to only include potential mates within a distance of four territories (*N*: Male, First pairing = 5202; Male, Later pairing = 5013; Female, First pairing = 4525; Female, Later pairing = 4686 possible pairings) to minimize overdispersion and since beyond this distance the likelihood of pairing with close relatives approaches zero (Fig. 1A, Fig. S2). We fit GLMMs using the function *glmer* in the R package *lme4* [41].

Third, to quantify deviations of distance and average relatedness of mates from expectations under 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. We then calculated the distance and kinship coefficient to mate using the same methods as above for each randomly generated pair. We ran 1,000 iterations per year and calculated the mean distance and kinship coefficient to mate for each year 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. Specifically, we quantified the proportion of simulations that had a mean distance to mate that was higher than the observed mean, and the proportion of simulations that had a mean kinship coefficient to mate that was lower than the observed mean.

Fourth, to examine how distance and relatedness to mate impacts lifetime fitness of Florida Scrub-Jays, we calculated three metrics of lifetime reproductive success for all breeders: the total number of offspring produced over an individual's lifetime that survived to day 30, day 90, and day 300, corresponding respectively to the ages at which Florida Scrub-Jays become physiologically capable of sustained flight, nutritional independence, and breeding [31,42–44]. Survival to these early life stages is governed by a varying degree of interactions between social and environmental factors, such as group and territory size, and offspring condition [42]. 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 [45,46]. The final dataset included individuals born between 1988-2006 and in 2009 (*N*: Males =196, Females =122).

We then fit six separate GLMMs (two sexes × three fitness metrics), with negative binomial error distributions (to account for overdispersion), lifetime reproductive success as the dependent variable, and distance moved for first pairing, weighted kinship coefficient to mates, and breeding lifespan as fixed effects (*N*: Males = 196, Females = 122). 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. Random effects included natal year to account for variation between birth cohorts. Further, to specifically examine the effect of moving away from the breeding territory, we also fit

six additional GLMMs with the same error structure, dependent variables, and random effects, with total distance moved for later pairings, weighted kinship coefficient to mates, and breeding lifespan as fixed effects with a truncated dataset that only included individuals that had switched mates in their lifetimes (*N*: Male = 92, Female = 51). All GLMMs were fit using the function *glm.nb* in the R package *MASS* [47].

Next, to examine the impact of distance moved on breeder survival, we fit two Cox proportional hazards models, one for each sex, with distance moved for first pairing as the fixed effect and natal year as a random effects using the *Surv* and *coxme* functions in the R packages *survival* [48] and *coxme* [49]. For the subset of individuals that switched mates at least once in their lifetime (*N*: Male = 92, Female = 51), we also examined the effect of territory loss (*i.e.*, 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 the fixed effect and natal year as random effects.

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 fit separate GLMMs by sex and pairing type using the function *glmer* in the R package *lme4* [41]. Fixed effects for all models were standardized using *z* scores [50], and variance inflation factor was < 2 for all fixed effects in all GLMMs [51].

Results

The number of available mates ranged from 14-42 females and 13-45 males across our study period with an average (± SD) of 26.2 (± 7.70) males and 25.2 (± 7.44) 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 (51 out of 122) and 47% of males (92 out of 196) switched mates at least once in their lifetime (mean ± SD number of mate switching instances per lifetime: Males = 0.83 ± 1.17, range: 0-6; Females = 0.73 ± 1.04, range: 0-4). Females, on average, moved farther than males, though more so for first pairings (Male = 1.05 ± 1.54, Female = 2.04 ± 2.61 territories crossed; *t*-test t = 6.52, df = 631.23, P < 0.001; [32]) than later pairings (Male = 0.34 ± 0.91, Female = 0.62 ± 1.29 territories crossed; *t*-test t = 3.73, df = 765.87, P < 0.001). In 212 out of 869 (24%) instances of later pairings, the focal individual (60% 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 187, Females = 31 of 171 events) were due to divorce, not mate death, a similar proportion to that found previously [31]. The kinship coefficient to mate ranged from 0 (unrelated) to 0.25 (*i.e.,* either siblings or parent-offspring). Across all years, only 44 out of 1443 (3%) of observed breeding pairs were comprised of individuals that were at least as closely related as first cousins (*i.e.*, had a kinship coefficient ≥ 0.0625). 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: $Z = -11.40$, $P < 0.001$; Females, Natal: $Z = -14.79$, $P < 0.001$; Males, Breeding: $Z = -8.49$, $P < 0.001$; Females, Breeding: $Z = -10.38$, $P < 0.001$; Fig. 1).

