

Breeding dispersal in a resident boreal passerine can lead to short- and long-term fitness benefits

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Abstract. Whether an individual disperses or remains site-faithful between breeding seasons can have important impacts on individual fitness and population dynamics. While several studies have identified factors influencing the probability of breeding dispersal, the consequences of dispersal are much less certain, particularly over an individual's lifetime. Here, we use 81 cases (13 paired and 55 single dispersals) of breeding dispersal across 55 yr of breeding and re-sighting data from an individually marked population of Canada jays (*Perisoreus canadensis*) at the southern edge of their range in Algonquin Provincial Park, Ontario to determine both the short- (year after dispersal) and long-term (lifetime) consequences of breeding dispersal. In the year following dispersal, adults had larger brood sizes and higher nest success compared to the year prior to dispersal. However, when adults dispersed during the fall/winter, they had significantly later lay dates and lower rates of nest success than adults that dispersed during the summer. Additionally, most breeders dispersed to territories of higher quality and individuals that dispersed to a territory of lesser quality experienced lower rates of nest success. Importantly, individuals that dispersed at least once in their lifetime produced an average of 2.7 more young and recruited an average of 0.9 more juveniles into the population compared to individuals that remained site-faithful. Our study provides rare evidence of both the short- and long-term benefits of breeding dispersal in Canada jays and demonstrates how the timing of dispersal can also have consequences for individual reproductive performance.

Key words: Canada jay; long-term data; *Perisoreus canadensis*; site fidelity; territory quality.

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INTRODUCTION

Dispersal is a key ecological and evolutionary process that can have significant consequences for individual fitness, population dynamics, and gene flow (Ronce 2007, Bonte et al. 2012). Traditionally, two types of dispersal are recognized: natal dispersal, the movement of juveniles from their birth site to the site of first reproduction, and breeding dispersal, the movement of adults between breeding locations (as opposed to remaining site-faithful; Greenwood and Harvey 1982). Breeding dispersal has been far less studied than natal dispersal, partly because it is less

common than natal dispersal but also because of challenges involved with monitoring breeding individuals across space and time (Pärt and Gustafsson 1989, Forero et al. 1999, Robertson et al. 2017).

Previous work on wild animal populations has demonstrated both costs and benefits of breeding dispersal. Dispersal can be costly due to energy used to travel to a new breeding site and find food in unfamiliar surroundings (Stamps et al. 2005, Öst et al. 2011, Mestre and Bonte 2012, Robertson et al. 2017). Suboptimal timing of dispersal can lead to delays in settlement on new territories and thus set back the initiation of

reproduction (Stamps et al. 2005), resulting in a decrease in reproductive output (Robertson et al. 2017, Sutton et al. 2019). For example, Robertson et al. (2017) showed that in a race of snail kites (*Rostrhamus sociabilis plumbeus*), a species dependent on wetland hydrology for reproductive success, individuals that dispersed late in the breeding season settled on territories with lower water depths, which led to increased nest failure. Individuals can also be prone to high rates of mortality when in transience or settlement stages of dispersal (Jack and Fedigan 2004, Stamps et al. 2005, Palestis and Hines 2015). In contrast, breeding dispersal can be beneficial when it leads to the acquisition of a higher-quality territory or mate or improved breeding position; upgrades that can lead to improvements in reproductive performance and probability of survival (Pärt and Gustafsson 1989, Payne and Payne 1993, Forero et al. 1999, Jack and Fedigan 2004, Rosenfield et al. 2016, Weitzman et al. 2017, Williams and Boyle 2019). For example, adult grasshopper sparrows (*Ammodramus savannarum*) that exhibit within-year breeding dispersal have higher nest survival than site-faithful breeders (Williams and Boyle 2019). Additionally, adult male white-faced capuchins (*Cebus capucinus*) that disperse display longer tenure as a dominant breeder and, thus, a greater number of reproductive opportunities compared to site-faithful counterparts (Jack and Fedigan 2004).

Even though the immediate consequences of breeding dispersal can be either positive or negative for individual performance, much less is known about the lifetime consequences of dispersal (Berteaux and Boutin 2000). Part of the reason for this is that most breeding dispersal studies are primarily restricted to cost-benefit analyses over short time frames (Payne and Payne 1993, Pasinelli et al. 2007, Valcu and Kempenaers 2008, Öst et al. 2011, Palestis and Hines 2015, Weitzman et al. 2017, Williams and Boyle 2019). Typically, such studies compare performance the year before and year after dispersal (e.g., Payne and Payne 1993, Pasinelli et al. 2007, Valcu and Kempenaers 2008, Öst et al. 2011) and face challenges with tracking individuals over large spatial scales or throughout an individual's lifetime. Long-term studies, though far and few between, provide the rare opportunity to examine the reproductive consequences of breeding dispersal

immediately after an individual settles on a new territory and over the course of its lifetime. For example, Berteaux and Boutin (2000) used long-term data from a resident population of red squirrels (*Tamiasciurus hudsonicus*) in Kluane, Yukon, Canada to demonstrate that breeding dispersal leads to higher survival and lifetime juvenile recruitment among adult females.

In this study, we used 55 yr of data from a population of individually marked Canada jays (*Perisoreus canadensis*) in Algonquin Provincial Park (APP), Ontario to examine how breeding dispersal influenced reproductive success and recruitment. Canada jays are year-round resident passerines of North American boreal forests. During late-summer and fall in APP, Canada jays scatter-hoard perishable food items such as berries, arthropods, fungi, and vertebrate flesh (Strickland and Ouellet 2020) that they rely on for over-winter survival and late-winter breeding (Waite and Strickland 2006, Sutton et al. 2019, Strickland and Ouellet 2020). Being perishable, food cached by Canada jays is susceptible to degradation over time, especially when exposed to warm temperatures during normally below-freezing periods (Sutton et al. 2019). This degradation of perishable cached food causes Canada jays to experience lower reproductive success when the fall and winter preceding the breeding season has had warmer temperatures and/or more freeze-thaw events than normal (Waite and Strickland 2006, Sutton et al. 2019, 2021a).

