REPRODUCTION IN STELLER'S JAYS (*CYANOCITTA STELLERI*): INDIVIDUAL CHARACTERISTICS AND BEHAVIORAL STRATEGIES

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Abstract.—We explored the consequences of male and female explorative and risk-taking behaviors that are components of a behavioral syndrome, as well as basic demographic and physical characteristics of three measures of reproductive performance in Steller's Jays (*Cyanocitta stelleri*). Older individuals of both sexes performed slightly better in measures of annual reproductive performance. Age was also positively correlated within pairs. In some years, males in better winter body condition performed better, whereas higher-performing females were in worse condition. Because winter body condition was negatively correlated within pairs, males in better condition possibly enabled their mates to invest more in reproduction in a given year, losing more body mass than low-performing females. Overall, variation in individual male and female traits, especially behavioral traits, explained little of the variation in annual reproductive performance. That age was identified as the single most consistent factor, which was correlated within pairs, suggests that experience and compatibility may be more important than inherent individual traits. By contrast, when examining reproductive performance over multiple years, less explorative and risk-averse males produced more offspring over the 3-year study period; the direction of relationships of the four behavioral traits in the syndrome was highly consistent. This suggests an advantage for linkage of these traits in a syndrome, supporting the hypothesis that the combination of traits in behavioral syndromes may be a target for selection. *Received 11 October 2011, accepted 24 April 2012.*

Key words: age, behavioral syndrome, *Cyanocitta stelleri*, exploration, reproductive performance, risk taking, Steller's Jay.

La reproduction chez *Cyanocitta stelleri* : caractéristiques individuelles et stratégies comportementales

Résumé.—Nous avons exploré les conséquences des comportements exploratoires et à risque des mâles et des femelles qui sont des composantes d'un syndrome comportemental, ainsi que les caractéristiques démographiques et physiques de base de trois mesures de performance reproductive chez *Cyanocitta stelleri*. Les individus plus âgés des deux sexes ont légèrement mieux performé dans les mesures de la performance reproductive annuelle. L'âge était également positivement corrélé au sein des couples. Certaines années, les mâles en meilleure condition corporelle hivernale ont mieux performé, alors que les femelles ayant le mieux performé étaient en moins bonne condition. Puisque la condition corporelle hivernale était négativement corrélée au sein des couples, les mâles en meilleure condition ont possiblement permis à leurs partenaires d'investir davantage dans la reproduction lors d'une année donnée, en perdant plus de masse corporelle que les femelles performant moins bien. Dans l'ensemble, une variation dans les traits individuels mâles et femelles, particulièrement les traits comportementaux, ont peu expliqué la variation dans la performance reproductive annuelle. Le fait que l'âge ait été identifié comme le facteur le plus constant, corrélé au sein des couples, suggère que l'expérience et la compatibilité peut être plus important que les traits individuels inhérents. Par contre, en examinant la performance reproductive sur plusieurs années, les mâles moins explorateurs et prenant moins de risques ont produit une progéniture plus nombreuse au cours de la période d'étude de trois ans; la direction des relations des quatre traits comportementaux dans le syndrome était très constante. Ceci suggère qu'il y a un avantage du couplage de ces traits dans un syndrome, supportant l'hypothèse que la combinaison des traits dans les syndromes comportementaux peut être une cible pour la sélection.

Reproductive performance in monogamous birds typically varies among individuals in a population (Darwin 1871; Newton 1989, 1998). Differences in reproductive performance have been attributed to a variety of individual characteristics, such as age, body condition, social status, or breeding experience (Lamprecht 1986, Chastel et al. 1995, Pärt 1995, Angelier et al. 2007, Black et al. 2007). However, the importance of these characteristics can differ between the sexes because energetic costs of reproduction are often higher for females (Clutton-Brock et al. 1982, Clutton-Brock 1988, Cox 2006, Nussey et al. 2009). Consequently, selective advantages of individual characteristics may be related to sex-specific strategies and behaviors (Partridge 1994, Weimerskirch et al. 1997).

How individuals behave in different situations—described as coping styles, personalities, or behavioral syndromes—adds

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further complexity to the description of phenotypic variation in reproductive performance (Sih et al. 2004, Dingemanse and Réale 2005, Smith and Blumstein 2008). Individuals in a variety of bird populations have been ranked along gradients of aggressive to submissive, bold to shy, inquisitive to inattentive, neophobic to neophilic, and risk prone to risk averse, in which correlations of behavioral types over two or more gradients constitute behavioral syndromes (Koolhaas et al. 1999, Carere and Eens 2005, Réale et al. 2007, Stamps 2007). When multiple traits in a syndrome are genetically or physiologically correlated, selection may act on the syndrome as a whole (Bult and Lynch 2000, Sih et al. 2004, van Oers et al. 2004, Carere and Eens 2005). This can be an advantage when selective benefits for the traits align with the suite of traits in the syndrome, thus selecting for the syndrome itself (Barton and Turelli 1991, Cheverud 1996, Bell 2005, Blows 2007). However, a disadvantage can arise when increasing the quality of one trait decreases adaptation of another trait that is linked in the same syndrome (Sih et al. 2003, Johnson and Sih 2005).

