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REVIEW

Proximate mechanisms of detecting nut properties in a wild population of Mexican Jays (*Aphelocoma ultramarina*)

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Abstract In contrast to extensive research on optimal foraging in birds, the proximate mechanisms by which birds estimate the properties of nuts or seeds have not been well studied. Using slow-motion video-recording and experiments with modified peanuts presented to birds in their natural habitat, we explored these issues in a wild population of the Mexican Jay (*Aphelocoma ultramarina*). Jays evaluated each peanut by performing fast movements of the head combined with additional fast movements of the beak, which may open and subsequently close producing sound at the moment of hitting the shell. These movements seemed to provide Jays with additional sensory information that led to a more strict discrimination against non-preferred peanuts. We presented Jays with two types of peanuts that looked similar but differed in weight and found that, after handling the nuts, Jays consistently preferred the heavier nuts. In another experiment, the visually larger nuts with atypically lower mass (due to experimental alteration) were picked up easily but subsequently were rejected during handling, while the smaller peanuts with the weight typical for the size were easily accepted leading to the preferences for nuts with higher nutmeat density. This indicates that birds may have a concept of how much a nut of a given size should weigh, or alternatively that simple correlation between density of nut content and the properties of sound produced during handling lead to the ability of choosing denser nuts. We discuss further experimental studies that may bring more understanding of the proximate mechanisms of nut content assessment by birds.

Keywords Mexican Jay · Corvidae · Heaviness · Proximate mechanisms · Nuts · Foraging · Food preferences

Introduction

Although preferences for specific food items by foragers have been at the very center of the classical optimality approaches to foraging (Stephens and Krebs 1986; Stephens et al. 2007), the relative paucity of research about proximate sensory mechanisms is puzzling considering the importance of proximate mechanisms in understanding the

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evolution of behavior (Stamps 1991; Crawford 1993). The question of how foraging animals detect the properties of food items is especially intriguing for the species that forage on nuts and other items that have the nutritious part hidden from direct sensory evaluation inside their protective walls or shells. Many corvids cache seeds, acorns and nuts. These birds choose items for caching or consumption by comparing several items without opening them before deciding which one to accept and which one to reject, and are known to prefer nuts/acorns with heavier or denser content (Hubbard and McPherson 1997; Langen and Gibson 1998; Langen 1999; Lutbeg and Langen 2004; Moore and Swihart 2006; Pons and Pausas 2007). Similar abilities have been documented in Bullfinches foraging on sunflower seeds (Greig-Smith and Crocker 1986).

How do the birds know which acorn/nut has a nutritious content? Although several studies included some experiments on proximate mechanisms of nut/seed assessment (e.g., Bossema 1979; Johnson et al. 1987), we are aware of only two experimental studies that specifically focus on the sensory mechanisms that allow birds to evaluate nut/seed content, and only one of them is on corvids (Ligon and Martin 1974), while the other is on chickadees and nuthatches (Heinrich et al. 1997). Forty years ago, Ligon and Martin (1974) used experimentally altered pine nuts and suggested that Pinyon Jays (*Gymnorhinus cyanocephalus*) pay attention to visual cues when choosing a nut to pick up, and that they probably use weight and sound cues while handling the nut in their beak. The latter involve “bill-clicking”, a specific manner of handling the seeds by quickly opening and closing the beak, which produces a clicking sound. Twenty years ago, experimental presentations of normal, empty and plaster-of-Paris-filled sunflower seeds to two species of non-corvid birds, Black-capped Chickadee (*Parus atricapillus*) and the Red-breasted Nuthatch (*Sitta canadensis*), by Heinrich et al. (1997) suggested that sound, mass and rigidity of the shell may somehow be perceived by these birds when evaluating the seed. We are not aware of other experimental studies of this phenomenon in birds, and neither Ligon and Martin (1974) nor Heinrich et al. (1997) used experimental food items that differed in only one cue at a time (e.g., sound) while keeping the other cues (mass, shell rigidity) unchanged. However, the continued interest in the proximate mechanisms of nut evaluation by mammals resulted in an elegant piece of experimental evidence of the importance of auditory cues and sensory perception of heaviness in evaluating nut contents (Visalberghi and Neel 2003). This research brought the area of psychology of heaviness perception (Amazeen and Turvey 1996; Turvey 1996) into the study of wild animals.

We intended to follow this path of inquiry using the Mexican Jay (*Aphelocoma ultramarina*) as our study subject. The Mexican Jays, like many corvids, handle unopened acorns and peanuts, which they often cache for later use without directly inspecting the contents. We therefore expected that they may also be able to evaluate nut content without opening the nuts. Here, (1) we report results of field experiments to test the idea that Mexican Jays may be able to detect differences in the content (differences in the nutmeat mass inside of the shells) between identically looking peanuts without opening them, and (2) we briefly discuss the proximate mechanisms of nut evaluation that the Jays may use.

