



Correlates and Consequences of the Pair Bond in Steller's Jays

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Abstract

Individuals that maintain pair bonds over multiple breeding attempts are often able to improve reproductive success compared to conspecifics that switch partners. However, the behavioral mechanisms driving this 'mate familiarity effect' are still largely unknown. We investigated whether long-standing pairs in the long-lived, socially monogamous Steller's jay improved their coordination of movements and behaviors, invested more time in pair bond maintenance, or became more compatible in their tendency to take risks over time compared to newly established pairs. We then compared these pair bond characteristics for successful and unsuccessful partnerships in terms of producing offspring. Jay partners regularly perched together, gave soft contact calls and travelled as a pair even in the non-breeding season. However, the proportion of observations jay partners spent in each other's company (pair tenacity) was unrelated to risk-taking behavior of pair members, pair bond duration, or the performance of subtle pair bond maintenance behaviors (i.e., a principle component of behaviors, including soft contact calls, proximity to mates, and frequency of arrival and departure flights with mate). However, evidence suggests that reproductive performance still improved in continuing compared to new pair bonds in Steller's jays. Variation in pair tenacity and frequency of pair bond behaviors may be inconsequential because of jays' overall high level of contact with partners. Additionally, if jays are able to maximize familiarity early in the pair bond through high overall pair tenacity, the additional benefit of increasing coordination and familiarity with increasing pair bond age may be limited.

Introduction

Variation in pair bonds is described in a variety of ways, including short-term, annual to long-term, perennial associations where partners may be in each other's company for brief forays during reproductive seasons to continuous contact even during long migrations (Kleiman 1977; Rowley 1983; Black 1996a). Pair bond members that keep the same partner for multiple breeding attempts are usually able to produce more offspring over time than those with multiple new mates (Ens et al. 1996; Black 2001). The improvement in reproductive prospects that comes with persistent pair bonds has been referred to as the mate familiarity effect (Black 1996b), but mechanisms behind the effect are largely unknown (Ens et al. 1996; Van de Pol et al. 2006). In socially

monogamous species, behavioral coordination and cooperation between partners may be particularly important for successful reproduction, including continuing and mutual responsiveness between pair members (Hirschenhauser 2012). Perhaps familiar partners are better able to coordinate energetically expensive routines on a daily or annual basis (Coulson 1972), or they may become more efficient and effective at winning resources because they stay together more and assist each other in competitive situations (*sensu* Scott 1980). Testing these ideas requires opportunities to witness subtle behaviors that are difficult to observe in highly mobile species.

Steller's jays are non-migratory and can be found on their territories throughout the year, although they are more mobile during the non-breeding season (Brown 1963; Greene et al. 1998; Gabriel & Black

2010). They often reside in urban settings allowing close observation. Unlike some North American jays, juveniles forgo prolonged association with parents to prospect and locate potential mates and breeding opportunities at the end of their first and into the second year (Greene et al. 1998). Both males and females defend territorial boundaries, and pair members have the opportunity to associate throughout the year.

In this study, we tested the prediction of the mate familiarity effect concept that coordination of movements and behaviors should increase with duration that partners spend in a pair bond. In particular, we quantified the arrival and departure of pair members at territories throughout the annual cycle, explored how these movements alone or as a pair varied among pairs and throughout the annual cycle, and asked whether long-standing pairs were seen more often with pair bond partners than newly established pairs (referred to as pair tenacity). We also quantified a number of subtle behaviors occurring only between partners (contact calling, perching nearby and traveling together) and tested whether pairs that spent more time with their partners performed these behaviors more often. In the long-term partnerships of geese and swans, pairs that engage more frequently in pair bond behaviors have competitive and reproductive advantages (Scott 1980; Dittami 1981; Black & Owen 1988; Lamprecht 1989; Black et al. 1996). Another prediction derived from the mate familiarity hypothesis is that pairs become increasingly compatible with time, whereby pair members behave or respond similarly during daily challenges. We tested this idea by examining whether established pairs were more likely to share similar behavioral traits measured in terms of their willingness to take risks and explore novel situations. We did this by measuring each bird's trappability when entering a bird feeder-trap where they had been previously captured. Animals are often identified along a gradient of being trap happy to trap shy, and this measure has recently been included in a suite of traits that describe individual temperaments or personalities within a population (Réale et al. 2000; Garamszegi et al. 2009a; Gabriel & Black 2010). Prior research has shown that jay partners with similar personality traits, including their willingness to enter a feeder-trap, were more compatible in terms of showing better reproductive performance than pairs with dissimilar personalities (Gabriel & Black 2012a). If a mate familiarity effect in Steller's jays is a function of pair bond maintenance (expressed in pair tenacity and pair bond behaviors) or of behavioral adaptation to a partner

