

Original Article

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

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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, whereas 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. *Key words*: behavioral syndrome, *Cyanocitta stelleri*, foraging, neophobia, risk-taking, sampling, Steller's jay. [*Behav Ecol* 23:676–683 (2012)]

INTRODUCTION

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 et al. 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 et al. 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 et al. 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 et al. 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 et al. 2003; Van Oers et al. 2004, 2005), and accumulating evidence suggests that natural selection favors contrasting responses under different ecological conditions (Wilson 1998; Dall 2004; Dall et al. 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 et al. 1996; Dingemanse and de Goede

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2004; Minderman et al. 2009), readily investigate novel objects (Webster and Lefebvre 2001), react aggressively toward conspecifics or threats (Verbeek et al. 1996; Dingemanse and de 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).

Although 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 with 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 et al. 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.

Furthermore, body size may be an important factor contributing to an individual's foraging behavior (Wikelski and Trillmich 1994; Barbraud et al. 1999; Weise et al. 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 et al. 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 center 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 3 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 km², 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 nonmigratory, defending territories with vocalizations, and displays throughout the year. They cache items year round for short- and long-term storage (Greene et al. 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 (Black JM and Gabriel PO, 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.

MATERIALS AND METHODS

To locate suitable field experiment sites, we used daily observations in 2009 and previous resighting data to determine pair status and territorial center (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 et al. 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 3 field trials, with minimum 6 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 6 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 et al. 1999). The feeding station

was a 50 cm × 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 center 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 3 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 4 peanuts remained (platform was replenished to 6 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 (Black JM and Gabriel PO, 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 of items taken. Trials lasted 30 min; if jays removed all items, we replenished the choice set back to 6 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 (minute) to perform each of the following behaviors in the 30-min trial: coming within 10, 5, 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, whereas 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 reenter.

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 2–11 years ($X + \text{standard error [SE]} = 4.0 + 0.23$).

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 3 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 4, 5, or 6 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 2 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 3 months and a longer period of 1 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 gage the relative importance of the 3 factors (behavior type, age, and body size) on the 3 foraging behaviors (average sample actions, average visit duration, and taking multiple items). We constructed 14 models using 5 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 (GLMs), 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 2 or 3 nuts in one or more visits. We ranked both sets of models according to corrected Akaike Information Criterion (AICc). We gaged 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 ($1 - \text{specificity}$). 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 reentry 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 2 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 2 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%), whereas 2 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: $r_s = 0.72$, degrees of freedom [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 2 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

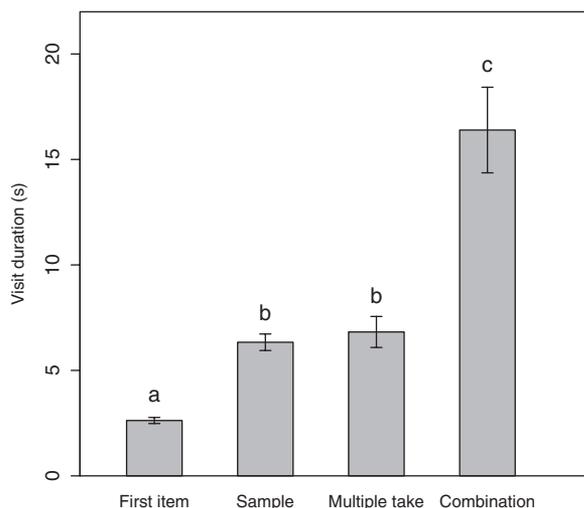


Figure 1

Average visit duration (s) \pm 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 2 or more items before choosing ($n = 62$), removing 2 or more items simultaneously ($n = 19$), or a combination of sampling and taking multiple items ($n = 22$). Letters depict which groups were statistically different.

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 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 and 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 to 0.637, $n = 11$). Individual average visit duration did not differ with the predator mount present compared with absent ($r = 0.104$, 95% CI = –0.186 to 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 to 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 5 variables of the full model (Table 1). Initial platform latency and age each had approximately 1.3 times more Akaike weight than the 3 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 2 AICc points greater than 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.

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-averse jays ($r_s = 0.442$, 95% CI = 0.168–0.648, df = 46; Figure 2b).

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

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) + PCI + sex	0.00	0.66	6
Log(platform latency) + log(age)	2.17	0.22	3
Log(platform latency) + PCI + sex	5.04	0.05	4
Log(risk-taking) + log(age) + PCI	6.00	0.03	4
Log(risk-taking) + log(age)	7.36	0.02	3
Log(risk-taking) + PCI	11.29	0.00	3
Take multiple items			
Risk-taking + age	0.00	0.32	3
Age	0.14	0.29	2
Risk-taking + age + PCI	2.18	0.11	4
Age + PCI	2.24	0.10	3
Age + PCI + sex	4.62	0.03	4
Risk-taking	4.96	0.03	2

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

(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 reentry 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 to 0.608, $n = 39$) than birds that avoided entering the trap.