We found that both distance and relatedness to mate influence mate choice decisions in the Florida Scrub-Jay. The likelihood of pairing with a potential mate increased at shorter geographical distances for both sexes at both life stages (Males, First pairing: $Z = -21.02$, $P < 0.001$; Females, First pairing: $Z = -18.65$, $P < 0.001$; Males, Later pairing: $Z = -23.83$, $P < 0.001$; Females, Later pairing: $Z = -23.77$, $P < 0.001$; Fig. 2B), and males at the first pairing and females at the both life stages showed evidence of discriminating against more related mates (Males, First pairing: $Z = -4.41$, $P < 0.001$; Females, First pairing: $Z = -4.35$, $P < 0.001$; Males, Later pairing: $Z = -0.49$, $P = 0.62$; Females, Later pairing: $Z = -2.83$, $P = 0.005$; Fig. 2A). Nevertheless, the effect of weighted kinship coefficient to mate remained considerably smaller than the effect of geographical distance on mate choice across sexes and pairing types (Fig. 2).

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). The kinship coefficient to mates for both sexes was never lower than predicted by the random mating model ($P > 0.05$ across all categories). Mates from later pairings were more closely related than expected by chance for both sexes (Males: $P = 0$; Females: $P = 0$; Fig. 3B), but not for first pairings (Males: $P = 0.25$; Females: $P = 0.30$; Fig. 3B).

Finally, we quantified the fitness consequences of different mate choice decisions using three metrics of lifetime reproductive success. We found that a higher weighted kinship coefficient to mates over an individual's lifetime resulted in significantly fewer offspring that survived to the independence and yearling stages for males, but not females (Fig. 4B, Table S1). This effect extended to offspring surviving to the fledgling stage when only males that switched mates at least once in their lifetime were considered (Fig. 5B, Table S2). Conversely, females, but not males, that moved farther from their natal territory for their first pairing had significantly fewer offspring that survived to independence (Fig. 4A, Table S1), and those that moved farther distances for later pairings had significantly fewer offspring that survived to the independence and yearling stage (Fig. 5A, Table S2).

Moreover, as we predicted, breeding lifetime—*i.e.*, the number of years an individual spends as a breeder—had the largest effect on lifetime reproductive success for both sexes: longer breeding lifetimes resulted in more total offspring that survived to all three life stages (Table S1-2). For both sexes, we found that neither distance moved for first pairing (Male: $Z = -0.01$, $P = 0.99$; Female: $Z = 0.92$, $P = 0.36$) nor dispersal away from an established breeding territory in the event of mate switching (Male: $Z = 1.02$, $P = 0.31$; Female: $Z = -0.25$, $P = 0.81$) impacted breeder survival. The kinship coefficient to their mate had no effect on the likelihood of divorce in any scenario (Males, First pairing: $Z = 0.47$, $P = 0.64$; Males, Later pairing: $Z = -0.03$ $P = 0.98$; Females, First pairing: $Z = -0.14$, $P = 0.89$; Females, Later pairing: $Z = 0.66$, $P = 0.51$).

