

Patterns and causes of breeding dispersal in a declining population of Canada jays, *Perisoreus canadensis*, over 55 years



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Breeding dispersal can influence fitness as well as the dynamics and genetic architecture of populations, but the patterns and causes of dispersal in most species are still poorly understood. Here, we used 55 years of re-sighting and breeding data from 530 individually marked adult Canada jays at the southern edge of their range in Algonquin Provincial Park, Ontario, Canada to evaluate factors that influence the probability of breeding dispersal occurrences and distances. Breeding dispersal within the study area was rare, occurring in 3% ($N = 81$) of the 2477 cases in which individuals were observed defending a territory in consecutive years, and only 13% ($N = 68$) of individuals dispersed at least once in their lifetime (mean age of dispersers = 4.75 ± 2.8). Of the 81 breeding dispersal cases, 68% ($N = 55$) involved a single bird, while the remaining 32% ($N = 26$) involved 13 cases of a mated pair dispersing together. The probability of breeding dispersal was similar between sexes, but females tended to disperse farther. Surprisingly, almost half of breeding dispersal events occurred during the autumn and winter when all or most food had already been cached. However, 70% ($N = 57$) of breeding dispersal events involved settlement on a neighbouring territory, which may have allowed adults to retrieve previously cached food on their original territory. Overall, adults were most likely to disperse locally when they lost a mate, had originally occupied a lower-quality territory, and a vacant position was available nearby. While the distance and rates of breeding dispersal did not change over time ($N = 55$), breeding dispersal events caused by mate loss, were highest in years with the steepest population decline, suggesting that a diminishing pool of mate replacements influenced breeding dispersal decisions.

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Breeding dispersal, defined as the movement of adults between successive breeding locations (Clobert et al., 2001; Greenwood, 1980), is considered an important behaviour because it can influence individual fitness (Pärt & Gustafsson, 1989; Payne & Payne, 1993), population dynamics (Dieckmann et al., 1999; Johnson & Gaines, 1990) and genetic structure (Waser & Elliot, 1991). While breeding dispersal has received more attention in recent decades (Berteaux & Boutin, 2000; Forero et al., 1999; Naves et al., 2006; Valcu & Kempnaers, 2008; Weitzman et al., 2017), it still remains one of the least understood life history phases. This is because individuals can be difficult to track over successive breeding periods and, in some species, breeding dispersal happens infrequently (Bowler & Benton, 2005). Thus, our most comprehensive understanding of the drivers of breeding dispersal typically comes from long-term studies that involve tracking movements and monitoring

the success of individually marked animals (Berteaux & Boutin, 2000; Forero et al., 1999; Pärt & Gustafsson, 1989; Weitzman et al., 2017).

Several demography-based hypotheses have been proposed to explain the probability of breeding dispersal and variation in dispersal distances (Table 1). For example, the probability of local breeding dispersal can be positively influenced by local density because higher densities lead to elevated intraspecific competition (Mattisson et al., 2013; Öst et al., 2011; Pasinelli et al., 2007). In contrast, the frequency of local breeding dispersal might be higher at lower densities if there are few replacement mates in the population, forcing individuals to leave their local areas to find future breeding opportunities. Breeding dispersal can occur when an individual is evicted or displaced by a more dominant breeder (Mattisson et al., 2013), or if individuals decide to move in response to nest failure or in order to acquire a different partner (Forero et al., 1999; Naves et al., 2006; Payne & Payne, 1993). There is also evidence that loss of a breeding partner can induce breeding dispersal (Paris et al., 2016; Wiklund, 1996), which is presumably beneficial

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Table 1
Summary of hypotheses and predictions examined to determine causes of breeding dispersal and variation in dispersal distances

Hypothesis	Hypothesized mechanism	Predictions	Source
Probability of breeding dispersal			
Site choice	Individuals disperse from a lower-quality territory	Dispersal is negatively correlated with territory quality on the originating territory	Montalvo & Potti (1992); Stanback & Rockwell (2003)
Mate loss	Individuals disperse to seek a new mate after loss of previous mate	Dispersal is positively correlated with mate loss	Forero et al. (1999); Paris et al. (2016); Wiklund (1996)
Age	Individuals disperse more when they are young because they are more easily evicted	Dispersal is negatively correlated with age	Greenwood & Harvey (1982); Naves et al. (2006)
Territory availability	Individuals have a higher probability of dispersal if breeding vacancies are close by because of the ability to access caches on originating territories	Dispersal is positively correlated with distance to nearest territory	Serrano et al. (2001); Spindelov et al. (1995)
Intraspecific competition	Individuals disperse to escape high levels of intraspecific competition	Dispersal is positively related to population density	Mattisson et al. (2013); Payne & Payne (1993)
Sex bias	Females show higher rates of dispersal because males invest more in resource defence	Dispersal is more frequent among females	Greenwood (1980); Greenwood & Harvey (1982)
Dispersal distance			
Site choice	Individuals disperse farther to access higher-quality territories	Dispersal distance is positively correlated with territory quality	Forero et al. (1999); Pasinelli et al. (2007)
Age	Individuals that are older disperse shorter distances because they gain dominance with age and can more easily acquire a territory	Dispersal distance is negatively correlated with the age of individuals	Forero et al. (1999); Greenwood & Harvey (1982)
Territory availability	Individuals disperse shorter distances to more readily access caches on the originating territory	Dispersal distance is positively related to distance to available territories	Serrano et al. (2001)
Intraspecific competition	Individuals disperse further to escape high levels of intraspecific competition	Dispersal distance is positively correlated with population density	Mattisson et al. (2013); Öst et al. (2011); Serrano et al. (2001)
Sex bias	Females disperse farther than males because they are smaller and traveling is less energy consuming than males	Dispersal distances are positively associated with females	Greenwood (1980); Greenwood & Harvey (1982)
Year	Dispersal distances decline over time because of the population has declined, leaving a larger proportion of territories vacant	Dispersal distance is positively associated with year	Waite & Strickland (2006)

when the probability of finding a new mate via actively searching for a partner is higher than waiting for one to arrive. Lastly, the causes of breeding dispersal can be a function of age (Andreu & Barba, 2006; Bried & Jouventin, 1998; Serrano et al., 2001), personality (Cote et al., 2010) and sex (Greenwood, 1980; Öst et al., 2011), with breeding dispersal often being female-biased in birds and occurring more often in younger individuals either because they are often evicted by dominant breeders or because they are paired with low-quality mates and, thus, are more likely to upgrade their situation when the opportunity arises.