Methods

Study site, species and general information

The research was conducted in January and February 2008, 2009 and 2012. We studied 9 groups of Mexican Jays near the Southwestern Research Station of the American Museum of Natural History located in the Cave Creek Canyon on the eastern slopes of the Chiricahua Mountains, near Portal, Arizona, USA (Fig. 1a). This population has been studied since 1969 by Jerram and Esther Brown (Fig. 1b; Brown 1970, 1972; Brown et al. 1999). The birds are trained to approach the feeding arenas (one per flock) in response to the sound of police whistle and most birds are individually marked (color bands). They accept a variety of food items such as acorns, bread, sunflower seeds, and peanuts. Most of these items are carried away by birds from the feeding arenas and are cached nearby. This creates a situation when Jays take away a peanut from the feeding arena without opening the nut, hence without directly checking what is inside of the shell.

Observations and slow-motion videos

For the slow-motion filming of the birds’ behavior, we used one group of the Mexican Jays at the Cave Creek Ranch (located at the mouth of the Cave Creek Canyon), where birds are extremely used to humans. We used a portable high-speed camera (Troubleshooter) at 250 fps, and occasionally 500 or 1000 fps, to capture the details of nut handling by the Jays visiting a feeder containing a pile of randomly chosen nuts (without any experimental modification). The movies were taken in January and February 2012. These movies were analyzed to quantify the behavior of handling the nuts by Jays.

First, we noted if handling was associated with beak opening and subsequent closing, and how many beak opening–closing movements were present in handling of a peanut before deciding to drop or accept it. In order to evaluate the association between beak opening and the

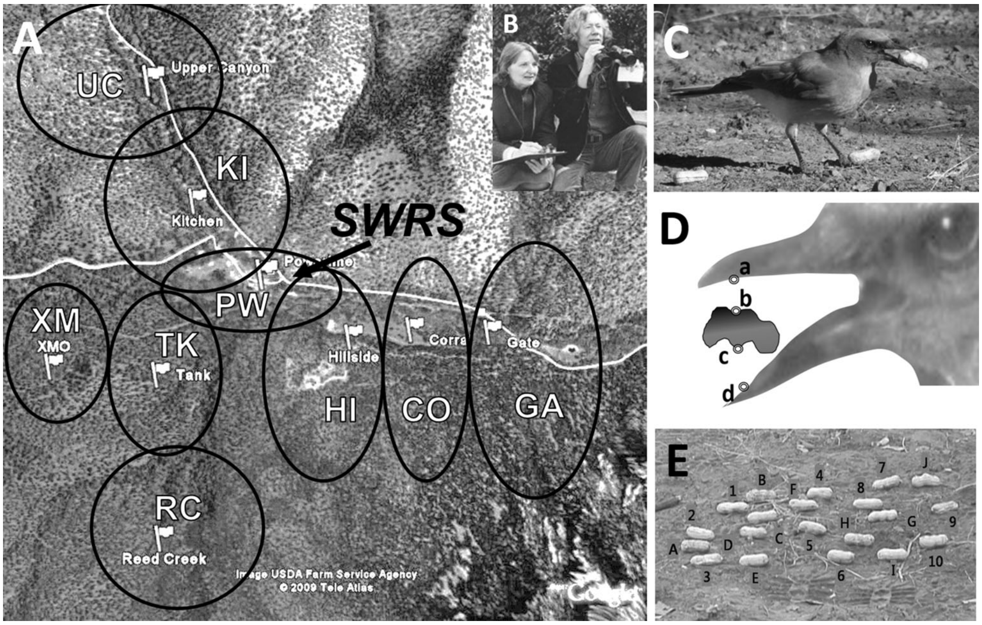

Fig. 1 Study site and methods. **a** Satellite view (source: Google maps; Image USDA Farm Service Agency, ©Tele Atlas) of the neighborhood of the Southwestern Research Station (SWRS) with schematic distribution of the social groups (flocks) of Mexican Jays: *UC* Upper Canyon, *KI* Kitchen, *PW* Powerline (recently PW seemed to have merged with KI), *XM* XMO flock, *TK* Tank, *RC* Reed Creek, *HI* Hillside, *CO* Corral, *GA* Gate. The *flag icons* show the location of feeding arenas. **b** Young Esther and Jerram Brown who initiated the long-term study of those groups in 1969 (Photo, courtesy of University at Albany). **c** Mexican Jay adult handling a peanut; **d** the velocity of the closing beak movements against the peanut shell was calculated by measuring the distance *ab* (for upper beak; and respectively *cd* for lower beak) two frames (8 ms) before the moment when *a* and *b* overlapped (point *a* on a beak got in touch with the shell at point *b*). The location of the points *a*, *b*, *c*, and *d* varied among beaks and peanuts depending on how the Jay grasped the peanut. **e** Example of 20 peanuts (10 empty and 10 normal treatment) randomly distributed in space in the feeding arena

proportion of nuts accepted, we ran Fisher's exact test (http://www.graphpad.com/quickcalcs/contingency2/).