Breeding dispersal in the APP Canada jay study population is uncommon, only occurring in 3% of all cases ($n = 2477$; 1964–2019) where territories were monitored in consecutive years (Fuirst et al., *in press*). Of 81 cases of breeding dispersal reported in a previous paper (Fuirst et al., *in press*), 26 (32%) were accounted for by 13 intact pairs that abandoned their “originating territory” (the territory a breeding individual occupied immediately before dispersal) and moved together into a newly vacant “receiving territory” (the territory an individual settles in after dispersing) adjacent to where they dispersed from (i.e., right next to the receiving territory). The other 55 cases involved the dispersals of single birds, 7 (13%) of which resulted from the eviction of the disperser by another bird that claimed the “originating” territory and paired with the disperser's mate. All of the 48 remaining

cases of breeding dispersal of single birds occurred when a breeder lost its mate and a replacement failed to appear. A striking feature of the breeding dispersals observed in the long-term APP study is that, with the exception of the seven cases of eviction, most of them resulted in the originating territory usually remaining vacant for several years, with some never becoming re-occupied. There was also an even distribution of dispersal events between fall/winter ($n = 38$) and summer ($n = 43$; Fuirst et al., *in press*).

Fuirst et al. (*in press*) reported that 70% of breeding dispersals were to adjacent territories (median distance: 1.1 km), a finding attributed to the strong likelihood that overwintering Canada Jays depend on memory to retrieve specific food items that they themselves have cached the previous summer and fall (Bunch and Tomback 1986, Strickland 1991, Waite and Strickland 2006). Because food stored by other individual jays is therefore not reliably discoverable, viable fall or winter options for dispersing jays appear to be largely limited to nearby territories from which the dispersers are able to frequently return to their originating territories to exploit their remembered but otherwise hidden stored food items.

Our goal was to examine several hypotheses to explain the short- and long-term consequences of breeding dispersal in APP Canada jays. Since most dispersing breeders appear to settle on higher quality receiving territories (Fuirst et al., *in press*), we hypothesized that breeding dispersal leads to short- and long-term improvements in reproductive performance after dispersal. Following this hypothesis, we predicted that dispersing adults would have higher rates of nest success, earlier lay dates, and larger brood sizes in the breeding season following dispersal. We also predicted that dispersing adults would have higher juvenile recruitment and offspring production over their lifetimes because, given high levels of site-fidelity due to reliance on cached food, such benefits of acquiring a new territory should persist over the lifetime of many dispersers. An alternative hypothesis is that breeding dispersal leads to short-term declines in reproductive performance because, despite the potential of improving territory quality, dispersing individuals must expend extra energy retrieving cached food on their originating territory or systematically search for food on their new, unfamiliar, territory.

Following this hypothesis, we predicted that dispersing adults would have lower rates of nest success, later lay dates, and smaller brood sizes in the breeding season following dispersal.

Additionally, we hypothesized that breeding dispersal of Canada jays would be costly when individuals disperse in the late fall or winter because settling on a new territory so late in, or after, the summer-fall food-storage season would correspondingly limit or eliminate the opportunity to stock the receiving territory with the caches necessary to support over-winter survival and late-winter reproduction. We, therefore, predicted that, compared to individuals that dispersed in the summer (and that therefore had the opportunity to build up food stores on their receiving territory), individuals dispersing in fall/winter would have lower reproductive success in the succeeding breeding season. We similarly predicted that, compared to individuals dispersing in fall/winter to adjacent territories, individuals dispersing in fall/winter to more distant territories would have lower reproductive success because such longer-distance dispersers would find themselves farther away from the remembered stored food locations on their originating territories. An alternative hypothesis is that breeding dispersal in fall/winter does not carry-over to negatively impact reproductive performance if there is little cost to individuals dispersing to a neighboring territory that is incurred when they access food previously cached on their originating territory. We tested predictions associated with these hypotheses using information on whether individuals dispersed or not, along with their respective dispersal distances, the timing of dispersal, and the change in habitat quality between originating and receiving territories to predict reproductive performance from the 81 breeding dispersal events detected from 1964 to 2019. Using data from 104 breeding adults, we also compared metrics related to lifetime fitness between individuals that did and did not disperse during the study period.

MATERIALS AND METHODS

Study area and focal species

We studied dispersal of Canada jays at the southern edge of their range in Algonquin

Provincial Park, Ontario (APP; 45.590°, -78.517°). In APP, an individually marked population of Canada jays located along the APP's highway 60 corridor has been monitored since

1964 with data on reproductive performance and survival collected annually (Fig. 1; Rutter 1969, Strickland and Waite 2001, Derbyshire et al. 2015, Sutton et al. 2021a). The study area covers

