

Foraging dynamics in Steller's jays: size and viability of cacheable food items



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Several species of birds and mammals cache food items, which in harsh conditions may translate into improved survival or reproductive success. Animals may benefit from evaluating the quality of cache items in terms of size, nutrition and storage viability. Steller's jays, *Cyanocitta stelleri*, which cache seeds for later consumption, may handle multiple food items with their beak prior to making a selection. By picking items up, individuals may use visual and tactile cues to evaluate size and shell condition. The number of items an individual jay handles is repeatable, reflecting consistent individual-specific foraging behaviours that may differentiate success at selecting high-quality cache items. In this study we quantified population-level preferences for food items based on size and shell integrity, and individual Steller's jay sampling behaviour when presented with these choices. Using field trials with free-ranging subjects, we quantified sampling frequency in a variety of choice tests and measured individuals' success at choosing higher-quality items. We found that Steller's jays selected items of greater weight and items with intact shells, and preferences for these properties were of comparable magnitude. Jays sampled more nuts during choice sets involving cracked and intact shells, resulting in individuals selecting more profitable nuts for caching. These results may suggest that Steller's jays evaluate cache items based on both current and future expected energetic values, and that sampling behaviour may enable them to choose more valuable forage items.

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Caching food items for later consumption is a specialized behaviour observed in some bird and mammal species, allowing individuals to exploit abundant yet ephemeral resources (Vander Wall 1990). Use of caches potentially translates into improved reproductive success or increased survival during harsh conditions (Vander Wall 1990). Keeping track of multiple caches requires a large and refined spatial memory that is likely a result of adaptations in brain morphology and function driven by life history demands (Sherry et al. 1989; Sherry & Hoshooey 2010). Aside from the demands of relocating caches, an individual may benefit from evaluating the quality of food items in terms of nutrition and viability while in storage. Western scrub-jays, *Aphelocoma californica*, and Steller's jays, *Cyanocitta stelleri*, sample multiple food items before choosing items for caching (Langen & Gibson 1998; Langen 1999; Rockwell et al. 2012), and several studies across a range of species have demonstrated that individuals preferentially choose larger items to cache (Heinrich et al. 1997; Jansen et al.

2004; Vander Wall 2008; Zhang et al. 2008). The spoiling of cached nuts and seeds caused by insects and fungus diminishes the cacher's benefit (Frank 1988; Gendron & Reichman 1995; Gerber et al. 2004). The perishability hypothesis suggests that animals make optimal decisions based not only on immediate rewards but on storage durability of food items (Hadj-Chikh et al. 1996). This hypothesis has been tested using seeds with different germination times or physical traits (Scarlett & Smith 1991; Hadj-Chikh et al. 1996; Smallwood et al. 2001; Moore & Swihart 2006; Pons & Pausas 2007) and with seeds from the same species but of differing characteristics (Bossema 1979; Steele et al. 1996; Dixon et al. 1997; Cristol 2001). Yet few studies have examined preferences for item size and item perishability within the same experiment.

In a previous study, the number of times that individual Steller's jays handled food items with their beaks prior to a final choice was moderately predictable, reflecting consistent individual-specific foraging tactics (Rockwell et al. 2012). A jay that samples multiple nuts may gather visual and tactile information on weight and shell integrity, while one that takes the first item handled makes a less informed decision but saves time. Heinrich et al. (1997) and Langen (1999) examined sampling behaviour in relation to item size but did not test shell integrity, which may influence the viability of the cached item. In this study we quantified population-level

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preferences for food items varying in size and shell integrity, and determined free-ranging Steller's jay sampling behaviour when presented with these choices. We tested viability over time for cached items with intact and cracked shells using simulated caches, which enabled us to evaluate expected energetic costs and payoffs when coupled with foraging trials. We comment on the optimality of individual Steller's jay's decisions in the context of sampling and how this relates to other phenotypic and life history characteristics (age, body size and sex). If sampling behaviour enables jays to assess item quality, we predicted that birds that sampled more items would choose the best class of nut more often than birds that showed little or no sampling behaviour.

