

Survival throughout the annual cycle of first year Canada Jays in the context of sibling competition, expulsion, and adoption

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ABSTRACT

For most birds that exhibit delayed dispersal (remaining on the natal territory rather than dispersing to seek a breeding opportunity), siblings appear free to stay or leave the natal area. However, in rare cases, delaying dispersal is determined via conflict among siblings, with the dominant individual remaining on the natal territory. We used radio-tracking to examine brood reduction, and subsequent juvenile survival, of first-year Canada Jays (*Perisoreus canadensis*) in Algonquin Provincial Park, Ontario, Canada. Soon after juveniles become nutritionally independent, intra-brood struggles lead to one “dominant juvenile” remaining on the natal territory after permanently expelling the subordinate siblings (“ejectees”). Males in above-average condition when nestlings were the most likely to become the dominant juveniles and females did so only when broods were all-female at the time of the expulsion. Dominant juveniles were much more likely to survive their first summer compared to ejectees (survival probabilities = 0.84 and 0.45, respectively), suggesting that ejectees are especially vulnerable to mortality risk in the critical interval between their expulsion from the natal territory and their settlement on a new territory. However, if ejectees lived to autumn, they had only a slightly lower probability of first-winter survival (0.73) than dominant juveniles (0.85). These results suggest that the survival advantage gained by dominant juveniles is greatest during the first summer after hatching, with a much smaller difference over the first winter after ejectees have settled on non-natal territories. Our work provides insight into potential evolutionary and ecological mechanisms driving social dominance hierarchies in wild birds.

Keywords: delayed dispersal, mortality risk, natal dispersal, *Perisoreus canadensis*, social dominance

How to Cite

Furst, M., D. Strickland, N. E. Freeman, A. O. Sutton, B. A. Graham, T. Burg, and D. R. Norris (2024). Survival throughout the annual cycle of first year Canada Jays in the context of sibling competition, expulsion, and adoption. *Ornithology* 141:ukae013.

LAY SUMMARY

- The Canada Jay is a resident passerine that relies on cached food for overwinter survival and late-winter reproduction.
- Six to 7 weeks after leaving the nest, juvenile Canada Jays engage in a dominance struggle ending with one bird, the “dominant juvenile,” remaining on the natal territory for an average of ~13 months after expelling its former nest-mates (ejectees).
- Dominant juveniles are more likely to be males and, among males, individuals in the best physical condition.
- Using radio-tracking, we showed that dominant juveniles were twice as likely to survive their first summer compared to ejectees, but had similar first-winter survival, partly because most surviving ejectees were adopted by unrelated adults after being expelled from their natal territory.
- Our work demonstrates the survival benefit of winning the fight to stay on the natal territory in this rare, post-fledging brood reduction behavior.

Survie des juvéniles de première année de *Perisoreus canadensis* au cours du cycle annuel dans le contexte de la compétition entre membres d’une fratrie, de l’expulsion et de l’adoption

Submission Date: May 24, 2023. Editorial Acceptance Date: March 1, 2024

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RÉSUMÉ

Chez la plupart des oiseaux qui présentent une dispersion retardée (restent sur le territoire natal plutôt que de se disperser à la recherche d'une opportunité de reproduction), les membres d'une fratrie semblent libres de rester ou de quitter la région natale. Cependant, dans de rares cas, le retardement de la dispersion est déterminé par un conflit au sein de la fratrie, l'individu dominant demeurant sur le territoire natal. Nous avons utilisé la radiotéléométrie pour étudier la réduction de la taille de la couvée et de la survie subséquente chez des juvéniles de première année de *Perisoreus canadensis* au parc provincial Algonquin, en Ontario, au Canada. Peu de temps après que les juvéniles soient devenus indépendants sur le plan nutritionnel, les luttes au sein de la couvée ont conduit à ce qu'un « juvénile dominant » demeure sur le territoire natal après avoir expulsé de façon permanente ses frères et sœurs subordonnés (« expulsés »). Les mâles dont la condition corporelle était supérieure à la moyenne lorsqu'ils étaient oisillons étaient les plus susceptibles de devenir les juvéniles dominants et les femelles ne le devenaient que lorsque les couvées étaient exclusivement composées de femelles au moment de l'expulsion. Les juvéniles dominants étaient beaucoup plus susceptibles de survivre à leur premier été que les expulsés (probabilités de survie = 0,84 et 0,45, respectivement), ce qui suggère que les expulsés sont particulièrement vulnérables au risque de mortalité dans l'intervalle critique entre leur expulsion du territoire natal et leur établissement dans un nouveau territoire. Cependant, si les expulsés survivaient jusqu'à l'automne, ils avaient seulement une probabilité légèrement plus faible de survie au premier hiver (0,73) que les juvéniles dominants (0,85). Ces résultats suggèrent que l'avantage de survie acquis par les juvéniles dominants est plus le plus important au cours du premier été suivant l'éclosion, avec une différence beaucoup plus faible au cours du premier hiver après que les expulsés se soient établis sur des territoires non nats. Notre travail donne un aperçu des mécanismes évolutifs et écologiques potentiels qui régissent les hiérarchies de dominance sociale chez les oiseaux sauvages.

Mots-clés: dispersion retardée, risque de mortalité, dispersion natale, *Perisoreus canadensis*, dominance sociale

INTRODUCTION

Family living occurs across a wide range of taxa and often results from offspring remaining on the natal area with their parents instead of dispersing in their first year (Koenig et al. 1992, Nelson-Flower et al. 2012, Mumme et al. 2015, Kingma et al. 2016, Suh et al. 2020). If delaying dispersal increases a juvenile's probability of acquiring a high-quality breeding territory (Ekman et al. 2001, Kokko and Ekman 2002) or surviving their first year (Tarwater and Brawn 2010, Groenewoud et al. 2016), it may be more advantageous to stay rather than leave the natal territory in the first year of life (Ekman et al. 1999, Griesser et al. 2006, Furst et al. 2023). However, in some cases, there may not be enough resources on a territory to sustain an entire family group consisting of the breeding adults and their young-of-the-year (Campbell et al. 2005, Eikenaar et al. 2007, Mumme et al. 2015). In such cases, siblings may compete for access to the natal territory if remaining at home leads to fitness benefits (Strickland 1991, Ekman and Griesser 2002).

Sibling competition most often occurs before young are fully independent and can lead to brood reduction via the death of 1 or more offspring through either sibling conflict or parent-offspring conflict (Mock 1994, Mock and Parker 1997, Tanner et al. 2008). In the vast majority of bird species, this type of sibling competition occurs in the nest and is typically won by a brood member who is able to monopolize parental food deliveries (Ploger 1997) because it hatched earlier (Tanner et al. 2008), is in above-average body condition (Camacho et al. 2019, Freeman et al. 2021), and/or is of the socially dominant sex (Bortolotti 1986, Drummond et al. 1991). In contrast, sibling expulsion can also occur outside of the nest once individuals have fledged; as is the case for Canada Jays (*Perisoreus canadensis*) and Siberian Jays (*Perisoreus infaustus*; Strickland 1991, Ekman et al. 2002, Iida 2003). In birds, these rare cases can be considered a form of brood reduction that results in one individual forcing its siblings to disperse from the natal territory (Strickland 1991, Ekman et al. 2002, Sorensen et al. 2022).

