



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

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ARTICLE INFO

Article history:

Received 2 April 2010

Initial acceptance 3 May 2010

Final acceptance 16 June 2010

Available online 13 August 2010

MS. number: A10-00230

Keywords:

behavioural syndrome

Cyanocitta stelleri

exploration

personality

repeatability

risk taking

Steller's jay

trapping success

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 the presence of a predator mount and while 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 recaptured 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.

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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 & Réale 2005). For example, individuals' relative aggressiveness and boldness scores often covary in a population (Réale 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 has been questioned (Höjesjö et al. 2002; Bell & Stamps 2004; Dingemanse & 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

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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 an open cup nest and subsequently cooperate in feeding nestlings. After fledging, birds show 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 defence 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 we 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 nontarget 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 coloration 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 one-third 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 3 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 (short-term assessment) and compared this with a bird's willingness to re-enter a baited trap where it had been captured previously (long-term annual assessment). We quantified an index of exploration behaviour by presenting a novel foraging situation within each bird's territory (short-term assessment) and compared this with a bird's propensity to explore beyond territorial boundaries (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 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 neighbouring jays that subsequently participated in mobbing activities. Participation of territorial birds in alarm calling was independent of

attending neighbours (chi-square test: $\chi^2_1 = 0.14$, $N = 28$, $P = 0.705$). 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 \pm 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 we initiated the experiment when the focal territorial pair arrived alone. To begin a trial, we placed seven peanuts on the ground inside the box, partially underneath the lid, and three peanuts on top of the lid, then retreated 15 m away. Birds were observed for the subsequent 20 min.

In accordance with similar tests of exploration behaviour (e.g. Dingemans 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

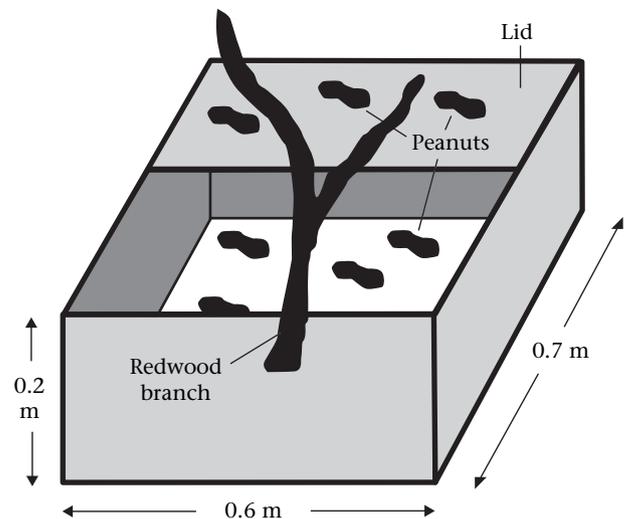


Figure 1. Schematic of experimental configuration used to test short-term exploration of a novel feeder. We placed peanuts inside and on top of a box with half a lid and no bottom, offering a foraging opportunity not unlike situations experienced in the forest, where jays enter enclosed spaces created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

2 min increments, to perform each of the seven behaviours, and we assigned an arbitrary latency score of 25 for any behaviours not 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 that they did not perform. 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 readily explored a large area of the novel feeder for an extended period. 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 have 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 \pm SE = 40.0 ± 2.2 , range 17–84, $N = 55$). If more than one nest location was known, the midpoint (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-ranks 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 to estimate repeatability of this trait (see below), but were 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 (recaptured/not recaptured).

Statistical Analyses

We tested the predictive power of short-term experimental tests for long-term annual measures of individual differences in the population and for 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) are 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 & 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 11 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, probably 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 & 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 reflected those relationships. To present effect sizes that are meaningful and comparable not only within our 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 nonparametric 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; Supplementary Table S1).

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 No. 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 3 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 per cent of the birds ($N = 43$) participated in alarm-calling behaviour while in presence of the raven mount. Mean \pm SE annual risk-taking score while approaching the baited trap was 3.2 ± 0.1 (range 0–5, $N = 109$). Mean \pm SE exploration score during the novel feeder set-up was 80.2 ± 8.3 (range 0–169, $N = 60$). Maximum annual travel distances ranged from 77 m to 520 m (mean \pm 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).