METHODS

We studied foraging behaviour in free-ranging Steller's jays on the Humboldt State University campus and surrounding residential areas of Arcata, CA, U.S.A. (40°59'N, 124°06'W). The study area was 2.2 km², bordered to the east by forest dominated by California redwood (*Sequoia sempervirens*). Steller's jays cache items year round for short- and long-term storage, to be retrieved and consumed at a later time (Greene et al. 1998). They are a useful species for behavioural studies, as they are relatively tolerant of human proximity, allowing close behavioural examination. The local nonmigratory population of Steller's jays was part of an annual banding programme since 1998, in which all birds wore a unique combination of colour leg bands (Gabriel & Black 2010, 2012). Year-round band resightings in 2009 and resighting data from previous years were used to determine pair status and territory occupancy of approximately 45 breeding pairs and 30–40 nonterritorial individuals. Birds received a wild bird seed mix including peanuts in the shell, sunflower seeds and millet from 21 feeder traps distributed across the study area in addition to feeders provided by local landowners. Details on trapping techniques and population monitoring are described in the methods of Rockwell et al. (2012).

Foraging Trials

We used peanuts in the shell as food items in all field experiments as a surrogate for acorns, a natural cache item in parts of the Steller's jay geographical range (Greene et al. 1998). Peanuts are protein-rich and highly sought-after cache items for Steller's jays, allowing us to maintain continual and repeated participation throughout trials despite the free-roaming status of subjects. A Steller's jay that procured a peanut typically flew out of sight of other jays to cache. A jay typically cached a peanut by pushing the nut beneath the soil surface and covering the exposed end with soil or leaves. At times a jay hulled and ate the nut or cached the cotyledons; in all observations of hulling behaviour the jay flew to a nearby perch and the shell breaking was clearly audible.

For the foraging trials, each jay was presented with an experimental feeding station within its territory. The feeding station was a 50 × 50 cm wooden platform with a 3 cm high rim, placed on the ground 5 m from cover (Rockwell et al. 2012). Six peanuts were evenly spaced within a 15 cm diameter circle on the platform. Peanuts were concealed under a Styrofoam dome until the trial's initiation. A single observer (C. Rockwell) stood 15 m from the feeding station. Baseline trials consisted of three trials per bird, beginning 16 October 2009, where all six nuts were the same size and shell integrity class (Table 1). A series of choice tests, in which two classes of nut size or integrity were available, were initiated upon the completion of baseline trials. These choice tests were conducted from 5 December 2009 to 30 March 2010. Each bird was offered three nuts each of two different sizes or shell integrities,

Table 1

Masses and shell conditions of peanuts offered to 60 Steller's jays in Arcata, CA during field trials to measure forage item preferences and jay sampling behaviour

	Class 1		Class 2	
	Mass (g)	Integrity	Mass (g)	Integrity
Baseline test	2.40±0.20	Intact	—	—
Choice test				
Medium vs small	2.40±0.20	Intact	1.60±0.20	Intact
Large vs medium	2.95±0.15	Intact	2.35±0.15	Intact
Intact vs cracked	2.40±0.20	Intact	2.40±0.20	Cracked
Medium intact vs large cracked	2.35±0.15	Intact	2.95±0.15	Cracked

The choice set in the baseline trials consisted of six intact peanuts of similar size. Each of the four choice tests consisted of three peanuts from Class 1 and three peanuts from Class 2. Small peanuts were single-chambered nuts; medium and large peanuts were double-chambered nuts. Cracked peanuts had their shells split 50–65% along their lengths.

including medium (two-chambered peanuts) and small (one-chambered peanuts), large (two-chambered peanuts) and medium, or peanuts with intact and cracked shells (Table 1). The fourth choice test was a trade-off between size and shell integrity, using three medium-sized nuts with intact shells and three large nuts with cracked shells (Table 1). In choice tests, the three peanuts of one class were arranged on the platform to alternate with the three peanuts of the second class to ensure equal availability of both classes regardless of a jay's direction of approach.

We recorded the duration of each visit to the platform, the number of times a bird picked up a peanut in its beak (i.e. sample actions) and the total number of items it carried away. It was plausible that a jay's choice of an intact peanut or a cracked one depended on whether the item was intended for caching or immediate consumption, which would complicate determination of preferred nut condition. We noted whether a jay hulled the peanut directly after it left the platform. During choice tests the observer approached the platform immediately following a bird's departure to determine the class of item(s) taken. The observer replaced the missing item(s) and recorded the same information for the bird's successive visits. The trial continued until the bird had visited the platform six times or 30 min had passed.

