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Preference and motivation for different diet forms and their effect on motivation for a foraging enrichment in captive Orange-winged Amazon parrots (*Amazona amazonica*)

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ABSTRACT

Motivation tests were conducted to assess preference strength for diet form and a cage enrichment device by Orange-winged Amazon parrots (*Amazona amazonica*) held in individual cages, $N = 10$. Each cage was equipped with two trough-type feeders, one of which had a hinged lid that required lifting to access feeder content; cost of lifting the lid could be increased by the addition of up to 480 g upon it, ~1.5 times the mass of an Amazon parrot. Motivation tests were conducted using three different diet forms of pellets (regular-sized, 0.16 g/pellet (cylindrical-shaped); large-sized, 3.4 g/pellet (cylindrical); and over-sized, 3–5 g/pellet (cuboid-to-spheroid)) manufactured from the same diet formulation. When regular pellets were concomitantly freely available, birds were still highly motivated to gain access to either large-sized or over-sized pellets, with 7 of 10 birds lifting the maximum weight of 480 g. In motivation tests comparing over-sized vs. large-sized pellets, birds worked more for over-sized pellets (when large-sized pellets were freely available) than vice versa: motivation for over-sized pellets exceeded that for large-sized pellets by approximately 242.67 ± 64.4 g ($F = 14.2$, $P = 0.0055$; Sign Test, $P = 0.0078$). Additional tests assessed motivation to access 2.5 cm/side wooden cube enrichment devices when regular or over-sized pellets were freely available. Birds removed more cubes when fed regular pellets (Sign Test, $P = 0.0078$) and lifted an average of 221.33 ± 64.62 g more to access them ($F = 11.73$, $P = 0.009$; Sign Test, $P = 0.0063$), than when over-sized pellets were freely available, suggesting that enrichment devices may act as foraging substitutes. Likewise, both wooden cubes and over-sized pellets elicited comparable podomandibulation (handling with beak and foot) behavior, and podomandibulation was reduced when parrots were fed regular as opposed to over-sized pellets (58 ± 10 s [mean ± SE] vs. 4.27 min ± 31 s; $P < 0.0001$). Finally, there was no evidence of contrafreeloading: in control experiments, birds only removed pellets which were freely available, when the same pellets were concomitantly available in weighted-lid feeders ($F = 120.20$, $P < 0.0001$). In summary, these results show that captive Orange-winged Amazon parrots strongly prefer pellet forms that are substantially larger than what is commercially recommended for them; preferred forms more closely resemble that of native wild foods, such as palm fruits.

1. Introduction

Approximately 2.7 million large parrots are kept as companion animals in the United States; the estimated yearly expenditure on products for their maintenance and well-

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being costs bird owners 1.4 billion dollars (American Pet Products Manufacturers Association, Inc., 2007; American Veterinary Medical Association, 2002). Unfortunately, items purchased for companion birds, including cages, food, and enrichment devices, may often be designed more for the convenience and appeal of the owner rather than the welfare of the animal (Graham, 1998; Young, 2003). If parrots are kept in barren environments, certain natural behaviors (e.g., foraging, flight, allogrooming) will not be expressed, possibly resulting in the development of abnormal behavior and poor welfare (Graham, 1998; Mason, 1991).

A limited number of empirical studies focus directly on preferences of captive parrots for various enrichments or aspects of cage design. Topics of these have included nest box selection (Martin and Millam, 1995), cage enrichment devices (Kim et al., 2009; Webb et al., 2010), pellet size (Rozek et al., 2010), social contact (Fox, 2006), and food preferences (Fa and Cavalheiro, 1998). In particular, Kim et al. (2009) described the preferences of Orange-winged Amazon parrots (*Amazona amazonica*) for wooden cube enrichment devices and based on the preferred qualities proposed that they may serve as a foraging substitute.

Even though some parrots have been bred in captivity for generations, they may have many of the same physical and behavioral needs as wild parrots (Davis, 1998; Graham, 1998). Knowledge of species-specific wild behaviors and diurnal patterns of behavior may therefore serve as a useful reference against which to gauge the normalcy of behavior in captivity.

For example, the wild parrots may spend 40–75% of their waking time searching for and accessing food items (e.g., Magrath and Lill, 1983; Renton, 2001; Westcott and Cockburn, 1988). However, in captivity, Orange-winged Amazon parrots may spend only approximately 42 min of a 12 h day consuming their food (Rozek et al., 2010). In part, this is due to the fact that captive birds do not have to travel to locate feeding grounds; also, energy requirements of birds in captivity are generally lower than for the same species in the wild (Koutsos et al., 2001). In addition, captive parrots are often fed a nutritionally balanced, energy-dense pelleted diet, enabling them to meet their nutritional needs with minimal foraging and ingestive behavior. While captive diets, particularly pelleted diets, require some foraging, the consequences of such limited foraging/ingestive behavior in captivity are not known. A common goal of many environmental enrichment programs is to foster the expression of natural behaviors (Young, 2003); a more stringent goal could be the expression of natural behaviors at levels comparable to those seen in the wild.

