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MECHANISMS OF CACHE DECISION MAKING IN FOX SQUIRRELS (*SCIURUS NIGER*)

Stephanie D. Preston* and Lucia F. Jacobs

Department of Psychology, 530 Church Street, University of Michigan, Ann Arbor, MI 48109, USA (SDP)
Department of Psychology, 3210 Tolman Hall, University of California–Berkeley, Berkeley, CA 94720, USA (LFJ)

The cache decisions of scatter-hoarding animals are influenced by a number of factors, including satiety, food quality, number of competitors, and the risk of predation and pilferage. However, it is unknown how animals assess these variables. We investigated this process experimentally in free-ranging fox squirrels (*Sciurus niger*) by measuring the effects of nut characteristics and social context on nut-handling behavior and subsequent cache decisions. We found that a behavior involved in nut handling, the head flick, was correlated with nut quality, shell presence, the decision to cache rather than eat the nut, and the time and energy spent caching. In contrast, a 2nd nut-handling behavior, the paw maneuver, was correlated with the social context but not the cache decision, and may instead reflect a response to social competition. Our results suggest that fox squirrels assess nut quality using overt, observable nut-handling behaviors. The experimental study of these behaviors can help us understand how animals use information about food and the social context to make adaptive food-storing decisions.

Key words: behavioral ecology, caching, decision, economic investment, food-storing, foraging, scatter-hoarding

To maximize fitness, animals must make accurate foraging decisions (Stephens and Krebs 1986). Obligate scatter-hoarding species rely on the success of thousands of cache decisions during a seasonal harvest to survive subsequent periods of extreme drought or cold (Andersson and Krebs 1978; Smith and Reichman 1984; Vander Wall 1990). For example, North American fox (*Sciurus niger*) and eastern gray (*S. carolinensis*) squirrels do not hibernate and must cache intensely during the fall masting season to have enough food to survive the winter (Cahalane 1942; Stapanian and Smith 1978; Steele et al. 2006; Thompson 1978), a period of up to 9 months that includes their major breeding season (Koprowski 1994a, 1994b). Thus, in a short period of time, and in the midst of intense social competition, tree squirrels make thousands of economic investments that affect immediate survival and long-term reproductive fitness.

In response to this strong selective pressure, tree squirrels should tailor their cache investment (i.e., the amount of time and energy spent caching) to the context, such as the quality of the nut, food availability, and social competition (Vander Wall 1990). Indeed, extensive research has demonstrated effects of seed size, fat content, and tannin concentration on cache decisions. Larger seeds (Jansen et al. 2004) and seeds with higher fat or lower tannin concentrations or both (Moore et al. 2007; Xiao et al. 2006) are removed more quickly than smaller seeds. Larger seeds also are more likely to be scatter-hoarded than eaten (Jansen et al. 2004; Muñoz and Bonal 2008; Xiao et al. 2005, 2006), are recached more often, and are eaten more quickly after caching (Xiao et al. 2005). These effects are adaptive for both scatter-hoarding animals and trees because larger nuts not only provide more energy, but survive longer as caches, and result in a higher proportion of emerged seedlings (Jansen et al. 2004; Xiao et al. 2004; but see Zhang et al. 2008). Scatter-hoarders' selection and dispersal decisions have also been shown to be sensitive to food availability (Jansen et al. 2004; Moore et al. 2007; Tamura et al. 1999), the size of the seed relative to the animal (Muñoz and Bonal 2008), handling time (Jacobs 1992), and perishability (Steele et al. 2006). Social factors also affect caching because squirrels take food farther from the source when pilferage is more likely (Leaver et al. 2007; Tamura et al. 1999), even turning their backs to potential competitors (Leaver et al. 2007).

Thus, extensive evidence shows that squirrels use information about the quality of nuts when making cache decisions, but it is unknown which features they attend to or how they process the information perceptually. There are many possible indicators of nut quality that squirrels could use, including sensory indices of species (texture and color), size, weight, density, or presence of a shell (associated with decreased

* *Correspondent: prestos@umich.edu*

perishability). Although many experiments show effects of seed size, size is highly confounded with weight, which has not been dissociated. Two nut-handling behaviors (described below) could potentially function to assess the size or weight of a nut—the previously described ''paw maneuvers'' (PMs) or the previously undescribed ''head flick'' (HF).

There is a precedent for food-assessment behaviors. Pinyon jays (*Gymnorhinus cyanocephalus*) and Clark's nutcrackers (*Nucifraga columbiana*) use ''bill-clicking'' (the mandibles are clicked against a seed in the mouth), which may be an auditory assay of seed quality, and ''bill-weighing'' (a seed is picked up and retained or quickly dropped), which could assess weight (see Johnson et al. [1987] for nutcrackers and Ligon and Martin [1974] for jays). Bill-clicking was observed in hand-raised juvenile jays, suggesting that the behavior is partially independent of experience, but it must also be subject to learning because its use changed with seed-handling experience (Eibl-Eibesfeldt and Kramer 1958). Extensive testing has not confirmed these hypotheses.