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, whereas 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 ob-

served 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 2 foraging behaviors to the established syndrome. Birds that took greater risks at the familiar trap sampled more and tended

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 (PCI)	0.76	0.30
Sex	0.72	0.08

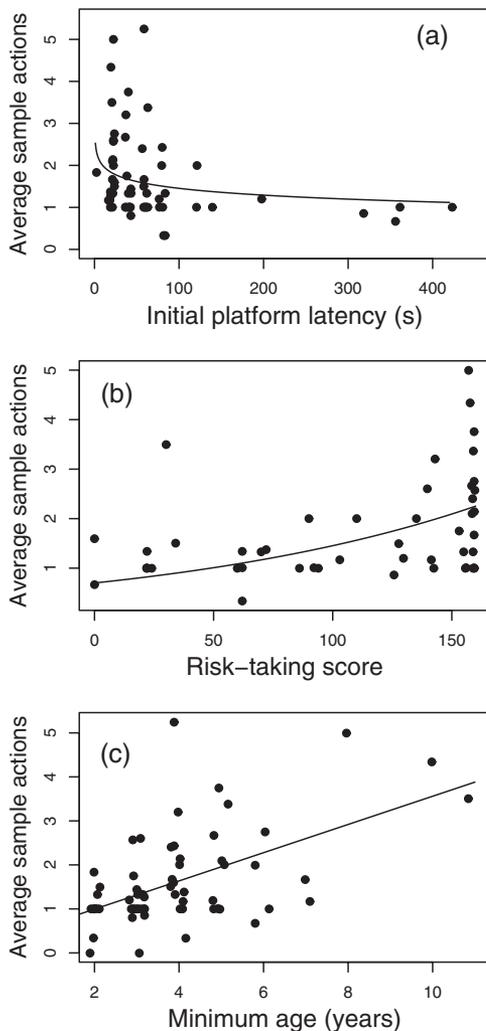


Figure 2
Relationship between individuals' average number of sample actions for Steller's jays in relation to (a) neophobia: latency (s) to approach a novel feeding platform ($n = 62$), (b) risk-taking score: response to a raccoon mount ($n = 48$), and (c) bird age in years ($n = 63$).

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 with 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.

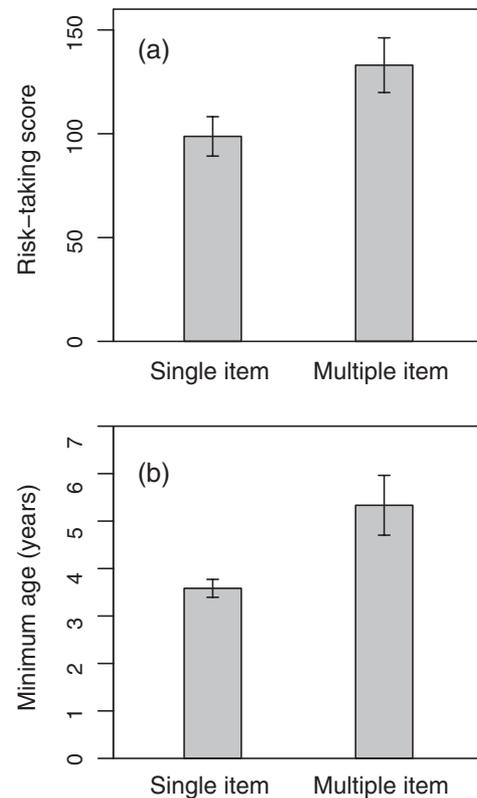


Figure 3
Comparison of Steller's jays that took a single item in all visits with jays that took multiple items in one or more visits for (a) risk-taking score ($n = 35, 13$; $\bar{X} \pm \text{SE}$) and (b) age ($n = 48, 15$; $\bar{X} \pm \text{SE}$).

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 2 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 et al. 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 et al. 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 2 peanuts and carrying them in the bill (Gabriel PO and Rockwell C, personal observation). The majority of jays were apparently capable of carrying 2 peanuts (Rockwell C, 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 gaging 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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REFERENCES

Alatalo RV, Moreno J. 1987. Body size, interspecific interactions, and use of foraging sites in tits (Paridae). *Ecology*. 68:1773–1777.

Barbraud C, Weimerskirch H, Robertson GG, Jouventin P. 1999. Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). *J Anim Ecol*. 68:1179–1192.

Bekoff M, Allen C, Grant MC. 1999. Feeding decisions by Steller's jays (*Cyanocitta stelleri*): the utility of a logistic regression model for analyses of where, what, and with whom to eat. *Ethology*. 105:393–406.