We describe a behavioral syndrome in a population of long-lived, monogamous Steller's Jays (*Cyanocitta stelleri*; hereafter "jays"), measured during field tests of tendencies to explore and take risks in different contexts (Gabriel and Black 2010). We found that breeding pairs tended to mate assortatively for behavioral traits, and pair members that were ranked similarly in any of the behaviors enjoyed reproductive advantages (Gabriel and Black 2012), conferring a selective advantage to the suite of traits in the syndrome. In the present study, we focus on the reproductive importance of traits for males and females, including their age, size, and body condition as well as their propensity to explore and take risks. We also tested whether jays showed assortative mating tendencies for age, size, or body condition and examined how this combination of individual traits and behaviors influenced reproductive performance across years.

Methods

We studied individually marked jays that lived along the interface of suburban neighborhoods and Redwood (*Sequoia sempervirens*) forest in Arcata, California (40°59′N, 124°06′W; elevation 10 m), from January 2006 to September 2008. Jays in this population are typically year-round residents that maintain continuous territory ownership and pair bonds. Birds were initially captured during annual trapping seasons (December–February) in feeders outfitted with a sliding trap door and were fitted with a unique combination of colored leg bands. Minimum known age for each bird was based on its age classification at date of first capture (hatch-year or after-hatch-year), which was based on gape coloration and typical juvenile plumage patterns and shapes (retrices and secondaries; Pyle et al. 1987). We measured wing chord with a ruler to the nearest millimeter, tarsometatarsus and gape length (distance from corner of mouth to tip of beak) with calipers to the nearest 10 μm, and weighed birds with a Pesola spring scale to the nearest gram. We used a principal component analysis of wing chord, tarsometatarsus, and gape lengths to describe body size as a composite of the three variables (LaBarbera 1989, Rising and Somers 1989). We used the size composite variable PC1 (first principal component), which accounted for 73% of total variance. Body

condition was assessed using residuals of a regression of winter (December–February) body mass against PC1 (i.e., size).

Reproductive performance.—We monitored jay territories on a near-daily basis and recorded resighting locations, behavior, pairing and nesting status, and reproductive performance for all color-marked individuals. We quantified nest initiation date and fledging success as indices of reproductive performance.

Sensitivity of jays to disturbances at the nest did not allow us to reliably assess number or condition of offspring for all broods (J. M. Black and P. O. Gabriel unpubl. data). However, early breeders have been widely shown to produce more and fitter offspring in a variety of other birds (Murphy 1986, Krementz et al. 1989, Hochachka 1990, Visser and Verboven 1999, Naef-Daenzer et al. 2001), and relative breeding date is therefore routinely used as an important reproductive variable (Norris et al. 2004). Date of first nest initiation was used as an indirect measure of potential reproductive performance.

Observations of reproductive behavior and parental care (Greene et al. 1998, Gabriel and Black 2012) were used to estimate initiation dates for the first known nest attempt of each jay pair. We calculated mean initiation date of first nests across the entire study population for each of 3 years and subtracted these means from respective estimated individual dates to obtain relative date of nest initiation as days before or after mean initiation in the appropriate year.

Successful fledging was attributed to birds that traveled with and/or fed fledglings in a breeding season (Vigallon and Marzluff 2005, Marzluff and Neatherlin 2006). Fledging success was assigned as an annual bivariate measure (fledged–not fledged). For a subset of birds, we could determine the number of offspring fledged in at least 2 of the 3 study years. Number of offspring fledged was determined mostly by repeated observations of families after fledging, and in few cases by observations of the fledging event. For these individuals, we calculated the mean number of fledglings produced over 2 or 3 years.

Behavioral measures.—We investigated two indices of exploration and two indices of risk taking, measured in four separate contexts. Because we showed (Gabriel and Black 2010) that the personality traits investigated are highly consistent within this population of individuals over time, behavioral scores that were repeatedly measured (maximum annual travel distances, n = 1–3 years; risk taking at a familiar trap, n = 1–2 years, mean n ± SD within years = 3.4 ± 2.1) were averaged over all observations per individual to obtain a single score for each of the four behavioral traits. Behavioral observations were made by a single experimenter (P.O.G.). Experimental procedures for all behavioral measures are described in detail in Gabriel and Black (2010) and are summarized here.

The jay's social system can be described as site-centered dominance, whereby socially monogamous pairs defend an area close to their nests but lose dominance with increasing distance from the territorial center, resulting in extensively overlapping home ranges without clear territorial boundaries (Brown 1963, Greene et al. 1998). After the breeding season concludes, birds exhibit even weaker territoriality and some individuals travel widely, sometimes with their partners but often alone. Maximum annual travel distances from territorial centers were used as a repeatable measure of a bird's propensity to travel and its opportunity for exploration

beyond the home territory. Travel distances were calculated for birds with known nest sites and ≥17 annual resighting locations, and the likelihood of resighting a bird was independent of maximum annual travel distances ($r = 0.004–0.28$; 95% confidence intervals [CIs] widely overlapping zero). On the basis of site-centered territorial behavior of jays (Brown 1963), we defined birds that were found farther away from their territorial centers as more explorative. We measured the distances between a bird's territorial center (midpoint between all known nest locations in a given year) and all resighting locations in the respective year. We used the mean of the five longest resighting distances from the territorial center for each year (2006–2008) as an annual index for exploration beyond home territories. This mean index struck a balance between representing how far and frequently a bird traveled while avoiding inclusion of biased resightings at known nest sites and feeders within a bird's territory. The average across all years was then calculated to obtain a single habitat-exploration score per individual jay.