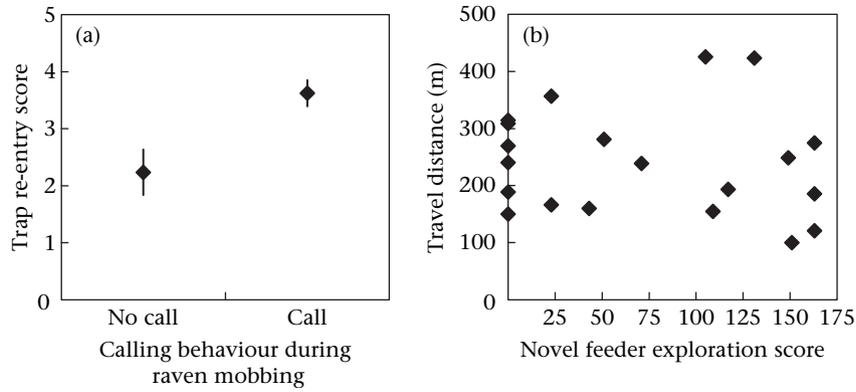


Figure 2. Relationships between short-term and long-term behavioural responses within two ecological contexts: (a) short-term risk taking facing a simulated predator and an index of long-term risk taking at a familiar trap ($r_{34} = 0.53$, 95% CI = 0.25–0.74, $P = 0.008$) and (b) an index of short-term exploration of a novel feeder and long-term exploration of unfamiliar environments ($r_5 = 0.20$, 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.

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%

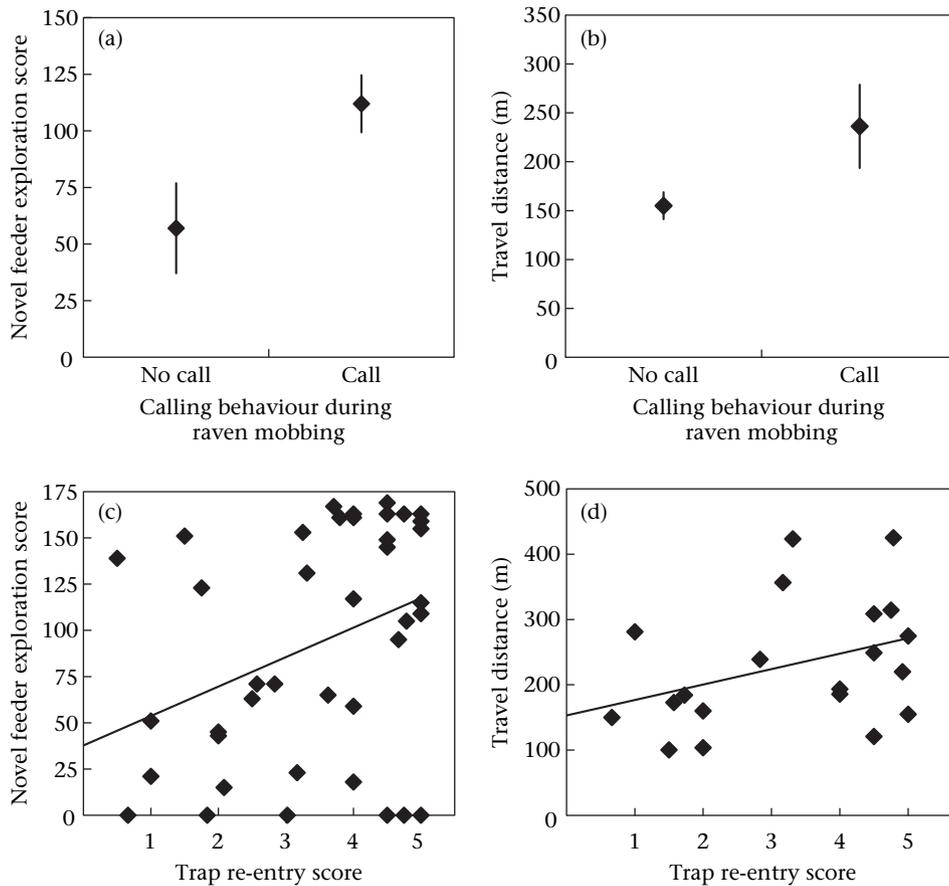


Figure 3. Relationships between behaviours measured in four ecological situations: (a) short-term risk taking and short-term object exploration ($r_{22} = 0.53$, 95% CI = 0.16–0.77, $P = 0.035$), (b) short-term risk taking and long-term habitat exploration ($r_9 = 0.69$, 95% CI = 0.16–0.91, $P = 0.045$), (c) long-term risk taking and short-term object exploration ($r_5 = 0.33$, 95% CI = 0.02–0.58, $N = 40$, $P = 0.037$) and (d) long-term risk taking and long-term habitat exploration ($r_5 = 0.37$, 95% CI = -0.08–0.70, $N = 20$, $P = 0.106$). Diamonds with error bars indicate means and SEs.

