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Behavioural Syndromes, Partner Compatibility and Reproductive Performance in Steller's Jays

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Abstract

The concept of partner compatibility in monogamous animals implies that individuals may reproduce better when paired to a partner with similar traits than to a higher quality, but dissimilar individual. We investigated whether partner similarities in traits that are linked in a behavioural syndrome influence reproductive performance in a wild population of Steller's jays. In some years, pairs more similar in explorative tendencies and in willingness to take risks initiated nests earlier and were more likely to fledge offspring than dissimilar pairs. Benefits of behavioural similarity differed among breeding seasons, being most pronounced in a year with late breeding onset after a severe winter. Pairing patterns for behavioural traits also varied among years and traits, and assortative pairing of behaviourally similar partners was not only common overall, but was also correlated across the three explorative and risk-taking tendencies. Pair members with behavioural similarities may yield more compatible and complementary partnerships. Our results indicate that compatibility across a suite of behavioural traits (i.e. a behavioural syndrome) may be beneficial for assortative pairs and support the hypothesis that the combination of traits in behavioural syndromes in itself might be a target for selection.

Introduction

When studying how monogamous animals choose a mate, individuals in a variety of species have been found to prefer partners with traits similar to their own phenotype (Burley 1983; Cooke & Davies 1983; Marzluff & Balda 1988). If they are high-quality traits yielding advantages (e.g. large body size), then assortative pairing may result when high-quality competitors acquire their preferred partners, and the less desirable individuals are left to pair with one another (Johnson 1988; Davies 1989). Alternatively, the idea of compatibility or complementarity between partners implies that individuals may reproduce better when paired to a similar type of partner than to a higher quality, but dissimilar individual. For example, in male and female barnacle geese, *Branta leucopsis*, large individuals generally live longer and achieve higher lifetime reproductive success (Black et al. 2007), but when small females are with small males they perform better than pairs comprised of small females and large males, and vice versa (Choudhury et al. 1996). Furthermore, in some years, pairs comprised of small–small partners outperformed all others (Choudhury et al. 1996). Compatibility between partners can therefore override the influence of intrinsic individual quality (Coulson 1972; Black 1996). Within pairs, similarity in physical traits may reduce aggression and stress, yielding enhanced behavioural coordination (Marzluff & Balda 1988; Black & Owen 1995; Choudhury et al. 1996; Marzluff et al. 1996). Improved fitness has been linked to compatibility and familiarity of partners predominantly in species with long-lasting monogamous pair bonds (Rowley 1983; Ens et al. 1996; Black 2001; Ryan & Altmann 2001; Spoon et al. 2006).

Partner compatibility, although often measured in genetic, morphological, physiological or demographic properties, is thought to be ultimately attributable to similar or complementary behaviours of both partners (Coulson 1972; Bateson 1983; Ens et al. 1996; Spoon et al. 2004). Behavioural personalities or syndromes may therefore represent an important aspect of partner compatibility. Behavioural syndromes describe suites of behavioural traits that are consistent over time and functional contexts, for example mating, antipredator, exploratory and competitive contexts (Sih et al. 2004; Dingemanse & Réale 2005). Traits that are part of a syndrome may show considerable heritable variation (Dingemanse et al. 2002) and are thought to be linked by common underlying physiological mechanisms (Ketterson & Nolan 1999; Bell & Stamps 2004; Kralj-Fišer et al. 2010). Recent studies examining the exploratory behaviour of great tits (*Parus major*) showed that pair members with similar exploratory tendencies had the highest reproductive success (Dingemanse et al. 2004; Both et al. 2005). If behavioural traits are linked in a specific behavioural syndrome, pair compatibility and fitness could be influenced either in similar or in opposing directions by different traits. For example, highly explorative individuals that are also risk-prone might do well when paired assortatively because engaging in similar foraging activities and travel habits may allow partners to spend much of their time together and thus improve behavioural coordination and familiarity (Spoon et al. 2006; Schuett & Dall 2009; Gabriel & Black 2010). Linking of these behavioural traits in a syndrome in this case would enhance compatibility and reproductive success of assortative pairs. Alternatively, if explorative and risk-prone individuals are also highly aggressive (Verbeek et al. 1996; Garamszegi et al. 2009a), assortative pairings could decrease compatibility through high levels of intrapair aggression (Ens et al. 1993; Spoon et al. 2004).