Several studies have outlined the benefits of providing increased foraging opportunities for captive parrots, suggesting that a deficit of foraging behavior may exist. For example, foraging enrichments prevent and reduce feather-damaging behavior (FDB) and stereotypy in young Orange-winged Amazon parrots (Meehan et al., 2003, 2004), as well as improve feather score and foraging time in African grey parrots (*Psittacus erythacus*) (Lumeij and Hommers, 2008). In these studies, parrots were fed pelleted diets but were still motivated to engage in additional foraging opportunities, supporting the view that pelleted diets do not completely satisfy the behavioral needs of the parrots.

Offering Amazon parrots dramatically over-sized pellets (~20–30 times larger than the manufacturer's recommended size for Amazon parrots) increased their daily foraging/ingestive time from 5.8% to 25.7% of daylight hours, a figure that more closely resembles foraging times of wild parrots; in addition, parrots consistently selected over-sized over regular pellets in choice preference trials (Rozek et al., 2010). Over-sized pellets elicited longer durations of podomandibulation, a natural behavior described as an active manipulation of the food item with the foot, beak and tongue (Harris, 1989; Rozek et al., 2010). Finally, when Amazon parrots were offered over-sized pellets they showed a significant decrease in enrichment device use, further supporting the idea (Kim et al., 2009) that certain enrichment devices serve as foraging substitutes (Rozek et al., 2010).

However, preference tests are limited in that they do not quantify the *strength* of preference. It has been argued that denying animals' access to a strongly preferred choice impacts their welfare more than denying them access to a choice that they only mildly prefer (Fraser and Matthews, 1997). Motivation tests can be an important tool for the assessment of animal welfare as they lend unique information that cannot be obtained by other experimental methods (Kirkden and Pajor, 2006). As discussed by Kirkden and Pajor (2006), motivation tests allow animals to express their priorities and are highly sensitive to differences between treatments (Dawkins, 1988, 1990; Rushden, 1996).

Motivation tests have been used to assess behavioral priorities in a range of animals. For example, using passage through a weighted door as a measure of motivation, it was determined that farmed American mink (*Neovison vison*) value access to food and bath more than access to toys or a tunnel (Mason and Cooper, 2001). Weighted doors were also used to determine that female laboratory rabbits (*Oryctolagus cuniculus*) value limited social contact and access to a platform similarly to food (Seaman et al., 2008). Laying hens (*Gallus gallus domesticus*) are motivated to access a perch to roost at night, again, as measured by pushing through a weighted door (Olsson and Keeling, 2002).

In consideration of the preference data of Rozek et al. (2010), we here test the motivation of captive Amazon parrots for a commercially recommended size of pelleted diet and two larger pellet sizes as well as wooden cube enrichment devices. We characterized motivation by employing a feeder apparatus that required lifting a lid to gain access to pellets; the lid allowed for the addition of incremental mass units weighing up to ~1.5 times the mass of an Amazon parrot.

2. Methods

2.1. Subjects, caging and management

Experiments were conducted between September 2009 and April 2010. Subjects were 10 Orange-winged Amazon parrots (*A. amazonica*); eight (five male, three female) ranging in age from 8 to 10 yrs and one male and one female, each 19 yrs. All birds were used in a pellet preference study (Rozek et al., 2010); eight birds were previously used in novelty and neophobia studies (Fox and Millam, 2004) and studies of cage enrichment devices (Kim et al., 2009; Webb et al., 2010). Birds were held on a 12L:12D photoperiod with light onset at 06:00 h. Room temperature was maintained between 23 and 27 °C. Adult Orange-winged Amazon parrots weigh 298–469 g (Forshaw, 1989).

Birds were individually housed in white, powder-coated steel wire cages (0.84 m wide × 0.64 m deep × 1.73 m high). All cages were located in the same room allowing visual and vocal contact among all birds in the study. Each cage was equipped with two 4 cm × 9 cm × 0.81 m Douglas fir perches placed approximately 1.14 m and 1.55 m from the floor, two feeders (see below) and a nipple drinking fount.

