How western scrub-jays (*Aphelocoma californica*) select a nut: effects of the number of options, variation in nut size, and social competition among foragers

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Abstract  Western scrub-jays (*Aphelocoma californica*) often visually assess and handle several whole (unshelled) peanuts before selecting one to transport and cache; this behavior is a search for a preferred heavy nut. I repeatedly video-taped individually identifiable jays as they landed on a feeding platform and chose from presentations of peanuts that varied in the number of items or in the distribution of sizes. I examined how differences among these presentations and a bird’s social status affected the amount of assessment and the economic consequences of choice. I also examined the specific patterns of handling peanuts, called sampling, to quantify the degree to which sampling sequences were typified by repeated comparisons among sampled peanuts (retrospective sampling), or sequential assessment and rejection of peanuts (prospective sampling). Peanut assessment was more extensive and prospective when there were many options from which to choose than when there were few. Peanut assessment was more extensive and retrospective when options were similar in size than when they varied. Scrub-jays were more likely to make repeated comparisons immediately before selecting a peanut than elsewhere in a sampling sequence. Subordinate scrub-jays, who were at the greatest risk of pre-emption by competitors, assessed peanuts less extensively and were more prospective in their sampling than dominants. Unless peanuts were very similar in size, jays were more accurate at selecting a high-quality peanut and achieved a higher rate of food storage than if they had not assessed. These results show that scrub-jays can adaptively modify how they search to improve their rate of food storage, and also suggest some of the specific search tactics used by jays when assessing peanuts.

Key words  Assessment · Dominance · Foraging · Optimal choice behavior · *Aphelocoma californica*

Introduction

Animals may evaluate multiple candidates before selecting a food item (Menge 1974; Elnor and Hughes 1978), mate (Gibson and Langen 1996), or home (Elwood and Neil 1992; Boulanger et al. 1996). To understand how animals make such decisions, one must investigate both the economic and the psychological factors affecting choice behavior.

Relevant economic models of choice in non-human animals have focused upon two general topics: optimal diet selection and mate choice. Optimal diet selection models explore the conditions under which it is adaptive to reject a potential food item in favor of continued search for more profitable items. Standard models for rate-maximizing foragers that encounter potential food items sequentially predict all-or-none selectivity: either always harvest a particular food item upon encounter or never include it in the diet (reviewed in Stephens and Krebs 1986; McNamara and Houston 1987). Related models investigate the conditions under which animals should appear to change preferences (e.g., Orians and Pearson 1979; Houston 1997), or the conditions under which partial preferences should be expected (a partial preference is a lower than 100% probability of accepting or rejecting a particular food item, a frequent empirical observation, e.g., Lucas 1987). Some principal reasons why rate-maximizing foragers might show partial preferences include: (1) food-types are hard to distinguish, and thus mistakes are common; (2) variables that affect choice are uncertain or changing, which can make it economical to select items that appear suboptimal to acquire information about them; and (3) the foraging bout is at risk of ending, in which case there may be little remaining opportunity to find a more profitable option if an encountered less-profitable item is passed-over (Lucas 1983, 1985; McNamara and Houston 1987).
Models of optimal mate choice investigate how animals might economically search through a pool of candidates to find a high-quality partner or breeding site. Some theoretical analyses have assumed that a candidate’s quality is accurately estimated upon a searcher’s initial inspection, and have analyzed the efficacy of choice thresholds or comparison tactics for finding the most economical candidate under differing assumptions about search costs or uncertainties about the candidate pool (Janetos 1980; Wittenberger 1983; Parker 1983; Real 1990; Mazalov et al. 1996; Johnstone 1997; Boulanger and Danchin 1997). Other analyses have focused on the issue of how an animal ought to conduct a search if the initial estimate of a candidate’s quality is inaccurate but can be improved through further assessment (Getty 1995, 1996; Luttbeg 1996); these models are closely related to others on the economics of information-gathering (Enquist and Leimar 1983; Getty 1985; Stephens 1989; Elwood and Neil 1992; Johnstone and Grafen 1992; Wiley 1994).

Seed-harvesting birds use both visual cues and tactile cues provided by handling seed with the beak to select high-quality food items (Ligon and Martin 1974; Gregg-Smith and Crocker 1986; Johnson et al. 1987; Heinrich et al. 1997; Fleck and Woolfenden 1997). Western scrub-jays (Aphelocoma californica) scatter-hoard acorns, usually loading a single acorn at a time for transport (Bent 1946; Carmen 1988; Fleck and Tomback 1996). Scrub-jays readily transfer this behavior to whole (unshelled) peanuts provided at bird feeders, food items that are similar in size and mass to stored acorns. Before making a selection, jays often handle with the beak multiple peanuts in succession, a behavior I call sampling. When they are offered several peanuts simultaneously, I have witnessed scrub-jays sample as many as 25 different candidates before choosing one, and some peanuts are sampled repeatedly before a selection is made.

Langen and Gibson (1998) repeatedly presented pairs of peanuts that differed in size to individually identifiable scrub-jays and concluded that jays prefer the heavier option. Accuracy at selecting the heavier peanut is lowered, however, when the relative difference in mass between options is small: most of our subjects achieved an accuracy of 75% “correct” when the heavier was about 50% larger than the alternative. Scrub-jays assess peanut relative size by visual scanning and sampling; the initial visual scan improves the likelihood of first handling the larger peanut over random choice, and further sampling improves a jay’s accuracy at selecting the larger peanut when relative differences in size are small.