When the bird's mate was within 15 m of the platform during the trial, we distracted the mate away with a peanut so the focal bird's visit would not be influenced. If nonresident birds approached, we either distracted the visitor as above or, if this was unsuccessful, ended the trial. The sequence of experiments was kept constant for all individuals: three baseline trials followed by one trial each for medium versus small, intact versus cracked, medium intact versus large cracked, and finally large versus medium choice tests. Each bird participated in at most one trial per day, with at least 6 days between trials. Trials could be repeated as necessary to record a minimum of four visits per choice test with no other birds present (within 15 m of the platform).

Cache Item Viability

To test whether intact food items had longer viability than cracked items when cached in the local environment, we buried pairs of intact and cracked peanuts on 2 January and 8 February 2010 to simulate observed depth and location of caches. Three cache simulation sites were selected within the boundaries of the Arcata Community Forest, dominated by California redwood in the overstory with sword fern (*Polystichum munitum*) and redwood sorrel (*Oxalis oregana*) dominant ground cover. Local temperatures from January to March 2010 averaged 9.7 °C (range 3.9–14.4 °C) and precipitation averaged 0.66 cm/day (range 0–4.7 cm/day). Sites were under redwood canopy less than 50 m from forest edge.

To imitate jay caches, we buried peanuts 1–2 cm beneath the soil surface inside soil-filled enclosures, in three rows 4.5 m apart parallel to slope. Enclosures were made of wire mesh screen (30.5 × 7.6 × 7.6 cm), each containing two intact and two cracked peanuts (mass known to 0.01 g) spaced 7.6 cm apart. We buried 42 pairs in the January session, collecting a third of the enclosures each at 1-, 2- and 4-week intervals. In February we buried 66 pairs and collected enclosures at 2-, 4- and 8-week intervals. We removed the cotyledons from the shells and counted any arthropod adults or larva detected. After 2 days of ambient drying, cotyledons were placed in a Fisher Scientific Isotemp Oven 637G at 70 °C for 24 h. Dried cotyledons were weighed to the nearest 0.001 g.

Statistical Analyses

We determined population-wide preferences for nut size and condition based on visits in which one peanut was taken. Using chi-square proportion tests, we compared the total number taken of the two classes presented in each of the four choice tests. We used a Fisher's exact test to determine tendency to hull cracked versus intact nuts.

Each bird's sample actions and visit durations were averaged across visits in the baseline trial and for each choice test experiment (sensu Rockwell et al. 2012); we used Wilcoxon signed-ranks tests to compare the average number of items individuals sampled during each choice test with their average sample actions from the baseline trials. Repeatability of foraging behaviour across experiments, a measure of variation within an individual compared to variation among individuals, was determined with a one-way ANOVA derivation (Lessells & Boag 1987). Repeatability estimates range from 0 to 1, with 1 meaning no variation within individuals. In animal behaviour studies, values greater than 0.25 are typically interpreted as moderately repeatable and values greater than 0.50 as highly repeatable (Dingemans & Réale 2005).

To determine whether birds made optimal choices, we needed to assess which food items were most valuable. Larger items predictably provide more energy, but we needed to compare intact and cracked peanuts after accounting for caching. In particular, we wanted to determine whether medium intact nuts or large cracked nuts would have more mass after caching. Initial masses of cotyledons inside sown peanuts were unknown. Based on whole nut mass (m_w) and dried cotyledon mass (m_c) of 250 unburied peanuts (2.100–3.200 g), we constructed a linear regression to predict cotyledon mass of cached peanuts prior to their burial: $m_c = 0.032 + 0.74 \times m_w$. We used the ratio of actual post-burial cotyledon mass and projected pre-burial cotyledon mass in a two-way factorial ANOVA to compare the effects of time and shell condition on decomposition rate and the dipteran larva abundance inside the peanuts. We assumed a constant decomposition rate across all initial nut sizes.

To incorporate economic costs into our considerations for optimal foraging choices, we calculated the expected payoff for maximizing storage rate similar to Langen & Gibson (1998), in which expected payoff = energy/(handling time + travel time). In our experiment, energy was the predicted total mass of peanut cotyledons taken during the trial, handling time was the sum of visit durations at the feeding platform during the trial, and travel time was handling time subtracted from total trial duration, which encompassed time to cache the peanuts and travel back and forth to the platform. While all other analyses operated at the visit level, using trial duration meant we could only use trials with little to no participation from birds other than the focal bird so that travel time was comparable across trials. Presence of a mate or neighbour in the general area may influence the distance a Steller's jay travels to cache items (R. Kalinowski, P. O. Gabriel & J. M. Black, unpublished data).

