



## Research

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# Early-life sibling conflict in Canada jays has lifetime fitness consequences

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While delaying natal dispersal can provide short-term benefits for juveniles, lifetime fitness consequences are rarely assessed. Furthermore, competition for limited positions on a natal territory could impose an indirect fitness cost on the winner if the outcome has negative effects on its siblings. We use radio-tracking and 58 years of nesting data in Ontario, Canada to examine the lifetime fitness consequences of sibling expulsion in the Canada jay (*Perisoreus canadensis*). Six weeks after fledging, intra-brood dominance struggles result in one 'dominant juvenile' (DJ) remaining on the natal territory after expelling its subordinate siblings, the 'ejectees' (EJs). Despite an older age-at-first-reproduction, DJs produced more recruits over their lifetime and had higher first-year survival than EJs, leading to substantially higher direct fitness. Even though DJs incurred an indirect fitness cost by expelling their siblings and there was no evidence that their presence on the natal territory increased their parents' reproductive output the following year, they still had substantially higher inclusive fitness than EJs. Our results demonstrate how early-life sibling conflict can have lifetime consequences and that such fitness differences in Canada jays are driven by the enhanced first-year survival of DJs pursuant to the early-summer expulsion of their sibling competitors.

## 1. Introduction

Delayed dispersal of juveniles and forgoing the direct fitness benefits of breeding at the first opportunity is often attributed to potentially greater indirect benefits of helping parents to raise younger siblings [1–6]. However, there are some species where juveniles delay dispersal but show little or no helping behaviour [7–10], suggesting that direct fitness benefits, such as accessing limited resources or using the natal territory as a safe haven while searching for breeding vacancies [9,11], are sufficient to explain delayed dispersal [12–15]. Even though delayed dispersal can yield both direct and indirect fitness benefits [8,9], such benefits could be reduced or cancelled out by the negative consequences of kin competition. In many cases, the consequences of kin competition are the death of some siblings within the nest [16,17]. A much less common outcome of kin competition can result in a reduction in brood size after fledging, whereby siblings compete to remain on the natal territory, eventually leading to a winner who could impose a fitness cost to its siblings via their expulsion from the natal territory [7,11,16,17]. While previous studies have shown that delayed dispersal can lead to short-term reproductive or survival benefits [9,12,18,19], less is known about the lifetime fitness benefits of delayed dispersal [8,18] or the potential costs of denying those benefits to siblings [15].

We used radio-tracking and long-term mark-resighting data from Canada jays (*Perisoreus canadensis*) in Algonquin Provincial Park (APP), Ontario, Canada to

examine the inclusive fitness consequences of sibling competition after fledging from the nest. The Canada jay is a resident, scatter-hoarding passerine of North American boreal and subalpine forests that relies on remembering the locations of previously made caches of perishable food for over-winter survival and, to a variably lesser extent, for its late-winter breeding [20]. Approximately six weeks after fledging, juvenile brood members begin to relentlessly attack each other in apparent attempts to drive siblings away from the family group [7]. After approximately 10 days, the struggle ends with a single 'dominant juvenile' (DJ), usually the individual with the highest body condition as a nestling, and a male if the brood still contains one at the time of the expulsion, effectively expelling its subordinate siblings, the 'ejectees' (EJs), from the natal territory [7]. This is a unique form of brood reduction because in virtually all other species where brood reduction occurs, siblings are attacked during the nestling stage, not after fledging [16,17]. After losing the expulsion struggle, EJs do not float or attempt to remain on the natal territory away from the parental-DJ trio. Instead they normally seek to establish a close relationship with an unrelated pair on an 'adoptive' non-natal territory where the same-year nesting attempt was unsuccessful and where there is consequently no DJ that can resist the arrival of an EJ [7]. The palaeartic Siberian jay (*Perisoreus infaustus*) shares these same brood-reduction behaviours [8,11] and, to our knowledge, is the only other bird in the world to do so.