Short-term exploration of a novel foraging opportunity was used to assess individual differences in solving the ecological tradeoff between time investment of exploring an unfamiliar situation and potential energetic benefits of a new food source. The experiment, described in detail in Gabriel and Black (2010), mimicked opportunities experienced by jays foraging in the forest among downed branches, leaf litter, and logs. In February and March of 2007, we attracted pairs to an experimental feeder (a four-sided wooden box without a floor and only half a lid) baited with peanuts (7 on the ground inside the box, partially underneath the lid, and 3 on top of the lid) that was set up close to their respective territorial centers, and observed behavioral responses for 20 min (Gabriel and Black 2010). We recorded latency of birds to perform a number of exploratory behaviors that represented an increasing degree of exploration, classified in accordance with similar tests (e.g., Dingemanse et al. 2002, Fox et al. 2009, Garamszegi et al. 2009b): (1) coming within 1 m of the novel feeder; (2) perching on top without taking a peanut; (3) taking a peanut from the top; (4) going inside the box for <2 s without taking a peanut; (5) taking a peanut from inside, spending <2 s; (6) going inside the box for >2 s without taking a peanut; and (7) taking a peanut from inside, spending >2 s. We translated these latencies into a cumulative exploration score, ranging from zero to 169; high-scoring birds entered and explored the feeder (Gabriel and Black 2010).

Risk-taking at a familiar trap was assessed throughout the non-trapping seasons (annually March–November; birds could freely enter and exit feeder traps) of 2006 and 2008 by recording individual jays' behavioral responses to feeders in which they had previously been trapped (Gabriel and Black 2010). On the basis of a systematic, categorical assessment of how far and for how long birds entered the familiar trap, we assigned scores between zero and 5 at each observed visit (zero = no approach, 1 = perched on top; 2 = perched at entrance; 3 = entered halfway; 4 = entered all the way for <2 s; 5 = entered all the way for >2 s) and calculated average individual scores, higher scores describing greater willingness to re-enter the trap.

Alarm-calling behavior in the presence of a predator model (mount of an adult male Common Raven [*Corvus corax*]) was used to assess individual differences in solving the ecological tradeoff between injury risk and energy investment of mobbing a potential predator, and potential fitness benefits of protecting offspring (Gabriel and Black 2010). Common Ravens are regular nest predators on jays in our study population and are frequently mobbed by breeding jays (P. O. Gabriel and J. M. Black unpubl. data). In February and March of 2008, pairs were attracted to a location close to their territorial centers by peanut bait and, upon arrival, exposed to a Common Raven mount suspended in flight posture for a 30-min observation period. We used alarm-calling behavior as a measure of mobbing activity. Once a bird joined an alarm-calling chorus, the length of calling bouts appeared to be reinforced by and dependent on the calling bouts of other jays participating in the mobbing. The number of calls given by a particular focal bird during this experiment (a continuous measure of mobbing activity) was therefore correlated among participants in the same experiment. By contrast, whether a bird present at the experiment did or did not participate in alarm calling at all was an independent measure of its mobbing activity (Gabriel and Black 2010). We therefore used alarm-calling behavior as a bivariate measure (call–no call), whereby birds that alarm called were taking a greater risk than those that did not alarm call (Gabriel and Black 2010).

Statistical analyses.—We calculated correlation coefficients to investigate the direction and strength of relationships between measures of annual reproductive performance, estimated by nest initiation date and fledging success, and age, size, winter body condition, and behavioral traits of male and female jays. Separate analyses for each year allowed comparisons among years but also avoided pooling (20 individuals contributed data in all 3 years, and 45 individuals in 2 different years). To test whether relationships between age and reproductive effort were attributable to differential performance of yearling breeders only, we repeated the tests after removing yearling birds from the data. We also calculated correlation coefficients for relationships between the mean number of fledglings produced over 2 or 3 years and age, size, winter body condition, and behavioral traits of a subset of males and females. We standardized the direction of relationships, such that a positive correlation signified that an individual that was older, larger, in better condition, more explorative, and more risk prone, initiated nests earlier, successfully fledged young, and produced more fledglings. We used correlation coefficients as standardized, directly comparable effect sizes, obtained from regressions either directly (expressed as Spearman r_s) or from related effect sizes obtained from Mann-Whitney U-tests (calculated as d and converted into r; Cohen 1988) and contingency tables (expressed as w; Cohen 1988). In combination with 95% CIs, effect sizes are used to interpret the relative magnitude of relationships on a continuous scale and the certainty that can be derived from current data (Garamszegi 2006, Nakagawa and Cuthill 2007, Garamszegi et al. 2009a). In accordance with Cohen (1988), we interpreted effect sizes of r or $w = 0.1$ as small, r or $w = 0.3$ as medium, and r or $w = 0.5$ as large. This approach is consistent with the methods we used in parallel studies to determine the contribution of behavioral traits of interest to a behavioral syndrome in jays (Gabriel and Black 2010), whether breeding pairs mated assortatively for behavioral traits, and the reproductive consequences of assortative mating for personality traits (Gabriel and Black 2012). Strength and direction of relationships between reproductive performance and traits of male and female breeders explored in the present study are therefore directly comparable.