Three experiments were performed, each testing 1 hypothesis associated with increased caching of higher-quality nuts and 1 hypothesis proposing a role for the HF or PM in assessing such qualities. Experiment 1 proposed that caching and the cache investment increase for nut species with higher nutritional content, and that HFs and PMs assess nuts for caching. Experiment 2 proposed that the presence of the shell reduces perishability, which increases caching and the cache investment, and that HFs and PMs increase for nuts in the shell (when the status of the nut is less certain). Experiment 3 proposed that squirrels increase caching and the cache investment for heavier nuts, holding size constant, and that the HF is used to assess weight by applying a known force, not by causing an audible rattle of the nut inside the shell.

Materials and Methods

All research on live animals was approved by the Animal Care and Use Committee of the University of California, Berkeley (protocol R188) and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Study sites and animals.—All experiments were conducted on 2 sites on the University of California, Berkeley, campus (Jacobs and Shiflett 1999) consisting of bluegum eucalyptus (*Eucalyptus globulus*), redwood (*Sequoia sempervirens*), and coast live oak (*Quercus agrifolia*) trees. Location A was a grassy field approximately 15 m in diameter, bordered on the eastern side by a eucalyptus grove and on the western side by a small campus road. Location B was approximately 300 m north of location A, with a lower density of trees (of the same species) in planting beds and grassy areas among campus buildings. The locations are independent, with different resident squirrels that were never observed at the opposing location. Campus fox squirrels are habituated to the presence of humans and can be observed at close distances. To individually identify the animals for testing, squirrels were marked by applying a small amount of a permanent black dye (Nyanzol D, Albinal Dyestuff Inc., Jersey City, New Jersey) to the fur of the back or flanks by gently squirting the liquid from a distance with a disposable syringe or bulb pipette.

Procedures.—All experiments consisted of individual sessions where the experimenter gave a single focal squirrel 1 nut at a time, from a single feeding location, placing the nut on the ground when the squirrel approached. The next nut was not given until the prior nut was eaten or cached. The session continued until the squirrel failed to return or the experimental nut sequence was exhausted. Multiple sessions across days ensured that a single individual received sufficient nuts for analysis. Each day 1 or 2 squirrels were tested, within approximately 2 h.

All experiments began with a prefeeding stage whereby squirrels were fed peanuts removed from the shell to increase the probability of caching during the experiment. After prefeeding, the focal squirrel received the experimental series of up to 4 nut types, with the shell already removed or intact, including peanuts (*Arachis hypogaea*), almonds (*Prunus dulcis*), and hazelnuts (*Corylus avellana*). We use the term ''nut'' throughout, even though peanuts are technically woody, indehiscent legumes.

Behavioral measurements.—The foraging decision was recorded for each nut (eat or cache). Squirrels never rejected an item, eating or caching all items. Typically, squirrels ate the nut at the feeding location or left to cache. Once the squirrel left the feeding location, the experimenter followed it at the farthest distance possible to record the number of digs and the total cache distance. A dig was defined as a discrete event, where the squirrel stops with a nut in its mouth, digs with its front paws as if to cache, but continues to a new location.

Statistics.—Data were analyzed using JMP 5.2.1 for Macintosh (SAS Institute Inc., Cary, North Carolina). Because this study took place in a free-ranging population, we could not perfectly control the subject pool, sample size, or trial numbers. To account for this heterogeneity in sampling, and the effect of the individual, all analyses were done using the general linear model (GLM) with the standard least-squares fit and reduced with the restricted maximum-likelihood (REML) procedure, entering squirrel identity as a nominal, random effects factor. The alpha level for all analyses was 0.05.

We recorded 2 types of nut-handling behaviors, the PM and the HF. PMs are manipulations of the food item by the front paws while the item is held loosely in the mouth and front paws. The movements occur among all possible axes, rolling the nut along its horizontal and longitudinal axis while braced against the mouth and rotated using the front paws. The PM was previously observed in hand-raised naïve Eurasian red squirrels (*S. vulgaris*) in response to their 1st nut at the age of 2.5 months (Eibl-Eibesfeldt 1951, 1963), suggesting it is independent of experience. Because the behavioral phenotype of the PM involves multiple movements that are not stereotyped or sequenced, we predict that the PM is necessary for basic goal-directed movements (opening, eating, and placing in teeth for caching) and to assess superficial qualities

(species and shell presence and integrity) to make cache decisions.

The HF is a sudden, saccadic movement of the entire head while a food item is held in the mouth, without support from the paws (see videos available online at http://dx.doi.org/10.1644/08-MAMM-A-254.s1). This behavior is only observed after the squirrel has taken a food item into its mouth and has ceased PMs, virtually always while the animal is situated upright, resting on 2 hind legs, and in no other context. This behavior has not been previously described in any species of *Sciurus*, nor in any mammalian scatter-hoarder, despite lengthy monographs on the Eurasian red squirrel and eastern gray squirrel (Eibl-Eibesfeldt 1951, 1956, 1963). We recorded any instances of the PM or HF from the time the squirrel received the nut until caching. In contrast to the PM, the HF is a single, stereotyped movement whereby the squirrel applies rapid sideways acceleration to the nut. Because of this, we predict that the HF is necessary, once the PM has determined that a nut is worth caching, to assess the weight of the nut, in order to tailor the cache investment to the weight.