In Canada jays, the early expulsion of subordinate siblings by DJs and the post-expulsion behaviour of EJs are both thought to be adaptive because they maximize the competition-free time individuals in each juvenile class have, during their first summer, to accumulate the food caches on which their first-winter survival will depend [7,21]. DJs and EJs both occasionally replace disappeared breeders in their first summer, but normally they remain on their respective natal and adoptive territories as part of essentially identical-pair non-breeder trios until their second summer, at which point they typically disperse to their first breeding position (on the second territory to be occupied by DJs and the third by EJs). One-year-old DJs still on their natal territory are aggressively excluded by their parents from the area around their active nest [22], but they occasionally feed fledglings [23].

To determine the inclusive fitness of juvenile Canada jays, we first estimated their direct fitness by combining 58 years of data on adult reproductive success (ARS) of DJs and EJs with estimates of the probability of reaching adulthood (i.e. first-year survival) from radio-tracking [24]. In most cases, calculating indirect fitness is associated with a 'positive' action, commonly as a result of helping a relative raise their young [17,25–27]. However, indirect fitness could also arise from a 'negative' action on relatives. For example, Lucas *et al.* [27] demonstrated a negative indirect fitness effects in a social species, but there have been very few examples in wild animals [27]. Here, we calculate the indirect fitness consequences of a negative action via the ejection of siblings from the natal territory, a behaviour that has never before been linked to inclusive fitness.

To estimate possible indirect fitness effects of DJs, we calculated the potential benefit of remaining on the territory via alloparenting behaviour in the fledgling period and the potential cost of expelling siblings out of the natal area via

a decrease in survival of expelled siblings. We then used long-term data to determine whether the presence of a one-year-old DJ increased the reproductive output of its parents the following year and then combined long-term reproductive data with survival rates to determine the indirect fitness cost of the DJ ejecting its siblings. We then used the measures of direct and indirect fitness to estimate inclusive fitness for DJs and EJs. Given that siblings fight aggressively to stay on the natal territory [7], we hypothesized that DJs would have higher inclusive fitness than EJs due to differences in direct fitness, despite the cost of prevailing in the struggle and expelling their siblings from the natal territory.

## 2. Methods

### (a) Study area, study species and data collection

We estimated inclusive fitness of DJs and EJs in a resident population of Canada jays in Algonquin Provincial Park (APP), Ontario, Canada (45° N, 78° W; 760 000 ha) that has been monitored along the Highway 60 corridor from 1964 to 2022 [28]. In the late summer and early fall, APP Canada jays begin to scatter-hoard perishable food items under tree bark or lichens, which they rely on for over-winter survival and nesting beginning in the late winter [18]. As many as 30 territories have been monitored twice each year (from mid-February to approx. end of April and then in October [29]), but since the 1980s, the number of occupied territories has declined, with only 14 remaining in 2022. Nests were located while under construction (mid-February to mid-March) and monitored every 3–5 days until failure or the banding of nestlings, at 11–14 d, with a unique combination of a Canadian Wildlife Service aluminium band and three colour leg bands. DJs in the long-term dataset (1964–2022) were birds banded as nestlings and found in our fall censuses as the sole brood-member still on the natal territory closely associated with its parents. EJs were identified as such if they satisfied one of three criteria: (i) birds banded as nestlings but found to be resident in their first fall on a non-natal territory (as either a 'third bird' with unrelated adults or as an apparent replacement for a former local breeder) while at the same time, a DJ was still present on the natal territory; (ii) birds banded as nestlings but found to be resident in their first fall on a non-natal territory as a 'third bird' with unrelated adults while at the same time no DJ was still resident on the natal territory; (iii) initially unbanded immigrants to the study area that were aged as first-year birds when they were captured and banded in the fall census as 'third birds' on territories where the same-year nesting was known to have failed or the nestlings had been banded. Among 561 first-fall individuals so identified, 49 DJs and 41 EJs eventually became breeders in our study area.