(expressed in increasing behavioral similarity), then individuals that spend more time with each other, perform pair bond behaviors more often, or become more similar in behavioral personalities with increasing pair bond duration may be expected to reproduce more successfully.

Methods

We studied individually marked Steller's jays living along the interface of suburban neighborhoods and redwood (*Sequoia sempervirens*) forest in Arcata, California (40°59'N, 124°06'W, elevation: 10 m), from Jan. 2006 to Sept. 2008. All birds in the study area were captured in feeder-traps outfitted with a sliding trap door and fitted with a unique combination of colored leg bands. Minimum known age for each bird was assigned (hatch-year or after-hatch-year) based on gape coloration and typical juvenile plumage patterns (rectrices and secondaries; Pyle et al. 1987). The study area contained between 130 and 170 individually marked jays annually.

Pair Bond Age and Pair Tenacity Measures

We monitored jay territories on a near-daily basis and recorded resighting locations, behavior, pairing and nesting status, and reproductive performance. Monitoring consisted of systematic searches of the study area; whenever a jay was encountered, behaviors were recorded until visual contact with the bird was lost, or the bird remained inactive for a prolonged period of time. Starting points for searches were rotated so as to equalize the search effort across the study area. Reproductive behaviors and pair bond behaviors such as courtship feeding, courtship displays, sex-specific vocalizations, regular proximity, and defense of the same territory were used to determine pair status. Pair bond durations were determined from the first to the last date, and color-marked partners were recorded together (simultaneously). Pair bond age was classified as new (established in current year) or continuing (established previously). All jay pairs were part of a year-round resident study population that has been continuously monitored since Jan. 2005. Thus, the bivariate classification of pair bond age could be assigned to all pairs in the current study, including pairs in the first year of study (2006).

Focusing on male records, which were more prevalent, we calculated the proportion of resightings where partners were observed together for each season (breeding: Mar.–Aug., or non-breeding: Sept.–Feb.) and territorial context (within or outside a bird's

own territory). Territories were defined as the area in which territory owners were always socially dominant over neighbors (habitually vocalized, challenged and chased neighbors; Brown 1963). Analyses were limited to birds with ten or more resightings within the period and context of consideration ($\bar{x}[n] \pm SD$: within territories during breeding = 25.6 ± 13.8 , within territories during non-breeding = 15.1 ± 3.7 , outside of territories during breeding = 17.9 ± 7.1).

We recorded the frequency of occasions when partners perched in close proximity (≤ 1 m) to each other and occurrences of mutual soft contact calling that was directed at each other. Both of these behaviors have only been observed between breeding or prospective partners in Steller's jays (Brown 1964; Hope 1980; Greene et al. 1998). We also recorded whether pair members travelled as a pair (i.e., arriving or departing the territory at the same time and direction). For males with at least ten observations within their territories during breeding seasons in the presence of their mate ($\bar{x}[n] \pm SD = 17.5 \pm 9.5$), we calculated the proportion of sightings where pair members were observed engaging in each of these subtle pair bond behaviors.