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 increase the likelihood of inbreeding, such as limited dispersal [21]. Inbreeding may instead be tolerated, and behaviors such as sex-biased dispersal and kin recognition may evolve to prevent inbreeding [6,52,53]. In cooperatively breeding species, where offspring often delay dispersal from their natal territory for one or more years and often breed near home, the fitness benefits of familiarity with the surrounding area and nepotism 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]. Both sexes may thus exhibit little propensity for movement away from their natal and breeding territories, thus 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. We found that dispersal distance had a greater impact on mate choice than relatedness. Next, we examined how limited dispersal, and its fitness consequences, drives inbreeding in this species. We found that fidelity to their breeding territory, rather than limited movement away from the natal territory, 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 the natal and breeding territories had a negative impact on lifetime reproductive success but not survival, though the effects varied by sex. Overall, our results suggest that although sex-biased natal dispersal acts as an inbreeding avoidance mechanism in Florida Scrub-Jays, the fitness benefits of remaining on established breeding territories may outweigh the costs of breeding with close relatives, resulting in inbreeding tolerance.

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]. 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), though both sexes are significantly more related to potential mates at dispersal distances of ≤ 4 territories away from their natal territory than potential mates > 4 territories away. 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 [33], and similar to other communal or cooperatively breeding species [54,55], 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 driven primarily by distance to mate, with a very small, if any, effect of relatedness to mate. Both sexes were more likely to pair with a geographically closer mate when breeding for the first time or switching mates as an experienced breeder. This degree of 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], lower competition due to nepotism [56,57], and high physiological costs of dispersal [58]. Although we expected to find a pattern of kin avoidance given that inbred Florida Scrub-Jay offspring have a lower probability of survival [3], we found a relatively small negative effect of kinship on mate choice. Theoretical work suggests that if the frequency and/or cost of inbreeding is low, inbreeding avoidance mechanisms—such as avoiding mating with kin—may not evolve [21]. Further, the cost threshold for the evolution of inbreeding avoidance can be fairly high, especially in the absence of many viable mates [21]. 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. Our results do indicate that males breeding for the first time and females switching mates discriminate against closely related mates to some extent, suggesting that relatedness to mate may be a factor in mate choice in a more nuanced way that merits further study.

To further understand the extent to which limited movement away from natal and breeding territories in mate choice leads to inbreeding, we compared observed means of distance moved and kinship coefficient to mate to those expected under a random mating scenario. We used a similar approach to simulating a random mating scenario as previous studies of breeding populations of territorial birds where most, if not all, individuals were uniquely marked [7,22,25]. 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. Thus, there was no evidence of inbreeding avoidance. Though we found that the distances moved for first and later pairings are both lower than expected under a random mating scenario for both sexes, female bias in distance moved for first pairing prevents higher relatedness between breeders in first pairings than expected by random chance. We found no sex bias in distance moved for later pairings, which likely leads to the observed higher relatedness to mate than expected under a random mating scenario. Thus, our results suggest that fidelity to the breeding territory, rather than limited natal dispersal, is a driver 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 driving 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 should thus take later life stages into account.

Finally, we investigated the lifetime fitness outcomes of dispersal distance and relatedness to mates in Florida Scrub-Jays. As predicted, we found a negative effect of both dispersal distance and relatedness on

lifetime reproductive success, but the effects varied by sex and were only apparent at later offspring survival stages. This result is consistent with previous work in Florida Scrub-Jays which found that the effect of inbreeding on offspring survival increased with number of life stages considered [3]. The total number of offspring fledged—the standard metric of reproductive success in birds—was only significantly lower for males with higher weighted kinship coefficient to mates when the data excluded males with only one mate in their lifetime. However, the number of offspring that survived to independence and yearling stages was consistently 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 affect female lifetime reproductive success. Instead, females that moved longer distances for both their first and later pairings had lower lifetime fitness (measured as the total number of independent or yearling offspring produced). We did not find any evidence of lower male or female breeder survival with higher distance moved for first or later pairings. These results are contrary to previous work in this population that found that both sexes had lower lifetime reproductive success and annual survival at greater dispersal distances, with a stronger effect in males compared to females [35]. However, unlike the previous study, we did not include immigrants from outside of the study tract in our analysis of lifetime fitness, since, in the context of mate choice, we are not able to account for all possible mates within their natal population nor accurately measure distance moved.

