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Steller's Jay (*Cyanocitta stelleri*) Behavioural Syndromes – Correlates and Consequences of Individual Behavioural Strategies

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Acknowledgments

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Zusammenfassung

Verhaltensreaktionen zeigen oftmals individuelle Variation innerhalb von Tierpopulationen. Wenn solche Verhaltensunterschiede in systematischer Weise über die Population verteilt sind, wo Variationen in spezifischen Gradienten angeordnet sind und innerhalb von Individuen über längere Zeiträume hinweg konstant bleiben, so werden sie als individuelle Verhaltenstrategien, Spezialisierungen oder Persönlichkeiten beschrieben. Die Koexistenz alternativer Verhaltensstrategien, beispielsweise von risikofreudigen und risikoscheuen Individuen in einer Population deutet an dass Life-history Trade-offs alternative Lösungen für ökologische Herausforderungen ermöglichen. Besonders wenn Verhaltensunterschiede im Sinne eines Syndroms eine große Spannweite von ökologischen Kontexten umfassen und mit anderen fitnessrelevanten Merkmalen korrelieren, ist zu erwarten dass diese Verhaltensvariationen Konsequenzen für Ökologie, Evolution und Artenschutz haben. In dieser Studie wurde die Beschaffenheit und Stabilität von individuellen Verhaltensreaktionen und deren Wechselbeziehungen zueinander an einem langlebigen Rabenvogel, dem Diademhäher, untersucht. Ich studierte die Zusammensetzung und Spannweite eines Verhaltenssyndroms in einer Vielzahl von ökologischen Zusammenhängen, unter anderem Erkundungstrieb, Risikofreude, Nahrungserwerb, und Fangerfolg, und über mehrere Jahre mit unterschiedlichen Umweltbedingungen. Ich untersuchte die Fitnesskonsequenzen individueller Verhaltensstrategien durch Messungen des Reproduktionserfolgs der unterschiedlichen Phänotypen, und von Paarungsmustern in Hinsicht auf den Verhaltenstyp des Partners. Diademhäher zeigen ein breit gefächertes, langzeitlich stabiles Verhaltenssyndrom, in dem risikofreudige, weitwandernde, erkundungsfreudige Individuen die komplexe Futtererwerbsstrategien anwenden mit risikoscheuen, nicht wandernden, erkundungsscheuen, simplen Futtersuchern koexistieren. Häher deren Partnerwahl in übereinstimmenden Persönlichkeiten resultierte, hatten

Reproduktionsvorteile die von kompatiblen Verhaltensmustern in allen Dimensionen des Syndroms resultierten. Ein Großteil der Häherpopulation nutzte diesen Kompatibilitätsvorteil und paarte sich assortativ für Verhaltentypen, wodurch die Vielfalt an Verhaltensstrategien durch disruptive Selektion aufrechterhalten wurde. Die Stabilität und berechenbare Zusammensetzung von Verhaltensmerkmalen im Syndrom des Diademhähers macht assortative Paarungen leichter erzielbar und lohnender, was sich als Selektion auf das Syndrom selbst auswirkt. Diese Berechenbarkeit ermöglicht außerdem die Feinabstimmung von Managementmaßnahmen, die den Diademhäher als eine Vogelart von weitreichender Bedeutung im Artenschutz betreffen. Erkenntisse zur Struktur eines Verhaltenssyndroms können in diesem Zusammenhang gewinnbringend in unser Verständnis der Ökologie dieser Art eingebunden werden.

Abstract

Behavioural responses to specific stimuli often vary among individual animals in a population. When such behavioural variations are distributed in a systematic fashion, where behavioural differences form particular gradients and remain consistent within individuals over time, they are described as individual behavioural strategies, specializations or personalities. The co-existence of alternative behavioural strategies, e.g. risk-prone and risk-averse individuals in a population suggests selection for alternative solutions of ecological challenges via trade-offs. Especially when behavioural differences span a broad range of contexts to form a syndrome and covary with other fitness-relevant traits, they may be expected to have important ecological, evolutionary and conservation implications. I studied the distribution, stability and covariation patterns among individual behavioural responses in a long-lived corvid, the Steller's jay. The shape and breadth of a behavioural syndrome was assessed over multiple contexts, including exploratory tendency, risk-proneness, foraging behaviour, and trappability, and over several years with varying environmental conditions. I investigated the fitness consequences of individual behavioural strategies by measuring the reproductive performance of different behavioural phenotypes, and of mating decisions regarding a partner's behavioural type. Steller's jays display a broad behavioural syndrome that is very stable over time, where risk-prone, far-travelling, explorative birds that use complex foraging techniques co-exist with risk-averse, travel-shy, non-explorative, simple foragers. Birds that were able to find a partner of matching personality experienced reproductive advantages of their behavioural compatibility across all behavioural axes. Jays often took advantage of this compatibility benefit by pairing assortatively for behavioural phenotypes, perpetuating the diversity of personality types via disruptive selection. The stability and predictable combination of behavioural traits in the Steller's jay syndrome makes assortative pairings more easily achievable and more rewarding, thus selecting for the syndrome itself. This predictability also enables the fine-tuning of management actions for this species of wide-spread management concern, incorporating knowledge on the structure of a behavioural syndrome into our understanding of Steller's jay ecology.

1 Introduction

1.1 The ecology of individual behavioural differences

Behavioural variation among individual animals has traditionally been regarded as adaptive only when it resulted from individuals adjusting their behaviour to current conditions. Since the 1980s and 1990s however, the concept that individuals in the same population may behave differently because they solve the same ecological challenges through different adaptive strategies has gained increasing attention and acceptance (Endler 1986, Wilson 1998). A growing body of research demonstrates that inter-individual variation in behaviour is often distributed in a non-random fashion, for example forming particular behavioural categories or gradients (Gosling & John 1999), which remain consistent over time (Black & Owen 1987, Bell & Stamps 2004). The specific nature of this variation suggests that it likely has consistent ecological and evolutionary consequences and is a focus for selection (Dall et al. 2004).

Exploration of consistent individual differences has led to the description of a variety of behavioural axes or gradients, such as aggressive to submissive, bold to shy, inquisitive to inattentive, neophobic to neophilic, and risk-prone to risk-averse. Individuals at either end of these behavioural spectra are thought to pursue alternative life-history strategies selected for by strong ecological trade-offs (Sih et al. 2004a, Dingemanse & Réale 2005). An aggressive phenotype, for example, may be at an advantage when competing for mates and thereby improve its reproductive success, but it may be penalized by predators (Sih et al. 2004b, Stamps 2007). The genetic foundation of such behavioural differences has been demonstrated most clearly in great tits, where artificial selection amplified separation of exploratory tendencies into “bold” and “shy” lineages (Drent et al. 2003). The heritability of behavioural differences has significant evolutionary and ecological implications. Understanding how genetic variability can be maintained despite strong selection is not only an outstanding issue in evolutionary biology (Dall et al. 2004), but a key issue in conservation biology. The ability of species to adapt to rapidly changing anthropogenic environments can depend on genetic and behavioural diversity (Nicolakakis et al. 2003). Moreover, behavioural types may show differential propensity for successful breeding in captivity (Smith & Blumstein 2008), and differential survival after reintroduction into the wild (Bremner-Harrison et al. 2004, McDougall et al. 2005). Most importantly, behavioural phenotypes may have differential propensity to enter traps and be captured for research and conservation purposes in the first place (Réale et al. 2000, Garamszegi et al. 2009a, Gabriel & Black 2010). Pools of captured or reintroduced animals may therefore represent a biased genetic sample.

Despite their prevalence in a wide variety of animals and their apparent ecological significance, the origin and maintenance of consistent individual differences in behaviour is poorly understood. Theoretical frameworks and experimental studies addressing adaptive explanations encompass frequency dependent fitness payoffs for competing behavioural strategies (Maynard Smith 1982, Dall et al 2004), fluctuations of behavioural optima across different environmental conditions (Mangel 1991, Réale & Festa-Bianchet 2003, Dingemanse et al. 2004), and behavioural specialization interacting with internal or social states (Rands et al. 2003, van Oers et al. 2005). The finding that behavioural specializations are often also consistent across contexts, where for instance highly explorative individuals also take higher risks (Garamszegi et al. 2009, Gabriel & Black 2010), has important implications for these adaptive explanations and their potential limits.

1.2 Behavioural syndromes

A behavioural syndrome describes a suite of behavioural traits which are consistent over time and functional contexts (Dingemanse and Réale 2005). The significance of a syndrome should increase as the stability over an animal’s lifetime and the variety of the contexts it spans increases. That is, behaviours that are correlated broadly e.g. across mating, antipredator, exploratory and competitive contexts are expected to have farther reaching consequences for an individual’s life history and fitness. In a context specific syndrome on the other hand, aggression towards potential mates and rivals for example may be correlated only within the mating context, but unrelated to defense behaviour in an antipredator context (Sih et al. 2004). Studies have documented correlations both across contexts (e.g. Hessing et al. 1993, Koolhaas et al. 2001, van Oers et al. 2004) and context specific syndromes (e.g. Coleman & Wilson 1998, Réale et al. 2000), but general conclusions on typical ranges of correlations await more extensive study. The question whether trapping success should be regarded as a typical component of behavioural syndromes for example has important consequences for assessment and interpretation of behavioural traits requiring capture, and, depending on the expected breadth of a syndrome, any other potentially covarying traits that are measured in captivity.

Traits that are part of a syndrome are often thought to be linked by common underlying physiological mechanisms, implying a genetic link (Ketterson & Nolan 1999; Bell & Stamps 2004; Kralj-Fišer et al. 2010). This entails that fitness effects observed to operate on one trait could be due to selection on other, correlated traits. Fitness could be influenced either in similar or in opposing directions by different traits in the syndrome. In a mating context for example, highly explorative individuals that are also risk-prone may reproduce well with partners of a similar phenotype because engaging in similar foraging activities and travel habits may allow partners to spend much of their time together (Spoon et al. 2006; Schuett & Dall 2009). 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 and fitness benefits of the syndrome through high levels of intra-pair aggression (Ens et al. 1993; Spoon et al. 2004).

Where fitness benefits for the different traits in a syndrome operate in compatible directions, the whole suite of traits found in a syndrome may itself be selected for (Eaves et al 1990, Bell 2005). This adaptive hypothesis of behavioural syndromes is an alternative to the hypothesis of a genetic link between correlated traits, without the two hypotheses being mutually exclusive (Lande 1986, Dingemanse & Réale 2005). Evidence supporting either of these hypotheses and allowing examination of their relative importance in shaping the distribution of individual behavioural traits and their covariation in animals is scarce. Quantification of behavioural traits over multiple contexts, multiple environmental conditions, and sufficiently long time frames in an animal’s life, coupled with fitness measures are required to understand the origin, function and relationships of behavioural specializations within animal populations (Smith & Blumstein 2008).

1.3 Study goals

The goals of this study were to describe the nature, stability, and covariation patterns among individual behavioural responses in a long-lived bird with a complex behavioural repertoire, and explore the ecological correlates and fitness consequences of the interaction of these individual strategies in a behavioural syndrome.

Behavioural traits including exploration and travel behaviour, willingness to take risks, and foraging strategies were measured over a variety of contexts to characterize the extent of individual behavioural variation in a wild population of urban Steller’s jays (*Cyanocitta stelleri*). I used repeated measures of the same behavioural response and comparisons between short-term experimental tests and long-term, annual measures of behaviours within the same ecological context. I investigated the stability of individual strategies and the usefulness of different types of measures, specifically short-term experiments in the wild, to assess an individual’s true phenotype. The shape and breadth of a behavioural syndrome was assessed using correlations among behavioural types within and across ecological contexts.

Assessing the role of trapping success in the behavioural syndrome informed interpretation of the significance of this relationship for studying individually captured and marked animals in the wild and in captivity.

I investigated selection on behavioural types by measuring the reproductive consequences of individual strategies, and of mating decisions regarding a partner's behavioural type. The question whether reproductive advantages for different behavioural types and combinations of types fluctuated with different environmental conditions was investigated across several years. The significance of behavioural specializations for fitness in foraging and reproductive contexts was compared to the significance of other fitness-relevant traits measured in the same population.

The question how the nature of this behavioural syndrome itself may have originated and is maintained was addressed by investigating directional selection on its component traits. I expected that fitness benefits of component traits would align with the direction of trait combinations in the syndrome, if the syndrome itself was selected for. If the suite of traits in the syndrome was a result of selection, covariation of traits may also be expected to enhance single fitness effects. Further I considered whether behavioural differences resulted from adaptations to different internal and social circumstances or were more likely to be stable, innate phenotypes. For this purpose I investigated interactions of behavioural traits and their fitness effects with individual and pair-specific traits such as age, sex, pair duration and pair tenacity.

2 Studying behavioural syndromes in Steller's jays

2.1 The ecology of urban Steller's jays

Throughout this study, I used free-living, individually marked Steller's jays as model organisms. The Steller's jay is a small corvid ranging from arid woodlands in Central America and the southwestern United States to coniferous forests, forest edges and urban habitats in northwestern North America (Greene at al. 1998). Similar to many other long-lived corvids, Steller's jays form long-term socially monogamous pair bonds that are rarely dissolved through any other cause than death (Brown 1964, P. O. Gabriel & J. M. Black, unpublished data). Pairs typically remain resident on breeding areas year-round, especially in low-elevation populations (Bent 1946, Brown 1964). In late March to early April both sexes build the open cup nest, and subsequently cooperate in feeding nestlings. After fledging, birds exhibit weaker territoriality and some individuals travel widely.

The interaction of Steller's jay breeding pairs in a very loose form of territoriality, described as site-centred dominance, creates a rather unique social environment. Each monogamous pair is dominant over all other jays close to its territorial centre but gradually loses dominance with distance from the nest site (Brown 1963). This form of organization and the high tolerance of residents towards regular territorial intrusions by conspecifics create a pattern of extensively overlapping homeranges among neighboring pairs. This social system combines some social advantages of flocking, such as finding temporary rich food sources and communal predator mobbing, with retaining priority of usage in core areas, similar to true territoriality (Brown 1974). Thus, regular encounters among pairs and small groups provide a platform for frequent behavioural interactions in complex, site-dependent dominance hierarchies (Brown 1963).

As omnivores consuming a wide variety of animal and plant food, including arthropods, seeds, fruits, small vertebrates, nest contents and human refuse (Greene et al. 1998, Vigallon and Marzluff 2005a), jays concentrate their activities in structurally complex, patchy habitats (Marzluff et al. 2004, Vigallon and Marzluff 2005a). This background makes them well adapted to urban and suburban environments, where plentiful, ephemeral and often unpredictable anthropogenic resources result in high habitat heterogeneity. Steller's jays take advantage of these habitats throughout the Pacific Northwest, occurring in suburban and recreationally used landscapes often at high densities (Marzluff et al. 2004).

Life in suburban environment creates or shifts emphasis of a number of ecological challenges for jays: Firstly, frequent disturbances by human activity, and the high density of potential nest predators such as crows, ravens, domestic and feral cats, raccoons and rats make jay nests much more susceptible to abandonment and predation in comparison to exurban and wildland areas (Vigallon & Marzluff 2005b). Thus, securing enough resources for frequent re-nesting attempts and choosing well-concealed nest sites become important factors for successful reproduction. Secondly, through the attraction of jays to profitable, patchily distributed anthropogenic resources, home range overlap among neighboring pairs can be dramatically higher than in wildlands (W. Goldenberg, J. Black & L. George, unpublished data), increasing the frequency of interactions, resource competition and possibly adding to the predation pressure on nests incidentally discovered by conspecifics. Lastly, the diversity and novelty of many anthropogenic resources encountered by jays, and the heightened competition for them provide unique opportunities to study the role of the complex individual behavioural specializations these corvids employ to exploit and compete for these resources.

2.2 Measuring behaviour in the wild

Behavioural phenotypes are usually measured as short-term responses to environmental stimuli under laboratory conditions (Verbeek et al. 1994, Dingemanse et al. 2002, López et al. 2005, Martins et al. 2007, Fox et al. 2009, Schuett & Dall 2009) or, more rarely, in the wild (Brown et al. 2005, Garamszegi et al. 2009a). Those short-term measures have enabled researchers to compare large numbers of traits with little time investment and consequently describe behavioural syndromes in many functional contexts. However, studies failing to find a link between fitness components and behavioural traits measured in captive situations suggest that laboratory studies may only provide limited insight into the fitness consequences of animal personality in the wild (Höjesjö et al. 2002, Martins et al. 2007, Fox et al. 2009, but see Herborn et al. 2010). Moreover, the relevance of a measured trait for the behavioural syndrome of a study species, or more importantly the detection of that relevance, can critically depend on the time frame of measurement, the specific ecological circumstance, and the general nature of the chosen trait (Bell & Stamps 2004). For example, investigations into different fitness components of bighorn ewes and their relation to two different and only weakly related traits, boldness and docility, showed that age at first reproduction acted on both boldness and docility, whereas weaning success was only related to boldness, and a third fitness index, survival, was affected by both behavioural traits, but only in years of high predation pressure (Rèale et al. 2000, Rèale & Fest-Bianchet 2003). The interpretation of well established personality traits such as exploration speed in a laboratory setting can also not necessarily be generalized over different species, because differences in ecological requirements and life-styles affect both the significance and the nature of a trade-off that is measured in a particular test (Mettke-Hofmann et al. 2005, Fox et al. 2009, Minderman et al. 2009). Since the nature of the trade-off is usually assumed instead of measured (e.g. that flight distance from a human observer reflects a trade-off between territorial defense and predator avoidance; Blumstein 2006) the interpretation of the absence of an expected effect can be difficult because the measured traits might be irrelevant to the behavioural syndrome of the investigated species, a behavioural syndrome might be absent altogether or the traits might have been measured in unsuitable circumstances (Mettke-Hofmann et al. 2005, Mettke-Hofmann 2007).

In a review of studies addressing natural selection on animal personality, Dingemanse and Rèale (2005) emphasize the importance of addressing selection gradients on personality traits and their comparative strength to other suites of traits, and thus encourage the publication of both the evidence and the absence of evidence for selection on behavioural traits. In this context the applicability of short-term behavioural measures to the life-history of the studied species is of critical importance. In fact, Dingemanse and Rèale (2005) suggest that selection studies on behavioural syndromes should be performed over the long-term to account for fluctuation of selection pressures and understand both immediate consequences and longer-term effects. If and how typically simple and practical short-term behavioural measures actually express life-history trade-offs assumed to be important in the long-term decision making of a species is therefore an important component in the study of behavioural syndromes.

Taking advantage of the longevity, behavioural complexity and easy habituation of urban jays to human observers, I developed protocols to measure behavioural traits in a variety of ecological short-term and long-term contexts that closely reflected real trade-offs encountered by jays in our study population. During ongoing studies on the mating system and life history of Steller’s jays, long-term data on several behavioural traits was collected, which after repeated field observations were suspected to vary strongly between individuals. Long-term behavioural observations spanned several years, providing opportunities for assessment of fitness effects under different environmental conditions. Both short-term and long-term behavioural measures were collected in the wild, without the need to take birds into captivity. This enabled me and my collaborators to create experimental situations that represented real ecological contexts for jays in urban-fringe populations as closely as possible, while avoiding the potential confounding effects of heterogeneity in trappability between behavioural types (Garamszegi et al. 2009a).

3 Materials and methods

3.1 Study population and demographic and morphological measures

The marked population of Steller's jays used in this study was first initiated in 1998, and expanded to a size of approximately 55 breeding pairs and 30-40 transient individuals by 2006. The marked birds were resident on the Humboldt State University campus and surrounding residential neighborhoods of Arcata, California (40º59'N, 124º06'W). In this contiguous study area of 3.5 km^2 all territories and nests were located within 750 m of redwood forest (*Sequoia sempervirens*). 28 feeders distributed across the study area were regularly baited with bird seed and peanuts and served as experimental sites and trapping stations (Figs. 1 and 5). Steller's jays in this region, as is typical for low-elevation populations, are non-migratory, defending territories with vocalizations and displays throughout the year. In contrast to most migratory passerines, both sexes in Steller's jays may exercise mate choice and territory defense and have a similar behavioural repertoire.

I attempted to trap all birds within the study area once annually after the completion of molt and before the onset of breeding activity, typically between December and March. Unbanded individuals were fitted with a unique combination of colour leg bands and aged as hatch-year or after-hatch-year birds, based on gape colouration and plumage patterns (Pyle et al. 1987). In all captured individuals, a variety of standard morphological traits, plumage characteristics and indices of parasite infestation were measured. Data on wing length, tarsometatarsus length, gape length and body mass were used in this study. For indices of body size, size measures that correlated well with body mass were either used directly, or where body size was of more central interest to the study hypothesis, calculated as a composite of all three size measures using principle component analysis (La Barbera 1989, Rising and Somers 1989). Body condition was assessed using residuals of regressions of size variables against body mass. Since the two

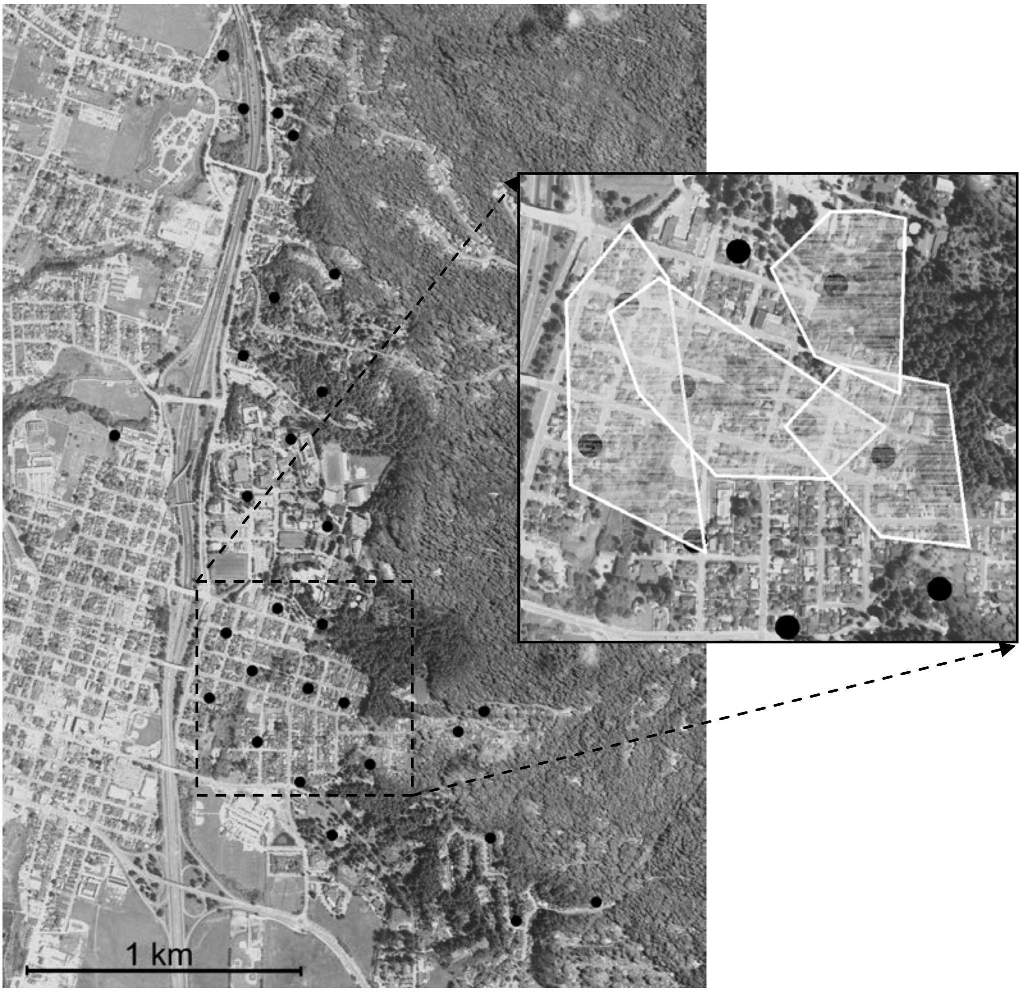

Figure 1. Study area in Arcata, California, U.S.A. Black circles denote locations of regularly baited feeders that could function as traps during 2006-2008. White, shaded polygons in the magnified detail depict approximate home ranges of four Steller's jays in 2007.

sexes in Steller's jays are largely monomorphic, with the exception of body size differences detectable in population means (Greene et al. 1998), sex was determined after banding individuals by observations of sex-specific calls given in territorial disputes (females "rattle", and males "creak"; Hope 1980).

3.2 Behavioural traits

Jay territories were monitored on a near-daily basis from January 2006 to September 2010 to obtain resighting locations and behavioural data for all colour-marked birds. Efforts were made to find each bird at least once per week throughout the breeding seasons (March – August) and once every three weeks outside the breeding seasons. From 2006 to 2008, one to five resighting locations per day were recorded for a given individual, depending on duration of the observation and flight distances. Adult jays that held a breeding territory between 2006 and 2008 were characterized for exploration tendency and risk-taking tendency, each measured in one short-term experiment and one repeatedly assessed long-term behaviour. I also recorded the success or failure to recapture them in baited feeders. Adult breeders in the study area between 2008 and 2010 were characterized for foraging behaviours in three different contexts.