To rule out an alternative hypothesis, that nut-handling behaviors are simply displacement movements reflecting an anxious state (cf. Maestripieri et al. 1992), we recorded the extent to which the squirrel demonstrated a defensive posture while retrieving the nut. The defensive posture was recorded categorically as a ''1'' or ''2'' according to the degree to which the squirrel's tail was curled back over its dorsal surface. A ''1'' was entered if the tail was raised, but more vertical than horizontal; a ''2'' was entered if the tail was fully curled and placed forward, horizontal over the surface of its back.

To assay the level of social competition, we recorded the number of animals in the general area (within 15 m of the feeding location; chosen because it captured the space within which squirrels typically attended to the experimenter and focal squirrel).

In each experiment, we 1st performed a GLM to model the relationship between nut quality and the cache decision (eat versus cache). Except where noted, nut type was entered as a nominal independent variable, the identity of the squirrel was entered as a nominal, random effects factor, and the decision to eat (0) or cache (1) was entered as the dependent variable.

Subsequently, we restricted analysis to cached nuts (not eaten) and performed 2 GLMs to separately test the effect of nut type on the cache investment based on the number of digs before caching, and the total cache distance in meters. Again, nut type was entered as a nominal independent variable, squirrel identity as a nominal, random effects factor, and the number of digs and total distance as continuous dependent variables.

Next, we performed a GLM on cached nuts to test the hypothesis that social context affects the number of digs before caching. The number of conspecifics in the area at the time of testing was entered as a continuous independent variable, squirrel identity as a nominal random effects factor, and number of digs as a continuous dependent variable.

We similarly performed a series of tests to investigate the role of nut-handling behaviors (HF and PM) on the cache decision and investment. Two GLMs were performed to separately test the effect of the presence of HF or PM on the decision to eat versus cache. HF and PM were entered as nominal independent variables, squirrel identity as a nominal, random effects factor, and the decision to eat (0) or cache (1) as the dependent variable.

Subsequently, we looked to see if nut type affected the likelihood of a HF or PM. Two GLMs were performed to separately test the effect of the nut type on the likelihood of a HF or PM. Nut type was entered as a nominal independent variable, squirrel identity as a nominal, random effects factor, and the presence (1) or absence (0) of the nut-handling behavior as the dependent variable.

To test the alternative hypothesis that the HF and PM simply reflect anxiety, we performed a GLM to determine if the social context affected the presence of the HF or PM. Two GLMs were performed to separately test the effect of the number of squirrels in the area on the likelihood of a HF or PM. Two additional GLMs were performed to separately test the effect of the defensive posture while retrieving the nut on the likelihood of a HF or PM. For these tests, the number of squirrels in the area was entered as a continuous independent variable, defensive posture as a nominal independent variable, squirrel identity as a nominal, random effects factor, and the presence (1) or absence (0) of the nut-handling behavior as the dependent variable.

Experiment 1: Influence of Nut Species

Experiment 1 tested the hypothesis that caching and the cache investment increase for nuts with higher nutritional content (see Table 1 for the nutrition information on the 3 nut types). In brief, hazelnuts are highest across multiple relevant features including average weight per nut, water, energy, total lipids, sugars, thiamin, and vitamin B-6. Almonds are intermediate, being highest in proportional shell weight (refuse), carbohydrates, fiber, multiple minerals (calcium, magnesium, phosphorus, and potassium), riboflavin, and 4 amino acids. Peanuts are generally the smallest, and lower in most salient features, but are higher in almost all amino acids. Other sources confirm that for total fat content, dry matter, and calories, peanuts $<$ almonds $<$ hazelnuts (Kornsteiner et al. 2006; Kris-Etherton et al. 1999). Therefore, this ordering also was expected in the rate of caching and the cache investment. Experiment 1 also tested the hypothesis that HFs and PMs are nut-assessment techniques applied across species to tailor the investment to the weight of the nut; as such, these behaviors predict the cache outcome.

Methods.—Six squirrels participated in this study at location A. After a squirrel began caching unshelled peanuts, they were offered peanuts, almonds, and hazelnuts, all removed from the shell.

Results.—The decision to eat or cache differed by nut species (Fig. 1). Peanuts and hazelnuts were eaten more often than almonds, the latter of which were almost always cached (least squares mean [LSM] proportion cached: peanuts = 0.29,

Table 1.—Comparison of nutrients in the edible portion of peanuts (*Arachis hypogaea*), almonds (*Prunus dulcis*), and hazelnuts (*Corylus*). Data were taken from the United States Department of Agriculture *National Nutrient Database for Standard Reference*, *Release 21*, using the following identification numbers: 12061, 16390, and 12120 (United States Department of Agriculture, Agricultural Research Service 2008). Nutrients with negligible values or without data for all 3 types were excluded. Average weight per nut was not listed for peanuts (NA), but was assumed to be less than that of the other types. Data are highly variable depending on the source and the exact nut type. Other sources (Kris-Etherton et al. 1999; Kornsteiner et al. 2006) indicate that for total fat, fat content (percent of dry weight), dry matter (percent dry weight), and calories, peanuts < almonds < hazelnuts.