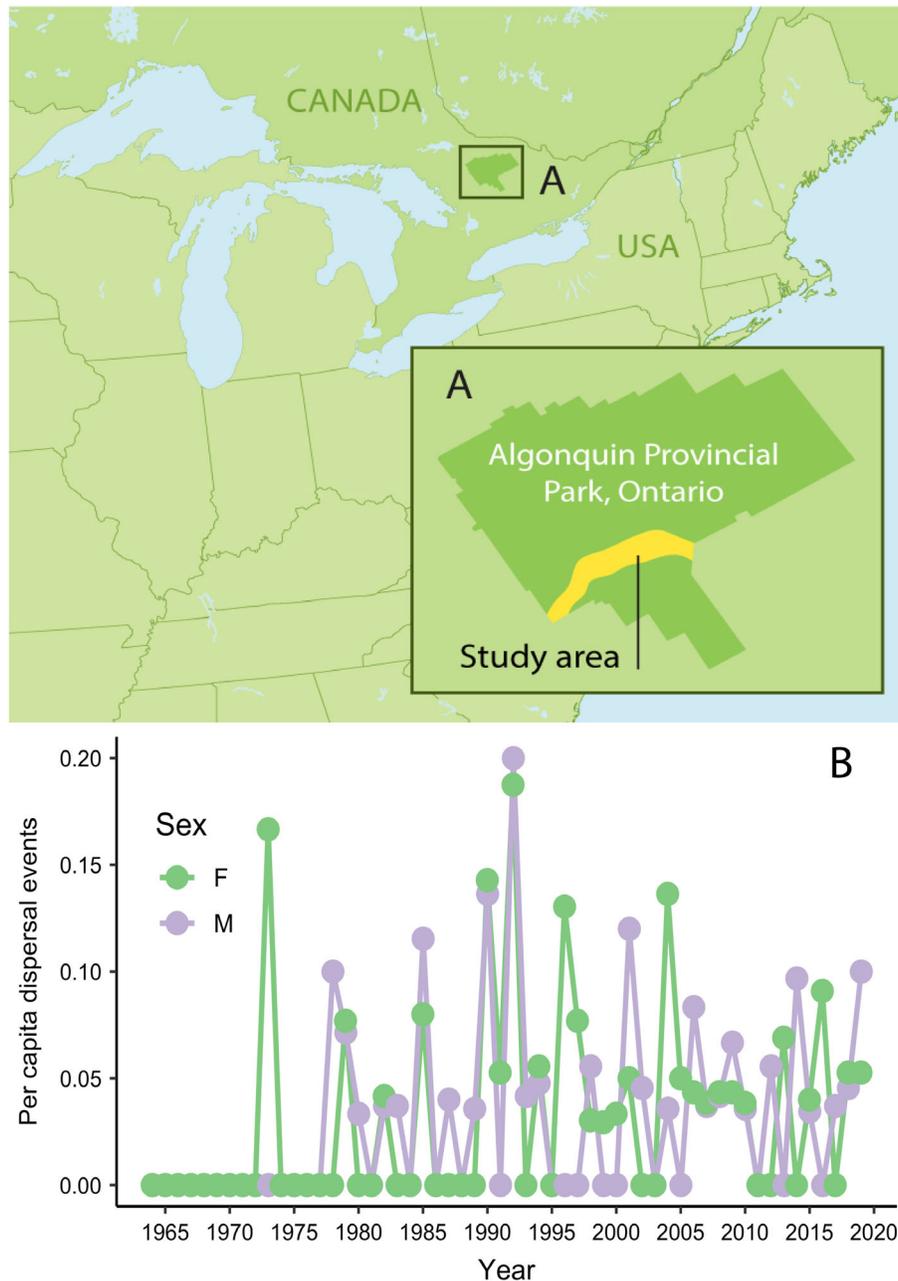


Fig. 1. (A) The location of the Canada jay (*Perisoreus canadensis*) study area, shown as a 1 km buffer on either side of Highway 60 within Algonquin Park in Ontario, Canada. (B) Per capita breeding dispersal events, by sex, each year from 1964 to 2019.

an east–west distance of approximately 55 km and extended a maximum distance of 8 km north or south of the highway 60 corridor. Canada jays occupy year-round territories and can live up to 18 yr (Strickland and Ouellet 2020). Each year ($n = 56$; 1964–2020), an average of 18 occupied territories (range 2–48) were censused twice, once at the beginning of the breeding season in late winter (~ March 1 \pm 1 week, hereafter “March census”) and once during the fall (~ October 15 \pm 1 week, hereafter “October census”). Since Canada jays actively defend their breeding territory in fall and winter and often nest in close proximity to previous years nests, we determined an individual to be an occupant with breeding status if it was seen within a given territory without being chased off by other individuals. During the March census, nests were accessed when nestlings were approximately 11 d old. At this time, we determined brood size, collected morphometric measurements and blood samples, and gave all nestlings a unique combination of a standard Canadian Wildlife Service aluminum band and three colored leg bands. Nest locations were recorded on subsequently geo-referenced high-resolution aerial photographs or using handheld GPS units with 5–10 m error (e.g., Garmin GPS Map 64st; Garmin International, Olathe, Kansas, USA). In June, ca six weeks post-fledging, intense intra-brood dominance struggles result in the retention of a single dominant juvenile on the natal territory and the expulsion of the subordinate siblings (ejectees), some of which succeed, singly, in forming close associations with unrelated breeding pairs elsewhere (Strickland 1991). In the October census, all territories were surveyed to determine which birds remained on each territory, had dispersed within the study area, or had disappeared between the March and October censuses (i.e., during the summer). Any unmarked individuals located during either census were captured using a potter trap and color-banded, provisionally sexed by weight (Strickland 1991), and aged based on rectrix shape (Strickland and Ouellet 2020).

Dispersal measurements

Breeding dispersal was defined as any case where an adult attempted to breed (i.e., at least built a nest with an opposite-sex individual

sharing the same territory) on an “originating territory” and then did so on another “receiving territory” within the study area in the following year. Our two annual censuses (March 1 and October 15) and observations of breeding each year also allowed us to identify two categories of dispersal events: “summer” dispersals (those occurring between the end of the breeding season (ca May 1) and before October 15) or “fall/winter” dispersals (those occurring between October 15 and March 1). In addition, we measured breeding dispersal distance by calculating the Euclidean distance (km) between the nests on the originating and receiving territories. We analyzed data only from breeders that were present in the study area in two consecutive breeding seasons. Thus, any instances where individuals were observed breeding in one year and then went undetected for two or more censuses before being observed breeding again on a different territory within the study area were excluded from all analyses. These data were excluded because we were unable to determine the reproductive performance or breeding status of such individuals while they were out of the study area. We recognize that not detecting dispersal movements from originating territories in the study area to receiving territories outside the study area leads to an underestimate of dispersal events involving study area territories, but we see no a priori reason why this would lead to biased estimates when comparing reproductive performance before and after dispersal or comparisons between individuals that dispersed vs. those that remained site-faithful. If any individuals dispersed more than once in their lifetime, all cases of dispersal for that individual were included in the analysis (with the random effect of individual ID accounting for multiple dispersal events within an individual’s lifetime). Additionally, since there were no differences in breeding dispersal frequency between sexes (Fuirst et al., *in press*), we counted paired dispersal events as one data point to avoid double counting spatially autocorrelated movements in relevant statistical models.