In this paper, I examine three factors that may affect how western scrub-jays assess options before choosing a peanut, by investigating how each factor affects the total amount of assessment, the quantity of food acquired at each visit to a feeder, and the rate of hoarding food. I also analyze the specific patterns of sampling, because sampling sequences can provide insight into the actual tactics used in making a selection (Wittenberger 1983; Wiegmann et al. 1996). In terms of pattern, I quantify the degree to which sampling sequences are prospective, consisting of sequential assessment and rejection of candidates until a choice is made, versus retrospective, consisting of repeated comparisons of peanuts via resampling before one is selected.

The three factors I examine are:

1. The number of peanuts from which to choose. When there are many unsampled options, it may be more economical for a jay to sample a new, potentially high-quality peanut about which it has little information than to resample a previously inspected candidate to improve an already-accurate quality estimate. When the candidate pool is small, however, it may be worthwhile to resample repeatedly the most promising candidates to discriminate more accurately the highest quality among them before making a selection. Thus sampling sequences should be longer and more prospective when there are many peanuts from which to choose than when there are few, but the number of samples should be greater for each sampled peanut when there are few options than when there are many.

2. The variation among peanuts from which to choose. When candidates are very discriminable in quality, it will be relatively easy for a jay to select a high-quality peanut without prolonged assessment, so sampling sequences should be short and prospective, and result in accurate selection of a high-quality peanut. When there is little variation among peanuts, however, sampling sequences should be long and retrospective, and result in less frequent selection of the highest-quality option than when the variation is large.

3. Social status. Dominant individuals may be interrupted less frequently by competitors during choice than subordinates, and therefore prolong assessment because it is less costly for them. Likewise, dominants may be more retrospective during sampling and subordinates more prospective (Wittenberger 1983). As a consequence, dominants should be more accurate at selecting a high-quality peanut each feeder visit and may hoard peanuts at a higher rate than subordinates.

Materials and methods

Study sites and general methods

I studied color-banded western scrub-jays at three sites in Los Angeles County, California [the Mildred Mathias Botanical Gardens at the University of California Los Angeles, residential Van Nuys, and the University of California's Santa Monica Mountains (Stunt Ranch) Reserve]. The study sites and general methods were the same as those described in Langen and Gibson (1998). At each site, I placed feeding platforms in scrub-jay territories and regularly stocked them with whole (unshelled) peanuts. Platforms were 60x60 cm, painted flat grey and mounted on a post 1.6 m high. After jays had begun visiting a feeder, I habituated them to the experimental procedures by mounting a video camera on a tripod 1.5 m away while an observer sat nearby and intermittently stocked the feeder with peanuts. At Van Nuys, the observer entered a house after putting peanuts on the feeder but at the other two locations she or he remained unconcealed.

During the experiments described below, jays were video-taped as they removed peanuts from the feeder platform. The following
Table 1 The number and distribution of peanuts used in the four presentations of experiment 1, with SD. The distribution of mass in a random sample of peanuts from the same lot was $1.57 \pm 0.489$ (SD) g ($n = 228$).

<table>
<thead>
<tr>
<th>Presentation</th>
<th>Mass (g)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1.0–1.1</td>
<td>1.2–1.3</td>
</tr>
<tr>
<td>Six-High variance</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Six-Low variance</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Two-High variance</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Two-Low variance</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Data were scored from the video record for each peanut removal: (1) total time spent on the feeder, (2) latency from landing until handling the first peanut, (3) time from handling the first peanut until leaving the feeder, (4) the sequence of handling peanuts until making a selection, and (5) the time from leaving the feeder until the bird next landed to make a choice (return time). Each instance in which a peanut was lifted from the platform by the bird’s beak was counted as a sample; a sampling sequence could include repeats of consecutive pick-ups of the same peanut and switches (handling a different peanut from the previous one). Sequences in which a jay removed more than one peanut at a time were not included in the analyses, nor were sequences in which a subject selected the feeder without removing a peanut (usually to avoid a more dominant individual); 7 ± 3.3% (SE) of trials per feeder were excluded for these reasons.

The feeders attracted territorial pairs and some floaters. If a feeder was located near the boundaries of a scrub-jay’s territory (e.g., Van Nuyes), sometimes neighboring pairs also visited it. Dominance status was determined by displacements on or near the feeder. Territorial males were dominant over their mates (sex determined by gender-specific calls and body size), and territorial birds displaced floaters (T.A. Langen, unpublished work). In this paper, all territorial males are classified as dominants, and territorial females and floaters are classified as subordinates.

Experiment 1: how peanut number and variability in peanut size affect choice

I repeatedly placed a selection of peanuts on the feeder in a randomized block of four presentation-types. Each presentation contained peanuts with the same mean mass (1.55 g) but differing in the total number of peanuts or the variation in mass among them (Table 1). Peanuts were weighed to the nearest 0.1 g. Whole-peanut mass was an accurate predictor of the mass of nut meat contained within the peanut ($F_{1,226} = 4939, P < 0.0001, r^2 = 0.96$, nut meat mass = (0.80 x whole mass) – 0.054, $n = 228$ randomly sampled peanuts from a lot used in the experiment).

The peanuts for the next trial were placed on the feeder 3 min after a removal in the previous trial. This inter-trial interval was included to eliminate any incentive for jays to quickly select a peanut in order to increase the renewal rate. The actual mean time between trials for a subject was 7.6 ± 0.36 (SE) min, or 97.9 ± 0.18% of a whole caching cycle (i.e., from landing on a feeder until the next return). Trial days were terminated when the jays stopped returning to the feeder (mean trials per day = 17 ± 1.7, mean trials per bird per day = 10 ± 2.7). I acquired sufficient data (more than five trials per presentation-type) on nine subjects (Van Nuyes: two dominants and one subordinate at one feeder, 8 days in September and December 1996; Reserve: one dominant and subordinate at one feeder, 7 days in September 1996; UCLA: three dominants and one subordinate among three feeders, 26 days in February-June 1996 and February-March 1998). Each subject participated in 22 ± 1.6 trials per presentation-type (range 7–42).