Habitat quality may also influence the probability of breeding dispersal and local dispersal distance. Breeding dispersal allows individuals to upgrade to better-quality breeding sites, which can improve future breeding performance (Mestre & Bonte, 2012; Montalvo & Potti, 1992; Spindelov et al., 1995). Whether or not to upgrade to better-quality breeding sites can depend partly on how risky it is to disperse locally. Even though breeding dispersal can provide the opportunity to upgrade to higher-quality sites, such upgrades are not guaranteed and individuals may be at risk of mortality during transience (Jack & Fedigan, 2004; Palestis & Hines, 2015). Additionally, the decision to attempt a territory upgrade can depend, in part, on how much investment has been made on the original territory. Such investments could include food storage (Sutton et al., 2019), creating safe locations to raise young (Doucet et al., 1994) and building structures for courtship (Jones, 1988). Among species that make a substantial investment in their territories, individuals may not be able to afford to abandon a breeding site unless breeding dispersal results in a

significant upgrade of individual fitness. For example, acorn woodpeckers, *Melanerpes formicivorus*, collect acorns and chisel out granaries, which makes switching territories energetically costly unless there is potential for improving a breeding position (MacRoberts, 1970). Additionally, North American red squirrels, *Tamiasciurus hudsonicus*, exhibit high frequencies of breeding dispersal, particularly when food availability is high (Berteaux & Boutin, 2000). However, little is known about the causes of breeding dispersal in resident species that rely on large quantities of cached food on their territories.

In this study, we used data from individually marked Canada jays censused twice annually (mid-October and early March) over a period of 55 years in Algonquin Provincial Park (APP), Ontario, Canada, to document the patterns and understand the causes of breeding dispersal. Canada jays occupy permanent territories in North America's boreal and subalpine forests (Strickland & Ouellet, 2020). In APP, they begin caching food as early as late summer and rely on this food for overwinter survival and, at least in part, for reproduction that takes place under still wintry conditions from February through late April (Sutton et al., 2019; Whelan et al., 2017). In addition to reporting patterns of breeding dispersal and breeding dispersal distances over time, we also examined the factors that influenced (1) the probability of breeding dispersal occurring locally, (2) the timing of local breeding dispersal, and (3) variation in local dispersal distances. Using data from 530 breeding adults between 1964 and 2019, we tested predictions from four hypotheses previously used to explain the probability of breeding dispersal and variation in breeding dispersal distances (Table 1).

METHODS

Study Area and Population

Breeding dispersal data on Canada jays were collected in Algonquin Provincial Park (APP), Ontario, Canada (45°N , 78°W ; 7.6×10^5 ha; Fig. 1), where a population has been monitored since 1964 (Sutton et al., 2019; Waite & Strickland, 2006; Whelan et al., 2017). Canada jay territories are occupied year-round and, in APP, have a mean area of ca. 146 ha (Strickland & Ouellet, 2020). The study site runs along the Highway 60 corridor in APP. From 1964 to 2019, an average of 18 occupied territories (range 1–48) were monitored in a given year. This study area has an east–west linear

shape, meaning that our results are limited to detecting local dispersal events north and south of the study area. All territories were censused twice each year, once at the commencement of the breeding season in late winter (~ 1 March ± 1 week) and once during the autumn (~ 15 October ± 1 week). During the late winter census, we monitored all breeding pairs throughout the entire duration of the breeding season (February–April) starting from nest building to fledging of young. During this census, we visited each occupied territory once every 2–3 days. This census provided information on which pairs attempted and/or successfully bred and which remained together. For the autumn census (~ 2 weeks long), we visited every historically occupied territory in the study area to determine which adults remained on each territory, dispersed