			Value per 10 g			
Category	Nutrient	Unit	Peanuts	Almonds	Hazelnuts	Ordering
	Typical weight/nut	g	NA	1.2	1.4	P < A < H
	Refuse (shells)	%	27[a]	60	54	P < H < A
Proximates	Water	g	0.16	0.47	0.53	P < A < H
	Energy	kcal	56	58	63	P < A < H
	Energy	kJ	245	241	263	A < P < H
	Protein	g	2.37	2.12	1.5	H < A < P
	Total lipid (fat)	g	4.97	4.94	6.08	A < P < H
	Carbohydrate	g	2.15	2.17	1.67	H < P < A
	Fiber, total dietary	g	0.8	1.2	1	P < H < A
	Sugars, total	g	0.42	0.39	0.43	A < P < H
Minerals	Calcium	mg	5	26	11	P < H < A
	Iron	mg	0.23	0.37	0.47	P < A < H
	Magnesium	mg	18	27	16	H < P < A
	Phosphorus	mg	36	48	29	H < P < A
	Potassium	mg	66	70	68	P < H < A
	Zinc	mg	0.33	0.31	0.25	H < A < P
	Copper	mg	0.067	0.100	0.173	P < A < H
	Manganese	mg	0.208	0.229	0.618	P < A < H
Vitamins	Thiamin	mg	0.044	0.021	0.064	A < P < H
	Riboflavin	mg	0.010	0.101	0.011	P < H < A
	Niacin	mg	1.353	0.339	0.180	H < A < P
	Pantothenic acid	mg	0.140	0.047	0.092	A < H < P
	Vitamin B-6	mg	0.026	0.014	0.056	A < P < H
	Folate, total	mcg	14	5	11	A < H < P
Lipids	Fatty acids, total:					
	Saturated	g	0.689	0.373	0.446	A < H < P
	Monounsaturated	g	2.464	3.089	4.565	P < A < H
	Polyunsaturated	g	1.569	1.207	0.792	H < A < P
Amino acids	Tryptophan	g	0.023	0.021	0.019	H < A < P
	Threonine	g	0.081	0.060	0.050	H < A < P
	Isoleucine	g	0.083	0.070	0.055	H < A < P
	Leucine	g	0.154	0.149	0.106	H < A < P
	Lysine	g	0.085	0.058	0.042	H < A < P
	Methionine	g	0.029	0.015	0.022	A < H < P
	Cystine	g	0.030	0.019	0.028	A < H < P
	Phenylalanine	g	0.123	0.112	0.066	H < A < P
	Tyrosine	g	0.096	0.045	0.036	H < A < P
	Valine	g	0.099	0.082	0.070	H < A < P
	Arginine	g	0.283	0.245	0.221	H < A < P
	Histidine	g	0.060	0.056	0.043	H < A < P
	Alanine	g	0.094	0.103	0.073	H < P < A
	Aspartic acid	g	0.289	0.291	0.168	H < P < A
	Glutamic acid	g	0.495	0.681	0.371	H < P < A
	Glycine	g	0.143	0.147	0.072	H < P < A
	Proline	g	0.104	0.103	0.056	H < A < P
	Serine	g	0.117	0.095	0.073	H < A < P

[a] Data from different source (Leonard 1903).

hazelnuts = 0.60, almonds = 0.83; GLM: $F = 10.00$, $d.f. = 2, 142$, $P < 0.0001$).

Among cached nuts, the investment into the cache episode did not differ significantly by species, but was always in the direction of greater effort as quality increased. On average, squirrels took better nuts farther (LSM cache distance in meters: peanuts = 5.68, almonds = 9.82, hazelnuts = 12.55; GLM: $F = 2.01$, $d.f. = 2, 84$, $P = 0.14$) and made more digs (LSM number of digs: peanuts = 1.28, almonds = 1.87, hazelnuts = 2.02; GLM: $F = 0.98$, $d.f. = 2, 84$, $P = 0.38$).

Table 2.—Frequencies and proportions of each possible behavioral sequence by fox squirrels (*Sciurus niger*), broken down by trials where the nut is eaten or cached. This information demonstrates the relative importance of each behavior, and their typical sequencing. For example, no behaviors at all (''none'') were typical in experiment 2 when squirrels were offered 2 clearly different nuts (peanuts and hazelnuts), whereas paw maneuver (PM) and head flick (HF) behaviors were frequent when the choices were more similar and more difficult to distinguish (e.g., all almonds of the same size varying in weight in experiment 3). Typically, cached nuts received a HF then a PM, but almost never the other way around. Only the 1st and 2nd behaviors in a sequence are included (e.g., PM followed by HF), ignoring additional behaviors that took place in a minority of trials (e.g., PM followed by HF, followed by another PM and another HF).

Behavior sequence		Frequency	% of total	No. eaten	No. cached	% cached
Experiment 1	None	57	38	25	32	56
	PM only	14	9	13	1	7
	HF only	29	19	13	16	55
	PM, HF	39	26	6	33	85
	HF, PM	11	7	2	9	82
	Total	150	100	59	91	61
Experiment 2	None	87	33	47	40	46
	PM only	39	15	15	24	62
	HF only	65	25	8	57	88
	PM, HF	60	23	20	40	67
	HF, PM	14	5	2	12	86
	Total	265	100	92	173	65
Experiment 3	None	20	7	5	15	75
	PM only	101	34	30	71	70
	HF only	24	8	0	24	100
	PM, HF	150	50	6	144	96
	HF, PM	5	2	1	4	80
	Total	300	100	42	258	86

Replicating previous findings for social context (Leaver et al. 2007), squirrels made more digs when there were more squirrels in the area (GLM: $F = 6.16$, $d.f. = 1, 89$, $P = 0.015$).