Using data from baseline trials with similar peanuts, we used a Wilcoxon two-sample test to compare time spent handling peanuts to time spent caching and travelling to the platform. Using data from variation trials, we calculated two expected average payoffs of caching medium intact and large cracked nuts, including a brief cache duration (1 week) and a long cache duration (8 weeks). This allowed us to determine the more optimal choice in the absence of a clear preference shown by the tested jay population. We tested for correlations between the expected payoff and the proportion of large cracked nuts taken using Spearman rank correlations, then Wilcoxon two-sample tests to compare individuals that chose more than 60% large cracked nuts against those that chose more than 60% medium intact nuts.

Individual jays' optimality scores for the four choice tests were calculated as the proportion of visits a bird chose the more profitable option (i.e. class of nuts with greater mass, intact condition, or greater payoff). We considered large cracked items more profitable than medium intact items, although superiority of large cracked nuts diminished over long cache durations. We used Spearman rank correlations to test for relationships between optimality scores and average sample actions, average visit time, age and body size. To account for the possibility that existing relationships may not be linear and may operate more at the extreme ends of the spectrum, we also grouped birds into 'good' choosers (optimality score >0.60) and 'poor' choosers (optimality score <0.40) for each choice test, as we did for the expected payoff analysis. This approach omitted birds with optimality scores approaching 0.50 for a given scenario. Since optimality was universally high for the medium versus small choice test, we grouped birds as >0.80 or <0.60 to increase sample size in the 'poor' group. We compared average sample actions, average visit time, body size and age of 'good' versus 'poor' choosers in each choice test with Wilcoxon two-sample tests. Minimum age of each bird was determined from banding data for the population (Gabriel & Black 2010). The body size measure was a principal component (PC) combining wing, tarsometatarsus and gape lengths to the nearest 0.01 mm; PC1 accounted for 71% of total variance. We tested whether optimality scores were related to sex with Wilcoxon two-sample tests and whether optimality scores were similar between pair bond partners using Wilcoxon signed-ranks tests. We only used two-tailed tests. Statistical tests were performed in program R 2.7.2 (R Development Core Team 2008).

Ethical Note

All study practices were conducted with appropriate licenses for the capture and marking of birds, and were approved by Humboldt State University's Institutional Animal Care and Use Committee (Protocol 08/09.W.39.A). The experiments in this study did not require capturing individuals, as they were designed to assess natural behaviours without the potential stressors of a captive environment. However, each bird in this study had been previously captured at least once for colour-marking and morphological measurements. Time in captivity was kept to a minimum, with birds released typically within 30–45 min after capture.

RESULTS

Item Preference and Selectivity

Sixty adult, territorial Steller's jays (34 males and 26 females) were tested in baseline foraging trials and four sets of choice tests. Only 52 of these birds participated in the large versus medium choice test. Of visits in which a single nut was taken (90.8% of all visits), birds selected medium (double-chambered) nuts over small

(single-chambered) nuts at a ratio of 10.3 to 1 (chi-square test: $\chi_1^2 = 198.5$, $N = 295$, $P < 0.001$; Fig. 1a). Birds chose large nuts over medium nuts (2.5:1; $\chi_1^2 = 52.5$, $N = 288$, $P < 0.001$; Fig. 1b) and intact nuts over cracked nuts (2.5:1; $\chi_1^2 = 52.8$, $N = 296$, $P < 0.001$; Fig. 1c). Birds showed no preference for medium intact nuts compared to large cracked nuts (1:1; $\chi_1^2 = 0.0$, $N = 318$, $P = 1.00$; Fig. 1d). Peanuts with cracked shells were immediately hulled marginally more frequently than intact nuts (4% versus 1%, respectively, of $N = 613$ total nuts; $N = 13$ hulled; Fisher's exact test: $P = 0.04$).

Increased variation between peanut classes (size and shell integrity) led to increased sampling activity in some but not all experimental scenarios. Individuals sampled significantly more peanuts during the intact shell versus cracked and the medium intact versus large cracked choice tests compared to baseline trials (Wilcoxon signed-ranks test: $T = 995$, $N = 59$, $P < 0.001$; $T = 831$, $N = 57$, $P = 0.001$, respectively). Unlike the other choice experiments, sampling behaviour during the medium intact versus large cracked choice test was directly related to item choice. A disproportionate number of visits in which large cracked nuts were chosen involved sampling, while medium intact nuts were chosen more frequently in visits without sampling ($\chi_1^2 = 5.7$, $P = 0.017$; Fig. 1d). Across baseline trials and the four choice experiments, the number of items sampled and the average visit duration were highly repeatable within individuals (repeatability for sampling: $r = 0.50$; visit duration: $r = 0.59$). Visit duration was strongly correlated with sample actions in all five scenarios (Spearman rank correlation: $r_s = 0.76$ – 0.88 , $N = 51$ – 60 , all $P < 0.001$).