In this study, we investigated the prevalence for and reproductive consequences of assortative pairing in a suite of behavioural traits in Steller's jays (*Cyanocitta stelleri*). In this species, a variety of risk-taking and explorative behaviours are correlated, yielding a behavioural syndrome of highly explorative, risk-prone, far-travelling individuals on one end and non-explorative, risk-averse, travel-shy jays on the other end of the gradient (Gabriel & Black 2010). We used three of these personality traits to test whether individuals were more likely to be paired with a behaviourally similar partner, and whether pairs with similar behaviours had improved reproductive performance. In accordance with the idea that the specific combination of behavioural traits in a syndrome may be selected for (Sih et al. 2004; Bell 2005), we assessed behavioural partner similarity across the three personality traits, and considered the consequences of compatibility or incompatibility across the entire syndrome for reproductive fitness. We also examined the influence of annual changes in environmental conditions on selection for behavioural similarities. In great tits, a selective advantage of assortative pairing for exploratory behaviour was apparent only in years when high winter food availability resulted in high overall recruitment compared to years of low recruitment (Dingemanse et al. 2004; Both et al. 2005). We investigated whether reproductive advantages of behavioural similarity varied with annual fluctuations in population productivity to evaluate overall apparent patterns of selection on and mate choice for partner similarity with respect to exploratory and risk-taking behaviours in Steller's jays.

Methods

We observed individually marked Steller's jay pairs living on the fringe of the redwood (*Sequoia sempervirens*) forest in Arcata, California (40°59′N, 124°06′W, elevation: 10 m) from Jan. 2006 to Sept. 2008. As year-round residents, jays in our study population typically maintained continuous territory ownership and pair bonds. Birds were initially captured in feeders outfitted with a sliding trap door and fitted with a unique combination of coloured leg bands. We actively monitored jay territories on a near-daily basis to obtain resighting locations, behavioural data, nesting status and reproductive performance for all colour-marked pairs. Pairing status was determined by behavioural observations of close association, courtship displays, nest building and nest attendance of individual jays during the 2 mo preceding breeding onset (Jan. and Feb.) and during breeding seasons (Mar.–Aug.) when courtship activity and formation of new pairs were most intense (J. M. Black & P. O. Gabriel, unpubl. data).

Reproductive Performance

We quantified nest initiation date or fledging success (in most cases both) for 34 individually marked Steller's jay pairs in 2006, 46 pairs in 2007 and 44 pairs in 2008. In these 3 yr, nests were initiated on average on 6 April, with a range from 5 Mar. to 30

May (SD = 15 d), and 51–59% of pairs successfully fledged young.

The sensitivity of Steller's jays to disturbances at the nest did not allow us to directly assess differences in the number or condition of offspring (J. M. Black & P. O. Gabriel, unpubl. data). However, differences in the seasonal onset of breeding have long been suggested to be a primary source for variance in reproductive success in monogamous species (Darwin 1871; Fisher 1958; O'Donald 1972). Individual birds that initiate breeding earlier in the season have indeed been widely shown to produce more offspring or offspring in better condition that have a better chance for recruitment into the breeding population (e.g. Murphy 1986; Møller 1988, 1990; Hochachka 1990; Tinbergen & Boerlijst 1990; Winkler & Allen 1996; McGraw et al. 2001). We therefore used the date of first nest initiation as an indirect measure of potential reproductive performance.

Steller's jays build their open cup, mud-lined nests within about 8 d and lay clutches of two to six eggs, laying one egg per day (Greene et al. 1998). Egg incubation lasts about 18 d, and hatchlings take about 17 d to fledge (Greene et al. 1998; J. M. Black & P. O. Gabriel, unpubl. data). Observations of nest building, carrying of nest material, egg incubation and food provisioning to hatchlings and fledglings were used to estimate initiation dates for the first known nest attempt of each jay pair. We calculated the mean initiation date of first nests across the entire study population for each of the 3 yr and subtracted this mean from the estimated individual dates to obtain relative measures of nest initiation that were comparable across years. The resulting measure is reported in days before or after mean annual nest initiation.