Depending on the experimental protocol, birds were fed three different sizes/shapes of pellets of identical nutrient composition; all pellets were formulated from Roudybush low fat maintenance diet (Roudybush Inc., Woodland, CA, USA). Pellet sizes included: regular (modal mass, 0.16 g; a cylindrical shape of 4.25 mm dia. × 5–15 mm in length, steam pelleted, same as manufacturer's size "small"); large-sized (modal mass, 3.4 g; a cylindrical shape of 12.5 mm dia. × 17–24 mm in length, steam pelleted, same as manufacturer's size "large"); or over-sized (bimodal mass, 3 g and 5 g; a spherical-to-cuboid shape of 15–17 mm dia. × 17–22 mm in length, a custom-sized pellet extruded from the same diet formulation as the steam pelleted diets). Experimental protocols and standard operating procedures were approved by the University of California, Davis, Institutional Animal Care and Use Committee; the university is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care International.

2.2. Feeder apparatus

Two, 14 cm wide-mouth "L"-shaped feeders (Bass Equipment Co., Healdsburg, CA, USA) were mounted side-by-size on the center rear wall of the cage and were accessible from the lower perch (Fig. 1). Each feeder mouth was fitted with a clear acrylic, hinged lid measuring 15.5 cm × 9 cm × 0.6 cm; the lid was slightly over-sized, creating a 1.3 cm overhang around the feeder mouth which birds could grasp or nudge to open the lid. When the lid was in the "closed" position (closed feeder), the feeder contents could only be accessed by the task of lifting the lid and simultaneously removing content. The lids would not remain open without being held open, thus requiring one lift per feeder visit. However, the experimenters could lock lids in the "open" position (free feeder), allowing free access to the contents.

Each lid had two 6.35 cm long machine screws projecting upward from the front center, allowing for the attachment of up to 480 g of mass to the lids, in ~21 g increments; weights were 6.4 cm × 3.5 cm metal mending braces (Ace Hardware, Oak Brook, IL, USA). These each weighed 33.3 g, but because of the mechanical advantage by their placement on the lids and as confirmed by measurement with a Pesola spring scale, each added only 21.1 g of weight to the hinged lids in their lowest position. The weight of the lid was 38.3 g. All birds became proficient in opening the lids (with and without additional weight) 4 months before testing began.

2.3. Experiment 1 – motivation for over-sized or large-sized pellets when regular pellets were freely available

All testing periods began 1 h after light onset and lasted 3 h. Captive Orange-winged Amazons tend to concentrate meal bouts into morning and evening periods, with little to no feeding occurring in the first hour after light onset (Rozek et al., 2010). During test periods, feed was removed approximately 1 h before lights out and presented 1 h after lights on. Each test period was preceded by one acclimation day during which birds received the same removal/presentation schedule of feed and the same pellet combinations in their feeders as would occur in the subsequent testing day. This acclimation day was originally instituted anticipating that birds would consume more feed the first morning following evening feed removal (birds were fed regular pellet diet *ad libitum* during non-test days); in fact, birds did not consume compensatory food on acclimation days, but, for consistency, the acclimation day remained in the protocol.

The experiment was divided into two, 8-day trials separated by 2–3 non-test days. Birds were randomly divided into groups to account for possible order effects of pellet order and task proficiency. In the first trial, birds received one of two treatments: both treatments received 120 g regular pellets in one feeder, while the other feeder (Group A) contained 200 g of over-sized pellets or (Group B) 200 g of large-sized pellets. These amounts represented more than 2 days worth of food and were enough to fill the trough of the feeder. Over-sized/large-sized pellets were placed in the closed feeder (birds had to lift lids to gain pellet access) and regular pellets were in the free feeder (allowing free access to pellets). Starting on day 2, three weights (63.4 g) were added to the closed lid each consecutive day (e.g., day 1 – no weight; day 2 – three weights; day 3 – six weights, etc.) so that during the testing period birds needed to lift the weighted lid in order to gain access to either an over-sized or a large-sized pellet. After the 3 h morning test period, birds received only regular pellets in the free feeder; this created a closed economy in which the resources being tested were only available during testing periods. After the first trial, the experiment was repeated with groups receiving the opposite treatment for a crossover design. The feeder (left or right) which would have the closed/weighted lid was randomized among birds and birds were randomly assigned to groups. To eliminate novelty effects, birds received both over-sized and large-sized pellets regularly for at least 2 months prior to the start of the study.