Optimality

Based on predictions of initial weights, lost cotyledon mass of cached nuts was dependent on integrity of the outer shell (ANOVA: $F_{1,102} = 35.6$, $P < 0.001$), burial duration ($F_{3,102} = 39.7$, $P < 0.001$), and the interaction of shell integrity and burial duration ($F_{3,102} = 13.5$, $P < 0.001$; Fig. 2). Difference in mass between buried pairs of intact and cracked nuts was greatest after 8 weeks in the ground (Wilcoxon signed-ranks test: $T = 120$, $N = 30$, $P < 0.001$). Numbers of dipteran larvae detected within a peanut ranged from 0 to 45. Number of larvae increased with burial time (ANOVA: $F_{3,112} = 4.9$, $P = 0.003$), but not by initial shell integrity ($F_{1,112} = 2.4$, $P = 0.12$). Based on the linear model of average post-burial mass, assuming decomposition rate to be independent of initial mass, large cracked nuts would be projected to weigh more (1.71–1.93 g)

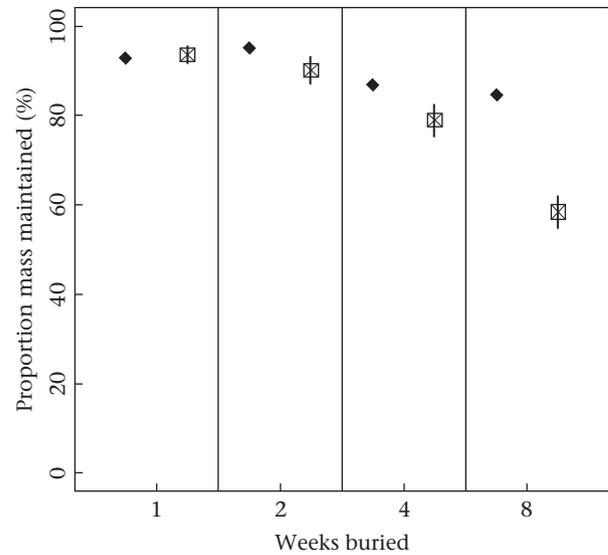


Figure 2. Fifty-six pairs of peanuts consisting of one intact peanut (black diamonds) and one peanut cracked 50–65% along its length (white squares) were buried as artificial caches at the redwood forest edge in Arcata, CA. The masses of unearthed cotyledons (mean \pm SE) after 1, 2, 4 and 8 weeks were compared to predicted masses prior to burial to determine the proportion of mass maintained.

4 weeks after caching than medium intact nuts (1.41–1.63 g), even though the cracked nuts would proportionately lose more mass. Yet after 8 weeks in a cache, we would predict the large cracked nuts to deteriorate to similar masses (1.34–1.56 g) as the medium intact nuts (1.37–1.60 g).

The energy in joules gained is only one component that determines the final energetic payoff for a jay. Using data from baseline trials (peanuts similar) for jays that were alone during the entire trial, we found that jays spent significantly more time caching and travelling between visits to the platform than they did selecting a peanut (Wilcoxon two-sample test: $W = 0$, $N = 21$, $P < 0.001$). Expected payoff declined as travel time increased, while handling time was a comparatively minor cost for the jays (Fig. 3).

Jay preference between medium intact nuts and large cracked nuts was similar (Fig. 1d). Therefore, we evaluated the optimal peanut class by calculating the expected payoff from nuts chosen during this trial after caching for 1 week and after caching for