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 recaptured 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). Recaptured birds travelled further beyond their home territories (Fig. 4c) and received higher exploration scores during the novel feeder experiment (Fig. 4d) than birds that were not captured.

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 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-Fiser 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 lifestyles (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 syndromes 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).

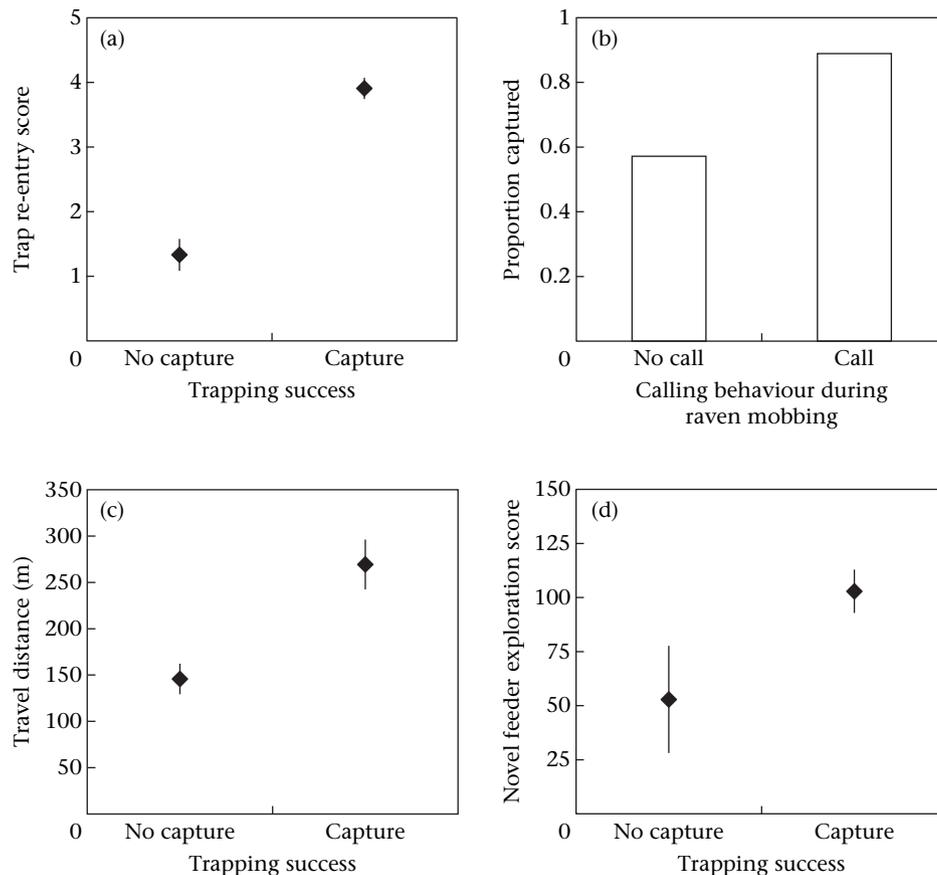


Figure 4. Relationships between trapping success and (a) long-term risk taking ($r_{19} = 0.65$, 95% CI = 0.27–0.85, $P = 0.036$), (b) short-term risk taking ($w_{25} = 0.36$, 95% CI = -0.06–0.86, $P = 0.11$), (c) long-term habitat exploration ($r_{42} = 0.34$, 95% CI = 0.04–0.59, $P = 0.026$) and (d) 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.

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 the long-term (re-entering a baited trap) contexts, 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 the findings of Herborn et al. (2010), in which two behavioural traits in blue tits, *Cyanistes caeruleus*, were correlated between measures in captivity and the wild, 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 are 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 than that gathered by 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 are highly explorative of a novel feeder at home are also good qualitative exploiters of novel foraging situations, regardless how far away from home such items are found. On the other hand, jays that travelled far might be expected to be superficial, quantitative explorers. These behavioural responses may represent two alternative exploratory strategies that are unrelated because time investment in one strategy might not allow simultaneous investment in the other strategy.