Overall, though effects differed by sex, our results suggest a trade-off in Florida Scrub-Jays between nearly equivalent costs of mating with close relatives and moving farther distances away from their natal and breeding territories. We note that our analysis likely underestimates the cost of moving farther distances, since it does not include individuals that die in transit or fail to establish as breeders and also excludes dispersers out of the study tract [59]. Thus, since the cost of inbreeding does not outweigh the benefit of limited dispersal, the population seems to exhibit inbreeding tolerance in accordance with theoretical expectations [21]. Our results are similar to that found in a range of other animal taxa—including insects such as the field cricket (*Teleogryllus commodus*) [60] and the parasitoid wasp *Venturia canescens* [61]; birds such as the Eurasian blue tit (*Cyanistes caeruleus*) [23], great tit (*Parus major*) [26], medium ground finch (*Geospiza fortis*) [25], collared flycatcher (*Ficedula albicollis*) [14], and red-cockaded woodpecker (*Leuconotopicus borealis*) [22]; and mammals such as reindeer (*Rangifer tarandus*) [62], grey wolf (*Canis lupus*) [63], and arctic fox (*Vulpes lagopus*) [63]—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 mates, suggesting that breeding with close relatives is not simply a response to lack of mate availability [16]. Further, since reproductive success increases with pair experience in Florida Scrub-Jays [31], 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 [21,64].

In summary, we show that a mate choice that maximizes individual lifetime fitness—*i.e.*, relatively 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 limited dispersal away from the natal territory, that drives 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.

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Figures

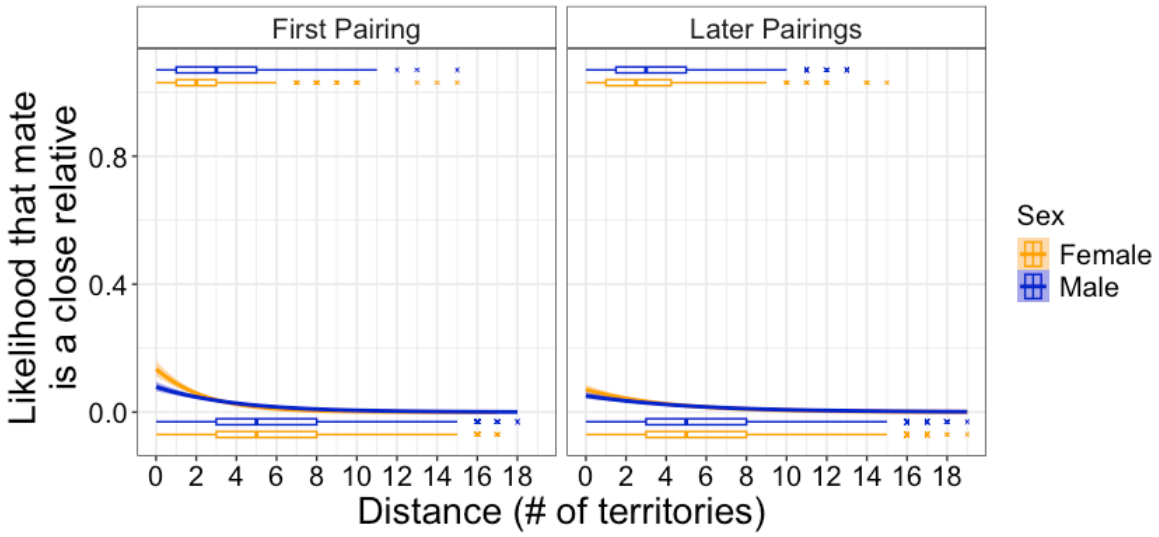

Figure 1. For both male (blue) and female (orange) Florida Scrub-Jays, mates at shorter distances from both their natal ("First Pairings") and breeding territories ("Later Pairings") are more likely to be close relatives. Lines indicate model fits, shaded areas 95% confidence intervals, and boxplots 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 = 421; Male, Later pairing = 249; Female, First pairing = 391; Female, Later pairing = 256 instances).