Differences in the timing of dispersal from the natal territory due to sibling rivalries can have immediate (Braun and Hunt 1983, Trillmich and Wolf 2008, Griesser et al. 2008, Griesser et al. 2014) and far-reaching (Ekman et al. 1999, Sorensen et al. 2022, Furst et al. 2023) consequences for survival and lifetime reproductive output. Unfortunately, in many species,

early-life movements and social interactions are poorly understood because dispersing juveniles can be difficult to track (Cooper et al. 2008, Norris et al. 2013, Cox et al. 2014) and are less conspicuous than adults (Thompson 1991) that are defending resources and breeding positions. Directly tracking individuals via remote sensing devices, such as radio transmitters, provides the opportunity to not only estimate survival of juveniles that dispersed outside a traditional study area, but also follow juveniles during a period when most mortality occurs. Understanding temporal variation in mortality can provide key insights into when survival is most limiting across the annual cycle (Cox et al. 2014), which has rarely been determined for birds in their first year (Sillert and Holmes 2002).

The Canada Jay is a resident passerine of North America's boreal and subalpine forests and relies on perishable stored food such as berries, fungi, invertebrates, and vertebrate flesh for overwinter survival and late-winter breeding (Strickland and Ouellet 2020). At the southern edge of their range, Canada Jays begin breeding in mid-February with incubation starting in early March. Females lay between 1 and 5 eggs, with a median and mode of 3 eggs (Strickland and Ouellet 2020). Juvenile behavior is characterized by a forced expulsion of subordinate brood members from the natal territory between early June to mid-July and the creation of 2 classes of juveniles, "dominant juveniles" and "ejectees" (Strickland 1991, Sorensen et al. 2022, Furst et al. 2023). Based on observations of 6 separate aggressive post-fledging struggles (Strickland 1991), the "dominant juvenile" expels its siblings ~6 weeks post-fledging (less frequently, it is the only brood member that survives that long) and remains closely associated with its parents. Dominant juveniles are most often males when arising from a mixed-sex nestling brood (Strickland 1991) but the influence of nestling condition on social dominance is less clear (Freeman et al. 2021). Some "ejectees," the expelled siblings forced out of their natal territories by the dominant juvenile, settle, separately, on territories occupied by an unrelated breeding pair whose same-year nesting attempt has failed and where, consequently, there is no dominant juvenile present (Strickland 1991, Sorensen et al. 2022). Dominant juveniles and ejectees normally remain as nonbreeders on their respective natal and adoptive territories for a year or longer (usually remaining longer if the following year's nesting attempt by the existing breeders fail; M.F., D.S., and D.R.N. personal observations) and then undertake a

“voluntary” (i.e., non-forced) dispersal to a breeding position on another territory (the second to be occupied since fledging in the case of dominant juveniles, and the third territory by ejectees; Strickland 1991). During the occupancy of the natal or non-natal territory, both dominant juveniles and ejectees may help the breeder pair defend the territory from other juveniles or adults (Strickland and Ouellet 2020). Only 3 cases have been observed in 58 years where more than one juvenile from the same brood was seen on the natal territory after 6–7 weeks post-fledging (~1% of all cases where at least one juvenile remained; D.S. and D.R.N. personal observations).

In this study, our goal was to better understand the delayed dispersal and sibling expulsion process of Canada Jays in a declining population at the southern edge of the range in Ontario, Canada (Waite and Strickland 2006, Sutton et al. 2021a). To accomplish this goal, we used radio-tracking to estimate survival and dispersal of dominant juveniles and ejectees both within and beyond our study area throughout their first year of life. Doing so allowed us to ask two primary questions: (1) what factors contribute to an individual becoming a dominant juvenile? and (2) what periods of the year drive differences in first-year survival between dominant juveniles and ejectees? To address the first question, we examined 2 hypotheses: First, sex determines whether an individual becomes a dominant juvenile because of the differences in body size between juvenile male and female Canada Jays, with males having greater average body mass (Strickland 1991, Strickland and Ouellet 2020). Following this hypothesis, we predicted that the probability of becoming a dominant juvenile would be higher in males than females. Second, nestling condition drives the determination of dominant juveniles because better physical condition would allow juveniles to win more fights and thus retain access to the natal territory. Following this hypothesis, we predicted that, among males only, the probability of becoming a dominant juvenile would be higher in individuals of better nestling body condition.

For the second question of what time period drives differences in first-year survival between dominant juveniles and ejectees, we hypothesized that ejectees would have lower survival in the summer because, unlike dominant juveniles that remain on their natal territory, they must disperse through unfamiliar habitat and find suitable territories immediately after they are ejected from the natal territory. Furthermore, it is imperative that they find a place to settle by the late summer because they presumably must have sufficient time to cache food prior to the onset of winter. Following this hypothesis, we predicted that ejectees would face higher instantaneous mortality risk in their first summer compared to dominant juveniles but have similar survival rates over the winter when almost all individuals of both social classes have settled on territories.

METHODS

Study Area and Field Methods

We used re-sighting and radio-tracking data from 2016 to 2021 (mean \pm standard deviation [SD] number of occupied territories each year = 17 ± 2) to quantify post-fledging Canada Jay delayed dispersal and sibling expulsion processes and subsequent juvenile survival in Algonquin Provincial Park (APP), Ontario, Canada (45°N, 78°W; 7.6×10^5 ha). We monitored 101 nests and radio-tagged 96 (27% of nestlings alive at banding were not tagged either due to a limited

number of deployable tags on hand or because nestlings were too small on day 14) of the 130 nestlings that survived to banding (2016: $n = 4$, 2017: $n = 5$, 2018: $n = 29$, 2019: $n = 19$, 2020: $n = 26$, 2021: $n = 13$). APP is situated within the central Ontario transition zone between the boreal forest and Great Lakes-St. Lawrence lowlands (Strickland et al. 2011). The study area runs along the Highway 60 corridor in APP and has an east-west linear configuration. Canada Jays occupy territories of ~130 ha year-round with a mean home-range of 84 ha (± 48 ha; Strickland and Ouellet 2020; Furst et al. 2022). From 1964 to 2022, all territories were monitored twice each year across all years with a mean of 18 territories being occupied (range: 1–48) each monitoring season (from mid-February to the end of April and then again in October; Norris et al. 2013, Sutton et al. 2021b). However, since the 1980s, the number of occupied territories has declined, with only 14 remaining in 2022, which is, in part, due to warmer fall temperatures and an increase in freeze-thaw events, which reduces the quality of cached food, and negatively influences population growth rate and territory occupancy (Waite and Strickland 2001, Sutton et al. 2021b). During the breeding season, nests on territories within the study site were located and monitored beginning mid-February until fledging late-April–mid-May. The location of each nest was recorded using a variety of handheld GPS devices (Garmin GPS Map 64st; Garmin International, Inc., Olathe, KS, USA) with 5–10 m error. Once a nest was found, it was checked regularly every 2–4 days until nestlings were ~14 days old (nestlings remain in the nest for ~23 days). At this time, nestlings ($n = 96$; 2016–2021) were banded with a unique combination of a Canadian Wildlife Service aluminum band and three colored leg bands (Haggie Engraving, Crumpton, MD, USA) to allow for subsequent individual identification.