In addition, 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). If this interpretation is correct, it would suggest that the two exploratory behaviours that we measured are probably selected for in unrelated behavioural axes, consistent 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 rank 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) rarely travelled beyond the home territory, and might thus have 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 & Stewart 2003). Future research could address whether birds that frequently explore beyond their home territories are more likely to switch social partners or territories or to participate in more extrapair copulations (Kempnaers et al. 1992) and whether they are more likely to lose a mate or territory or to be cuckolded because they spend less time with their mate in the home territory (Gowaty 1996; Brylawski & 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 probably indicated a lack of common proximate mechanisms. In addition, the strength of the 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 probably 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 the relatively short study period of 3 years, limited our ability to obtain behavioural sampling of 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 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, annual scores for re-entering a baited trap and distances travelled from territory centres were meaningful measures of individuals' willingness to take risks and their 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). Variation in some environmental factors such as weather and presence of conspecifics was 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 can influence behavioural responses (Bell & Stamps 2004; Mettke-Hofmann 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 that showed highly explorative behaviours were more likely to be captured in 2006 and recaptured 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 is likely to contain a different distribution of behavioural types than the entire population, this has important consequences for design and interpretation of studies of behavioural syndromes and 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-Fiser 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 because of 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 when 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).

Acknowledgments

We thank Jeff Jacobsen, Ryan Kalinowski, Jeff Zirpoli, Christina Rockwell, Lindsay Greene and students in the undergraduate program of Humboldt State University's Wildlife Management Program for assistance during fieldwork. We are also grateful to private landowners and residents throughout Arcata for permission to access their properties for trapping, observations and experiments. P.O.G. is very thankful to her doctoral supervisor Wolf Schröder, who encouraged and enabled the international

cooperation making this study possible. Funding for materials was provided by Humboldt State University's Sponsored Programs Foundation (grant nos 1.57-5712 and D05740).

Supplementary Material

Supplementary material for this article is available in the online version at doi:10.1016/j.anbehav.2010.07.004.

References

- Bell, A. M. & Stamps, J. A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **68**, 1339–1348.
- Biro, P. A. & Dingemanse, N. J. 2008. Sampling bias resulting from animal personality. *Trends in Ecology & Evolution*, **24**, 66–67.
- Black, J. M. 1996. *Partnerships in Birds. The Study of Monogamy*. Oxford: Oxford University Press.
- Black, J. M. & Owen, M. 1987. Determinants of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour*, **102**, 129–146.
- de Bono, M. & Bargmann, C. I. 1998. Natural variation in a neuropeptide Y receptor homolog modifies social behavior and food response in *C. elegans*. *Cell*, **94**, 679–689.
- Both, C., Dingemanse, N. J., Drent, P. J. & Tinbergen, J. M. 2005. Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology*, **74**, 667–674.
- Brand, L. A. & George, T. L. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. *Auk*, **118**, 678–686.
- Briffa, M., Rundle, S. D. & Fryer, A. 2008. Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B*, **275**, 1305–1311.
- Brooker, M. & Rowley, I. 1995. The significance of territory size and quality in the mating strategy of the splendid fairy-wren. *Journal of Animal Ecology*, **64**, 614–627.
- Brown, C. & Braithwaite, V. A. 2004. Size matters: a test of boldness in eight populations of bishop, *Brachyraphis episcopi*. *Animal Behaviour*, **68**, 1325–1329.
- Brown, C., Jones, F. & Braithwaite, V. 2005. In situ examination of boldness—shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, **70**, 1003–1009.
- Brown, J. L. 1963. Aggressiveness, dominance and social organization of the Steller's jay. *Condor*, **65**, 460–484.
- Brylawski, A. M. Z. & Whittingham, L. A. 2004. An experimental study of mate guarding and paternity in house wrens. *Animal Behaviour*, **68**, 1417–1424.
- Buss, D. M. 1995. Psychological sex differences: origins through sexual selection. *American Psychologist*, **50**, 164–168.
- Carere, C., Groothuis, T. G. G., Mostl, E., Daan, S. & Koolhaas, J. M. 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Hormones and Behavior*, **43**, 540–548.
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour*, **50**, 413–429.
- Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*. Hillsdale, New Jersey: L. Erlbaum.
- Cote, J. & Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B*, **274**, 383–390.
- Curio, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypothesis and predictions. *Zeitschrift für Tierpsychologie*, **48**, 175–183.
- Dingemanse, N. J. & Réale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.
- Dingemanse, N., Both, C., Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2002. Repeatability and heritability of exploration behaviour in great tits from the wild. *Animal Behaviour*, **64**, 929–938.
- Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B*, **271**, 847–852.
- Drent, P. J. 2006. Avian personalities: the great tit story. *Journal of Ornithology*, **147**, 6.
- Farwell, M. & McLaughlin, R. L. 2009. Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behavioral Ecology*, **20**, 913–921.
- Fort, K. T. & Otter, K. A. 2004. Territorial breakdown of black-capped chickadees, *Poecile atricapillus*, in disturbed habitats? *Animal Behaviour*, **68**, 407–415.
- Fox, R. A., Ladage, L. D., Roth, T. C. II & Pravosudov, V. V. 2009. Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, **77**, 1441–1448.
- Frost, A. J., Winrow-Giffen, A., Ashley, P. J. & Sneddon, L. U. 2007. Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proceedings of the Royal Society B*, **274**, 333–339.
- Garamszegi, L. Z. 2006. Comparing effect sizes across variables: generalization without the need for Bonferroni correction. *Behavioral Ecology*, **17**, 682–687.
- Garamszegi, L. Z., Erritzøe, J. & Møller, A. P. 2007. Feeding innovations and parasitism in birds. *Biological Journal of the Linnean Society*, **90**, 441–455.