All remaining pellets were weighed after each testing period and the amount removed (g) was recorded. Only data for birds that were continuing to perform the task were analyzed. Birds were no longer tested after two consecutive days of failure to lift the lid; the last day on which lids were lifted to gain food was considered the final data

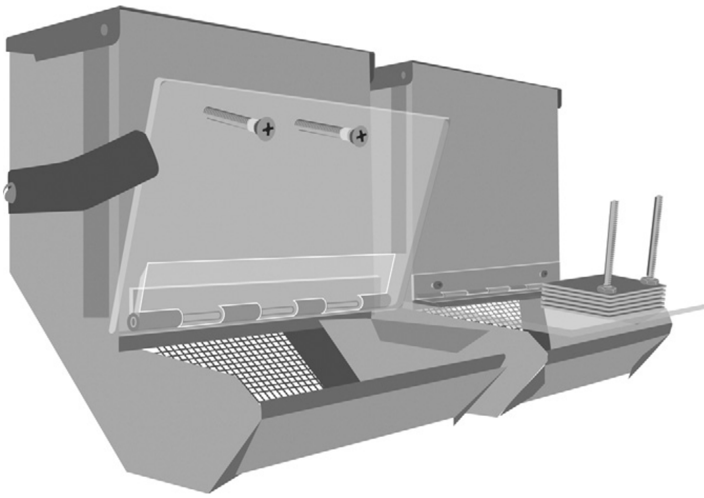

Fig. 1. Feeders as mounted on the center rear wall of each subject's cage. The feeder on the left is shown in the free position (lid locked open), while the feeder on the right is in the closed position, with several 33 g weights positioned on two machine screws to increase the cost of access to pellets or wooden cubes.

point and the grams lifted on that day were considered the maximum for each individual.

2.3.1. Data analysis

For all experiments in this study, data were analyzed using SAS (9.2, Cary, NC, USA). Each model fit was determined via graphical analysis and Shapiro–Wilk test. Data were normally distributed and all interactions were non-significant unless otherwise stated. Parrots were included in each analysis model as a random factor.

Maximum price data were compared using the mixed effects model with a random statement to specify a repeated measures model: grams = group treatment trial. Due to the nature of the experimental design in having a predetermined maximum (480 g) and minimum (0 g, assigned if a bird failed to lift the lid for the duration of trial) cost, these results were also verified with the non-parametric Sign Test.

Pellet removal data were analyzed using the mixed effects model and a random statement to specify a repeated measures model: amount = trial treatment group day trial × day treatment × day group × day. In experiment 1, data for over-sized/large-sized pellet removal were normally distributed; data for regular pellet removal were log transformed to meet normality standards. Means reported for regular pellet removal are de-transformed least squares means when indicated.

To estimate the number of lid lifts birds performed to gain access to pellets, the total mass of the removed pellets was divided by the average mass of one pellet. With a sample N of >50 for each pellet type, average masses were 0.15, 2.92 and 3.60 g for regular, large-sized and over-sized pellets, respectively.

2.4. Experiment 2 – motivation for over-sized or large-sized pellets when the opposite size pellets were freely available

The same trial schedule, pellet removal/presentation sequence, groups, and lid weight additions were followed as in experiment 1. In the first trial of experiment 2, birds received one of two treatments: either 200 g large-sized pellets (group A) or 200 g over-sized pellets (group B) in the closed feeder and 200 g of the opposite pellet type in the free feeder. After the first trial, the experiment was repeated with groups receiving the opposite treatment. All remaining pellets were weighed after each testing period and the amount removed (g) was recorded as well as the maximum grams lifted.

2.5. Experiment 3 – motivation for destructible wooden cube enrichment devices when regular pellets or over-sized pellets were freely available

The same trial schedule, pellet removal/presentation sequence, and lid weight additions were followed as in experiment 1. In the first trial of experiment 3, birds received one of two treatments: either 200 g over-sized pellets (group A) or 120 g regular pellets (group B) in the free feeder and 10, 2.5 cm/side wooden cubes in the closed feeder. Birds routinely received similar 5 cm wooden cubes as cage enrichment devices and had regularly received 2.5 cm cubes for at least 2 months prior to the start of the study. After the first trial, the experiment was repeated with groups receiving the opposite treatment. After the 3 h testing period, the amount of wooden cubes removed and maximum grams lifted were recorded and used for analysis. Because only three of the 10 birds removed cubes when over-sized pellets were freely available, the non-parametric Sign Test was used to compare difference between cubes removed under each treatment.

2.6. Experiment 4 – contrafreeloading: motivation for regular pellets when regular pellets were freely available

To ensure that the parrots were lifting the lids to access resources and not for the interaction/success of lifting a lid, we tested the birds with the same resource in both feeders. The same removal/presentation and testing period schedule was followed, as above. All birds received regular pellets in both the free feeder and the closed feeder for three consecutive days; for the first two days, birds had to lift only the lid (38.3 g), for the third day, three weights (63.4 g) were added to the lid for a total of 101.7 g.

2.7. Podomandibulation time determination

For three consecutive days parrots received a randomized order of the three pellet types, receiving a different pellet type each day. To determine podomandibulation times, parrots were visually observed in random order between 07:00 h and 09:00 h. For each pellet type, podomandibulation time of three retrievals/parrot was recorded for a total of 30 retrievals/pellet type. These data were analyzed using the general mixed effects model with a random statement to specify a repeated measures model: time = treatment day treatment × day. To meet normality standards, these data were log transformed.