To monitor post-fledging and natal dispersal movements within and outside of the study area, we used a combination of ground-based and aerial radio-tracking (via aircraft). At the time nestlings were banded (mean age = 14 days \pm standard error [SE] 2 days), we fitted all brood members with 2.5-g radio-transmitters (Model PipAg393, Lotek Wireless Inc., Newmarket, ON, Canada) using adjustable leg-loop harnesses made of Kevlar thread (Rappole and Tipton 1991). We delayed placing transmitters (mean weight = $2.5 \text{ g} \pm 0.1 \text{ SE}$; battery life: 8.5 months) until day 14 when mean nestling body mass was $53.5 \text{ g} (\pm 0.6 \text{ SE})$ to minimize the impact transmitters may have on an individual's behavior and survival (Fair et al. 2010). If a nestling appeared to be smaller than a typical 14-day old, it was not fitted with a transmitter for fear of constricting subsequent growth. Transmitters were deployed on surviving dominant juveniles in autumn 2016 and on nestlings between 07 April and 13 May from 2017 to 2021 resulting in 5 years of both nestling and post-fledging data and 1 additional year of post-sibling expulsion data.

After nestlings were fitted with radio-transmitters, nests were monitored every 3 days until fledging. Fledge date was defined as the first day that one or more young were seen alive outside of the nest or the first day a nest was observed empty if the nest appeared intact and not damaged. To record post-fledging juvenile movements and confirm survival, fledglings were tracked throughout the entire extent of their natal territory (~120 ha) 1–2 times per week until ~late-June to early-July when ejectees left the natal territory and then once per month until the end of the calendar year. We determined that an individual was on the natal territory if it was still being

seen within the boundaries of the natal territory, which is defined by a 450-m buffer around the mean location of all nests on that territory over the entire study period (Strickland et al. 2011, Furst et al. 2022). If an individual was consistently seen away from those areas, it was determined to have dispersed from its natal territory. To track birds on the ground, we followed individuals on foot, by canoe, or a combination of both, and used VHF receivers (SRX600; Lotek Wireless Inc.) and 3-element Yagi directional antennas (Lotek Wireless Inc.) to follow the signal strength of the radio-transmitter until the individual was located visually and its identity confirmed. We also recorded whether it was alone or, if not, the identity of all other accompanying individuals. We considered that a death had occurred if tracking led us to remains of a focal individual or if a radio signal was detected in a log, tree, or burrow for more than one visit and the individual could not be seen.

We estimated the date of sibling expulsion as the mid-point between the last date an individual was detected on the natal territory and the first date it was detected off the natal territory. In most cases, by early- to mid-July of their first year, ejectives had moved sufficiently far (>500 m) that aerial telemetry was required to locate individuals. Aerial telemetry was conducted in a Turbo Beaver fix-winged aircraft with antennas attached to each wing. Telemetry flights followed a series of concentric circles around natal territories and locations of previous detections. We focused efforts of each search generally within 15 km, but occasionally as far as 30 km from an individual's last known location. In the summers of 2016–2018, one aerial flight was conducted once per month from July to September. From 2019 to 2021, we conducted 1 aerial telemetry flight between early-July to late-August to determine where ejectives had settled after expulsion from their natal territory. In all years, after locating individuals with aerial telemetry, we used ground-based radio-telemetry within 48 hr of each flight to determine the fate of ejectives (i.e., alive/dead) and whether the focal individual was with any other jays. A final telemetry flight and subsequent ground-based telemetry was conducted in autumn (approximately late October) to confirm the location that individuals dispersed to in summer and determine their fate (i.e., alive or dead). In autumn, any juvenile still on its natal territory (i.e., a dominant juvenile) was caught using a Potter trap baited with suet and then fitted with a replacement transmitter to permit continued monitoring. The timing of dispersal of dominant juveniles was estimated the following year using a combination of weekly radio-tracking and re-sightings. One-year-old dominant juveniles ($n = 27$) typically remained on their natal territory through the breeding season, but, as reported by Strickland and Waite (2001), they were prevented daily from occupying the area immediately surrounding (within ~100–200 m) the new nest by their parents.

We considered juveniles to be “ejectives” ($n = 19$) if they satisfied one of 3 criteria: (1) Any bird banded as a nestling but was no longer resident on its natal territory after confirming to be alive during expulsion in June or later, while, at the same time, one banded sibling (i.e., the dominant juvenile) remained on the natal territory. (2) Any bird banded as a nestling and later found as a nonbreeding “third bird” (in addition to the resident pair of breeders) on a non-natal territory even if no dominant juvenile remained on the natal territory. We were confident that any such non-natal “third bird” was an ejective because no case has ever been observed

of a dominant juvenile “voluntarily” dispersing from its natal territory merely to become a nonbreeding “third bird” with unrelated adults elsewhere. (3) Any unbanded immigrant found in our study area autumn population counts that was aged as a first-year bird (based on rectrix shape; Pyle 1997). All animal sampling and handling protocols were approved by Environment Canada (Permit #10416) and the University of Guelph's Animal Care Committee (AUP #4003).

To document post-fledging home-ranges, we calculated 100% minimum convex polygons (MCP), which is used to estimate home-ranges of individuals with limited locations (Johnson and Gillingham 2008) for all fledgling Canada Jays with ≥ 10 pre-dispersal locations ($n = 20$). For dominant juveniles ($n = 19$), we estimated natal dispersal distance as the straight-line Euclidean distance (km) between its last observed location on the natal territory and its first location where, in the fall of its second year, it was detected paired with an opposite-sex bird on its first breeding territory (Greenwood and Harvey 1982). For ejectives that were tracked to their first breeding site ($n = 7$), we estimated natal dispersal distance as the straight-line Euclidean distance (km) from the natal territory to the first location on the first breeding territory (i.e., ignoring the intermediately occupied adoptive territory). Because dispersal is considered complete when an individual obtains a breeding position (Greenwood and Harvey 1982), we have included dispersal distances from the natal territory to the first territory in which they bred, but we did not include the distance from the natal territory to an adoptive territory where individuals exist as nonbreeders after their first year.