When comparing birds, I used each subject’s mean or median (latency only) of the trials. The statistical significance of differences among presentations was examined via three-way ANOVAs in which subject was used as an unreplicated randomized blocking factor and number of peanuts (six or two) and variation among peanuts (high or low) were the two balanced treatment factors.

Experiment 2: choice when the number of peanuts is unlimited

The feeder tray was completely covered with peanuts to a depth of 2 cm, resulting in a presentation of 1000–1200 peanuts, and jays were filmed as they removed peanuts for storage. During a trial day, peanuts were constantly available. Thus a bird could begin selection immediately upon arrival. Every 5 min the peanuts on the feeder were mixed and a few additional peanuts were added to compensate for removals. From the video record, besides recording data on the sampling behavior of each visiting jay, I also measured the rate of feeder visitation by birds (number of jays landing on the feeder per minute).

Twenty jays were repeatedly observed among the three sites (Reserve: four dominants and four subordinates, March 1996 and January 1998, 4 days among three feeders; UCLA: three dominants and three subordinates, March 1996, May 1997 and February 1998, 6 days among three feeders; Van Nuyes: three dominants and three subordinates, February-March 1996 and January 1998, 7 days at one feeder). Each jay was filmed removing 27 ± 2.4 (SE) peanuts (range 12–62). The feeders averaged 0.6 ± 0.09 visits per min, and each jay visited its feeder every 6.0 ± 0.88 min.

Comparison of sampling patterns

For a sequence of samples from the initial pick-up to the removal of the selected peanut, I treated each pick-up as a separate decision step. Each decision step was treated as a hierarchical set of dichotomous actions: (1) leave with the peanut or drop it and sample again; (2) if sampling again, repeat sampling the same peanut or switch to another; (3) if switching, select a new peanut or return to a previously sampled one; and (4) if returning to a previously sampled peanut, handle the most recently or a less recently sampled peanut of the sequence (two or more previous).

Using all of the sampling sequences of a jay, I estimated the probability of taking one of the actions by dividing the total number of instances that the action was chosen by the total number of times the decision point was reached. I only included those decision points for which both alternatives were possible; e.g., to estimate the probability of selecting a new peanut when switching, I excluded the first switch in a sequence since the other alternative (return to a previously sampled option) was impossible at this stage. To maintain a minimum level of precision, I only included probability estimates based on five or more counts per dichotomous choice.

I statistically compared presentations using ANOVA, in which the unit of replication was the arcsine-square root transformed mean proportion of trials a subject selected one course of action of a dichotomous choice. I included status (dominant or subordinate) as a fixed factor along with the fixed factor of presentation type.

During a peanut-sampling sequence, it is possible that the probability of taking an action depends on how many samples have preceded it. For the sequences from unlimited presentations, I calculated the proportion of trials that a jay left with a peanut after each sample (i.e., the proportion of trials that a bird only sampled once, the proportion of the remaining trials that a bird only sampled twice, and so on). I then used the arcsine-square-root-transformed proportions as dependent variables in linear regressions, done separately for each jay, in which the independent variable was the step in a sampling sequence. Because there was a signifi-
cant increase in the probability of leaving with each step (see Results, experiment 2), only the probability of leaving at the first decision step (after the initial pick-up) was compared among presentations. Data from the other presentations and for other actions were insufficient to make a separate probability estimate at each sequence step.

I also examined whether the likelihood of taking certain actions differed after the penultimate decision-step before peanut removal from elsewhere in a sequence by calculating the ratio of the two probability estimates (the null ratio, or no difference, would equal 1). Relatively few subjects had sufficient sequence data to calculate this ratio for any given presentation, so statistical power to detect small deviations from unity were low. Because the data were homogeneous in the mean direction of deviations among presentations, I pooled the results among presentations in these instances. To avoid pseudoreplication, I selected the presentation that had the largest sample size of last choices for each of the few subjects that was represented more than once.

Payoffs from assessment

As in Langen and Gibson (1998; see also Waite and Ydenberg 1996), I estimated the rate at which scrub-jays stored edible peanut meat in experiment 1 as the ratio of the mean amount of nut meat removed per choice over the mean time from first landing on a feeder to initiate choice until the bird's next return to the feeder (time on the feeder plus return time). I compared the jays' actual storage rates to the hypothetical rates if (1) they removed a random peanut as quickly as possible (= 0.2 s), and (2) they removed the first handled peanut after the initial latency. Nut meat was estimated from total peanut mass by a regression model (see experiment 1 methods, above). The calculated rates are “ratio of expectations” estimates of long-term hoarding rates (Stephens and Krebs 1986; Bateson and Kacelnik 1996). The conclusions are unaffected if the ratio is computed for each choice cycle and then averaged across trials (“expectation of ratios”, Bateson and Kacelnik 1996).

Because the masses of the peanuts removed in experiment 2 were unknown, a different approach was used. I weighed a random sample of 228 peanuts from a lot used in the experiment to determine the mean and distribution of nut mass, and then calculated the theoretical board rate if birds were not selective (= mean nut mass/return time = 0.2 s). Using the observed mean total time actually spent on the feeder, I calculated the minimum nut mass that would have resulted in each bird “breaking even”, i.e., having the same hoard rate as a random chooser by selecting a peanut large enough to compensate for the time spent in assessment. The “break-even” mass was compared to the actual distribution of peanut masses to determine the abundance of sufficiently large peanuts.