In addition, the nature of effect sizes as standardized measures that have certain attributes when tabulated across multiple variable correlations allowed us to use simple meta-analytical methods to investigate a number of general patterns in the matrix of correlations (Garamszegi 2006). We calculated overall correlation coefficients and 95% CIs from individual effect sizes and sample sizes of different subsets of trait relationships with separate reproductive indices in separate years (Hedges and Olkin 1985, Garamszegi 2006). First, we investigated the separate effects of male and female traits (age, size, winter body condition, and behavioral traits) on annual reproductive performance across all reproductive indices (nest initiation date and fledging success) and years. Because effect sizes for these comparisons were estimated from overlapping samples of individuals, associations between different variables at the level of individuals may confound meta-analysis of effect sizes at the level of variables. Before combining effects across several response variables, we therefore tested whether response variables were correlated across years within the individuals studied in these 3 years (Garamszegi 2006). Fledging success was unrelated to timing of nest initiation in all 3 years (all 95% CIs widely overlapping 0; reported in Gabriel and Black 2012); relative nest initiation dates were unrelated among years (2006–2007: $r = -0.24$, 95% CI: -0.72 to 0.39, $n = 12$; 2006–2008: $r = 0.19$, 95% CI: -0.54 to 0.76, $n = 9$; 2007–2008: $r = 0.20$, 95% CI: -0.26 to 0.58, $n = 21$), as was fledging success (2006–2007: $w = 0.31$, 95% CI: -0.13 to 0.66, $n = 17$; 2006–2008: $w = 0.35$, 95% CI: -0.25 to 0.95, $n = 9$; 2007–2008: $w = 0$, 95% CI: -0.45 to 0.45, $n = 21$). For the purpose of interpretation of overall effects, single effects of relationships with these reproductive measures could thus be treated as statistically independent. Second, we tested whether the direction of the relationship with annual reproductive variables was consistent across behavioral traits for males and females. In order to enhance selection of the behavioral syndrome, we expected that the trait relationships with reproductive performance needed to show a consistent direction within a given reproductive index and year, but not necessarily across years and indices; selection on traits or suites of traits operating in opposing directions under different circumstances can actually sustain the coexistence of alternative behavioral strategies (Dingemanse et al. 2004) and would not preclude selection for the entire suite of traits; we therefore adjusted the signs of relationships so that the most common direction of relationships for a given reproductive index in a given year was positive before combining trait relationships in this analysis. Third, we repeated this assessment for longer-term reproductive success, testing whether the direction of the relationship with mean fledgling number produced over multiple years was consistent across behavioral traits for male and female jays.

We used correlation coefficients and 95% CIs to investigate whether jays mated assortatively for age, size, or winter body condition and whether these traits covaried within either sex. Because age and body size were correlated in both sexes, we also tested whether relationships persisted in a longitudinal analysis for birds measured in more than 1 year using Wilcoxon signed-rank tests. Only one pair of measurements per individual (the first two available) was used in this comparison to avoid pseudoreplication.

Statistical analyses were performed in R, version 2.10.1 (R Development Core Team 2009), and Microsoft EXCEL 2007.

RESULTS

We captured, color marked, measured, and monitored 130 male and 103 female jays and recorded at least one behavioral and reproductive index for 68 individuals in 2006, 92 in 2007, and 88 in 2008. For 23 males and 21 females, belonging to 32 unique pairs over the 3 years, we determined mean number of fledglings produced in 2 years ($n = 20$) or all 3 years ($n = 24$) of the study. In these 3 years, first nests were initated between 5 March and 30 May, 51–59% of pairs successfully fledged young, and chicks fledged between 25 May and 28 August.

The correlation matrix between male and female traits and two annual reproductive indices in 3 years was mainly constructed to inform a set of meta-analyses. However, examination of Table 1 revealed that relationships between any individual traits and nest initiation or fledging success were rare. Male jays that were older, larger, or in better winter body condition sometimes had higher reproductive performance, primarily in 2007, whereas females in worse winter body condition initiated nests earlier in 2007 and 2008. Regarding correlations between personality traits and reproductive performance, none of the 24 potential relationships in males and only 2 of 24 in females showed effects and had 95% CIs that did not overlap zero. Females that fledged young in 2006 were less explorative of a novel feeder, but they called more in the presence of a predator model (Table 1).

When examining the correlations between male and female traits and mean number of fledglings produced, two male behavioral traits showed strong relationships. Males that were less explorative of a novel foraging opportunity and took less risk at a familiar trap produced more fledglings over multiple years (Table 2).

The first set of meta-analyses revealed that older male and female jays had overall higher annual reproductive performance (across all reproductive indices and years) with small effect sizes (Fig. 1). The effect of age on annual reproductive performance in both sexes was not significant after removing hatch-year breeders from the analysis (males: $r = 0.12$, 95% CI: -0.02 to 0.26; females: $r = 0.12$, 95% CI: -0.03 to 0.27).