3. Results

3.1. Experiment 1 – motivation for over-sized or large-sized pellets when regular pellets were freely available

Overall, parrots were highly motivated to access both over-sized and large pellets, even when regular pellets were freely available. For the first 4 days (with lid weights accumulating from 38.3 to 228 g) all 10 birds lifted the lid for access to both over-sized and large-sized pellets. Seven of the 10 birds went on to lift lids for all 8 days, including the maximum amount of weight (480 g), for access to the over-sized and large pellets. There was no difference between the maximum price paid for over-sized pellets vs. large-sized pellets ($F(1,8) = 2.26$, $P = 0.1710$; Sign Test, $M = -1$, $P = 0.5$), though because of the limitation of the capacity of the lids to hold additional weights, the 480 g estimate is conservative, a true maximum price cannot be calculated.

There was a significant effect of treatment in terms of the mass of pellets removed: birds removed more over-sized (85.07 ± 16.35 g) than large-sized pellets (64.43 ± 16.24 g) ($F(1,16.5) = 5.33$, $P = 0.0345$). However, over the course of the experiment, birds lifted lids to access pellets 24 times/day, regardless of pellet type (Fig. 2). In addition, as days passed and lid weight increased, lesser amounts of pellets were removed ($F(7,84.6) = 3.85$, $P = 0.0011$). There were no order effects or group effects ($F(1,16.5) = 2.42$, $P = 0.1390$; $F(1,8.12) = 0.11$, $P = 0.74575$).

Pellet type had a pronounced effect on the removal of freely available regular pellets (−0.236 ± 0.279 g vs. 1.197 ± 0.279 g (log transformed means ± SE); $F(1,21) = 12.78$, $P = 0.0018$). For clarity these data are de-transformed in Fig. 2. Birds removed only 0.58 ± 1.97 g regular pellets/day (de-transformed) when working for over-sized pellets compared to 15.74 ± 1.9 g regular pellets/day (de-transformed) when working for large-sized pellets.

For these data there were also no order or group effects ($F(1,12.1) = 0.76$, $P = 0.3930$; $F(1,9.34) = 2.61$, $P = 0.1213$). There was one significant interaction, trial × day ($F(7,83) = 2.29$, $P = 0.0220$), but this interaction was not significant if day 2 was removed from the analysis ($F(6,72.1) = 1.17$, $P = 0.3330$). For unknown reasons, there was a noticeable drop in regular pellet removal on day 2 in trial 2 for birds in group A, causing the interaction result to be significant. The analysis was run both ways (with and without day 2) but this did not have any effect on the significance of the results.

3.2. Experiment 2 – motivation for over-sized or large-sized pellets when the opposite size pellets were freely available

When over-sized pellets were freely available and large-sized pellets were offered in closed feeders an average of three birds worked for large-sized pellets over days 1, 2 and 3. For 9 of 10 birds, the mass of large-sized pellets removed was less than 8 g; the exceptional tenth bird was also the only bird that continued to work for large-sized pellets from days 4 through 8. Conversely, an average of 8 birds worked for over-sized pellets for the first 3 days; six birds continued to work for over-sized pellets through the maximum weight (480 g). On average, birds removed 20.64 ± 7.87 g more over-sized pellets than large-sized pellets. Overall, the maximum price paid for over-sized pellets exceeded that for large-sized pellets by 242.67 ± 64.4 g ($F(1,8) = 14.2$, $P = 0.0055$; Sign Test, $M = 4$, $P = 0.0078$).

3.3. Experiment 3 – motivation for wooden cube enrichment devices when regular pellets or over-sized pellets were freely available

The size of freely available pellets strongly influenced maximum price paid for wooden cube enrichment devices. Birds paid an average of 221.33 ± 64.62 g more for wooden cubes when regular pellets were freely available than when over-sized pellets were freely available ($F(1,8) = 11.73$, $P = 0.009$; Sign Test, $M = 3.5$, $P = 0.0063$). Motivational strength was also reflected in the number of birds willing to lift lids to access cubes. Eight of the 10 birds worked for wooden cubes when regular pellets were freely available, compared to three of 10 birds when over-sized pellets were freely available; two birds did not access cubes under either pellet condition. As illustrated in Fig. 3, a total of 243 cubes were removed when the parrots were fed regular pellets, compared to only 41 when they were fed over-sized (Sign Test, $M = 4$, $P = 0.0078$); the second total is heavily skewed by one bird which removed 38 of the 41 removed cubes.