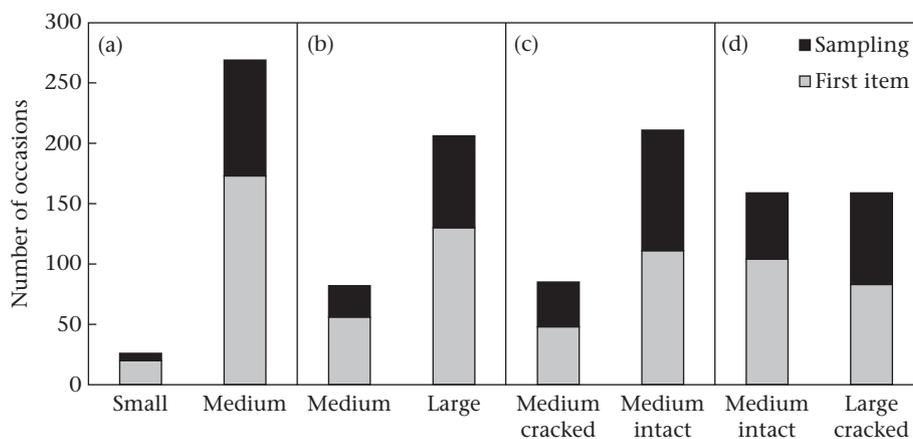


Figure 1. Total number of peanuts chosen across four choice tests, each with two classes of peanuts presented to Steller's jays ($N = 52$ – 60), and presence or absence of sampling behaviour during each visit: (a) small intact and medium intact nuts, (b) medium intact and large intact nuts, (c) medium cracked and medium intact nuts, (d) medium intact and large cracked nuts.

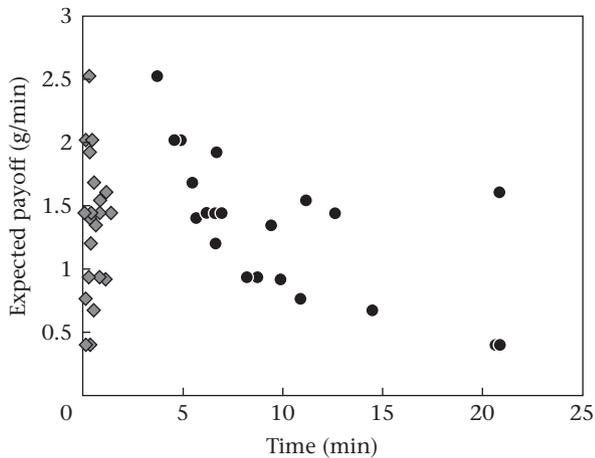


Figure 3. Expected payoff (grams of edible cotyledon per minute of effort) for 21 Steller's jays after caching items for 1 week, based on trials with similar-sized peanuts in which the jay was alone throughout the trial. Time costs of handling (grey triangles) and caching/travel (black circles) are displayed as separate components of expected payoff.

8 weeks. The expected payoff was not significantly correlated with the proportion of large cracked nuts taken under scenarios of 1 week (Spearman rank correlation: $r_s = 0.34$, $N = 11$, $P = 0.166$) or 8 weeks ($r_s = 0.21$, $N = 11$, $P = 0.409$). When we omitted the non-discriminating jays and compared those that preferentially selected medium intact nuts or large cracked nuts, there was a significantly greater expected payoff to choose large cracked nuts over medium intact nuts if cached for 1 week (Wilcoxon two-sample test: $W = 1$, $N = 11$, $P = 0.018$; Fig. 4). The payoff did not persist to the eighth week after the large cracked nuts substantially deteriorated ($W = 4$, $N = 11$, $P = 0.072$).

Individual optimality scores that we derived from the proportion of the more profitable item class chosen (possible range 0.0–1.0) were highest when choosing between medium and small nuts (mean \pm SE = 0.91 ± 0.02). Optimality scores were the same when choosing large over medium nuts and when choosing intact over cracked nuts (mean \pm SE = 0.69 ± 0.03). Optimality scores were lowest in the medium intact versus large cracked trial (mean \pm SE = 0.49 ± 0.03). In the intact versus cracked experiment, the proportion of intact items chosen was positively correlated with

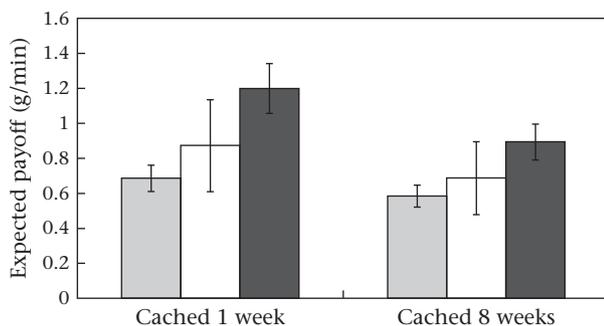


Figure 4. Average expected payoff (mean \pm SE) in grams of peanut cotyledon per minute of effort based on Steller's jay performance during a choice test between medium intact versus large cracked peanuts ($N = 18$ jays) from nuts cached for 1 week and nuts cached for 8 weeks. Effort included time handling the peanuts and caching the chosen nut. It does not factor in time spent retrieving the cache. Pale grey bars: jays that chose medium intact peanuts in more than 60% of visits ($N = 7$); white bars: jays that chose large cracked and medium intact nuts in similar proportions ($N = 7$); dark grey bars: jays that chose large cracked peanuts in more than 60% of visits ($N = 4$).