Additional statistical details

Initial exploratory data analyses showed that latency was independent of the other activity measures, but these other measures (the time on the feeder after the latency, the number of samples, the number of switches and, in experiment 2, the number of different peanuts sampled) were all highly correlated. These activity measures were therefore reduced into a composite variable of assessment activity via principal components analysis, done separately for each experiment and only including trials with more than one sample. One significant principal component (PC) accounted for most of the variation among the variables in each experiment [experiment 1: χ² = 7,555, P < 0.0001, n = 478 trials, PC1 = 78% of the variance, (unrotated) score weights: In time at latency = 0.382, In number of samples = 0.396, In number of switches = 0.351; experiment 2: χ² = 2,389, P < 0.0001, n = 407, PC1 = 89% of the variance, (unrotated) score weights: In time at latency = 0.249, In number of samples = 0.269, In number of switches = 0.272, In number of different peanuts = 0.271]. The PC scores were saved and used in the analyses of assessment behavior.

All data have initially been inspected for temporal trends (systematic changes in activity measurements within or among trials). In ANOVA models, the interaction term has been removed if non-significant (P > 0.05). P-values are two-tailed, except as specifically noted when directional hypotheses are tested. Summary statistics express the mean ± SE. Variables have been transformed if necessary before performing parametric statistical tests.

Results

Experiment 1: how peanut number and variability in peanut size affect choice

Causes of variation in assessment behavior

The latency between landing and handling the first peanut was longer in low than high-variance presentations (Tables 2, 3). The jays were more likely to continue sampling after the first pick-up in six- than two-peanut presentations, and when they did continue the assessment behavior (as measured by the “assessment” PC) was more extensive when birds had six peanuts from which to choose or when the variation in size was small (Tables 2, 3).

There were significant differences among subjects in the amount of assessment activity (i.e., latency, % sampled, and the assessment PC; Table 3). Some of these differences were associated with dominance status (Table 2). Although there were no significant differences in latency associated with dominance status (each presentation: t₁,ₛ > 1.0, Ps > 0.3), the probability of sampling again after handling the first peanut was higher for dominants (each presentation: t₁,ₛ > 2.3, Ps < 0.05). When sampling continued after the initial pick-up, dominants performed significantly more assessment behavior (i.e., had higher PC scores) than subordinates in the six-peanut-high-variance presentation (t₁,ₛ = 3.7, P = 0.01; other presentations: t₁,ₛ < 1.7, Ps > 0.1; one subordinate excluded that did not sample multiply). Among birds, the mean time spent on a feeder selecting a peanut was not significantly correlated with the mean length of time between visits (each treatment combination: rₛ < 0.2, Ps > 0.6, n = 9).

Results of assessment

The first-sampled peanut was significantly heavier than random on average (greater than 1.55 g) in each of the four presentations (Fig. 1; each presentation: one sample t₁,ₛ > 2.3, one-tailed Ps < 0.025). A higher proportion of initial selections were heavier than random in high-variance than low-variance presentations, however (Fig. 1; Tables 2, 3). When birds sampled more than one peanut, there was significant improvement between the initial selection and the final (removed) peanut in the high-variance but not the low-variance presentations (Fig. 1; two high-variance presentations: t₁,ₛ > 2.5, one-tailed Ps < 0.02; two low-variance presentations: t₁,ₛ < 0.9, one-tailed Ps > 0.2; see also Tables 2, 3).

Although by visually scanning and sampling peanuts the jays acquired items that provided significantly more food than random, assessment increased the time spent in...
Table 2 Behavioral measures of peanut assessment during the four presentations for each dominance class (n in parentheses) [% Sampled the proportion of trials that a bird continued sampling after the first pick-up, Assessment PC principal component that expresses the amount of activity on the feeder after the initial latency (see Methods: Additional statistical details), % Improvement difference between the first handled peanut and the peanut removed in the probability that it is heavier than the mean]. The subordinate excluded from Assessment and % Improvement was sampled more than once only in two trials.

<table>
<thead>
<tr>
<th>Latency</th>
<th>% Sampled</th>
<th>Assessment PC</th>
<th>% Improvement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dominant</td>
<td>Subordinate</td>
<td>Dominant</td>
</tr>
<tr>
<td></td>
<td>(6)</td>
<td>(3)</td>
<td>(6)</td>
</tr>
<tr>
<td>Six-High</td>
<td>1.6 ± 0.34</td>
<td>1.4 ± 0.36</td>
<td>76 ± 8.0</td>
</tr>
<tr>
<td>Six-Low</td>
<td>2.1 ± 0.49</td>
<td>2.0 ± 0.33</td>
<td>81 ± 8.7</td>
</tr>
<tr>
<td>Two-High</td>
<td>1.3 ± 0.13</td>
<td>1.5 ± 0.15</td>
<td>69 ± 11.9</td>
</tr>
<tr>
<td>Two-Low</td>
<td>1.5 ± 0.27</td>
<td>1.8 ± 0.47</td>
<td>75 ± 9.0</td>
</tr>
</tbody>
</table>

Table 3 Summary of F statistics from ANOVAs testing the effects of presentation type and subject on measures of peanut assessment (see Table 2 for description of the variables).

<table>
<thead>
<tr>
<th></th>
<th>Latency</th>
<th>% Bigger (initial)</th>
<th>% Sampled</th>
<th>Assessment⁹</th>
<th>Improvement⁹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variance</td>
<td>(df = 1,25)</td>
<td>4.9 *</td>
<td>8.6 **</td>
<td>2.5</td>
<td>6.2 *</td>
</tr>
<tr>
<td>Number</td>
<td>(df = 1,25)</td>
<td>1.8</td>
<td>0.2</td>
<td>5.9 *</td>
<td>15.7 ***</td>
</tr>
<tr>
<td>Subject</td>
<td>(df = 8,25)</td>
<td>8.4 ***</td>
<td>1.0</td>
<td>29.7 ***</td>
<td>12.0 ***</td>
</tr>
</tbody>
</table>

*P < 0.05, **P < 0.01, ***P < 0.001

*Variance and number df = 1,22, subject df = 7,22 (excluded individual sampled more than once just twice among all treatments).