Second, for the 31 best movies with a good side view of a bird, we traced the trajectories of the ear, eye, beak base, lower beak tip and upper beak tip using a coordinate system based on the location of a wrist bend (the frontal "tip" of a folded wing) as the point of origin (0, 0 point in the coordinate system; Fig. 2a). Measurements were done at 12-ms time intervals (every third frame in a 250-fps movie) starting with the frame just before the first frame in which the movement was noticeable. Pixels were transformed to centimeters based on known average beak and tarsus length in this population.

Third, for the six carefully chosen best close-ups, we estimated the velocity with which the beak closes against the nutshell. For this, we measured the distance between the point on the upper beak surface (point "a" in Fig. 1d) that gets in contact with the nutshell and the point on the nutshell (point "b" in Fig. 1d) that gets in contact with the upper beak 8 ms (2 frames in the 250-fps video) before these two surfaces get in contact. By dividing this distance by 8 ms, we obtained a rough estimate of the speed with which the beak hits the nut. We did the same for the lower beak (points "c" and "d" in Fig. 1d).

Experiment 1: effect of mass on nut acceptance I (empty vs. normal)

The experiments were conducted in January and February 2008 in five flocks (Gate, Hillside, Kitchen, Powerline, and Upper Canyon). In each flock's feeding arena, we set up an arrangement of 20 peanuts (Fig. 1e). Ten of them were empty (treatment "empty"; 0.56 ± 0.09 g, evaluated from $n = 14$ randomly chosen experimental nuts, mean ± SD). They were prepared by opening, removing the nuts, and gluing the two halves of the shell together using a small amount of superglue gel. The remaining ten were prepared in a similar manner, but instead of removing the nuts we glued them to the shell interior with a drop of glue to prevent the rattling noise (treatment "normal": 2.10 ± 0.23 g, $n = 14$). Hence, normal peanuts were almost four times heavier than empty ones. The two groups differed in mass but did not differ in other characteristics such like visual features (nut length for 14 randomly chosen nuts from the experiments was 42.4 ± 4.3 and 41.2 ± 3.8 mm for empty and normal peanuts respectively), or with respect to the absence of rattling noise (originally present in some peanuts due to loose nuts inside). The foraging Jays were filmed for later analyses.