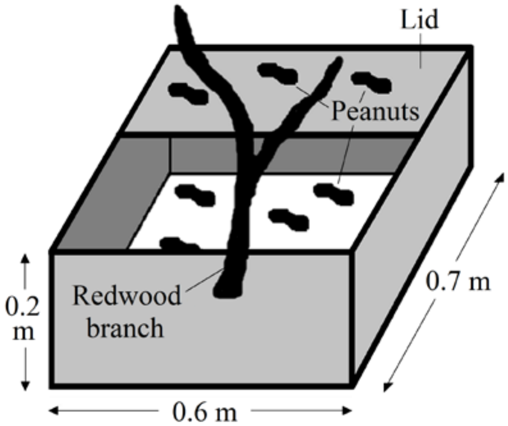

Figure 2. Experimental feeder that jay pairs were exposed to close to respective territorial centres for 20 min observation periods. Jays were scored on exploration tendencies according to amount of area explored, time spent exploring, and peanuts taken. Cumulative scores ranging from 0 to 169 were calculated from latencies to perform these explorative behaviours (from Gabriel & Black 2010).

Short-term and foraging experiments were designed to closely mimic ecological circumstances that birds in our study population would likely encounter, whereas long-term behaviours were measured under regular daily monitoring conditions. Exploration tendencies were assessed by experimentally exposing jay pairs to a novel feeding opportunity (short-term; see Fig. 2) and by annual measures of travel distance beyond territorial boundaries (long-term; see Fig. 3).

Figure 3. Resighting locations (circles) and nest sites (stars) of two jays in 2007 in Arcata, California. The mean of the five longest distances from the nest (depicted by lines connecting resighting and nest location) were used as an annual index of how far and how frequently individual birds explored beyond their home territory (black: far-travelling individual; white: travel-shy individual).

The propensity to take risks was measured in the contexts of confrontation with a potential predator (short-term; see Fig 4) and willingness to re-enter a familiar trap (long-term; see Fig. 5).

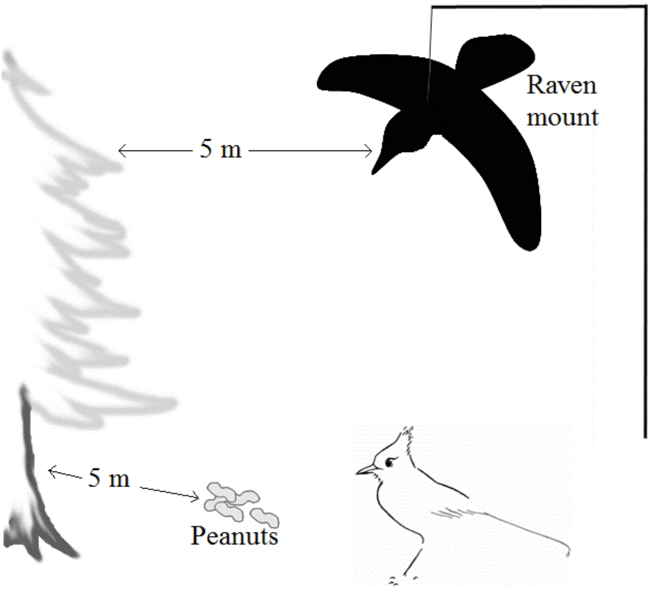

Figure 4. Experimental mount of a raven (*Corvus corax*), a common predator of jay nests and juveniles, suspended in flying posture for predator mobbing experiment. Jays were attracted to peanuts close to respective territorial centres. After revealing raven mount risk taking tendency was scored during 30 min observation periods according to individual jays' mobbing activity (bivariate measure: alarm calling / no alarm calling).

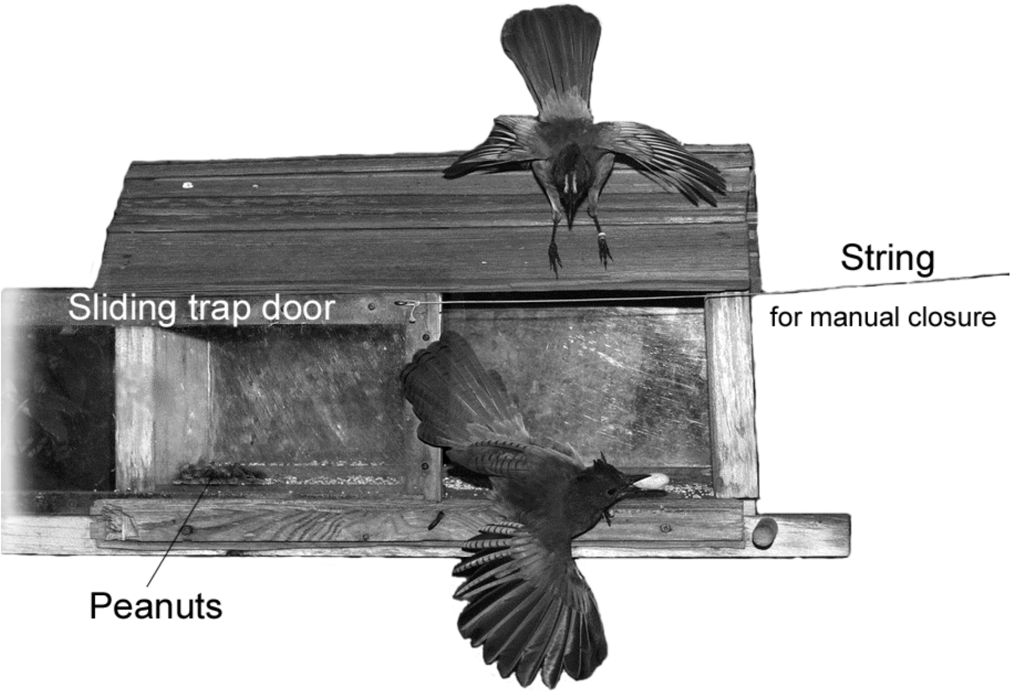

Figure 5. Regularly baited feeder for trapping and behavioural experiments. Jays were assigned a score at each visit observed: 0 = no approach; 1 = perched on top; 2 = fed at entrance; 3 = entered halfway; 4 = entered all the way < 2s; 5 = entered all the way > 2s. For previous successful capture, birds had to enter the feeder at least once all the way corresponding to a score of at least 4. Birds scored for risk taking were thus all familiar with the trapping risk associated with attending the feeder. Mean score per individual over all observations within a year was used as annual index for long-term risk taking.

Foraging strategies were assessed as the propensity to sample and choose multiple food items and were compared among contexts of encountering a novel feeding situation and encountering a potential predator (see Fig. 6). The short-term experiments and the foraging experiments were conducted during non breeding seasons when pair bond and territorial displays were at a maximum prior to nest building. In 2007 recapturing effort was most intensive and consistent throughout the study area. I therefore used the success or failure to trap an individual that had been captured in the same trap the previous year and survived to the 2007 capturing season as a bivariate measure of trapping success (trapped / not trapped).

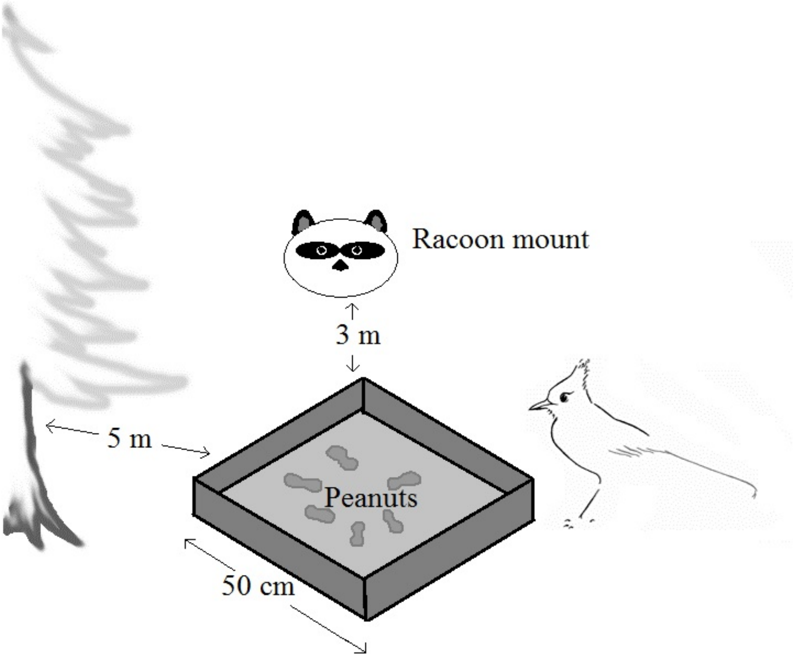

Figure 6. Feeder platform repeatedly presented to jays close to respective territorial centres for 30 min observation periods. In absence of the raccoon mount, first latency to approach platform (explorative tendency), number of sample actions and number of peanuts carried away were assessed (complexity of foraging strategy). In presence of the raccoon mount, number of sample actions and number carried away (foraging strategy), and a cumulative risk-taking score according to latencies and distances to approach the mount were assessed (risk-taking tendency).

3.3 Pair bonds and reproductive performance

Behavioural and resighting data collected during regular monitoring of the study population was used to assess pairing and nesting status, reproductive performance, and pair bond characteristics. A male and female jay associating regularly, engaging in pair bond behaviours such as courtship feeding, soft and loud contact calls, courtship displays, regular proximity, and defense of the same territory, and later attempting to nest were determined to be a pair. Territories were defined as the area where a pair regularly performed sex-specific territorial vocalizations, displays, cached food items nearby, and displaced intruding jays (Brown 1963, 1964; Greene et al. 1998).

According to the idea that coordination of movements and behaviours should increase with the time that partners spend in a pair bond, known as the mate familiarity effect (Black 1996), I measured characteristics of jay pair bonds and their interactions with compatibility and stability of behavioural traits in a pair. Pair bond duration and age were estimated from the dates when partners were first recorded associating as a pair, and, if the pair bond ended within the study period, the last date recorded together. The frequency with which partners were observed associating and engaging in a number of subtle pair bond behaviours were used as measures of tenacity and maintenance of the pair bond.

I quantified nest initiation dates and fledging success as indices of reproductive performance in 2006, 2007 and 2008. Nest initiation relative to conspecifics in the same population is a widely used indicator of reproductive success, because individuals that initiate breeding earlier usually 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 & Boerlist 1990; Winkler & Allen 1996; McGraw et al. 2001). Observations of reproductive behaviour and parental care (Greene et al. 1998) were used to estimate initiation dates for the first known nest attempt of each jay pair, relative to annual mean date across the entire study population. Successful fledging was attributed to birds that travelled with and/or fed fledglings in a breeding season (Vigallon and Marzluff 2005b, Marzluff and Neatherlin 2006).

3.4 Statistical analyses

Consistency of behavioural responses within individuals over time as an important criterion for individual behavioural differences and syndromes was measured as repeatability. Repeatability estimates the ratio of among-individual variance to the total variance in the measured samples. These variance components were calculated from appropriate mean squares obtained from ANOVAs using individual as the main effect (Lessells and Boag 1987). Repeatability scores range from zero to one, where a higher score indicates that a greater proportion of the variance is explained by the variation among individuals than by the variation within individuals. Values greater than 0.25 are considered moderately repeatable and values greater than 0.50 are considered highly repeatable (Dingemanse and Réale 2005), with a value of 1 indicating no variation within individuals.

For comparisons of strength and direction of relationships between different behavioural traits, and between behavioural traits and a number of other characteristics of Steller's jay individuals and pairs, I calculated effect sizes and 95% confidence intervals around these effects. In contrast to conventional hypothesis testing based on significance levels that allow only dichotomous decisions whether a biological effect is observed or not, this approach allows interpretation of the relative magnitude of relationships on a continuous scale and the certainty that can be derived from current data (Nakagawa 2004, Garamszegi 2006, Nakagawa and Cuthill 2007, Garamszegi et al. 2009b). I used correlation coefficients as standardized, directly comparable effect sizes. These were either obtained directly from regressions between two continuous variables (expressed as Pearson's or Spearman r), from related effect sizes obtained in comparisons of means and variances for categorical variables (calculated as d and converted into r; Cohen 1988) or from proportions in contingency tables (expressed as w; Cohen 1988). 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 methods used in recent behavioural research (see e.g. Garamszegi et al. 2009a). It enabled me to determine the relative contribution of a range of behavioural traits to a behavioural syndrome in Steller's jays, reproductive consequences of individual traits, reproductive consequences of assortative mating for personality traits, and relationships between pair bond characteristics, individual behaviours and reproductive performance. The magnitude of effects among these relationships in the same population and to relationships found in other studies and other species are directly comparable.

In addition to their usefulness for the interpretation of biological significance, effect sizes can be used in analyses that follow the pattern of meta-analytical approaches to estimate effects of a predictor variable across multiple comparisons (Hedges and Olkin 1985, Garamszegi 2006). In accordance with the nature of effect sizes as standardized measures that have a certain statistical distribution with measurable attributes when tabulated across multiple variables I used simple meta-analytical methods to investigate general patterns in different matrices of correlations (Garamszegi 2006). General effect sizes were calculated for relationships of several individual and pair characteristics with reproductive performance across two reproductive indices and three years, for assortative mating tendencies across multiple traits and years, and for certain trait combinations. Overall correlation coefficients and confidence intervals were calculated from individual effect sizes and sample sizes of the relevant trait relationships. Depending on whether the variables included in these meta-analyses were correlated within individuals and pairs, resulting overall effect sizes were either interpreted as absolute effects, or only in relation to each other (Garamszegi 2006).

In analyses of foraging strategies, several demographic and morphological characteristics as well as behavioural traits influenced foraging selectivity. Model selection techniques according to corrected Akaike Information Criteria (AICc) were therefore used to gauge the relative importance of personality type, body size and experience on individual foraging decisions.

4 Results and discussion

4.1 Structure and correlates of a behavioural syndrome

Interpreting and understanding the function and consequences of behavioural syndromes, where individual behavioural differences are correlated within individuals over time and across behavioural traits and ecological contexts, requires detailed assessment of these correlations (Sih et al. 2004). In this study, 133 individual jays over five years were characterized for eight different behavioural traits in short-term and repeated long-term measures for a comprehensive assessment of a Steller's jay syndrome across multiple ecological contexts and time frames. Individual behavioural responses covaried across three different ecological contexts to form a behavioural syndrome in a wild population of urban Steller's jays. The willingness of individual jays to take risks when mobbing a potential predator and at a familiar feeder trap was positively correlated with their exploration behaviour of both novel objects and environments (Fig. 7). Choice of foraging strategy was correlated with risk-taking traits, where jays that sampled and/or took multiple items were risk-prone birds, exhibiting short latency periods for approaching the novel foraging platform and the predator mount, while risk averse-birds with long latencies used simple strategies (Fig. 8.). Moreover, tendency to use complex foraging strategies (sampling and/or take of multiple items) correlated with risk-prone and highly explorative tendencies in long-term behaviours (trap re-entry and travel distance; Table 1).

Long-term measures of exploration, risk-taking, and complexity of foraging behaviour were moderately to highly repeatable within individual jays over time and this consistency predicted accurately that these measures were also meaningful contributors to the behavioural syndrome described. It could be confirmed that separate measures of the same behavioural trait that were strongly correlated with each other, and therefore likely mediated by the same trade-off, would also have very similar relationships to other behavioural traits. This was evident from measures of risk-taking, which were strongly positively correlated between the contexts of predator mobbing and trap re-entry (*r* = 0.53, 95% *CI* = 0.25 - 0.74), and were both positively related to novel feeder exploration and to travel distance (Fig. 7).

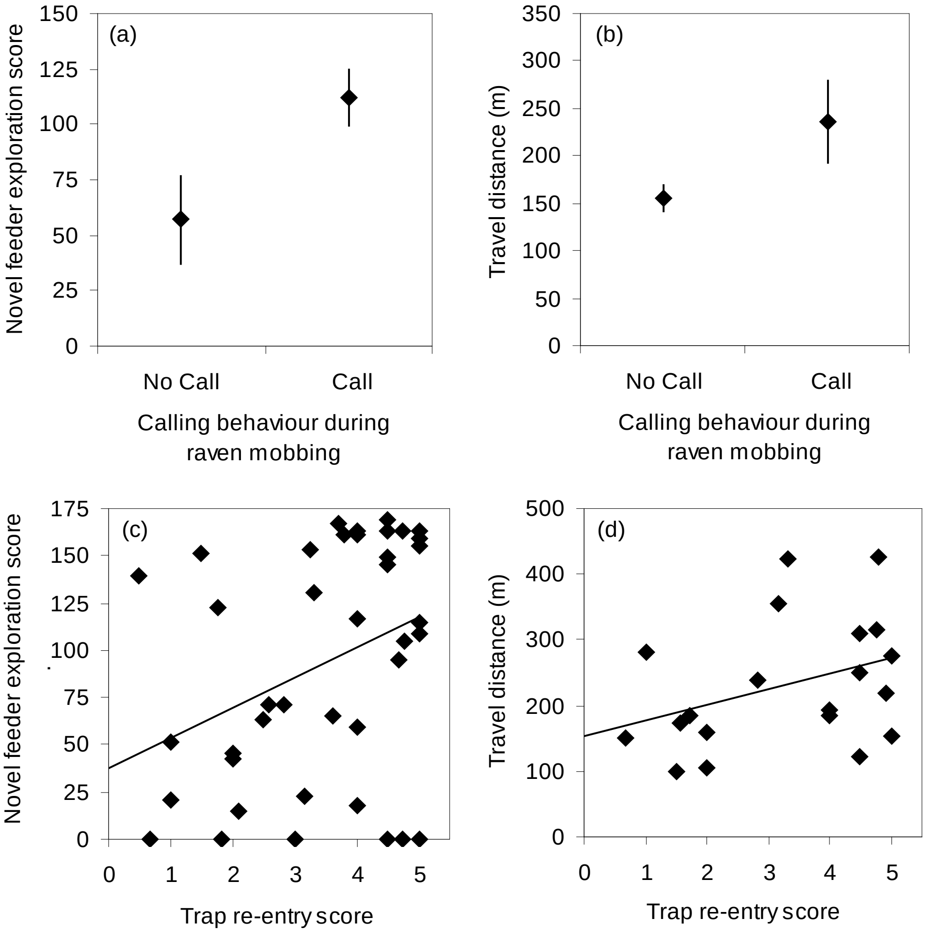

Figure 7. Relationships between behaviours measured in four ecological situations: (a) short-term risk taking and short-term object exploration (*r* = 0.53, 95% *CI* = 0.16 - 0.77), (b) short-term risk taking and long-term habitat exploration (*r* = 0.69, 95% *CI* = 0.16 - 0.91), (c) long-term risk taking and short-term object exploration (*r* = 0.33, 95% *CI* = 0.02 - 0.58), and (d) long-term risk taking and long-term habitat exploration (*r* = 0.37, 95% *CI* = -0.08 - 0.70). Diamonds with error bars indicate means and SEs (from Gabriel & Black 2010).

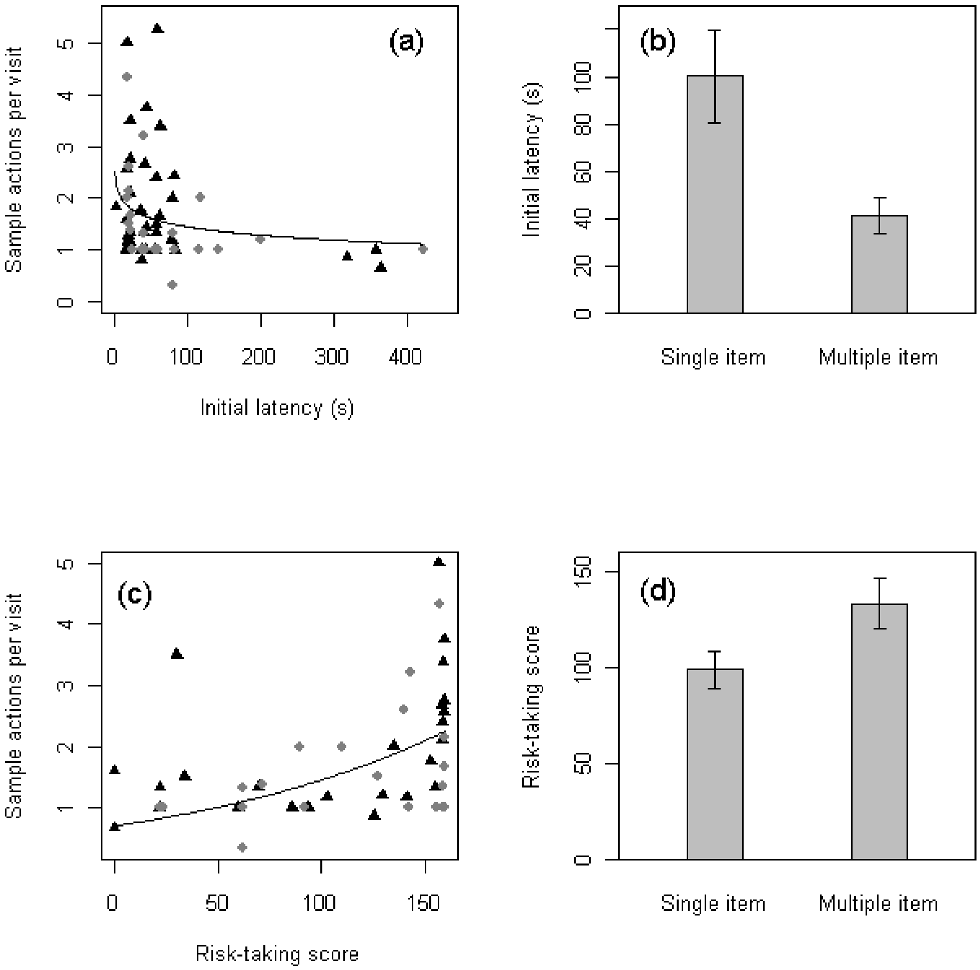

Figure 8. Use of simple (taking first item handled) and complex (sampling or taking multiple items) foraging strategies in 63 Steller's jays in relation to two boldness tests (black triangles: males, gray circles: females). Relationship between latency to approach a novel feeding platform and: (a) average number of sample actions (*r* = -0.48, 95% *CI* = -0.66 – -0.26), (b) birds that took a single item in all visits compared to birds that took multiple items in one or more visits (*r* = -0.25, 95% *CI* = -0.34 – -0.12). Relationship between risk-taking score (response to a raccoon mount and: (c) average sample actions (*r* = 0.44, 95% *CI* = 0.17 – 0.65), (d) birds that took single items compared to birds that took multiple items in one or more visits (*r* = 0.29, 95% *CI* = 0.03 – 0.54; modified from Rockwell et al. 2012)

Table 1. Relationships between Steller's jay foraging behaviours (sampling and taking multiple items) and long-term exploratory and risk-taking traits.

	Sampling behaviour			Taking multiple items		
	r	*n*	95% *CI*	*r*	*n*	*95% CI*
Travel distance[a]	0.81	16	0.53 – 0.93	0.64	11, 5	0.31 – 0.88
Trap re-entry[b]	0.36	39	0.05 – 0.60	0.28	30, 9	-0.02 – 0.60

[a] Average of five longest distances from territory centre in one year of resightings
[b] Annual score of how far a jay entered a familiar trap following a capture event

Interestingly, the two measures of exploration were not correlated with each other (*r* = 0.20, 95% *CI* = -0.26 – 0.59) but also showed similar covariations with both risk-taking behaviours (Fig. 7). The same was true for measures of exploration and risk-taking in a foraging context, where latency to approach the novel platform was unrelated to risk taking in presence of the racoon mount (*r* = -0.17, 95% *CI* = -0.26 – 0.42), but both behavioural traits had similar relationships to foraging behaviour (Fig. 8). This implies that the investigated exploratory and risk-taking strategies are of similar importance to a behavioural syndrome in Steller's jays. However, because short-term responses in seemingly related contexts were not necessarily related and did not necessarily predict long-term behavioural strategies, the expression of behavioural types and assumed underlying trade-offs should be regarded as context specific (Martins et al. 2007, Fox et al. 2009, Minderman et al. 2009). The complexity of relationships between the behaviours we measured suggests that behavioural responses on one hand generally co-evolved to form syndromes, but on the other hand may compete for resources allocated to separate behaviours that don't share genetic and physiological pathways (Roff 1997, Réale et al. 2007). Behavioural responses in the two explorative contexts seem to represent two alternative exploratory strategies that are unrelated because time investment into a qualitative strategy (thorough exploration of a novel foraging opportunity) might not allow simultaneous investment into the alternative, quantitative strategy (exploration beyond the home territory). Lack of correlation between latency to approach the novel platform and risk-taking score may be explained by a large mismatch in risk magnitude, resulting in independent physiological and thus behavioural responses (Coleman and Wilson 1998, Réale et al. 2007).

Expression of behavioural types was independent of pair membership. The independence of behavioural responses between jay partners validated the approach to assess birds under natural conditions in the wild, which sometimes required the simultaneous testing of partners. Moreover, it provided reasonable cause to assume that behavioural differences were not based on differences in habitat quality among territories that were shared by partners (Riechert & Hall 2000). Explorative and risk taking tendencies of individual jays were also independent of sex and age, whereas male, older, and larger jays tended to show more complex foraging strategies. Increased foraging efficiency with age is reported in many species (Jansan 1989; Desrochers 1992; Heise and Moore 2003; Wheelwright and Templeton 2003). However, increased familiarity with foraging and available food seems to allow individual Steller’s jays to not simply improve efficiency, but develop alternative strategies (Bennetts and McClelland 1997), disproportionately among risk-prone compared to risk-averse individuals. Since more complex foraging behaviours were more time consuming, larger and male jays were likely able to spend more time on profitable, complex strategies without the risk of displacement due to their higher social dominance position when competing with their mates and neighbors for food (Brown 1964). Behavioural differences between males and females even in foraging strategies were rather small, however. Thus, male and female Steller’s jays appear to solve adaptive problems with similar behavioural strategies, as may be predicted from their very similar life styles (Brown 1963, 1964, Buss 1995, van Oers et al. 2004). Such behavioural and ecological similarity between the sexes is rare (Kurvers et al. 2009). It provides a relatively unique perspective on the investigation of behavioural syndrome and mating strategies, because selection on correlated behavioural characters in a syndrome should not be constrained by conflicting selection on different trait optima between the sexes (Partridge 1994, Dingemanse et al. 2004, Pruitt & Riechert 2009).