Fig. 1 Changes in accuracy at selecting a heavy peanut between the initial and final selection for the four presentations (H high variance, L low variance); n = 9 subjects, random choice P = 0.5

hoarding each peanut by 9.2 ± 0.80 s, or 2 ± 0.2% of a caching cycle (from landing on a feeder until the next return). If birds had immediately removed the first sampled peanut after visual scanning, they would have achieved higher rates of food storage than if they had immediately removed randomly selected peanuts (Fig. 2; both six-peanut and the two-peanut-high-variance presentations: paired t₈s > 2.3, one-tailed Ps < 0.03; two-peanut-low-variance: t₈ = 1.6, P = 0.08). Additional assessment improved the jays' rates of storage over what they would have attained had they immediately removed the first-sampled peanut in the high-variance presentations but not the low-variance presentations (Fig. 2; high-variance presentations: paired t₈s > 2.4, one-tailed Ps < 0.03; low-variance presentations: paired t₈s < 0.7, one-tailed Ps > 0.15). Experiment 2: choice when the number of peanuts is unlimited

Causes of variation in assessment behavior

There were significant differences among birds in both the latency to handling the first peanut (F₁₉,₅₁₃ = 15.4, P < 0.0001, mean of subjects = 2.2 ± 0.21 s, n = 20) and subsequent assessment (assessment PC: F₁₉,₃₇₅ = 11.2, P < 0.0001, mean of subjects = 1.5 ± 0.13, n = 20). Jays that had long latencies were also more likely to continue sampling after the first pick-up (r = 0.62, P = 0.003, n = 20). Unlike the findings of Langen and Gibson (1998), there was no significant relationship between the median la-
tency of birds and the total rate of visitation to the feeder
\( r = -0.17, P = 0.5, n = 20 \), nor with dominance status \( t_{18} = 0.8, P = 0.4 \). However, the proportion of trials in which a bird sampled more than once was greater for dominants than subordinates \( t_{18} = 2.1, P = 0.05; \) dominants \( 0.86 \pm 0.033, \) subordinates \( 0.68 \pm 0.080 \), and during such trials, birds at feeders with high rates of visitation performed less assessment (as measured by the assessment PC) than those at feeders with low visitation rates (Fig. 3; \( r = -0.52, P = 0.02, n = 20 \)). This relationship was strong for subordinates \( r = -0.71, P = 0.02, n = 10 \) but non-significant for dominants \( r = -0.23, P = 0.5, n = 10 \). The probability of leaving the feeder increased with each additional sample [slope of the linear regression (see Methods): one-sample \( t_{19} = 5.1, P < 0.0001, \) mean slope \( 0.046 \pm 0.009 \)]. However, this rate of increase did not differ by dominance status \( t_{18} = 0.2, P = 0.8 \) or the total rate of visits to the feeder \( r = 0.30, P = 0.2, n = 20 \). Among birds, the mean time spent on a feeder selecting a peanut was not significantly correlated with the mean length of time between consecutive visits \( r = 0.17, P = 0.5, n = 20 \).

**Results of assessment**

The birds could have hoarded nut meat at a rate of \( 0.27 \pm 0.330 \) g min\(^{-1} \) by randomly selecting a peanut. To break even given the actual mean time spent on the feeder (9.1 ± 0.98 s), the birds would need to have selected a peanut a mere 4% heavier than the mean nut mass (1.25 ± 0.033 g nut meat), or slightly greater than the 50th percentile. The maximum break-even estimate was 10% heavier than the mean for one jay.

**Patterns of sampling compared**

**General patterns of sampling sequences**

A summary of the estimated probabilities of taking a particular action at a decision step is presented in Table 4. After the initial pickup, the birds were significantly more likely to leave in presentations with few peanuts than many, and subordinates were more likely to leave than dominants (presentation \( F_{4,50} = 2.9, P = 0.03, \) status \( F_{1,52} = 31.6, P < 0.0001 \). The probability that the same peanut would be resampled when a bird sampled again also decreased with the number of presented peanuts, and subordinates repeated less frequently than dominants (presentation \( F_{1,46} = 2.7, P = 0.04, \) status \( F_{1,49} = 5.6, P = 0.02 \). The birds were more likely to select a new peanut when switching if presented many peanuts than few, and subordinates were more likely to switch to a new peanut than dominants (presentation \( F_{2,28} = 18.9, P < 0.0001, \) status \( F_{1,28} = 6.6, P = 0.02 \).

When returning to a previously sampled candidate, scrub-jays were significantly more likely to choose the one sampled immediately before than one earlier in the sequence (Fig. 4). This peanut was frequently not the closest, but jays did sometimes move a peanut next to another to facilitate comparison. There was no difference among presentations or dominance status in the likelihood of returning to the immediately prior candidate (presentation \( F_{2,16} = 0.5, P = 0.6; \) status \( F_{1,17} = 0.2, P = 0.7 \).

The number of peanuts sampled increased with the number of options and was somewhat higher for dominants (Fig. 5a), but the number of samples per sampled peanut declined with presentation size and was much lower for subordinates (Fig. 5b). The peanut that was most frequently sampled within a sequence was also significantly more likely to be selected (one-sample t-test pooled across conditions: \( t_{15} = 4.2, P = 0.0008, \) mean likelihood over random = 1.7 ± 0.16 or 50 ± 5.3% of the maximum); the magnitude of this bias did not differ across presentations \( F_{4,23} = 0.9, P = 0.5 \).