The HF was associated with the decision to cache, because squirrels were twice as likely to HF before caching (LSM = 0.58) than eating (LSM = 0.27; GLM: $F = 13.30$, $d.f. = 1, 143$, $P = 0.0004$; Table 2). Conversely, there was no relationship between caching and PMs (GLM: $F = 2.50$, $d.f. = 1, 143$, $P = 0.12$). The likelihood of HFs and PMs did not differ by nut (GLM: $F < 2.07$, $d.f. = 2, 65$, $P > 0.13$) and did not predict the number of digs (GLM: $F < 0.22$, $d.f. = 1, 85$, $P > 0.64$) or cache distance (GLM: $F < 0.61$, $d.f. = 1, 85$, $P > 0.43$).

The defensive posture of the squirrel while taking the nut was not related to HFs or PMs (GLM: $F < 3.87$, $d.f. = 1, 143$, $P = 0.051$). There was also no relationship between the number of squirrels in the area and HFs (GLM: $F = 1.05$, $d.f. = 1, 143$, $P = 0.31$), although PMs occurred more when more squirrels were nearby (GLM: $F = 5.33$, $d.f. = 1, 143$, $P = 0.02$).

Experiment 2: Influence of Nut Shell

In experiment 1, the HF highly predicted caching and was not associated with defensive behavior or social competition, whereas the PM showed the opposite pattern. If the HF indeed functions to assess nuts, the incidence should increase when nuts are in the shell. Experiment 2 tested this hypothesis. Peanuts and hazelnuts were provided with and without the shell. Squirrels were predicted to cache nuts in the shell more than nuts without shells, supporting handling time (Jacobs 1992) and perishability (Steele et al. 2006) hypotheses, and the HF was expected to increase for nuts in the shell, when information about nut quality is less available. To address possible issues of power for null effects, 2.5 times more squirrels were tested in experiment 2 than in experiment 1.

Methods.—Fifteen squirrels from 2 locations participated in this study. After a squirrel began caching unshelled peanuts they were offered a random series of peanuts and hazelnuts, shelled or unshelled. All other procedures were as described for experiment 1.

Statistics.—Statistics were identical to those in experiment 1, but with 2 independent variables tested simultaneously using a fully factorial model. Nut type was entered as a nominal independent variable with 2 levels (peanut, hazelnut), presence or absence of the shell was entered as a nominal independent variable with 2 levels (0, 1), and their interaction was entered separately (as with all previous tests, squirrel identity was entered as a nominal random effects factor). Total cache distance was not recorded in this study, so only the number of digs indicated cache investment.

Results.—Squirrels again increased effort for better nuts (LSM likelihood of caching: peanuts out of the shell = 0.29, peanuts in the shell = 0.51, hazelnuts out of the shell = 0.36, hazelnuts in the shell = 0.63; Fig. 2). Hazelnuts were cached more often than peanuts (GLM, effect of nut: $F = 7.65$, $d.f. = 1, 248$, $P = 0.006$) and nuts in the shell were cached more often than nuts removed from the shell (GLM, effect of shell: $F = 6.98$, $d.f. = 1, 246$, $P = 0.009$), but nut type and shell did not interact (GLM, interaction: $F = 0.16$, $d.f. = 1, 246$, $P = 0.69$).

As in experiment 1, the investment into cached nuts (digs) did not differ significantly by nut type, but was in the

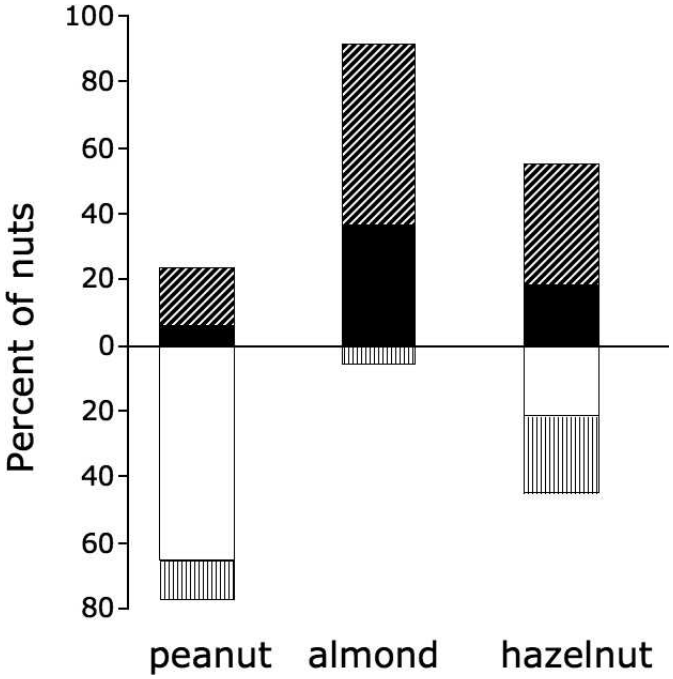

Fig. 1.—The effect of nut species on cache decision by fox squirrels (*Sciurus niger*). Each bar represents an average, across individual squirrels, of the percent of trials where the nut was subjected to a behavioral treatment. In the positive direction, the total percent reached (e.g., 22% for peanuts) represents the average percent of trials where the nut was cached. This measure of caching is further broken down by the proportion of trials without a head flick (HF; filled black region) and with a HF (black region with white diagonal stripes). In the negative direction, the total percent reached (e.g., 78% for peanuts) represents the average percent of trials where the nut was eaten. This measure of eating is further broken down by the proportion of trials without a HF (unfilled region), and with a HF (unfilled region with black vertical stripes).