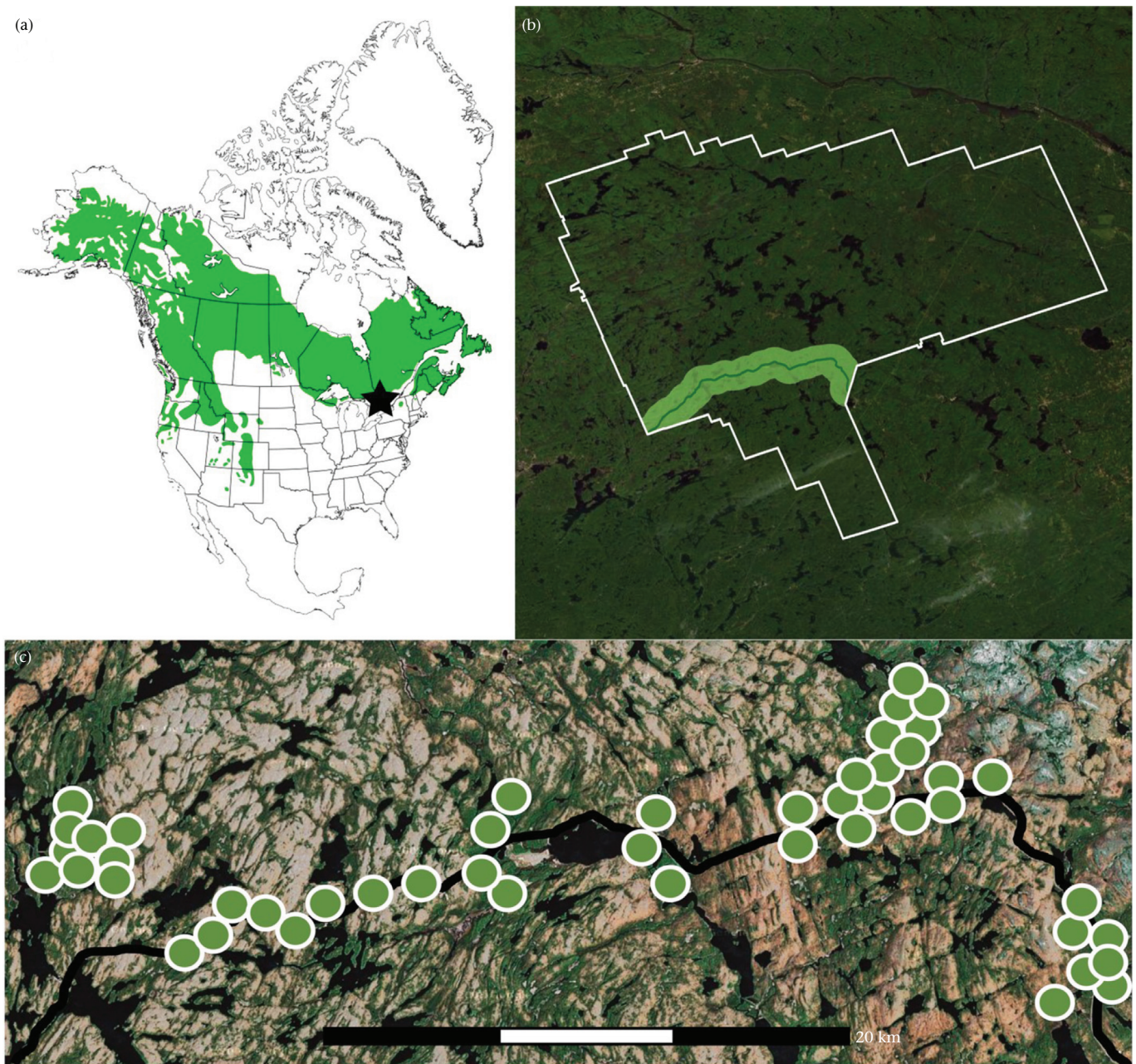


Figure 1. (a) Breeding distribution of Canada jays across North America. The black star denotes the study area in Algonquin Provincial Park, Ontario. (b) The park boundary and location of the Highway 60 corridor. (c) Location of 48 historically occupied and monitored Canada jay territories along Highway 60 (black line) and associated secondary roads. Leafless photography shows areas dominated by tolerant hardwoods (light tan), chiefly sugar maple, *Acer saccharum*, and areas dominated by various conifers (green).

locally within the study area or disappeared between the winter and autumn censuses (i.e. during the summer). Canada jays are monogamous and new pairs may form at any time of the year through the replacement of a lost breeder (Strickland & Ouellet, 2020). Additionally, the apparent survival of adult Canada jays in APP is higher in autumn/winter (~92%) compared to summer (~79%; Norris et al., 2013).

At or following the 1 March census, we determined the breeding status and reproductive success of all individuals on each territory by searching and checking each occupied territory every 2–3 days. The location of each nest was recorded using a variety of hand-held GPS devices (Garmin International, Inc., Olathe, KS, U.S.A.) with 5–10 m error or, prior to 1990, with aerial photos. When nestlings were approximately 11 days old, nests were accessed to band, blood sample and measure the young. In June, approximately 6 weeks postfledging, intrabrood dominance struggles result in delayed dispersal of a single dominant juvenile on the natal territory and the ejection of the subordinate siblings (ejectees). Some of these ejectees succeed in forming close associations with unrelated breeding pairs elsewhere or becoming a breeder at the end of their first year (Strickland, 1991). Because females rarely depart the nest once egg laying has begun (Strickland & Ouellet, 2020), we estimated lay date as the first day the female was seen sitting on the nest for at least 30 min. After individuals completed building their nest, we checked the nest every 1–2 days to determine the exact lay date. Since incubation lasts ca. 18 days from the last-laid egg (Strickland & Ouellet, 2020), we were then able to project the hatching date and subsequent date that offspring reached 11 days old. As with adults, all nestlings within the study area were given a unique combination of a Canadian Wildlife Service aluminium band and three coloured leg bands.

During the autumn census, all territories (mean = 18, range 1–48) were surveyed to determine which individuals were still present, including whether they were still on the territory they occupied the previous breeding season or whether they had moved to a new territory. During this census, any unbanded jays (replacement breeders or immigrant nonbreeders) were colour-banded, measured, blood-sampled, provisionally sexed by weight (Strickland, 1991) and aged as hatch-year (HY) or after-hatch-year (AHY) based on rectrix shape (Strickland & Ouellet, 2020). All jays were caught using a Potter trap with a suet bait placed inside (100% capture success rate). During capture, jays were kept in small cloth bags when not being measured in order to minimize stress. All animal sampling and handling protocols were approved by Environment Canada (Permit No. 10416) and the University of Guelph's Animal Care Committee (AUP No. 4003).

Dispersal and Site-fidelity

Breeding dispersal events and distances were recorded only for reproductively active adults (i.e. breeders) that dispersed locally within the study area because we could not reliably survey and track individuals that moved outside of the study area. We considered local breeding dispersal to have occurred when an adult attempted to breed (i.e. at least built a nest with an opposite-sex individual sharing the same territory) on one territory and then did so on another territory within the study area in the next year (Table 2). Due to the large territory size (mean = 146 ha; Strickland & Norris, 2015) of Canada jays in the study area, any permanent movement between territories was obvious and clearly indicated local breeding dispersal. We defined individuals as paired if they were breeding with a mate or occupying a territory with another opposite-sex adult. Because we conducted a second, autumn census every year (~ 15 October), we were able to classify local breeding dispersal as occurring either during the 'summer'

(between 1 March and 15 October) or the 'autumn/winter' (between 15 October and 1 March). We refer to the territory that a disperser left from as the 'originating territory' and the one it dispersed locally to as the 'receiving territory' (Table 2). If an adult dispersed locally alone it was referred to as 'single' whereas if an individual moved with its mate to another territory it was considered 'paired'. Individuals that remained on the same territory between late-winter censuses were considered 'site-faithful'. We analysed data only from breeders that were detected in two successive breeding seasons, including those that dispersed more than once in their lifetime. Thus, instances where individuals were observed breeding in year t and then went undetected for two or more censuses before being observed breeding on a different territory within the study area were excluded from any analyses. To quantify breeding dispersal distance, we measured the Euclidean distance (km) between the nests on the originating and receiving territories (Greenwood & Harvey, 1982).