Reproductive performance and territory quality

To examine the consequences of breeding dispersal occurring, as well as the timing and distance of dispersal, we considered three different

metrics of reproductive performance: (1) *lay date*, which was the Julian date of the first egg laid (Whelan et al. 2017), (2) *brood size*, which was the total number of nestlings in the nest at the time nests were accessed (Sutton et al. 2019), (3) *nest success*, which was, whether or not the nest had nestlings alive during the time nestlings were banded (Sutton et al. 2019), and (4) *juvenile recruitment*, which was the number of offspring that remained in the study area over an individual's lifetime.

For each dispersal event, we also determined the change in territory quality by calculating the difference in proportion of conifers between the receiving and originating territories. Following Strickland et al. (2011), territory quality was estimated as the proportion of land covered by conifers within each territory. A prior experiment using artificial storage chambers containing mealworms and raisins designed to simulate food cached by Canada jays on trees provided evidence that conifers, particularly black spruce (*Picea mariana*), performed best at preserving food over 4–5 months compared to deciduous trees (Strickland et al. 2011) and analyses of Canada jays in Algonquin Park showed that nest success was positively related to the proportion of conifers on territories (Strickland et al. 2011, Whelan et al. 2017).

Statistical analysis

To investigate whether breeding dispersal in Canada jays led to immediate improvements or reductions in reproductive performance, we constructed linear mixed effect models (LMEs; Bates et al. 2015) for lay date (Gaussian) and generalized linear mixed effect models (GLMMs; Bates et al. 2015) for brood size (Poisson) and nest success (binomial) and used a likelihood ratio to compare a model with a binomial fixed effect “before or after dispersal” (0 = before vs. 1 = after dispersal. $n = 68$ paired cases) to an intercept-only model (Vuong 1989). Both models included individual ID as a random effect since some individuals dispersed multiple times throughout their lifetime. Support for the “before-and-after dispersal” model would suggest that reproductive performance improved after breeding dispersal.

One possibility with the above modeling approach is that improvement of reproductive

measures might be due to age-related experience (i.e., the year after dispersal, by definition, is always later in life than the year before). To address this, we constructed similar mixed effect models and used likelihood ratio tests to compare a model with the binomial fixed effect “time after dispersal” (0 = first year after dispersal vs. 1 = second year after dispersal; $n = 68$ paired events) to an intercept-only model. Both models included individual ID as a random effect. Lack of support for the “time after dispersal” variable would suggest that, if there was support for improvement of reproductive performance related to dispersal in the previous model, it was likely not due to age-related experience. To test whether birds preferentially dispersed to higher-quality territories, we also used binomial tests to compare the percentage of paired and single dispersers that moved to a receiving territory that was of higher quality than the originating territory against a null 50:50 ratio.

We then examined how changes in territory quality, dispersal distance, and the time of year that individuals disperse influenced reproductive performance after breeding dispersal ($n = 68$) using a series of GLMMs with brood size (Poisson distribution with identity link function), nest success (binomial distribution with logit link function), and lay date (Gaussian distribution with identity link function) as response variables. The predictor variables included in each set of models were dispersal distance (km), individual age (quadratic), change in territory quality (i.e., the difference in percent spruce between the originating and receiving territory), and timing of dispersal (i.e., summer or fall/winter). Age was included as a quadratic variable because breeding performance of Canada jays in APP peaks at 8 yr and then declines as birds senesce (M. Sorensen, *unpublished manuscript*). We also included individual identity as a random effect because some individuals in the dataset dispersed multiple times.

We further examined whether breeding dispersal influenced lifetime reproductive success using a series of GLMMs. For this set of models, we compared lifetime reproductive success of individuals that dispersed at least once during their lifetime to those that remained site-faithful throughout the rest of their lives ($n = 104$; 37 dispersers and 67 site-faithful). We analyzed only

individuals that were 8 or more years old to ensure that we did not include young individuals, some of whom may have disappeared because they dispersed outside of the study area (and, thus, would have otherwise been considered site-faithful in the dataset). We used eight years as a cutoff since that age has been shown to be around when peak reproductive performance occurs in this Canada Jay population (M. Sorensen, *unpublished manuscript*). We examined two response variables: the number of locally produced offspring recruited into the study population (Poisson distribution) and the total brood size over an individual's lifetime (Poisson distribution). Offspring recruited into the population were any banded juveniles detected within the study area during the fall of their first year and did not include juveniles that dispersed out of the study area their first year and were never detected again. For each series of models, the explanatory variables were the binary variable of whether or not that individual dispersed once during its lifetime (1 = dispersed, 0 = site-faithful), sex, and lifespan (i.e., maximum age of the focal individual). We also included territory ID as a random effect since multiple individuals bred on the same territory during their lifetime and territory boundaries in this population are relatively stable over time, irrespective of the composition of occupants (Strickland and Ouellet 2020, Sutton et al. 2021b).