Successful fledging was attributed to pairs that travelled with and/or fed at least one fledgling in a breeding season (Vigallon & Marzluff 2005; Marzluff & Neatherlin 2006). Fledging success was assigned as an annual bivariate measure (fledged/not fledged).

Behavioural Measures

We investigated two different indices of exploration in separate contexts and one index of risk-taking behaviour. A second index of risk-taking behaviour when approaching the mount of a nest predator was also found to be a component of behavioural syndromes in Steller's jays (Gabriel & Black 2010), but was not included in this analysis because of insufficient samples. As the personality traits investigated were shown to be consistent within individuals over time (Gabriel & Black 2010), behavioural scores were averaged over all observations per individual to obtain a single score for each of the three behavioural traits. All behavioural observations were made by a single experimenter (P.O.G.). Experimental procedures for all behavioural measures are described in detail in Gabriel & Black (2010) and are summarized here.

The Steller's jay social system can be described as site-centred dominance, where socially monogamous pairs defend an area close to their nests but lose dominance with increasing distance from the territorial centre, resulting in extensively overlapping home ranges (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 also alone. Maximum annual travel distances from territorial centres (mid-point between all known nest locations in a year) 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 at least 17 annual resighting locations, where the likelihood of resighting a bird was independent of maximum annual travel distances. Based on the site-centred territorial behaviour of Steller's jays (Brown 1963), we defined birds that were found farther away from their territorial centres as more explorative. We used the mean of five longest resighting distances for each year (2006–2008) from the territorial centre as an annual index for exploration beyond home territories. This mean index represented on average 14% (range: 6–29%) of annual resightings and struck a balance between representing how far and frequently a bird travelled 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 trade-off between time investment of exploring an unfamiliar situation and potential energetic benefits of a new food source. The experiment mimicked opportunities experienced by jays foraging in the forest among downed branches, leaf litter and logs. We attracted jay pairs to an unfamiliar feeder (a four-sided wooden box without a floor and only half a lid) baited with peanuts (seven on the ground inside the box, partially underneath the lid, three on top of the lid) that was set on the ground close to their respective territorial centres, and observed behavioural responses for 20 min. We recorded the latency of birds to perform a number of exploratory behaviours and translated these latencies into a cumulative exploration score, ranging from 0 to 169, where high-scoring birds explored a large proportion of the novel feeder, spent extended time exploring and were fast to do either.

Risk-taking at a familiar trap 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' behavioural responses to the feeders they had previously been captured in during trapping seasons (annually Dec.–Feb.). Depending on how far and for how long birds entered the familiar trap, we assigned scores between 0 and 5 at each observed visit and calculated average individual scores, where higher scores described greater willingness to re-enter the trap.

Statistical Analyses

We predicted that if partners' similarity in exploration and risk-taking behaviours contributed to behavioural compatibility, then partners with similar behaviour would have enhanced reproductive performance. If behavioural similarity enhanced reproductive success, we also expected assortative mating for behavioural traits.

Partner similarity in each of the three personality traits was expressed as the absolute value of the difference between the behavioural scores of partners in each pair, where smaller values indicated greater similarity in a personality trait between partners.

To investigate direction and strength of relationships between behavioural personality traits within pairs, and between intrapair behavioural similarities and reproductive performance, we calculated correlation coefficients. Analyses were performed separately by years, which allowed comparisons among years, but also avoided pseudoreplication (10 pairs contributed data in all 3 yr and 21 pairs in 2 different yr). Consistent with the approach that was used to determine the contribution of the behavioural traits of interest to a behavioural syndrome in Steller's jays (Gabriel & Black 2010), we used effect sizes and 95% confidence intervals to interpret the relative magnitude of biological relationships and the certainty with which the current data reflect those relationships (Garamszegi 2006; Nakagawa & Cuthill 2007; Garamszegi et al. 2009b). The effect sizes presented are directly comparable among each other and also to other studies that make use of the effect size theorem. Variables were checked for normality and homoscedasticity, and non-parametric tests were applied when parametric criteria were not met. Therefore, we calculated correlation coefficients from regressions either directly (expressed as Pearson's or Spearman's *r*) or from related effect sizes obtained from unpaired *t*-tests or Mann–Whitney *U*-tests (calculated as *d* and converted into *r*; Cohen 1988) and contingency tables (expressed as *w*; Cohen 1988). In accordance with the reports of 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. P values of the underlying statistical tests are reported for reference but not emphasized in our interpretation of results, because significance testing based on critical p values often does not well represent biological relevance, especially in studies of behavioural ecology (Nakagawa 2004; Garamszegi 2006).