Steller’s jays that were highly explorative and willing to take greater risks were more likely to be captured than less explorative and risk-averse individuals (Fig. 9). These findings affirm the suspicion that trapping success has to be regarded as a component of behavioural syndromes (Wilson et al. 1993, Mills & Faure 2000, Réale et al. 2000, Malmkvist & Hansen 2001, Garamszegi et al. 2009a). Since a pool of captured animals likely contains a different distribution of behavioural types than the entire population, this has important consequences for design and interpretation of studies of behavioural syndromes and any covarying traits in captivity (Garamszegi et al. 2009a). For example, behavioural syndromes may affect stress responses (Carere et al. 2003, Kralj-Fišer et al. 2007), levels of parasitism (Garamszegi et al. 2007), or morphological and physiological characteristics that are widely studied for their evolutionary and ecological significance (Krause et al. 1998, Wilson 1998, Brown & Braithwaite 2004, López et al. 2005). Since those traits can only be assessed in captive animals, such studies likely miss one end of the natural distribution of phenotypes. For example, annual measures of body mass and size, secondary sexual plumage characteristics and parasite load are taken of all captured individuals in this study population of Steller’s jays. Since any of these characteristics may interact with the behavioural syndrome described in this study, equalizing the sampling, i.e. trapping success over all phenotypes in the population is an important prerequisite for accurate interpretations of results. The longevity and year-round residence of our study species provides a great advantage for addressing this problem, because it allows repeated, long-term, and if necessary, individually focused trapping efforts.

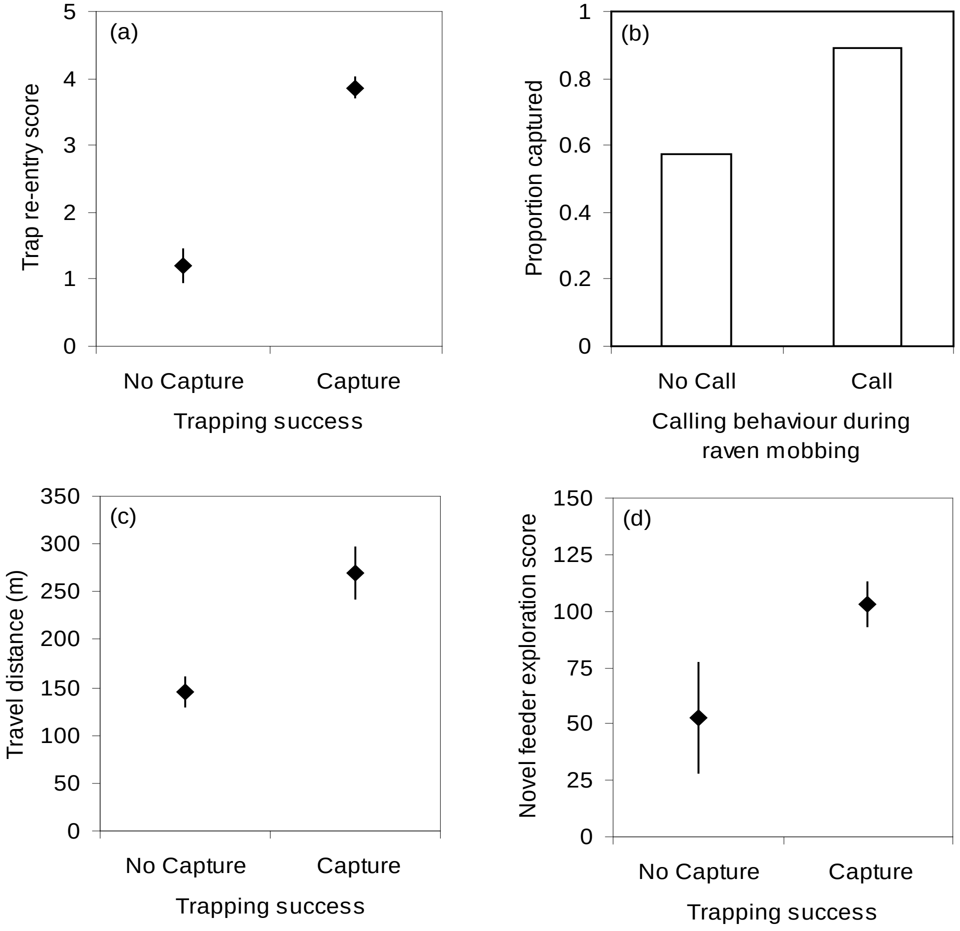

Figure 9. Relationships between trapping success and (a) long-term risk taking (*r* = 0.65, 95% *CI* = 0.27 - 0.85), (b) short-term risk taking (*w* = 0.36, 95% *CI* = -0.06 - 0.86), (c) long-term habitat exploration (*r* = 0.34, 95% *CI* = 0.04 - 0.59), and (d) short-term object exploration (*r* = 0.82, 95% *CI* = 0.71 - 0.89). Diamonds with error bars indicate means and SEs (from Gabriel & Black 2010).

4.2 Fitness consequences for the individual and the pair bond

I explored the consequences of male and female explorative and risk-taking traits, as well as basic demographic and physical characteristics on two measures of reproductive performance in 130 male and 103 female Steller's jays. In both sexes, age had the most consistent, although only small to moderate influence on reproductive performance. Relationships between behavioural characteristics and nest initiation or fledging success were generally absent or weak and inconsistent, with the exception of females that were less explorative in a novel feeding situation performing slightly better overall (Fig.10).

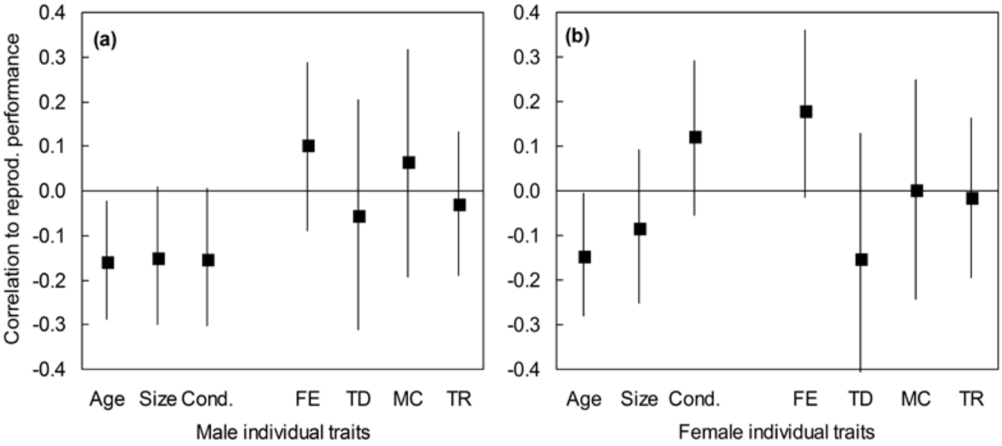

Figure 10. Correlation coefficients *r* and 95% *CI*s (indicated by error bars) of meta analyses for Steller’s jay males (a) and females (b) describing relationships between individual traits (age, body size, body condition (Cond.), exploration of a novel feeder (FE), travel distance beyond home territory (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 three years (2006, 2007, 2008; from Gabriel & Black 2012).

This tendency for better reproductive performance of less explorative females may be related to the observation that nest predation and abandonment due to disturbance are very important variables determining reproductive success in this urban population (J.M. Black & P.O. Gabriel, unpublished data). Jays who are “conservative” in their exploration and become intimately familiar with local resources might more often re-use known nest areas which have remained unchanged in a typically dynamic anthropogenic environment. Such sites would have more predictable patterns of predation and disturbance risk, sometimes allowing earlier nest initiation or better fledging success. Overall, variation in individual male and female traits, especially behavioural traits, explained little of the variation in nest initiation and fledging success. Consequently it was not surprising that there was no evidence of covariation in the direction of selection, measured in reproductive variables, on the four behavioural traits investigated that were known to form a behavioural syndrome (overall covariation in males: $r = 0.03$; in females: $r = 0.08$). Selection on this behavioural syndrome in the form of differential reproductive performance by individual jays with different suites of behavioural traits was therefore not apparent. Our study population has access to an abundance of readily available anthropogenic and natural food sources year-round, which can ameliorate the fitness effects of individual quality (Schielzeth et al. 2011). Moreover, environmental factors such as the distribution of cats and the alteration or removal of nesting trees, leading to many failed and abandoned nests, are so unpredictable that effects of individual parental strategies might be masked by random environmental influences on ultimate reproductive outcome in a given year. This effect was evident when comparing the relative influence of male and female traits on the two different reproductive measures: The consequences of individual traits were weaker for fledging success than for nest initiation date. Differences in parental quality might become apparent only if resource availability is more limited and unevenly, but predictably distributed over space and time (Dingemanse et al. 2004; Boon et al. 2007). Indeed, the strongest influence of male and female qualities on reproductive performance was apparent in 2007 (2006: $r = 0.13$, 2007: $r = 0.21$, 2008: $r = 0.\ 11$), when jay pairs initiated nests later than in the other two years ($F_{2,107} = 4.63$, $P = 0.012$), indicating that nesting conditions were less favourable. The winter preceding the 2007 breeding season was colder, with freezing periods unusual for the region, which likely diminished insect availability in the spring.

In contrast to weak fitness effects of individual characteristics, behavioural similarity between Steller's jay partners in exploratory and risk-taking tendencies had strong reproductive benefits. Partners that showed similar behavioural responses in either of two exploration contexts or in risk-taking at a familiar trap had higher reproductive performance in at least one of the reproductive components investigated (nest initiation date and fledging success) in at least two out of three years (Fig. 11). This finding indicates that personality similarity in all three traits enhanced behavioural compatibility under certain circumstances, and similarity in any trait was not selected against. Thus, the linkage of these traits in a behavioural syndrome would generally be beneficial for individuals that mate assortatively. Recent studies have shown that an individual's mate choice may depend on the match of the chooser's behavioural characteristics to its prospective partner (Forstmeier & Birkhead 2004; Groothuis & Carere 2005; Schuett 2008), and that behaviourally amicable partners may have higher reproductive success and mate fidelity (Spoon et al 2006, 2007). Results in this study complement these findings, demonstrating that partner compatibility, which has long been used to account for variation among pairs in fitness, mate choice or mate retention, especially in species with long-term pair bonds (Coulson 1972; Choudhury 1995; Black 1996; Spoon et al. 2006, 2007; Weiß et al. 2010), can be a direct result of behavioural similarity in a suite of linked personality traits. This interpretation is supported by the finding that highly explorative and risk-prone individuals were equally likely to pair assortatively as less explorative and risk-averse individuals (Novel feeder exploration score: w = 0.13, 95% CI = -0.15 – 0.39; Travel distance: w = 0.22, 95% CI = -0.37 – 0.37; Trap re-entry score: w = 0.14, 95% CI = -0.12 – 0.36). This means that mate choice for behaviourally similar partners, and the resulting compatibility benefits of partner similarity, were independent of personality types per se. This is in contrast to pairing patterns in zebra

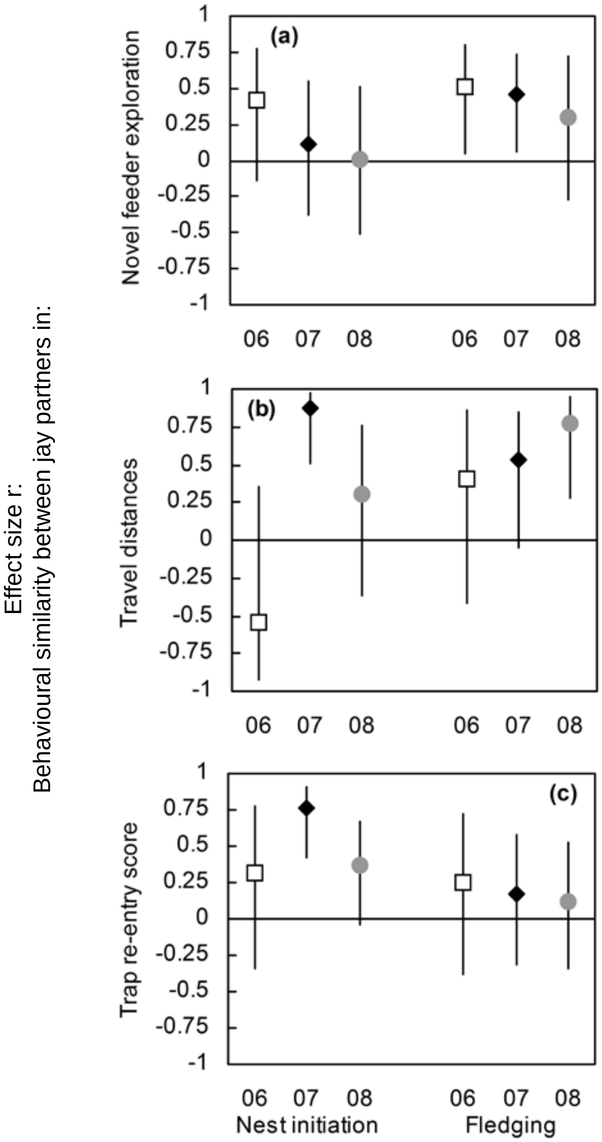

Figure 11. Correlation coefficients *r* and 95% *CI*s (indicated by error bars) of relationships between reproductive performance measured across two reproductive indices (Nest initiation date, fledging success) and three years (2006, 2007, 2008) and partner similarity in behavioural responses during a) exploration of a novel feeder, b) travel distance beyond home territory, and c) and risk taking at a familiar trap.

finches (*Taeniopygia guttata*) and great tits, where only highly explorative individuals preferred similar mates (Groothuis & Carere 2005; Schuett 2008). In context with the finding that expression of these behavioural types was independent of a jay's age, sex and body condition, the relationships between personality similarity and pair fitness in the long-term perennial pair bonds of Steller's jays are attributable to the effects of compatibility emerging directly from behavioural similarity of partners.

The influence of mate similarity in personality traits on reproductive success varied strongly among years. In 2007, a positive relationship between mate similarity and measures of reproductive success was expressed in four out of the six trait relationships we investigated, whereas in both 2006 and 2008 expression of such a relationship was rarer and weaker in some cases when it did occur. Population-wide nest initiation after an unusually cold winter was later in 2007 than in the other two years. Thus, the benefits of behavioural compatibility and coordination appear to be most important when jay pairs are constrained by environmental conditions and resource availability. This parallels the finding that individual male and female characteristics, including an explorative personality trait, were most important for a pair's reproductive performance in 2007. However, the fitness effects of behavioural similarity were much stronger and more consistent (overall $r = 0.38$) than any effect of individual traits of either sex, with age the most consistently important individual trait (males: $r = 0.16$, females: $r = 0.15$). Moreover, 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. More similar partners did not experience a decrease in reproductive success 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 (overall $r = 0.37$). But similar to selection pressure on behavioural similarity, pairing for behavioural similarity itself fluctuated across years and traits. The strongest assortative pairing patterns for the three behavioural traits overlapped well with the selection patterns for these pairings. Thus, although an overall tendency for assortative pairing is obviously maintained in this population because of its average benefit, Steller's jay pairs seem to adjust pairing and/or breeding decisions to some degree to the immediate benefit. This could explain the discrepancy between the lack of assortative pairing among all studied pairs averaged across all years and the clear overall assortative tendency when taking only known breeders in separate years into account. Pairs that are more dissimilar in certain traits might fail to even attempt breeding in years where such similarities and their compatibility benefits are more important. The question remains however, why not all jay pairs would mate assortatively in all years. The simplest answer might be that individual jays seeking a partner are constrained by the limited choices available in a sedentary, long-lived population where territorial openings are rare.

Assortative pairing in jays was also apparent with respect to age. Long-lived species often improve their reproductive performance continuously for several years (Clutton-Brock 1988; Forslund & Pärt 1995; Reid et al. 2003), as was the case in our jay population. Especially in an omnivorous species with a complex behavioural repertoire, the development of foraging skills and familiarity with resources that may constrain reproductive investment (Forslund & Larsson 1992; Wheelwright & Schultz 1994) likely are long-term processes. This is illustrated by older jays in this same study population taking more time examining food items before making a selection. Similarly, behavioural coordination of partners improves over the life-time of long-term monogamous birds (Black 1996). The positive correlation between male and female age within jay pairs was thus not surprising, and supports the idea that mate familiarity with increasing pair-bond duration is a likely component of the age-effect on reproductive performance.

The idea that coordination of movements and behaviours should increase with the time that partners spend in a pair bond, known as the mate familiarity effect (Black 1996), was investigated by measuring characteristics of jay pair bonds and their interactions with compatibility and stability of behavioural traits in a pair. Continuing pairs nested earlier and fledged more young than new pairs in some years. Overall, this resulted in a consistent, but relatively weak benefit of continuing pair-bonds (Fig. 12), which persisted after controlling for the effects of bird age.

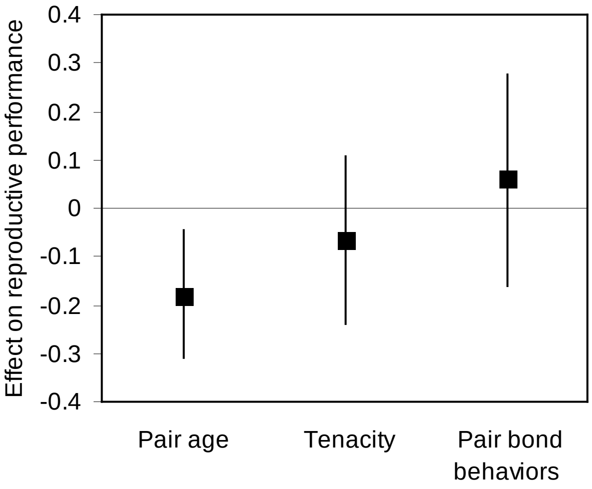

Figure 12. Overall effects (correlation coefficients and 95% *CI*s) of pair age (new or continuing pairs), pair tenacity (proportion of time males were observed with partner), and pair bond behaviours (composite variable of time pairs spent in close proximity, softcalling and travelling together) on reproductive performance, obtained from meta analyses on relationships across two reproductive indices (nest initiation date, fledging success) and three years (2006, 2007, 2008; from Gabriel & Black in submission).

Risk-taking behaviour at a familiar trap and the combination of these risk-taking tendencies, representing a component of the syndrome that was known to influence reproductive performance of the pair, was measured in 10 new and 14 continuing pairs. Partner similarity in this personality trait did not differ in new and continuing pairs, or in pairs that varied in tenacity. Thus, the observation that breeding partners in this jay population are behaviourally similar to each other is not the result of adaptation through prolonged exposure to behaviours of a partner, but rather suggests that jays mate assortatively for pre-existing behavioural traits. This result confirms that this behavioural trait is indeed relatively fixed in adult jays. Partner similarity in risk-taking at a familiar trap, and the specific combination of the trait with other behavioural traits in the described syndrome have reproductive advantages for jay pairs, as described above. Consequently, the inflexibility of traits in this syndrome conforms to the idea that distinct personality types and their covariation in syndromes can persist when the benefit of being predictable (consistent) is large (Dall et al. 2004, Sih et al. 2004).

Jay pairs varied considerably in the proportion of time spent in each other's presence (pair tenacity), yet pair tenacity and the frequency of subtle pair bond behaviours performed between partners were not only unrelated to pair age, but had hardly any effect on reproductive performance. The extent of variation in tenacity and frequency of pair bond behaviours may be inconsequential for reproductive performance because of the overall high frequency of these behaviours in Steller's jays. Jays live in year-round partnerships; during non-breeding partners spend the overwhelming majority of their time together, and during breeding seasons almost half their time. In comparison to most other, commonly 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 and coordination, limited only by the amount of breeding experience the partners have accumulated on their own (influence of bird age) and as a pair (influence of pair age). The observation that reproductive effects of pair age were relatively weak in comparison to effects of pair similarity in behavioural traits amends 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 tenacity, the additional benefit of increasing coordination and familiarity with increasing pair bond age is likely limited. Secondly, behavioural similarity as a very important factor for reproductive performance did not change over time, and the compatibility benefits of this similarity are thus not expected to increase with age. Lastly, it appears that compatibility, expressed in behavioural similarity, trumps the role of improved coordination over time, possibly because as a behaviourally complex species readily adapting to a complex anthropogenic environment, the Steller's jay avoids the intense, relatively homogeneous competition within species that experience dramatic increase of reproductive success with pair-bond duration (e.g. many waterfowl species (Collias & Jahn 1959, Lamprecht 1989, Black 2001) by various behavioural specializations that often match their partner, but not many of their neighbors.

5 Conclusions and perspectives

If an individual is consistent in its behavioural responses over time, and over different functional behavioural categories (ecological contexts), its behaviour will appear less than optimal in at least some situations (Sih et al. 2004b, Schuett et al. 2010). Consequently, the question arises why individual behavioural strategies evolved in animal populations and how they are maintained. As discussed by Stamps (2007), if one specific behavioural pattern results in highest fitness, a combination of both low intra-individual and inter-individual behavioural variation would be expected in a population (i.e. high repeatability of individual behaviours, but no distinct personalities). If more than one behavioural pattern results in equally high fitness, a combination of high intra- and inter-individual variation would be expected (i.e. individual responses optimized to individual situations). Instead, the pattern observed in many animal populations combines low intra-individual with high inter-individual variation, resulting in behavioural personalities and syndromes (reviewed e.g. in Dall et al. 2004, Sih et al. 2004a, Dingemanse & Réale 2005). A number of recent hypotheses attempt to explain this observation from a functional perspective, meeting with the considerable challenge of identifying mechanisms that create inter-individual variation (e.g. life-history trade-offs; Stamps 2007, Wolf et al. 2007) and simultaneously interact with mechanisms maintaining intra-individual consistency (e.g. benefits of predictability; Dall et al. 2004, McNamara et al. 2009). In addition, Sih, Bell, and Johnson (2004) suggested that interpretations and explanations of individual behaviour and performance, especially in situations where they appear suboptimal, will only be accessible through tracking these behaviours across many ecological and environmental situations, i.e. by taking account of an overall syndrome in an integrated fashion. In accordance with the concept of behavioural syndrome, ecologically broad, long-term investigations of behavioural traits in an urban population of Steller’s jays revealed the significance of intra-individual consistencies and correlations, similar as has been established in the comprehensive study of the great tit (Drent 2006), with important differences attributable to distinct ecologies of the two species.

In Steller's jays, behavioural syndromes shaped individual strategies across several separate ecological contexts. Both short-term and long-term behavioural measures in the wild were found to be practical, repeatable and meaningful for the assessment of individual strategies, establishing an important prerequisite to successfully integrate behavioural personality into the study of Steller's jay ecology (Réale et al. 2007). However, because short-term responses did not necessarily predict long-term behavioural strategies in related contexts, the expression of behavioural types and assumed underlying trade-offs should be regarded as species and context specific (Minderman et al. 2009). The complexity of relationships between these behaviours demonstrates that individual responses can show some plasticity across ecological contexts, and even within contexts, that can be functionally separated by complex trade-offs. Similar to the variable consequences of individual exploratory strategies on selection in great tits tracked over multiple years (Dingemanse et al. 2004, van Oers et al. 2005), these results emphasize the significance of comprehensive long-term studies of behavioural strategies in multiple contexts for the investigation of selection on behavioural syndrome in itself (Sih et al. 2004b, Dingemanse & Réale 2005). The Steller's jay may represent a good model system for such investigations, because the demonstrated limitations on adequately sampling a population for many fitness-relevant traits due to biased trapping success can be overcome more easily in a long-lived, resident animal (Dingemanse et al. 2004, Sih et al. 2004b, Both et al. 2005, Frost et al. 2007).

Similarity in correlated exploratory and risk-taking behaviours had reproductive advantages for jay partners in some years. Separate effects of trait similarities appeared to be enhanced by the interaction of these traits in behavioural syndromes, where jay partners shared similarities simultaneously across several behaviours. Thus, linkage of these traits in a syndrome was beneficial for assortatively paired jays. This finding lends support to the idea that the combination of behavioural characteristics in a behavioural syndrome in itself might be selected for and not just the result of genetic or mechanistic linkage (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). In general, individual behavioural strategies identified in this jay population were relatively fixed in adult individuals. This predictability of traits and their combinations is an important prerequisite for the manner in which selection operated on the syndrome in jays: behavioural compatibility in exploratory and risk-taking tendencies among partners had a large impact on reproductive pair performance, and breeding jays exploit this advantage by preferably pairing with partners that are behaviourally reliably similar, both across time and compatible contexts. This pattern reveals a role for both natural and sexual selection operating on Steller’s jay syndromes, and is consistent with the recent theory that sexual selection on behavioural traits may both maintain inter-individual differences and maintain or even generate intra-individual consistency (Schuett et al. 2010).