Molecular Sexing

We sexed all radio-tagged nestlings molecularly since they could not be sexed morphologically as nestlings. DNA was extracted from blood stored in lysis buffer using a modified Chelex protocol (Walsh et al. 1991, Burg and Croxall 2001). Individuals were then sexed using Z43BF/Z43BR primers (Dawson et al. 2016); the forward primer modified with M13 to allow incorporation of a fluorescent marker to run on Licor gel. All polymerase chain reactions (PCRs) were conducted in 10 μ L reactions with genomic DNA, 1 \times μ L clear Flexi buffer (Promega), 2.5 mM MgCl₂, 200 μ M dNTP, 1 μ M each primer, 0.05 μ M M13 primer, and 0.5 units GoTaq (Promega). We used the following thermocycler conditions: 1 cycle of 30 s at 94°C; 35 cycles of 30 s at 94°C, 45 s at 55°C, and 45 s at 72°C, with a final extension for 5 min at 72°C. All PCR products were run on a 6% acrylamide gel. All gels included known positives (1 male and 1 female) to maintain consistency across gels.

Statistical Analyses

Nestling body condition was defined as mass given body size of a nestling at the time of banding (usually ~14 days after hatching) and calculated following Derbyshire et al. (2015) by first quantifying body size with a principal component analysis (PCA; Dunteman 1989, Rising and Somers 1989) from a correlation matrix of length of tarsus, seventh primary feather, and bill. We then used an asymptotic exponential model to regress the body size estimates against mass (see Supplementary Material). The residuals from this regression were used as an estimate of nestling body condition (Derbyshire et al. 2015, Freeman et al. 2021). Negative residuals represented individuals that were assumed to be of below-average nestling

condition compared to individuals with positive residuals that had above-average nestling condition.

To determine the effect of nestling condition on the probability of an individual becoming the dominant juvenile, we used binomial generalized linear mixed effect models (GLMMs) using the *lme4* package (Bates et al. 2015) in the program R version 4.1.1 (R Core Team 2019). Data were analyzed from 28 males (a subset of the 96 radio-tagged individuals) that were alive at the time of sibling expulsion and models were run with a binary response variable (1 = dominant juvenile and 0 = ejectee). We decided to do the analysis on just males because the sample size of known-sex females with a confirmed social status was too small. We included nestling condition as a predictor and territory was included as a random effect to account for multiple sibling groups arising from the same territory over the course of the study. We then compared the model with the nestling condition term against the intercept-only model.

To calculate cumulative annual survival rates of juveniles, we used staggered entry Kaplan-Meier (hereafter K-M) models in the *survival* package in R (Therneau 2015, R Core Team 2019). K-M survival estimates are non-parametric estimates that provide survival probabilities at different times and can only incorporate one predictor, which is different from semi-parametric Cox regression models that can include multiple predictors to understand causes of mortality risk (Therneau 2015, Fox and Weisberg 2019). K-M models were generated for all radio-tagged individuals combined ($n = 96$; this was also the total number of molecularly sexed individuals, a subset of the total 130 nestlings monitored) and then separately for individuals of known social status ($n = 46$) and between sexes (male, $n = 44$; female, $n = 52$). To do this, we created encounter histories for each radio-tagged individual (mean number of time points for each individual = 6.55 ± 0.58 SE; range: 2–35), which included day of transmitter deployment, approximate last day an individual was detected, and if the individual was alive or dead (0 = survived, 1 = mortality). The data were both left-censored (defined by having differences in “entry times” into the survival data) to account for staggered radio-tagging of birds into the sample, and right-censored (defined by having uncertain “exit dates” in dataset) to account for potential transmitter failures. Since multiple individuals were tracked from the same territory, we included territory ID as a random effect in all survival models. We used log-rank tests to compare K-M curves between sexes (male, $n = 44$; female, $n = 52$) and social status (dominant juvenile, $n = 27$; ejectee, $n = 19$).

We then estimated survival rates across separate time periods over the year: banding to fledging (hereafter “late-stage nestling” survival), fledging to sibling expulsion (hereafter “fledgling” survival), sibling expulsion in June to the autumn population count in October (hereafter “first-summer survival”), and autumn population count to the beginning of the following breeding season at approximately 01 March (hereafter “first-winter survival”). To do this, we used raw radio-telemetry detections because the K-M model only calculates survival probabilities over the detection period (i.e., a year in our case), not survival rates for part of the year. Additionally, Cox proportional hazard models are unable to quantify stage-specific rates of survival or account for partial brood losses. Our equations for stage-specific survival complement our K-M and Cox proportional hazard models because they, at a life-stage level, estimate the rate of individuals

that survived, while accounting for differences in dispersal outcomes. It is important to account for partial brood losses and stage-specific survival rates because after expulsion, and even before the expulsion, partial brood losses occur at the expense of the number of potential ejectees.

To estimate late-stage nestling survival ($\phi_{\text{late-stage nestling}}$), we divided the total number of radio-tagged birds at fledging (f) by the total number of birds (inclusive of nestlings that were not tagged but were in the nest with radio-tagged individuals) at banding (t):

$$\phi_{\text{Late-stage nestling}} = \frac{f}{t} \quad (1)$$

To estimate fledgling survival across all individuals in the study ($\phi_{\text{Fledgling}}$), we divided the total number of radio-tagged birds at expulsion (e) by the total number of radio-tagged birds at fledging (f):

$$\phi_{\text{Fledgling}} = \frac{e}{f} \quad (2)$$

First-summer survival ($\phi_{\text{DJ first-summer}}$) for dominant juveniles (DJ) was calculated by dividing the total number of radio-tagged dominant juveniles detected in the autumn population count (d) by the total number of sibling groups on natal territories across the study area at the time of sibling expulsion (g):

$$\phi_{\text{DJ first-summer}} = \frac{d}{g} \quad (3)$$

The number of sibling groups accurately represented the number of dominant juveniles alive at expulsion because one offspring from each brood becomes a dominant juvenile.

To estimate first-summer survival for ejectees ($\phi_{\text{EJ first-summer}}$), we first calculated the number of radio-tagged ejectees alive at expulsion by subtracting the number of sibling groups at expulsion (i.e., number of dominant juveniles at expulsion; g) from the total number of juveniles alive at the time of expulsion (j). We then divided the number of ejectees alive in autumn (a) by the number of ejectees present at expulsion ($j - g$).

$$\phi_{\text{EJ first-summer}} = \frac{a}{j - g} \quad (4)$$

To estimate first-winter survival ($\phi_{\text{DJ first-winter}}$) for dominant juveniles, we divided the total number of radio-tagged dominant juveniles at the start of the breeding season (d_w) by the total number of radio-tagged dominant juveniles the previous autumn (d).

$$\phi_{\text{DJ first-winter}} = \frac{d_w}{d} \quad (5)$$

Similarly, to estimate first-winter survival of ejectees ($\phi_{\text{EJ first-winter}}$), we divided the total number of radio-tagged ejectees at the start of the breeding season following banding, (a_w) by the total number of radio-tagged ejectees the previous autumn (a):

$$\phi_{\text{EJ first-winter}} = \frac{a_w}{a} \quad (6)$$

To determine how the instantaneous risk of mortality may be influenced by intrinsic and extrinsic factors (Johnson et al. 2004, Murray and Patterson 2006), we used Cox proportional hazards model (*coxph* function in the *survival* package in Program R; Therneau 2015) with the encounter data for individuals of known social status and sex ($n = 46$). Proportional hazard functions measure the instantaneous risk of mortality per observation, given that an individual has

survived to that point. Cox proportional hazard models are advantageous as they left-censor individuals that entered the sample at different times (i.e., when nestlings were banded and tagged) and have the ability to right-censor radio-tag failures (Johnson et al. 2004). The encounter history dataset included day of entry, approximate day of exit, and absolute duration in days for that interval. Prior to running hazard models, we examined whether the assumptions of Cox proportional hazard models were met by the survival data using model diagnostics on scaled Schoenfeld residuals with the *cox.zph* function in Program R (Fox and Weisberg 2019). All proportional hazard models included predictors such as sex, social status, fledge date, and nestling body condition and an interaction between social status and sex. We also included year as a random effect to account for varying number of transmitter deployments each year. The assumptions of proportional hazards were met for the global model that included the predictors: sex, social status, fledge date, and nestling body condition ($\chi^2 = 3.5, p = 0.10$).