Potential Causes of Breeding Dispersal

We tested predictions from six hypotheses explaining the causes of breeding dispersal for Canada jays within the study area (listed in Table 1). Mate loss (1 = mate loss, 0 = mate present) was defined as any instance where a mate was no longer on the originating territory between censuses, having either dispersed locally within the study area or disappeared (i.e. was no longer detected in the study area; Table 2). Any instance where both breeders left the originating territory between two censuses was considered a 'double disappearance' (Table 2). Age was included as a quadratic function to examine whether senescence played a role in dispersal since, in APP, Canada jay reproductive performance improves until 8 years of age and then declines thereafter (Sorensen et al., 2020). Following Strickland et al. (2011), territory quality was defined as the proportion of conifers present within each territory. A previous field experiment using artificial storage chambers containing perishable foods known to be cached by Canada jays provided evidence that conifers, specifically black spruce, *Picea mariana*, performed best at preserving food over 4–5 summer–autumn months compared to deciduous trees (Strickland et al., 2011). Analyses of Canada jays in APP also demonstrated that nest success was positively related to the proportion of conifers on territories (Strickland et al., 2011; Whelan et al., 2017). The distance to the nearest territory was estimated by calculating the Euclidean distance from an individual's territory centre (centroid of previous known nest locations) to the closest historically occupied territory in the study area. We used population density at year t as a predictor because high local densities could promote dispersal due to saturation of breeding spots (Fletcher, 2009; Lindberg et al., 1998). In contrast, low densities might promote local breeding dispersal if an individual loses a mate that is not promptly replaced from a local pool of nonbreeders. Because of the small sample size of dispersal events, we encountered model convergence issues with nest success, which prevented us from testing hypotheses related to previous reproductive output as a cause of breeding dispersal. All breeding dispersal distances were log-transformed to achieve normality.

Statistical Analyses

To evaluate how patterns of local breeding dispersal in the study area changed over time, we used logistic regression models to test whether the number of per capita double disappearances and the number of per capita dispersal events each year changed over the 55 years of monitoring. Additionally, we used a weighted linear regression with the sample size of dispersed birds each year as a

Table 2

Summary of definitions and potential outcomes of adult Canada jays' movements in Algonquin Provincial Park, Ontario, Canada

Term	Definition
Breeding dispersal	Occurs when an individual breeds on an 'originating' territory and, in a following late-winter census, breeds on a different, 'receiving' territory such that: On the originating territory, in year $t + 1$ (1) Disperser is replaced by a new breeder (2) Former mate is alone without a breeding partner (3) Former mate is also no longer present, either because it has dispersed within the study area or disappeared (death or dispersed out of study area) (4) New pair occupies the originating territory On the receiving territory in year $t + 1$, the disperser (1) Occupies a formerly vacant territory with a new bird with which it breeds (2) Fills a same-sex vacancy and subsequently breeds with the already-resident, opposite-sex bird (3) Occupies a vacant territory alone
Double disappearance	Occurs when both members of an apparent breeding pair are present on an 'originating' territory at one autumn, or late-winter, census but are both absent from that territory at the following census. It includes cases where: (1) Both birds disperse together to another territory within study area (2) Both birds disperse to, and occupy, separate territories elsewhere in the study area (3) One bird disperses within study area and the other bird disappears (through either death or dispersal out of study area) (4) Both birds disappear from the study area (through either death or dispersal out of study area)

weighted factor, to test whether mean dispersal distances each year changed over the long-term study. The per capita number of dispersal events each year was calculated by taking the number of birds that dispersed locally each year divided by the total number of breeding individuals within the study area during that breeding season. The per capita number of double disappearances each year was calculated by taking the number of double disappearances each year divided by the total number of breeding pairs in the study area each year.

We examined the factors that influenced the probability of breeding dispersal using a series of generalized linear mixed models (GLMMs; Bates et al., 2015) with a binomial distribution and logit link function. To examine factors that determined breeding dispersal, we used all 2477 observations of adults and incorporated a binary response for every observation for each individual (dispersed = 1, site-faithful = 0). The explanatory variables used were mate loss, individual age, individual age (quadratic), distance to the nearest territory, sex, territory quality and breeding density. We also considered individual identity (ID) and year as random effects since individuals were observed over multiple years and the frequency of local dispersal events varied by year. Because this data set had a large number of zeros relative to the total sample size, zero-inflation models were considered instead of GLMMs. However, the zeros in these data were 'structural' zeros (ecologically relevant) and recorded with no error rather than representing an absence of an individual that could be recorded with error (Blasco-Moreno et al., 2019), meaning that it would be unlikely that zeros were 'inflated'. Nevertheless, to confirm this, we ran zero-inflation models and there was no evidence that any of our parameters were causing zero-inflation ($\beta \pm SE = -18.03 \pm 5589$, $P = 0.99$), so we proceeded to use binomial GLMMs.

We also tested what factors might have influenced breeding dispersal timing (summer versus the autumn/winter) using GLMMs with a binomial distribution and logit link function. For this analysis, we used only local breeding dispersal events ($N = 81$) and a binary response variable for each dispersal event such that summer dispersal = 0 ($N = 43$) and autumn/winter dispersal = 1 ($N = 38$). The fixed effects used were as follows: mate loss, individual age (quadratic), distance to the nearest territory, sex, territory quality and breeding density. Individual ID and year were included as random effects for this set of models.

To identify variables that influence variation in breeding dispersal distance, we used a linear mixed effect model (LME), with

log-transformed dispersal distance (km) as the normalized response variable ($N = 81$). The fixed effects were distance to the nearest territory, sex, percentage of conifers on the receiving territory, breeding density, individual age and year. Individual identity was used as a random effect because some individuals dispersed more than once in their lifetime.

For all three models sets, we constructed models that represented all possible combinations of fixed effects in addition to each variable alone. There was no evidence that any of the fixed effects in the models used to predict dispersal probability or dispersal distance were collinear ($r < 0.3$), and all possible interactions were examined prior to analyses. For all GLMMs, we used the second-order Akaike's information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002) to rank competing models. We considered any model with $\Delta AICc < 2$ to be a candidate model (Burnham & Anderson, 2002). In addition, Akaike weights (w_i) gave cumulative support for each model when accounting for all competing models. When there was no clear top model, to determine the direction and magnitude of the effect of each explanatory variable, we performed full model averaging over a candidate set of models using the 'model.avg' function in the 'MuMIn' package (Burnham & Anderson, 2002). Statistical analyses were run in R v.3.3.2 (R Core Team, 2017) using the 'lme4' (Bates et al., 2015), 'nlme' (Pinheiro et al., 2020), 'MuMIn' (Bartón, 2018) and 'AICcmodavg' (Mazorelle, 2017) packages. All statistical tests were considered significant at $P < 0.05$. To further avoid the inclusion of uninformative parameters in our model selection, we report the 85% confidence intervals (CIs) and explanatory variables when the unconditional CIs did not include zero (Arnold, 2010). Confidence intervals of 85% are more appropriate than those of 95% when using AIC model selection because 95% CIs could discard variables in best-approximating models that are supported by lower AIC values (Arnold, 2010).