Similarity of Behavioral Traits

Risk taking was assessed during non-trapping seasons (annually Mar.–Nov., where birds could freely enter and exit feeder-traps) throughout 2006 and 2008 by recording individual jays' behavioral responses to feeder-traps in which they had been previously captured during trapping seasons (annually Dec.–Feb.). Based on a systematic, categorical assessment of how far and for how long birds entered the feeder-trap that was regularly baited with peanuts, we assigned scores between 0 and 5 at each observed visit ([0] no approach; [1] perched on top; [2] perched at entrance; [3] entered halfway; [4] entered all the way for <2 s; and [5] entered all the way for more than 2 s), where higher scores described greater willingness to reenter the feeder-trap (details in Gabriel & Black 2010). Because risk-taking tendency is a highly consistent personality trait within this population of individuals (Gabriel & Black 2010), the repeatedly measured score ($\bar{x}[n] \pm SD$ within years = 3.4 ± 2.1) was averaged over all observations per individual to obtain a single score. Partner similarity in this behavioral trait was expressed as the absolute value of the difference between the behavioral scores of partners in each pair, where smaller values indicated greater similarity in a personality trait between partners (more details in Gabriel & Black 2012a).

Reproductive Performance

We quantified nest initiation date and fledgling success as indices of reproductive performance. Sensitivity of Steller's jays to disturbances at the nest did not allow us to directly assess the number or condition of offspring (J. M. Black & P. O. Gabriel, unpubl. data). Because in passerines, early breeders have been shown to generally produce more and fitter offspring (e.g., O'Donald 1972; Murphy 1986; Hochachka 1990; Tinbergen & Boerlijst 1990; Winkler & Allen 1996; McGraw et al. 2001) date of first nest initiation is a widely used indirect fitness measure (Norris et al. 2004; Blums et al. 2005; Chalfoun & Martin 2007).

We used observations of reproductive behavior and parental care (Greene et al. 1998; Gabriel & Black 2012a) 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 yr and subtracted these means from respective estimated individual dates. Resulting relative measures of nest initiation are reported in days before or after mean annual initiation date.

Successful fledging was attributed to birds that travelled with and/or fed fledglings in a breeding season (Vigallon & Marzluff 2005; Marzluff & Neatherlin 2006). Fledgling success was assigned as an annual bivariate measure (fledged/not fledged). Additional measures of reproductive performance were limited due to ethical reasons (see Ethical Notes below).

Statistical Analyses

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). Effect sizes were used in combination with 95% confidence intervals that did not or only marginally overlapped zero to interpret the relative magnitude of relationships on a continuous scale and the certainty that can be derived from current data (Garamszegi 2006; Nakagawa & Cuthill 2007; Garamszegi et al. 2009b). Following Cohen's (1988) guidelines, 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 used in recent behavioral research (see, e.g., Garamszegi et al. 2009a) and with the methods we used in parallel studies to determine the contribution of a range of behavioral traits to a behavioral syndrome in

Steller's jays (Gabriel & Black 2010), reproductive consequences of assortative mating for personality traits (Gabriel & Black 2012a), and reproductive consequences of individual traits (Gabriel & Black 2012b); strength and direction of relationships between pair bond age, pair tenacity, pair bond and individual behaviors and reproductive performance explored in this study are, therefore, directly comparable.

Time spent <1 m apart was positively correlated with the proportion of time engaging in mutual soft vocalizations ($r_s = 0.53$, $n = 24$, 95% CI = 0.16–0.77) and traveling together ($r_s = 0.45$, $n = 24$, 95% CI = 0.06–0.72). We, therefore, constructed a composite variable from all three behaviors in a principle component analysis (La Barbera 1989; Rising & Somers 1989) and used the composite variable PC1 (referred to as subtle pair bond behaviors), which accounted for 62% of total variance, in all following comparisons.

We compared the proportion of observations when males were seen with their mate among observations when males were in their territory during breeding seasons, in their territory during non-breeding seasons, and outside their territory during breeding seasons; sample sizes were insufficient to include observations when males were outside their territory during non-breeding seasons. Because the proportion of observations males spent with their mate differed among the three contexts (see Results), we used only observations within a bird's territory during breeding seasons as a measure of pair tenacity for further comparisons, because our monitoring effort yielded the most observations for these circumstances.