3.4. Experiment 4 – contrafreeloading: motivation for regular pellets when regular pellets were freely available

When there were regular pellets in both the free and closed feeders, birds worked for only token quantities of regular diet, an amount likely within measurement error due to removing and weighing the food (closed feeder, 0.57 ± 0.10 g vs. free feeder, 17.06 ± 1.47 g; $F(1,9) = 120.20$, $P < 0.0001$). There was no difference in pellet removal from the free feeder when birds were offered regular pellets in the closed feeder,

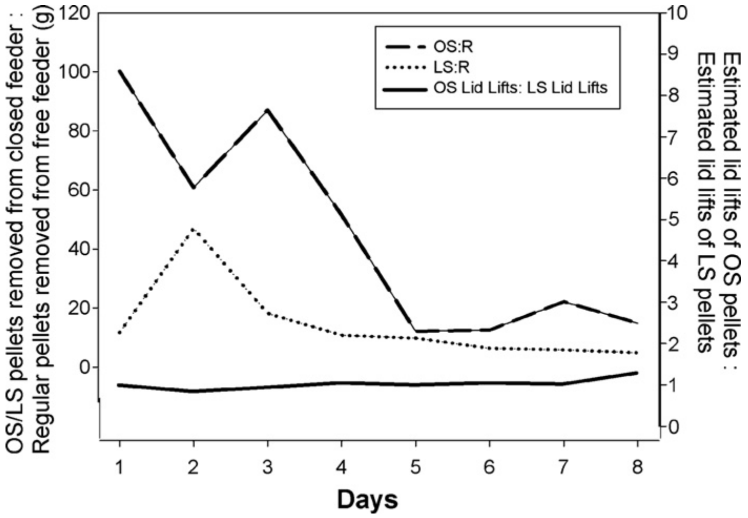

Fig. 2. Ratio (left *y*-axis) of mass of over-sized pellets (OS, broken line) or large-sized pellets (LS, dotted line) removed to regular pellets (R) removed (when the latter are freely available) as costs increase from day 1 (38.3 g) to day 8 (480 g), and the ratio (right *y*-axis) of the estimated number of over-sized pellet lid lifts (solid line) to large-sized pellet lid lifts over the same time period. Parrots removed a significantly greater mass of over-sized pellets than large-sized overall ($F = 5.33$, $P = 0.0345$), but the number of estimated lid lifts per day for either pellet type was essentially identical. Regular pellet data is de-transformed.

with or without 101.7 g lid weight cost ($F(2,18) = 0.33$, $P = 0.5768$).

3.5. Podomandibulation time determination

Pellet type significantly affected podomandibulation time ($F(2,13.2) = 40.69$, $P \leq 0.0001$); moreover, each pellet type differed from every other type with respect to podomandibulation time (over-sized vs. large-sized, $t = 4.79$, $P = 0.003$; over-sized vs. regular, $t = 9.02$, $P < 0.0001$; large-sized vs. regular $t = 4.23$, $P = 0.0009$). Parrots spent the most time podomandibulating over-sized pellets with an average of 4.27 min ± 31 s (log transformed mean is 2.41 ± 1.491) per retrieval bout. This was about 4.5 times greater than the podomandibulation time of regular pellets (58 ± 10 s; log transformed mean is 1.763 ± 1.000) and twice as long as large-sized pellets (2.08 min ± 21 s); log transformed mean is 2.096 ± 1.322. There was no effect of pellet order or interactive effects between pellet order and pellet type ($F(2,13.2) = 1.63$, $P = 0.2323$; $F(4,18.5) = 0.44$, $P = 0.7775$).

4. Discussion

These experiments were designed to test motivation by requiring parrots to incrementally lift up to 480 g (~1.5 times the body weight of an adult Amazon parrot) to gain access to food pellets or wooden cubes. However, because of the 480 g price ceiling caution is warranted; the maximum prices in the analyses are conservative and