Behavioral-trait relationships with measures of annual reproductive performance did not show a consistent direction among the four behavioral traits in males ($r = 0.03$, 95% CI: -0.05 to 0.12) or females ($r = 0.08$, 95% CI: -0.02 to 0.17). Behavioral traits had a strongly consistent relationship to the mean number of fledglings produced over several years: less explorative and risk-averse individuals produced more offspring in males ($r = -0.51$, 95% CI: -0.70 to -0.25) but not in females ($r = -0.003$, 95% CI: -0.33 to 0.33).

Composite body-size variable PC1 was moderately positively correlated with age in males ($r_s = 0.41$, 95% CI: 0.13 to 0.63, $n = 44$; Table 3), but not significantly so in females ($r_s = 0.31$, 95% CI: -0.02 to 0.58, $n = 36$; Table 3). Longitudinal analysis of individuals in multiple years showed that this relationship was not due to continued growth of individuals; body size PC1 did not change over time (males: $r = 0.09$, 95% CI: -0.16 to 0.32, $n = 33$; females: $r = 0.23$, 95% CI: -0.09 to 0.50, $n = 20$), and winter body condition was not related to age (males: $r_s = -0.07$, 95% CI: -0.36 to 0.24, $n = 44$; females: $r_s = 0.05$, 95% CI: -0.29 to 0.38, $n = 35$) or body size (males: $r_s = 0.03$, 95% CI: -0.27 to 0.32, $n = 44$; females: $r_s = -0.03$, 95% CI: -0.36 to 0.30, $n = 35$).

TABLE 1. Correlation coefficients (*r*) for relationships between male and female Steller's Jay traits (age, size, winter body condition [Cond.], novel feeder exploration [FE], travel distance beyond home [TD], alarm calling toward predator mount [AC], risk taking at trap [TR]), and two reproductive indices in 3 years (*n* = sample size; 95% confidence intervals in parentheses, calculated for individual relationships). Effect sizes are in bold where |*r*| ≥ 0.25, and in italics where confidence interval does not overlap zero.

		Nest initiation date			Fledging success		
		2006	2007	2008	2006	2007	2008
Male	Age	**0.32**	0.16	0.19	0.05	***0.32***	−0.11
		n = 28	*n* = 38	*n* = 42	*n* = 34	*n* = 43	*n* = 37
		(−0.06 to 0.62)	(−0.17 to 0.46)	(−0.12 to 0.47)	(−0.30 to 0.38)	(0.03 to 0.57)	(−0.42 to 0.23)
	Size	0.01	***0.40***	0.13	−0.11	**0.29**	0.01
		n = 20	*n* = 30	*n* = 31	*n* = 24	*n* = 36	*n* = 29
		(−0.44 to 0.44)	(0.04 to 0.66)	(−0.23 to 0.47)	(−0.49 to 0.31)	(−0.05 to 0.56)	(−0.36 to 0.38)
	Cond.	−0.01	***0.48***	**0.28**	−0.05	0.01	0.07
		n = 20	*n* = 30	*n* = 31	*n* = 24	*n* = 36	*n* = 29
		(−0.44 to 0.44)	(0.14 to 0.72)	(−0.08 to 0.48)	(−0.44 to 0.36)	(−0.32 to 0.34)	(−0.30 to 0.43)
	FE	−0.20	0.21	−0.20	−0.09	−0.24	−0.06
		n = 18	*n* = 19	*n* = 19	*n* = 22	*n* = 25	*n* = 18
		(−0.61 to 0.30)	(−0.27 to 0.61)	(−0.60 to 0.28)	(−0.44 to 0.36)	(−0.58 to 0.17)	(−0.51 to 0.42)
	TD	−0.03	0.06	−0.20	0.41	0.19	−0.06
		n = 9	*n* = 13	*n* = 14	*n* = 10	*n* = 15	*n* = 12
		(−0.68 to 0.65)	(−0.51 to 0.59)	(−0.66 to 0.37)	(−0.30 to 0.83)	(−0.35 to 0.64)	(−0.61 to 0.53)
	AC	−0.08	−0.22	−0.21	−0	0.03	0.14
		n = 7	*n* = 14	*n* = 16	*n* = 9	*n* = 14	*n* = 14
		(−0.79 to 0.72)	(−0.68 to 0.35)	(−0.64 to 0.32)	(−0.65 to 0.65)	(−0.42 to 0.47)	(−0.37 to 0.67)
	TR	−0.07	0.18	−0.08	0.22	0.05	−0.10
		n = 19	*n* = 26	*n* = 32	*n* = 25	*n* = 31	*n* = 30
		(−0.51 to 0.40)	(−0.22 to 0.53)	(−0.42 to 0.28)	(−0.19 to 0.57)	(−0.31 to 0.40)	(−0.45 to 0.27)
Female	Age	0.19	**0.26**	0.19	0.13	0.05	0.08
		n = 27	*n* = 35	*n* = 40	*n* = 32	*n* = 40	*n* = 36
		(−0.21 to 0.53)	(−0.08 to 0.55)	(−0.13 to 0.47)	(−0.23 to 0.46)	(−0.27 to 0.35)	(−0.26 to 0.40)
	Size	0.07	0.11	0.24	0.12	−0.07	0.07
		n = 17	*n* = 29	*n* = 26	*n* = 20	*n* = 32	*n* = 21
		(−0.42 to 0.54)	(−0.27 to 0.46)	(−0.16 to 0.57)	(−0.34 to 0.54)	(−0.41 to 0.28)	(−0.38 to 0.48)
	Cond.	0.18	***−0.38***	***−0.44***	0.13	0.08	−0.07
		n = 16	*n* = 28	*n* = 26	*n* = 19	*n* = 31	*n* = 21
		(−0.35 to 0.62)	(−0.66 to −0.01)	(−0.71 to −0.06)	(−0.34 to 0.55)	(−0.28 to 0.43)	(−0.49 to 0.37)
	FE	0.18	−0.06	−0.18	***−0.74***	0.07	−0.09
		n = 17	*n* = 20	*n* = 19	*n* = 21	*n* = 24	*n* = 17
		(−0.33 to 0.61)	(−0.49 to 0.40)	(−0.59 to 0.30)	(−0.89 to −0.45)	(−0.34 to 0.46)	(−0.55 to 0.41)
	TD	0.24	**−0.26**	0.32	0.40	0.34	−0.15
		n = 8	*n* = 11	*n* = 13	*n* = 9	*n* = 14	*n* = 12
		(−0.56 to 0.81)	(−0.74 to 0.40)	(−0.28 to 0.74)	(−0.37 to 0.84)	(−0.23 to 0.74)	(−0.67 to 0.46)
	AC	−0.02	−0.18	0.13	***0.79***	−0.21	**−0.29**
		n = 8	*n* = 15	*n* = 17	*n* = 9	*n* = 15	*n* = 15
		(−0.72 to 0.69)	(−0.63 to 0.37)	(−0.37 to 0.58)	(0.54 to 1.13)	(−0.70 to 0.30)	(−0.82 to 0.22)
	TR	−0.12	0.03	0.18	−0.19	−0.06	0.13
		n = 17	*n* = 23	*n* = 28	*n* = 18	*n* = 26	*n* = 24
		(−0.57 to 0.38)	(−0.39 to 0.44)	(−0.21 to 0.52)	(−0.60 to 0.31)	(−0.44 to 0.33)	(−0.29 to 0.51)