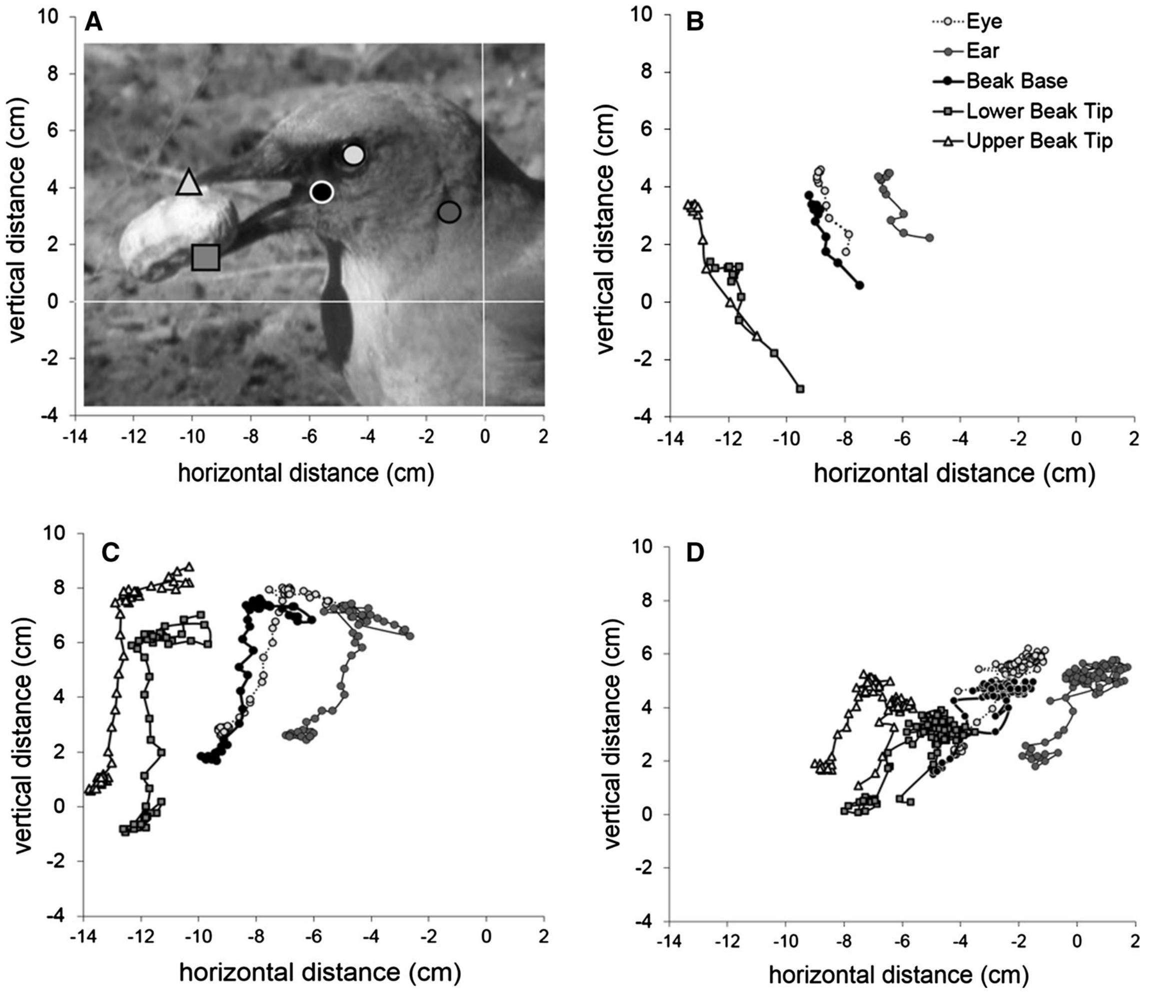

Fig. 2 Examples of the trajectories of the movements of ear, eye, beak base, lower beak tip and upper beak tip in a side view using coordinate system based on the location of a wrist bend (the frontal "tip" of a folded wing) as the point of origin (0, 0 point in the coordinate system). Measurements done at 12-ms time intervals (every third frame in a 250-fps movie). **a** Explanations of the corresponding points that were tracked: *triangle* upper beak tip, *square* lower beak tip, *black circle* beak base, *light circle* eye, and *gray circle* approximate location of ear opening. Examples (**b**–**d**) were chosen to represent a variety of patterns seen in the 31 shaking events analyzed from slow-motion movies (see Supplementary Videos 1–6 for examples)

Experiment 2: effect of mass on nut acceptance II (heavy vs. normal)

This experiment was conducted in 2009 using a different shipment of peanuts than the ones used in Experiment 1. The experimental setup was similar to that of Experiment 1, except ten normal peanuts (length 38.2 ± 2.2 mm, mass 2.1 ± 0.2 g) were compared with ten heavy peanuts (length 38.2 ± 2.5 mm, mass 3.4 ± 0.4 g). Hence, heavy peanuts were 1.6 times heavier than normal ones. We prepared heavy peanuts by opening the shell and adding to the interior of the nut some amount of non-toxic clay (Crayola Air-dry Clay) in which the actual nuts were embedded. The shell was closed and glued just like for normal and empty peanuts, and the clay was dried before using the nuts in the field. Hence, we attempted to create two groups of peanuts with the same amount of nutmeat inside but different with respect to their weight. In our evaluation, the two groups of peanuts appeared also similar to each other with respect to other characteristics such like visual features or absence of rattling noise. We tested five flocks (Gate, Corral, Hillside, Kitchen and Tank).

Experiment 3: effect of visual cues on nut acceptance (single vs. triple)

In this experiment, we asked whether and how Jays incorporate visual information in their decisions to pick up a nut. The design of the experiment was the same as for Experiment 1 and Experiment 2. The two treatments comprised: visually small peanuts containing only one nut (treatment "single") and the visually large peanut (peanut that normally contains 3 nuts) containing also only one nut (treatment "triple"). In both treatments, the nut has been glued to the interior shell surface to prevent rattling. The two groups of peanuts were prepared such that their mean mass is as similar as possible without creating differences in the nutmeat content. Triple peanuts were more than two times longer (length 41.4 ± 2.2 mm for triple and 19.0 ± 0.9 mm for single) and 1.2 times heavier (mass 0.97 ± 0.07 g for triple and 0.83 ± 0.08 g for single) than the single ones. If Jays use visual cues and prefer to lift larger peanuts, we expected that triple peanuts would be lifted earlier than single ones. If Jays are able to distinguish the weight difference between triple and single peanuts triple peanuts should be taken away from the feeding arena sooner than single ones. However, if Jays are unable to detect the relatively small weight difference between single and triple peanuts, then both types of peanuts would be accepted after handling at a similar rate. Finally, if Jays somehow pay attention to the density (mass relative to visual size) we may expect that they prefer to accept the single peanuts. This experiment was conducted in January and February 2008 in nine flocks (Gate, Kitchen, Hillside, Upper Canyon, Powerline, Corral, Tank, Reed Creek and XMO).

Data analysis and statistics

Analysis focusing on nuts

For each nut, we obtained the following four variables:

1. Latency from the arrival of the first bird to the feeding arena until the moment when the nut was lifted for the first time [latency until the first lift (s)].
2. Latency from the moment when a nut was lifted for the first time until the moment when a nut was accepted (by one of the birds in the flock) and was taken away by a bird from the feeding arena [latency until acceptance (s); this variable was calculated only for those peanuts which were taken away, the peanuts that were not taken away by the moment of test termination were not accounted for in this variable].
3. The number of times the nut was picked up, handled, and dropped (number of rejections; this variable was calculated only for those nuts that were lifted at least once; if a nut was never lifted, it did not contribute to the variable).
4. The binary variable indicating whether the nut was accepted or not at the first lift for that nut (acceptance at the first lift). This variable had value only for the peanuts that were lifted at least once. Similarly the latency until the first lift was only calculated for the peanuts that were actually lifted at least once, but, occasionally, when the peanut was immediately pecked while on the ground (which means it was opened without handling), we ignored this nut for the analysis of acceptance at the first lift while it contributed to the analysis of the latency until the first lift. Almost all peanuts were lifted at least once because in most cases we were able to run the test for sufficiently long time to ensure that all peanuts were lifted.