Selection must act jointly on the correlated traits in a syndrome (Carere & Eens 2005), creating an adaptive advantage when selective advantages for the traits align with trait combination in the syndrome (Barton and Turelli 1991; Cheverud 1996; Bell 2005; Blows 2007), but resulting in a disadvantage 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). No particular exploratory or risk-taking personality type seemed to be selected for in the context of reproductive performance in Steller’s jays. By contrast, selection on particular exploratory phenotypes in great tits was generally strong, but acted in opposite directions between 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). The correlation of behaviours in the Steller’s jay syndrome may thus have constrained theoretical reproductive advantages of single traits in any environmental circumstance if they acted in opposing directions than favored by the syndrome. The finding that assortative pairing and its reproductive benefits were not confined to a particular behavioural phenotype (e.g. only to highly risk-prone and highly explorative partners) seems to confirm that neither of the alternative exploratory and risk-taking phenotypes are intrinsically of higher quality. If a particular behavioural trait signals higher quality, but is costly to produce (which is normally assumed for a trait to signal quality reliably; Zahavi & Zahavi 1997), behavioural variation in the population would still be maintained by inherent and condition-dependent differences in individual quality. However, assortative pairings would only be expected to occur and be profitable at one end of the behavioural spectrum. This seems to be the case in the only other two bird species whose mating patterns in relation to behavioural personalities have been studied (great tits: Groothuis & Carere 2005; zebra finches: Schuett 2008), but not in Steller’s jays. Behavioural variation within populations in some species is apparently maintained by varying directional selection on behavioural traits with changing environmental conditions (Réale & Festa-Bianchet 2003; Dingemanse et al. 2004, Both et al. 2005). In contrast, distinct behavioural strategies in Steller’s jays seem to be maintained by a lack of directional selection on particular personality types, coupled with disruptive selection on behavioural phenotypes resulting from assortative pairing patterns in the breeding population (sensu Schuett et al. 2010).

A notable exception to the pattern of high stability of individual behavioural strategies was found in foraging strategies employed by jays. Although still moderately repeatable and strongly correlated to risk-taking and exploratory traits, the complexity of foraging strategies (sampling and taking multiple items compared to take of the first item sampled) increased with age. Thus, jays adopt more complex strategies as they acquire the necessary experience, or birds innately employing complex strategies survive better, suggesting a fitness benefit of complex foraging strategies over simple strategies in either case. Regardless of the mechanism, the idea that the increase of a particular foraging strategy with age is likely the result of overall benefits for this strategy can be tested by comparing profitability of the alternative strategies. In a recent experiment, Steller's jays in this population that frequently chose higher quality food items sampled more items (i.e. were more complex foragers) than birds that chose lower quality food items (where a higher quality food item was defined as the class of item chosen significantly more often across all observed occasions, see Fig. 13; Rockwell, Black & Gabriel in preparation).

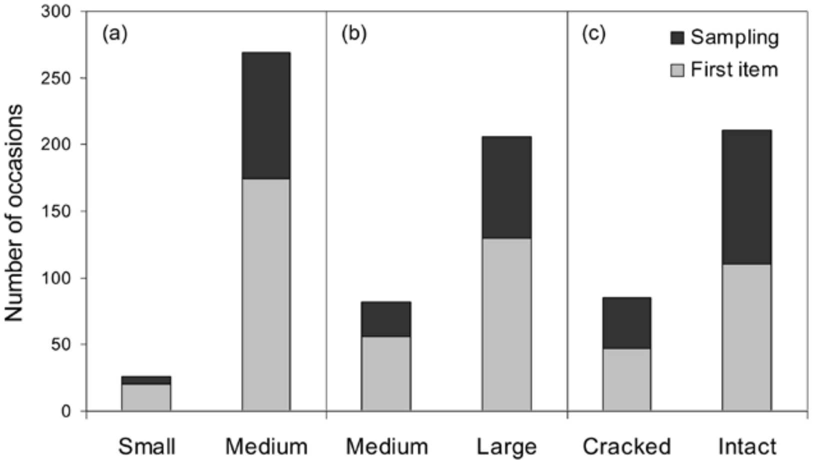

Figure 13. Total number of peanuts chosen across three experimental choice sets presented to 60 Steller's jays, and prevalence of sampling behaviour during each visit to experimental sets. Choice sets included a) 3 small (1.6 ± 0.2 g), single-chambered and 3 medium (2.4 ± 0.2 g), double-chambered peanuts (42 % of birds frequently choosing small sampled, 75% of birds frequently choosing medium sampled, *P* = 0.839), b) 3 medium (2.4 ± 0.2 g), double-chambered and 3 large (4.0 ± 0.2), double-chambered peanuts (33 % of birds frequently choosing small sampled, 78% of birds frequently choosing medium sampled, *P* = 0.039), and c) 3 double-chambered nuts with a cracked shell and 3 intact, double-chambered peanuts, where all nuts weighed 2.4 ± 0.2 g (57% of birds frequently choosing cracked sampled, 92% of birds frequently choosing intact sampled, *P* = 0.006; modified from Rockwell et al. in preparation).

These results are in accordance with studies in western scrub-jays (*Aphelocoma californica*), where the food item finally selected during choice experiments weighed more than the first item handled (Langen & Gibson 1998, Langen 1999).

Thus, foraging selectivity seems to convey advantages over simple grab-and-go foraging techniques, which raises the question why complex foraging techniques are not more wide-spread in the jay population. Several factors likely contribute to the maintenance of inter-individual variation in foraging strategies. Firstly, social dominance mediated by body size and sex may enable larger and male jays to engage in time consuming complex strategies more readily than subordinate individuals (Richner 1989, Langen 1999). Secondly, the learning of new, complex behavioural patterns is seldom achieved evenly across all individuals in a population, especially if highly developed cognitive abilities seem to be involved in problem solving (Reader 2003, Heinrich & Bugnyar 2005, Keagy et al. 2009). The ability to develop complex skills may often be tied to other behavioural personality types, as for example in great tits, where bold, fast-exploring individuals adopted new foraging habits more readily than shy, slow-exploring birds (Marchetti & Drent 2000). Indeed, this seems to be the case in jays, where risk-prone and highly explorative individuals were more likely to employ complex foraging strategies. This connection to the overall syndrome, especially in the absence of clear selection on specific risk-taking or exploratory tendencies in the same syndrome, is likely to contribute to the maintenance of inter-individual variation in foraging behaviour.

It remains to be investigated whether the apparent advantages of complex foraging strategies translate into general fitness benefits. Measuring survival of individual behavioural types in jays, including for foraging, exploratory and risk-taking tendencies, will be necessary to add to our interpretation of the origin, maintenance and relationships of these individual behavioural strategies. The abundance but simultaneous unpredictability of resources encountered by urban Steller's jays may ameliorate reproductive fitness effects of individual quality, as data from this study suggests, but may at the same time favour survival of more explorative, risk-prone personality types, as related research on urban wildlife suggests (Møller 2008, Short & Petren 2008). Information on annual survival and general longevity of urban Steller's jays is becoming accessible as monitoring on this long-lived, marked population continues.

Finally, the finding that foraging strategies are a strong component of the Steller's jay behavioural syndrome has potentially important conservation implications. Steller's jays are nest predators on many bird species throughout their range, including a variety of threatened and endangered species such as the marbled murrelet (*Brachyramphus marmoratus*) in the Pacific Northwest. Jays do not perform targeted searches for bird eggs or nestlings, but instead prey incidentally on nests they encounter during searches for invertebrate or plant food (Vigallon & Marzluff 2005a). Reproductive losses of vulnerable species to predation by increasing jay populations in increasingly fragmented habitats can nevertheless be substantial (George and Brand 2002, Golightly & Gabriel 2009, Golightly & Schneider 2011). In a recent experiment, 52 adult Steller's jays were held in temporary captivity and offered chicken eggs that were coloured to closely resemble marbled murrelet eggs. Only 54% of the birds opened and consumed whole eggs, whereas 10% consumed only eggs previously punctured by observers (so as to expose contents) and 36% did not consume any eggs. Among a subset of these birds, risk-taking tendency when entering a familiar trap was assessed in a very similar manner as described for this study. Preliminary results show that 100% of jays that consumed eggs entered the trap far enough to be recaptured, whereas only 40% of birds that did not consume any eggs did so ($w = 0.72$, 95% $CI = 0.17 - 1.00$; Gabriel & Golightly 2011). These results suggest that egg predation may be a specialized behaviour among jays which is linked to the behavioural syndrome. Risk-prone, highly explorative birds may be more likely to sample rare food sources such as bird eggs. Thus, simple behavioural tests, similar to those developed in this study, may be used to assess prevalence and identity of behavioural types in a wild population of conservation interest. Investigations are under way how this information may inform planning and direction of efficient, precise and cost-effective management actions, such as targeted taste aversion conditioning.

In conclusion, risk-prone, far-travelling, explorative birds that use complex foraging techniques co-exist with risk-averse, travel-shy, non-explorative, simple foragers in an urban-fringe population of Steller's jays. These behavioural specializations likely ameliorate competition, especially in the densely packed, highly overlapping territories of urban jay populations. Birds that can find a partner of matching personality enjoy reproductive advantages of their behavioural compatibility across all behavioural axes, perpetuating the diversity of personality types via disruptive selection. The stability and predictable combination of behavioural traits in this syndrome makes assortative pairings more easily achievable and more rewarding, thus selecting for the syndrome itself. This predictability also enables the fine-tuning of management actions for a species of wide-spread management concern, incorporating knowledge on the breadth, structure, and stability of a behavioural syndrome into our understanding of Steller's jay ecology.

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Curriculum vitae

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Behavioural syndromes in Steller's jays:
the role of time frames in the assessment of behavioural traits

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ABSTRACT—Behavioural syndromes describe consistent and correlated individual differences in behavioural traits. Quantifying individual differences often requires researchers to capture and hold animals in captivity while short-term behavioural assays are recorded. We compared behavioural responses of adult, territorial Steller's jays in short- and long-term field assessments of behavioural traits in two ecological contexts, risk taking and exploration. Individuals' risk taking was similar in short-term and long-term contexts (i.e. alarm calling in presence of a predator mount, and re-entering a trap, respectively). However, a measure of short-term exploration of a novel object in a feeding context was not related to a long-term index of annual habitat exploration (i.e. travel distance outside home territory). Risk taking and exploration indices were correlated across ecological contexts, indicating that these traits contributed to a behavioural syndrome in jays. Annual assessments of risk taking and exploration behaviours were repeatable. Individuals with high scores in risk taking and exploration were more likely to be re-captured in a familiar trap. We conclude that short-term experiments are adequate measures of specific behavioural strategies, but because short-term responses did not necessarily predict long-term annual behaviours in related contexts, expression of behavioural types and associated ecological strategies should be regarded as species and context specific. Long-lived residents are useful study species to overcome sampling biases for traits measured in captivity, because they provide opportunity to evenly sample a population over all personality types, including trap-shy individuals.

KEYWORDS—behavioural syndrome, *Cyanocitta stelleri*, exploration, personality, repeatability, risk taking, Steller's jay, trapping success.

Consistent differences in individual behavioural traits have been described in a wide variety of species and taxa, from worms, crabs and spiders (de Bono & Bargmann 1998; Riechert & Hall 2000; Briffa et al. 2008) to fish, birds, and mammals (Black & Owen 1987; Hessing et al. 1993; Wilson et al. 1993). Differences have been described along a variety of behavioural gradients such as aggressive to submissive, bold to shy, inquisitive to inattentive, neophobic to neophilic, and risk prone to risk averse. When two of these gradients are correlated across contexts, the suite of behavioural traits constitutes a behavioural syndrome (Sih et al. 2004), or personality (Dingemanse and Réale 2005). For example, individuals' relative aggressiveness and boldness scores often covary in a population (Reale et al. 2007). Individuals at either end of these behavioural spectra are thought to pursue alternative life-history strategies selected for by strong ecological trade-offs, with different optima under different environmental conditions (Réale & Festa-Bianchet 2003; Dingemanse et al. 2004).

Personality traits are usually quantified using short-term responses to environmental stimuli under laboratory conditions (Verbeek et al. 1994; Dingemanse et al. 2002; López et al. 2005; Martins et al. 2007; Fox et al. 2009; Quinn et al. 2009; Schuett & Dall 2009) or, more rarely, in the wild (Brown et al. 2005; Garamszegi et al. 2009a). However, when describing the adaptive significance of behavioural syndromes, the usefulness of traits measured in captive situations over short periods of time has been questioned (Höjesjö et al. 2002; Bell & Stamps 2004; Dingemanse and Réale 2005; Smith & Blumstein 2008; but see Herborn et al. 2010). In this study we compare short and long-term observations of risk taking and exploration responses in a long-lived passerine with an elaborate behavioural repertoire, the Steller's jay, *Cyanocitta stelleri*. Our goal was to assess the relationship between short-term experimental tests, performed in the wild, and long-term, annual measures of individual differences in the population. We predicted that short-term and long-term responses would covary positively across individuals if both represented meaningful measures of the same behavioural trait. We tested whether individuals' behaviours would be consistent across the two different ecological contexts, risk taking and exploration, to describe whether and how the traits might contribute to a behavioural syndrome (sensu Sih et al. 2004) in Steller's jays. Specifically, if a short-term measure was a good predictor of the long-term assessment of a behavioural trait (i.e. if short-term and long-term measures within a context were strongly correlated), we expected short-term and long-term measures of this trait to have similar relationships across ecological contexts, confirming that the specific short-term and long-term assessments might be regarded as interchangeable measures of the same trait. We investigated the repeatability of long-term behavioural observations, and how it varied among different time frames. Repeatability of behaviours over time has been widely used as an indicator for a trait’s relevance to a behavioural syndrome (e.g. Verbeek et al. 1994; Mettke-Hofmann et al. 2005; Minderman et al. 2009; Schuett & Dall 2009; Herborn et al. 2010). However, repeatability estimates over short time intervals can be confounded by stochastic variation in test conditions (Dingemanse et al. 2002), and can differ substantially from estimates taken over longer periods (Réale et al. 2000; Kurvers et al. 2009). We predicted that measures of individual differences that contribute to the behavioural syndrome (i.e. traits that covary across contexts) would be repeatable among individuals and that repeatability would increase with the time-frame of assessment. Lastly, we investigated whether individual differences in risk taking and exploration contexts had consequences for the trappability of individuals, which may have implications for studies that rely on experiments in captivity (Biro & Dingemanse 2008). Although some workers suggest that more risk-averse and less explorative individuals may be more difficult to capture (Wilson et al. 1993; Mills & Faure 2000; Réale et al. 2000), to our knowledge such a link has been directly demonstrated only once (Garamszegi et al. 2009a).

METHODS

We observed individually marked Steller’s jay pairs on year-round territories on the fringe of the redwood (*Sequoia sempervirens*) forest in Arcata, California (40°59’N, 124°06’W) from January 2006 to September 2008. Steller’s jays are particularly strongly associated with patches and edges of forested habitat (Brand & George 2001, Marzluff et al. 2004). All territories and nests in this study were located within 750 m of the forest edge. 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). In late March to early April both sexes build the open cup nest, and subsequently cooperate in feeding nestlings. After fledging, birds exhibit weaker territoriality and some individuals travel widely. In contrast to most migratory passerines, both sexes in Steller's jays may exercise mate choice and territory defense and have a similar repertoire of explorative, risk taking and aggressive behaviours (P.O.G. & J.M.B. unpublished data). We expected that sex would not influence the expression of individual behavioural traits in this species (Buss 1995; van Oers et al. 2004) and included both sexes in the study.

Birds were initially captured in feeders outfitted with a sliding trap door. Manual operation of the trap door allowed us to selectively capture individuals and also minimize the likelihood that non-target birds would observe a capture event. Unbanded individuals were given a unique combination of coloured leg bands and classified as hatch-year or after-hatch-year birds, based on gape colouration and typical juvenile plumage patterns and feather shapes (rectrices and secondaries, Pyle et al. 1987). Minimum known age for each bird was based on its age classification at the date of its first capture. We measured wing length with a ruler to the nearest millimeter and weighed birds with a Pesola spring scale to the nearest gram. Body condition was assessed using residuals of wing length / body mass regression. Sex was subsequently determined by sex-specific calls given in territorial disputes (females "rattle", and males "creak"; Hope 1980).

We actively monitored jay territories on a near-daily basis from January 2006 to September 2008 to obtain resighting locations and behavioural data for all colour-marked birds. Systematic resighting surveys typically covered 1/3 of all territories per day and were conducted along the existing grid of roads, allowing near-even access and search effort among territories. We made efforts to find each bird at least once per week throughout the breeding seasons (March – August) and once every three weeks outside the breeding seasons, and recorded one to five locations per day, depending on duration of the observation and flight distances.

We quantified an index of risk taking behaviour in the presence of a nest predator (a short-term assessment) and compared this with a bird's willingness to re-enter a baited trap where it had been captured previously (a long-term, annual assessment). We quantified an index of exploration behaviour by presenting a novel foraging situation within each bird's territory (a short-term assessment) and compared this with a bird's propensity to explore beyond territorial boundaries (a long-term, annual assessment). Assessments of short-term indices were made in the winters of 2007 and 2008, when the jays were establishing territories prior to the nesting season, whereas long-term behaviours were measured throughout the year.

Short-term Risk Taking during a Predator Model Presentation

For an index of short-term risk taking we tested the behavioural response of territorial jay pairs to a predator model (mount of an adult, male raven, *Corvus corax*). Predation on adult Steller's jays in our study area was rare, but eggs and fledglings were regularly taken by ravens (P.O.G. & J.M.B. unpublished data). During the breeding season we regularly observed breeding jays engaging in mobbing behaviour towards ravens (alarm calling, close following, approach to about 2 m). Mobbing is thought to be an energetically expensive and potentially risky behaviour (Curio 1978; Sordahl 1990; Markman et al. 2002). Siberian jays (*Perisoreus infaustus*) are reported to show considerable individual variation in mobbing activity, and mobbing intensity of parents is related to the inclusive fitness benefit achievable from protecting offspring (Griesser & Ekman 2004).

Mobbing responses were measured from February to March 2008. Experimental locations were close to the territorial centres of focal pairs and

5 m from cover. The raven was mounted in soaring flight posture and suspended at a height of 2.5 m by clear nylon line, held by a vertical pole and small supporting platform. The experiment was initiated by setting up the support pole without the raven mount and attracting jay pairs to a pile of peanuts on the ground at a distance of 3 m from the base of the pole. Once the focal territorial pair had arrived and detected the peanuts the raven mount was attached and revealed. The observer retreated 15 m and started a 30 min observation period. During this period we recorded jay alarm calls and several other behaviours (not presented here). No birds performed alarm calls or mobbing behaviours while presented with only the support pole, and all birds took peanuts from the experimental set-up within a few minutes after the raven mount was removed. The raven mount seemed to be perceived as a risk because only 18 out of 87 birds took peanuts in presence of the raven mount, over half of the birds engaged in alarm calling and no bird came within 2 m of the mount.

Alarm calling at the raven mount sometimes attracted neighboring jays that subsequently participated in mobbing activities. Participation of territorial birds in alarm calling was independent of attending neighbors (Chi-Square test: $X^2_1 = 0.14$, $n = 28$, $P = 0.705$). We used alarm calling behaviour as a bivariate measure of mobbing activity (call / no call), assuming that birds that actively alarm called were taking a greater risk than those that did not alarm call.

Long-term Risk Taking at a Familiar Trap

During weekly territory monitoring we recorded individual jays' behavioural responses to the feeders they had previously been trapped in to obtain an index of long-term risk taking. We assigned scores between 0 and 5 depending on whether and how far birds entered the familiar trap (0: no approach; 1: perched on top; 2: perched at entrance; 3: entered halfway; 4: entered all the way for less than 2 s; 5: entered all the way for more than 2 s;). We calculated average individual scores for 2006 and 2008 (number of scores per bird: mean ± SE = 3.4 ± 0.2, range 2-12, n = 109 birds), where higher scores described greater willingness to take the risk of re-entering the trap.

Annual trap re-entry scores were negatively correlated with time since last capture in 2008 (Spearman rank correlations: 2006: $r_s = 0.16$, $n = 43$, $P = 0.32$; 2008: $r_s = -0.29$, $n = 65$, $P = 0.018$), and positively correlated with number of previous captures in both years (2006: $r_s = 0.36$, $n = 44$, $P = 0.02$; 2008: $r_s = 0.46$, $n = 65$, $P = 0.0001$). The directions of these correlations are opposite to expectations if individual jays' willingness to re-enter a trap would have been confounded by previous captures. This implies that jays that were more willing to take greater risks at a familiar trap were also more likely to be captured more often and in shorter time intervals, foreshadowing and confirming a covariation between this index of risk taking and trapping success.

Short-term Exploration of a Novel Feeder

Presentation of a novel feeder allowed us 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 (peanuts). The experiment was designed to assess birds' readiness to explore a novel feeding situation not unlike opportunities experienced by jays foraging in the forest among downed branches, duff, and logs.

In February and March 2007 we conducted experiments close to the territorial centre of focal pairs and 5 m from the nearest cover. The experimental feeder consisted of a four-sided wooden box without a floor and only half a lid (Fig. 1). These dimensions allowed a jay to move on top, look inside, and to go inside on the ground underneath the lid. A Y-shaped redwood branch (5 cm diameter) was provided as a perch spanning both the covered and uncovered portions of the box. We attracted birds to the set up by a familiar whistle, that all study birds had previously been trained to, and initiated the experiment when the focal territorial pair arrived alone. The experiment began when 7 peanuts were placed on the ground inside the box, partially underneath the lid, and 3 peanuts on top of the lid, and the observer had retreated 15 m. Birds were observed for the subsequent 20 min.

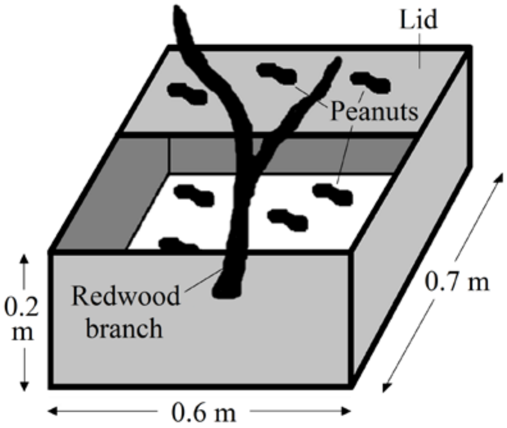

Figure 1. Schematic of experimental configuration used to test short-term exploration of a novel feeder. We placed peanuts inside and on top of a box with half a lid and no bottom, offering a foraging opportunity not unlike situations experienced in the forest, where jays would enter enclosed spaces created by downed trees, branches and heavy duff.

In accordance with similar tests of exploration behaviour (e.g. Dingemanse et al. 2002; Fox et al. 2009; Garamszegi et al. 2009a) we assumed that the following behaviours represented an increasing degree of exploration: 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 less than 2 s without taking a peanut, 5) taking a peanut from inside, spending less than 2 s, 6) going inside the box for more than 2 s without taking a peanut, and 7) taking a peanut from inside, spending more than 2 s. We recorded each jay’s initial latency, in 2 min increments, to perform each of the seven behaviours, and assigned an arbitrary latency score of 25 for any behaviours the jay never performed during the 20 min observation period. If birds performed a higher ranking behaviour at any time during the experiment they received a latency score of 0 for lower ranking behaviours they never performed. We summed incremental latency scores in each of the seven behavioural categories to obtain an overall cumulative score for each bird. Birds that did not perform any of the behaviours described during presentation of the novel feeder consequently received a maximum cumulative score of 175. Low cumulative latency scores represented a high degree of exploration, because birds with low scores explored a large area of the novel feeder, spent extended time exploring, and were fast to do either. For conceptual clarity, we then inverted this scale so a low score represented low exploration by subtracting all scores from 175, resulting in a range of exploration scores between 0 and 169; i.e. more exploration yielded high scores.

Long-term Exploration beyond Home Territories

Maximum annual travel distances from territorial centres were used as a measure of a bird's propensity to travel and its opportunity to explore beyond the home territory. We used travel distances for established breeders in years of stable territory ownership, because new breeders and birds that change territories within a year had inflated travel distances (P.O.G. & J.M.B. unpublished data). Maximum annual travel distances were calculated for birds with known nest sites and at least 17 annual resighting locations (mean ± SE = 40.0 ± 2.2, range 17-84, $n = 55$). If more than one nest location was known, the mid-point (centroid) between them was used as territorial centre. A pilot analysis comparing breeding home range centroids based on resightings to centroids based on nest locations confirmed that home range centroids underestimated annual travel distances (Wilcoxon signed-rank-test: W = 20, $n = 17$, $P < 0.01$). Based on the site-centred territorial behaviour of Steller's jays (Brown 1963) we assumed that the farther a bird was from its territorial centre the more unfamiliar it would be with its environment. Birds that were found farther away from their territorial centres were consequently defined as more explorative. We used the mean of five longest resighting distances for each year (2006-2008) from the territorial centre (nest location or nest centroid) as an annual index for long-term exploration beyond home territories. Travel distances measured in 2008 were used only to estimate repeatability of this trait (see below), but excluded from other analyses, because data collection in 2008 did not encompass the entire calendar year.

Trapping Success

We used the success or failure to trap surviving individuals in both 2006 and 2007 as a bivariate measure of trapping success (re-captured / not re-captured).

Statistical Analyses

We tested the predictive power of short-term experimental tests for long-term annual measures of individual differences in the population, and the consistency of responses over time and over different ecological contexts as a basis for the description of a behavioural syndrome in Steller’s jays.

We predicted that if readiness to re-enter a ‘risky’ trap and exploration beyond a home territory (travel distance) were meaningful long-term measures of a behavioural syndrome, then those measures should be repeatable within individuals. If behavioural responses vary with stochastic environmental influences, we predicted that repeatability would increase with the time frame of assessment. Repeatability was estimated from the ratio of among-individual variance to the total variance (the sum of among-individual and within-individual variances), calculated from appropriate mean squares obtained from ANOVAs using individual as the main effect (Lessells and Boag 1987). Repeatability scores R can range from zero to one, where a score above 0.5 indicates that a greater proportion of the variance is explained by the variation among individuals than by the variation within individuals. We assessed consistency of the long-term variable of re-entering a trap by calculating repeatability scores within years. For a measure of consistency over a longer time frame, repeatabilities of annual indices of both re-entering a trap and maximum travel distance were calculated across multiple years. For the calculation of repeatability of maximum travel distances we used data for 2008 in addition to data for 2006 and 2007 to boost sample size. We obtained maximum annual travel distances for eleven birds in two different years and for seven birds in three different years. We assumed that this repeatability estimate was conservative, because the time interval for the calculation of maximum annual travel distances was shorter in 2008 than in 2006 and 2007, likely inflating within-individual variation. Since measurements for both long-term variables, travel distance and re-entering a trap, were highly repeatable within individuals between years we used the means of all valid observations per individual for comparisons with other behavioural traits.