TABLE 2. Correlation coefficients *r* for relationships between male and female Steller's Jay traits (age, size, winter body condition [Cond.], novel feeder exploration [FE], travel distance beyond home [TD], alarm calling toward predator mount [AC], risk taking at trap [TR]), and mean number of fledglings produced over at least 2 years between 2006 and 2008 (*n* = sample size; 95% confidence intervals in parentheses). Effect sizes are in bold where |*r*| ≥ 0.25, and in italics where confidence interval does not overlap zero.

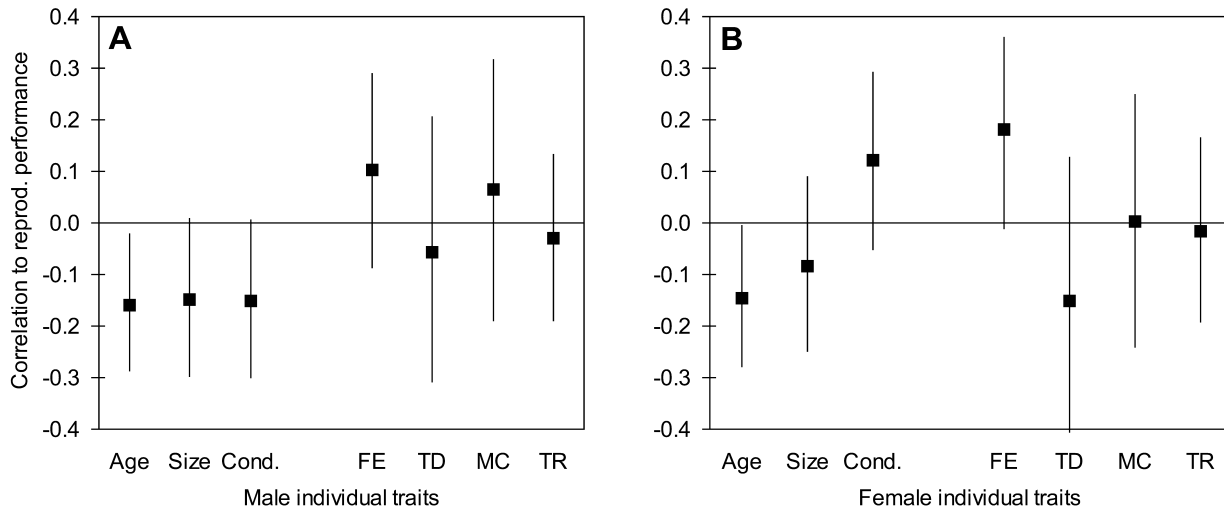|	Age	Size	Cond.	FE	TD	AC	TR
Male	0.04	0.12	0.05	***−0.50***	**−0.52**	**−0.40**	***−0.79***
	n = 23	*n* = 21	*n* = 21	*n* = 16	*n* = 9	*n* = 19	*n* = 8
	(−0.38 to 0.44)	(−0.33 to 0.52)	(−0.39 to 0.47)	(−0.82 to −0.01)	(−0.88 to 0.22)	(−0.72 to 0.07)	(−0.96 to −0.18)
Female	0.20	**0.40**	−0.03	−0.08	**−0.39**	0.12	**0.31**
	n = 21	*n* = 18	*n* = 17	*n* = 15	*n* = 8	*n* = 14	*n* = 8
	(−0.25 to 0.58)	(−0.09 to 0.73)	(−0.51 to 0.45)	(−0.57 to 0.45)	(−0.86 to 0.43)	(−0.44 to 0.61)	(−0.50 to 0.83)