For the analyses predicting the dominant juvenile and mortality risk, we used the *MuMIn* package (Bartón 2020) to construct a set of models that represented all possible combinations of fixed effects in addition to each variable alone. We found no evidence that any predictors of the probability of becoming the dominant juvenile (nestling condition) or Cox proportional hazards (nestling condition, sex, social status, or fledge date) were colinear ($r < 0.3$). We did have data on seven female dominant juveniles and while these were not included in the analyses examining causes of social dominance, they were included in the survival analyses. To rank models for each model set, we used an information-theoretic framework (Burnham and Anderson 2002). We used the function *aictab* from the *AICmodavg* package (Mazorelle 2020) to rank models according to the second-order Akaike information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002) and Akaike weights (w_i), which provides cumulative support for each model when accounting for all other models. We considered any model with $\Delta AIC_c < 2$ to be a competing model (Burnham and Anderson 2002). When there was no clear top model, we performed model averaging over the candidate set of models using the *MuMIn* (Bartón 2020) and the *AICmodavg* package (Mazorelle 2020) to determine the direction and magnitude of the effect of each explanatory variable using relative variable importance from summed model weights (Burnham and Anderson 2002). We made model inferences for all mixed effect models using 85% confidence intervals (Arnold 2010). All confidence intervals were calculated using the *stats* package in R (R Core Team 2019). All statistics from stage-specific survival estimates and Cox proportional hazard and K-M models are reported as means \pm standard errors (SE).

RESULTS

Fledging Phenology and Dispersal Movement

Of the 96 radio-tagged individuals (from the total 130 nestlings banded on days 11–14), 46 survived to be assigned as either dominant juveniles or ejectees. Among all nests monitored over the 5-yr period, fledging dates of nestlings ranged from 17 April to 26 May with a mean of 01 May \pm 8 days. The average number of days between banding and fledging was 10 \pm 4 days. Across radio-tagged individuals with at least 10 ground-based telemetry locations ($n = 20$ individuals; mean:

TABLE 1. Model selection results for predicting the probability of becoming a dominant juvenile in male Canada Jays. Fixed effects for each model are shown, as well as the total number of parameters in a model (k), AIC_c , ΔAIC_c , and AIC_c weight (w_i).

Model	k	AIC_c	ΔAIC_c	w_i
Nestling condition	3	33.1	0.00	0.96
Intercept	2	39.6	6.54	0.03

15 \pm 5 locations per individual), the mean MCP home-range of fledglings still on their natal territories was 48 ha \pm 33 ha (range: 10–140 ha). For individuals tracked into their second year, dominant juveniles ($n = 19$) dispersed a median of 2.4 km (inter-quartile range: 2.9) after leaving their natal territory to their first place of reproduction. Ejectees ($n = 7$) dispersed a median of 4.5 km (inter-quartile range: 3.3) from their natal territory to where they acquired breeder status (i.e., ignoring the intermediate adoptive territory).

Predictors of Social Status

Of the 46 radio-tagged individuals of known social status tracked in their first year, 30 individuals originated from mixed-sex broods. Twenty-seven individuals were dominant juveniles, with 74% (20 of 27) being male (very close to the proportion of male dominant juveniles considered to be males based on comparisons of their weights with those of behaviorally-sexed breeding adults [0.76; $n = 207$] recorded in the long-term [1980–2022] APP data, D.S. and D.R.N. personal observations). Of the radio-tagged males, 75% (15 of 20) originated from mixed-sex broods. In contrast, of the 7 cases (26%, 7 of 27) where the dominant juvenile was female, only 2 were from mixed-sex broods, and no males remained in these broods at the time of expulsion.

The model that included nestling condition best predicted whether an individual male nestling became a dominant juvenile (Table 1). Male nestlings that were of better body condition ($\beta = 0.39, z = 1.71, 85\%$ CIs: 0.10, 1.28; Figure 1) were more likely to become the dominant juvenile than males of poorer nestling condition.

Timing of Sibling Expulsion

Between 2016 and 2021, we observed 4 fights between siblings during the post-fledging stage. We determined that dominant juveniles had finished expelling their subordinate siblings from the natal territory by 6.8 \pm 2.7 weeks after fledging (see Methods). For ejectees ($n = 19$), median dates between the last detection on the natal territory and the first detection outside the territory ranged from 01 June to 13 July with a mean of 22 June \pm 10 days. After expelling their siblings, dominant juveniles remained on the natal territory for an average of ~13 months after expelling their siblings (dispersed on 29 July \pm 60 days in their second year) with a range of 4 months (i.e., October of their first year) to as long as 28 months (October of their third year).

Estimates of Survival and Predictors of Mortality Risk

We estimated survival from the date of transmitter deployment (14 days after hatching) to the end of an individual's

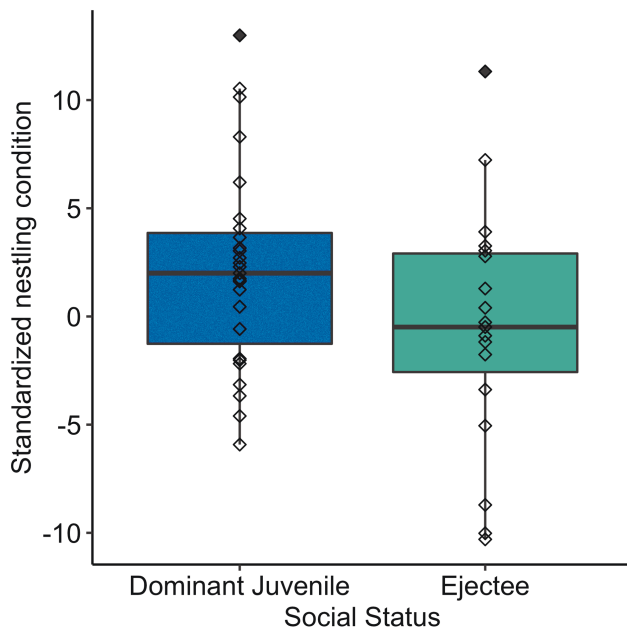


FIGURE 1. A boxplot comparing the standardized nestling body condition (i.e., residual body condition ~11–14 days after hatching) between first-year Canada Jays that become the dominant juvenile ($n = 27$) and individuals that were ejectees ($n = 19$). Thick lines for each box represent the median, the upper and lower limits of each box represent the 25th and 75th quartiles, vertical lines represent the standard error of the data, and solid black points are outliers. Canada Jay graphic was created by Young Ha Suh.