number of items sampled (Spearman rank correlation: $r_s = 0.28$, $N = 58$, $P = 0.035$). There were no other relationships among optimality scores and number of items sampled, visit duration, bird's age, or its body size ($r_s = -0.027$ – 0.28 , $N = 47$ – 59 , $P = 0.125$ – 0.957 ; see Supplementary material, Table S1).

Birds that were relatively 'good' choosers (optimality score >0.60) sampled more nuts than 'poor' choosers (optimality score <0.40) during the large versus medium choice test (Wilcoxon two-sample test: $W = 147$, $N = 38$, $P = 0.039$) and during the intact versus cracked choice test ($W = 215$, $N = 44$, $P = 0.006$), although good and poor choosers spent similar amounts of time deciding before leaving with a peanut ($W = 124$ – 188 , $N = 37$ – 52 , $P = 0.091$ – 0.768 ; see Supplementary material, Table S2). In the large versus medium choice test, 'good' choosers were older compared to 'poor' choosers ($W = 149$, $N = 37$, $P = 0.019$).

Individuals' optimality scores were unrelated to the bird's sex (Wilcoxon two-sample test: $W = 385$ – 480 , $N = 52$ – 59 , $P = 0.128$ – 0.740 ; Supplementary material, Table S2) or their mates' optimality scores (Wilcoxon signed-ranks test: $T = 43.5$ – 220 , $N = 21$ – 25 , $P = 0.051$ – 0.721 ; Supplementary material, Table S2).

DISCUSSION

Steller's jays expressed noticeable preferences for larger nuts and those that were structurally intact. Selection was strongest when items were easily distinguishable (one-chambered versus two-chambered nuts). This is reasonable given that animals seem to perceive relative differences in size (Langen & Gibson 1998; O'Brien et al. 2005). The medium peanuts were 50% larger than the small, whereas the large peanuts were only 25% larger than the medium. Similar size and weight preferences have been documented in other birds including parids and other corvid species (Heinrich et al. 1997; O'Brien et al. 2005; Pons & Pausas 2007). However, large item size may not be universally beneficial when factoring in handling time. Out of six oak species, blue jays, *Cyanocitta cristata*, preferred pin oak acorns, *Quercus palustris*, which are relatively small but can be hulled easier than thick-shelled acorns such as red and black oak species (Scarlett & Smith 1991; Moore & Swihart 2006).

Several studies have indicated that qualities affecting storage viability play an important role in food preference for caching species (e.g. Hadj-Chikh et al. 1996; Pons & Pausas 2007). Steller's jays avoided cracked items in choice trials, and our artificial caches demonstrated that cracked items had a greater likelihood of being damaged by insects after caching than did intact items. Past studies have demonstrated that insect infestation or fungal colonization on cache items is undesirable to jays and squirrels (Bossemma 1979; Steele et al. 1996; Dixon et al. 1997). Cristol (2001) found that common ravens, *Corvus corax*, distinguished between both size and shell condition, preferring to eat walnuts that were already cracked and to cache small, intact nuts. Similarly, the Steller's jays in our study hulled and ate nuts with cracked shells more frequently than they did nuts with intact shells.

We tested the plasticity of sampling behaviour in individuals under different choice sets. Compared to baseline trials, individuals sampled at higher rates when cracked items were possible options (choice tests 3 and 4). This may suggest that Steller's jays sample in order to tactilely assess shell condition in addition to using visual cues. Pinyon jays, *Gymnorhinus cyanocephalus*, shake pinyon pine seeds in their beaks, apparently to assess seed ripeness as well as weight (Ligon & Martin 1974). Yet both the tendency to sample and visit duration were highly repeatable across all our experiments. Rather than adapt their foraging behaviour based on items presented, individuals instead sampled at a similar rate as in trials in which all items were similar. We found that time costs of sampling

had relatively little influence on energetic payoff compared to time spent caching items. Given the proportionately large time costs required to cache the nuts, it would likely optimize energetic payoff to marginally increase handling time if it resulted in choosing a more profitable item. Tendencies for individuals to show consistent, apparently suboptimal, responses have been well documented in behavioural syndrome experiments (Sih et al. 2004; Gabriel & Black 2010). There is considerable interest in behavioural syndrome research to explain how a gradient of responses persists in a population (Sih et al. 2004; Smith & Blumstein 2008). Steller's jays in our population were consistent in nut sampling frequency even in the presence of a mock predator (Rockwell et al. 2012). Fluctuations in fitness effects may also apply to the benefits and costs of sampling.