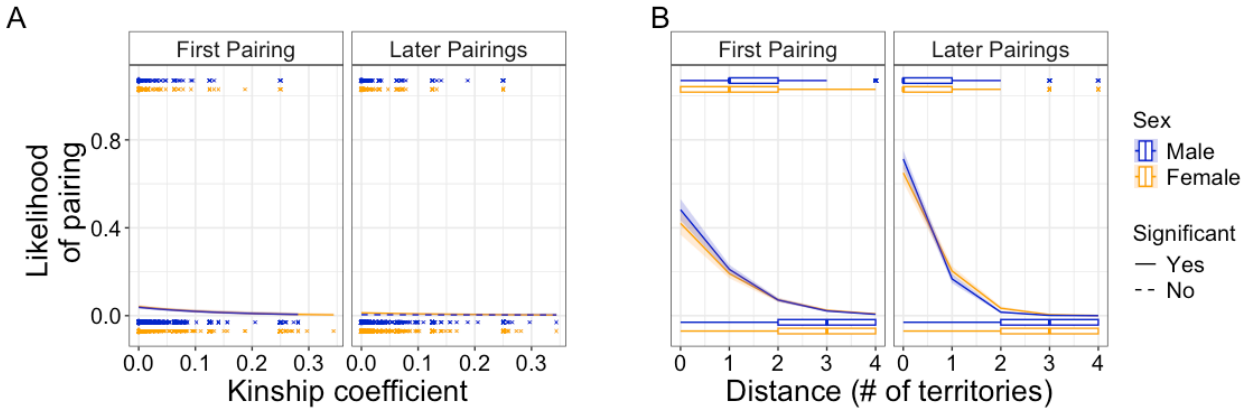

Figure 2. The predicted effect of (A) relatedness and (B) distance to mate (solid line = significant, dashed line = not significant effect) on mate choice in both sexes (blue = male, orange = female) of Florida Scrub-Jays. We only included potential mates located four or fewer territories away (*N*: Male, First pairing = 5202; Male, Later pairing = 5013; Female, First pairing = 4525; Female, Later pairing = 4686 possible pairings) to prevent overdispersion in the models, and because 95% of pairings occur with mates within that distance (Fig. S2). While relatedness to mate significantly lowered likelihood of pairing for males at the first pairing and females at the first and later pairing stages, the effect of relatedness to mate was minimal compared to that of distance to mate. Both sexes were more likely to pair with mates at shorter distances for both first and later pairings. Shaded areas around predicted fits depict 95% confidence intervals and boxplots indicate distribution of raw data, with points indicating outliers. Since kinship coefficients for 78% of all possible pairs equaled 0, the interquartile range for boxplots in panel A is 0.