first year using K-M cumulative survival models. Cumulative first-year annual survival (ϕ) for Canada Jays was 0.28 ± 0.04 (95% CIs: 0.20, 0.37) and was significantly lower for females ($\phi = 0.12 \pm 0.06$; 95% CIs: 0.05, 0.27) than males ($\phi = 0.41 \pm 0.05$; 95% CIs: 0.29, 0.55; log-rank test, $\chi^2 = 4.1$, $p = 0.04$; Figure 2A) without controlling for dominance status, and lower for ejectees ($\phi = 0.47 \pm 0.12$; 95% CIs: 0.28, 0.78) than dominant juveniles ($\phi = 0.80 \pm 0.07$; 95% CIs: 0.66, 0.97; log-rank test, $\chi^2 = 6.7$, $p = 0.01$; Figure 2B).

We then estimated survival rates for separate life-stages for all radio-tagged individuals. Across all individuals combined (2016–2021), survival for late-stage nestlings (i.e., 14 days after hatching to fledging) was 0.92 (120 of 130) and survival for fledglings (i.e., from fledging to sibling expulsion) was 0.61 (74 of 120; Figure 3B). The first-summer survival (i.e., sibling expulsion to the autumn population count) of radio-tagged dominant juveniles (0.84; 27 of 32) was substantially higher than ejectees (0.45; 19 of 42; Figure 3B), but the first-winter survival rate (i.e., autumn population count to the beginning of the following breeding season) for radio-tagged dominant juveniles (0.85; 23 of 27) was similar to that of ejectees (0.73; 14 of 19; Figure 3B).

Finally, we used Cox proportional hazard models to determine factors influencing mortality rates of juveniles between the date of transmitter deployment to the end of an individual's first year. All four top models within $2\Delta AIC_c$ included social status (dominant juvenile or ejectee) while 3 of the 4 included sex, 2 of the 4 included nestling body condition, and 1 included fledge date (Table 2). Based on model-averaging, the mean relative variable importance (RVI) of social status, sex, nestling body condition, and fledge date were 1.0, 0.75, 0.52, and 0.20, respectively. The model-averaged coefficients suggested

TABLE 2. Model selection results for explaining the probability of mortality risk in Canada Jays using Cox Proportional Hazard models. Factors examined in the top models included social status (dominant juvenile or ejectee), fledge date, sex of the focal individual and nestling body condition (body condition in the nest prior to dispersal). Fixed effects for each model are listed as well as the total number of parameters in a model (k), AIC_c , ΔAIC_c , and AIC_c weight (w_i).

Model	k	AIC_c	ΔAIC_c	w_i
Social status + sex + nestling condition	4	97.13	0.00	0.23
Social status + sex + fledge date	4	97.66	0.53	0.18
Social status + sex	3	97.91	0.79	0.16
Social status + nestling condition	3	98.11	0.98	0.14
Social status + fledge date	3	99.40	2.27	0.08

that mortality risk was substantially higher in females than males ($\beta = 1.14$, $z = 1.93$, 85% CIs: 0.29, 2.00). Individuals of above-average nestling condition had lower mortality risk compared to individuals with below-average nestling condition ($\beta = -0.10$, $z = 1.83$, 85% CIs: -0.17, -0.02). The day-to-day mortality risk of dominant juveniles was slightly lower than ejectees ($\beta = -0.66$, $z = 1.03$, 85% CIs: -1.57, 0.25). Individuals that fledged later in the season were also slightly more likely to die compared to jays that fledged earlier in the season ($\beta = 0.04$, $z = 1.67$, 85% CIs: 0.006, 0.08).

DISCUSSION

In several ways, our results increase and improve our understanding of how sibling conflict can lead to differences in dispersal behavior and consequently rates of juvenile survival in group-living species (Ligon and Stacey 1991, Ekman et al. 1999, Sparkman et al. 2011, Kingma et al. 2016). First, we were able to estimate survival during each life-stage for first-year juvenile Canada Jays and found very high (92%) late-stage nestling survival, lower (61%) fledgling survival, substantially greater first-summer survival of dominant juveniles (84%) than ejectees (45%), and a smaller difference in their first-winter survival rates (85% in dominant juveniles vs 73% in ejectees). As hypothesized, the large difference between our dominant juvenile and ejectee first-summer survival rate estimates drives their overall difference in first-year survival and provides support that juveniles forced to leave their natal territories 6–7 weeks after fledging suffer significantly greater mortality than the philopatric dominant juveniles that were responsible for expelling their siblings. Concerning the sex of dominant juveniles, Strickland (1991) suggested that if male Canada Jay fledglings are invariably dominant over females as in some other jays (Ekman et al. 2002, Griesser et al. 2008, Suh et al. 2020), then female dominant juveniles should only arise from all-female broods. Our results support this idea but only with the crucial further clarification that it is the sex composition of the fledgling brood at the time of expulsion that matters. In other words, a mixed-sex nestling brood can give rise to a female dominant juvenile only if it loses its male(s) before the time of expulsion.

Our results are consistent with previous studies on group-living species (Gienapp and Merilä 2011, Cozzi et al. 2018, Sparkman et al. 2011, Suh et al. 2020) that show juveniles who retain access to the natal territory are more often males