We investigated the direction and strength of the relationships between pair bond age and proportion of observations spent with mate (pair tenacity) in a cross-sectional and longitudinal analysis. For these analyses, pair tenacity was calculated separately for each of the three breeding seasons (2006, 2007, 2008). In the cross-sectional analysis, each pair was included once with their first available tenacity measure, comparing pair tenacity between new and continuing pairs. In the longitudinal analysis, we tested whether pair tenacity changed over time in pairs with measures in two separate years.

We investigated the relationships of pair bond age, pair tenacity, and pair bond behavior with pair similarity in risk-taking behavior at a feeder-trap (Gabriel & Black 2010). This measure of risk taking was included in a suite of traits describing a behavioral syndrome in Steller's jays (Gabriel & Black 2010). For the comparison of pair bond age, we tested similarity

in performance between new and continuing pairs using *U*-test, whereas Spearman rank correlations were used for comparisons with pair tenacity and pair bond behavior.

We tested whether pair bond age (using *U*-tests), pair tenacity, and pair bond behavior (using Spearman rank correlations) influenced reproductive performance across the two indices, nest initiation date and fledging success, and across the 3 yr. For a consistent interpretation, the direction of effects of these pair bond characteristics on the bivariate measure of fledging success was matched to the direction of relationships with nest initiation date. Thus, a negative effect size signifies that pairs in a continuing pair bond, spending more time together, or engaging in pair bond behaviors more frequently initiated nests earlier or fledged young more often. The nature of effect sizes as standardized measures that have certain attributes when tabulated across multiple variables allowed us to use simple meta-analytical methods to investigate general patterns in this matrix of correlations (Garamszegi 2006). As 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 among individuals (Garamszegi 2006). Fledging success was unrelated to timing of nest initiation within individuals in all 3 yr (all 95% CIs widely overlapping 0; reported in Gabriel & Black 2012a); relative nest initiation dates were unrelated within individuals among years (2006/2007: $r_s = -0.24$, $n = 12$, 95% CI = -0.72–0.39; 2006/2008: $r_s = 0.19$, $n = 9$, 95% CI = -0.54–0.76; 2007/2008: $r_s = 0.20$, $n = 21$, 95% CI = -0.26–0.58), as was fledging success (2006/2007: $w = 0.31$, $n = 17$, 95% CI = -0.13–0.66; 2006/2008: $w = 0.35$, $n = 9$, 95% CI = -0.25–0.95; 2007/2008: $w = 0$, $n = 21$, 95% CI = -0.45–0.45). For the purpose of interpretation of overall relationships, single effects of relationships with these reproductive measures could thus be treated as statistically independent. We calculated overall correlation coefficients and confidence intervals from individual effect sizes and sample sizes of the trait relationships with separate reproductive indices in separate years for pair bond age, pair tenacity, and pair bond behavior (Hedges & Olkin 1985; Garamszegi 2006).

As we demonstrated in an earlier study that bird age influences reproductive performance (Gabriel & Black 2012b), relationships between pair bond age and reproduction may be confounded by bird age.

We, therefore, tested whether pair bond age was related to male age. Males in continuing pairs tended to be older than males in new pairs (2006: $r = 0.26$, $n = 42$, 95% CI = -0.05 – 0.52 ; 2007: $r = 0.34$, $n = 44$, 95% CI = 0.04 – 0.58 ; 2008: $r = 0.21$, $n = 44$, 95% CI = -0.09 – 0.48). This relationship was due to all first-year breeders necessarily being members in new pairs: Male age did not differ between new and continuing pairs after the removal of yearlings (2006: $r = 0.18$, $n = 32$, 95% CI = -0.18 – 0.50 ; 2007: $r = 0.23$, $n = 40$, 95% CI = -0.09 – 0.50 ; 2008: $r = 0.16$, $n = 42$, 95% CI = -0.15 – 0.44). To test whether relationships between pair bond age and reproductive performance across the 2 indices and 3 yr were independent of male age, we, therefore, repeated these comparisons after the removal of yearlings.

