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Early-life experience shapes patterns of senescence in a food-caching passerine

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For many species, breeding performance increases through early adulthood followed by declines later in life. Although patterns of age-specific decline have been shown to vary between individuals, the factors that lead to this individual variation in the intensity of reproductive senescence are yet to be fully understood. We investigated whether early-life social status influenced age-related trends in the breeding performance of male Canada jays (*Perisoreus canadensis*), year-round residents of North America's boreal and sub-alpine forests. Shortly after young become nutritionally independent, intra-brood dominance struggles lead to one juvenile (Dominant Juvenile) remaining on the natal territory after expelling its subordinate siblings (Ejectees). First, we show via radio tracking that in our declining range-edge population Ejectees either join an unrelated pair (67%), form a breeding pair with another bird (28%) or occupy a territory alone (5%). Second, using 39 years of breeding data, we demonstrate that Ejectee males advanced laying dates and increased the annual number of nestlings until 6 years of age before declining, whereas Dominant Juvenile males advanced laying dates until 11 years and increased annual number of nestlings until 12 years of age before declining. This study documents clear variation in ageing patterns between dominant and expelled young, with implications for the role of early-life experiences and phenotypic quality in determining patterns of ageing.

1. Introduction

Reproductive senescence has been commonly observed across iteroparous animals [1]. Young individuals typically improve their reproductive performance through early adulthood, likely driven by improved foraging skills or access to resources [2], followed by reproductive senescence as cellular damage accumulates [3,4]. There is increasing empirical evidence that age-related reproduction patterns vary between individuals within a species [5]. Such variation has been linked to early-life environmental conditions and trade-offs between reproductive effort and cellular maintenance [5,6]. However, the factors driving individual variation in senescence have yet to be fully understood [5,6]. Identifying such factors remains a central issue in understanding both the evolution of ageing and population ecology of iteroparous organisms [7].

Using 39 years of breeding data from individually marked Canada jays (*Perisoreus canadensis*), we asked whether juvenile social status affected the onset of reproductive senescence. Canada jays are year-round residents of North America's boreal and sub-alpine forests where they rely on food cached during the summer and autumn to support over-winter survival and reproduction during the late winter and early spring [8]. Just after the juveniles reach nutritional independence in mid-June, intra-brood dominance struggles lead to the expulsion of all subordinate siblings (hereafter 'Ejectees') by the dominant juvenile (hereafter 'Dominant Juveniles') [9]. The majority of Ejectees is thought to settle, singly, on territories

Table 1. A priori candidate models (linear, cubic, threshold) testing the effect of age on lay date and annual number of nestlings in Canada jay males. All models included individual ID and year as a random effect and partner age as a fixed effect. Partner age was included as a fixed effect. AIC_c = Akaike's information criterion with a correction for small sample size; ω_i = model weight; numbers in brackets indicate the breakpoint of the top threshold models. Top models within <2 ΔAIC_c are shown in italics.

	model structure	d.f.	AICc	logLik	ΔAICc	ω_i
lay date	**Dominant Juveniles**					
	cubic	7	*667.98*	*−326.37*	*0.00*	*0.79*
	threshold (11)	7	670.64	−327.71	2.66	0.21
	linear	6	682.35	−334.72	14.37	0.00
	Ejectees					
	threshold (6)	7	*1075.21*	*−530.22*	*0.00*	*0.72*
	cubic	7	1077.80	−531.52	2.59	0.20
	linear	6	1079.62	−533.52	4.41	0.08
number of nestlings	**Dominant Juveniles**					
	threshold (12)	9	*292.88*	*−136.46*	*0.00*	*0.67*
	cubic	9	*294.83*	*−137.44*	*1.96*	*0.25*
	linear	8	297.27	−139.86	4.39	0.07
	Ejectees					
	threshold (6)	9	*474.66*	*−227.77*	*0.00*	*0.96*
	cubic	9	481.16	−231.03	6.51	0.04
	linear	8	484.73	−233.92	10.07	0.01

where no Dominant Juvenile is present and form a close association with the local unrelated breeders, while Dominant Juveniles typically remain on the natal territory until, and sometimes beyond, the end of the following breeding season.