Separate from these 90 individuals analysed from the long-term dataset, we used seven years (2016–2022) of radio-tracking data [24] from 27 DJs and 19 EJs to quantify DJ versus EJ differences in first-fall status (single non-breeder on natal or adoptive territory versus filling a breeding vacancy on a non-natal territory versus possibly being alone on an otherwise vacant territory; table 1) and first-year survival. Of the radio-tracked individuals, 89% (41/46) did not have data on survival and ARS because they left the study population, while 11% (5/46) became breeders in the study area and were included in the 90 individuals analysed from the long-term dataset. We used estimates of the probability of reaching adulthood for direct fitness calculations (see below) since DJs and EJs have similar survival rates once they have achieved breeding status (mean lifespans of DJs and EJs that achieve breeding status according to the long-term data were, respectively,  $4.49 \pm 0.47$  years and  $5.34 \pm 0.54$  years). All animal sampling and handling

**Table 1.** Post-expulsion fates of radio-tagged, first-year juvenile Canada jays in Algonquin Provincial Park, ON from 2016 to 2022. Data only include individuals that survived until their first fall.

post-expulsion fate	DJs	EJs
1. remained on natal territory through first fall	89% (24/27)	0% (0/19)
a. moved to breeding position in second year	71% (17/24)	–
b. failed to find a mate after dispersing in second year	8% (2/24)	–
c. died after first winter while still on natal territory	21% (5/24)	–
2. left natal territory before first fall	11% (3/27)	100% (19/19)
a. settled with unrelated pair by first fall	0% (0/3)	53% (10/19)
b. found alone on new territory by first fall	0% (0/3)	21% (4/19)
c. found on new territory with apparent mate by first fall	100% (3/3)	26% (5/19)

protocols were approved by the Canadian Wildlife Service (permit no. 10416) and the University of Guelph's Animal Care Committee (AUP no. 4003).

### (b) Inclusive fitness of dominant juveniles and ejectees

To calculate inclusive fitness, we added estimates of direct ( $d$ ) and indirect fitness ( $f$ ) using a combination of long-term data and previously published radio-tracking data [24]. Below, we describe calculations of both direct and indirect fitness.

#### (i) Estimating direct fitness

To calculate direct fitness ( $d$ ), we multiplied the estimate of first-year survival from radio-tracking data [24] for EJs ( $\phi^{\text{AnnualEJ}}$ ) and DJs ( $\phi^{\text{AnnualDJ}}$ ) by ARS (defined as the observed total reproductive output [determined by juvenile recruits] produced by birds that survived to make it to a breeding position). from the long-term data ( $o$ ):

$$d^{\text{DJ}} = \phi^{\text{AnnualDJ}} * o^{\text{DJ}} \quad (2.1)$$

$$d^{\text{EJ}} = \phi^{\text{AnnualEJ}} * o^{\text{EJ}} \quad (2.2)$$

For  $\phi$ , we used radio-tracking data analysed from 19 EJs and 27 DJs over seven years to estimate first-year survival for individuals that either remained in the study population ( $n=5$ ) or dispersed out of the study area ( $n=41$ ) [24]. To estimate  $o$ , we used long-term reproductive data from individuals of known juvenile social status that became breeders within the study population ( $n=49$  DJ (male = 34, female = 15),  $n=41$  EJ (male = 19, female = 22)). Five of the 41 EJs were first-year immigrants into the study population. As an estimate of  $o$ , we used the mean total number of recruits, defined as the total number of offspring sired by that individual that were observed in the study population during the October population counts. It is important to note that  $o$  was a conservative estimate of ARS because EJs and DJs will have produced offspring that dispersed out of the study area. To determine whether ARS (defined by the mean total recruits) differed between DJs and EJs, we ran a series of

generalized linear models (GLMs, Poisson distribution, log link function) with total number of recruits per individual as the response variable and social status (DJ or EJ), sex (determined with molecular methods; [24]), and maximum known age (oldest confirmed age of an individual before disappearance) as fixed effects. Due to limited sample size, we could not include environmental variables known to influence reproductive performance as predictors [28,29]. We then took the mean number of recruits for each juvenile class from the raw long-term data to estimate  $o$ . As a second estimate of  $o$ , we also followed the same procedure as above for the total number of nestlings that survived to banding (approx. day 11–14).