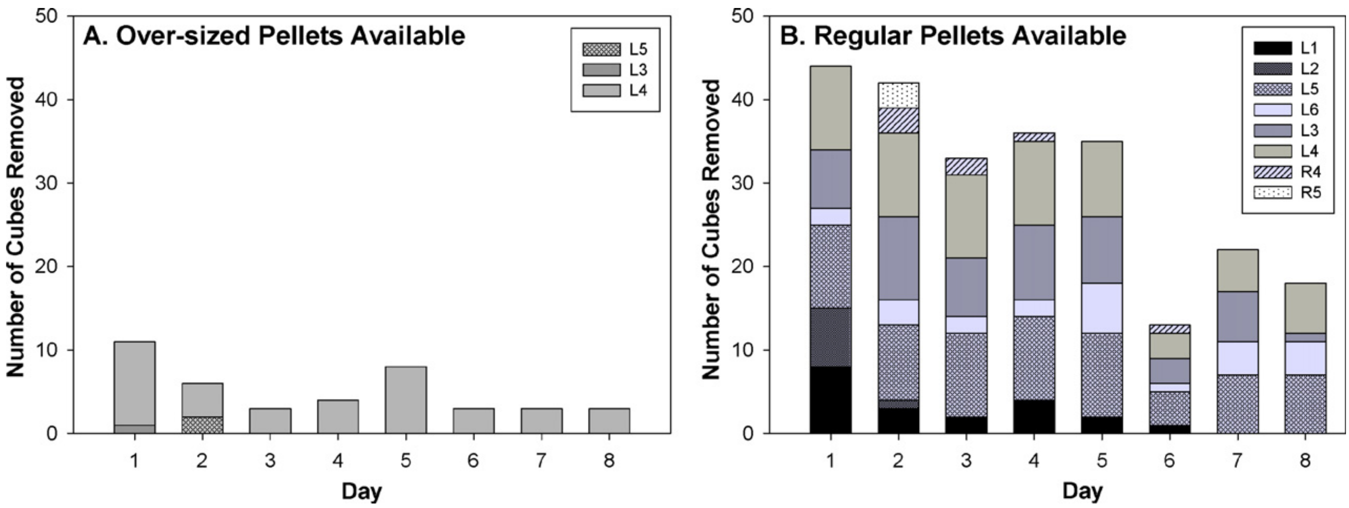

Fig. 3. Total number of wooden cubes removed/day when parrots had free access to either (A) over-sized pellets or (B) regular pellets as costs increased from day 1 (38 g) to day 8 (480 g). Box in each figure lists identification number of individual birds that actually removed wooden cubes, i.e., only three individuals removed cubes when over-sized pellets were freely available (A) compared to eight when regular pellets were freely available (B). In total, parrots removed 243 cubes when fed regular pellets and just 41 when fed over-sized ($P = 0.0078$); of those 41 cubes, it is important to note that one individual removed 38 cubes. The difference in motivation for wooden cubes may suggest an appetite for podomandibulation that is not met when fed regular pellets.

likely understate the true maximum price the parrots were willing to pay. The price ceiling did not affect resolving motivational differences for either large or over-sized pellets vs. regular pellets – the motivation for both larger pellets was strong – but the price ceiling may well have handicapped the ability to resolve a motivational difference for large vs. over-sized pellets. Support for this possibility is found in the mass of regular pellets removed when they were freely available: 0.58 ± 1.97 g were removed when working for over-sized pellets compared to 15.74 ± 1.9 g removed when working for large-sized pellets. This suggests that over-sized pellets were preferred to large pellets. Inspection of Fig. 2 reveals that the ratio of removal of over-sized pellets to regular pellets is much higher than the ratio of removal of large-sized pellets to regular pellets; this is despite the fact that estimated lid lifts for access to either larger pellet is essentially the same, with a ratio of ~1.

A stronger motivation to obtain over-sized pellets than large pellets was also suggested in how many birds paid the maximum price of 480 g for access to the larger pellets. In experiment 2, when large-sized pellets were freely available, six birds lifted the maximum weight for over-sized pellets, but when over-sized pellets were freely available, only one bird lifted more than 163 g for large-sized pellets.

It should be noted that because wastage of food by parrots is high and individually variable, pellet consumption was not measured; pellet removal was measured because it was more accurately quantifiable. Additionally, the birds were not weighed as catching and restraining birds is stressful and could interfere with food consumption. Thus, we do not want to speculate on energy intake yet cannot rule out that pellet size may have altered food consumption. However, close anecdotal observation did not suggest body mass change over the course of the experiments. In summary, the motivation for specific pellet sizes we observed are based on the amount of pellets removed from the feeders.

Over-sized pellets are 1.2–2.2 times larger than large-sized pellets and elicited twice as much podomandibulation time, which may have been a determining factor in preference. The two pellets also had different shapes. Large-sized pellets, being cylindrical like regular pellets, were observed to be held only one way by parrots: with the toes wrapped around the circumference of the pellet and the parrots breaking off pieces from the distal end. In contrast, the more cubic-to-spheroid shape of over-sized pellets prompted many rotations of a pellet throughout a feeding bout with parrots continuously changing the location of where they bit the pellet.

The two larger pellet sizes, although of identical formulation, were manufactured differently: over-sized pellets (cubic-to-spheroid in shape) were extruded, while regular and large pellets (cylindrical) were steam pelleted. Therefore, the preference of large-size pellets vs. regular pellets is a simple comparison of mass and volume, as shape and density of these pellet types is identical. In contrast, the preference of over-sized pellets over large or regular pellets could be based on differences in shape (cubic-to-spheroid vs. cylindrical, respectively), density (undetermined), surface texture (relatively rough vs. relatively smooth, respectively), nutritional density (undetermined, but extruded pellets might be expected to have slightly different nutrient composition than steamed pellets; (e.g., Amornthewaphat et al., 2005; Cutlip et al., 2006)), or size, i.e., mass and volume. Which of these parameters may govern preference is not yet resolved, but we can speculate by extrapolation: as the preference for large over regular pellets was based on mass and volume (i.e., size), then it is consistent that the preference of over-sized pellets over regular and large pellets is also based on size.