We investigated the overall tendency for assortative or disassortative mating for behavioural traits among known breeders in a meta-analysis. The standardized effect sizes and sample sizes of the pairing patterns detected in separate years and behavioural traits were used to calculate an overall correlation coefficient and confidence interval (Hedges & Olkin 1985; Garamszegi 2006). We used the same technique to test whether assortative pairing was correlated across all three behavioural traits.

The reproductive fitness effects of behavioural similarities within pairs were stronger in some years than in others. We investigated whether this variation may be the result of variations in environmental conditions that would be reflected in fluctuations of population-wide reproductive performance among years. To this end, we compared population-wide nest initiation dates and fledging success rates among years, using an ANOVA and Chi-square test, respectively. We also tested whether nest initiation and fledging success were related in any year using *t*-tests and calculating correlation coefficients and confidence intervals as described earlier.

To determine whether particular behavioural types contributed to partner similarity more than others (e.g. if risk-prone individuals were more likely to be assortatively paired than risk-averse individuals) as a factor potentially confounding our interpretation of the effects of partner similarity, we tested whether individual behavioural types differed between pairs that were behaviourally similar and pairs that were dissimilar in behavioural measures of exploration and risk-taking. Pairs were categorized as similar if they had similarity values in novel feeder exploration scores between 0 and 64 (minimum to mean similarity score of all pairs), in travel distances between 1 and 54 m, and in trap re-entry scores between 0 and 1.0. Pairs were categorized as dissimilar with similarity values in novel feeder exploration scores between 64 and 163 (mean to maximum), in travel distances between 54 and 127 m and in trap re-entry scores between 1.0 and 5. Birds were non-explorative/risk-averse with novel feeder exploration scores 0–88, travel distances 99–234 m and trap re-entry scores 0–3.27. Birds were explorative/risk-prone with novel feeder exploration scores 88–163, travel distances 234–456 m and trap re-entry scores 3.27–5.

Ethical Note

All procedures were conducted under appropriate state and federal licences for the capture and marking of birds, and were approved by Humboldt State University's Institutional Animal Care and Use Committee (Protocol # 08/09.W.14.A). The majority of experimental and observational approaches did not require capture of individuals, but were explicitly designed to allow the assessment of behavioural traits in the wild, without exposing animals to stress associated with captivity assays. However, each bird in this study was captured at least once for colour-marking and morphological measurements that were reported elsewhere (Gabriel & Black 2010). Time in captivity was kept to the minimum required for procedures, and birds were released typically within 30–45 min after capture.

Results

Evidence for Assortative Pairing for Behavioural Traits Separately and across All Traits

Whereas travel distances of partners were positively correlated (i.e. similar) for pairs breeding in all 3 yr of the study (Fig. 1), pair member scores for tendency to explore during the novel feeder experiment and re-enter a familiar trap (i.e. risk-taking score) were positively correlated in 1 yr (2006 and 2007, respectively; Fig. 1).

The meta-analysis of effect sizes of the within-pair correlation of behavioural traits in general revealed a positive association. To test whether this association was due only to the strong relationships between travel distances, the analysis was repeated without them, with very similar results (Fig. 1).