Biondi LM, Bó MS, Vassalo AI. 2010. Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Mikvago chimango*). *Anim Cogn*. 13:701–710.

Black JM, Prop J, Larsson K. 2007. Wild goose dilemmas. Groningen, The Netherlands: Branta Press.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am Nat*. 161:1–28.

Brown JL. 1963. Aggressiveness, dominance and social organization in the Steller jay. *Condor*. 65:460–484.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed.. New York: Springer-Verlag.

Cohen J. 1988. Statistical power analysis for the behavioral sciences. Hillsdale (NJ): L. Erlbaum.

Coleman K, Wilson DS. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim Behav*. 56:927–936.

Dall SRX. 2004. Behavioral biology: fortune favours bold and shy personalities. *Curr Biol*. 14:470–472.

Dall SRX, Houston AI, McNamara JM. 2004. The behavioral ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett*. 7:734–739.

Dall SRX, McNamara JM, Cuthill IC. 1999. Interruptions to foraging and learning in a changing environment. *Anim Behav*. 57:233–241.

Desrochers A. 1992. Age-related differences in reproduction by European blackbirds: restraint or constraint? *Ecology*. 73:1128–1131.

Dingemanse NJ, Both C, Drent PJ, van Oers K, van Noordwijk AJ. 2002. Repeatability and heritability of exploratory behavior in great tits from the wild. *Anim Behav*. 64:929–938.

Dingemanse NJ, de Goede P. 2004. The relationship between dominance and exploratory behavior is context-dependent in wild great tits. *Behav Ecol*. 15:1023–1030.

Dingemanse NJ, Réale D. 2005. Natural selection and animal personality. *Behaviour*. 142:1165–1190.

Drent PJ, van Oers K, van Noordwijk AJ. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proc R Soc Lond B Biol Sci*. 270:45–51.

Farwell M, McLaughlin RL. 2009. Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behav Ecol*. 20:913–921.

Gabriel PO, Black JM. 2010. Behavioral syndrome in Steller's jays: the role of time frames in the assessment of behavioral traits. *Anim Behav*. 80:689–697.

Greenberg R. 2003. The role of neophobia and neophilia in the development of innovative behavior of birds. In: Reader SM, Laland KN, editors. *Animal innovation*. Oxford: Oxford University Press. p. 175–196.

Greenberg R, Mettke-Hofmann C. 2001. Ecological aspects of neophobia and neophilia in birds. *Curr Ornithol*. 16:119–178.

Greene E, Davison W, Muehter V. 1998. Steller's jay (*Cyanocitta stelleri*), no. 343. In: Poole A, Gill F, editors. *The birds of North America*. Washington DC: Academy of Natural Sciences and American Ornithologists' Union. p. 1–20.

Heinrich B. 1995. Neophilia and exploration in juvenile common ravens, *Corvus corax*. *Anim Behav*. 50:695–50704.

Heinrich B, Joerg CC, Madden SS, Sanders EW Jr. 1997. Black-capped chickadees and red-breasted nuthatches "weigh" sunflower seeds. *Auk*. 114:298–299.

Heise CD, Moore FR. 2003. Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration. *Condor*. 105:496–504.

Herborn KA, Macleod R, Miles WTS, Schofield ANB, Alexander L, Arnold KE. 2010. Personality in captivity reflects personality in the wild. *Anim Behav*. 79:835–843.

Jansan A. 1989. Acquisition of foraging skills by Heron Island silver-eyes *Zosterops lateralis chlorocephala*. *Ibis*. 132:95–101.

Johnson JC, Sih A. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Anim Behav*. 74:1131–1138.

Kacelnik A. 1984. Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *J Anim Ecol*. 53:283–299.

Kontianen P, Pietiäinen H, Huttunen K, Karell P, Kolunen H, Brommer JE. 2009. Aggressive Ural owl mothers recruit more offspring. *Behav Ecol*. 20:789–796.

Krebs JR, Erichsen JT, Webber ML, Charnov EL. 1977. Optimal prey selection in the great tit (*Parus major*). *Anim Behav*. 25:30–38.