Natal dispersal is an important life-history process [10]. Dispersing individuals may incur costs resulting from different environmental, social and individual factors [11]. For instance, movement and settlement in unfamiliar areas may result in reduced feeding efficiency [12], higher susceptibility to predators [13], or exposure to aggression from resident conspecifics [14]. Dispersing meerkats (*Suricata suricata*) had lower body mass and higher glucocorticoid concentrations post-dispersal than resident meerkats [15] and Mauritius kestrels (*Falco punctatus*) that dispersed farther had lower lifetime reproductive success compared to those that settled closer to home [16]. Empirical evidence has also linked exposure to stressors during early life with earlier senescence [17–19]; therefore, we should expect the costs of an imposed early dispersal to continue even after breeding status is reached. A relationship between the timing of senescence and early-life social status could also arise if differences in individual quality affect senescence. Nestlings that become Dominant Juveniles tend to be heavier than Ejectees [9] which may lead to higher lifetime breeding productivity [20,21]. Such weight differences may be partly explained by the long-term predominance of males among Dominant Juveniles and, at least for adults, by the approximately 10% greater body masses of males compared to those of females [22]. Given the potential for phenotypic differences related to social dominance and the costs of early independence, we predicted that reproductive senescence in Canada jays would occur earlier in Ejectees forced to leave their natal territories barely six weeks after fledging than it does in Dominant Juveniles that leave much later.

2. Material and methods

We studied Canada jays at the southern edge of their range in Algonquin Provincial Park, Canada (45.590°, −78.517°). The reproductive performance of a population of Canada jays in Algonquin Park has been monitored since 1964 along the park's highway 60 corridor [9,23]. Canada jays are relatively long lived, with some individuals surviving 18 years [8]. In Algonquin Park, first clutches have been initiated as early as 22 February and clutch sizes range between one and five eggs (modal = three eggs; [8], with additional data from 1991 to 2018). Both sexes contribute to provisioning young [8]. No evidence of extra-pair paternity (EPP) has been found in 15 nestlings from eight nests in Algonquin Park [8] or in nine nestlings from three nests on Anticosti Island, Quebec [24]. Additionally, there is no evidence of EPP in the closely related Siberian jay (*Perisoreus infaustus*) [25]. All individuals in the population are uniquely marked with three colour bands and one aluminium USFWS/CWQ band as nestlings or when discovered as newly dispersed immigrants into the study area. Beginning in 1994 ages of immigrants to the study area were determined as either juvenile (first-year) or adult (second-year or older), using rectrix shape. Nests within the study area were found beginning in mid-February and monitored until the end of the breeding season in early May. Once a nest was found, it was checked regularly every 2–4 days until young were marked at approximately 11–14 days old. The date that the first egg was laid (laying date) and the number of young present in the nest at banding (number of nestlings) were used as measures of reproductive performance. As is common in many species, earlier laying dates in Canada jays are associated with higher reproductive success [26,27]. Only juveniles marked as nestlings in the study area and still on their natal territory in the autumn census were assigned the status of 'Dominant Juvenile'. 'Ejectee' status was assigned to either (i) any non-breeder found in the autumn to be in a close, continuing association with an unrelated breeding pair or (ii) any juvenile found in its first autumn to be part of an apparent breeding pair on a non-
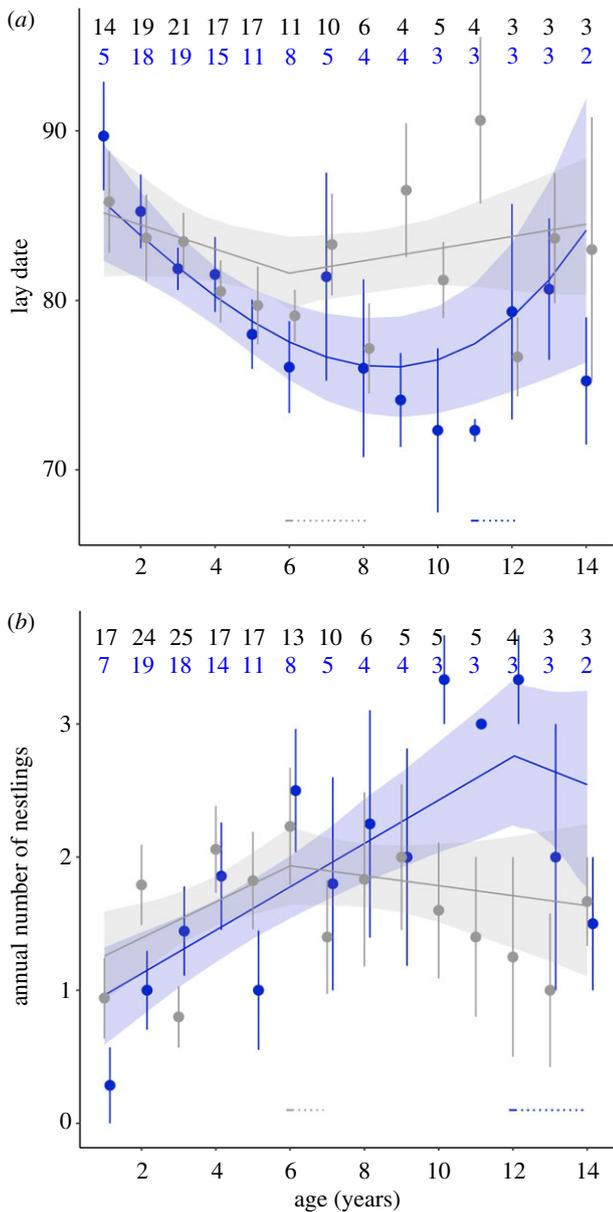
Figure 1. The relationship between age and reproductive performance of Dominant Juveniles (blue) and Ejectee (grey) juvenile Canada jay males. Mean reproductive performance is shown (circles ± s.e.). (a) Laying date with a fitted cubic model (±95% CI) for Dominant Juveniles, and a threshold model (±95% CI) for Ejectees and (b) annual number of nestlings with fitted threshold models (±95% CI). The solid bars above the x-axis in (a) and (b) reflect the breakpoints of the top threshold models and the dotted lines indicate 95% confidence intervals [28]. Sample sizes for each age group are indicated for Dominant Juvenile (blue text) and Ejectee (grey text) males.