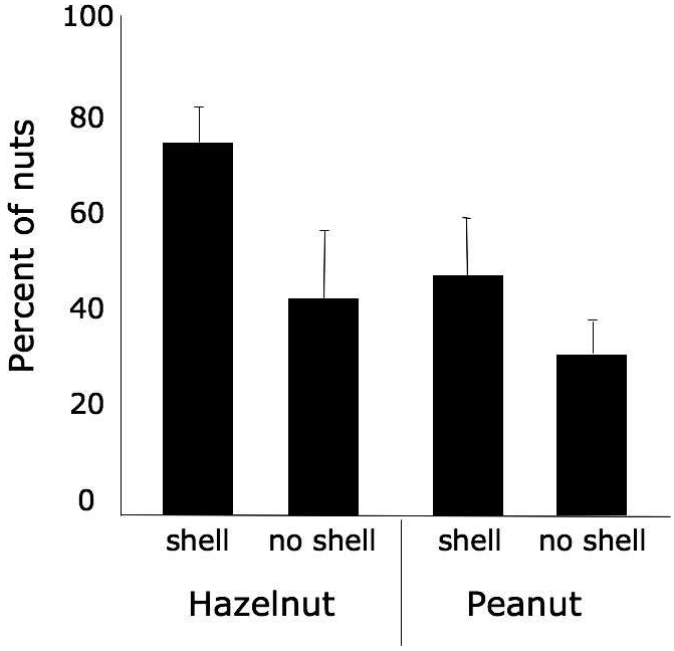

Fig. 2.—The effect of nut shell on cache decision by fox squirrels (*Sciurus niger*). Bars indicate the percent of nuts of each type (hazelnuts and peanuts) given a head flick, separated by whether the nut had the shell intact or not. Bars are averages of the percent of trials for each individual, with error bars representing the variation in *SE* across individuals in this proportion.

predicted direction (LSM number of digs: peanuts out of the shell = 1.69, peanuts in the shell = 1.73, hazelnuts out of the shell = 1.99, hazelnuts in the shell = 2.12). On average, squirrels made more digs before caching the hazelnuts than peanuts (GLM: $F = 1.75$, $d.f. = 1, 156$, $P = 0.19$), but did not make more digs for nuts in the shell versus out of the shell, and the 2 variables did not interact (GLM: $F < 0.09$, $d.f. = 1, 156$, $P > 0.75$). In contrast to experiment 1, squirrels did not increase digs with the number of competitors present (GLM: $F = 1.57$, $d.f. = 1, 159$, $P = 0.21$).

Mirroring the effects from experiment 1, the HF and PM occurred in different contexts (Table 2). The decision to eat or cache was associated only with the HF, occurring twice as often for cached (LSM = 0.64) than eaten (LSM = 0.34) nuts (GLM: $F = 15.73$, $d.f. = 1, 249$, $P < 0.0001$). Again, there was no relationship between caching and PMs (GLM: $F = 2.13$, $d.f. = 1, 249$, $P = 0.15$).

The likelihood of the HF for cached nuts increased with quality (LSM likelihood of HF: peanuts out of the shell = 0.26, peanuts in the shell = 0.47, hazelnuts out of the shell = 0.56, hazelnuts in the shell = 0.75; Fig. 2). Squirrels HF hazelnuts more than peanuts (GLM: $F = 12.86$, $d.f. = 1, 246$, $P = 0.0004$) and nuts in the shell more than nuts removed from the shell (GLM: $F = 4.51$, $d.f. = 1, 246$, $P = 0.03$), but nut type and shell did not interact (GLM: $F = 0.002$, $d.f. = 1, 246$, $P = 0.96$). PMs were only more likely to occur for nuts in the shell than removed from the shell (GLM: $F = 11.28$, $d.f. = 1, 246$, $P = 0.0009$), but did not differ by species or the interaction with shell (GLM: $F < 1.97$, $d.f. = 1, 246$, $P > 0.15$; LSM likelihood of PM: peanuts out of the shell = 0.27, peanuts in the shell = 0.48, hazelnuts out of the shell = 0.25, hazelnuts in the shell = 0.68). HFs and PMs again did not predict digs (GLM: $F < 1.00$, $d.f. = 1, 159$, $P > 0.31$).

Head flicks increased when squirrels were less hesitant retrieving the nut (GLM: $F = 6.80$, $d.f. = 1, 249$, $P = 0.0097$). The defensive posture was unrelated to PMs (GLM: $F = 0.013$, $d.f. = 1, 249$, $P = 0.91$). The number of competitors did not affect HFs or PMs (GLM: $F < 2.53$, $d.f. = 1, 249$, $P > 0.10$).