Ethical Note

All procedures were conducted under appropriate State and Federal licenses for the capture and marking of birds and were approved by Humboldt State University's Institutional Animal Care and Use Committee (Protocol number 08/09.W.14.A). The majority of experimental and observational approaches did not require capture of individuals, but were designed to allow assessment of behaviors in the wild, without exposing animals to stress associated with captivity. However, each bird in this study was captured at least once for color-marking and morphological measurements. Time in captivity was kept to the minimum required for the procedures, and birds were released typically within 30–45 min after capture. Due to sensitivity of Steller's jays to disturbances at the nest, we did not approach and inspect nest sites directly but assessed reproductive success in two measures, described above, that were accessible through behavioral observations of adults and fledglings away from the nest.

Results

We observed 44 Steller's jay pairs in 2006, 47 pairs in 2007, and 49 pairs in 2008; 19 of these were paired in all 3 yr, and 19 others in 2 yr. Ten males were paired with two different females, and three males with three different females, resulting in 83 unique pair bonds during the 3 yr. The subset of males from these pair bonds with available behavioral and reproductive data varied between analyses and is indicated in the sample sizes given for each analysis.

When on territories during the breeding season, pair members were simultaneously recorded on 47%

(SE = 2%) of observations using the male as the focal bird (range, 20–71%, $n = 44$). This compared to 38% (SE = 3%), outside territory boundaries during the breeding season (range, 11–69%, $n = 27$; $r = 0.29$, 95% CI = 0.06 – 0.49), and 80% (SE = 6%), within territorial boundaries during the non-breeding season (range, 43–100%, $n = 9$; $r = 0.64$, 95% CI = 0.44 – 0.77).

Pair tenacity scores (i.e., proportion of simultaneous observations of pair bond members) did not differ between males in new ($50\% \pm 0.03$, $n = 12$) and continuing pairs ($47\% \pm 0.02$, $n = 30$; $r = -0.12$, 95% CI = -0.41 – 0.19). The longitudinal analysis confirmed this assessment: pair tenacity score did not change for males over time ($r = -0.11$, $n = 15$, 95% CI = -0.45 – 0.26). Pair tenacity score was not related to the proportion of observations when pairs performed subtle pair bond behaviors ($r_s = -0.07$, $n = 24$, 95% CI = -0.46 – 0.34).

Male and female partners in new pair bonds behaved similarly when entering feeder-traps (1.21 ± 0.24 mean similarity in re-entry score, $n = 10$) to partners in continuing pairs (1.88 ± 0.38 , $n = 14$; $r = 0.28$, 95% CI = -0.14 – 0.61). Pair similarity in willingness to reenter a feeder-trap was not related to pair tenacity ($r_s = -0.08$, $n = 20$, 95% CI = -0.50 – 0.38) or the composite of subtle pair bond behaviors ($r_s = -0.03$, $n = 14$, 95% CI = -0.55 – 0.51).

Continuing pairs initiated nests earlier than new pairs in 2006 and 2008 (2006: $r = -0.38$, $n = 29$, 95% CI = -0.66 to -0.02 ; 2007: $r = -0.20$, $n = 38$, 95% CI = -0.50 – 0.13 ; 2008: $r = -0.21$, $n = 42$, 95% CI = -0.49 – 0.09 ; Fig. 1a), and fledged young from more nests in 2007 (2006: $r = -0.08$, $n = 35$, 95% CI = -0.33

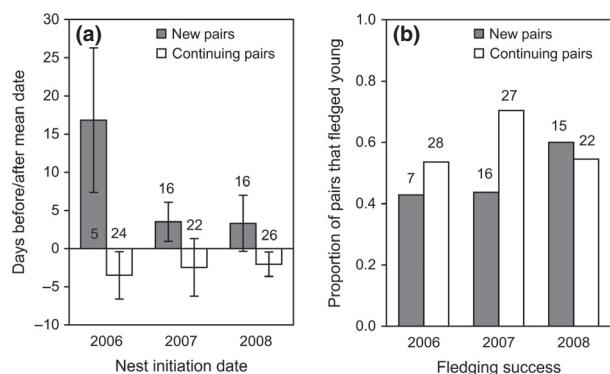


Fig. 1: Reproductive performance of new pairs (established in same year) and continuing pairs (established previously) of Steller's jays measured across the reproductive indices, nest initiation date (a) and fledging success (b), in 3 yr. Bars with error bars indicate $\bar{x} \pm SE$. N shown inside or above bars.