#### (ii) Estimating indirect fitness

To calculate indirect fitness of DJs,  $f$ , we used the following equation:

$$f = (\rho - \varepsilon) \quad (2.3)$$

where  $\rho$  is the increase in offspring recruited by parents that is attributable to the presence of a DJ (possibly through provisioning of younger siblings during the fledgling period) and  $\varepsilon$  is the cost of ejecting siblings. To determine whether  $\rho > 0$ , we used generalized linear mixed models (GLMMs; Poisson distribution, log link function) to examine whether the presence of a DJ influenced the number of recruits of its parents in a given breeding season ( $n=125$  nesting attempts with a DJ present,  $n=652$  nesting attempts of breeders without a DJ). In these models, we also included ages of the breeders [30] and territory quality (defined as the proportion of conifers on the territory; [31]) as fixed effects and individual identity of each parent and year as random effects because reproductive output varies between years. If there was no significant effect of DJ presence on parent reproduction, we assumed the value for  $\rho$  to be zero. We also used the same GLMM model structure as we did to test the effect of DJ presence on parent reproduction to test the assumption that EJs do not have any indirect fitness benefits to the unrelated breeders that they join. For this analysis, we examined whether the presence of an EJ influenced the number of recruits of the adoptive breeders in a given breeding season ( $n=52$  nesting attempts with an EJ present,  $n=652$  nesting attempts of breeders without an EJ). Similar to the analysis on DJs, if there was no significant effect of EJ presence on unrelated breeder reproduction, we assumed that EJs have zero indirect fitness benefits on their adoptive territory. To estimate  $\varepsilon$ , we used the following equation:

$$\varepsilon = (e) * (s) * (r) * (o^{\text{EJ}}) \quad (2.4)$$

where  $e$  is an estimate of the mean number of subordinate siblings (imminent EJs) present at the time of expulsion,  $s$  is the difference in survival between DJs and EJs,  $r$  is the average degree of relatedness (assumed to be 0.5 given there is no evidence that Canada jays have extra-pair paternity [18]) and  $o^{\text{EJ}}$  is the ARS of the DJ's ejected siblings. To calculate  $e$ , we used the following equation:

$$e = (b * \phi^{\text{Bandingtoexpulsion}}) - 1, \quad (2.5)$$

where  $b$  is mean brood size at banding, calculated from the long-term data, and  $\phi^{\text{Bandingtoexpulsion}}$  is the survival rate of first-year birds from banding to expulsion, calculated previously from radio-tracking [24]. One was subtracted from this estimate to account for the fact that, at the time of expulsion, one bird per brood was destined to become the DJ. To calculate  $s$ , we used the following equation:

$$s = \phi^{\text{DJFirst-summervs survival}} - \phi^{\text{EJFirst-summervs survival}}, \quad (2.6)$$

where  $\phi^{\text{DJFirst-summervs survival}}$  is the first-summer (expulsion to fall) survival rate of DJs and  $\phi^{\text{EJFirst-summervs survival}}$  is the first-summer (expulsion to fall) survival rate of EJs. This estimate evaluates

the reduction in first-summer survival of EJs as a consequence of being expelled from their natal territory. The indirect fitness of EJs was assigned the value of zero since EJs can only join an unrelated pair.

### (c) Additional details about statistical analyses

Statistical models were constructed and run using the *lme4* package [32] in R [33]. For all model sets, we used the *MuMIn* package [34] to assess all possible combinations of fixed effects and the *aictab* function from the *aicmodavg* package [35] to rank models according to second-order Akaike information criterion corrected for small sample sizes (AICc) [36]. Models with  $\Delta\text{AICc} < 2$  were considered candidate model [36]. Akaike weights ( $w_i$ ) provided cumulative support for each model when accounting for all other competing models. We based our inferences on coefficients from the top-ranked model rather than model-averaged coefficients because model-averaging can produce inaccurate coefficients, particularly when including interaction terms [37]. We considered a covariate to be an important predictor if the confidence interval of the coefficient did not overlap with 0. There was no evidence that any predictors in the models were colinear ( $r < 0.3$ , variance inflation factor = 1.08). Means are reported with  $\pm$  standard error (s.e).