Kurvers RH, Prins HH, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC. 2010. The effect of personality on social foraging:

- shy barnacle geese scrounge more. *Proc R Soc Lond B Biol Sci.* 277:601–607.
- LaBarbera M. 1989. Analyzing body size as a factor in ecology and evolution. *Annu Rev Ecol Syst.* 20:97–117.
- Lang A, Black JM. 2001. Foraging efficiency in barnacle geese: a functional response to sward height and an analysis of sources of individual variation. *Wildfowl.* 52:7–20.
- Langen TA. 1999. How western scrub-jays (*Aphelocoma californica*) select a nut: effects of the number of options, variation in nut size, and social competition among foragers. *Anim Cogn.* 2:223–233.
- Langen TA, Gibson RM. 1998. Sampling and information acquisition by western scrub-jays, *Aphelocoma californica*. *Anim Behav.* 55:1245–1254.
- Lemon WC, Barth RH Jr. 1992. The effects of feeding rate on reproductive success in the zebra finch, *Taeniopygia guttata*. *Anim Behav.* 44:851–857.
- Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities: a common mistake. *Auk.* 104:116–121.
- Ligon JD, Martin DJ. 1974. Piñon seed assessment by the piñon jay, *Gymnorhinus cyanocephalus*. *Anim Behav.* 22:421–429.
- López P, Hawlena D, Polo V, Amo L, Martin J. 2005. Sources of individual shy-bold variations in antipredator behavior of male Iberian rock lizards. *Anim Behav.* 69:1–9.
- Marchetti C, Drent PJ. 2000. Individual differences in the use of social learning in foraging by captive great tits. *Anim Behav.* 60:131–140.
- Marzluff JM, Millsbaugh JJ, Hurvitz P, Handcock MS. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology.* 85:1411–1427.
- Marzluff JM, Neatherlin E. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biol Conserve.* 130:301–314.
- McElreath R, Strimling P. 2006. How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Anim Behav.* 72:1135–1139.
- Minderman J, Reid JM, Evans PGH, Whittingham MJ. 2009. Personality traits in wild starlings: exploration behavior and environmental sensitivity. *Behav Ecol.* 20:830–837.
- Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol Rev.* 82:591–605.
- Partridge L. 1976. Individual differences in feeding efficiencies and feeding preferences of captive great tits. *Anim Behav.* 24:230–240.
- Pyke GH, Pulliam HR, Charnov EL. 1977. Optimal foraging: a selective review of theory and tests. *Q Rev Biol.* 52:137–154.
- Quinn JL, Cresswell W. 2005. Personality, anti-predatory behavior, and behavioral plasticity in the chaffinch *Fringilla coelebs*. *Behaviour.* 142:1377–1402.
- R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Richardson H, Verbeek NAM. 1987. Diet selection by yearling north-western crows (*Corvus caurinus*) feeding on littleneck clams (*Venerupis japonica*). *Auk.* 104:263–269.
- Richner H. 1989. Phenotypic correlates of dominance in carrion crows and their effects on access to food. *Anim Behav.* 38:606–612.
- Rising JD, Somers KM. 1989. The measurement of overall body size in birds. *Auk.* 106:666–674.
- Ritchie ME. 1990. Optimal foraging and fitness in Columbian ground squirrels. *Oecologia.* 82:56–67.
- Schoener TW. 1971. Theory of feeding strategies. *Annu Rev Ecol Syst.* 2:369–404.
- Short KH, Petren K. 2008. Boldness underlies foraging success of invasive *Lepidodactylus lugubris* geckos in the human landscape. *Anim Behav.* 76:429–437.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol.* 19:372–378.
- Stephens DW, Krebs JR. 1986. Foraging theory. Princeton (NJ): Princeton University Press.
- Van Buskirk J, Smith DC. 1989. Individual variation in winter foraging of black-capped chickadees. *Behav Ecol Sociobiol.* 24:257–263.
- Van Oers K, Drent PJ, de Goede P, van Noordwijk AJ. 2004. Realized heritability and repeatability of risk-taking behavior in relation to avian personalities. *Proc R Soc Lond B Biol Sci.* 271:65–73.
- Van Oers K, Klunder M, Drent PJ. 2005. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behav Ecol.* 16:716–723.
- Verbeek MEM, Boon A, Drent PJ. 1996. Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour.* 133:945–963.
- Waite TA, Ydenberg RC. 1994. What currency do scatter-hoarding gray jays maximize? *Behav Ecol Sociobiol.* 34:43–49.
- Webster SJ, Lefebvre L. 2001. Problem-solving and neophobia in a columbiform-passeriform assemblage in Barbados. *Anim Behav.* 62:23–32.
- Weise MJ, Harvey JT, Costa DP. 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology.* 91:1004–1015.
- Wheelwright NT, Templeton JJ. 2003. Development of foraging skills and the transition to independence in juvenile savannah sparrows. *Condor.* 105:279–287.
- Wikelski M, Trillmich F. 1994. Foraging strategies of the Galapagos marine iguana (*Amblyrhynchus cristatus*): adapting behavioral rules to ontogenetic size change. *Behaviour.* 128:255–279.
- Wilson DS. 1998. Adaptive individual differences within single populations. *Philos Trans R Soc B-Biol Sci.* 353:199–205.