FIG. 1. Correlation coefficients *r* and 95% confidence intervals (indicated by error bars) of meta analyses for (A) male and (B) female Steller's Jays, describing relationships between individual traits (age, body size, winter body condition [Cond.], exploration of a novel feeder [FE], travel distance beyond home territory [TD], alarm calling in presence of predator mount [MC], and risk taking at a familiar trap [TR]), with reproductive performance measured across two reproductive indices (nest initiation date, fledging success) and 3 years (2006–2008).

Age was positively correlated within breeding pairs (r_s = 0.45, 95% CI: 0.24 to 0.62, *n* = 73), whereas winter body condition was negatively correlated (r_s = −0.45, 95% CI: −0.69 to −0.11, *n* = 31). Body size was not correlated between male and female pair members (r_s = −0.20, 95% CI: −0.51 to 0.16, *n* = 32).

DISCUSSION

We explored the consequences of male and female behavioral, demographic, and physical characteristics on three measures of reproductive performance in Steller's Jays. In both sexes, age was the only trait with an overall consistent, although small, influence on annual reproductive performance. Behavioral characteristics were generally not related to annual measures of nest initiation date or fledging success. However, less explorative and risk-averse male jays produced, on average, more offspring over multiple years during our study, and the direction of relationships with the four behavioral traits in the syndrome was highly consistent.

It is well known that reproductive performance improves with age in many animals (Clutton-Brock 1988, Forslund and Pärt

1995). In long-lived monogamous birds, factors such as breeding experience and territory tenure are often closely associated with age, although they reflect very different biological phenomena (Newton 1989, Pärt 1995, Cam and Monnat 2000, Pyle et al. 2001). Similar to reproductive patterns in the related Red-billed Chough (*Pyrrhocorax pyrrhocorax*; Reid et al. 2003), jays in our study showed little variation in age at first breeding and do not typically miss breeding seasons or change mates or sites once established as breeders (J. M. Black and P. O. Gabriel unpubl. data). Thus, increase in reproductive effort with age in both male and female jays is difficult to separate from breeding experience or territory occupation and is probably shaped by both. Furthermore, behavioral coordination of partners may improve over the lifetime of long-term monogamous birds (sensu Black 1996, 2001). The positive correlation between male and female age within pairs was not surprising, and it supports the idea that mate familiarity with increasing pair-bond duration is a likely component of the age effect on reproductive performance. Similarly, Pinyon Jay (*Gymnorhinus cyanocephalus*) pairs showed assortment for age, which was based on assortative formation of pair bonds, even among older birds

TABLE 3. Means (± SE; mm) of wing chord, tarsometatarsus, and gape (distance from corner of mouth to tip of beak) in three age classes of male and female Steller's Jays (*n* = sample size).

	Male age			Female age		
	1–2 years	3–4 years	≥5 years	1–2 years	3–4 years	≥5 years
Wing	138.1 ± 1.1	143.2 ± 0.5	144.1 ± 1.1	134.0 ± 0.5	137.4 ± 0.6	136.8 ± 1.4
	n = 6	*n* = 29	*n* = 11	*n* = 8	*n* = 21	*n* = 7
Tarsus	43.7 ± 0.3	44.0 ± 0.2	44.4 ± 0.2	42.7 ± 0.3	42.9 ± 0.2	42.4 ± 0.5
	n = 13	*n* = 39	*n* = 11	*n* = 19	*n* = 33	*n* = 8
Gape	34.6 ± 0.2	35.2 ± 0.2	35.2 ± 0.4	33.0 ± 0.2	33.3 ± 0.1	33.3 ± 0.4
	n = 13	*n* = 33	*n* = 11	*n* = 19	*n* = 25	*n* = 7

(Marzluff and Balda 1988). It remains to be investigated whether age correlation within Steller' Jay pairs is also the result of assortative pairing, which would suggest a role for compatibility of similarly aged partners (Marzluff and Balda 1988), or mostly a result of high mate fidelity among initial pairs of yearlings.

Older jays of both sexes were larger in the cross-sectional analysis. The longitudinal analysis indicated that this relationship was not due to individual jays growing larger over time; instead, larger individuals may survive better. Benefits of large size are widely documented (Roff 1992, Andersson 1994, Blanckenhorn 2000) and may indicate that larger jays, particularly males for whom the relationship was more pronounced, are better competitors that can secure more or better resources (Searcy 1979, Maynard Smith and Harper 1988, Richner 1989, Rockwell et al. 2012).