-0.20 ; 2007: $r = -0.26$, $n = 43$, 95% CI = -0.55 – 0.03 ; 2008: $r = 0.05$, $n = 37$, 95% CI = -0.26 – 0.37 ; Fig. 1b). Meta-analysis revealed that continuing pairs had overall higher reproductive performance, with a small effect size, than new pairs (i.e., categorical variable, pair bond age, Fig. 2). These relationships remained similar after removal of pairs with yearling male breeders (Fig. 3).

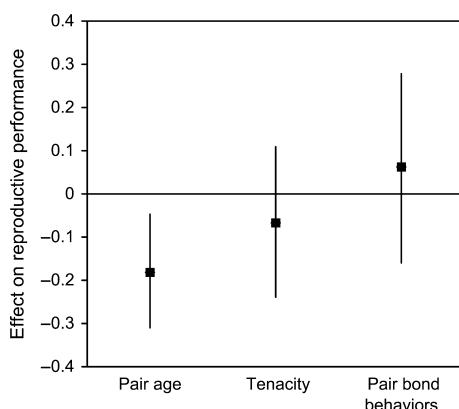


Fig. 2: Overall effects (correlation coefficients and 95% CIs) of pair bond age (new or continuing pairs), pair tenacity (proportion of time males were observed with partner), and pair bond behaviors (composite variable of time pairs spent in close proximity, soft calling, and traveling together) on reproductive performance, obtained from meta-analyses on relationships across 2 reproductive indices (nest initiation date, fledging success) and 3 yr (2006, 2007, 2008). A negative effect signifies that pairs in a continuing pair bond, with higher tenacity, or engaging in pair bond behaviors more frequently initiated nests earlier or fledged young more often.

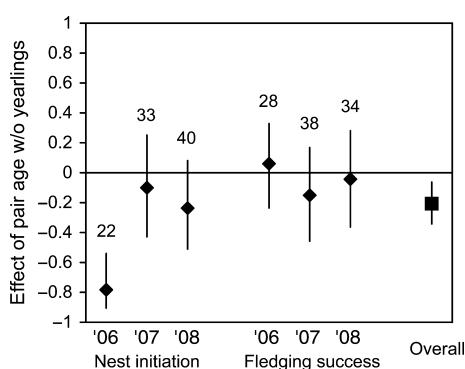


Fig. 3: Correlation coefficients and 95% CIs of relationships between pair bond age (new or continuing pairs) and reproductive performance of Steller's jay pairs after the removal of pairs with yearling males, measured in 2 reproductive indices (nest initiation date, fledging success) and 3 yr, and overall effect obtained from meta-analysis across all indices and years (Overall). N shown above CI bars. A negative effect signifies that pairs in a continuing pair bond initiated nests earlier or fledged young more often.

In 2008, males that fledged young were recorded more often with partners (had higher tenacity) than males that did not fledge young, with intermediate effect ($r = -0.38$, $n = 20$, 95% CI = -0.70 – 0.08). In other years, pair tenacity had no effect on reproductive performance ($r = -0.36$ – 0.17 , $n = 20$ – 30 , all 95% CIs widely overlapping 0), which was confirmed in a meta-analysis (Fig. 2).

In 2006, males who performed fewer subtle pair bond behaviors with partners initiated nests earlier ($r = 0.51$, $n = 14$, 95% CI = -0.03 – 0.82). Otherwise, subtle pair bond behaviors had little detectable influence on reproductive performance ($r = -0.25$ – 0.28 , $n = 14$ – 21 , all 95% CIs widely overlapping 0), and no overall effect of pair bond behavior on reproduction was found (Fig. 2).