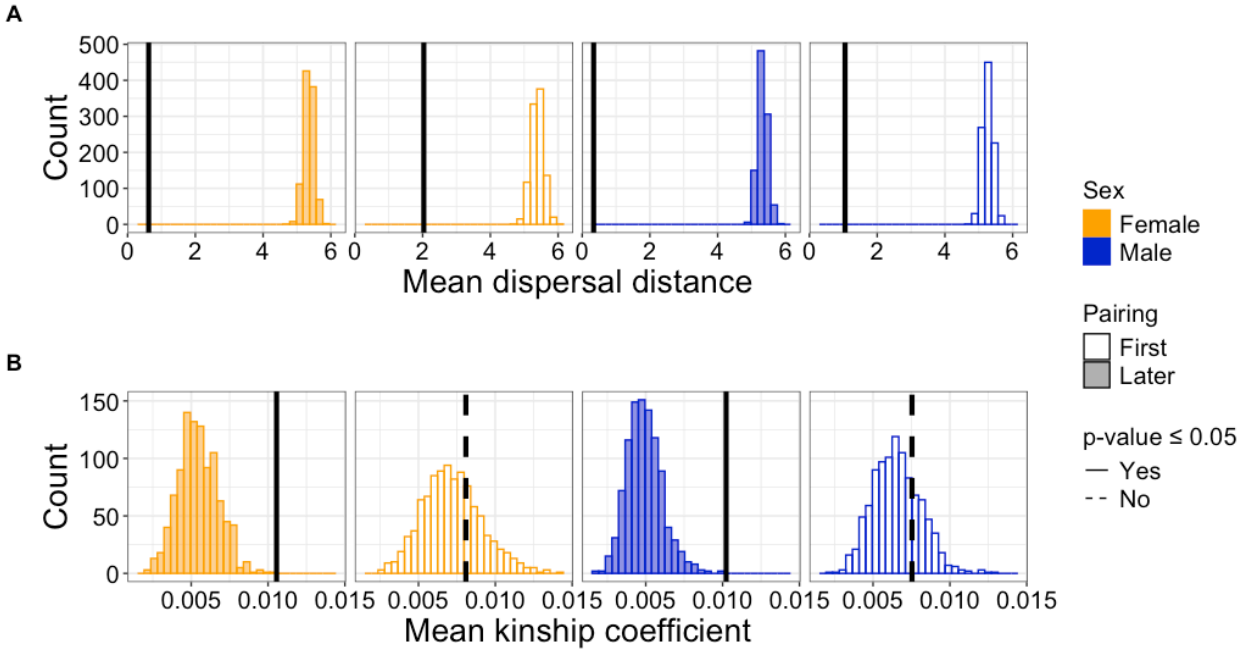

Figure 3. Observed and expected (under random mating) (A) dispersal distance and (B) relatedness to mate for male (blue) and female (orange) Florida Scrub-Jays at both the first (filled bars) and later (unfilled bars) pairing stages. Histograms show the distributions of expected means under 1000 simulations 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). 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, but not first, pairing stages.

