Animal Behaviour 86 (2013) 783–789

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 1 April 2013
Initial acceptance 30 May 2013
Final acceptance 16 July 2013
Available online 23 August 2013
MS. number: A13-00284R

Keywords:
caching
Cyanocitta stelleri
food preference
optimal foraging
perishability
sampling
Steller's jay

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.

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 & Hoshooley 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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0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2013.07.018

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 km^2, 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, 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.

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.

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.