Discussion

A review of long-term studies by Ens et al. (1996) encouraged researchers to find the subtle behaviors responsible for improved reproductive success in long-term pair members. Few studies have identified behavioral mechanisms behind the presumed mate familiarity effect (Fowler 1995; Black 1996a; Van de Pol et al. 2006; Hatch & Westneat 2008). Our study indicates that performance is slightly improved in continuing compared to new pairs in a long-lived corvid and that this effect is likely due to pair bond duration rather than individual bird age, but we were unable to identify subtle behaviors that may be responsible for the improvement. The proportion of observations jay partners spent in each other's company varied among seasons and territorial context (discussed in detail below), but this measure of pair tenacity was unrelated to the duration of the pair bond, pair bond maintenance behaviors, or similarity in risk-taking behavior. Consequently, there was no relationship between pair tenacity or the performance of subtle pair bond behaviors and a pair's reproductive performance. These results match patterns in some related species, where long-lasting pairs had higher reproductive success (Marzluff & Balda 1988), but behavioral coordination between partners did not increase with pair bond duration (Marzluff et al. 1996), but contrasts with other species where pair tenacity was an important predictor for the stability of the pair bond (Dhondt & Adriaensen 1994).

Jays spent time in each other's company within territorial boundaries more often during non-breeding season than during the breeding season (on average 80% compared to 47%). That females spend a large proportion of time on the nest (Greene et al. 1998),

and that jays in this study area initiate up to four nest attempts annually, best explains why pair members were observed 'together' only in about half of all observations during breeding seasons. Pair tenacity was also somewhat lower when birds travelled outside their own territories (38%) which can similarly be attributed to females making only short trips in between incubation bouts (J. M. Black & P. O. Gabriel, unpubl. data) and thus rarely being with their mate outside the territory during incubation. With few exceptions, mainly in some waterfowl and parid species (Scott 1980; Ficken et al. 1981; Dhondt & Adriaensen 1994; Lemmon et al. 1997; Black et al. 2007), the rates and consequences of pair tenacity between monogamous partners especially outside the breeding season are largely unknown. In both aforementioned bird groups, the main benefit of continual proximity (80–100%) has been identified as higher dominance ranks for paired individuals in aggressive encounters and improved foraging opportunities (Scott 1980; Teunissen et al. 1985; Lamprecht 1989; Ekman 1990; Lemmon et al. 1997; Black 2001). The finding that jay partners were in each other's presence during most observations outside the breeding season suggests similar social benefits and has important implications for familiarity among partners, discussed in detail below. Observations of agonistic interactions with neighbors indeed indicate that resident jay pairs are more successful in retaining, for example, priority access to feeders than territory owners engaging intruders on their own (J. M. Black & P. O. Gabriel, unpubl. data).

Simultaneous observations of Steller's jay pair members varied considerably during breeding seasons (ranging 20–71%), yet this measure of pair tenacity did not differ between new and continuing pairs. Similarly, subtle pair bond behaviors were not more common among pairs that spent more time in each other's presence. In the barnacle goose (*Branta leucopsis*), long-term pairs performed more loud calls and spent more time on the perimeter of foraging flocks where there was more food (Black et al. 1996), but they were not recorded in proximity to each other more than younger pairs (Black et al. 2007). In cockatiels, *Nymphicus hollandicus*, pair members not participating in extra-pair copulations (EPC) were more behaviorally compatible than pairs in which at least one member was involved in EPC (Spoon et al. 2007). Compatibility was attributed to pairs with lower within-pair aggression, less distance between mates, and greater within-pair allopreening responsiveness (Spoon et al. 2006, 2007). Pair tenacity and the frequency of pair bond maintenance behaviors,

rather than being functions of increasing familiarity between partners, may be functions of individual traits and the combination of both partners in the pair. This is supported by the longitudinal analysis where Steller's jay pair tenacity remained constant within the same pairs over the years.

We quantified risk-taking tendencies in ten new and 14 continuing pairs, yet partner similarity in this personality trait did not differ in new and continuing pairs or in pairs that varied in pair tenacity. Thus, the previous finding that the most successful breeding partners in this jay population are behaviorally similar to each other (Gabriel & Black 2012a) is not the result of continuous adjustments to behaviors of a partner, but rather suggests that jays mate assortatively for preexisting behavioral traits. Partner similarity in this and other traits in the Steller's jay behavioral syndrome have reproductive advantages for jay pairs (Gabriel & Black 2012a). Similar benefits of behavioral trait stability and behavioral similarity among partners have been demonstrated in zebra finches (*Taenopygia guttata*; Schuett et al. 2011a,b). Consequently, the inflexibility of traits in this syndrome conforms to the idea that stable, correlated behavioral specializations within a population can persist when the fitness benefit of being predictable is large (Dall et al. 2004; Sih et al. 2004; Royle et al. 2010; Schuett et al. 2010; Gabriel & Black 2012a).