For the analyses that addressed how changes in territory quality, dispersal distance, and the season of dispersal influence reproductive performance on the receiving territory, and for analyses addressing whether breeding dispersal influenced lifetime reproductive success, we used an informatic-theoretic approach (Burnham and Anderson 2002) to evaluate each set of models. We used the second-order Akaike information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) to rank competing models and considered any model with $\Delta\text{AICc} < 2$ to be a candidate model (Burnham and Anderson 2002). In addition, Akaike weights (w_i) gave cumulative support for each model when accounting for all competing models. We used the Shapiro-Wilk normality test to determine whether response variables fit a normal distribution and Levene's test to determine homogeneity of variances. All GLMMs and

LMEs were constructed using the *lme4* (Bates et al. 2015) package. When there was no clear top model, we performed model averaging over the candidate set of models using the *MuMIn* (Bartón 2020) and the *AICcmodavg* (Mazorelle 2020) package to determine the direction and magnitude of the effect of each explanatory variable using relative variable importance from the summed model weights (Burnham and Anderson 2002). We made model inferences using 85% confidence intervals (Arnold 2010). All likelihood ratio tests were run using the *lmtest* package (Zeileis and Hothorn 2002). Statistical analyses were run in R v. 3.3.2 (R Core Team 2017), and all statistical tests were deemed significant at $P < 0.05$. Predictors in each model were not highly correlated (all $r < 0.3$; Dingemanse and Dochtermann 2013).

RESULTS

Summary of breeding dispersal and reproductive metrics

From 1964 to 2019 inclusive, we recorded 81 individual breeding dispersals associated with 68 different individuals across 39 different originating territories. Of the 68 dispersing individuals, 56 dispersed once in their lifetime, 11 dispersed twice, and one dispersed three times. Of the 11 birds that dispersed twice, at least one of their movements were motivated by mate loss, while the other dispersal of that individual was either via paired dispersal, eviction, or divorce. For the individual that dispersed three times, the first two cases occurred with its mate and the third occurred after its partner disappeared.

Among all breeding dispersal events, 68% (55/81) of cases involved an individual that dispersed alone while 32% (26/81) involved 13 breeding pairs that dispersed together into a recently vacated receiving territory, all but one of which was adjacent to the dispersing pair's originating territory. Concerning single-bird dispersal events, 87% (48/55) occurred when a mate had previously been lost and 12% (7/55) involved the disperser's mate being left on the originating territory (i.e., divorce by (2/7, or eviction of (5/7), the disperser). The frequency of single-bird breeding dispersals was relatively similar for males ($n = 31$) and females ($n = 24$) and the age

of dispersers ranged from 1 to 13 yrs (mean 4.8 ± 2.9).

The number of dispersal events that occurred in the summer (i.e., between the breeding season of year t and the fall of the same year, $n = 43$) vs. the fall/winter (i.e., between the fall of year t and the breeding season of year $t + 1$; $n = 38$) was similar. Among all dispersal events ($n = 81$), distances ranged from 0.5 to 7.0 km (median = 1.1 km) and, in 70% ($n = 57$) of cases, individuals dispersed to adjacent territories (mean territory size ~ 130 ha; Strickland et al. 2011). Both paired (62%, 8/13) and single (70%, 39/55) dispersers settled on receiving territories that were of higher quality than the originating territories more often than expected (i.e., when compared to the expected higher/lower of 50:50 ratio (Binomial test; pairs: $P = 0.02$, single: $P < 0.007$). Receiving territories had, on average, 7% (SE = $\pm 17\%$) greater percent conifer coverage (estimate of territory quality) compared to originating territories.

Short-term consequences of dispersal

The inclusion of the binary variable for breeding dispersal (0 = before dispersal, 1 = after dispersal) improved model fit for brood size ($X^2 = 3.8$, $df = 1$, $P = 0.04$; Appendix S1: Table S1) and nest success ($X^2 = 3.9$, $df = 1$, $P = 0.04$; Fig. 2; Appendix S1: Table S1) for dispersing adults ($n = 68$). Parameter estimates in both models were positive, suggesting that nest success and brood size were, on average, higher during the breeding season after dispersal. However, breeding dispersal did not significantly improve model fit for lay date.

The variable representing the first vs. second year after dispersal (0 = first year after dispersal vs. 1 = second year after dispersal) did not significantly improve model fit for any of the models predicting lay date, brood size, and nest success, suggesting that individuals did not have higher reproductive performance in the second year after dispersal compared to the first year after dispersal ($n = 68$; Appendix S1: Table S2).