- Garamszegi, L. Z., Eens, M. & Török, J. 2009a. Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Animal Behaviour*, **77**, 803–812.
- Garamszegi, L. Z., Calhim, S., Dochtermann, N., Hegyi, G., Hurd, P. L., Jørgensen, C., Kutsukake, N., Lajeunesse, M. J., Pollard, K. A., Schielzeth, H., Symonds, M. R. E. & Nakagawa, S. 2009b. Changing philosophies and tools for statistical inferences in behavioral ecology. *Behavioral Ecology*, **20**, 1363–1375.
- Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, **127**, 45–86.
- Gowaty, P. A. 1996. Multiple mating by females selects for males that stay: another hypothesis for social monogamy in passerine birds. *Animal Behaviour*, **51**, 482–484.
- Greenberg, R. & Mettke-Hofmann, C. 2001. Ecological aspects of neophobia and neophilia in birds. *Current Ornithology*, **16**, 119–178.
- Greene, E., Davison, W. & Muether, V. R. 1998. Steller's Jay (*Cyanocitta stelleri*). In: *The Birds of North America*, No. 343 (Ed. by A. Poole & F. Gill), pp. 1–20. Ithaca, New York: Cornell Lab of Ornithology.
- Griesser, M. & Ekman, J. 2004. Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, **67**, 933–939.
- Hale, A. M., Williams, D. A. & Rabenold, K. N. 2003. Territoriality and neighbour assessment in brown jays (*Cyanocorax morio*) in Costa Rica. *Auk*, **120**, 446–456.
- Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L. & Arnold, K. E. 2010. Personality in captivity reflects personality in the wild. *Animal Behaviour*, **79**, 835–843.
- Hessing, M. J. C., Hagelso, A. M., van Beek, J. A. M., Wiebkema, P. R., Schouten, W. P. G. & Krukow, R. 1993. Individual behavioural characteristics in pigs. *Applied Animal Behaviour Science*, **37**, 285–295.
- Höjesjö, J., Johnsson, J. I. & Bohlin, T. 2002. Can laboratory studies on dominance predict fitness of young brown trout in the wild? *Behavioral Ecology and Sociobiology*, **52**, 102–108.
- Hope, S. 1980. Call form in relation to function in the Steller's jay. *American Naturalist*, **116**, 788–820.
- Kempenaers, B., Verheyen, G. R., van den Broeck, M., Burke, T., van Broeckhoven, C. & Dhondt, A. A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature*, **357**, 494–496.
- Kralj-Fiser, S., Scheiber, I. B. R., Blejec, A., Moestl, E. & Kotrschal, K. 2007. Individualities in a flock of free-roaming greylag geese: behavioral and physiological consistency over time and across situations. *Hormones and Behavior*, **51**, 239–248.
- Krause, J., Loader, S. P., McDermott, J. & Ruxton, G. D. 1998. Refuge use by fish as a function of body-length related metabolic expenditure and predation risk. *Proceedings of the Royal Society B*, **265**, 2373–2379.
- Kurvers, R. H. J. M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C. & Prins, H. H. T. 2009. Personality differences explain leadership in barnacle geese. *Animal Behaviour*, **78**, 447–453.
- Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- López, P., Hawlena, D., Polo, V., Amo, L. & Martín, J. 2005. Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards. *Animal Behaviour*, **69**, 1–9.
- Malmkvist, J. & Hansen, S. W. 2001. The welfare of farmed mink (*Mustela vison*) in relation to behavioural selection: a review. *Animal Welfare*, **10**, 41–52.
- Markman, S., Pinshow, B. & Wright, J. 2002. The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and offspring care. *Proceedings of the Royal Society B*, **269**, 1931–1938.
- Martins, T. L. F., Roberts, M. L., Giblin, I., Huxham, R. & Evans, M. R. 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Hormones and Behavior*, **52**, 445–453.