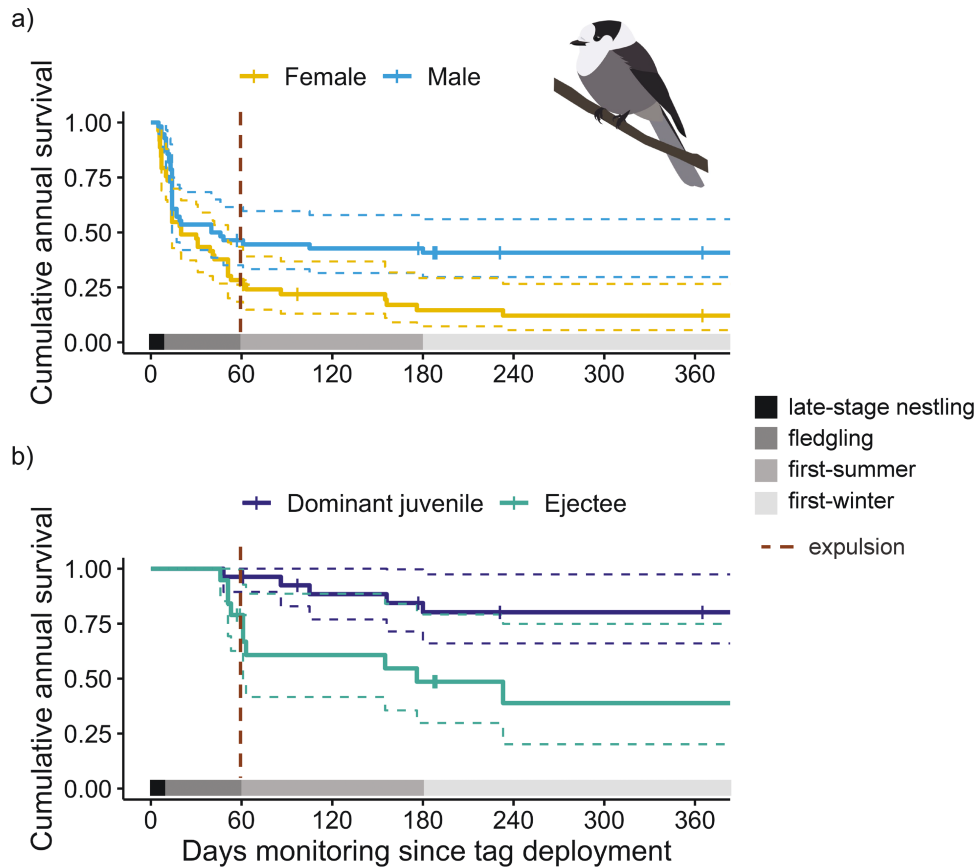


FIGURE 2. Kaplan-Meier plots of the cumulative annual survival of (A) male and female ($n = 96$) and (B) dominant juvenile and ejectee ($n = 46$) radio-tagged juvenile Canada Jays in Algonquin Provincial Park, Ontario, 2016–2021. Solid lines indicate the estimates of cumulative annual survival and dotted lines represent upper and lower 95% confidence intervals. Vertical ticks represent right-censored data points. Shading on the bottom of each panel indicates the different life-stages of first-year Canada Jays and the dotted line represents time of sibling expulsion.

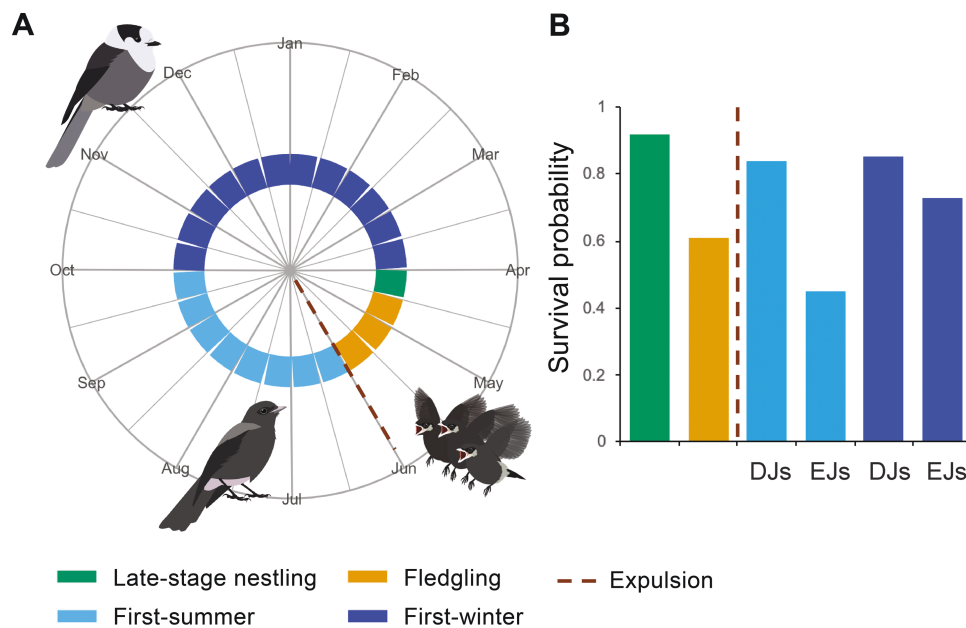


FIGURE 3. Stage-specific survival probabilities for late-stage nestling, fledgling, first-summer, and first-winter survival of first-year Canada Jays. Panel (A) shows a circular schematic of when each life stage occurs (thick lines) and panel (B) shows survival probabilities for each life stage for juveniles with first-summer and first-winter survival probabilities shown separately for dominant juveniles and ejectees. Dotted line in both panels indicates sibling expulsion. Canada Jay graphics were created by Young Ha Suh.

or individuals of above-average nestling condition due to their competitive advantage over siblings. Such relationships between retaining access to the natal territory and individual quality may be driven by evolutionary strategies to maximize individual fitness. For example, in 1 of 2 other species that are in the same genus as Canada Jays, Siberian Jay siblings that were bigger and more dominant were more likely to remain on the natal territory after expelling its siblings, which ultimately led to the acquisition of higher-quality breeding territories than subordinates (Ekman et al. 2001, Ekman et al. 2002, Gienapp and Merilä 2011). Interestingly, our results differed from those of Freeman et al. (2021), who provided evidence that nestling condition did not predict juvenile social status in Canada Jays. This is likely because the analysis of Freeman et al. (2021) was restricted to first-summer survivors, whereas our sample included all individuals regardless of whether they survived to the fall.

An important potential limitation of Strickland's (1991) estimates of first-year survival was that ejectees disappear from their natal territories < 2 months after fledging with no guarantee that surviving individuals will settle on territories within the study area. Strickland (1991) attempted to circumvent this problem by assuming that the number of ejectees banded as nestlings within the study site that had dispersed and survived unobserved outside of the study area would equal the number of unbanded juvenile immigrants nonbreeders observed in autumn (i.e., assumed to be ejectees dispersing into the study area from outside). Using this approach, it was estimated that the overall first-summer (banding to fall) survival was at least 0.48 for dominant juveniles and at least 0.15 for ejectees. However, Strickland (1991) was unable to quantify the numbers of potential dominant juveniles and ejectees just before the expulsion and instead relied on the number of nestlings that were banded in the nest, which does not account for mortality between banding and expulsion. Using radio-telemetry, we were able to build on the work of Strickland (1991) by tracking juvenile both within and outside of the study area using a combination of re-sighting data and aerial and ground telemetry. In doing so we gained valuable insights on the timing of sibling expulsion, rates of first-year survival, and outcomes of dominant juveniles and ejectees.