**Table 4 Decisions during peanut assessment, expressed as the percentage of instances that one alternative of a dichotomous decision was chosen. The percentage for the first decision-step is reported for Leave. The number of birds is in parentheses**

<table>
<thead>
<tr>
<th></th>
<th>Leave (first sample)</th>
<th>Repeat if sampled</th>
<th>New if switched</th>
<th>One previous if resampled</th>
</tr>
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<tr>
<td></td>
<td>Dominant</td>
<td>Subordinate</td>
<td>Dominant</td>
<td>Subordinate</td>
</tr>
<tr>
<td>Two-High</td>
<td>35 ± 9.7 (6)</td>
<td>75 ± 8.8 (3)</td>
<td>60 ± 12.1 (6)</td>
<td>30 ± 30.0 (2)</td>
</tr>
<tr>
<td>Two-Low</td>
<td>25 ± 6.3 (6)</td>
<td>74 ± 12.1 (3)</td>
<td>50 ± 9.4 (6)</td>
<td>27 ± 10.9 (2)</td>
</tr>
<tr>
<td>Six-High</td>
<td>24 ± 5.7 (6)</td>
<td>71 ± 11.6 (3)</td>
<td>52 ± 10.9 (6)</td>
<td>30 ± 30.0 (2)</td>
</tr>
<tr>
<td>Six-Low</td>
<td>21 ± 6.1 (6)</td>
<td>63 ± 22.5 (3)</td>
<td>33 ± 8.4 (6)</td>
<td>24 ± 20.3 (2)</td>
</tr>
<tr>
<td>Unlimited</td>
<td>15 ± 3.0 (10)</td>
<td>32 ± 8.0 (10)</td>
<td>21 ± 3.8 (10)</td>
<td>18 ± 4.3 (9)</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>86 ± 2.5 (10)</td>
<td>91 ± 45 (8)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>80 ± 6.3 (6)</td>
<td>75 ± 12.6 (3)</td>
</tr>
</tbody>
</table>
Fig. 4 The likelihood (observed probability/random) of sampling the option handled immediately previously when returning to a previously handled peanut (filled bars). The null likelihood = 1.0 and the maximum likelihood (i.e., the previous peanut is always chosen) is shown by open bars. Significance values are from one-sample r-tests of whether the observed likelihood differs from the null hypothesis († P < 0.1; **P < 0.01)

Fig. 6 The likelihood (observed probability/random) of selecting the last new peanut sampled when more than one was sampled (filled bars). The null likelihood = 1.0 and the maximum likelihood (i.e., the last peanut is always selected) is shown by open bars. Significance values are from one-sample r-tests of whether the observed likelihood differs from the null hypothesis (*P < 0.05, **P < 0.01, ***P < 0.0001)

Fig. 5 Differences due to presentation-type and status in a the mean number of peanuts sampled (ANOVA on ln-transformed data: peanut number F_{4,50} = 13.6, P < 0.0001; status F_{1,50} = 4.9, P = 0.03), and b the mean number of samples per sampled peanut (ANOVA on ln-transformed data: peanut number x status F_{4,46} = 3.4, P = 0.02, peanut number F_{4,46} = 2.1, P = 0.10; status F_{1,46} = 42.6, P < 0.0001) (presentations: 2L two-peanut-low-variance, 2H two-peanut-high-variance, 6L six-peanut-low-variance, 6H six-peanut-high-variance, U unlimited)

Patterns near the end of a sampling sequence

The last sample before leaving with a peanut was more frequently a repeat of the penultimate than elsewhere in a sequence (one sample t_{20} = 3.4, P = 0.003, mean likelihood last over elsewhere = 1.4 ± 0.21 or 39 ± 4.9% of the maximum). The likelihood did not differ among presentations (F_{4,37} = 0.4, P = 0.8). If the last sample before leaving was the result of a switch, it was less likely to be a switch to a new peanut, and therefore more likely to be a return to a previously sampled candidate, than elsewhere in a sequence (one-sample t_{16} = 2.8, P = 0.01, mean likelihood last over elsewhere = 0.8 ± 0.07). This change in switching pattern was greater for six-peanut-high-variance than unlimited presentations, the only two that could be compared (t_{17} = 2.3, P = 0.04; mean likelihood six-high = 0.6 ± 0.18 n = 4, unlimited = 0.9 ± 0.06 n = 15). The likelihood of removing the last sampled peanut varied markedly among presentations: with a candidate pool of two peanuts, jays were no more likely to remove the last than first sampled peanut, but with unlimited options they were far more likely to remove the last sampled peanut than expected by chance (Fig. 6).

Discussion

These results can be summarized by five main points:

1. Western scrub-jays assess peanuts more extensively when there is a large pool from which to choose and when options are similar in size.

2. The actual pattern of sampling is typified by frequent resampling of previously sampled peanuts (retrospective sampling) when the candidate pool is small and by sequential assessment and rejection of peanuts (prospective sampling) when the pool is large.

3. Scrub-jays are more likely to make repeated comparisons immediately before peanut removal than elsewhere in a sampling sequence.
Fig. 7 Summary of the factors that affect the length and pattern of sampling sequences when western scrub-jays search for a high-quality peanut. Retrospective searches include frequent resamples of previously sampled candidates, prospective searches are composed primarily of sequential assessment and rejection of new candidates.