RESULTS

Prevalence of Breeding Dispersal

Between 1964 and 2019, there were 2477 events of 530 adults (271 males, 259 females) breeding on or actively defending a given territory in a given year. In only 3% (81/2477) of these cases did an individual locally disperse as an adult to a different breeding territory within the study area the following year. Of the 530 adults, only 68 (13%) individuals exhibited breeding dispersal at least once

in their lifetime. Of the 2477 breeding events, mate loss prior to the breeding event occurred in 12% (298/2477) and, of those instances, 12% (36/298) were followed by a breeding dispersal event. Among all dispersal events, 32% (26/81) involved both members of a pair moving to a nearby vacant territory together and 68% (55/81) involved an individual that locally dispersed alone. Of the single-bird dispersal events, 78% ($N = 43$) occurred when a mate had been lost beforehand and 22% ($N = 12$) resulted in the mate being left on the originating territory. There was no evidence for sex bias in the frequency of local breeding dispersal (males: $N = 44$; females: $N = 37$) and there was a similar number of local dispersal events in the summer ($N = 43$) versus the autumn/winter ($N = 38$).

Concerning the originating territory, of the 55 cases where an adult dispersed alone, 13% (7/55) involved a disperser that was found to have been replaced by a new breeder that paired with the disperser's former mate (that remained on the originating territory). After dispersing, 60% (49/81) of breeding dispersal events resulted in the originating territory being completely vacant in the next census and 23% (19/81) were followed by two new breeders taking over the vacated territory. In a further 16% (13/81) of cases, at the census following breeding dispersal, we found the former mate or remaining juvenile from the previous breeding event or a new adult alone on the originating territory.

Concerning the receiving territories, in 20% (16/81) of breeding dispersal events, breeders moved to territories that were known to be completely vacant before breeding dispersal occurred (8 dispersal events of paired birds and 8 of individual birds) and another 7% (6/81) of cases involved individuals that filled same-sex breeding positions known to have been vacant before dispersal. In addition, 67% (37/55) of single-bird dispersers were found breeding with partners that were known to have been breeding with a different partner on the receiving territories the year before the local dispersal event.

The per capita number of breeding dispersal events (mean = 0.03 per year, range 0–0.2), per capita double disappearances (mean = 0.12, range 0–1) and mean breeding dispersal distance (mean = 1.7 km per year, range 0.6–3.4 km) per year did not significantly increase over time (per capita dispersal events: $\beta = 0.02$, $t = 0.53$, $N = 55$, $P = 0.59$; Appendix, Fig. A1a; double disappearances per year: $\beta = 0.003$, $t = 0.15$, $N = 55$, $P = 0.87$; Appendix, Fig. A1b; distance: $\beta = -0.002$, $t = -0.35$, $N = 55$, $P = 0.72$; Appendix, Fig. A1c).

Factors Influencing the Probability of Dispersal

To explain the probability of breeding dispersal, there were four models within 2 Δ AICc of the top model (Table 3, Appendix, Table A1). All of these models included mate loss, territory

quality and distance to the nearest territory as fixed effects. Based on model averaging, the mean relative variable importance (RVI) of mate loss, distance to the nearest territory, territory quality, age, density and sex were 1.00, 0.90, 0.29, 0.50, 0.28 and 0.27, respectively. The model-averaged coefficients suggested the probability of breeding dispersal within the study area was positively related to mate loss (Appendix, Table A1); individuals dispersed more often when their mate was not present anymore (Fig. 2). Additionally, the probability of dispersal was inversely related to the distance to the closest territory (Table 3, Appendix, Table A1). There was some evidence that breeding dispersal was higher when individuals occupied low-quality territories, although the 85% confidence interval overlapped with zero (Table 3, Appendix, Table A1).

Timing of Breeding Dispersal

Next, we examined the factors that influenced the timing of local breeding dispersal within the study area. For this analysis, there were two top models within 2 Δ AICc and both included mate loss, sex, density and age as predictors (Appendix, Tables A2, A3). Based on model averaging, the RVI of mate loss and sex were both

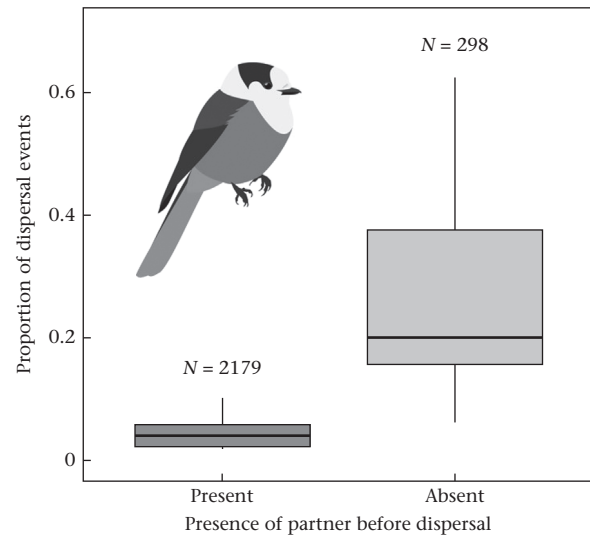


Figure 2. Proportion of times in which Canada jay breeding dispersal occurred prior to a breeding event ($N = 2477$ total events) in relation to whether the original mate was present on the originating territory between breeding seasons or the mate was absent (i.e. dispersed out of the study area or died). Numbers above boxes represent sample sizes for each category. The thick line in each box represents the median, the upper and lower limits represent the standard error and the vertical lines are the standard deviation.

Table 3

Model selection results for demographic and environmental factors that influence the probability of breeding dispersal of Canada jays

Model	K	AICc	Δ AICc	w_i
Territory quality + nearest territory + mate loss	6	506.99	0.00	0.35
Territory quality + nearest territory + mate loss + sex	7	508.58	1.58	0.16
Territory quality + nearest territory + mate loss + (age) ²	7	508.71	1.72	0.15
Territory quality + nearest territory + mate loss + density	7	508.99	2.00	0.13
Territory quality + nearest territory + sex + (age) ² + density	8	510.35	3.35	0.07
Territory quality + nearest territory + mate loss + sex + density	8	510.58	3.58	0.06
Territory quality + nearest territory + mate loss + density + (age) ²	8	510.70	3.71	0.05
Territory quality + nearest territory + mate loss + sex + density + (age) ²	9	512.35	5.35	0.02
Territory quality + mate loss	5	515.14	8.15	0.01
Territory quality + (age) ² + mate loss	6	516.61	9.62	0.00

Mate loss: loss of mate due to dispersal or death (binary); nearest territory: distance (km) to the nearest vacant territory; territory quality: habitat quality of territory measured as the percentage of coniferous trees on territory; age: age of focal individual at breeding (quadratic); density: the number of individuals within the population in year t ; sex: sex of focal individual). Fixed effects for each model are listed as well as the total number of parameters in a model (K), AICc, Δ AICc and AICc weight (w_i).