To investigate direction and strength of relationships between behavioural traits, we calculated correlation coefficients. We followed recommendations of Garamszegi (2006), Nakagawa and Cuthill (2007) and Garamszegi et al. (2009b) to use effect sizes and 95% confidence intervals to interpret the relative magnitude of biological relationships and the precision and certainty with which the current data reflects those relationships. To present effect sizes that are meaningful and comparable not only within this study but also to other studies that make use of the effect size theorem, we calculated correlation coefficients from regressions either directly (expressed as Spearman r_S) or from related effect sizes obtained from non parametric two sample tests (calculated as d and converted into r) and contingency tables (expressed as w; Cohen 1988). 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. Statistical significance testing based on critical P values often does not satisfy the conceptual quest for biological relevance, especially in studies of behavioural ecology (Nakagawa 2004; Garamszegi 2006). P values of the underlying statistical tests are reported here for reference but not emphasized in our interpretation of results.

To determine whether risk taking and exploration behaviours were related to potentially confounding factors other than individuality, we tested both short- and long-term indices of risk taking and exploration for correlations with sex, age, body condition and between members of the same breeding pair (hereafter: pair membership). None of the behavioural traits we measured were significantly related to sex, age, body condition, or pair membership ($P > 0.1$ in all cases).

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 # 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. Time in captivity was kept to the minimum required for the procedures, and birds were released typically within 30 - 45 min after capture.

RESULTS

We observed 114 individually marked Steller's jays over three years quantifying their short-term behavioural responses to a simulated predator (raven mount) and a novel feeder, and average annual indices of risk taking (re-entering a trap where they had been captured) and explorative behaviour (travel distance away from the home territory). Seventy seven percent of the birds (N = 43) participated in alarm calling behaviour while in presence of the raven mount. The average annual risk taking score while approaching the baited trap was 3.2, where 5 was the max possible score (SE = 0.1, range 0 – 5, $n = 109$). The average exploration score during the novel feeder setup was 80.2 with a range between 0 and 169 (SE = 8.3, $n = 60$). Maximum annual travel distances ranged from 77 m to 520 m (mean ± SE = 231.2 ± 13.5, $n = 55$), indicating a wide range of propensities and opportunities for exploration beyond the home territory.

Correlations among Behavioural Responses

Comparisons within ecological contexts (short- and long-term measures)

Birds that performed repetitive alarm calls in the presence of a simulated predator (a short-term measure of risk taking) more readily re-entered baited traps throughout the year (a long-term measure of risk taking) than birds that were silent with the predator (Fig. 2a). Exploration scores while investigating a novel feeder placed within the home territory (a short-term measure of exploration) were not related to maximum annual travel distances beyond the home territory (a long-term measure of exploration; Fig. 2b).

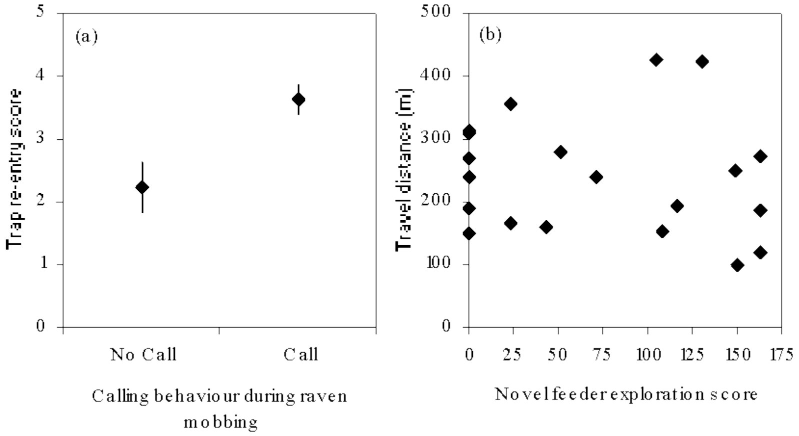

Figure 2. Relationships between short-term and long-term behavioural responses within two ecological contexts: (a) short-term risk taking facing a simulated predator and an index of long-term risk taking at a familiar trap (r_{34} = 0.53, 95% *CI* = 0.25 - 0.74, *P* = 0.008), and (b) an index of short-term exploration of a novel feeder and long-term exploration of unfamiliar environments (r_s = 0.20, 95% *CI* = -0.26 - 0.59, *n* = 20, *P* = 0.391). Diamonds with error bars indicate means and SEs.

Comparisons between ecological contexts (risk taking and exploration)

Jays that called in the presence of the raven had higher exploration scores at the novel feeder (Fig. 3a), and travelled longer distances outside their territory (Fig. 3b) than birds that did not alarm call, with large effect sizes for both relationships. The readiness with which jays re-entered baited traps throughout the year was positively correlated with exploration of the novel feeder (Fig. 3c), and with maximum annual travel distances (Fig. 3d), with medium effect sizes in both cases.

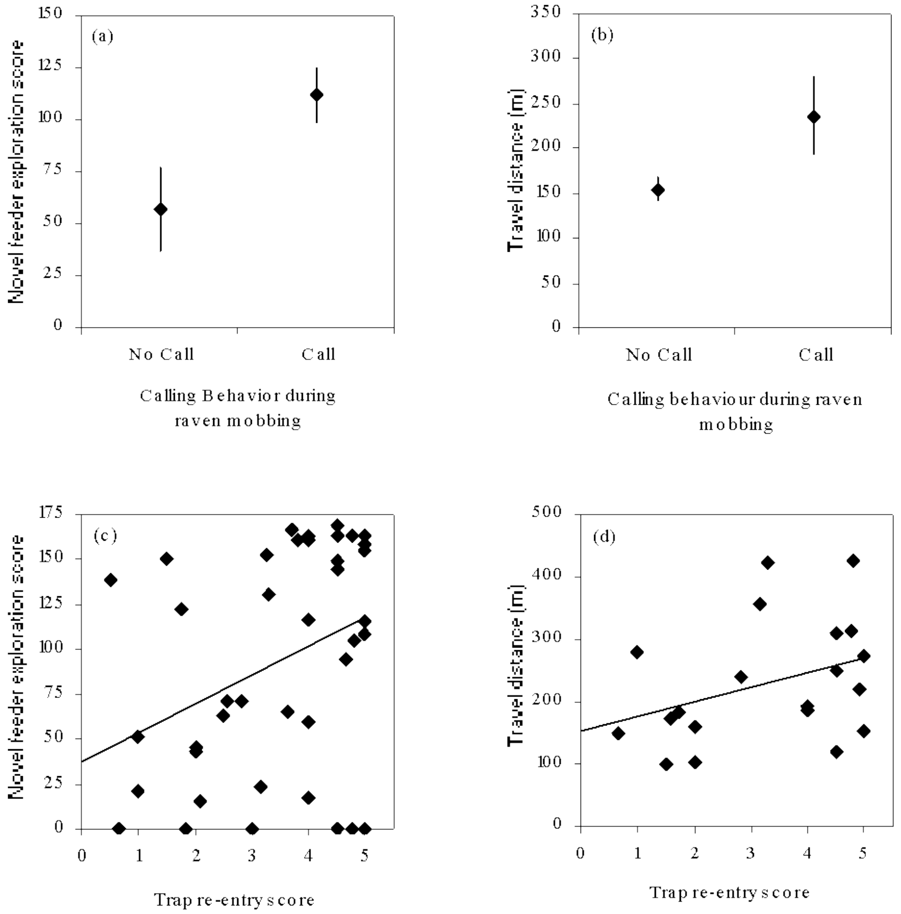

Figure 3. Relationships between behaviours measured in four ecological situations: (a) short-term risk taking and short-term object exploration (r_{22} = 0.53, 95% *CI* = 0.16 - 0.77, *P* = 0.035), (b) short-term risk taking and long-term habitat exploration (r_9 = 0.69, 95% *CI* = 0.16 - 0.91, *P* = 0.045), (c) long-term risk taking and short-term object exploration (r_s = 0.33, 95% *CI* = 0.02 - 0.58, *n* = 40, *P* = 0.037), and (d) long-term risk taking and long-term habitat exploration (r_s = 0.37, 95% *CI* = -0.08 - 0.70, *n* = 20, *P* = 0.106). Diamonds with error bars indicate means and SEs.

Repeatability of Long-term Behavioural Traits

Readiness to re-enter baited traps was moderately repeatable within individual jays within both years (2006: R = 0.49, 95% *CI* = 0.33 - 0.64, $F_{43,105}$ = 4.37, $P < 0.0001$; 2008: R = 0.41, 95% *CI* = 0.28 - 0.54, $F_{64,159}$ = 3.43, $P < 0.0001$), and highly repeatable across years (R = 0.74, 95% *CI* = 0.49 - 0.88, $F_{22,23}$ = 6.77, $P < 0.0001$).

Maximum annual travel distances were highly repeatable within individual jays (R = 0.60, 95% *CI* = 0.28 - 0.80, $F_{17,25}$ = 4.53, $P < 0.001$).

Trapping Success of Behavioural Types

Birds that were re-captured in 2007 were more likely to re-enter the baited trap throughout the year (Fig. 4a), and tended to be more likely to alarm call in the presence of the raven mount (Fig 4b). Re-captured birds travelled further beyond their home territories than birds that were not captured (Fig. 4c), and received higher exploration scores during the novel feeder experiment (Fig. 4d).

DISCUSSION

We demonstrated how individual behavioural responses can covary across ecological contexts to form a behavioural syndrome in a wild population of urban Steller's jays. The willingness of individual jays to take risks in two situations was positively correlated with their exploration behaviour of a novel feeding situation within the home territory and of environments beyond the home territories. Annual long-term indices of risk-taking (re-entering a trap) and exploration (travel distances outside the territory) were highly repeatable over time and this consistency reflected accurately that both measures were also meaningful contributors to the behavioural syndrome we described. The significance of such consistencies and correlations for the concept of behavioural syndrome has been established in the comprehensive study of the great tit (Parus major; Drent 2006), but

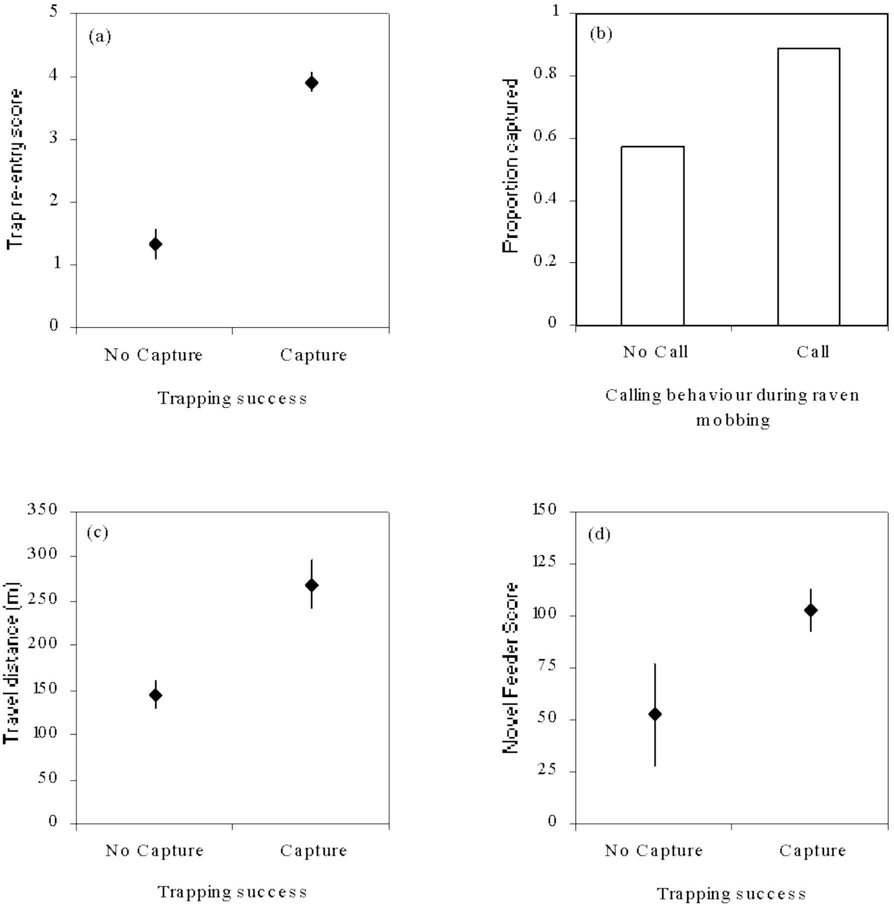

Figure 4. Relationships between trapping success and (a) long-term risk taking (r_{19} = 0.65, 95% *CI* = 0.27 - 0.85, *P* = 0.036), (b) short-term risk taking (w_{25} = 0.36, 95% *CI* = -0.06 - 0.86, *P* = 0.11), (c) long-term habitat exploration (r_{42} = 0.34, 95% *CI* = 0.04 - 0.59, *P* = 0.026), and (d) short-term object exploration (r_{54} = 0.82, 95% *CI* = 0.71 - 0.89, *P* < 0.0001). Diamonds with error bars indicate means and SEs.

similar relationships in species with a different ecology have usually been demonstrated only for single traits or single measures of traits (Pruitt et al. 2008; Garamszegi et al. 2009a; Kurvers et al. 2009; but see Kralj-Fišer et al. 2007). Expression of behavioural types was independent of potential covariates such as age and body condition, and also of a jay’s sex and the behaviour of its mate. We could thus confirm that male and female Steller’s jays solve ecological trade-offs with similar behavioural strategies, as might be predicted from their almost identical life styles (Brown 1963, Greene et al. 1998). Such ecological and behavioural similarity between the sexes is rare (Kurvers et al. 2009). It opens a relatively unique perspective on the investigation of behavioural syndrome and mating strategies, because selection on correlated behavioural characters in a syndrome should not be constrained by conflicting selection on different trait optima between the sexes, in contrast to behaviourally dimorphic species (Partridge 1994; Dingemanse et al. 2004; Pruitt & Riechert 2009). The independence of behavioural responses between pair members validated our approach to assess birds under natural conditions in the wild, which required the simultaneous testing of mates in some experiments. Moreover, the unrelatedness of responses between mates occupying the same territory makes it unlikely that behavioural differences were based on differences in habitat quality among territories (Riechert & Hall 2000), which can influence especially individual travel distances (Brooker & Rowley 1995; Fort & Otter 2004).

Predictive Significance of Short-term Measures

We confirmed that risk taking in Steller’s jays could be adequately assessed in a short-term experiment, which was a good predictor of long-term risk taking behaviour. Individual risk taking responses were strongly positively correlated between the short-term (alarm calling in presence of a predator) and long-term context (re-entering a baited trap), and both measures were positively related to investigation of a novel feeder and to exploration of habitats beyond the home territory (travel distance) across individual jays. Together with findings of Herborn et al. (2010) that two behavioural traits in blue tits (*Cyanistes caeruleus*) were correlated between measures in captivity and the wild, this indicates that some behavioural traits may be reliably measured in controlled, short-term tests.

Interestingly, the two indices of exploration, which were not correlated with each other, also showed similar covariations with risk taking when in view of the raven mount and when re-entering a trap. This implies that both exploratory strategies are of similar significance to a behavioural syndrome in Steller’s jays. However, the two different contexts of exploration behaviour (i.e. investigating the novel feeder and travelling beyond the home territory) appear to be driven by separate ecological trade-offs. Active and fast responses of individual animals to novelty is often equated with a willingness to explore new food sources and habitats simultaneously (Gosling 2001; Réale et al. 2007; Smith & Blumstein 2008; Farwell & McLaughlin 2009; Schuett & Dall 2009). Measures of habitat exploration are typically short-range measures (Dingemanse et al. 2002; van Oers et al. 2005; Pruitt et al. 2008; Garamszegi et al. 2009a). Garamszegi et al. (2009a) for example interpreted the willingness of a bird to approach a familiar nestbox outfitted with an unfamiliar object as exploration of a novel environment. The conceptual difference between novel object and novel environment exploration in such experiments is therefore not apparent, which might contribute to generally strong correlations between the two traits (Verbeek et al. 1994, 1996; Dingemanse et al. 2002). In contrast, findings of Fox et al. (2009) and Minderman et al. (2009) indicate that exploration behaviour can be selected for in unrelated behavioural axes, that represent separate ecological strategies. Fast explorers may move through the environment more quickly and encounter a larger area, but the information gathered might be more superficial compared to slow explorers. This distinction is interpreted as a trade-off between quality and quantity of exploration. Our results can support and extend this argument because jays that travelled further were not particularly better at investigating the novel feeder at the home territory. Subsequent experiments could test whether jays that were highly explorative of a novel feeder at home are good qualitative exploiters of novel foraging situations, regardless how far away from home such items are found. Jays that travelled far on the other hand might be expected to be superficial, quantitative explorers. These behavioural responses may represent two alternative exploratory strategies that are unrelated because time investment into one might not allow simultaneous investment into the other strategy.

Additionally, the strength of exploration of novel objects in jays may be mediated mostly by neophobia (Greenberg & Mettke-Hofmann 2001; Réale et al. 2007), whereas habitat exploration may be shaped more strongly by social dominance, since far travelling jays regularly encounter and compete with conspecifics (Brown 1963). This interpretation would confirm that the two exploratory behaviours we measured are likely selected for in unrelated behavioural axes, and agrees with suggestions of Mettke-Hofmann et al. (2002) that neophobia in a feeding context and exploration in a neutral context might be functionally independent in many animal species. Mettke-Hofmann et al.'s (2002) finding that exploration, but not neophobia was related to intraspecific dominance ranks in parrot species also supports our interpretation that social dominance might drive habitat exploration in Steller's jays. Notably, jays with the shortest annual travel distances (~75 – 150 m from territorial centres) hardly travelled beyond the home territory at all, and might thus have very limited opportunities to encounter alternative territories and mates (Hale et al. 2003). This could have important implications for mating strategies and alternatives to social partnerships (Choudhury 1995; Black 1996; Westneat and Stewart 2003). Future research could address whether birds that explore far and often beyond their home territories might be more likely to switch social partners and territories and might participate in more extra-pair copulations (Kempenaers et al. 1992), but might also be more susceptible to loose a mate and territory or to be cuckolded, if they spend less time with their mate in the home territory (Gowaty 1996; Brylawski and Whittingham 2004).

The relationships of individual jays' behavioural traits between ecological contexts also varied in strength (as indicated by medium effect values, sensu Cohen 1988). Response to the raven mount was strongly related to both exploration indices. All these behavioural measures may have had a component of novelty, and thus were by definition driven to some degree by neophilia. In contrast, risk-taking at a familiar trap explicitly contained minimal novelty, which may explain why the relationship of this trait to both exploration behaviours was only of moderate strength. Similarly, Garamszegi et al. (2009a) suspected that the strong correlation of risk taking and exploration in wild male collared flycatchers (*Ficedula albicollis*) was due to shared elements of neophobia and risk in the performed experiments, whereas weak associations of both those traits with aggression likely indicated a lack of common proximate mechanisms. In addition, the strength of relation between our long-term behavioural measures, risk-taking at a familiar trap and habitat exploration, was subject to uncertainty, evident from the large confidence interval around the effect size. While relatively small sample sizes likely contributed to some uncertainty in most of our behavioural comparisons, we attribute the particularly large margin in this relationship to variability in individual behaviours between years, driven by a variable environment. The patterns of repeatability in these long-term behaviours, discussed below, suggest that reliability of a behavioural measure is maximized by repeated sampling over the greatest variety of conditions. Logistic constraints in combination with a study period of only three years limited our ability to even out behavioural sampling among all birds in all relevant time periods and environmental conditions, emphasizing the importance of continuing observations and experiments over many years to reduce the influence of environmental variability even more and to increase reliability in the description of behavioural relationships.

Repeatability of Long-term Behavioural Traits

The consistency of a behavioural response over time, usually measured as repeatability, is used to judge the significance of a trait to a behavioural syndrome in a particular species (Mettke-Hofmann et al. 2005; Cote & Clobert 2007) or the suitability of the specific measure to detect such a significance (Farwell & McLaughlin 2009). In accordance with this interpretation, a jay's annual scores for re-entering a baited trap, and the distance individual jays travelled from their territorial centre were meaningful measures of an individual's willingness to take risks, and propensity to travel and explore unfamiliar environments, respectively. However, our estimate of repeatability increased with the time frame of assessment, where within year repeatability of risk-taking at baited traps was only moderate, whereas repeatability across years was strong. This may indicate that stochastic environmental and intrinsic influences confounded repeatability estimates over the short-term, which in turn can influence interpretation of the selective significance (Minderman et al. 2009; Schuett & Dall 2009) and genetic influences on a trait (Réale et al. 2000). Some environmental factors like weather and presence of conspecifics varied partially due to fluctuating experimental conditions in the wild, and would be easier to control in captivity. However, experimental snapshots in captivity cannot control for seasonal or developmental variation in motivation or differences in experience, which have been shown to influence behavioural responses (Bell & Stamps 2004; Mettke-Hoffmann et al. 2005). The long-term observation of behaviours, allowing for repeated sampling over a variety of conditions, might therefore be the most accurate approach to determine the significance of a trait for the description of a behavioural syndrome.

Differential Trapping Success of Behavioural Types

Steller's jays that were willing to take greater risks and exhibited highly explorative behaviours were more likely to be captured in 2006 and again in 2007 than risk averse and less explorative individuals. These findings affirm the suspicion that trapping success and behavioural syndromes are generally strongly correlated, and that trappability should be regarded as a component of behavioural syndromes (Wilson et al. 1993; Mills & Faure 2000; Réale et al. 2000; Malmkvist & Hansen 2001; Garamszegi et al. 2009a). Since a pool of captured animals likely contains a different distribution of behavioural types than the entire population, this has important consequences for design and interpretation of studies of behavioural syndromes and any covarying traits in captivity (Biro & Dingemanse 2008, Garamszegi et al. 2009a). Although we were able to avoid a sampling bias for behavioural types in this study by using behavioural measures and experiments in the wild, a number of potentially fitness-relevant traits that may also covary with behavioural syndromes can only be measured in captivity (Krause et al. 1998; Wilson 1998; Carere et al. 2003; Brown & Braithwaite 2004; López et al. 2005; Garamszegi et al. 2007; Kralj-Fišer et al. 2007). Many studies may miss one end of the natural distribution of phenotypes for the wide array of morphological and physiological characteristics that are assessed. The longevity and year-round residence of our study species provides an advantage for addressing this problem. Our study included close to 100% of the population resident in the study area. Each individual was captured at least once initially to fit colour bands prior to the study, which was possible due to repeated, long-term, and if necessary individually focused trapping efforts. We therefore suggest that long-lived, resident species such as the Steller's jay are a suitable model species to explore fitness consequences and fitness-relevant correlates of behavioural syndromes, especially if such fitness consequences and the distribution of behavioural strategies are expected to fluctuate over time (Dingemanse et al. 2004; Sih et al. 2004; Both et al. 2005; Frost et al. 2007).

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Bolder, older, and selective: factors of individual-specific foraging behaviors in Steller's jays

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ABSTRACT—Several species of animals, particularly corvids, will sample from a collection of items before making a decision. There is an expected trade-off between investing effort in making better choices and increased exposure to risk. Little is known about individuals' consistency in sampling behavior and whether it covaries with other behavior traits. Risk-taking and neophobia are documented components of behavioral syndromes; we examined whether sampling behavior is comparable. We quantified food sampling behavior (i.e. number of items sampled, visit duration and number of items taken) of individual Steller's jays (*Cyanocitta stelleri*) during experimental field trials. Sampling behavior of individual jays was moderately repeatable within and between winter field seasons and was positively correlated with birds' willingness to approach a novel object and take food in front of a predator mount. These results suggest that food sampling is a measurable component in the suite of traits comprising the Steller's jay behavioral syndrome. Model selection techniques indicated that sampling behavior was more common in older, neophilic, risk-prone, larger jays, while jays that took multiple items were more likely to be older and risk-prone. This suggests that experience and size may additionally influence individuals' habitual foraging behaviors.

KEYWORDS—behavioral syndrome, *Cyanocitta stelleri*, foraging, neophobia, risk-taking, sampling, Steller's jay

Traditional optimal foraging theory predicts that an individual will make foraging decisions based on maximizing benefits, such as nutritional value, and minimizing costs, such as handling time and exposure to predation (Schoener 1971; Krebs et al. 1977; Stephens and Krebs 1986). However, it may be advantageous in the long-term for an individual to be explorative and "curious" if resources are variable or unpredictable, even if it means sacrificing immediate efficiency (Pyke, Pulliam, and Charnov 1977). By sequentially handling multiple food items, individuals sample and assess their options. Investing time in sampling behavior may increase their profit from a single foraging bout (Ligon and Martin 1974; Kacelnik 1984;

Heinrich et al. 1997; Langen and Gibson 1998; Langen 1999), but it is argued that such behavior should be employed only if an individual has surplus time and is not exposing itself to high risks (Dall, McNamara, and Cuthill 1999). After observing western scrub-jays (*Aphelocoma californica*) lift several items in turn before making a selection (with each lift considered a sample action), Langen (1999) concluded that the birds made comparisons to identify heavy, nutritionally valuable items. This sampling behavior might be practiced equally by all scrub-jays or only a subset.