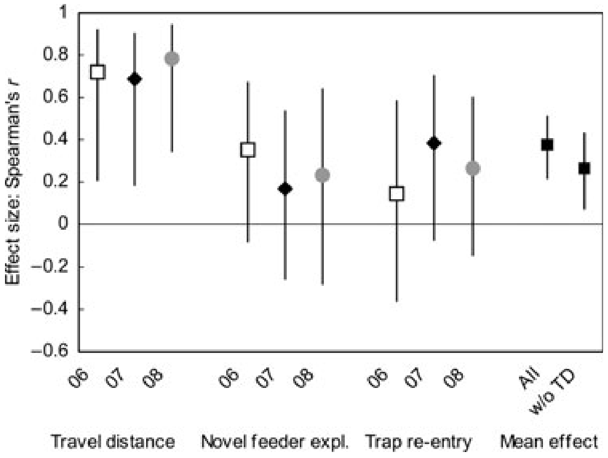

Fig. 1: Effect sizes of relationships between female and male partner's behavioural traits (annual habitat exploration distances: 2006: n = 11, p = 0.013, 2007: n = 12, p = 0.014, 2008: n = 11, p = 0.004; exploration scores during a novel foraging opportunity: 2006: n = 22, p = 0.105, 2007: n = 24, p = 0.438, 2008: n = 17, p = 0.377; and risk-taking at a familiar trap: 2006: n = 17, p = 0.579, 2007: n = 20, p = 0.096, 2008: n = 25, p = 0.195) for pairs known to attempt breeding in 3 yr, and a meta-analysis of these effect sizes overall (mean effect – all: $z = 4.49$, $p < 0.0001$) and after removal of relationships among travel distances (w/o TD: $z = 2.73$, $p = 0.006$). Symbols with error bars indicate correlation coefficients and 95% CIs.

A meta-analysis investigating the correlation of within-pair similarities across all three traits showed a moderate positive association ($r = 0.44$, 95% CI = 0.04–0.72, $z = 2.18$, $n_1 = 10$, $n_2 = 11$, $n_3 = 9$, $p = 0.03$).

Behavioural types were found to be equally distributed between similar and dissimilar pairs in respect to all three personality traits (Novel feeder exploration score: $w_{52} = 0.13$, 95% CI = −0.15 to 0.39, Chi-square test: p = 0.405; Travel distance: $w_{28} = 0.22$, 95% CI = −0.37 to 0.37, Chi-square test: $p > 0.999$; Trap re-entry score: $w_{66} = 0.14$, 95% CI = −0.12 to 0.36, Chi-square test: p = 0.344).

Relationships between Behavioural Similarities and Reproductive Performance

Relative nest initiation dates of jay pairs were strongly positively correlated with similarity in their travelling behaviour in 2007, but not in 2006 and 2008 (2006: $r_7 = -0.54$, 95% CI = −0.92 to 0.36, parametric regression: p = 0.211; 2007: $r_9 = 0.87$, 95% CI = 0.50–0.97, parametric regression: p = 0.002; 2008: $r_{11} = 0.30$, 95% CI = −0.36 to 0.76, parametric regression: p = 0.369; Fig. 2a). Pairs that fledged young were more similar in the distances that partners travelled beyond their home territories

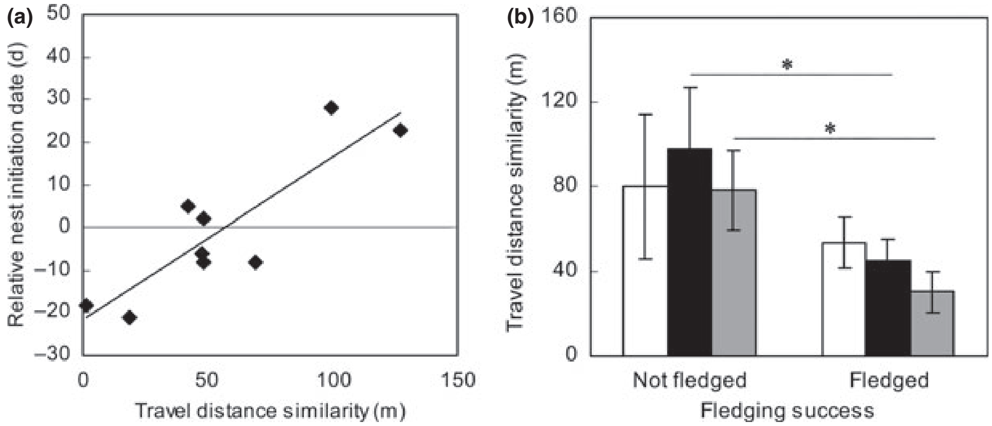

Fig. 2: Relationships between mate similarity in long-term habitat exploration and (a) annual nest initiation dates relative to the annual population mean, and (b) annual fledging success of Steller's jay pairs in 3 yr (white = 2006, black = 2007, grey = 2008). Columns with error bars indicate means and SEs. *Relationships with large effect sizes.