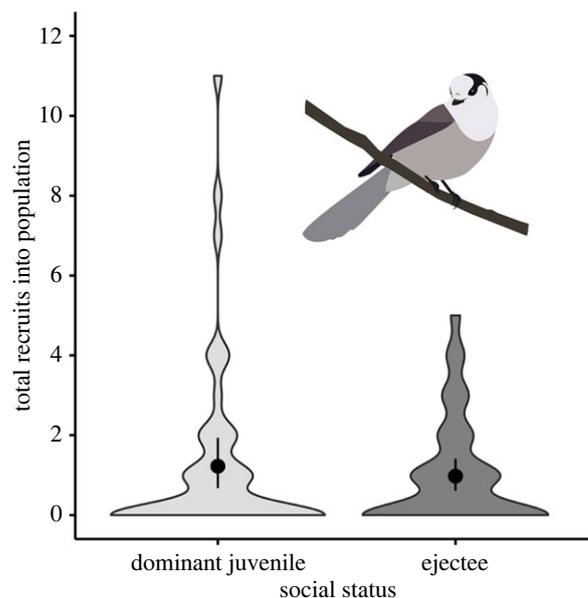
## 3. Results

### (a) Direct fitness

Despite EJs breeding earlier, on average, than DJs (DJs =  $2.05 \pm 0.13$  years, EJs =  $1.59 \pm 0.10$  years; electronic supplementary material, table S1), we found support that the total number of juveniles recruited throughout an individual's breeding tenure was considerably higher for DJs than for EJs (figure 1; electronic supplementary material, tables S2 and S3). The mean number of individuals recruited for DJs was  $1.22 (\pm 0.32)$  and for EJs was  $0.97 (\pm 0.20)$ . Multiplying these values by probabilities of reaching adulthood (DJs =  $0.80 \pm 0.07$ , EJs =  $0.47 \pm 0.12$ ; [24]) suggests that the direct fitness of DJs (0.98) was more than double that of EJs (0.46; table 2). When the number of nestlings produced over an individual's breeding tenure was used instead of the number of juveniles recruited, DJs still had substantially higher direct fitness (3.69) than EJs (2.61; electronic supplementary material, tables S4–S6).

### (b) Indirect fitness

We found no evidence that the presence of a DJ increased reproductive output (electronic supplementary material, tables S7 and S8), suggesting that the indirect fitness benefit for DJs delaying dispersal was zero. Similarly, we found no evidence that the presence of an EJ increased the reproductive performance of the unrelated breeders on their adoptive territory (electronic supplementary material, tables S9 and S10). To determine whether there were indirect fitness costs for DJs, we first calculated the mean number of imminent EJs ( $e = 0.41$ ) by multiplying mean brood size at banding ( $b = 2.52$ ) by survival to expulsion ( $\phi^{\text{banding to expulsion}} = 0.56$ ) and then subtracting 1 (equation (2.5)). The cost of ejecting siblings ( $\varepsilon = 0.08$ , equation (2.4) was the product of the mean number of imminent EJs ( $e = 0.41$ ), the difference in survival between DJs and EJs ( $s = 0.39$ ), the coefficient of relatedness ( $r = 0.5$ ) and the mean ARS of the DJ's ejected sibling (0.97 recruits). Thus, after subtracting the cost of ejecting siblings from indirect fitness benefit (= 0, equation (2.3), the total



**Figure 1.** A violin plot comparing the number of offspring recruited into the population between DJs ( $n = 49$ ) and EJs ( $n = 41$ ) that reached breeding status using the long-term re-sighting and nest monitoring data.

**Table 2.** A summary table of the direct, indirect and inclusive fitness estimates of DJ ( $n = 49$ ) and EJ ( $n = 41$ ) Canada jays. Calculations were based on a combination of radio-tracking and long-term demographic data (see Methods).