1.00, while age and density were 0.25. Individuals were more likely to disperse during the autumn/winter if they lost a mate ($\beta = 2.98$, 85% CI = [0.77, 5.24]; Appendix, Tables A2, A3) and were male ($\beta = 2.27$, 85% CI = [0.61, 3.95]; Appendix, Tables A2, A3).

Factors Influencing Dispersal Distance

Among all 81 local breeding dispersal events, distances ranged from 0.48 to 7.0 km (median = 1.1 km; Fig. 3). Only 11% ($N = 9$) of all detected breeding dispersal events within the study area were > 3 km. In 70% of cases ($N = 57$), receiving territories were directly adjacent to originating territories and in only 16% of cases ($N = 13$) was the receiving territory more than two territories away (range 3–6). Female dispersal ranged from 0.4 to 5.4 km (median = 1.3 km, $N = 37$), and male dispersal ranged from 0.5 to 7.0 km (median = 1.1 km, $N = 44$). There was one top model predicting variation in breeding dispersal distances, with distance to the nearest vacant territory and sex as predictors. Canada jays tended to disperse greater distances as the distance to the nearest vacant territory increased ($\beta = 1.03$, 85% CI = [0.44, 1.61]; Appendix, Tables A4, A5) and if they were female ($\beta = -0.42$, 85% CI = [-0.78, -0.05]; Fig. 3, Appendix, Tables A4, A5).

DISCUSSION

Using a 55-year data set, we provide evidence that adult Canada jays are highly site-faithful, with local breeding dispersal occurring in only 3% of the cases in which individuals were observed defending a territory in consecutive years and only 13% of all breeding individuals dispersing at least once during their adult life. Even among adults that lost a mate, which we identified as a motivating factor for local dispersal, only 12% ended up dispersing to a new territory. In those rare cases where local dispersal did occur, it appeared to come in two general forms: birds dispersing alone, which comprised 68% of all breeding dispersal events, or

birds dispersing with a mate, which comprised 32% of all events. Below, we discuss possible reasons for low breeding dispersal rates in this population, motivations behind dispersal, and why dispersal rates and distance did not change over time.

While we did not find any evidence for a linear increase in per capita dispersal rates over time, the steepest decline in the APP Canada jay population occurred between 1982 and 1995 (Sutton et al., 2021), which coincided with an increase in annual per capita dispersal frequencies, ‘double disappearances’ and dispersal distances (Fig. A1). The number of dispersal events caused by mate loss also peaked between 1990 and 1994, which would be consistent with the idea that there was a diminishing number of potential replacements for widowed birds during the period of decline, potentially causing birds to disperse in search of a new partner rather than to remain on their territory. Further research is needed to determine both the short- and long-term fitness consequences of breeding dispersal and what, if any, consequences it might have at the population level.

We propose that the primary reason for a low rate of local breeding dispersal is that overwintering Canada jays are critically dependent on the memory-accessed food items that they themselves cache on their territories during the summer and autumn. This constraint against abandoning their own cache-filled territories is supported by the fact that 70% of dispersers only moved to a neighbouring territory. Although we have no direct evidence, such short local breeding dispersal distances possibly allows individuals to retrieve food that was cached on their originating territory. Returning to the originating territory to access cached food may also explain the otherwise surprisingly high percentage of local breeding dispersal events that occurred in the autumn/winter (47%), when little or no fresh food is available sustain birds on a newly settled territory and the locations of caches made by previous occupants are unknown. Consistent with the idea that individuals may be more constrained by the availability of recovered cached food when dispersing in the autumn/winter, a slightly higher percentage of dispersal events were to neighbouring territories during the autumn/winter (76%) compared to the summer (65%), which could be attributed to the need to settle on an adjacent territory in order to access previously cached food. High levels of site-fidelity have been observed in other food-caching species, including Florida scrub-jays, *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick, 1984), wolverines, *Gulo gulo* (Aronsson & Persson, 2018), American pikas, *Ochotona princeps* (Morrison et al., 2009), blue tits, *Cyanistes caeruleus* (Valcu & Kempenaers, 2008), and Eurasian magpies, *Pica pica* (Molina-Morales, Martínez, & Avilés, 2012), suggesting that investment in cached food on a territory could be a common driver of high breeding site fidelity.

While mate loss is clearly not a predisposing factor contributing to the local breeding dispersal of intact pairs (pairs that dispersed together), our results provide evidence that it is one of the primary factors associated with single-bird dispersals. Among all local single-bird dispersal events, 78% ($N = 55$) involved loss of a mate prior to the local dispersal and, despite the fact that not all breeding dispersal events involved single dispersers, mate loss was still in the top model predicting the overall probability of breeding dispersal. Previous studies on birds have also found support for the ‘mate loss’ hypothesis as a driver of breeding dispersal (Forero et al., 1999; Kim et al., 2007; Pasinelli et al., 2007; Wiklund, 1996). Even though the overall probability of local breeding dispersal is low in this population, our results indicate that loss of a mate is the primary factor driving breeding dispersal among birds that disperse alone.

Interestingly, we also found that individuals were more likely to locally disperse after they lost a mate in the autumn/winter than in the summer. This may follow from the fact that, in summer, more

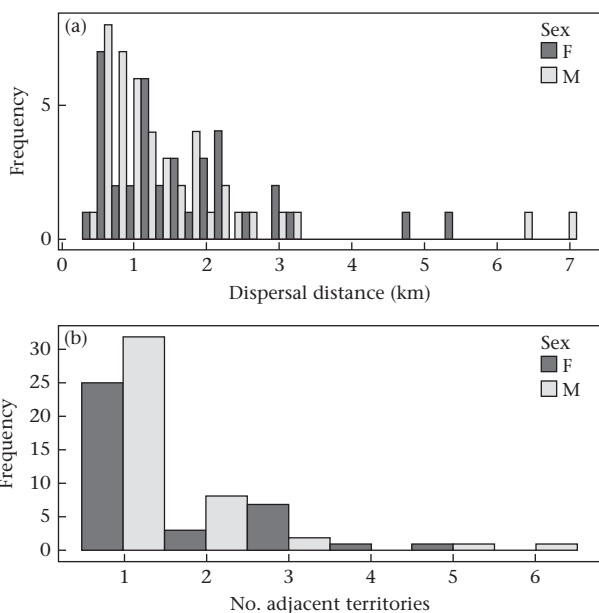


Figure 3. The frequency distribution of breeding dispersal distances (not log-transformed) as measured by (a) distance from the nest on the originating territory to the nest on the receiving territory in kilometres and (b) the number of territories between the originating and receiving territory for male and female dispersing adult Canada jays. A value of one indicates that the disperser moved to a neighbouring territory adjacent to the originating territory.