The trials in Experiment 2 were conducted multiple times per flock and the trial number nested in flock [TrialNr (flock)] was used as a random variable. We chose this method of analysis to be able to generalize over a population of similar feeding events in a population of flocks of Jays. In additional analyses, where TrialNr was used as a fixed factor, we checked that TrialNr did not modify the effect of peanut type on any of the variables (i.e. interactions between TrialNr and peanut type were not statistically significant). We used a general linear mixed model (PROC MIXED) to analyze the latency until the first lift and latency until acceptance, and a generalized linear mixed model (PROC GLIMMIX) to analyze Nr of Rejections (Poisson distribution) and acceptance at the first lift (binary distribution). Statistical analyses were conducted with SAS v.9.3 (SAS Institute, Cary, USA).

Analysis focusing on birds

In Experiment 2, we also analyzed the data by calculating variables for each individually identified bird. In four flocks (Kitchen, Gate, Hillside, and Tank), we analyzed 1727 peanut handling events by 25 birds (5 birds in Gate, 10 birds in Kitchen, 5 birds in Hillside, and 5 birds in Tank) that handled peanuts for at least 25 times/bird (total for all trials) and were clearly identifiable from color bands in the video. Each time a bird picked up a peanut, we noted whether the bird accepted or rejected the peanut (binary response variable "acceptance"). After arriving at the feeding arena, a bird would typically go through a sequence of lifting and dropping the peanuts (occasionally picking again a peanut that was already lifted earlier in the sequence) until accepting one peanut and flying away with it from the feeding arena (Supplementary Videos 1–6). First, in order to obtain results directly comparable to the other experiments, we analyzed the effect of treatment (normal vs. heavy) on the binary variable (nut accepted or not) for the dataset of 568 first pickups at each arrival of a bird at the feeding arena. We used bird ID as random factor and flock ID as a fixed factor (block). Then, we ran the same analysis for the whole dataset of all 1727 peanut handling events by individually identifiable birds in the four flocks. We used SAS PROC GLIMMIX for the statistical analysis.

Results

Observations in slow-motion videos

In approximately half of the 174 observed handling events (Fig. S1 in Supplementary Material), the birds shook the nut while firmly holding it in the beak, without opening the beak during handling. In the remaining handling events, a bird quickly opened and closed its beak at least once but often more times (up to 8 times). The speed of the beak closing relative to the nutshell just before contact with the shell reached 0.7 m/s (maximum), and on average it was 0.33 ± 0.06 and 0.36 ± 0.10 m/s (mean ± SE) for upper and lower beak respectively ($n = 6$ closing events). A total of 141 handling events were filmed long enough to contain the moment of either acceptance (birds flies away) or rejection (birds dropped the peanut) of the peanut. Among those, none of the 62 handling events with beak opening resulted in accepting a peanut, while 12 (15 %) out of the 79 handling events without beak opening resulted in nut acceptance. This indicates a significant association between beak opening and more strict (100 % rejection) evaluation of peanuts during handling (Fisher's exact two-tailed probability $P = 0.0012$). Examples of slow-motion movies of handling events are shown in the supplemental videos (Supplementary Videos 3–6). These movements, traced in the side view, followed a variety of trajectories that did not appear to possess a common feature. Some of them contained mostly the vertical or horizontal component, and some contained both (examples in Fig. 2).

Experiment 1: effect of mass on nut acceptance I (empty vs. normal)

Jays did not show stronger visual attraction to either empty or normal peanuts: the latency until the first lift did not differ (Fig. 3a; $F_{1,92} = 1.45$, $P = 0.2313$) confirming that, in accordance with our intentions, the experimental peanuts did not differ visually. The proportion of peanuts accepted at the first lift was larger for normal than for empty peanuts (Fig. 3b; $F_{1,90} = 23.31$, $P < 0.0001$). Normal peanuts were taken on average earlier from the feeding arena, and were rejected fewer times, than were empty ones (Supplementary Material, Fig. S2).

Experiment 2: effect of mass on nut acceptance II (heavy vs. normal)

Analysis focusing on nuts

Birds seemed to be visually less attracted to heavy peanuts as indicated by the longer latency until the first lift for heavy than for normal peanuts (Fig. 3c; $F_{1,658} = 7.71$, $P = 0.0057$; an ad hoc explanation of this is presented in Supplemental Material). Nevertheless, the conclusion of Experiment 2 is similar to Experiment 1: by handling the nuts in their beaks, Jays were able to distinguish heavier nuts. Proportion of peanuts accepted at the first lift was larger for heavy than for normal peanuts (Fig. 3d; $F_{1,658} = 34.55$, $P < 0.0001$). The heavy peanuts were taken away earlier, and after fewer rejections, from the feeding arena than were normal peanuts (Supplemental Material, Fig. S2).