	DJs	EJs
<i>direct fitness</i>		
probability of reaching adulthood	$0.80 \pm 0.07$	$0.47 \pm 0.12$
mean lifetime recruits	1.22	0.97
direct fitness estimate	0.98	0.46
<i>indirect fitness</i>		
benefit (helping parents)	0	–
cost (ejecting siblings)	0.08	–
indirect fitness estimate	– 0.08	0
<i>inclusive fitness</i>		
	0.90	0.46

indirect fitness for DJs was  $-0.08$  (table 2). Because EJs do not help raise offspring nor have any negative effects on their same-cohort DJs, we assumed their indirect fitness was zero.

### (c) Inclusive fitness

Combining the direct and indirect fitness values for DJs yielded an inclusive fitness estimate of 0.90, still substantially higher than the 0.46 inclusive fitness estimate of EJs (table 2).

## 4. Discussion

Our analysis suggests that DJ Canada jays have almost twice the inclusive fitness of the siblings (EJs) they expel from the natal territory just six weeks after fledging. Such

fitness differences are not associated with indirect benefits that might accrue to DJs remaining on their natal territories through enhancement of nest defense or through helping to feed next-cohort fledglings. Instead, higher direct fitness of DJs is mainly driven by their higher ARS, estimated either by the number of recruits or the number of nestlings produced, and higher rates of reaching adulthood, which is primarily manifested by elevated mortality rates of EJs in the summer months immediately following expulsion [24]. The higher ARS of DJs may be attributable to their later onset of reproductive senescence [21] and, compared to EJs, to their much higher, first-summer (post-expulsion) survival rate [24].

While DJs appear to gain significant fitness advantages over EJs, the post-expulsion lives and reproductive outputs of DJs and EJs can be quite similar. Although individuals of both juvenile classes sometimes disperse to vacant breeding positions in their first summer, they more typically remain on their respective natal and 'adopted' territories for their first year of life (table 1) and only disperse to their first breeding territories sometime in their second summer. Our data are consistent with the hypothesis [7,21] that both DJs and EJs seek to become the *only* juveniles on their respective natal and adoptive territories and to do so as early as possible. We speculate, that, in doing so, DJs and EJs can thereby maximize their competition-free opportunities during their first summer and fall to amass the food caches necessary to sustain them through their first winter. Additionally, by closely associating with the more experienced adult breeders, they may tap into an inadvertent 'parental' subsidy [7], again free of competition from other juveniles, by watching the adults and then pilfering and re-hiding some of the adults' caches [21]. The cohesive trios formed by EJs and unrelated adults are usually difficult to distinguish from those comprised DJs still with their own parents and, consistent with this observation, both radio-tracking and long-term mark-resighting data reveal similar first-winter (fall to spring) survival rates of DJs versus EJs (0.85 versus 0.73, [23]; 0.56 versus 0.47; D.S. & D.R.N. 2022, unpublished data).

Our work highlights how indirect fitness costs can be incorporated into calculations of inclusive fitness. In species where delayed dispersers do not directly cause the departure of 'early dispersers', there is no reason to assess indirect costs against the inclusive fitness of the delayed dispersers [17,38–41]. However, in a brood-reduction system, where the delayed disperser is responsible for the fitness losses of the subordinate juveniles [12,13], it is appropriate to charge the delayed dispersers for the damage they cause to their common genetic interest through imposing a fitness cost on the early dispersers. In the case of Canada jays, indirect costs were incurred through the DJ's expulsion of its siblings from the natal territory and the consequent decline in EJ survival. That said, for such costs to have an impact on inclusive fitness, the survival rate of early dispersers must be substantially lower than that of delayed dispersers. We found that, although the first-summer, post-Expulsion survival rate of EJs was only about half that of DJs, the consequent indirect cost incurred by DJs through expelling their siblings was still just 9% of their direct fitness (0.08 versus 0.90). Costs associated with ejecting siblings will also increase as the number of siblings negatively affected by competition grows. Canada jays have relatively small brood sizes (mode=3 in APP [18]), a number that is further reduced

when accounting for partial brood losses that occur between banding and expulsion.