4. Scrub-jays assess peanuts less extensively at feeders that attract many competitors. Dominant individuals assess peanuts more extensively and are more retrospective in their sampling than subordinates.

5. Jays improve their accuracy at selecting a high-quality peanut via the initial visual scan and the subsequent sampling behavior. Peanut sampling (using the beak to handle several peanuts in succession) results in a higher rate of food storage than is attainable by simple visual inspection, at least when options are not too similar.

These five findings indicate that western scrub-jays adaptively adjust how they search for a high-quality peanut both within and between feeder visits depending on the prospective value of information gained through sampling and the costs of assessment (Fig. 7). The sampling sequence data may also indicate how scrub-jays cognitively compare options.

Economics of peanut assessment

During this study, weather conditions were mild. The scrub-jays appeared to have abundant alternative sources of food to peanuts, and did not appear to be provisioning dependent offspring. The time during which jays could collect peanuts from a feeder was no greater than about 25% of the total time available for foraging on any trial day. Under such conditions, animals are expected to maximize the rate of food storage rather than the energetic efficiency of storage (Waite and Ydenberg 1996; Ydenberg 1998). Although this study was not designed to distinguish among different potential currencies, the scrub-jays' actual assessment behavior did generally result in a higher rate of food storage than alternative, simpler choice tactics. This conclusion differs from that of Langen and Gibson (1998), but in the former study only pairs of peanuts were presented, and the difference in size within a pairing was frequently quite small; in the present study also, jays did not improve the rate of storage by sampling when peanuts were all very similar in size.

One cost, the magnitude of the risk of pre-emption either by other competitors poaching better options or chasing the chooser from the feeder, has a significant effect on peanut assessment behavior (see also Langen and Gibson 1998). Consistent with optimal diet choice models, scrub-jays are more likely to leave with a low-quality peanut when the risk of interruption is high (Lucas 1983, 1985; McNamara and Houston 1987); and, consistent with models of optimal mate choice (e.g., Real 1990; Luttbeg 1996; Johnstone 1997), the duration of peanut assessment is shorter when there is a high risk of pre-emption. Similar results to these have been reported in other empirical studies (e.g., Lucas 1987; Dale et al. 1992). A more interesting finding is that the risk of pre-emption affects the form of a search: dominant individuals, who are at lowest risk, are more retrospective in sampling peanuts whereas subordinates are more prospective. This result is consistent with the suggestion of Wittenberger (1983) that pooled comparisons are more economical when costs are negligible but sequential decision-rules are better when there are significant risks of pre-emption (see also Real 1990; Dall et al. 1999).

Economic models of optimal choice behavior and peanut assessment

Models of optimal diet selection do not incorporate the option of returning to a previously rejected food item, although foragers may accept identical items encountered later in the foraging bout for various reasons (Lucas 1983, 1985; McNamara and Houston 1987). Most models of optimal mate choice assume that candidates are accurately assessed upon encounter, and hence predict that re-visits will be rare too except when a candidate is chosen. Scrub-jays, however, repeatedly resample peanuts that they have previously encountered, especially when the candidate pool is small or peanuts are similar in size. One hypothetical explanation is that searchers reject candidates that fail to meet a threshold of acceptance, and this cut-off rule is adjusted downward if search is fruitless (Real 1990; Wiegmans et al. 1996); under this scenario jays continue repetitive resampling of a whole pool until an encountered peanut finally meets an increasingly less stringent criterion. The results reported in Langen and Gibson (1998) and the present paper make this conjecture implausible: for the same relative difference in size, two large peanuts are resampled as repeatedly as two small; and when jays resample, they are much more likely to handle the immediately previously sampled peanut than one handled earlier in a sampling sequence.

Instead, repeated inspection serves to improve discrimination between similar peanuts. This appears to provide an example of the search tactic based on Bayesian inference modeled by Luttbeg (1996) which was shown to perform better than alternatives when search costs are low candidates can be relocated, and initial assessments are inaccurate but can be improved through further inspection. With low search costs, his model predicts that candidate will be re-inspected, sometimes repeatedly, and that assessment will be more prolonged when there is greater uncertainty about them. The decision of whether to in
pect a particular candidate at any decision step depends on the expected value of the information provided by assessing it versus the expected payoff from assessing other options or making a selection. Given the assumptions of the model of Luttbeg (1996), it can frequently be more economical to assess candidates that initially appear less promising if there is greater uncertainty about them. Consistent with the model:

1. Scrub-jays assess more when the variation among options is low than high, but are more accurate at selecting a high-quality peanut when the variation is high than low.

2. The pattern of assessment within a search sequence is nonrandom and frequently includes revisits to candidates that are ultimately rejected.

3. Except when the variation among options is very low, sampling repeatedly results in more accurate selection of a high-quality candidate than if the first-sampled peanut is removed without further assessment.

Scrub-jays have more information about the candidate pool at the initiation of a search than is assumed in most theoretical models, although a few can incorporate such information in principle (e.g., Luttbeg 1996). When presented with a small number of peanuts, jays may visually inspect all candidates simultaneously rather than sequentially as is normally assumed (Valone et al. 1997). In all presentations, the birds appear to estimate the size of the candidate pool and the variation among candidates upon initial inspection. As a result, better-quality peanuts are encountered more frequently than expected by random search because of cues perceived during the scan, and the choice tactics may be prospectively modified based on the apparent size of the pool and the variation among candidates. In some empirical studies of mate choice also, there is good evidence that candidates are not encountered randomly and choosers adjust their tactics based on long-range cues or other information acquired before the initiation of close inspection (reviewed in Gibson and Langen 1996).