Based on experimental caches, we found both shell condition and duration of cache influenced decomposition rate. Time and shell condition also influence nutrition of naturally occurring food items, such as acorn weevil larvae (*Curculio* spp. and *Conotrachelus* spp.) damaging acorns (Washington 2003). Optimal foraging theory is based on the premise that animals are capable of balancing benefits of energy content and costs of search and handling time (Pyke et al. 1977; Sih & Christensen 2001); caching species should also account for decreasing energetic value over time (Gerber et al. 2004). Expected payoff after factoring in time costs was not significantly correlated with the proportion of large cracked items taken as a continuous variable, potentially due to high variability among jays that chose both classes of nuts. When grouped according to type of items taken, the predicted energetic benefit for jays that took large cracked nuts over medium intact nuts was greater for short cache durations but statistically equivalent for long cache durations. Cache duration may vary depending on a jay's needs, yet we often observed jays retrieving cached peanuts shortly after a supply of peanuts had been cached, suggesting that many caches are for short-term use. Sampling during a visit increased the likelihood of a jay choosing a more profitable large cracked nut rather than a medium intact one. It is likely easier for jays to discern shell condition than mass using visual information. In contrast, birds that handle several items may detect differences in relative mass and make a different decision than those using visual information alone.

Making profitable choices was not as ambiguous in the other choice tests, reflected by strong population-wide preferences. When size differences between items were visually distinct (one-versus two-chambered nuts), nearly all birds chose the larger item. Optimality scores were lower when the choice was more visually subtle, as between two sizes of two-chambered nuts or between similar-sized intact and cracked nuts, and birds that frequently sampled multiple items had higher optimality scores than jays that did not sample. These results were in accordance with Langen (1999), who found that when free-ranging western scrub-jays sampled peanuts, the final selection weighed more than the first item handled.

Age may potentially influence the types of cache items chosen. In the large versus medium choice set, birds with higher optimality scores were older than birds with lower optimality scores. Previously we showed that sampling behaviour was positively correlated with age (Rockwell et al. 2012). We suggested that over time birds may fine-tune their sampling actions, and thus choose larger, more profitable food items (Rockwell et al. 2012). Yet while the experiments in this study also demonstrated consistent correlations between sampling activity and age, in several trials it did not translate to choosing higher-quality items more often. Many songbirds develop rapidly in their first year, both morphologically and behaviourally, to reach foraging efficiency akin to adults (Wheelwright & Templeton 2003). Perhaps the influence of

experience is most apparent in relatively sophisticated foraging behaviours when differences between food items are relatively subtle.

There were no relationships between tendency to take more profitable items and body size or sex. We did not necessarily expect to observe direct relationships, as size differences in jays are not large enough to preclude taking certain sizes of peanuts (Rockwell et al. 2012). However, we thought size and sex may indirectly influence freedom to make choices as more socially dominant jays have lower risk of displacement (Brown 1963; Langen 1999).

Note that relationships between optimality and individual traits (sampling behaviour, age) were detected more often when considering two extreme behaviour types ('good' choosers and 'poor' choosers) than when intermediate behavioural types were included in the comparison. This may be explained by extreme behavioural types actually representing two alternative strategies that are best expressed when a suite of supporting behavioural, morphological and life history traits correlate well within individuals. While no jays consistently chose smaller-sized items during trials, two out of 58 jays only took cracked items in the intact versus cracked trial. One of these jays (along with two others) only took large cracked items, and four jays only took medium intact items, perhaps reflecting different foraging or caching tactics. Contrasting behavioural strategies may result in different fitness advantages depending on ecological conditions (Dingemanse et al. 2004). An alternative explanation is that intermediate-performing birds that took an even mix of lower and higher profitable items performed as if not being selective: they essentially took items randomly. Birds choosing randomly, potentially seeking to minimize costs of handling time, might add noise to the data and obscure existing patterns between certain individual traits and decision making.

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Supplementary Material

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