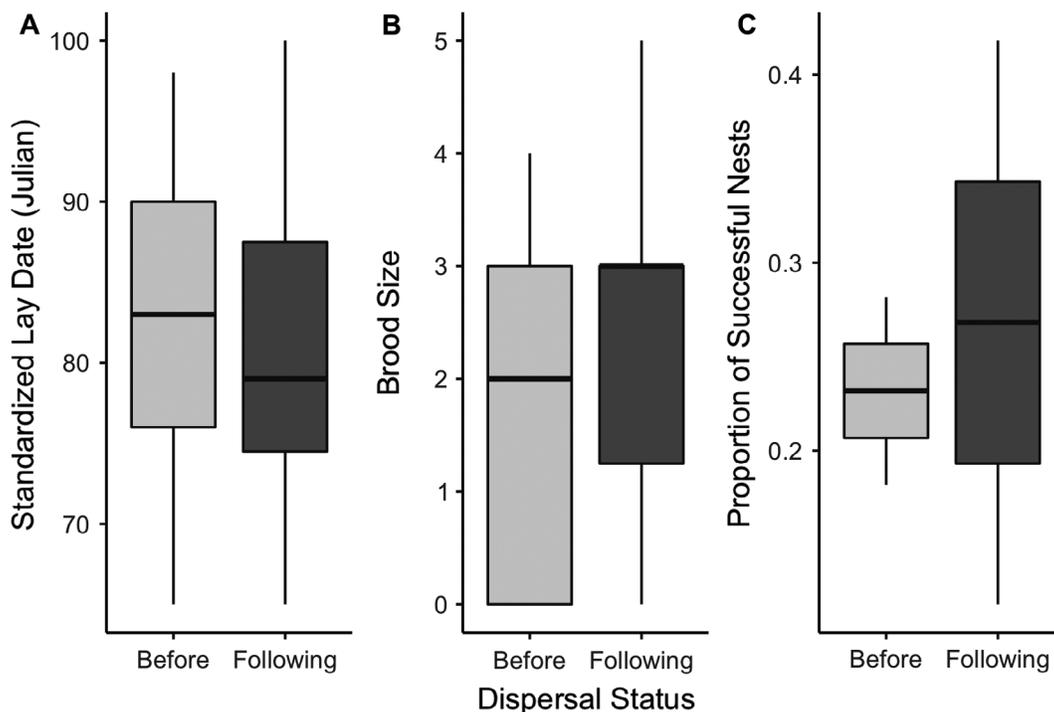


Fig. 2. From 1964 to 2019 adult Canada jays (*Perisoreus canadensis*; $n = 68$) did not improve (A) lay date after dispersal, but showed significant improvements in (B) brood size and (C) nest success after dispersal compared to the year prior. Thick lines in boxes represents the median, upper and lower limits represent the standard error, and vertical lines are the standard deviation.

This supported the notion that dispersal to a new territory itself (not greater age and, therefore, experience) was what improved reproductive performance.

Effects of dispersal timing, dispersal distance, and territory quality on reproductive success

There was one top model ($<2 \Delta\text{AICc}$) to explain variation in lay date, and it included only the binary dispersal timing variable (Appendix S1: Tables S3, S4). Canada jays that dispersed during the fall/winter tended to initiate clutches later than those that had dispersed in the previous summer ($n = 68$, $\beta = 0.40$, 85% CI = 0.08, 0.72; Fig. 2; Appendix S1: Tables S3, S4). On average, individuals that had dispersed during the previous summer began laying eggs 4 d earlier (March 20 ± 7 d) than individuals that dispersed in the fall/winter (March 24 ± 9 d).

We also examined factors that could influence variation in brood size after breeding dispersal ($n = 68$). There were nine models within $2 \Delta\text{AICc}$ of the top model (Appendix S1: Table S5). These models included change in territory quality, dispersal timing, dispersal distance, and age (quadratic) as predictors. Based on model-averaging, the mean relative variable importance (RVI) of dispersal timing, dispersal distance, change in territory quality, and age (quadratic) were 0.37, 0.37, 0.28, and 0.28, respectively. However, this support was weak because all model-averaged estimates overlapped with zero.

To explain the probability of nest success after breeding dispersal, there were five models within $2 \Delta\text{AICc}$ of the top model ($n = 68$; Appendix S1: Table S6). These models included fixed effects such as change in territory quality, dispersal timing, dispersal distance, and age (quadratic). Based on model-averaging, the mean relative variable importance (RVI) of change in territory quality, dispersal timing, dispersal distance, and age (quadratic) were 0.77, 0.72, 0.10, and 0.09, respectively. The model-averaged coefficients suggested the probability of nest success after breeding dispersal within the study area was negatively related to the change in territory quality ($\beta = -0.03$, 85% CI = -0.06 , -0.0005 ; Appendix S1: Table S6), suggesting that individuals that dispersed to a receiving territory of lower quality (compared to their originating

territory) were more likely to have unsuccessful nests. Additionally, the model-averaged coefficients suggested the probability of nest success after breeding dispersal within the study area was negatively correlated with dispersal timing ($\beta = -1.14$, 85% CI = -2.18 , -0.10 ; Fig. 3; Appendix S1: Table S6), indicating that individuals that dispersed in fall/winter were more likely to have unsuccessful nests compared to individuals that dispersed in the summer.

Long-term consequences of dispersal

We then examined whether breeding dispersal influenced lifetime reproductive success of adult jays ($n = 104$; 37 dispersers and 67 site-faithful). There was one top model ($<2 \Delta\text{AICc}$) to explain variation in the number of offspring that were recruited into the population and this model included both the variable indicating whether or not individuals dispersed at least once during their lifetime ($\beta = 0.55$, 85% CI = 0.28, 0.83; Appendix S1: Tables S7, S8) and lifespan ($\beta = 0.08$, 85% CI = 0.02, 0.13; Fig. 4; Appendix S1: Tables S7, S8), suggesting that individuals that dispersed and lived longer had higher rates of juvenile recruitment. Dispersing adults recruited an average of 0.92 more offspring throughout their lifetime than site-faithful adults. Similarly, there was one top model explaining variation in total number of nestlings produced by breeders over their lifetime and, similar to the recruitment model, it included the positive effect of the breeding dispersal variable ($\beta = 0.18$, 85% CI = 0.07, 0.29; Appendix S1: Tables S9, S10) and lifespan ($\beta = 0.06$, 85% CI = 0.04, 0.08; Appendix S1: Tables S9, S10), suggesting that both were positively related to offspring production. Dispersing adults produced an average of 2.71 more offspring during their lifetime compared to site-faithful adults.

DISCUSSION

Our study provides rare evidence that changes in breeding conditions due to dispersal carry over to improve reproductive performance immediately after dispersing and that dispersal can enhance fitness over an individual's lifetime. We propose that the reason Canada jays experienced both short- and long-term benefits from dispersing is because they are highly selective of