natal territory. To further investigate first-autumn social status differences between Dominant Juveniles and Ejectees, between 2016 and 2019, 35 nestlings were fitted with 2.5 g radio transmitters (PipAg393, Lotek, Newmarket, ON) at 14 days of age and tracked through spring/summer until the subsequent autumn (for additional details see electronic supplementary material, appendix S1).

(a) Statistical analysis

Data included males age 0–14 years with information on breeding attempts by 32 Dominant Juveniles (laying date: $n = 103$, number of nestlings: $n = 106$) and 46 Ejectees (laying date: $n = 154$, number of nestlings: $n = 174$). Dominant juvenile females are observed much less frequently than Dominant

Juvenile males (24% versus 76%; [9], with additional data from 1991 to 2019). Too few dominant juvenile females ($n = 11$) were present over the course of the study to allow a similar comparison for females.

First, to determine the age at which changes in breeding performance occurred, we identified the best threshold model for both laying date and number of nestlings separately, by ranking all breakpoint models with all possible breakpoints at yearly intervals using Akaike information criterion corrected for small sample sizes (AICc). Confidence intervals were estimated by maximum likelihood and placed around the breakpoint values at the 95% limit [28]. For laying date, the response variable was measured as a continuous variable and linear mixed models were run using the package 'lme4' [29]. For number of nestlings (total number of young produced per year), the response variable was entered as an ordinal factor (0, 1, 2, 3, 4, 5 young) and analysed using a cumulative link mixed model using the ordinal package [30].

Second, to identify the shape of the age function, we compared a variety of candidate models, including 'age' entered as either a linear, cubic, or threshold model (the best threshold model from the previous step) and ranked by AICc. Model predictions ±95% confidence intervals were generated using the ggeffects package for cubic models [31] and the mcp package for threshold models [32]. All models included year and individual ID as random effects and partner age as a fixed effect.

Finally, to examine whether observed trends in breeding performance could be explained by within-individual (individual age effects on breeding performance; i.e. years since first breeding) versus between-individual (selective appearance or disappearance of individuals; i.e. age at first or last breeding) effects, we conducted a longitudinal analysis ([33,34]; for additional details see electronic supplementary material, appendix S2). Statistical analyses were performed using R v. 3.6.0 [35].

3. Results and discussion

From a combination of radio tracking and long-term data, our results show that Ejectees that survived their first summer ($n = 36$), either joined an unrelated pair (67%), formed a breeding pair with another bird (28%), or occupied a territory alone (5%). In comparison, all tracked Dominant Juveniles ($n = 21$) remained on their natal territories throughout the first autumn. The most common behaviour for Ejectees, to join an unrelated pair, occurs chiefly when the same-year nesting of the unrelated pair has failed and when, consequently, there is no locally produced Dominant Juvenile. The benefit of this strategy may be that, in a manner similar to Dominant Juveniles accompanying their parents on the natal territory, the Ejectee can acquire a subsidy of stored food inadvertently provided by the adults by staying close to them and pilfering the food items they hide [9].

In agreement with our prediction, Dominant Juveniles began reproductive senescence later than Ejectees. Model comparisons of age-related variation in laying date highlighted support for cubic models for Dominant (only model within less than 2 ΔAICc = cubic model) and threshold models for Ejectee males (only model within less than 2 ΔAICc = threshold model; table 1) best representing the relationship between age and laying date. Where threshold models or polynomial terms best represented the relationship between age and laying date we went back to the threshold models to identify differences in the onset of senescence. Dominant Juvenile males showed evidence for a later-in-life decline in laying date (i.e. later laying date) than Ejectee

Table 2. Threshold models testing the effect of age on lay date and annual number of nestlings in Canada jay males. All models included individual ID and year as a random effect and partner age as a fixed effect. AIC$_c$ = Akaike's information criterion with a correction for small sample size; ω_i = model weight. Only models with ΔAIC$_c$ < 2 are shown.