Continuing Steller's jay pairs nested earlier and were more likely to fledge young in some years than new pairs. Given the lifespan of a jay (the oldest bird known in this population was 13 yrs old; J. M. Black & P. O. Gabriel, unpubl. data), a 3-year study of pair bonds is by no means exhaustive, and future studies may reveal more detailed effects of pair bond age. However, even our current, relatively simple comparison between new and continuing pairs revealed that the overall advantage of continuing pair bonds persisted after removing potentially confounding effects of bird age. Pair tenacity and the frequency of subtle pair bond behaviors performed between partners, on the other hand, were not only unrelated to pair bond age, but had little effect on reproductive performance. Sample sizes for some of these comparisons may not have been sufficient to detect weak relationships. However, our results are in accordance with Marzluff et al. (1996) reporting that behavioral coordination between Pinyon jay (*Gymnorhinus cyanocephalus*) partners did not increase with pair bond duration, although long-lasting pairs had higher reproductive success (Marzluff & Balda 1988). As staying with the same partner for Steller's jays usually also means staying in the same territory (J. M. Black & P. O. Gabriel, unpubl. data), the fitness benefits may also be

explained by a positive effect of territory familiarity (Ens et al. 1996; Naves et al. 2007). This explanation would not apply to Pinyon jays who do not defend territories (Marzluff & Balda 1992), and may not be an exhaustive explanation for Steller's jays, due to their loose form of territoriality in the non-breeding season (Brown 1963). Even if we assume a larger role of partner familiarity than territory familiarity in generating reproductive benefits of longer pair bonds, the extent of variation we observed in pair tenacity and frequency of pair bond behaviors may be inconsequential because of their overall high level of contact with partners.

Jays live in year-round partnerships; during the non-breeding season, partners spend the overwhelming majority of their time together, and during the breeding season, when females are regularly on the nest, almost half their time is spent together. In comparison with most other, part-time bird partnerships (e.g., Coulson 1972; Desrochers & Magrath 1996; Van de Pol et al. 2006), this might simply be more than enough time spent in the presence of their partner for even the least tenacious pairs to optimize familiarity, limited only by the amount of breeding experience the partners have accumulated on their own (influence of bird age; Gabriel & Black 2012b) and as a pair (influence of pair bond age; this study). The observation that the influence of pair bond age on reproduction was relatively weak (overall effect size $r = 0.18$) in comparison with the effects of pair similarity in behavioral traits (overall effect size $r = 0.38$, Gabriel & Black 2012a) expands this interpretation in several ways: Firstly, if jays are able to maximize their familiarity with each other relatively early in the pair bond through their high overall pair tenacity, the additional benefit of increasing coordination and familiarity with increasing pair bond age may be limited. Secondly, behavioral similarity as an important factor for reproductive performance did not change over time, and the compatibility benefits of this similarity are thus not expected to increase. Lastly, in contrast to waterfowl, where reproductive success has been shown to dramatically increase with pair bond duration, jays may experience less intense intraspecific competition. The social mechanism suspected to underlie the strong effect of pair bond duration on reproductive success is the constant need for female-male cooperation during the intense, relatively homogeneous competition experienced in breeding and foraging flocks of waterfowl (Collias & Jahn 1959; Scott 1980; Teunissen et al. 1985; Black & Owen 1989; Lamprecht 1989; Black et al. 1996, 2007). In contrast, the Steller's jay as a behaviorally complex species readily adapting to a complex anthropogenic environment

seems to ameliorate competition by various behavioral specializations that match often their partner (Gabriel & Black 2012a), but not many of their neighbors (Gabriel & Black 2010).

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