Experiment 3: Influence of Nut Weight and Movement

Size, volume, and species can be ascertained from visual cues or PMs, and thus likely drive the decision to cache. In contrast, weight is not directly observable, but could be determined from the HF and used to tailor the investment in nuts that will be cached. However, the HF causes the nut to collide with the shell, which could indicate infestation because infested nuts occupy less of the shell, or are detached, or both. The HF also could assist in weight determination by allowing

evaluation of the force of the nut against the shell or the resulting sound. Experiment 3 was designed to dissociate these hypotheses.

Nuts were created to vary in weight and movement of the nut inside the shell while holding size of the shell constant. Squirrels were predicted to cache heavier nuts but not nuts that rattled, and the HF, but not the PM, was expected to predict cache investment into heavier nuts. To further address possible issues with power for null effects, additional squirrels were tested.

Methods.—Eighteen squirrels participated in this study from locations A and B. Experimental almonds were created by sawing them open along their natural lengthwise seam and replacing contents of shells of a similar size with contents of known weight. Weight classes were continuous but were categorized by cutoffs (light: < 2 g; medium: < 3 g; heavy: > 3 g). For light, medium, and some heavy nuts, the interior was replaced with almond seeds that were shaven or taken from other shells to achieve the desired weight. To create the heaviest nuts (>4.5 g), while still fitting them into the shells, the contents were replaced with a ''hex nut'' (a hexagonal hardware fastener with a threaded hole) glued to pieces of gravel using Elmer's Wood Glue (nontoxic; Elmer's Products, Inc., Columbus, Ohio). To manipulate nut movement, in one-half of the nuts the replaced material was glued to the shell, in the other one-half the same amount of glue was applied to the shell without impeding nut movement.

Each trial began with a series of 6 single unshelled peanuts offered sequentially to the focal squirrel. The squirrel was then offered a series of light, medium, and heavy reconstructed almonds that either had a moving or immobile nut. Because the first 2 experiments found no effect of the defensive posture, this measure was excluded. We additionally recorded the number of conspecifics in the immediate area at the time of nut retrieval and the amount of time (in seconds) the squirrel spent caching.

Statistics.—Analyses were performed as in experiments 1 and 2. To additionally test our hypothesis, a GLM was performed to model the relationship between nut weight, movement of the nut, and their interaction on the decision to eat or cache the nut. Total nut weight including the nut and shell was entered as a continuous independent variable, the presence or absence of movement of the nut in the shell as a nominal independent variable, and the interaction between the 2 as separate factors with squirrel identity entered as a nominal, random effects factor. An additional test was run on the number of conspecific competitors, identical to tests of the other measure of competition. An additional test was run on the time spent caching, identical to tests of the number of digs.

Results.—Heavier nuts were more likely to be cached ($R^2 = 0.19$, GLM: $F = 5.59$, $d.f. = 1, 238$, $P = 0.02$) but movement of the nut inside the shell did not affect caching or interact with weight (GLM: $F < 0.14$, $d.f. = 1, 238$, $P > 0.70$).

Among cached nuts, squirrels carrying heavier nuts made more digs (GLM: $F = 5.36$, $d.f. = 1, 249$, $P = 0.02$), but did not spend more time caching (GLM: $F = 0.466$, $d.f. = 1, 94$, $P = 0.50$) or cache farther (GLM: $F = 0.43$, $d.f. = 1, 251$, $P = 0.51$). As in experiment 2, the number of conspecifics in the general area or in the immediate area during retrieval did not influence digs (GLM: $F < 1.13$, $d.f. = 1, 107$, $P > 0.29$).

Squirrels were again much more likely to HF before caching than before eating (GLM: $F = 32.94$, $d.f. = 1, 299$, $P = 0.0001$), which was not true of PMs (GLM: $F = 1.24$, $d.f. = 1, 298$, $P = 0.27$; Table 2). HFs also increased with nut weight (GLM: $F = 5.16$, $d.f. = 1, 241$, $P = 0.02$), but did not differ with movement of the nut or their interaction (GLM: $F < 0.13$, $d.f. = 1, 241$, $P > 0.71$). PM did not differ by weight, nut movement, or their interaction (GLM: $F < 2.62$, $d.f. = 1, 241$, $P > 0.11$).

In cache trials, HFs and PMs did not predict the number of digs (GLM: $F < 0.26$, $d.f. = 1, 254$, $P > 0.61$), but squirrels did spend more time caching if they had made a HF (GLM: $F = 8.08$, $d.f. = 1, 97$, $P = 0.006$), which was not true of the PM (GLM: $F = 0.21$, $d.f. = 1, 98$, $P = 0.65$). Squirrels also tended to take nuts farther after a HF (GLM: $F = 3.76$, $d.f. = 1, 256$, $P = 0.05$) and took nuts significantly farther after a PM (GLM: $F = 5.04$, $d.f. = 1, 256$, $P = 0.03$).

As in the previous 2 experiments, the number of animals in the general area did not influence HFs (GLM: $F = 0.07$, $d.f. = 1, 107$, $P = 0.80$) and the number of animals in the immediate area at the time of retrieval did not predict HFs or PMs (GLM: $F < 1.170$, $d.f. = 1, 103$, $P > 0.28$). As in experiment 1, PMs increased with the number of competitors in the general area (GLM: $F = 6.28$, $d.f. = 1, 107$, $P = 0.014$).