in 2007 and 2008 than unsuccessful pairs, with large effect sizes in both years (2006: $r_8 = 0.40$, 95% CI = −0.42 to 0.86, Mann–Whitney *U*-test: p = 0.655; 2007: $r_{12} = 0.54$, 95% CI = −0.05 to 0.85, *t*-test: p = 0.071; 2008: $r_{10} = 0.77$, 95% CI = 0.28–0.94, *t*-test: p = 0.040; Fig. 2b).

Relative nest initiation date of individual jay pairs was not related to partner similarity in exploration scores (2006: $r_{14} = 0.42$, 95% CI = −0.14 to 0.78, parametric regression: p = 0.137; 2007: $r_{18} = 0.11$, 95% CI = −0.37 to 0.55, parametric regression: p = 0.659; 2008: $r_{15} = 0.005$, 95% CI = −0.51 to 0.52, parametric regression: p = 0.986). Pairs that successfully fledged offspring were more similar in exploration of a novel feeder in 2006 and 2007 than pairs that were unsuccessful, showing large effect sizes in both years (2006: $r_{17} = 0.51$, 95% CI = 0.04–0.80, Mann–Whitney *U*-test: p = 0.149; 2007: $r_{23} = 0.46$, 95% CI = 0.06–0.73, *t*-test: p = 0.06; 2008: r_{16} = 0.30, 95% CI = −0.27 to 0.72, *t*-test: p = 0.515; Fig. 3).

Relative nest initiation dates were positively correlated with partner similarity in risk-taking at a familiar trap, with a strong effect in 2007, and intermediate effect in 2008 (2006: $r_{11} = 0.32$, 95% CI = −0.35 to 0.77, parametric regression: p = 0.340; 2007: $r_{16} = 0.76$, 95% CI = 0.42–0.91, parametric regression: p = 0.0007; 2008: $r_{24} = 0.37$, 95% CI = −0.04 to 0.67, parametric regression: p = 0.079; Fig. 4). Pairs that successfully raised a brood to fledging did not differ from unsuccessful pairs in partner similarity in risk-taking scores when approaching a familiar trap (2006: $r_{12} = 0.25$, 95% CI = −0.38 to 0.72, *t*-test: p = 0.662; 2007: $r_{19} = 0.16$, 95% CI =

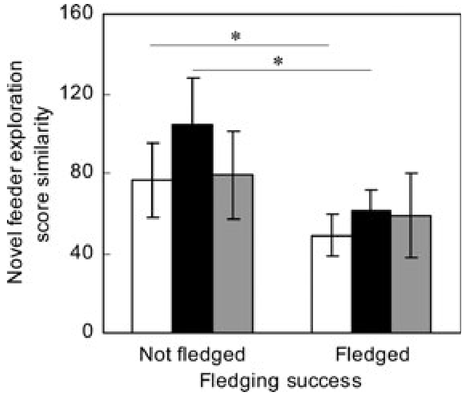

Fig. 3: Relationships between mate similarity in novel feeder exploration scores and annual fledging success of Steller's jay pairs in 3 yr (white = 2006, black = 2007, grey = 2008). Columns with error bars indicate means and SEs. *Relationships with large effect sizes.

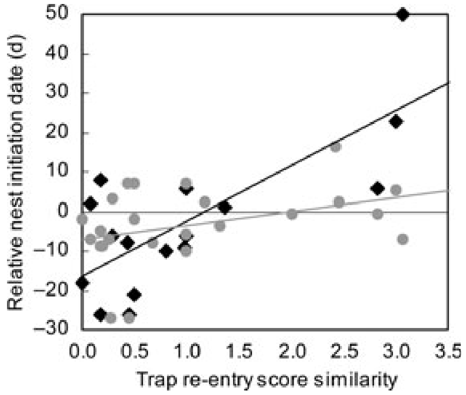

Fig. 4: Relationships between mate similarity in risk-taking at a familiar trap and annual nest initiation dates of Steller's jay pairs relative to the annual population mean in 2 yr (black = 2007, grey = 2008).