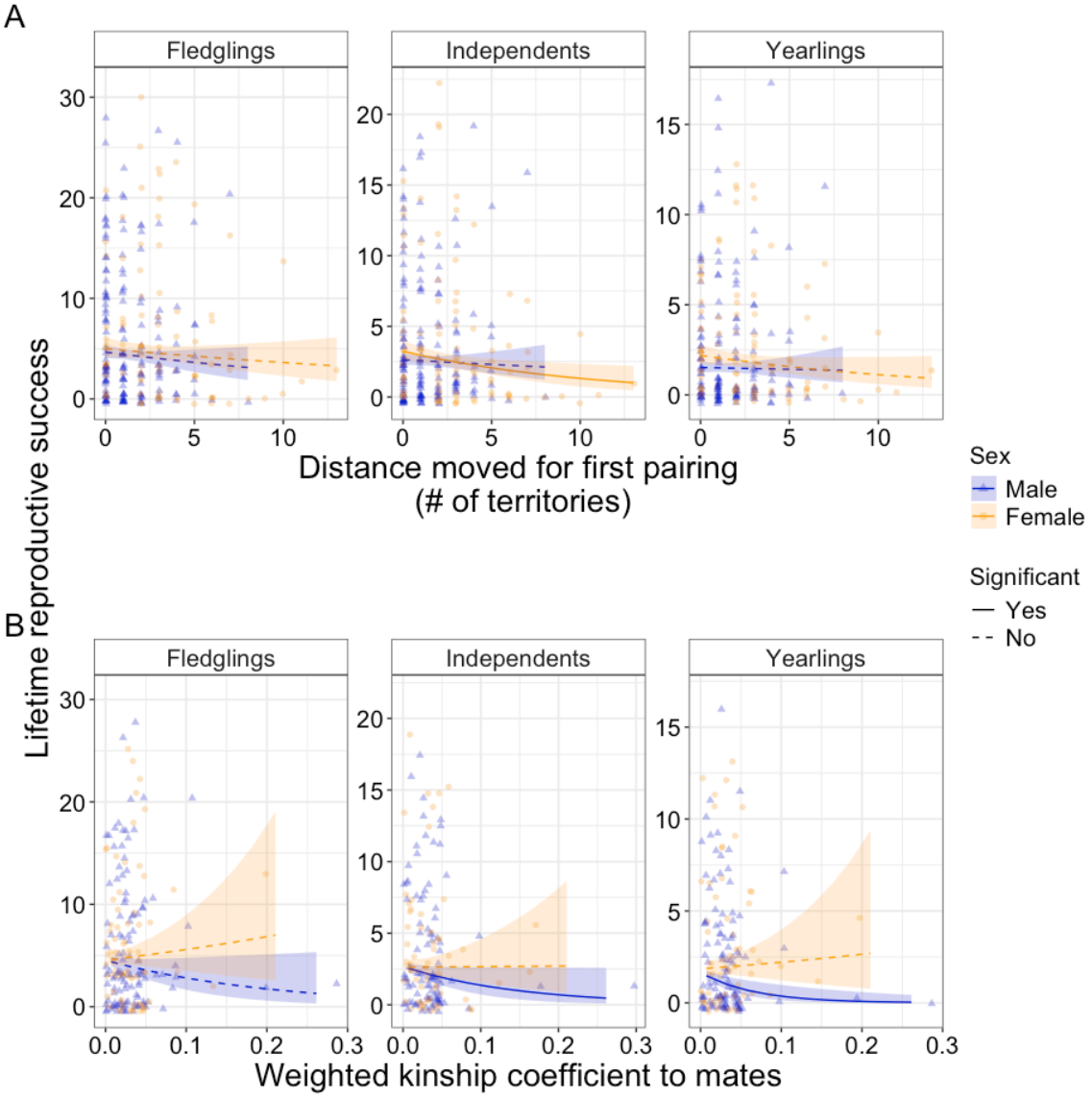

Figure 4. Predicted model fits investigating the effects (solid line = significant, dashed line = not significant) of (A) Distance moved for first pairing, and (B) Weighted kinship coefficients to mates on three metrics of lifetime reproductive success (LRS)—number of offspring surviving to fledgling, independence, and yearling stages—for males (blue, triangles) and females (orange, circles) (*N*: Males = 196, Females = 122). Breeding lifespan (not shown) was also included as a fixed effect in the model, since the longer a breeder lives the more chances it has to accrue greater LRS. Females had reduced LRS with increasing distance moved for first pairing, while males showed a relatively similar reduction in LRS with increased kinship to mates over their lifetime.