second-year nonbreeders (i.e. juveniles surviving from the year before) are available to replace disappeared breeders, resulting in a greater likelihood that breeding vacancies are promptly filled in summer and making it unnecessary for widowed breeders to move. In contrast, even though adult mortality is much lower in winter than in summer (Norris et al., 2013), an autumn or a winter vacancy is correspondingly less likely to be filled because the pool of possible replacements may well have been already exhausted, especially in our declining population (Sutton et al., 2021). This reduction in potential replacements, in combination with lower rates of mortality in autumn or winter, may explain why individuals disperse more often in autumn or winter when faced with mate loss.

Our results provide some evidence that breeding dispersal distances in Canada jays is sex-biased, which is in concert with Greenwood's (1980) evolutionary hypothesis for female-biased breeding dispersal distances in birds. The frequency of local breeding dispersal did not differ between sexes, but we provide evidence that female Canada jays tended to travel longer distances than males, which is consistent with studies of birds showing female-biased breeding dispersal distances (Newton & Marquiss, 1982; Paris et al., 2016; Pärt & Gustafsson, 1989). As suggested by Greenwood (1980), female-biased breeding dispersal distances may be due to differences in competitive ability and resource-holding potential between sexes. Canada jay females are smaller than males and might have to prospect further distances when searching for a new breeding site if existing pairs are more likely to fend them off compared to intruding males. Additionally, Greenwood (1980) suggested that dispersing adult males are more likely to remain close to the natal area than are females. In Canada jays, males delay natal dispersal more than females (Strickland, 1991), so for adults born in the study area, shorter dispersal distances in males might be due to higher philopatric tendencies than in females.

Our results demonstrate that territory quality appears to influence the local breeding dispersal of both paired and single dispersers. Paired dispersal appears to happen when a pair has the opportunity to upgrade the quality of their territory, particularly to one that is nearby and vacant (Carro, Llambías, & Fernández, 2017). Additionally, our results provide some evidence that dispersal may be more likely when an individual is occupying a low-quality territory. These results are consistent with previous work on this Canada jay population demonstrating that individuals are more likely to move from low-quality into high-quality territories than vice versa (Norris et al., 2013). While occupying low-quality territories does not seem to affect survival (Norris et al., 2013), it may result in food caches of lower quality or quantity (Strickland et al., 2011), which, in turn, probably has a negative impact on reproductive success (Sutton et al., 2019). However, even if higher territory quality facilitates improved reproductive success, it does not seem to entice adults to disperse very frequently, even when there is a vacant, high-quality territory nearby. This, again, suggests that the cached food investment that Canada jays make on their territories plays an important role in their high territorial fidelity.

We acknowledge that some aspects of our study limited our ability to gain a comprehensive picture of the patterns and causes of local breeding dispersal in Canada jays. Perhaps most significantly, we were unable to record successful breeding dispersal events of birds that dispersed to outside of the study area. This was likely accentuated by the east–west linear shape of the study area (it runs along the Highway 60 corridor through APP), which means that many local breeding dispersal events to the north or south of the study area would have been missed. For this reason, our estimates of the total number of breeding dispersal events and, therefore, the percentage of birds that dispersed in their lifetime

are almost certainly underestimates. However, the magnitude of this underestimate may be lower than expected given that most Canada jays do not switch territories once they have acquired a breeding partner and, when they do disperse, the vast majority of individuals move to neighbouring territories, less than 2 km away. It is also important to note that, because of low sample sizes, we were not able to include nest success as a predictor of breeding dispersal. Several previous studies have demonstrated that nest failure can be a precursor for dispersal (Forero et al., 1999; Öst et al., 2011), and while the exclusion of this variable inherently limits this study, we do not believe that it impacts the conclusions of our work. Among all dispersal events, only 19% (16/81) were known to be preceded by nest failure. Therefore, the low number of failed nests prior to local breeding dispersal suggest that this likely would not be a strong predictor of dispersal.

Author Contributions

M.F. and D.R.N. were responsible for conceptualization and data curation. Formal analysis was done by M.F. with the supervision of D.R.N. D.R.N. was responsible for funding acquisition and investigation. The methodology used was developed by D.R.N. and D.S. and data collection was done by M.F., D.R.N. and D.S. R.N. was in charge of project administration, resources, supervision and validation. M.F. wrote the manuscript and it was reviewed and edited by D.R.N. and D.S.

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Appendix

Table A1

Model-averaged results of GLMMs predicting factors that influence the probability of breeding dispersal in Canada jays

Coefficient	Estimate	Lower CI	Upper CI	z	RVI
Intercept	−3.03	−4.24	−1.83	3.63	–
Mate loss	2.60	2.21	2.99	9.54	1.00
Nearest territory	−1.34	−1.91	−0.77	3.38	0.90
Age	0.004	−0.05	0.05	0.02	0.50
Territory quality	−0.005	−0.01	0.00	0.63	0.29
Density	−0.003	−0.02	0.00	0.39	0.28
Sex	0.01	−0.30	0.47	0.12	0.27

Mate loss: loss of mate due to dispersal or death (binary); territory quality: habitat quality of territory measured as the percentage of coniferous trees on territory; nearest territory: distance to the nearest territory (km); sex: sex of focal individual; age: age of focal individual at breeding (quadratic); density: the number of individuals within the population in year *t*. Candidate models selected have a $\Delta AICc$ of 2 or less. For each explanatory variable, the variable coefficient, estimate, upper and lower 85% confidence interval (CI), z value and relative variable importance (RVI) are listed. Relative variable importance for each variable was calculated by summing the Akaike weights of the candidate models that included said variable.