Analysis focusing on birds

The previous analyses were easy to conduct and are suitable for a situation when individuals are not marked. In order to evaluate the validity of those analyses in generalizing our results to the population of birds, we looked at the subset of data from Experiment 2 focusing on clearly recognizable color-banded individuals. Birds accepted heavy peanuts more easily than normal peanuts at the first lifts (Fig. 4a, $F_{1,539} = 6.26$, $P = 0.0126$). This preference for heavy nuts was confirmed for all lifts by Jays (Supplementary Material Fig. S3A) and it was persistent over multiple trials repeated over 1 week period (Supplementary Material, Fig. S3B).

Experiment 3: effect of vision on nut acceptance (single vs. triple)

The birds were attracted to visually larger triple peanuts as indicated by shorter latency until the first lift for triple than for single peanuts (Fig. 3e, $F_{1,166} = 53.98$, $P < 0.0001$). At the first lift, visually smaller single peanuts were more likely to be accepted than were visually larger triple peanuts (acceptance at first lift was higher for singles than for triples; Fig. 3f, $F_{1,166} = 15.46$, $P = 0.0001$). The latency until acceptance was shorter, and number of rejections was smaller for singles than for triples (Supplementary Material, Fig. S2E, F), indicating that during handling Jays accepted singles more easily than triples.

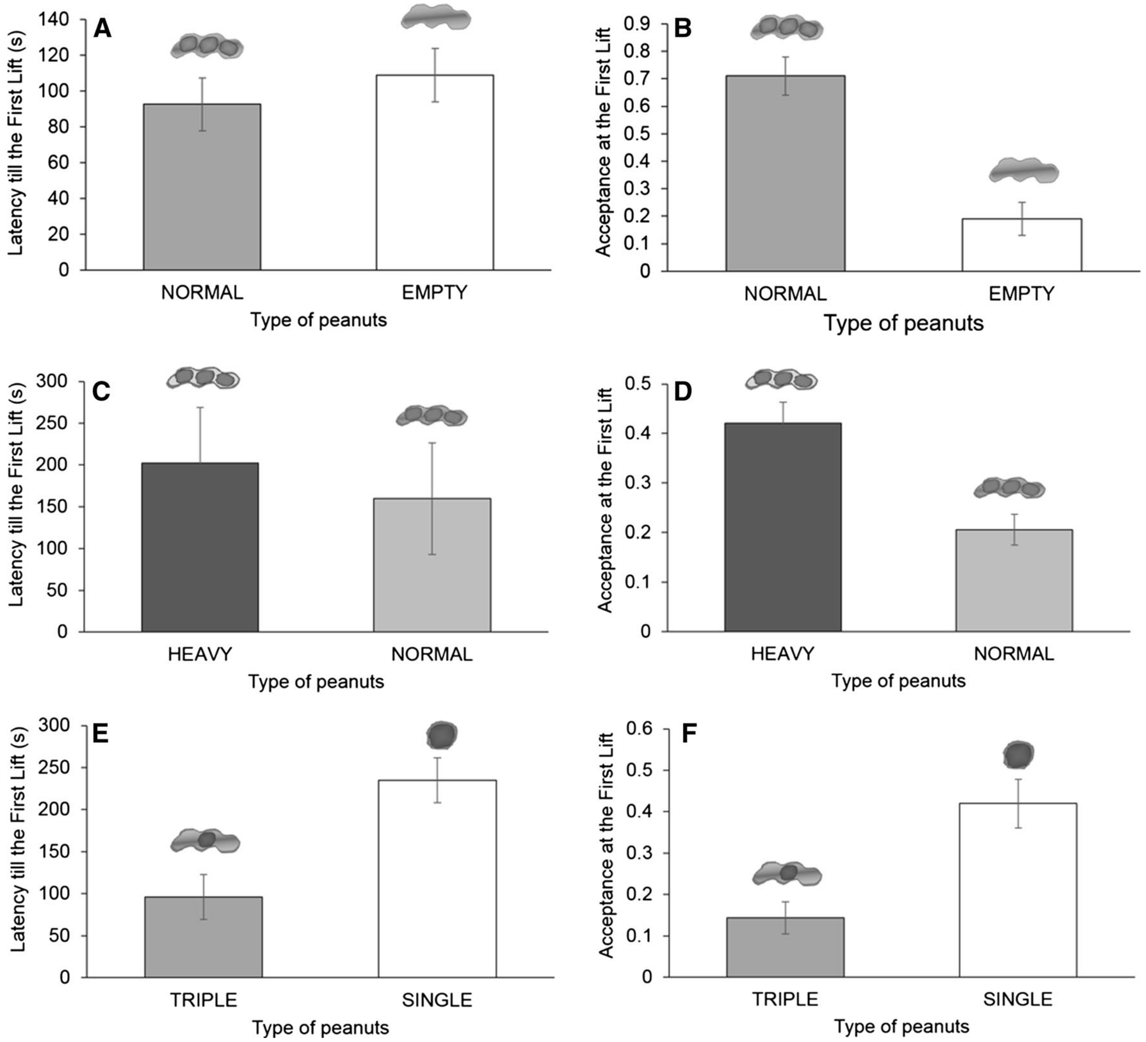

Fig. 3 Effect of experimental peanut type on the least square means and their standard errors of the latency until the frist lift (**a**, **c**, **e**), and the Acceptance at the First Lift (**b**, **d**, **f**) in Experiment 1 (**a**, **b**), Experiment 2 (**c**, **d**) and Experiment 3 (**e**, **f**)