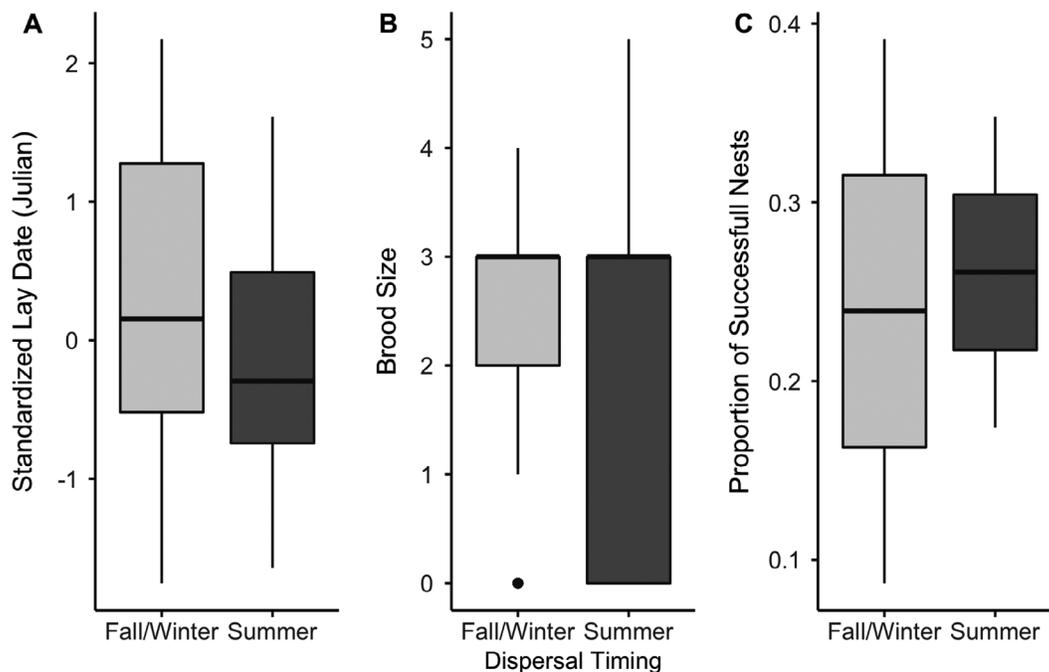


Fig. 3. From 1964 to 2019 adult Canada jays (*Perisoreus canadensis*) that dispersed in fall/winter had significantly (A) later lay dates compared to those that dispersed in summer but the timing of dispersal did not influence (B) brood size in the breeding season immediately after dispersal. (C) Individuals that dispersed in summer had higher rates of nest success. Thick lines in each box represent the median, upper and lower limits represent the standard error, vertical lines are the standard deviation, and the black dot is an outlier.

when they do disperse and that this selectivity is related to their unique reliance on food-storage. Since Canada jays are long-lived and do not often disperse, short-term benefits from breeding dispersal likely lead to lifetime improvements in reproductive performance because they are most often permanent changes in breeding conditions. In a recent companion paper (Fuirst et al., *in press*), we suggested that individuals are constrained in their dispersal options by the need to remain on or near the territory where, during summer and fall, they have cached the food they will later recover (through memory of specific cache locations) and use to survive the winter months. Dispersing long distances, therefore, could preclude access to caches on their originating territories and, depending on when dispersal occurred, make it difficult or impossible to accumulate food stores sufficient to ensure winter survival or successful reproduction on their receiving territories. For example, our results demonstrated that when breeders dispersed in

fall/winter, they had lower rates of nest success and later lay dates, likely due to increased energy expended to retrieve cached food. Despite these constraints in dispersal options and potential short-term effects, when breeders did disperse, a positive change in the proportion of conifers on the receiving territory (i.e., territory quality) usually led to improved reproductive performance.

Within these constraints, our results suggest that, depending on their circumstances, Canada jay breeders have wide latitude in their ability to choose whether to disperse and where to settle when they do disperse. Of the 81 dispersing breeders recorded in our study, 32% (13 intact pairs) moved into adjacent newly vacant territories and, since they were clearly not compelled to do so, it is reasonable to infer they were “voluntarily” choosing to occupy what they perceived as higher-quality habitat. In contrast, of the 55 single-bird dispersers, 7 (13%) were forced to leave by another breeder (Fuirst et al., *in press*). For the remaining 48 single-bird dispersers, it

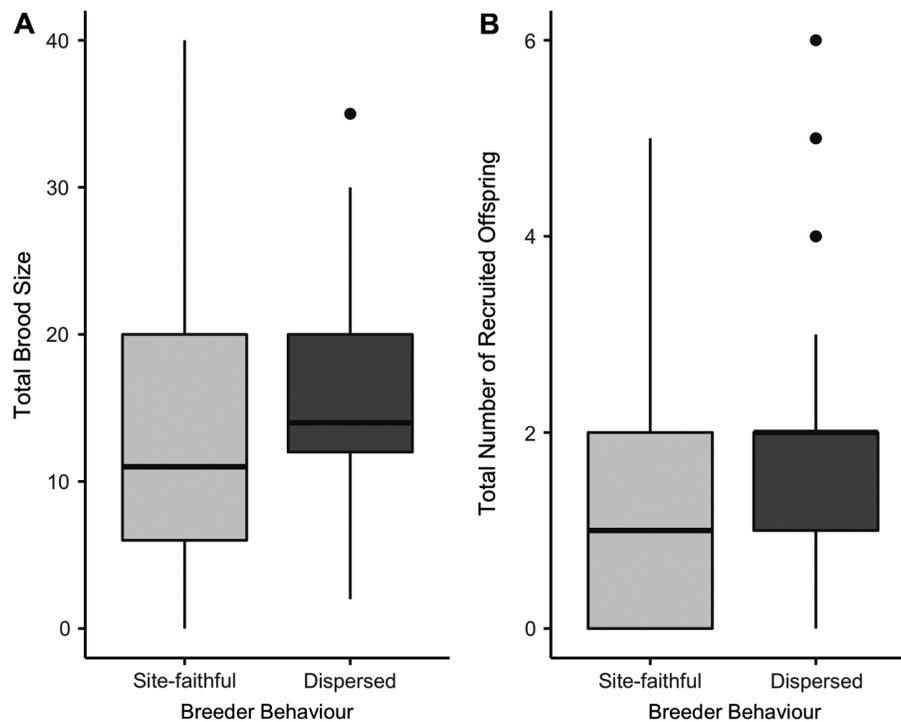


Fig. 4. Breeding Canada jays (*Perisoreus canadensis*; $n = 104$) that dispersed at least once in their lifetime showed higher (A) total brood size and (B) total number of offspring recruited into the population compared to site-faithful breeders (did not disperse as adults during their lifetime). The thick line in each box represents the median, the upper and lower limits represent the standard error, vertical lines are the standard deviation, and black dots are outliers.