Motivation for wooden cube enrichment devices was strongly influenced by freely available pellet size. Birds removed more cubes and paid higher prices to access them when regular pellets were freely available. This corresponds to our earlier findings showing that enrichment device interaction/destruction (operationalized as g of material removed from 3.8 cm/side wooden cubes) is dependent on pellet size; birds interacted with cubes more when over-sized pellets were absent and only regular pellets were available (Rozek et al., 2010). The 2.5 cm/side wooden cubes used in this study are slightly larger than over-sized pellets and although the cubes were not ingested, they evoked identical podomandibulation behavior.

Behaviors associated with foraging, such as oral manipulation, are linked to physiological factors such as food intake regulation and satiety (Toates and Halliday, 1980). For instance, rats (*Rattus norvegicus*) were motivated to ingest a substantial amount of water orally even though their daily water needs had been exceeded through intragastric or intravenous administration (Nicolaidis and Rowland, 1975). It has been argued that there may be an ethological need for oral manipulation, such that if normal oral activity is prevented then feedback cues may motivate redirected oral behavior (Hughes and Duncan, 1988; Wiepkema, 1985). Thus, an appetite for foraging behavior may not be met by feeding parrots only regular pellets; under these circumstances podomandibulating wooden cubes may satisfy an appetite that is met by podomandibulation of food when parrots are fed over-sized pellets.

When animals learn to perform a task for food reinforcement, the task itself may become associated with the primary reinforcer as a secondary reinforcer; this may lead the animal to perform the task even in the absence of motivation for food (Inglis et al., 1997). Such contrafreeloading, when animals work for food although identical food is freely available, has been observed in many different species and experimental conditions and has been suggested as a means for an animal to exert control over its environment (Hughes and Duncan, 1988; Inglis et al., 1997; Jensen, 1963). Animals may work for food sources in order to gain information about their environment, such as profitability estimates about uncertain food sources; therefore, acquiring the food itself may not act as the sole incentive for the work preformed, as the information about the earned food may be equally motivating (Inglis et al., 1997). To determine whether contrafreeloading was a factor in the present study, we conducted an experiment in which regular pellets were simultaneously offered freely and under closed lids; parrots only removed pellets from the open feeder, indicating that contrafreeloading was not confounding pellet choice. The sequential nature of the experiments could have introduced experimental confounds; for example, prior experiment effects may have reduced contrafreeloading.

It remains unclear which features of the larger pellets motivated the birds' preference. African grey parrots are able to discriminate both continuous and discrete quantities of food and choose the larger amount in addition to being able to discriminate objects based on relative size (Al Ain et al., 2009; Pepperberg and Brezinsky, 1991). Other birds, such as pigeons (*Columbia livia*), have been documented to choose larger sizes of feed in choice trials (Killeen et al., 1993). The preference we observed may have been motivated by amount of food.

Animals may exhibit temporary reactions (i.e., avoidance, attraction) when presented with unfamiliar items and preferences may change as animals gain long-term experience with them (Fraser and Matthews, 1997). For these reasons, parrots were given both over-sized and large-sized pellets, and wooden cubes regularly for at least 2 months prior to the start of the experiment. For the preference trials between over-sized and regular pellets in Rozek et al. (2010), we cautioned that the strong preferences observed for over-sized pellets may be transient as the study was limited to short-term preferences (over a matter of a few months). However, the current experiments show that the dramatic preference for over-sized over regular pellets persists after at least 11 months and is therefore more likely to be permanent.

5. Conclusion

Captive Orange-winged Amazon parrots strongly prefer pellets that are substantially larger than what is commercially recommended for species of their size, with seven of ten Orange-winged Amazons lifting more than their own body weight to access them. Of the two largest pellet types tested for maximum price, birds showed a strong preference for the greater one ("over-sized" pellets). The rank order in terms of price paid was over-sized > large-sized > regular-sized, and this same order held true for pellet mass and podomandibulation time. When regular pellets were freely available, birds were motivated to remove more wooden cube enrichment devices than when over-sized pellets were freely available. These findings suggest that parrots are highly motivated to access food forms that enable podomandibulation, a naturalistic foraging/ingestive behavior; further, parrots will substitute interaction with wooden cube enrichment devices as surrogates for food if their food diet doesnot enable podomandibulation. Further studies are needed to determine in what ways, if any, the opportunity to podomandibulate food may contribute to parrots' overall welfare.

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