Discussion

How a forager makes decisions is of great theoretical importance (Stephens and Krebs 1986), but in most studies we observe only the product of the decision with little insight into how those decisions are made. In this series of 3 experiments, we found that squirrels are highly influenced by nut quality when deciding to eat or cache. Nut quality can be inferred from the nut species, presence of a shell, and weight, but is unlikely to be affected by whether the nut moves inside the shell.

Previous studies emphasized the effect of nut size (Jansen et al. 2004; Muñoz and Bonal 2008; Xiao et al. 2005, 2006; Zhang et al. 2008), presumably because it is an easily observed variable; however, we propose that weight, handling time, and survivability are more important than size. Squirrels in experiment 2 preferred hazelnuts in the shell to peanuts in the shell; due to the configuration of peanuts, which have 2 nuts per shell, they are larger, but less dense, lighter, and lacking a hard shell. This makes them poorer candidates for caching because they are lighter, easier to eat, and unable to survive long-term caching. In addition, experiment 3 demonstrated that weight affected caching when size of the shell was held constant.

Across all experiments, the HF was strongly associated with caching rather than eating. In contrast, there was no evidence that the HF is a displacement movement associated with

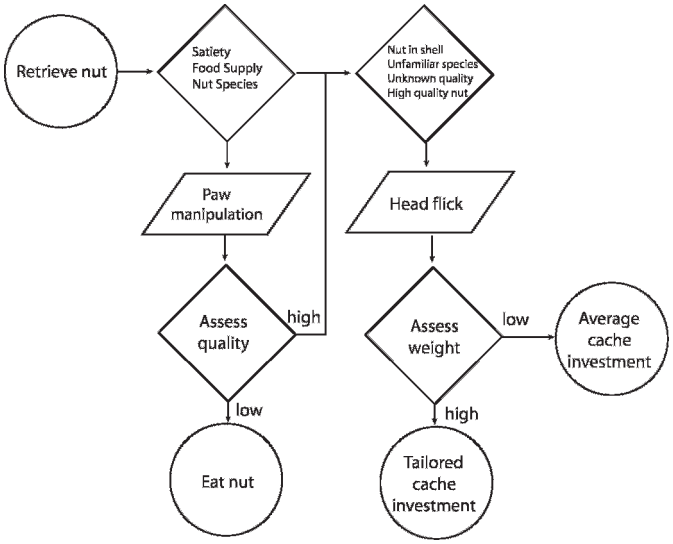

Fig. 3.—Schematic of the proposed sequence of events during a foraging decision by fox squirrels (*Sciurus niger*). Squirrels retrieve the nut, and on the basis of visual, olfactory, and tactile information that includes the paw maneuvers (PMs), animals decide whether to cache. Squirrels eat nuts of low quality, particularly when hungry, and cache nuts of higher quality, particularly when full. Nuts that will be cached are submitted to the head flick (HF), which functions as a secondary assessment, providing additional information about the weight of the nut to tailor the cache investment to the quality of the nut.

human experimenters or conspecific competitors. The PM, in contrast to the HF, was not associated with caching, and increased with conspecific competition in 2 of 3 experiments. However, PMs also increased when the nut was presented in a shell in experiment 2 and predicted cache distances in experiment 3. The PM is proposed to be part of an initial assessment process that can assess nut volume or shell presence, but may include movements that are purely instrumental, such as movements to grasp the nut for eating or for placing in the mouth. Future research needs to focus on the PM, differentiating movements of rotation versus placement, independently manipulating the size of the nut and handling difficulty.

In general, nut quality, likelihood of caching, and likelihood of performing a HF were highly intercorrelated—animals typically performed a HF and cached the vast majority of high-quality nuts, and failed to perform a HF and ate the majority of lower-quality nuts. This pattern suggests the following sequence of events (Fig. 3): Squirrels 1st decide whether to consume or cache the nut. This decision is largely based on immediately accessible cues such as the species of nut (which includes visual and olfactory cues), handling time, available food supply, and hunger. The PM also may be used in this preliminary stage, providing additional tactile cues to assess the nut quality based on size and perishability. Once the animal has decided to cache, a HF is made, which helps determine the weight, based on the resulting acceleration and deceleration after applying a known force. In turn, the result of this secondary assessment determines how much energy to invest while caching, carrying items farther to increase survival (Tamura et al. 1999). Thus, a higher-quality nut is subjected to more assessment, as the squirrel matches assessment expenditure to the quality of the nut.

Direct evidence for the assessment hypothesis of the HF is difficult to obtain, however, because of the almost complete association with caching. This tight correlation precludes a statistical demonstration that heavier nuts subjected to a HF are taken farther than ones that are not subjected to a HF, because there is no comparison group of nuts cached without HFs. In addition, the high correlation between the HF and caching could indicate that it is a motor ''spill over'' effect of increased arousal or motor preparation for caching. It would not be an ''intention movement,'' because it does not contain elements of the cache repertoire (cf. Tinbergen 1951), but it could relate to caching in a less functional way.

Research into the mechanisms of decision making in humans and nonhuman primates has recently flourished, emphasizing complex cognitive and neural (i.e., parietal, striatal, and prefrontal) processes required for adaptive choices. However, behaviors that are critical for survival, such as those related to the allocation of resources, can exert strong selective pressure not only on neural processes, but also on behavioral mechanisms for making adaptive decisions.

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