was not always clear to what extent their departures could be called “voluntary.” There were five dispersals (10%, $n = 48$) associated with “divorce” (i.e., the “divorcee’s” former mate was still alive and occupying the originating territory alone after the focal individual had dispersed) but the remaining 43 birds (90%) dispersed to a new territory only after losing their mate and failing to attract a replacement. Strictly speaking, these dispersers were not compelled to leave their originating territories but, given the apparently overwhelming importance of not missing a breeding season, it is questionable whether the dispersals of such widowed individuals may be termed “voluntary.” Over the 55 yr of data from APP, 88% of individuals that lost a mate remained on the same territory the following breeding season. The only individual breeders that dispersed were birds that, having lost their former mate, waited unsuccessfully, sometimes for many months and even missing a breeding

season, before finally dispersing to a new breeding position elsewhere (Fuirst et al., *in press*). This result reinforces the notion that the benefits of territory familiarity often outweigh the costs of dispersing to a new area (Stamps et al. 2005, Öst et al. 2011, Robertson et al. 2017).

While our measures of breeding dispersal are informative, we do recognize that aspects of our study design might have biased dispersal estimates. First and foremost, we only recorded dispersal events within the study area, limiting the chance of detecting longer-distance events. The linear shape of the study site likely also contributed to our inability to detect such dispersal events and determine their reproductive consequences. However, we suggest that the short-distance breeding dispersal events recorded here (median breeding dispersal distance of 1.1 km, with only 11% of breeding dispersal events >3 km; Fuirst et al., *in press*) are still fairly representative of the breeding dispersal patterns in

this population. We suspect that breeding dispersal in Canada jays, particularly when it occurs in the fall, is constrained by the need to retrieve cached food from originating territories, thereby preventing most individuals from moving too far from originating territories that they may need to access during winter months.

Importantly, with the exception of the 7 dispersals by evicted breeders, all other “voluntary” breeding dispersals recorded in our study population resulted in the originating territory being left temporarily, and often “permanently,” vacant in subsequent, post-dispersal breeding seasons. Given that breeding dispersals and the associated losses of occupied territories are triggered by the failure of nonbreeders to promptly fill territorial or single-bird breeding vacancies, we may question whether breeding dispersals would occur at all, or at least as much as they do, in a stable (non-declining) population in which vacancies are quickly filled from nonbreeder ranks. We correspondingly suggest that breeding dispersal may be viewed as a demographic signature of the decades-long, slow decline in the number of occupied Canada jay territories in APP (Waite and Strickland 2006, Sutton et al. 2019).

While high rates of breeding dispersal at low densities may be a signature of decline, it could positively affect population growth rates given that, on average, individuals improve reproductive performance immediately after switching territories. In other words, dispersal could act as a negative density-dependent mechanism preventing or slowing down the population from further decline. Of course, for breeding dispersal to be a factor at the population level, the improvement in individual reproductive success would have to be strong enough to affect population growth rates. This could be the case in some declining populations of other species where breeding dispersal has been shown to be beneficial at the individual level (Palestis and Hines 2015, Williams and Boyle 2019), but it is probably unlikely in Canada jays given their relatively low annual reproductive output (Sutton et al. 2021b). Breeding dispersal acting as a mechanism for negative density-dependence would also rest on the assumption that most dispersal at low densities would occur within the population (i.e., short distances). While this could be possible given the

high proportion of vacancies, other studies have noted the opposite pattern: an increase in emigration rates with declining population abundance (Matthysen 2005, Meester and Bonte 2010). Modeling the population consequences of adaptive dispersal strategies under different life histories would be a useful exercise for understanding how and when this behavior scales up to influence demography.

Among vertebrates, improvements in reproductive performance during the breeding season after dispersal can come about through various mechanisms including improvements in mate or territory quality (Payne and Payne 1993, Forero et al. 1999, Berteaux and Boutin 2000, Valcu and Kempenaers 2008). In Canada jays, both territory quality and age of the breeding partner could play a role in an increase in short- and long-term reproductive performance after dispersal. From our analysis, many dispersing Canada jays settled on a territory with a higher proportion of conifers than their originating territory, which has been previously shown to correlate with higher nest success (Strickland et al. 2011, Whelan et al. 2017). Nest success is likely influenced by the proportion of conifers on territories because conifers outperform deciduous trees at preserving cached food (Strickland et al. 2011) and prior experiments have shown that reproductive performance of Canada jays in APP is limited by the quantity and/or quality of food available during the late-winter breeding period (Derbyshire et al. 2015, Freeman et al. 2021). Alternatively, individuals may improve reproductive performance after moving to a territory with more conifers if higher densities of conifers are correlated with the quality or abundance of fresh food items. A second reason reproductive success could have improved after dispersal is that dispersers may have settled with an older, more experienced partner on the receiving territory compared to their originating territory. In Canada jays, reproductive success is correlated with age of both males and females (Whelan et al. 2017) and, in an analysis of male senescence, reproductive performance was found to continue at high levels until ages 10–12 yr for dominant juveniles and 6 yr for ejectives (M. Sorensen, *unpublished manuscript*). In our analysis, of the individuals that dispersed alone, 65% (36/55) joined a new breeder that was older than their

previous mate by an average of 3 yrs (Fuirst et al., *in press*). Due to the strong territorial fidelity of Canada jays, these improvements in habitat and mate quality probably carry through an individual's lifetime, thus contributing to increase long-term reproductive performance of dispersers.

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DATA AVAILABILITY

Data and analytical code are available from FigShare: <https://doi.org/10.6084/m9.figshare.15113325> and <https://doi.org/10.6084/m9.figshare.15115203.v1>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3747/full>