Each sampled peanut is assessed more carefully when there are few options than many. The birds appear to be sensitive to a tradeoff between improving estimates of the qualities of sampled peanuts and the opportunity to assess new ones. When there is an unlimited supply of candidates, it may be less economical to acquire a more accurate estimate of the quality of an encountered option by resampling than to continue search for a new candidate that is certain to surpass the previous one in quality. In some species, candidates are rarely or never revisited during mate search while in others (mostly birds) a majority of mate search sequences include repeated assessment (Gibson and Langen 1996); it would be worthwhile to investigate whether in the former species the candidate pool is inexhaustible given the time and energy allocated for mate assessment, and in the latter the candidate pool is small enough that choosers can afford to exhaustively compare most promising candidates.

Interestingly, scrub-jays are always relatively more likely to repeat sampling the same peanut or return to a previously sampled candidate near the end of a search than earlier in the sampling sequence. Even when options are unlimited, at some point during a search the benefit of acquiring a candidate that surpasses the current best will not compensate for costs incurred during the extensive search required to locate it (Real 1990). At this point, it may still be worth reducing uncertainty about the top encountered candidates if there is a possibility of having erred in the initial ranking of their quality and the costs of re-locating and reassessing them are low.

Psychological factors affecting peanut assessment

Scrub-jays make very fine comparisons between very similar peanuts to select accurately a high-quality item. Economic models of choice make rather simple and probably unrealistic assumptions about how animals perceive and recall differences among candidates (Shettleworth 1998). The fields of perceptual and cognitive psychology may provide clues for how to add greater biological realism to these economic models. Three areas are clearly relevant to how scrub-jays choose high-quality peanuts.

First, for the same absolute difference between stimuli, discriminability declines as the mean magnitude increases (Weber's Law) for many perceived quantities including the amount or size of food (Killeen et al. 1993; Bateson and Kacelnik 1995; Kacelnik and Bateson 1996). This appears to be true for western scrub-jays choosing between similar-sized peanuts as well (Langen and Gibson 1998). Relative scaling of sensory discriminations is probably the consequence of greater inherent uncertainty in estimates of large magnitude (the variance of an estimate increasing with the mean; Gescheider 1997). Because of this, the net value of information provided by assessment will vary depending on the magnitude of a stimulus being assessed; it will be more costly to reach the same level of accuracy at discriminating between two large candidates than two small candidates of the same absolute difference. For scrub-jays, this can result in a lower net benefit of accurate choice when discriminating between pairs of large peanuts, since more extensive assessment is required to attain the same expected increase in the amount of food above random choice than when choosing between two small peanuts with the same absolute difference in mass.

Second, some patterns of assessment may be more informative than others. Empirical evidence suggests that by alternating bouts of assessment between two stimuli, they can be more accurately discriminated than if the same quantity of assessment is performed as a single bout for one stimulus followed by a single bout for the other (Honey et al. 1994; Symonds and Hall 1995; Honey and Bateson 1996). Consistent with this idea, jays often repeatedly alternate samples between two peanuts when resampling candidates. Such runs are also observed in some studies of mate choice (e.g., Trail and Adams 1989; Bensch and Hasselquist 1992; Hovi and Ratti 1994; Fiske and Kålås 1995; Gibson 1996; Dale and Slagsvold 1997),
and may represent a strategy to maximize the information acquired during comparisons.

Finally, memory of a perception may become increasingly uncertain with time and intervening events, resulting in the estimate of its magnitude regressing toward some average value (Hellström 1985; Algom et al. 1985; Algom 1992). Likewise, when many similar stimuli are assessed in a series, recall error can be substantial, a phenomenon known as interference (Wright et al. 1986; Hampton et al. 1998). The search tactics of animals may correct for the loss of information that occurs during serial encounters of similar candidates by reassessment of selected, favored ones to refresh the animals’ memories. Regular reassessment may be economical even when an initial assessment of a candidate is accurate, if recall accuracy declines rapidly.

This may help explain why scrub-jays are much more likely, when resampling, to resample the peanut handled immediately previously in a search sequence, and why the peanut that is ultimately selected is often the most frequently sampled candidate. At least under conditions that promote retrospective searches, scrub-jays appear to select initially a promising candidate which is used as a standard of comparison. Sequentially, each new peanut is compared with this standard, and is either rejected or becomes the new standard if judged larger than the previous standard. A representative search sequence of five sampled peanuts resembles the following (where each letter corresponds to a different peanut): ABCACDCDECC. Thus, scrub-jays behave as if they only store in memory two size estimates based on sampling, a standard and the latest candidate in the search sequence, and they often refresh their estimate of the standard by resampling it before handling a new candidate.

Unresolved issues

Three major issues remain unresolved as to how scrub-jays select peanuts. First, it is unknown how scrub-jays develop the ability to economically sort through a pile of nuts. Young jays perform little sampling behavior and are very inaccurate at choosing a large peanut even when the risk of pre-emption is low (T.A. Langen, personal observation); considerable learning may be necessary to develop the motor, perceptual, and cognitive skills necessary for accurate, economical decision-making. Second, it is unclear to which cues scrub-jays principally attend during visual scanning and handling of peanuts. Visual size, color, mass, density, and tactile cues provided by shaking all appear to be used during choice (T.A. Langen, unpublished work). Since multiple cues can be integrated in various ways to make discriminations (Fetterman 1996), it remains an intriguing question as to how scrub-jays weight multiple sources of information when assessing the quality of a peanut. Finally, a model of choice behavior needs to be developed that makes quantitative predictions about how animals ought to assess options when faced with a problem qualitatively similar to that faced by a scrub-jay at a feeder. Besides revealing how well jays perform relative to an optimal assessor, it may also indicate what sampling patterns are to be expected when an assessor is subject to various economic and cognitive constraints.

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