Individual-specific preferences have been observed for food type, intake rate and foraging sites (Partridge 1976; van Buskirk and Smith 1989; Bolnick et al. 2003), yet little is known about an individuals' consistency in sampling food items. Some individuals may sample multiple food items at nearly every opportunity, others may sample occasionally, still others may never be observed sampling. This would result in a diversity of foraging behaviors within a population. Foraging is an important daily activity; the cumulative effects of differential foraging success and efficiency between individuals may influence reproductive fitness, social status or survival (Stephens and Krebs 1986; Ritchie 1990; Lemon and Barth 1992; Black, Prop, and Larsson 2007).

If an individual demonstrates a repeatable behavior when foraging, there are many potential factors that may influence its predilection. Recent research in behavioral syndromes or animal personality attempts to describe and explain variation around what was traditionally assumed a theoretical “optimal” behavior (Sih, Bell, and Johnson 2004; Dingemanse and Réale 2005). All individuals in a population do not necessarily respond with the ideal actions in all situations; reactions may be somewhat constrained by individual phenotype. Repeatability has been used in behavioral syndrome and personality studies to identify behavior traits that remain characteristic of an individual over time (Quinn and Cresswell 2005; Kontiainen et al. 2009; Minderman et al. 2009; Gabriel and Black 2010; Herborn et al. 2010). Behavioral variation between individuals has a heritable component

(Dingemanse et al. 2002; Drent, van Oers, and van Noorwikj 2003; van Oers et al. 2004; van Oers, Klunder, and Drent 2005), and accumulating evidence suggests that natural selection favors contrasting responses under different ecological conditions (Wilson 1998; Dall 2004; Dall, Houston, and McNamara 2004; Dingemanse and Réale 2005; McElreath and Strimling 2006; Kontiainen et al. 2009).

Researchers have often described behavioral responses along a bold to shy continuum, demonstrating correlated behaviors in a variety of contexts. Bold animals, which overall adapt more readily to new situations, are expected to quickly explore new environments (Verbeek, Boon, and Drent 1996; Dingemanse and Goede 2004; Minderman et al. 2009), readily investigate novel objects (Webster and Lefebvre 2001), react aggressively towards conspecifics or threats (Verbeek, Boon, and Drent 1996; Dingemanse and Goede 2004; Kontiainen et al. 2009), and are more likely to engage in risky behavior (van Oers et al. 2004; López et al. 2005; Quinn and Cresswell 2005). In contrast, shy animals are expected to explore new environments slowly and more thoroughly, be wary of novel objects, act less aggressively, and be hesitant to take risks. An individual's aversion to risk could also be an important factor in determining its realized foraging behavior (Stephens and Krebs 1986; van Oers et al. 2004; Johnson and Sih 2007).

While studies have examined individual willingness to forage in threatening situations (Wilson 1998; van Oers et al. 2004; Johnson and Sih 2007), the connection between behavioral syndromes and the subtleties of foraging decisions remains unexplored. We compared the use of simple (taking first item handled) and complex (sampling and taking multiple items) foraging behaviors in a suburban population of Steller's jays (*Cyanocitta stelleri*) to determine whether sampling behavior can be treated as a component of their behavioral syndrome. Jays in this study population exhibit a range of repeatable behaviors linked in a syndrome. Individuals that were fast explorers in a novel feeding situation and traveled far beyond their home territory were also more likely to be recaptured in a familiar trap (Gabriel and Black 2010). It seems reasonable that sampling different food items from a collection may be functionally similar to short-term exploration, and that investing more effort into information gathering may increase exposure to risk. We predicted that explorative, risk-taking jays would be more likely to sample or take multiple items compared to shy, risk-adverse jays.

Other factors besides behavior type could influence an individual's willingness or ability to sample food items, such as age and experience. Several studies have demonstrated improved foraging performance with age (Richardson and Verbeek 1987; Desrochers 1992; Heise and Moore 2003; Black, Prop, and Larsson 2007). Birds may develop more complex and selective foraging behaviors with age and experience. A bird that is familiar with variable food items may realize it can benefit by considering its options before deciding. Older jays would be expected to exhibit sampling behavior and take multiple items more frequently than younger individuals.

Further, body size may be an important factor contributing to an individual's foraging behavior (Wikelski and Trillmich 1994; Barbraud et al. 1999; Weise, Harvey, and Costa 2010). Steller's jays may carry one or multiple items simultaneously in the crop and bill; taking multiple items may double or triple the food-load in a single trip. Individuals with larger gapes might be expected to take multiple items more frequently, and perhaps sample more items as they attempt this manipulation. Similarly, male Steller's jays may sample more items than females due to their larger size (Greene, Davison, and Muehter 1998).

In Langen's scrub-jay studies, competition and dominance at communal feeders appeared to be factors determining how many items jays sampled, with the risk of displacement increasing the cost of sampling when conspecifics were present (Langen and Gibson 1998, Langen 1999). Other economic factors, such as distance to cache site (Waite and Ydenberg 1994), could potentially influence sampling decisions. In our Steller's jay study we tested territory owners at locations near their territory centre to better evaluate inherent individual differences in foraging behavior.

In this study we quantified sampling behavior and tendency to take multiple items in Steller's jays, determined repeatability of these behaviors within individuals, and evaluated relative influence of three factors: behavior type, age, and body size. We predicted individuals would be consistent in their foraging tactics and that one or more of the explanatory variables describes the variation in sampling behaviors between individuals. We expected more neophilic, risk-prone, older, or larger jays to exhibit sampling behavior and take multiple items with greater frequency than neophobic, risk-adverse, younger or smaller jays.

STUDY SYSTEM

We studied sampling behaviors in Steller's jays on the Humboldt State University campus and surrounding residential areas of Arcata, CA (40°59'N, 124°06'W). The study area was 2.2 km^2, bordered to the east by redwood forest (*Sequoia sempervirens*). An inhabitant of coniferous and mixed coniferous-deciduous forest edge, Steller's jays have taken advantage of campgrounds and suburban areas for foraging and breeding opportunities (Brown 1963; Marzluff et al. 2004; Marzluff and Neatherlin 2006).

Steller's jays in our study area are non-migratory, defending territories with vocalizations and displays throughout the year. They cache items year round for short and long-term storage (Greene, Davison, and Muehter 1998). The Arcata population is part of an annual banding program since 1998, in which all birds are fitted with a unique combination of color leg bands and body size measurements are taken (Gabriel and Black 2010). Approximately 45 breeding pairs and 30-40 transient individuals are residents (JM Black and PO Gabriel, personal communication). Birds regularly received a wild bird seed mix including peanuts, sunflower seeds, and millet, from 21 feeder traps distributed across the study area in addition to feeders provided by local landowners. This is a useful population for behavioral studies, as they are tolerant of human proximity and year-round observation. Jay territories within the study area are monitored at comparable frequencies.

METHODS

To locate suitable field experiment sites we used daily observations in 2009 and previous resighting data to determine pair status and territorial centre (Gabriel and Black 2010). A male and female bird associating regularly and later attempting to nest were considered a pair (Gabriel and Black 2010). Territory holders were identified by performance of sex-specific territorial vocalizations, displays, caching food items nearby, and displacing intruding jays (Brown 1963; Greene, Davison, and Muehter 1998).

From 19 December 2008 until 11 March 2009 we quantified initial latency to approach a novel feeding platform and food sampling behavior of Steller's jays; each bird participated in at least three field trials, with minimum six days between trials. From 10 February to 30 March 2009 we repeated the foraging experiment with a predator mount present to assess risk-taking (approach latency and minimum distance to mount) and how food sampling behavior changed with a predation threat present. Each bird participated in a single risk-taking trial. In January and February 2009 we captured the birds and measured their skeletal features. Foraging experiments were postponed for at least six days after capture. From March to September 2009 we monitored pair bond status and territorial behavior (see below). We conducted a second set of foraging experiments from 16 October to 24 December 2009 on previously-tested birds to measure repeatability of foraging behavior between winter field seasons.

Sampling experiment

Each jay was provided with an experimental feeding station within its territory, placed on the ground 5 m away from the nearest cover (sensu

Bekoff, Allen, and Grant 1999). The feeding station was a 50 cm x 50 cm wooden platform with a 3 cm high rim. Six items [peanuts in the shell] were evenly-spaced within a 15 cm diameter circle in the centre of the platform. Steller's jays in our study area typically cached peanuts rather than consumed them immediately, so participation in the experiment was assumed to be independent of bird hunger. We used visually similar peanuts in shape and length (3.2 – 4.1 cm) with a standardized mass (2.40 +/- 0.20 g). Peanuts were concealed under a Styrofoam dome prior to trial initiation; a trial began when a territory owner was present and attentive. Trials were held between the hours of 0900 and 1200. The observer stood 15 m from the feeding platform. A single observer collected all the data, practicing all real-time observation techniques on birds outside the study area in preparation for actual trials.

We recorded three measures of foraging behavior each time a jay landed on the platform. Number of sample actions was the count of instances a bird picked up a peanut in its bill. Visit duration was the time spent perched on the platform. Items taken was the total number of items carried away. We recorded the same information for successive visits; the trial ended when fewer than four peanuts remained (platform was replenished to six peanuts at most once during the session) or 30 min after the trial's initiation. We used each bird's latency (in 20 s intervals) to land on the feeding station during its first trial as a measure of neophobia toward a novel object. Jays with shorter approach latencies were considered more neophilic than jays with longer latencies.

Risk-taking experiment

We assessed risk-taking by measuring how quickly and closely each jay approached the feeding platform with a raccoon mount (*Procyon lotor*) placed 3 m away. Raccoons were one of the primary nest predators that jays would encounter in the study area (JM Black and PO Gabriel, unpublished data). Peanut arrangement and initial trial conditions were the same as the sampling experiment. If a jay visited the platform, we recorded number sample actions, visit duration, and number items taken. Trials lasted 30 min; if jays removed all items we replenished the choice set back to six peanuts twice during the session. Trials in which birds other than the territorial pair (see below) arrived were not included in analysis.

A jay's risk-taking score was calculated from the summation of latencies (min) to perform each of the following behaviors in the 30-min trial: coming within 10 m, 5 m, and 3 m of the mount and staying within these distances for longer than 2 s. Behaviors that were not performed received a latency score of 32. If a bird came within several distance boundaries in one action (e.g. bird flew from 12 m immediately to 3 m), the bird received a 0 for the longer boundaries (Gabriel and Black 2010). The index was inverted so high values represented birds exhibiting risk-prone behavior while low values represented risk-adverse birds. Since jay behaviors could potentially be influenced by the social mate's behavior or local site characteristics, we tested for independence between pair members. We used Spearman rank correlations to test whether birds' foraging behavior, latency to approach the platform, or risk-taking scores correlated with the mate's behavior.

To further compare sampling and taking multiple items in the context of the Steller's jay syndrome, we used a relevant measure from Gabriel and Black (2010), risk-taking at feeders in which color-marked jays had previously been trapped. Throughout 2006 and 2008, individual birds were assigned scores depending on how far and how long they ventured into familiar traps (0: no approach; 1: perched on top; 2: perched at entrance; 3: entered halfway; 4: entered all the way for less than 2 s; 5: entered all the way for more than 2 s), where higher scores described greater willingness to re-enter.

Age and size measures

Minimum age was determined for each bird based on historical banding data for the population. Test subjects were all at least in their second winter (all

AHY). Age range was 2 to 11 years (X + SE = 4.0 + 0.23). The relevant morphological measurements were tarsometatarsus length, wing length, and gape length, measured to nearest 0.01 mm. We used principle component analysis to compute a composite size variable from gape, tarsometatarsus, and wing lengths (LaBarbera 1989; Rising and Somers 1989). The size composite variable PC1 accounted for 72% of total variance.

Statistical analyses

We analyzed the food sampling behavior of jays that had at least three visits to the platform during which the bird was alone (no other jays detected within 12 m of the platform) and on its home territory. Birds had four, five, or six peanuts from which to choose. For each subject we calculated number of sample actions averaged across visits and average visit duration. For tendency to take multiple items, individuals were divided into two categories - birds that took one item in all visits and birds that took multiple items for at least one visit. Repeatability, the variation within an individual, was determined for a short time period spanning three months and a longer period of one year, using a one-way analysis of variance (ANOVA) derivation (Lessells and Boag 1987). Repeatability (R) estimates range from 0 to 1, with 1 implying no variation in behavior for each individual. Values greater than 0.25 are considered moderately repeatable and values greater than 0.50 are considered highly repeatable (Dingemanse and Réale 2005).

We used model selection techniques to gauge the relative importance of the three factors (behavior type, age, body size) on the three foraging behaviors (average sample actions, average visit duration, and taking multiple items). We constructed 14 models using five covariates: initial latency to approach the novel platform, risk-taking score during the predator mount experiment, sex, PC1, and age. To model individuals' average sample actions we used generalized linear models (GLM), log-transforming variables to meet normality assumptions. Applying log-transformations to the GLMs produced normally-distributed residuals. We used logistic regression to model the occurrence of birds taking one nut in all visits versus taking two or three nuts in one or more visits. We ranked both sets of models according to corrected Akaike Information Criterion (AICc). We gauged the relative importance of each predictor by summing Akaike weights of models containing that predictor (Burnham and Anderson 2002). We used total deviance to measure model fit. For logistic models we also used area under the receiver operating characteristic (ROC) curve. Based on observed data and model predictions, the ROC curve plots true positive rate (sensitivity) against false positive rate (1 – specificity). Due to missing data for some variables, the models were based on data for 44 birds.

For variables that appeared in the top models for sampling and taking multiple items, we calculated correlation coefficients for individual covariates. We also calculated correlations to compare sampling and taking multiple items with existing trap re-entry scores from Gabriel and Black (2010). Spearman rank correlation coefficients described sampling behavior and effect sizes were used directly (r_s). To compare birds that took one item in all visits with those that took two or more items, we converted the d statistic of two-sample test comparisons (Wilcoxon signed-rank and Wilcoxon rank-sum test) to r. To obtain 95% confidence interval for an effect size, we bootstrapped the data for 5000 iterations. We used Cohen's (1988) guidelines for interpreting effect size: $r = 0.1$ as small, $r = 0.3$ as medium, and $r = 0.5$ as large. The use of effect sizes and confidence intervals allowed us to interpret the magnitude and reliability of a biological effect without the conceptual problems of interpretations based on P-values (Nakagawa and Cuthill 2007). Results presented here are from the first year, as the second year of data supported the first year's results with similar correlations. All statistical tests and model evaluations were performed in program R 2.7.2 (R Development Core Team 2008).

RESULTS

Sampling experiment

Sampling experiments in the first year yielded 307 visits, made by 35 males and 28 females (X + SE = 4.9 + 0.25 visits/bird). In the second year, to assess repeatability (no predator mount), 462 visits made by 32 males and 25 females were included (X + SE = 7.5 + 0.6 visits/bird). Of the 63 subjects in the first year, 38 exhibited some degree of complex foraging behavior, including sampling multiple nuts (36.5%), taking two nuts in one visit (3.2%), or using a combination of these behaviors (20.6%). Twenty-four jays took the first nut picked up (i.e. simple behavior) in all visits (38.1%), while two birds avoided the platform and peanuts in all trials. Each bird's sample actions were averaged across visits; values ranged from 0.33 to 5.3 sample actions per visit.

Visit duration (X + SE = 4.65 + 0.29 s, n = 307) was strongly positively correlated with number of sample actions (Spearman's rank correlation: r_s = 0.72, df = 305, $P < 0.001$) and was dependent on foraging tactic: taking first item, sampling, taking multiple items, or combination of sampling and multiple take (ANOVA: $F_{3,289} = 290$, $P < 0.001$; Figure 1). Visit duration, number of sample actions, and number of items taken were moderately repeatable within individuals within the first and second field seasons (visit duration repeatability: R = 0.39, 0.41; sampling: R = 0.35, 0.41; multiple take: not applicable) and between the two field seasons (visit duration: R = 0.32; sampling: R = 0.38; multiple take: R = 0.31). Given the strong association between visit duration and sample actions, we focused the remainder of our analysis on number of sample actions as a discrete behavior that allowed clear categorization of individuals into samplers and non-samplers.

Risk-taking experiment

Risk-taking scores assessed during the predator mount experiment (approach latency and minimum distance to mount) among 48 subjects (26 males and

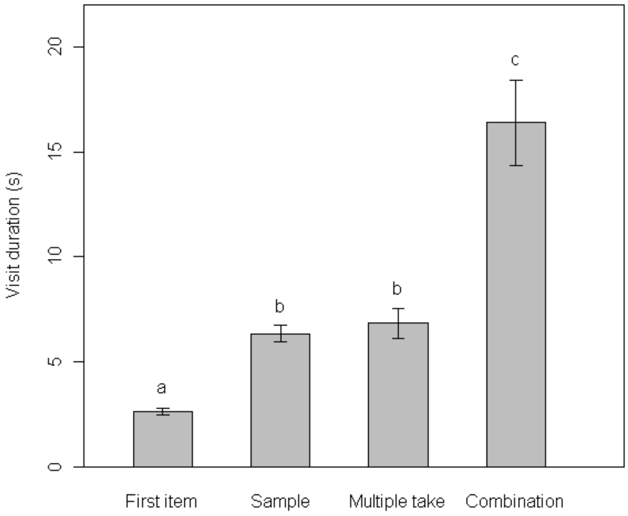

Figure 1. Average visit duration (s) ± SE of Steller's jays (*n* = 63) to a baited platform. Jays employed one of several foraging behaviors during a given visit: taking the first item handled (*n* = 190 visits), sampling two or more items before choosing (n = 62), removing two or more items simultaneously (*n* = 19), or a combination of sampling and taking multiple items (*n* = 22). Letters depict which groups were statistically different.

23 females) encompassed bold and shy extremes (range 0 - 159.7, X + SE = 108.0 + 7.9, *n* = 48). Twenty-four of these 48 individuals (12 males, 48). Twenty-four of these 48 individuals (12 males, 12 females) took a food item with the predator mount present; 18 of which had (1) sampled multiple items and/or (2) took multiple items simultaneously in trials without the predator mount. Nearly half of these 18 jays switched to taking the first item handled (44% and 46%, respectively). Jays that did not switch tactics (56% and 54%, respectively) continued to perform complex behaviors, but at a reduced frequency ((1) Wilcoxon signed-rank test: r = 0.851, 95% *CI* = 0.748 – 0.914, n = 18; (2) r = 0.294, 95% *CI* = -0.146 – 0.637, n = 11). Individual average visit duration did not differ with the predator mount present compared to absent (r = 0.104, 95% *CI* = -0.186 – 0.377, n = 24). Risk-taking scores from the predator mount experiment were not correlated with initial novel platform latency (r_s = -0.17, 95% *CI* = -0.26 – 0.415, df = 46).

Platform latency and risk-taking score were independent of sex, gape size, age (for platform latency), and mate response (r_s = 0.045 - 0.247, n = 25 - 63, all P > 0.1). Predator mount risk-taking score correlated positively with bird age (r_s = 0.341, 95% CI = 0.064 – 0.578, df = 48).

Multivariate analysis

The best candidate model for describing individuals' average sample actions included all five variables of the full model (Table 1). Initial platform latency and age each had approximately 1.3 times more Akaike weight than the three other predictors (Table 2). The full model accounted for 55% of total deviance (R^2 = 0.545). The second top model included only initial platform latency and age and was slightly more than two AICc points

Table 1. Top 6 of 14 model structures describing individual Steller's jays habitual foraging behaviors: tendency to sample items (log-transformed linear regression) and taking multiple items simultaneously (logistic regression).

Sampling behavior	Δ AICc	Akaike weight	Parameters
Log(platform latency) + log(risk-taking) + log(age) + PC1 + sex	0.00	0.66	6
Log(platform latency) + log(age)	2.17	0.22	3
Log(platform latency) + PC1 + sex	5.04	0.05	4
Log(risk-taking) + log(age) + PC1	6.00	0.03	4
Log(risk-taking) + log(age)	7.36	0.02	3
Log(risk-taking) + PC1	11.29	0.00	3

Take multiple items	Δ AICc	Akaike weight	Parameters
Risk-taking + age	0.00	0.32	3
Age	0.14	0.29	2
Risk-taking + age + PC1	2.18	0.11	4
Age + PC1	2.24	0.10	3
Age + PC1 + sex	4.62	0.03	4
Risk-taking	4.96	0.03	2

* Five variables describe three factors: (1) behavior type (initial latency to approach novel feeding platform, risk-taking score from predator mount experiment), (2) bird age, (3) body size (PC1 and sex).

greater that the full model. The second model accounted for 41% of total deviance (R^2 = 0.431). The ranking of the model set with average visit duration (highly correlated with average sample actions) as the response variable was very similar to the results using average sample actions.

The top model for taking multiple items contained age and risk-taking score during the predator mount experiment (Table 1) and accounted for 20% of total deviance. Age was the most descriptive variable in these models, with 1.8 times more Akaike weight than risk-taking score and 11.8 times more weight than sex or platform latency (Table 2). Area under the ROC curve was 0.80. The second top model carried similar weight and included bird age as the only variable; this model accounted for 15.5% of total deviance. Area under the ROC curve was 0.78.

Table 2. Summed Akaike weights across 14 candidate models for each variable describing sampling behavior and tendency to take multiple items in Steller's jays.

Predictor	Sampling	Take multiple items
Platform latency	0.95	0.07
Risk-taking	0.72	0.50
Age	0.94	0.89
Body size (PC1)	0.76	0.30
Sex	0.72	0.08

Pair-wise comparisons

Average sample actions prior to leaving with a nut was negatively correlated with platform latency: more neophilic jays sampled more items than more neophobic jays (r_s = 0.482, 95% *CI* = 0.264 – 0.661, df = 60; Figure 2a). Risk-taking scores were positively correlated with average sample actions: more risk-prone jays sampled more items than more risk-adverse jays (r_s = 0.442, 95% *CI* = 0.168 – 0.648, df = 46; Figure 2b).

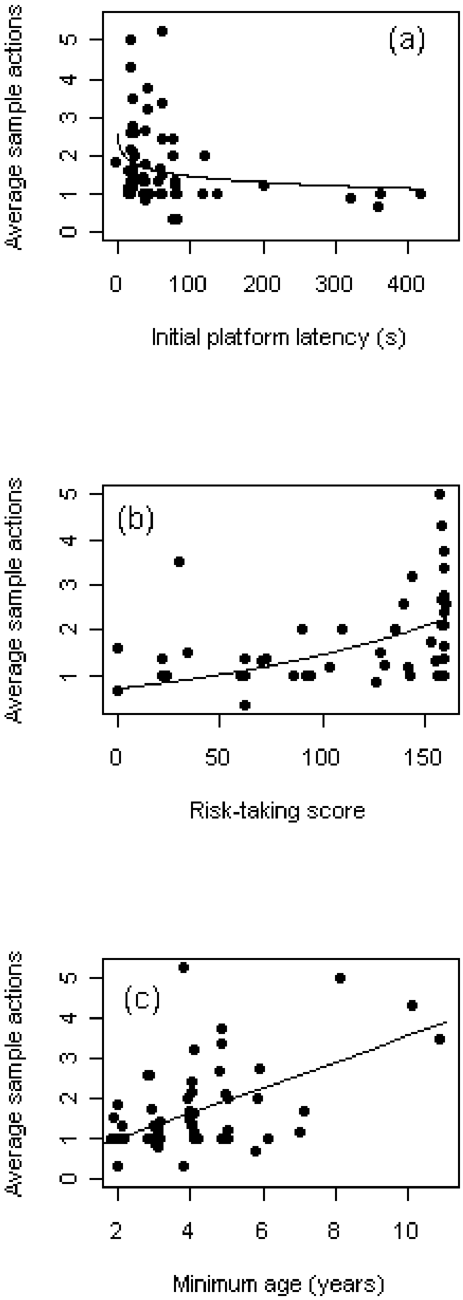

Figure 2. Relationship between individuals' average number of sample actions for Steller's jays in relation to (a) neophobia: latency (s) to approach a novel feeding platform (*n* = 62), (b) risk-taking score: response to a raccoon mount (*n* = 48), and (c) bird age in years (*n* = 63).

Age was positively correlated with average sample actions (r_s = 0.447, 95% *CI* = 0.211 – 0.644, df = 61; Figure 2c). Sampling was positively correlated with body size (PC1: r_s = 0.400, 95% *CI* = 0.142 – 0.610, df = 55). Male Steller's jays sampled peanuts more than females (*r* = 0.252, 95% *CI* = 0.041 – 0.518, *n* = 63).

Birds that took multiple items in a single foraging trip had higher risk-taking scores than those taking a single item (Wilcoxon rank-sum test: *r* = 0.290, 95% *CI* = 0.034 – 0.541, *n* = 48; Figure 3a). Birds that took multiple items were older than birds that took single items (*r* = 0.348, 95% *CI* = 0.141 – 0.533, *n* = 63; Figure 3b).

Finally, birds that had higher re-entry scores at a familiar trap sampled more in the current study (r_s = 0.359, 95% *CI* = 0.056 – 0.601, df = 35) and showed a weak to moderate tendency to take multiple items more often (*r* = 0.284, 95% *CI* = -0.029 – 0.608, *n* = 39) than birds that avoided entering the trap.

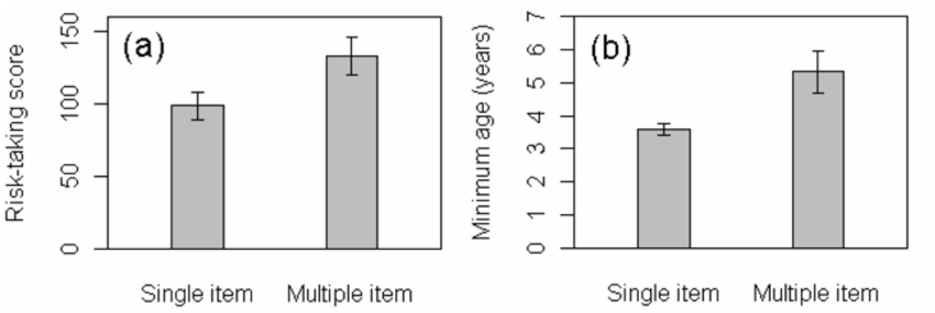

Figure 3. Comparison of Steller's jays that took a single item in all visits with jays that took multiple items in one or more visits for (a) risk-taking score (*n* = 35, 13; X ± SE) and (b) age (*n* = 48, 15; X ± SE).