We surmise that the significant survival benefits associated with forgoing reproduction and remaining as the "extra" bird in Canada Jays, may be attributed to the fact that nonbreeding individuals on their natal or non-natal territory are able to access the cached food of the existing breeders. Previous studies have hypothesized that one potential explanation for the development of juvenile social dominance rankings is that by fighting to remain on the natal territory and forcing siblings out, dominant juveniles get competition-free opportunities to accumulate enough cached food to make over-winter survival possible (Strickland 1991, Ragheb and Walters 2011, Sorensen et al. 2022). For instance, in Siberian Jays (Ekman et al. 2002) and Columbian ground squirrels (*Urocitellus columbianus*; Wiggett and Boag 1992), socially dominant juveniles drive subordinate siblings out of the natal territory, leading to access to cached food on the natal territory without competition of siblings. For Canada Jays, it may also be particularly beneficial for a dominant juvenile to acquire access, again free of competition, to an inadvertent "parental subsidy" of stored food through closely associating with the adults, watching them store food, and subsequently pilfering and re-hiding some parental caches (Strickland 1991,

Sorensen et al. 2022). Like dominant juveniles, ejectees must spend their first summer and autumn caching their own food and it was hypothesized by Sorensen et al. (2022) that through a close association with the local breeding pair, ejectees gain a similar benefit to dominant juveniles by pilfering cached food of adults, as well as profiting in other ways from their experience (e.g., learning appropriate foods and foraging tactics, predator identification). Although breeding pairs seem to gain no indirect fitness advantage by accepting the presence of an unrelated ejectee, such acceptance is common in Canada Jays (Strickland 1991, Sorensen et al. 2022; Furst et al. 2023), and our experience is that it is often difficult to discern behavioral differences between a trio composed of an ejectee with unrelated adults and one composed of a dominant juvenile with its parents.

In Canada Jays, dominant juveniles gain direct fitness benefits from ejecting their siblings, which outweighs the indirect fitness costs that they suffer from their siblings' increased risk of mortality after eviction (Furst et al. 2023). For dominant juveniles, the early timing of expulsion (i.e., ~6–7 weeks post-fledging) can be understood as permitting the dominant juvenile to maximize the length of time during the summer and autumn when it will be free of sibling competition as it accumulates critical food stores of berries, fungi, carrion, and invertebrates needed to survive its first winter. By the same token, the timing of expulsion in Canada Jays also results in maximizing the time, assuming they survive, that ejectees will have available for the same task on their adoptive territories. Our finding that the first-winter (Autumn to March) survival of ejectees (73%) was almost as high as that of dominant juveniles (85%) supports this idea. The reason ejectees had slightly lower first-winter survival than dominant juveniles were likely because our survival analysis included all ejectees, not just ejectees that were adopted, and, therefore, reaped the benefits of being in a trio.

One explanation for the acceptance of juveniles by either related or unrelated adults on their territories over the winter is that group-living arises in response to having a "safe haven" or increased vigilance for predators (Ekman et al. 1999, Kokko and Ekman 2002). In many vertebrate species, predation risk has been shown to be an important factor driving delayed dispersal (Ekman et al. 2000, Heg and Taborsky 2010, Groenewoud et al. 2016). With the absence of extended parental care and true cooperative breeding, in addition to improved survival of one of their offspring, predator detection may be another reason that parents allow the dominant juvenile to stay, and why ejectees are accepted by unrelated breeders on their territory, despite the fact that neither dominant juveniles nor ejectees help at the nest. However, even though the presence of dominant juvenile or an ejectee with an unrelated pair does not lead to long-term reproductive benefits for the breeders (Furst et al. 2023), the potential survival differences between pairs with a dominant juvenile or ejectee and those without have yet to be explored in Canada Jays.

In some species, delayed dispersers provide alloparental care to the offspring of the next generation, thus benefiting their own inclusive fitness (Koenig et al. 1992, Groenewoud et al. 2016). In most cooperatively breeding species, all nonbreeding members of a family group will contribute to helping at the nest (Koenig et al. 1992, Nelson-Flower et al. 2012, Suh et al. 2020). However, in Canada Jays, helping behavior has only been observed after the nestlings have fledged and then only rarely (Waite and Strickland 1997, Strickland and Waite 2001).

Thus, it is unlikely that the benefits of having a juvenile on the territory is related to post-fledging helping behavior. This is also reinforced by the fact that adults may accept the presence of an unrelated juvenile (ejectee) over the winter, which neither helps, nor indirectly improves, the long-term reproductive success of the breeders (Furst et al. 2023).

Our stage-specific survival estimates provide evidence that the fledgling period is a limiting juvenile life-stage for Canada Jays. This is consistent with other studies on juvenile birds that indicate that the fledgling period, particularly within the first 3 weeks after fledging, is when individuals experience the highest rates of mortality (Moore et al. 2010, Ausprey and Rodewald 2013, Cox et al. 2014). Shortly after leaving the nest juveniles are not skilled fliers and, for at least part of this time, are nutritionally dependent on their parents, making them more susceptible to predation and starvation (Ausprey and Rodewald 2013, Raybuck et al. 2020). In Canada Jays, juveniles may be vulnerable to predation by migratory raptors (e.g., Sharp-shinned Hawks [*Accipiter striatus*] and Merlins [*Falco columbarius*]) that usually return to their boreal forest breeding grounds around the time that Canada Jays fledge. By examining survivorship throughout the annual cycle, our new stage-specific measures of survival could have important implications for our understanding of the long-term dynamics of this declining population.

Together, this research quantifies the causes and consequences of early-life sibling rivalries in Canada Jays. We not only improve our understanding of early-life sibling conflicts in Canada Jays and its effect on stage-specific survival probabilities, but also provide new evidence to suggest that the benefits of remaining on the natal territory are driven by first-summer survival. We also demonstrate that this reduction in survival occurs in summer and that overwinter survival of dominant juveniles and ejectees are similar. Our work provides a valuable perspective on the social and environmental drivers of delayed dispersal in wild birds, particularly for species where group-living is not primarily governed by cooperative behaviors.

Supplementary material

Supplementary material is available at *Ornithology* online.

Acknowledgements

We thank Rick Stronks and David Legros for supplying equipment and granting permission to access backcountry sites. We thank all the students and field assistants throughout the years who have played pivotal roles in collecting and managing the long-term data. We thank Young Ha Suh for contributing beautiful graphics of Canada Jays. The authors acknowledge that they lived and worked on the traditional lands of the Omàmiwininiwag (Algonquin) and Anishinabewaki peoples for this study.

Funding statement

This research was supported by a Discovery Grant from the Natural Sciences and Engineering Council of Canada (D.R.N.), the American Ornithological Society (M.F.), the Society of Canadian Ornithologists (M.F.), the Wilson

Ornithological Society (M.F.), and the Animal Behaviour Society (M.F.). M.F. was supported by the Weston Family Foundation Fellowship Program, a program of the Wildlife Conservation Society Canada funded by the Weston Family Foundation.

Ethics statement

All animal sampling and handling protocols were approved by Environment Canada (Permit #10416) and the University of Guelph's Animal Care Committee (AUP #4003).

Conflict of interest statement

To the best of our knowledge, the named authors have no conflict of interest to declare.

Author contributions

M.F., D.S., A.O.S., N.E.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. The methodology used was developed by M.F., D.S., A.O.S., N.E.F., T.G., B.A.G., and D.R.N. and data collection was done by M.F., A.O.S., D.R.N., D.S., and N.E.F. D.R.N. was in charge of project administration, resources, supervision, and validation. M.F. wrote the manuscript, and it was reviewed and edited by all authors. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Analyses reported in this article can be reproduced using the data (<https://doi.org/10.6084/m9.figshare.25345210>) and code (<https://doi.org/10.6084/m9.figshare.25345357>) from figshare.

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