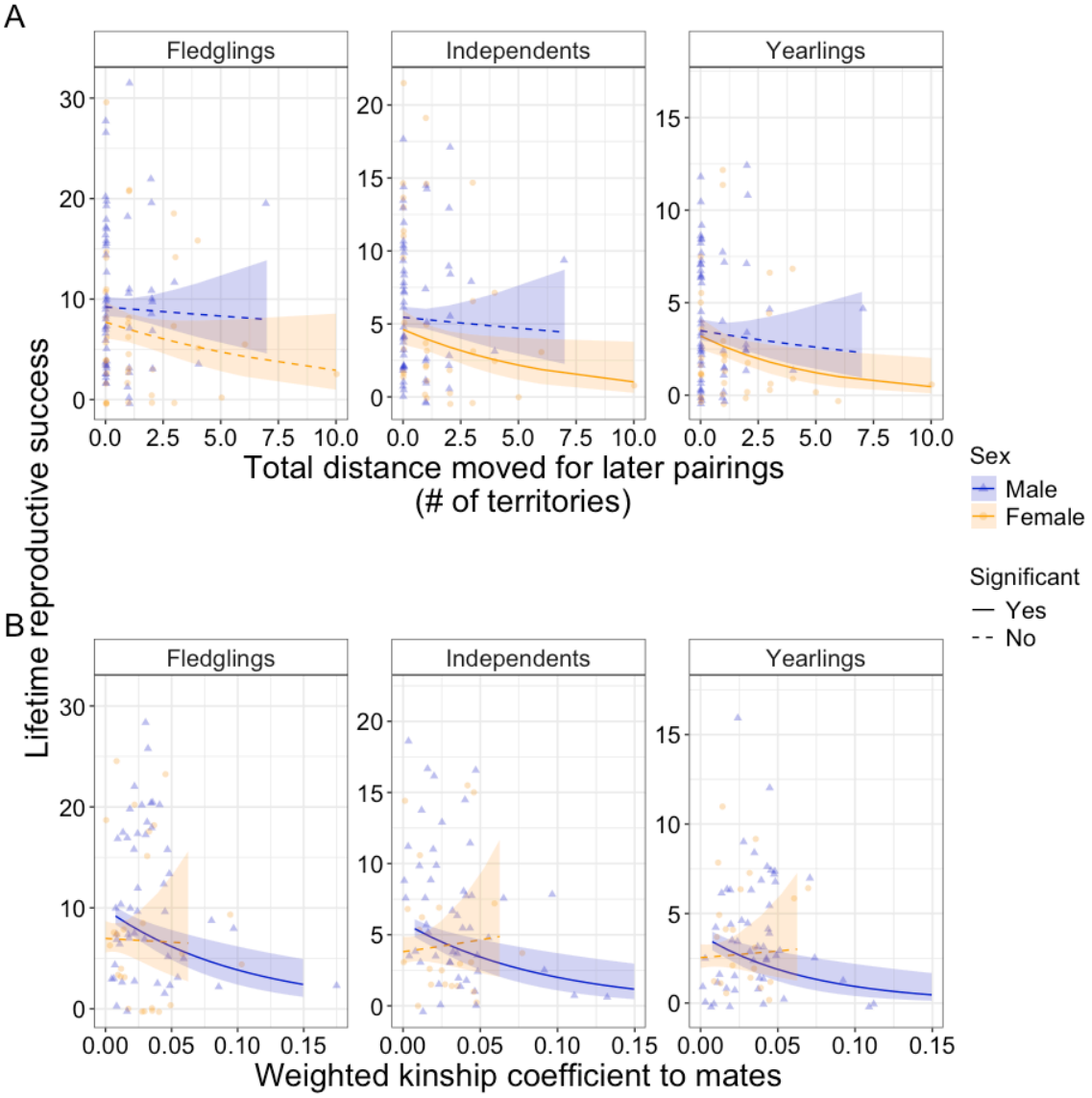

Figure 5. Predicted model fits investigating the effects (solid line = significant, dashed line = not significant) of (A) Total distance moved for later pairings, and (B) Weighted kinship coefficients to mates on three metrics of lifetime reproductive success (LRS)—number of offspring surviving to fledgling, independence, and yearling stages—for males (blue, triangles) and females (orange, circles) that paired with more than one mate in their lifetime (*N*: Males = 92, Females = 51). As in the previous model, breeding lifespan (not shown) was also included as a fixed effect since the longer a breeder lives the more chances it has to accrue more LRS. Females had reduced LRS with increasing distance moved for later pairings, while males showed a relatively similar reduction in LRS with increased kinship to mates over their lifetime.