DISCUSSION

Steller's jays in our urban population were moderately consistent in their sampling behavior, visit duration and number of items taken, repeatable over a few months and between winter field seasons. This satisfies a requirement of traits in a behavioral syndrome. Few studies to date have examined the repeatability of individual-specific foraging behaviors in relation to behavior type. High consistency in foraging tactics was also reported in barnacle geese (*Branta leucopsis*), in which bold individuals consistently located food patches while shy geese used a scrounger tactic (Kurvers et al. 2010). Even when a predator mount was present, half the jays in our study came to the platform and took peanuts. Of these, about half adjusted to the higher risk level by switching to a simple behavior, while the other half continued to sample nuts, take multiple items, or exhibit both complex behaviors. This demonstrates an individual's potential for flexibility between these tactics based on circumstances, yet strong tendencies in some individuals to remain consistent. Jays performing similar foraging behaviors even under different threat conditions may be indicative of routine-forming behavior, as has been observed in bold individual great tits (*Parus major*) (Marchetti and Drent 2000). The observation of highly variable responses between jays during these experimental trials suggests that sampling and taking multiple items are inherent individual behaviors related to behavior type.

However, multivariate analysis indicated that several bird attributes contribute to its tendency to sample or take multiple items. The relative importance of these attributes differed by behavior. Although many birds sampled and took multiple items in combination, it is possible these behaviors have fundamental differences. The avoidance or use of food sampling may reflect superficial versus thorough forms of information acquisition (Langen and Gibson 1998). All hypothesized factors appeared to influence sampling behavior, with neophobia and age describing the most variation. In comparison, taking multiple items may qualify as a more innovative behavior than sampling, perhaps limited by dexterity in manipulating large food items. Greater experience handling peanuts could explain the predominant effect of age. Similarly, birds that had been shown to take greater risks at a familiar trap in a different set of experiments

(Gabriel and Black 2010) sampled more in the current study but showed only a weak tendency to take multiple items more frequently. This may further suggest that sampling is more strongly influenced by behavior type while taking multiple items may be more influenced by experience. However, birds that take multiple items must be willing to invest more in handling time.

Tendency to sample and take multiple items was related to behavior type, according to moderately high effect sizes. Birds that sampled more peanuts per visit had shorter approach latencies to the novel feeding platform and predator mount, and birds that took multiple items had shorter latencies to the predator mount. These results are in accordance with Farwell and McLaughlin's (2009) study of brook charr (*Salvelinus fontinalis*), in which individuals foraging in open water were more willing to take risks (had a short latency to enter an unfamiliar environment) than those which used a sedentary, sit-and-wait foraging tactic.

As repeatable behaviors correlated to neophobia and risk-taking traits, sampling and taking multiple items can thus be characterized as components of a behavioral syndrome. The comparison with a behavior trait previously described as a component of the Steller's jay behavioral syndrome (Gabriel and Black 2010) could confirm this and connect the two foraging behaviors to the established syndrome. Birds that took greater risks at the familiar trap sampled more and tended to take multiple items more frequently. Findings in studies with blue tits (*Cyanistes caeruleus*), in which bolder individuals located new food sources more quickly, were interpreted as bold individuals being able to gather more information about new opportunities (Marchetti and Drent 2000; Herborn et al. 2010). Information gathering may not necessarily be limited to novel locations; it may apply to examination of valuable food items, here by neophilic, risk-prone jays. Behavior type may even be related to learning new foraging techniques. When presented with a tutor to mimic, bold, fast-exploring great tits quickly adopted new foraging habits compared to shy, slow-exploring individuals (Marchetti and Drent

2000). The ability to overcome neophobia, modify foraging behavior and learn from other individuals may expand opportunities and improve performance across a population (Greenberg 2003). Bold behavior types may have important advantages particularly in anthropogenic systems in which stimuli and conditions change rapidly (Short and Petren 2008). The roles of social learning and independent innovation in the development of sampling and taking multiple items are still unknown in Steller's jays.

The measure of neophobia was not correlated with risk-taking score, contrary to the prediction that birds would express similar levels of boldness in both tests. Lack of a relationship may be explained by neophilia or curiosity being constrained by perceived risk, with this interaction not constant across individuals. Nearly a third of subjects exhibited a short initial latency to the novel feeding platform, landing within the first minute, yet avoided the platform entirely with the raccoon mount present. Corvids have been identified as highly explorative and curious yet also highly neophobic (Greenberg and Mettke-Hofmann 2001). The two boldness tests of our study potentially had a sizable discrepancy in perceived risk. Coleman and Wilson (1998) encountered similar results with pumpkinseed sunfish (*Lepomis gibbosus*), in which individual responses to a threat stimulus was not correlated with response to a novel food source.

Our results also suggested that older jays use these complex behaviors more frequently than younger jays. While many studies report increased foraging efficiency with age (Jansan 1989; Desrochers 1992; Lang and Black 2001; Heise and Moore 2003; Wheelwright and Templeton 2003), many of these studies only consider the transition from juvenile to adult. Juvenile birds must learn what is edible, and have been documented as more explorative and neophilic than adults (Heinrich 1995; Biondi, Bó, and Vassalo 2010), implying younger birds may be more inclined to sample items. It is important to note that our study tested adult territory owners. Young Steller's jays that do not disperse typically spend a period of time as a floater before occupying a vacant territory. Submissive floaters have a high risk of displacement from feeding areas (Brown 1963), and would not have the opportunity to use complex, time-consuming foraging behaviors. Established territory owners have increased familiarity with available food items (and familiarity with the habitat and ambient risk), allowing individuals to develop habits of sampling and taking multiple items.

Body size contributes to the occurrence of specialized foraging behaviors and diet composition in a variety of other species (Alatalo and Moreno 1987; Wikelski and Trillmich 1994; Weise, Harvey, and Costa 2010). In Steller's jays, body size and sex are related to sampling behavior, although to a lesser extent than age or behavior type, but not taking multiple food items. There is anecdotal evidence that existing size limitations for taking multiple items can be circumvented by crossing two peanuts and carrying them in the bill (PO Gabriel and C Rockwell, personal observation). The majority of jays were apparently capable of carrying two peanuts (C Rockwell, unpublished data), yet failed to exhibit this behavior. To explore the size and sampling relationship, consider that dominance in Steller's jays is site-based. We tested birds on their home territories where they would typically initiate and win social interactions, and thus have a low risk of displacement (Brown 1963). Yet if body size plays a role in aggressive interactions (Richner 1989), a large individual may be freer to engage in sampling behavior both at home and in neighboring territories. Langen's (1999) observation that dominant scrub-jays sampled more items than subordinate jays may explain sex differences in Steller's jay sampling, although in our study sex was one of the least influential predictors. A female regularly faces the possibility of being displaced by her socially dominant mate (Brown 1963), therefore she may be less likely to use time-consuming sampling behavior.

This study is among the first to recognize the role of individual differences in foraging tactics, in addition to gauging the importance of behavior type relative to other factors. This study raises considerations for behavior traits that meet the criteria of behavioral syndromes yet are not independent of other attributes of the individual. Improved comprehension of this behavioral syndrome component has potential applications for wildlife management, such as corvid management that is sensitive to variation between individuals. Individual habits may be equally or even more important in determining realized foraging behavior than general characteristics of age and sex, particularly in species with complex behavioral repertoires.

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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.

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 out-perform all others (Choudhury et al. 1996). Compatibility between partners can therefore override the influence of intrinsic individual quality (Coulson 1972; Black et al. 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 and Altman 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 which are consistent over time and functional contexts, for example, mating, antipredator, exploratory and competitive contexts (Sih et al. 2004; Dingemanse and 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 intra-pair 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 in order 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 January 2006 to September 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 two months preceding breeding onset (January & February) and during breeding seasons (March – August) when courtship activity and formation of new pairs was most intense (J.M.B. & P.O.G. unpublished 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 three years, nests were initated on average on April 6, with a range from March 5 to May 30 (SD = 15 days), and 51 to 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.B. & P.O.G. unpublished 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 & Boerlist 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 days and lay clutches of 2 to 6 eggs, laying one egg per day (Greene et al. 1998). Egg incubation lasts about 18 days, and hatchlings take about 17 days to fledge (Greene et al. 1998; J.M.B. & P.O.G. unpublished 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 three years 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.

Since 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 (7 on the ground inside the box, partially underneath the lid, 3 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 March – November, 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 December - February). 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 intra-pair 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 three years, and 21 pairs in two different years). 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 reflects those relationships (Garamszegi 2006; Nakagawa & Cuthill 2007; Garamszegi et al. 2009b). The effect sizes presented are directly comparable amongst each other and also to other studies that make use of the effect size theorem. Variables were checked for normality and homoscedasticity, and nonparametric tests were applied when parametric criteria were not met. Therefore, we calculated correlation coefficients from regressions either directly (expressed as Pearson or Spearman *r*) or from related effect sizes obtained from two sample 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 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, since 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 if 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 above.

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 licenses 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 three years 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 one year (2006, 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). 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 – 0.39, Chi-Square test: *P* = 0.405; Travel distance: w_{28} = 0.22, 95% *CI* = -0.37 – 0.37, Chi-Square test: *P* > 0.999; Trap re-entry score: w_{66} = 0.14, 95% *CI* = -0.12 – 0.36, Chi-Square test: *P* = 0.344).

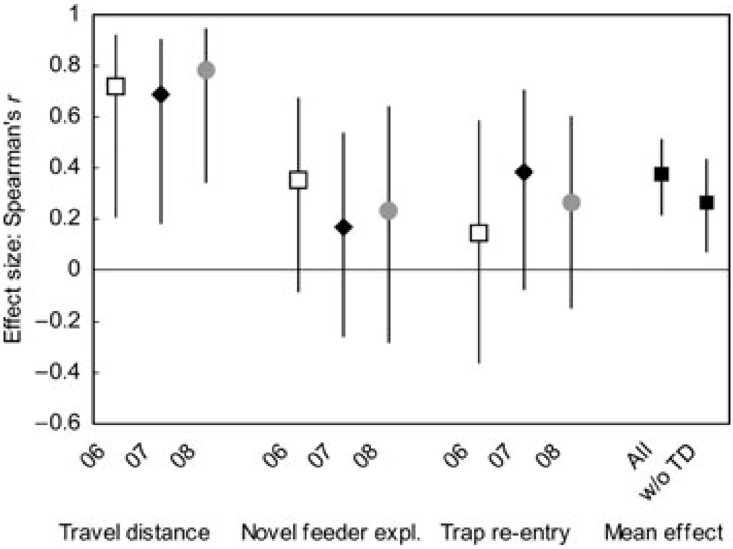

Figure 1. Effect sizes of relationships between female and male partner's behavioural traits (annual habitat exploration distances: 2006: *n* = 11, *P* = 0.013, 2007: *n* = 12, *P* = 0.014, 2008: *n* = 11, *P* = 0.004; exploration scores during a novel foraging opportunity: 2006: *n* = 22, *P* = 0.105, 2007: *n* = 24, *P* = 0.438, 2008: *n* = 17, *P* = 0.377; and risktaking 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% *CI*s.

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 - 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 - 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 in 2007 and 2008 than unsuccessful pairs, with large effect sizes in both years (2006: r_8 = 0.40, 95% *CI* = -0.42 - 0.86, Mann-Whitney U test: *P* = 0.655; 2007: r_{12} = 0.54, 95% *CI* = -0.05 - 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).

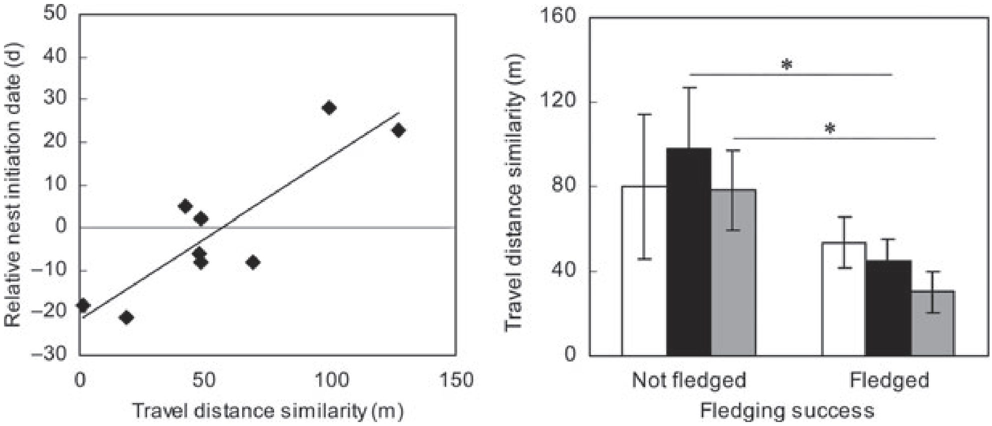

Figure 2. Relationships between mate similarity in long-term habitat exploration and (a) annual nest initiation dates relative to the annual population mean, and (b) annual fledging success of Steller's jay pairs in 3 yr (white = 2006, black = 2007, grey = 2008). Columns with error bars indicate means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

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 - 0.78, parametric regression: P = 0.137; 2007: r_{18} = 0.11, 95% CI = -0.37 - 0.55, parametric regression: P = 0.659; 2008: r_{15} = 0.005, 95% CI = -0.51 - 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 - 0.72, t test: P = 0.515; Fig. 3).

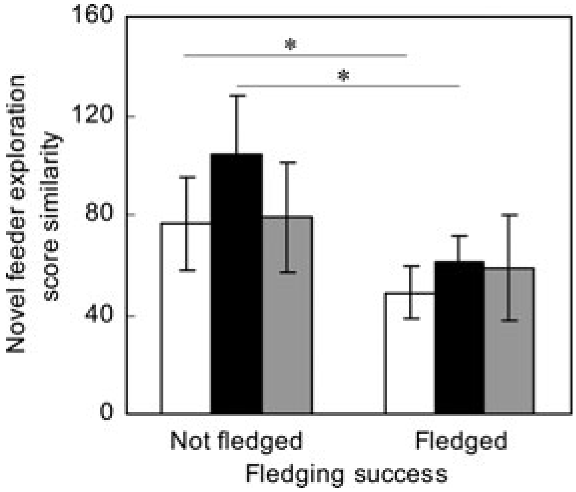

Figure 3. Relationships between mate similarity in novel feeder exploration scores and annual fledging success of Steller’s jay pairs in 3 yr (white = 2006, black = 2007, grey = 2008). Columns with error bars indicate means and SEs. *Relationships with large effect sizes.

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 - 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 - 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 - 0.72, t test: P = 0.662; 2007: r_{19} = 0.16, 95% *CI* = -0.31 - 0.58, t test: P = 0.636; 2008: r_{20} = 0.11, 95% *CI* = -0.35 - 0.53, t test: P = 0.711).

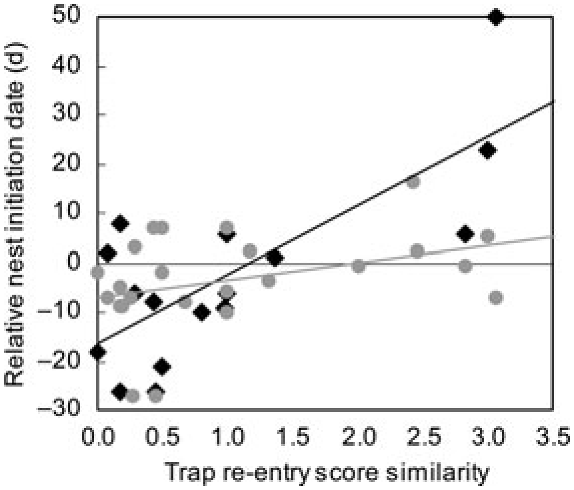

Figure 4. Relationships between mate similarity in risk-taking at a familiar trap and annual nest initiation dates of Steller's jay pairs relative to the annual population mean in 2 yr (black = 2007, grey = 2008).

Between-year differences in Reproductive Performance

Nest initiation in 2007 occurred on average 2 days later than in 2006 and 9 days 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 (X_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 - 0.47, t test: $P = 0.76$; 2007: $r_{37} = 0.13$, 95% $CI = -0.21 - 0.43$, t test: $P = 0.69$; 2008: $r_{35} = 0.10$, 95% $CI = -0.24 - 0.42$, 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 two out of three years. Although the precision and certainty with which these relationships were expressed was low in some cases, which is likely an effect of small sample sizes for some comparisons (Fig. 3a, 4; further discussion below), 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 one out of three years, partners that were both travelers, and partners that were both non-travelers 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 out 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 two years, 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 January 2007 were 1.5 - 2.5 °C below any other winter month in the 3-year 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 coordination 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 to 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 travelers and non-travelers. 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 byproduct 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 if traits are predictably related within individuals. This lends support to the idea that a correlated suite of behavioural traints (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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Reproduction in Steller's jays: individual characteristics and behavioral strategies

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ABSTRACT—Individual differences in reproductive performance within a bird population may be caused by a variety of traits. As reproductive strategies and costs often differ between the sexes, so can the selective advantages of individual traits. We investigated the reproductive importance of individual male and female traits in urban Steller's Jays (*Cyanocitta stelleri*), including age, size and body condition as well as their propensity to explore and take risks. Exploration and risk-taking traits are known to be correlated through a behavioral syndrome in jays, where selection must act jointly on the correlated characteristics, further constraining how male and female traits may operate to improve reproduction. We found older jays of both sexes, and less explorative female jays to have slightly better reproductive performance, where age was also positively correlated within pairs. Males in better body condition performed slightly better, whereas higher performing females were in worse condition. Since body condition was negatively correlated within pairs, males in better condition likely enabled their mates to invest more into reproduction, 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 reproductive performance. Correlation of behaviors in a syndrome may have constrained reproductive advantages of single traits if they acted in opposing directions than favored by the syndrome. More importantly, the reproductive influence of individual quality was likely diminished by high food abundance and unpredictability of nest loss in the anthropogenic environment experienced by this jay population.

KEYWORDS—age, behavioral syndrome, *Cyanocitta stelleri*, exploration, reproductive performance, risk taking, Steller's Jay.

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 since energetic costs of reproduction are often higher for females (Clutton-Brock et al. 1982; Clutton-Brock 1988).

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 further complexity when describing 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, where 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). Selection cannot improve the traits in a behavioral syndrome separately, but must act jointly on the correlated characteristics (Carere and Eens 2005). This can be an advantage when selective advantages for the traits align with trait combination in the syndrome, thus selecting for the syndrome itself (Barton and Turelli 1991; Cheverud 1996; Bell 2005; Blows 2007). However, a disadvantage arises 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 described a behavioral syndrome in a population of long-lived, monogamous Steller's Jays (*Cyanocitta stelleri*), measured during field tests describing tendencies to explore and take risks in different contexts (Gabriel and Black 2010). We found breeding pairs tended to mate assortatively for behavioral traits, and pair members ranked similarly in any of the behaviors enjoyed reproductive advantages (Gabriel and Black 2012), conferring a selective advantage to the trait combination in the syndrome. In this paper, we focused on the reproductive importance of individual male and female traits, including age, size and body condition as well as their propensity to explore and take risks. We tested whether Steller's 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 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 January 2006 to September 2008. Jays in this population are typically year-round residents maintaining 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 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) based on gape coloration and typical juvenile plumage patterns and shapes (retrices and secondaries; Pyle et al. 1987). We measured wing length with a ruler to the nearest millimeter, tarsometatarsus and gape length with calipers to the nearest 10 micrometers, and weighed birds with a Pesola spring scale to the nearest gram. Body size was calculated as a composite variable from wing, tarsometatarsus and gape lengths in a principle component analysis (La Barbera 1989; Rising and Somers 1989). We used the size composite variable PC1, which accounted for 73% of total variance. Body condition was assessed using residuals of a regression of body mass against PC1 size variable.

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 Steller’s Jays to disturbances at the nest did not allow us to directly assess number or condition of offspring (J. M. Black and P. O.

Gabriel unpubl. data). However, early breeders have been widely shown to produce more and fitter offspring (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 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 three years and subtracted these means from respective estimated individual dates. Resulting relative measures of nest initiation are reported in days before or after mean initiation in the respective 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).

Behavioral measures

We investigated two indices of exploration and two indices of risk taking, measured in four separate contexts. Since the personality traits investigated were shown to be highly consistent within this population of individuals over time (Gabriel and Black 2010), 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.

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 at least 17 annual resighting locations, where the likelihood of resighting a bird was independent of maximum annual travel distances (r = 0.004 – 0.28, 95% confidence intervals widely overlapping 0). Based on site-centered territorial behavior of Steller's Jays (Brown 1963) where pairs defend an area close to their nests but lose dominance with increasing distance from the territorial center, we defined birds that were found farther away from their territorial centers as more explorative. We used the mean of five longest resighting distances for each year (2006-2008) from the territorial center (mid-point between all known nest locations in the respective year) 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 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. Prior to the breeding season of 2007, we attracted jay pairs to an experimental feeder baited with peanuts that was set up close to their respective territorial centers, and observed behavioral responses for 20 min. 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. 2009a) by approach distances, times spent and bait items taken. We translated these latencies into a cumulative exploration score, ranging from 0 to 169, where high scoring birds entered and explored the feeder.

Risk taking at a familiar trap was assessed throughout 2006 and 2008 by recording individual jays' behavioral responses to feeders they had previously been trapped in. Based on a systematic, categorical assessment of 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.

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 trade-off between injury risk and energy investment of mobbing a potential predator, and potential fitness benefits of protecting offspring. 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). Prior to the breeding season of 2008, jay pairs were attracted to a location close to their territorial centers by peanut bait, and upon arrival exposed to a raven mount suspended in flight posture for a 30 min observation period. We used alarm calling behavior as a bivariate measure of mobbing activity (call / no call), where birds that alarm called were taking a greater risk than those that did not alarm call.

Statistical Analyses

We calculated correlation coefficients to investigate direction and strength of relationships between reproductive performance, estimated by nest initiation date and fledging success, and age, size, body condition and behavioral traits of male and female Steller's Jays. We standardized the direction of relationships to where a negative correlation would signify that an individual that was older, larger, in better condition, more explorative and more risk-prone initiated nests earlier, and successfully fledged young. Separate analyses for each year allowed comparisons among years, but also avoided pooling (20 individuals contributed data in all three years, and 45 individuals in two different years). To test whether relationships between age and reproductive effort were due to differential performance of yearling breeders only, we repeated the tests after removing yearling birds from the data. 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% confidence intervals, 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. 2009b). 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 Steller's jays (Gabriel and Black 2010), whether breeding pairs mated assortatively for behavioral traits, and 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 this 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 confidence intervals 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, body condition and behavioral traits) on reproductive performance across all reproductive indices and years. Since 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 in all three years (all 95% *CI*s widely overlapping 0; reported in Gabriel & Black 2012); relative nest initiation dates were unrelated among years (2006/2007: r = -0.24, 95% *CI* = -0.72 / 0.39, n = 12; 2006/2008: r = 0.19, 95% *CI* = -0.54 / 0.76, n = 9; 2007/2008: r = 0.20, 95% *CI* = -0.26 / 0.58, n = 21), as was fledging success (2006/2007: w = 0.31, 95% *CI* = -0.13 / 0.66, n = 17; 2006/2008: w = 0.35, 95% *CI* = -0.25 / 0.95, n = 9; 2007/2008: w = 0, 95% *CI* = -0.45 / 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 combined trait relationships from males and females with an effect revealed in the first set of meta-analyses ($|r| \geq 0.1$ and confidence interval that did not or only minimally overlapped 0) in a second set of analyses comparing the strength of combined influence of individual jay traits on the two separate reproductive indices, and in the three separate years. For these analyses, relevant male and female trait relationships were standardized for direction by assigning the common direction a positive sign. However, we excluded female body condition, since male and female body condition were not only negatively correlated, but instances of the relationship in females coincided with opposite relationships in males. Since several of the variables included in this set of analyses were correlated within individuals and pairs, resulting effect sizes would be expected to overestimate true effects, and were thus not interpreted as absolute effects, but only in relation to each other (Garamszegi 2006). Third we tested whether the direction of the relationship with 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; 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.

We used correlation coefficients and confidence intervals to investigate whether jays mated assortatively for age, size or body condition, and whether these traits covaried within either sex. Since 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 one year using Wilcoxon signed-rank tests. Only one pair of measurements per individual (the first two available) was used in this comparison to avoid pseudo replication.

Statistical analyses were performed in R Statistical Computing Package 2.10.1 and Microsoft Excel 2007.

RESULTS

We captured, color-marked, measured and monitored 130 male and 103 female Steller's Jays and recorded at least one behavioral and reproductive index for 68 individuals in 2006, 92 in 2007 and 88 in 2008.

The correlation matrix between male and female traits and two reproductive indices in three years was mainly constructed to inform a set of meta-analyses. However, certain patterns emerged when examining relationships in Table 1: male jays that were older, larger or in better condition had moderately higher reproductive performance in some years as did older females that were in worse condition; one to two out of the six relationships for each of these five traits showed effects and where confidence intervals did not or only minimally overlapped zero. Regarding correlations between personality traits and reproductive performance, none out of 24 relationships in males and only two of 24 in females showed effects and where confidence intervals did not or only minimally overlapped zero. Females that fledged young in 2006 were less explorative of a novel feeder, but called more in presence of a predator model (Table 1).