We acknowledge that our calculation of inclusive fitness makes a number of underlying assumptions. First, we assumed equal survival rates of DJs and EJs past their first year. As with DJ versus EJ differences in rates of reproductive senescence [21], it is possible that, later in life, some EJs experience higher mortality rates than DJs as a result of differences in phenotype or early-life experiences. However, given similar DJ and EJ first-winter survival rates (0.85 versus 0.73, [24]; 0.56 versus 0.47; D.S. & D.R.N. 2022, unpublished data) and similar average maximum lifespans of the 90 individuals analysed in this study (DJ mean lifespan =  $4.49 \pm 0.47$ , EJ mean lifespan =  $5.34 \pm 0.54$ ), differences in survival past this age seem unlikely. Second, it is important to note that our estimates of the probability of reaching adulthood based on radio-tracking were collected over six recent years, when the APP population has been declining, and therefore, may reflect a below-average survival rate of reaching adulthood compared to previous decades. Third, to estimate the cost of ejecting siblings, we assumed that the first-summer survival of EJs, had they not been ejected, would have been similar to that of DJs. This assumption receives some support in our 58 years of long-term data since the winter survival of single non-breeders (0.54,  $n = 330$ ) is not significantly different from the survival of fall non-breeders when there were two individuals on the same territory (0.46,  $n = 68$ ,  $X^2 = 0.476$ ,  $p = 0.57$ ; D.S. & D.R.N. 2022, unpublished data). Finally, estimates of juvenile recruitment were only based on individuals within the study area, which could have biased results. However, given the similarity of the surrounding landscape with the exception of relatively small negative effects on survival for individuals on territories that border the highway [42], we have no reason to believe that EJs settling outside the study area would have more or fewer recruits over the course of their time as a breeder than EJs settling inside the study area.

Canada jays and Siberian jays are not the only group-living species in which some members of juvenile broods delay dispersal while others leave early. However, to our knowledge, they are the only species where the most dominant brood member forces all its siblings to disperse from the natal territory (i.e. through 'true' brood reduction). By contrast, in species with variably early dispersal (e.g. red-cockaded woodpeckers, *Picoides borealis* [38]; acorn woodpeckers, *Melanerpes formicivorus* [43]; desert night lizards, *Xantusia riversiana* [44]; green woodhoopoes, *Phoeniculus purpureus* [45]; superb starlings, *Lamprotornis superbus* [46]; Mexican jays, *Aphelocoma ultramarina* [47]; red wolves, *Canis lupus* [48]), there may be more than one brood member that delays dispersal, the dispersers may leave at different times and they may do so apparently 'voluntarily' (i.e. not because they have been aggressively forced to leave by one or more stronger siblings). Overt fighting and attempts to stay are not features of such 'voluntary' dispersal systems, but a sex bias in the delayed disperser cohort versus those juveniles that leave early may nevertheless result. If females, for example, are usually or invariably lower in a juvenile dominance hierarchy, the benefit of staying (less with declining rank in the hierarchy) may be less than a fixed benefit obtained by leaving [4] and this could partially explain the preponderance of female-biased avian juvenile dispersal [49].

**Ethics.** 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).

**Data accessibility.** Data used for this study are available on Figshare at the following DOIs: <https://dx.doi.org/10.6084/m9.figshare.21135310> [50]; <https://dx.doi.org/10.6084/m9.figshare.21135463> [51]; <https://dx.doi.org/10.6084/m9.figshare.21135832> [52]; <https://dx.doi.org/10.6084/m9.figshare.21135946.v1> [53].

The data are provided in the electronic supplementary material [54].

**Authors' contributions.** M.F.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft and writing—review and editing; D.S.: conceptualization, data curation and writing—review and editing; N.E.F.: conceptualization, data curation and writing—review and editing; A.O.S.: conceptualization, data curation and writing—review and editing; D.R.N.: conceptualization, data curation, formal analysis, funding acquisition, project administration, supervision, validation, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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