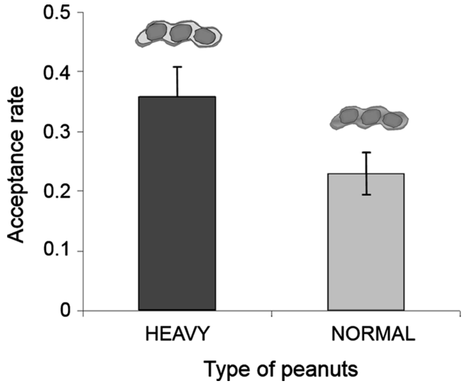

Fig. 4 Acceptance rate of heavy and normal peanuts in Experiment 2 for the first lifts by each Jay at each visit to the feeding arena by individually marked birds in five flocks (Gate, Corral, Hillside, Kitchen and Tank)

Discussion

We found out that the evaluation of each peanut during a nut-comparison sequence comprised very fast movements of the whole head combined with additional fast movements of the beak, which may open and subsequently close (loosening the grip of the peanuts for milliseconds). These movements seemed to provide Jays with sensory information sufficient to differentiate peanuts based on their mass: among similarly looking peanuts Jays consistently preferred the heavier ones in Experiment 1 and Experiment 2. Significant association between the presence of beak opening–closing moments and the strict discrimination among the peanuts suggests that the beak opening–closing causes birds to be more discriminatory or that birds use the opening–closing movements for a finer evaluation of those peanuts that are already perceived by birds as more likely to be rejected. What information may the Jays perceive during nut handling?

We hypothesize that, similar to humans (Turvey 1996), during the handling of a nut Jays may perceive inertia-related stimuli. The "inertia hypothesis" proposes that Jays apply the proximate mechanism that is similar in the basic aspects to the human's "dynamic touch" mechanism (Turvey 1996). Humans are able to perceive object heaviness by holding it in their hands and moving or rotating the object in alternating directions. This is because, during this type of handling, humans experience inertia by putting an object to motion and subsequently stopping the motion (Jones 1986; Amazeen and Turvey 1996; Carello et al. 1996; Turvey 1996). The strength of inertia depends on the mass and the speed of the object. It is believed that human's abilities to perceive heaviness are based on the sensory cues from exteroceptors (e.g., pressure sensing cells) and proprioceptors in muscles (Carello and Turvey 2004). If birds are indeed able to perceive inertia during handling of peanuts, then what senses do they use? Bird beaks are not comparable to the human hands in terms of the number and variety of sensory cells that may perceive various aspects of the objects held in hands (Johnson 2001). By analogy to humans, we hypothesize that proprioceptors in avian muscles involved in head and beak movements are differently stimulated depending on the weight of the object that is handled.

It is also possible that the heavy nuts differ from the empty ones in the sound that is produced when the beak closes and grasps the peanuts during handling, as shown in the slow-motion movies (Supplementary Videos 3–6). A bird handling a peanut may perceive the sound through the typical pathway for auditory cues: via air and ear. However, we suspect that the sound may be also perceived through the skeleton that may deliver vibrations from the beak to the inner ear. We are now analyzing a series of experiments that seem to indicate that sound is indeed taken into account by Jays handling the peanuts and that it may be more important than the perception of heaviness (Jablonski PG, Lee SI, Fuszara M, Fuszara E, unpublished). Hence, we think that Jays, like primates (Visalberghi and Neel 2003), may be able to use auditory/vibrational information to evaluate nut content without opening it.

Finally, the peanuts may differ in shell properties that affect the stiffness/softness of the shell, which hypothetically may be detected by Jays during grasping the peanuts in their beaks. While we cannot exclude this possibility, we think that the shell of raw peanuts of various content, including the empty ones, is relatively hard and that the beak hitting the shell with the speed estimated from the video would not bend it sufficiently to provide useful cues. This mechanism was already suggested by Heinrich et al. (1997) in their study of the Black-capped Chickadees and the Red-breasted Nuthatches handling sunflower seeds.