−0.31 to 0.58, *t*-test: p = 0.636; 2008: $r_{20} = 0.11$, 95% CI = −0.35 to 0.53, *t*-test: p = 0.711).

Between-year differences in Reproductive Performance

Nest initiation in 2007 occurred on average 2 d later than in 2006 and 9 d later than in 2008 (ANOVA: $F_{2,107} = 4.63$, p = 0.012). The proportion of pairs that successfully fledged young did not differ among years, with 51.4% successful pairs in 2006, 59.1% in 2007, and 56.8% in 2008 ($\chi^2_2 = 0.48$, p = 0.788). Timing of nest initiation did not differ between pairs that did and did not fledge young during this study (2006: $r_{29} = 0.13$, 95% CI = −0.25 to 0.47, *t*-test: p = 0.76; 2007: $r_{37} = 0.13$, 95% CI = −0.21 to 0.43, *t*-test: p = 0.69; 2008: $r_{35} = 0.10$, 95% CI = −0.24 to 0.42, *t*-test: p = 0.74).

Discussion

We demonstrated that Steller's jay partners that behaved similarly in exploratory and risk-taking situations enjoy improved reproductive prospects in four of six comparisons. Partners scoring similarly in behavioural assessments nested early or were more likely to fledge young in 2 of 3 yr. Although the precision and certainty with which these relationships were expressed were low in some cases, which is likely an effect of small sample sizes for some comparisons (Figs 2b and 4; further discussion later), effect sizes were generally large across all relevant relationships. Furthermore, behaviourally similar partners were likely to share similarities across all three of the measured personality traits contributing to successful reproduction, suggesting that partners with an equivalent combination of behavioural traits (i.e. a behavioural syndrome) experience this advantage.

Recent studies have shown that an individual's mate choice may depend on the similarity of the chooser's behavioural characteristics to its prospective partner (Forstmeier & Birkhead 2004; Groothuis & Carere 2005; Schuett 2008) and that behaviourally compatible partners may have higher reproductive success and mate fidelity (Budaev et al. 1999; Spoon et al. 2006, 2007). These findings suggest that individuals may choose compatible partners based on similarity to their own behavioural phenotype. In conjunction with findings of an earlier study, where we showed that expression of behavioural types was independent of a jay's age, sex and body condition (Gabriel & Black 2010), we suggest that the fitness benefits of assortative mating in long-term perennial pair bonds of Steller's jays are attributable to the effects of compatibility emerging directly from behavioural similarity of partners. In contrast with pairing patterns in zebra finches (*Taeniopygia guttata*) and great tits, where assortative mate choice was limited to highly explorative individuals (Groothuis & Carere 2005; Schuett 2008), highly explorative and risk-prone Steller's jays were just as likely to pair assortatively as less explorative and risk-averse individuals. This means mate choice for behaviourally similar partners and the resulting compatibility benefits of partner similarity were independent of individual behavioural strategies.

In 1 out of 3 yr, partners that were both travellers and partners that were both non-travellers established nest sites sooner than partners with dissimilar travel habits. Furthermore, jay partners that were well matched in their willingness to risk re-entering a familiar trap initiated nests earlier than unmatched pairs. An individual's propensity to take risks is likely to influence the types of habitats it chooses for foraging and other activities (Mettke-Hofmann et al. 2002; Farwell & McLaughlin 2009; Harcourt et al. 2009), as well as its social interactions (Díaz-Uriarte 1999; López et al. 2005; Harcourt et al. 2009; Schuett & Dall 2009). More importantly, partners that share a similar perception of disturbance and predation risk and with a similar amount of information from prospecting alternative sites might be quicker to agree on a nest location than dissimilar pairs. Jays that were well matched with partners in their explorative tendencies fledged nests more successfully, possibly because they might spend more time together engaging in mutual foraging and territorial activities (Verbeek et al. 1994; Dingemanse & de Goede 2004). The reproductive advantage for pairs in which partners have spent more time together in the pair bond has been demonstrated in a wide range of monogamous species (e.g. Spurr 1975; Coulson & Thomas 1983; Bradley et al. 1995; Ens et al. 1996; Black 2001; Spoon et al. 2006). Behaviourally similar Steller's jay partners seem to enjoy this benefit regardless if they follow a qualitative strategy of intense and fast object exploration or a quantitative strategy of far-ranging habitat exploration (Fox et al. 2009; Minderman et al. 2009; Gabriel & Black 2010).