- Marzluff, J. M., Milsaugh, J. J., Hurvitz, P. & Handcock, M. S. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology*, **85**, 1411–1427.
- Mettke-Hofmann, C., Winkler, H. & Leisler, B. 2002. The significance of ecological factors for exploration and neophobia in parrots. *Ethology*, **108**, 249–272.
- Mettke-Hofmann, C., Ebert, C., Schmidt, T., Steiger, S. & Stieb, S. 2005. Personality traits in resident and migratory warbler species. *Behaviour*, **142**, 1357–1375.
- Mills, A. D. & Faure, J. M. 2000. Ease of capture in lines of Japanese quail (*Coturnix japonica*) subjected to contrasting selection for fear and sociability. *Applied Animal Behaviour Science*, **69**, 125–134.
- Minderman, J., Reid, J. M., Evans, P. G. H. & Whittingham, M. J. 2009. Personality traits in wild starlings: exploration behavior and environmental sensitivity. *Behavioral Ecology*, **20**, 830–837.
- Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology*, **15**, 1044–1045.
- Nakagawa, S. & Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, **82**, 591–605.
- van Oers, K., Drent, P. J., de Jong, G. & van Noordwijk, A. J. 2004. Additive and nonadditive genetic variation in avian personality traits. *Heredity*, **93**, 496–503.
- van Oers, K., Klunder, M. & Drent, P. J. 2005. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, **16**, 716–723.
- Partridge, L. 1994. Genetic and nongenetic approaches to questions about sexual selection. In: *Quantitative Genetic Studies of Behavioral Evolution* (Ed. by C. R. Boake), pp. 126–141. Chicago: University of Chicago Press.
- Pruitt, J. N. & Riechert, S. E. 2009. Sex matters: sexually dimorphic fitness consequences of a behavioural syndrome. *Animal Behaviour*, **78**, 175–181.
- Pruitt, J. N., Riechert, S. E. & Jones, T. C. 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour*, **76**, 871–879.
- Pyle, P., Howell, S. N. G., Yunick, R. P. & DeSante, D. F. 1987. *Identification Guide to North American Passerines*. 1st edn. Bolinas, California: Slate Creek Press.
- Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A. & Sheldon, B. C. 2009. Heterogeneous selection on a heritable trait in a variable environment. *Journal of Animal Ecology*, **78**, 1203–1215.
- Riechert, S. E. & Hall, R. F. 2000. Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider. *Journal of Evolutionary Biology*, **13**, 541–550.
- Réale, D. & Festa-Bianchet, M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, **65**, 463–470.
- Réale, D., Gallant, B. Y., Leblanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, **60**, 589–597.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.
- Schuett, W. & Dall, S. R. X. 2009. Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, **77**, 1041–1050.
- Sih, A., Bell, A. & Johnson, J. C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.
- Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.
- Sordahl, T. A. 1990. The risks of avian mobbing and distraction behavior: an anecdotal review. *Wilson Bulletin*, **102**, 349–352.
- Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent differences in early exploratory behaviour of male great tits. *Animal Behaviour*, **48**, 1113–1121.
- Verbeek, M. E. M., Boon, A. & Drent, P. J. 1996. Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, **133**, 945–963.
- Westneat, D. F. & Stewart, I. R. K. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 365–396.
- Wilson, D. S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London, Series B*, **353**, 199–205.
- Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. 1993. Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.