	age threshold	d.f.	AICc	logLik	ΔAICc	ω_i
lay date	Dominant Juveniles					
	11	7	670.64	−327.71	0.00	0.52
	12	7	671.91	−328.34	1.27	0.28
	Ejectees					
	6	7	1075.21	−530.22	0.00	0.48
	8	7	1077.80	−531.05	1.66	0.21
number of nestlings	Dominant Juveniles					
	12	9	292.88	−136.46	0.00	0.51
	13	9	294.28	−137.16	1.40	0.25
	Ejectees					
	6	9	474.66	−227.77	0.00	0.86

males (figure 1a). Laying dates advanced until approximately 11 years of age before declining, whereas for Ejectees laying dates advanced until approximately 6 years of age before declining (table 2 and figure 1). Canada jay females have earlier than average laying dates when food-supplemented [36,37] and when paired with more experienced males [26]. Male age may influence laying dates via courtship feeding during the pre-breeding period [8,38]. Early-life improvement in the quality and quantity of food cached by males and subsequently fed to females may lead to earlier laying dates, followed by later laying dates in late-life as foraging ability deteriorates.

The annual number of nestlings showed a similar pattern of declining later in life for Dominant Juveniles compared to Ejectees. Model comparisons found exclusive support for threshold models to best represent the relationship between age and the annual number of nestlings for Ejectees (table 1). For Dominant Juveniles, the threshold model was the top model identified by AICc weight, with additional support for a cubic term (top model = threshold model, ΔAICc of cubic model = 1.96; table 1). While Dominant and Ejectee males both experienced age-related declines in the annual number of nestlings (figure 1b), threshold model breakpoints showed that Dominant Juveniles increased the annual number of nestlings until approximately 12 years of age before declining, whereas Ejectees increased the annual number of nestlings until approximately 6 years of age before declining (figure 1b; table 2 for top threshold models). Our longitudinal analysis indicated that within-individual trends had higher variable importance than between-individual trends (selective appearance) for both reproductive performance measures during early life. There was also no evidence to support that the decline in breeding performance in later life was driven by selective disappearance in Ejectees or by later laying dates as individuals age (see electronic supplementary material, appendixes S2 and S3). Although we show early-life improvement in male reproductive performance followed by late-life declines, the exact mechanism by which this occurs (changes in sperm quality, courtship feeding and/or nestling provisioning) requires further study.

The earlier age of senescence observed in Ejectees may be due to the stressors associated with early dispersal and independence. Challenging early-life experiences have been linked with earlier senescence [17–19]. For example, under experimental conditions, three-spined stickleback (Gasterosteus aculeatus) originating from a more benign early-life environment senesced at a slower rate than those that experienced a harsh early-life environment [17]. Indeed, first-summer (June–October) apparent survival rates for Ejectees are markedly lower than for Dominant Juveniles that remain on their natal territory (15% for Ejectees versus 48% for Dominant Juveniles; [9]). The stressors associated with dispersal, such as travelling over unfamiliar territory, uncertain access to resources, and higher susceptibility to predators, could be experienced by sub-dominant Canada jays at a young age and may be driving the observed difference in the timing of reproductive senescence between Dominant Juveniles and Ejectees [39,40].

The long-term effects of challenging early-life experiences are not always obvious. Some studies have found that poor early-life conditions can have favourable effects on survival and reproduction [41]. For example, compared to those born in good years, cohorts of male great tits (Parus major) born in poor years live longer and have greater reproductive success [42]. One proposed explanation is that selection is stronger during periods of hardship [42,43]. For Canada jays, stronger selection on Ejectees is likely given the lower first-summer survival rates of Ejectees compared to Dominant Juveniles. Nevertheless, surviving Ejectees show earlier ages of senescence than their socially dominant counterparts, suggesting that a poor start in life for Canada jays has long-term disadvantages rather than favourable effects [44,45].

Phenotypic differences between juveniles of different early-life social status may also be driving the observed patterns in senescence timing. As nestlings, Dominant Juveniles tend to be heavier than Ejectees [9] although sex itself may also be an important factor determining social status and likely provides an advantage in dominance contests between siblings (males are 10% heavier than females; [46]). Heavier individuals may also benefit from long-term advantages because the costs of reproduction have been shown to

decrease with increasing body mass [47]. How individual phenotypes are related to the timing of senescence is poorly understood [48]. It is likely that some combination of phenotype and dispersal history drives the observed differences in the onset of senescence between Dominant Juveniles and Ejectees. Our study provides unique insight into both the value of delayed juvenile dispersal and individual phenotypic heterogeneity as important factors influencing variation in the patterns of senescence.

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