When faced with nuts of visually different sizes, the Jays picked up the larger peanuts first (Experiment 3). This indicates that visual information is used in the choice of peanuts for handling as already shown in several corvids (Ligon and Martin 1974; Bossema 1979; Scarlet and Smith 1991; Hubbard and McPherson 1997; Langen 1999; Pons and Pausas 2007). However, Jays avoided taking away large peanuts that weighed less than the full peanuts of the same size. What proximate mechanisms may lead to this ability to choose only those nuts whose mass and visual size match? One possibility is that the birds use their memory formed from information collected through different sensory channels during the repeated exposure to the food items with various properties. This memory may provide the birds a concept of how much a nut of a given visual size should weigh. This would require substantial level of cognition, for which corvids are known (Emery and Clayton 2004). It is an exciting possibility that warrants further investigations. However, our preliminary analyses also suggest an alternative explanation. Although the peanuts in our experiments had similar mass and look, they produce different sounds during handling (Supplemental Material, Fig. S4; Jablonski PG, Lee SI, Fuszara M, Fuszara E, Jeong C, Lee WY, unpublished), and this suggests a simpler explanation. If heavy/full peanuts have consistently different auditory features than light/empty ones, then the Jays would also reject the artificially lighter triple peanuts, if they follow only the auditory cues without any cognitive processes about the match between weight and visual size.

The idea that corvids may use sounds to detect properties of nuts has already been proposed over 40 years ago by Ligon and Martin (1974), who studied Pinyon Jays evaluating pinyon nuts by "bill-clicking", which was also observed in Clark's Nutcrackers (Johnson et al. 1987). However, a brief review of the previous research on Jays and other corvids foraging on peanuts, acorns or seeds revealed that proximate mechanisms were relatively ignored during the last four decades (Fig. 5). The research focusing on proximate mechanisms disappeared from this literature in the 1970s (Fig. 5), i.e. in the same decade when "behavioral ecology" was "born" (Krebs and Davies 1978). We suspect that this is not a coincidence. Behavioral ecology put a high value on ultimate questions triggering a burst of novel research focusing on behavioral strategies and tactics and superficially giving an impression that proximate mechanisms, the typical 'black box' in optimality models, are not as important as the ultimate explanations.

Future studies on other birds that perform extraction foraging, such as parrots eating nuts or hard-shelled fruits,

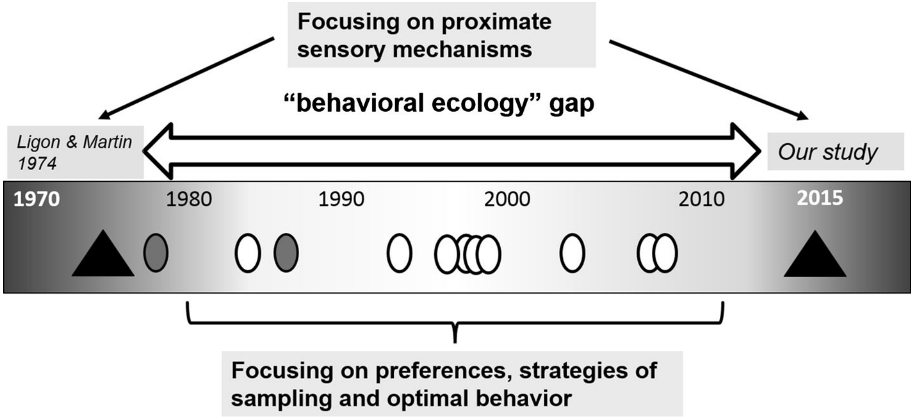

Fig. 5 Schematics summarizing the content of the papers dealing with Corvidae foraging on nuts, acorns, seeds, etc. This brief review may miss some papers, and the aim is to illustrate a trend rather than to provide exhaustive review. *Black triangle* research focusing on proximate mechanisms of evaluation of nut/acorn/seed content by birds; *gray oval* papers that study and/or discuss some elements of proximate mechanisms (Bossema 1979; Johnson et al. 1987); *white oval* research focusing and/or containing bird food preferences, strategic and optimality analyses and/or interpretations of birds choosing food items (Johnson and Adkisson 1986; Scarlet and Smith 1991; Johnson et al. 1993; Dixon et al. 1997; Langen and Gibson 1998; Langen 1999; Lutbeg and Langen 2004; Moore and Swihart 2006; Pons and Pausas 2007)

shorebirds foraging on shelled molluscs, or granivorous birds foraging on seeds, will reveal whether proximate mechanisms are similar or different across situations. We hypothesize that auditory stimuli are important for birds, like bullfinches, chickadees, Clark's Nutrackers or Pinyon Jays (Ligon and Martin 1974; Greig-Smith and Crocker 1986; Johnson et al. 1987; Heinrich et al. 1997), which handle smaller seeds that produce very weak inertia-based cues, while additional inertia-based perception of heaviness may be important for animals handling larger and heavier items. The future research should expand to mammals other than primates in order to reveal if the proximate mechanisms of nut evaluation are similar across a diversity of taxa. For example, fox squirrels appear to use head flick movements for the evaluation of a nut before deciding what to do with it, but the proximate sensory mechanisms involved are not known (Preston and Jacobs 2009). We also suggest that, in the future studies of proximate mechanisms, the simple nut-based (generally item-based) analyses of data from feeders visited by groups of unmarked individuals are sufficient, because in our study they were consistent with the analyses based on individually marked birds. In such a case, the research design should include sampling multiple groups/localities and treating them as random variables.

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