Table A2

Model selection results for demographic and environmental factors that influence the timing of breeding dispersal among Canada jays

Model	<i>K</i>	AICc	ΔAICc	<i>w_i</i>
Mate loss + sex	4	92.9	0.00	0.31
Mate loss + sex + (age) ²	4	94.9	1.96	0.11
Mate loss + sex + (age) ² + density	6	95.0	2.07	0.11
Mate loss + (age) ² + territory quality	5	96.3	3.42	0.05
Mate loss + sex + (age) ² + density + territory quality	7	96.6	3.71	0.05
Mate loss + sex + territory quality + nearest territory + density	7	96.7	3.82	0.04
Mate loss + sex + (age) ² + nearest territory	6	96.8	3.89	0.04
Mate loss + sex + (age) ² + nearest territory + density	7	96.9	4.02	0.04
Mate loss + density	4	97.1	4.22	0.03
Mate loss	3	97.7	4.76	0.02

Mate loss: loss of mate due to dispersal or death (binary); nearest territory: distance (km) to the nearest vacant territory; territory quality: habitat quality of territory estimated as the percentage of coniferous trees on territory; age: age of focal individual at breeding (quadratic); density: the number of individuals within the population in year *t*; sex: sex of focal individual). Fixed effects for each model are listed as well as the total number of parameters in a model (*K*), AICc, ΔAICc and AICc weight (*w_i*).

Table A3

Model-averaged results of GLMMs predicting factors that influence the timing of breeding dispersal in Canada jays

Coefficient	Estimate	Lower CI	Upper CI	<i>z</i>	RVI
Intercept	-3.57	-5.90	-1.03	2.15	–
Mate loss	2.98	0.77	5.24	1.92	1.00
Sex	2.27	0.61	3.95	1.94	1.00
Age	0.09	-0.34	0.67	0.20	0.25
Density	0.09	-0.17	0.89	0.20	0.25

Mate loss: loss of mate due to dispersal or death (binary); territory quality: habitat quality of territory estimated as the percentage of coniferous trees on territory; sex: sex of focal individual; age: age of focal individual at breeding (quadratic). Models with ΔAICc of 2 or less were considered competitive. For each explanatory variable, the variable coefficient, estimate, upper and lower 85% confidence interval (CI), *z* value and relative variable importance (RVI) are listed. Relative variable importance for each variable was calculated by summing the AICc weights of the candidate models that included said variable.

Table A4

Model selection results for factors that influence variation in breeding dispersal distances of Canada jays

Model	<i>K</i>	AICc	ΔAICc	<i>w_i</i>
Nearest territory + sex	5	260.1	0.00	0.60
Nearest territory	4	262.9	2.75	0.15
Nearest territory + (age) ²	5	264.1	3.98	0.08
Nearest territory + density	5	264.8	4.60	0.06
Nearest territory + (age) ² + sex	6	266.9	6.76	0.02
Nearest territory + year	5	267.2	7.00	0.01
Nearest territory + density + sex	6	267.5	7.35	0.01
Nearest territory + territory quality	5	268.3	8.16	0.01

Nearest territory: distance (km) to the nearest vacant territory; sex: sex of focal individual; territory quality: habitat quality of territory estimated as the percentage of coniferous trees on territory; year: year of dispersal event; age: age of focal individual at breeding (quadratic); density: the number of individuals within the population in year *t*). Fixed effects for each model are listed as well as the total number of parameters in a model (*K*), AICc, ΔAICc and AICc weight (*w_i*). Models with ΔAICc of 2 or less were considered competitive.

Table A5

Estimates and 85% confidence intervals of the top model (– nearest territory + sex + 1|ID) predicting what factors influence variation in breeding dispersal distances (km) of Canada jays

Variable	Estimate	Lower CI	Upper CI
Nearest territory	1.03	0.44	1.61
Sex	-0.42	-0.78	-0.05

Sex: sex of dispersing individual; nearest territory: distance in kilometres to the nearest territory.

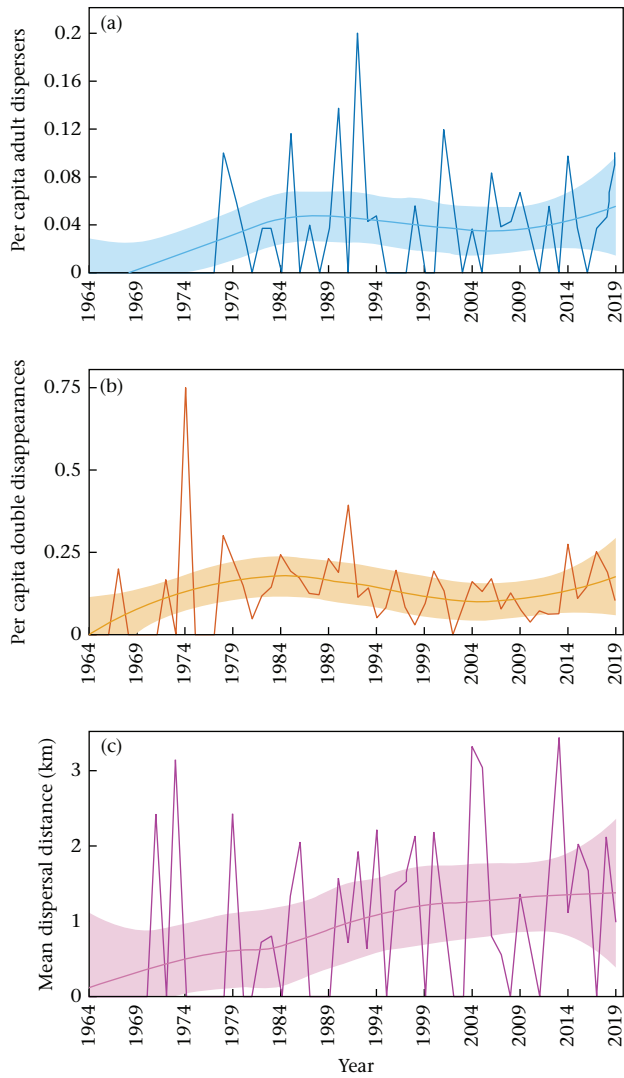


Figure A1. Annual variation (1964–2019; 55 years) in (a) the total number of breeding dispersers ($P < 0.001$), (b) the total number of double disappearances ($P < 0.001$), (c) the proportion of potential breeding opportunities ($P = 0.006$) and (d) the mean breeding dispersal distance (km) ($P = 0.006$) of Canada jays within the study area, Algonquin Provincial Park, Ontario. Shaded regions along the trend line represent the standard error.