The influence of partner similarity in personality traits on reproductive performance varied among years. In 2007, there was a positive relationship between partner similarity and reproductive performance in four of the six trait relationships, whereas in both 2006 and 2008 expression of such a relationship was rare and weaker in cases where it did occur (Fig. 3a). Nest initiation dates were later in 2007 than the other 2 yr, indicating that nesting conditions were less favourable. The winter preceding the 2007 breeding season was colder, with freezing periods that were unusual for the region (min., avg., and max. temperatures in Jan. 2007 were 1.5–2.5°C below any other winter month in the 3-yr study period and 3–3.5°C below long-term averages for the region; National Climatic Data Center 2010), which likely diminished insect availability in the spring. Thus, behavioural compatibility and co-ordination appear to be most important when breeders were constrained by environmental conditions and resource availability. Similarly, Both et al. (2005) found that selection for behavioural traits in great tit parents and their offspring was strongest in years of scarce resources and low survival. In great tits, fluctuating patterns of selection on behavioural types and combinations of types in a pair led to an overall pattern of disassortative mating for exploration tendency even though assortative pairs had highest reproductive performance in some years (Dingemanse et al. 2004; Both et al. 2005). In Steller's jays, however, the variation in selection pressure on partner similarity from year-to-year did not preclude an overall selective advantage of assortative mating for exploratory or risk-taking personality types. We found no evidence for a decrease in reproductive success for more similar partners in any year. Thus, assortative pairing seemed to bear no reproductive cost. The finding that jays which attempted breeding in any given year tended to pair assortatively across all behavioural traits confirms this assessment. The strongest and most consistent assortative pairing pattern was expressed in travel distance beyond the home territory, corresponding well with the strongest and most pervasive reproductive advantage of partner similarity in this trait compared with the other traits. Alternatively, pairs in habitats that might have enabled higher nesting success might also be able to forage together more often than pairs in poor habitat, resulting in more similar travel habits of pairs in good territories. However, if variation in habitat quality would indeed have been an important influence on travel habits in this population, birds in poor habitat would be expected to travel more widely to find adequate resources (Dunning et al. 1992; Fedy & Stutchbury 2004; Fort & Otter 2004), and a relationship between similarity in travel distances and high reproductive performance would be evident only in non-travelling birds. On the contrary, assortative pairs were equally distributed among travellers and non-travellers. Also, the strongest assortative pairing patterns for the remaining two traits overlapped relatively well with the temporal patterns of when these pairings had reproductive advantages. Thus, it seems that assortative mating in jay pairs is not a by-product of underlying factors such as habitat quality, but is maintained overall because of its reproductive benefit. Assuming sufficient heritability for explorative and risk-taking behaviour in jays, offspring of assortatively paired parents with phenotypes at either end of trait gradients would have similar, extreme phenotypes. Hence, these pairing patterns and their fitness consequences act as disruptive selection on the traits themselves (Both et al. 2005), supporting the diversity of individual strategies in the population.

In conclusion, similarity in all three exploratory and risk-taking behaviours had reproductive advantages for jay partners in some years, and jays exploited these advantages by pairing assortatively for these behaviours, often sharing similarities across all three. Thus, linkage of these traits in a syndrome seems beneficial for Steller's jays, because assortative pairings are more easily achieved and more rewarding when traits are predictably related within individuals. This lends support to the idea that a correlated suite of behavioural traits (i.e. a behavioural syndrome) might be selected for and not just the result of a genetic or mechanistic link (Barton & Turelli 1991; Brodie et al. 1995; Bell 2005). This adaptive hypothesis of behavioural syndromes has been rarely addressed to date, but is crucial to our understanding of the evolution of behavioural personalities and syndromes (Eaves et al. 1990; Dingemanse & Réale 2005).

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