Perhaps the negative correlation between male and female winter body condition, as well as the fact that females that initiated nests earlier were often in worse winter condition (which reflects condition both before and after breeding, given that winter body condition was highly correlated within individuals over the years; J. M. Black and P. O. Gabriel unpubl. data), may be due to high-performing females investing more effort into reproduction and, thus, expending more energy than low-performing female jays. Low-performing female breeders in some bird taxa survive better than good performers (Pugesek 1987, Desrochers and Magrath 1993, Hepp and Kennamer 1993, Black et al. 2007), which can be a consequence of high energetic costs of early and large reproductive investment (Afton 1979, Pugesek 1983, Dow and Fredga 1984). Male jays that were paired to females in relatively poor winter body condition, possibly because of high reproductive investment, were more likely to be in better condition. Given that both sexes participate in nest building and provisioning of nestlings, and that males feed females during incubation (Greene et al. 1998, J. M. Black and P. O. Gabriel unpubl. data), males in better winter body condition may enable partners to make a higher reproductive investment. In addition, males in good winter body condition may be attractive and females may invest more when mated to attractive males (Møller and Thornhill 1998). Alternatively, it is possible that relative body mass measured in the winter does not reflect body condition in jays. Higher-quality females, or females that occupy higher-quality territories, may instead be able to afford to carry less body fat in the winter, because their access to food is more secure (Pravosudov et al. 1999). Lower relative body mass may be advantageous, for example, in that it conserves energy in flight and facilitates escape from predators (Witter and Cuthill 1993, Gentle and Gosler 2001). However, the negative relationship between male and female body condition under this interpretation seems puzzling. Further investigation into the relationships of relative body mass, fat storage, food caching, and reproductive investment are needed to conclusively interpret the significance of winter body condition in jays (see, e.g., Koenig et al. 2005).

Overall, variation in individual male and female traits, especially behavioral traits, explained little of the variation in measures of annual reproductive performance in jays. Consequently, lack of covariation in the direction of selection on the four behavioral traits known to form a behavioral syndrome was not surprising (Gabriel and Black 2010). This apparent lack of selection on the syndrome when assessed by measures of annual reproduction

of individual jays stands in contrast to selection on the same syndrome in an analysis of jays that paired assortatively for behavioral traits (Gabriel and Black 2012). In the latter study, pair members with similar behavioral traits in risk taking and exploration initiated nests earlier and fledged young more often. Regarding the overall lack of reproductive consequences of individual behavioral strategies in the present study, we suspect that unpredictable environmental factors that are often exacerbated in urban habitats—for example, domestic cats (*Felis catus*) and anthropogenic changes to habitat that lead to many failed and abandoned nests—may mask effects of individual quality over the short term. This was evident when we compared the relative influence of male and female traits on two different annual reproductive measures: The consequences of individual traits were apparent more often for nest initiation dates than for fledging success. Moreover, jays had access to an abundance of food sources year round, which can ameliorate fitness effects of phenotype quality (Dingemanse et al. 2004, Boon et al. 2007, Schielzeth et al. 2011). Indeed, the influence of male and female qualities on measures of annual reproductive performance was apparent mostly in 2007. Elsewhere, we have documented that in 2007 our normally mild coastal climate was unusually cold and that population-wide nest initiation was delayed (Gabriel and Black 2012). Even in 2007, however, the individual traits of males and females seemed less important when describing annual reproductive performance than specific trait combinations experienced in the pair bond (Gabriel and Black 2012). It may be that pair compatibility or similarity of behavioral traits override individual quality in this long-lived, long-term monogamous bird thriving in an urban environment. That age was identified as the single most consistent factor in the present study, and was correlated within pairs, confirms the assessment that experience and compatibility, which build over time, are more important than inherent individual traits. Future research may identify whether this assessment remains valid when measuring lifetime reproductive success in jays.

In contrast to annual reproductive performance, average number of fledglings produced over multiple years was, overall, strongly correlated with behavioral characteristics in male jays. Less explorative and risk-averse males fledged more young. Males that were "conservative" in their exploration and risk taking likely became more familiar with local intricacies of their territory, including well-known close-by food sources. Perhaps these males provisioned partners on the nest more, enabling females to make a higher reproductive investment. The number of young produced from nests over several years was, thus, more sensitive to individual qualities, perhaps compensating, over the longer term, for the many random effects on individual nest failures. The strong covariation among male jays in the direction of selection on the four behavioral traits known to form a behavioral syndrome (Gabriel and Black 2010) suggests that linkage of these traits in a syndrome is beneficial for jays. This advantage applies both to male jays, which directly experience the benefits of compatible exploration and risk-taking behaviors, and to females that can achieve more rewarding partnerships when beneficial traits are reliably correlated within their male partners (Dall et al. 2004, Schuett at al. 2010). In parallel with an earlier study in which we found that pair members with similar behavioral traits in exploration and risk taking had higher annual reproductive performance (Gabriel and

Black 2012), this lends support to the idea that a correlated suite of behavioral traits might be selected for and may not just be the result of mechanistic linkage (Barton and Turelli 1991, Brodie et al. 1995, Dingemanse and Réale 2005).

Acknowledgments

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