The first set of meta-analyses revealed that males that were older, larger, and in better condition had overall higher reproductive performance (across all reproductive indices and years) with small effect sizes (Fig. 1a). Females that were older, in lower body condition, and less explorative of a novel feeder had overall higher reproductive performance with small effect sizes (Fig. 1b). The effect of age on reproductive performance in both sexes was slightly weakened, but maintained after removing hatch-year breeders from the analysis (males: *r* = -0.12, 95% *CI* = -0.26 / 0.02; females: *r* = -0.12, 95% *CI* = -0.27 / 0.03).

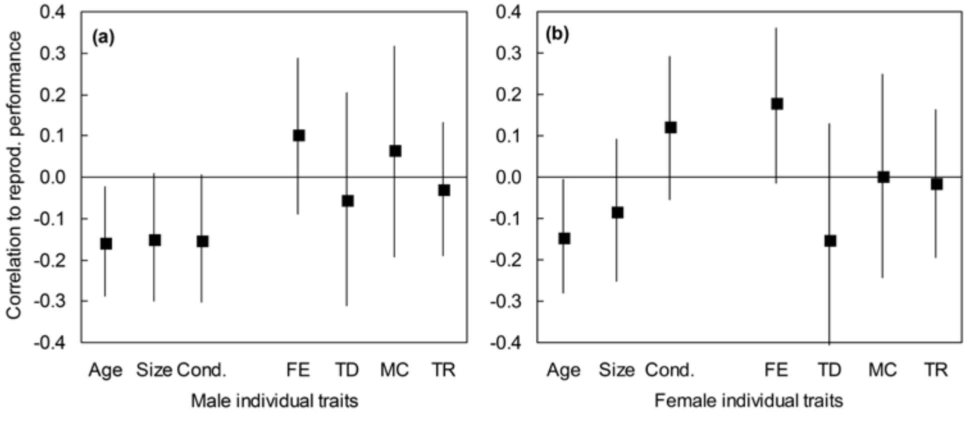

Figure 1. Correlation coefficients *r* and 95% confidence intervals (indicated by error bars) of meta analyses for (A) male and (B) female Steller's Jays, describing relationships between individual traits (age, body size, winter body condition [Cond.], exploration of a novel feeder [FE], travel distance 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).

Table 1. Correlation coefficients *r*, sample sizes (in subscript), and 95% *CI*s (shown below *r*) for relationships between male and female Steller's Jay traits (age, size, body condition (Cond), novel feeder exploration (FE), travel distance beyond home (TD), alarm calling towards predator mount (AC), risk taking at trap (TR)) and two reproductive indices in three different years. Effect sizes shown bolded where $|r| \geq 0.1$ and *CI*s not or minimally overlapping 0.

		Nest initiation date			Fledging success		
		2006	2007	2008	2006	2007	2008
Male	Age	**-0.32**$_{28}$ -0.62/0.06	-0.16_{38} -0.46/0.17	-0.19_{42} -0.47/0.12	-0.05_{34} -0.38/0.30	**-0.32**$_{43}$ -0.57/-0.03	0.11_{37} -0.23/0.42
	Size	-0.01_{20} -0.44/0.44	**-0.40**$_{30}$ -0.66/-0.04	-0.13_{31} -0.47/0.23	0.11_{24} -0.31/0.49	**-0.29**$_{36}$ -0.56/0.05	-0.01_{29} -0.38/0.36
	Cond	0.01_{20} -0.44/0.44	**-0.48**$_{30}$ -0.72/-0.14	**-0.28**$_{31}$ -0.48/0.08	0.05_{24} -0.36/0.44	-0.01_{36} -0.34/0.32	-0.07_{29} -0.43/0.30
	FE	0.20_{18} -0.30/0.61	-0.21_{19} -0.61/0.27	0.20_{19} -0.28/0.60	0.09_{22} -0.36/0.44	0.24_{25} -0.17/0.58	0.06_{18} -0.42/0.51
	TD	0.03_{9} -0.65/0.68	-0.06_{13} -0.59/0.51	0.20_{14} -0.37/0.66	-0.41_{10} -0.83/0.30	-0.19_{15} -0.64/0.35	0.06_{12} -0.53/0.61
	AC	0.08_{7} -0.72/0.79	0.22_{14} -0.35/0.68	0.21_{16} -0.32/0.64	0_{9} -0.65/0.65	-0.03_{14} -0.47/0.42	-0.14_{14} -0.67/0.37
	TR	0.07_{19} -0.40/0.51	-0.18_{26} -0.53/0.22	0.08_{32} -0.28/0.42	-0.22_{25} -0.57/0.19	-0.05_{31} -0.40/0.31	0.10_{30} -0.27/0.45
Fem.	Age	-0.19_{27} -0.53/0.21	**-0.26**$_{35}$ -0.55/0.08	-0.19_{40} -0.47/0.13	-0.13_{32} -0.46/0.23	-0.05_{40} -0.35/0.27	-0.08_{36} -0.40/0.26
	Size	-0.07_{17} -0.54/0.42	-0.11_{29} -0.46/0.27	-0.24_{26} -0.57/0.16	-0.12_{20} -0.54/0.34	0.07_{32} -0.28/0.41	-0.07_{21} -0.48/0.38
	Cond	-0.18_{16} -0.62/0.35	**0.38**$_{28}$ 0.01/0.66	**0.44**$_{26}$ 0.06/0.71	-0.13_{19} -0.55/0.34	-0.08_{31} -0.43/0.28	0.07_{21} -0.37/0.49
	FE	-0.18_{17} -0.61/0.33	0.06_{20} -0.40/0.49	0.18_{19} -0.30/0.59	**0.74**$_{21}$ 0.45/0.89	-0.07_{24} -0.46/0.34	0.09_{17} -0.41/0.55
	TD	-0.24_{8} -0.81/0.56	0.26_{11} -0.40/0.74	-0.32_{13} -0.74/0.28	-0.40_{9} -0.84/0.37	-0.34_{14} -0.74/0.23	0.15_{12} -0.46/0.67
	AC	0.02_{8} -0.69/0.72	0.18_{15} -0.37/0.63	-0.13_{17} -0.58/0.37	**-0.79**$_{9}$ -1.13/-0.54	0.21_{15} -0.30/0.70	0.29_{15} -0.22/0.82
	TR	0.12_{17} -0.38/0.57	-0.03_{23} -0.44/0.39	-0.18_{28} -0.52/0.21	0.19_{18} -0.31/0.6	0.06_{26} -0.33/0.44	-0.13_{24} -0.51/0.29

The second set of meta-analyses comparing the strength of combined influence of these relevant male (age, body size, body condition) and female traits (age, novel feeder exploration) on two separate reproductive indices and in the three separate years was instructive where strength of influence was assessed with *r* values when 95% confidence intervals did not or minimally overlapped zero. The relevant individual jay traits had larger influence on nest initiation date than on fledging success. Influence of relevant individual traits on reproductive performance was larger in 2007 than in 2006 and 2008 (Fig. 2).

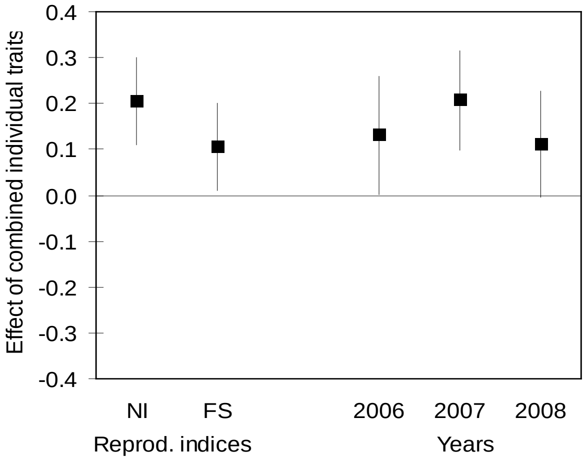

Figure 2. Correlation coefficients *r* and 95% *CI*s (indicated by error bars) of meta analyses comparing combined influence of relevant male traits (age, body size, body condition) and female traits (age, novel feeder exploration) of Steller's Jays on two reproductive indices (nest initiation date (NI), fledging success (FS)) across all three years, and in three separate years (2006, 2007, 2008) across both reproductive indices. Relevant traits were determined from trait relations with reproductive performance across all indices and years showing effect sizes $|r| \geq 0.1$ and *CI* not or minimally overlapping 0 (see Fig. 1).

Behavioral trait relationships with reproductive performance did not show a consistent direction among the four behavioral traits in males ($r = 0.03$, 95% $CI = -0.05 / 0.12$) or females ($r = 0.08$, 95% $CI = -0.02 / 0.17$).

In both sexes composite body size variable PC1 was moderately positively correlated with age (males: $r_s = 0.41$, 95% $CI = 0.13 / 0.63$, $n = 44$; females: $r_s = 0.31$, 95% $CI = -0.02 / 0.58$, $n = 36$). This was confirmed with longitudinal analysis of individuals in multiple years for females, where body size PC1 was slightly larger in later measurements (r = 0.23, 95% CI = -0.09 / 0.50, n = 20), but not for males (r = 0.09, 95% CI = -0.16 / 0.32, n = 33). Increase in body size PC1 in females over time was mainly due to increase in gape length (gape: r = 0.23, 95% CI = -0.08 / 0.51, n = 20; tarsus: r = 0.04, 95% CI = -0.23 / 0.30, n = 27; wing: r = 0.12, 95% CI = -0.15 / 0.37, n = 28). Body condition was not related to age (males: r_s = -0.07, 95% CI = -0.36 / 0.24, n = 44; females: r_s = 0.05, 95% CI = -0.29 / 0.38, n = 35) or body size (males: r_s = 0.03, 95% CI = -0.27 / 0.32, n = 44; females: r_s = -0.03, 95% CI = -0.36 / 0.30, n = 35).

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

DISCUSSION

We explored the consequences of male and female explorative and risk taking traits that are components of a behavioral syndrome, as well as basic demographic and physical characteristics on two measures of reproductive performance in Steller's Jays. We found that in both sexes, age had the most consistent, although only small to moderate influence on reproductive performance. Body condition had a detectable but overall weak and relatively inconsistent relationship with reproduction for both male and female jays. In addition, larger males, and females that were less explorative in a novel feeding situation tended to perform slightly better overall. Other behavioral characteristics were generally not related to nest initiation date or fledging success.

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 related Red-billed Chough (*Pyrrhocorax pyrrhocorax*; Reid et al. 2003), Steller's Jays in our study showed little variation in recruitment age 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. In contrast to some shorter-lived birds where improvement of reproductive performance with age is mainly due to poor performance of yearling breeders (Desrochers 1992; Wheelwright and Schultz 1994; Potti 2000), long-lived species often improve their performance continuously for several years (Clutton-Brock 1988; Black and Owen 1995; Forslund and Pärt 1995; Reid et al. 2003), as was the case in our jay population. Especially in an omnivorous species with a complex behavioral repertoire, the development of foraging skills that may constrain reproductive investment (Forslund and Larsson 1992; Wheelwright and Schultz 1994), as well as familiarizing with and ability to defend territorial resources likely are long-term processes. For example, Rockwell et al. (2012) show that older jays in this same study population took more time examining food items before making a selection. Furthermore, behavioral coordination of partners may improve over the life-time of long-term monogamous birds (Black 1996, 2001). The positive correlation between male and female age within jay pairs was not surprising, and supports the idea that mate familiarity with increasing pair-bond duration is a likely component of the age-effect on reproductive performance.

Older jays of both sexes were larger in the cross-sectional analysis. The longitudinal analysis indicated that in female jays, this was at least in part due to individual jays' beaks growing larger over time. Since beaks continue to grow slowly to offset wear, leading to variation in beak length between years and seasons in many passerines (Green 1981; Price and Grant 1984;

Richner 1989), the small amount of individual growth in female breeders is most likely due to decreased wear on female beaks compared to males who feed partners during multiple incubation periods in summer (Green 1981). Male jays, in contrast, did not show individual growth, suggesting instead that larger males may survive better. Benefits of large size are widely documented (Roff 1992; Anderson 1994; Blanckenhorn 2000), and probably also contribute to the relationship between age and size in female jays. The tendency of larger males to reproduce better is probably partly a consequence of the relationship between age and size, but may also indicate that larger males are better competitors that can secure more or better resources for reproduction (Searcy 1979; Maynard Smith and Harper 1988; Richner 1989).

Regarding assortative trait relationships within jay pairs, the negative correlation between male and female body condition, as well as the fact that females in worse condition tended to perform better, may be explained by high performing females investing more effort into reproduction and thus expending more energy than low performing female jays. Low performing female breeders have been found to survive better than good performers in a variety of bird taxa (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 condition, likely because of high reproductive investment, were more likely to be in better condition. Since both sexes participate in nest building and provisioning of nestlings, and males feed females during incubation (Greene et al. 1998; J. M. Black and P. O. Gabriel unpubl. data), males in better condition may enable partners to make a higher investment into reproduction. In addition, males in good condition may be attractive and females invest more when mated to attractive males (Møller and Thornhill 1998).

It has been suggested that life history trade-offs can maintain individual variation observed within populations (Stamps 2007; Wolf et al. 2007). Specifically, trade-offs between reproductive effort and mortality may lead to a range of solutions in reproductive patterns and in behavioral traits, and even encourage formations of syndromes involving different behaviors yielding the same trade-off. For example, highly explorative and highly risk-prone behaviors may both trade early reproductive success for increased mortality risk. However, trade-offs between productivity and survivorship mediated by variation in risk-taking behaviors are more likely in a population that evolved with, and currently faces, many predators (Biro and Stamps 2008). Corvids in general, and our urban study population of Steller's Jays in particular, experience relatively low predation pressure on adults (sensu Møller 2008), which may explain why individual risk-taking behaviors in breeding jays did not affect reproductive performance. However, an overall weak tendency suggested that female jays who were less explorative in a novel feeding situation might reproduce better. Nest predation and abandonment due to disturbance are important factors determining reproductive success in this urban environment (J. M. Black and P. O. Gabriel unpubl. data). Thus, jays who are "conservative" in their exploration and become more familiar with local intricacies of their territory might more often re-use known nest areas that would have more predictable patterns of predation and disturbance risk in a typically dynamic anthropogenic environment, sometimes allowing earlier nest initiation or better fledging success.

Overall, variation in individual male and female traits, especially behavioral traits, explained little of the variation in reproductive performance in Steller's 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 in individual jays stands in contrast to selection on the same syndrome in the form of differential reproductive performance by jays paired assortatively for behavioral traits (Gabriel and Black 2012). We describe in that analysis that pair members with similar behavioral traits in risk taking and exploration had higher reproductive performance. Regarding the overall lack of reproductive consequences of individual behavioral strategies in the present study, the correlation of the four behaviors in a syndrome may have constrained theoretical reproductive advantages of single traits if they acted in opposing directions than favored by the syndrome (Dall et al. 2004; Sih et al. 2004; Pruitt and Riechert 2009). More importantly for our study population, unpredictable environmental factors such as domestic cats and anthropogenic changes to habitat, leading to many failed and abandoned nests, may mask effects of individual quality. This was evident when comparing the relative influence of male and female traits on two different reproductive measures: The consequences of individual traits were stronger 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 phenotypic quality (Dingemanse et al. 2004; Boon et al. 2007; Schielzeth et al. 2011). Indeed, the strongest influence of male and female qualities on reproductive performance was apparent in 2007. Elsewhere we describe that 2007 was unusually cold for our normally mild coastal climate and population wide nest initiation was delayed (Gabriel and Black 2012).

Even in 2007, however these individual traits of males and females seemed less important when describing reproductive performance than specific trait combinations experienced in the pair bond (Gabriel and Black 2012). Therefore, it appears 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 this study, which also 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 detailed mechanisms of familiarity and compatibility that we suspect to ultimately drive fitness effects of age and behavioral similarity we observed in this population.

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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 contact calls and traveled 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 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.

KEYWORDS—behavioral similarity, compatibility, *Cyanocitta stelleri*, familiarity, pair bond, personality, reproductive success, risk taking, Steller's jay, tenacity.

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). 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 require 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 and Black 2010). They often reside in urban settings allowing close observation. Unlike other 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 a 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 (hereafter referred to as pair bond behaviors) and tested whether pairs that spent more time with their partners performed these behaviors more often. 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, Eens, and Török 2009, Gabriel and Black 2010). Prior research has shown that jay partners with similar personality traits, including their willingness to enter a feeder-trap, were more compatible, showing better reproductive performance than pairs with dissimilar personalities (Gabriel and Black 2012). Finally, we compared these pair bond characteristics for successful and unsuccessful partnerships in terms of producing offspring.

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 January 2006 to September 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 coloured leg bands. Minimum known age for each bird was assigned (hatch-year or after-hatch-year) based on gape colouration and typical juvenile plumage patterns (retrices and secondaries; Pyle et al. 1987). The study area contained between 130-170 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. 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 colour-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 January 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: March – August, or non-breeding: September – February) 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 10 or more resightings within the period and context of consideration (mean n ± 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 ($\leq$ 1m) 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 10 observations within their territories during breeding seasons in presence of their mate (mean n ± SD = 17.5 ± 9.5), we calculated the proportion of sightings where pair members were observed engaging in each of these subtle behaviors.

Similarity of Behavioral Traits

Risk taking was assessed during non-trapping seasons (annually March-November, 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 December-February). 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 less than 2 s; [5] entered all the way for more than 2 s), where higher scores described greater willingness to re-enter the feeder-trap (details in Gabriel and Black 2010). Because risk taking tendency is a highly consistent personality trait within this population of individuals (Gabriel and Black 2010), the repeatedly measured score (mean n ± 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 and Black 2012).

Reproductive Performance

We quantified nest initiation date and fledging success as indices of reproductive performance. Sensitivity of Steller’s Jays to disturbances at the nest did not allow us to directly assess number or condition of offspring (JM Black and PO Gabriel, unpublished data). Since in passerines, early breeders have been shown to generally produce more and fitter offspring (e.g. O’Donald 1972; Murphy 1986; Hochachka 1990; Tinbergen and Boerlist 1990; Winkler and 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 and Martin 2007).

We used observations of reproductive behavior and parental care (Greene et al. 1998; Gabriel and Black 2012) 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 three years 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 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). 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 and Cuthill 2007; Garamszegi, Calhim, et al. 2009). 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 methods used in recent behavioral research (see e.g. Garamszegi, Eens, and Török 2009), 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 and Black 2010), reproductive consequences of assortative mating for personality traits (Gabriel and Black 2012), and reproductive consequences of individual traits (Gabriel and Black, in press); 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 less than 1m apart was positively correlated to 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 and Somers 1989), and used the pair bond composite variable PC1, 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. Since 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 direction and strength of 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 and Black 2010). This measure of risk taking was included in a suite of traits describing a behavioral syndrome in Steller's jays (Gabriel and Black 2010). For the comparison of pair bond age, we tested similarity in performance between new and continuing pairs using Mann-Whitney U test, whereas Spearman Rank correlations were used for comparisons with pair tenacity and pair bond behavior.

We tested whether pair bond age (using Mann-Whitney 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 three years. 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). Since 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 three years (all 95% *CI*s widely overlapping 0; reported in Gabriel and Black 2012); 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 and Olkin 1985; Garamszegi 2006).

Since we demonstrated in an earlier study that bird age influences reproductive performance (Gabriel and Black in press), 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 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 two indices and three years were independent of male age, we therefore repeated these comparisons after 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 colour-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 three years, and 19 others in two years. Ten males were paired with two different females, and three males with three different females, resulting in 83 unique pair bonds during the three years. 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% ± 0.03, $n = 12$) and continuing pairs (47% ± 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 re-enter 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% $CI = -0.66 / -0.02$; 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% $CI = -0.33 / 0.20$; 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).

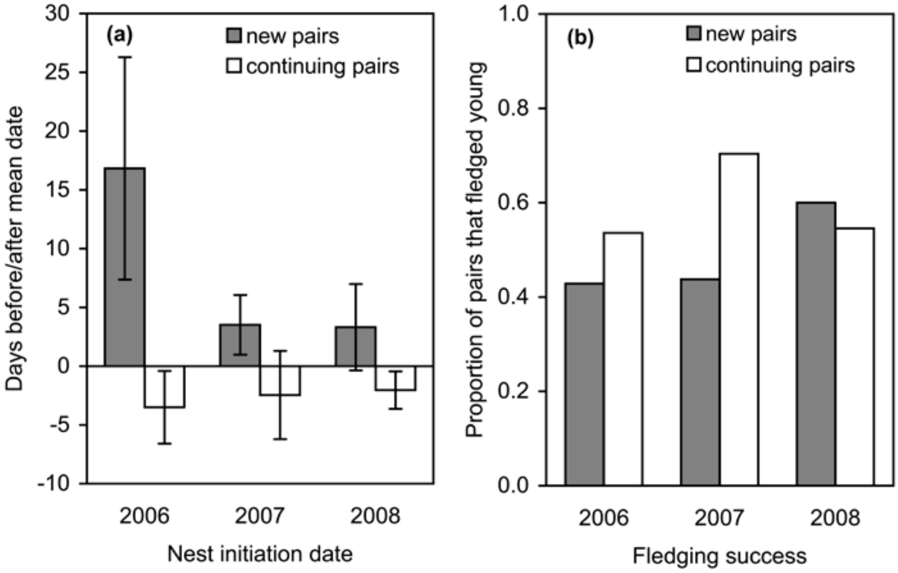

Figure 1. Reproductive performance of new pairs (established in same year) and continuing pairs (established previously) of Steller's jays measured across the reproductive indices nest initiation date (a) and fledging success (b) in three years. Bars with error bars indicate means ± SE.

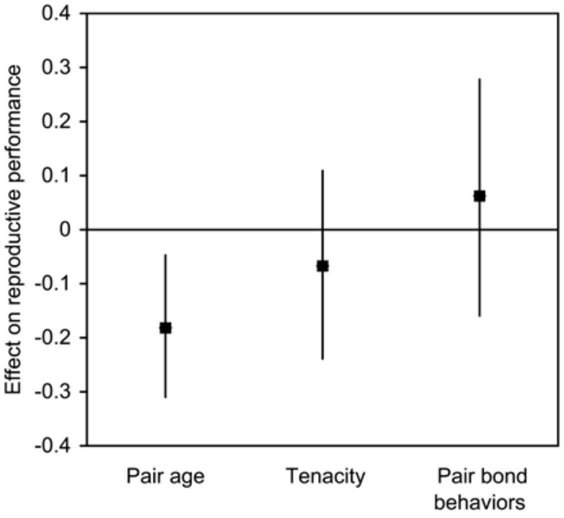

Figure 2. Overall effects (correlation coefficients and 95% *CI*s) of pair bond age (new or continuing pairs), pair tenacity (proportion of time males were observed with partner), and pair bond behaviors (composite variable of time pairs spent in close proximity, softcalling and travelling together) on reproductive performance, obtained from meta analyses on relationships across two reproductive indices (nest initiation date, fledging success) and three years (2006, 2007, 2008).

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% *CI*s 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% *CI*s widely overlapping 0), and no overall effect of pair bond behavior on reproduction was found (Fig. 2).

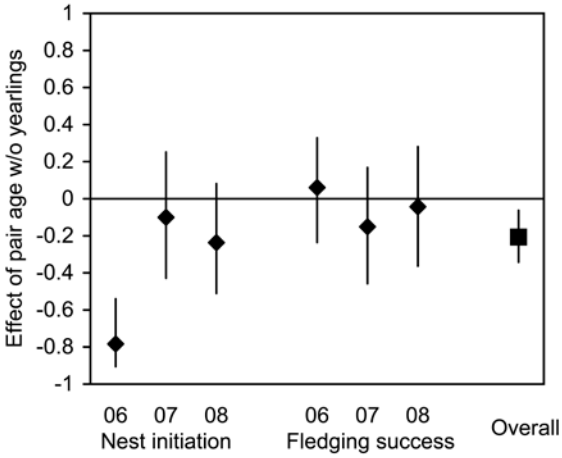

Figure 3. Correlation coefficients and 95% CIs of relationships between pair bond age (new or continuing pairs) and reproductive performance of Steller's jay pairs after removal of pairs with yearling males, measured in two reproductive indices (nest initiation date, fledging success) and three years, and overall effect obtained from meta analysis across all indices and years (Overall).

DISCUSSION

Ens, Choudhury and Black's (1996) review of long-term studies 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 and Westneat 2008). Our study confirms 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 and 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 and 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 traveled outside their own territories (38%) which can similarly be attributed to females making only short trips in between incubation bouts (JM Black and PO Gabriel, unpublished 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 and 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 to 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.

Simultaneous observations of Steller's jay pair members varied considerably during breeding seasons (ranging 20 to 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; Spoon et al. 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 10 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 and Black 2012) is not the result of continuous adjustments to behaviors of a partner, but rather suggests that jays mate assortatively for pre-existing behavioral traits. Partner similarity in this and other traits in the Steller's jay behavioral syndrome have reproductive advantages for jay pairs (Gabriel and Black 2012). Similar benefits of behavioral trait stability and behavioral similarity among partners have been demonstrated in zebra finches (*Taenipopygia guttata*; Schuett, Godin, and Dall 2011; Schuett, Dall, and Royle 2011). 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).

Continuing Steller's jay pairs nested earlier and were more likely to fledge young in some years than new pairs. 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. Samples 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 and Balda 1988). 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 to most other, part-time bird partnerships (e.g. Coulson 1972; Desrochers and 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 and Black in press) 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 to effects of pair similarity in behavioral traits (overall effect size r = 0.38, Gabriel and Black 2012) 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 and Jahn 1959; Teunissen et al. 1985; Black and 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 and Black 2012), but not many of their neighbors (Gabriel and Black 2010).

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