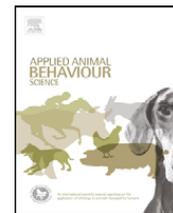




Contents lists available at ScienceDirect

Applied Animal Behaviour Science

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

Over-sized pellets naturalize foraging time of captive Orange-winged Amazon parrots (*Amazona amazonica*)

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ARTICLE INFO

Article history:

Accepted 7 March 2010

Available online 2 April 2010

Keywords:

Foraging behavior

Pelleted diets

Activity budget

Preference testing

Enrichment

Animal welfare

ABSTRACT

Parrots held in captivity experience distinctly different environmental demands, as compared to their wild conspecifics, particularly in regard to feeding. Cages equipped with computer-monitored infra-red beams (placed across a primary perch, in front of the feeder, in front of the drinking fount, and at the peak of the cage; interruption of a beam indicated a parrot's location) were used to supplement direct observation in characterizing activity budgets of adult male and female captive Orange-winged Amazon parrots (*Amazona amazonica*) fed pelleted diets. Parrots spent nearly all of their time perching, moving off the perch only a few times daily to drink and a few dozen times daily for pellet meals (each meal consisting of pellet retrieval and manipulation of the pellet(s) before swallowing). Such meals were temporally clumped, usually into 3–5 meal clusters per day, and clusters tended to be concentrated in morning and afternoon periods of a 12:12 LD light cycle, with a midday respite. Over-sized pellets formulated to be approximately 20–30 times larger than regular pellets (approximately 3–5 g each vs. 0.16 g each, respectively) exerted no detectable effect on the frequency distribution of off-perch bout lengths, but over-sized pellets dramatically increased post-pellet retrieval manipulation time approximately five-fold. In choice preference trials, parrots strongly preferred over-sized pellets to regular pellets, retrieving over-sized pellets approximately seven-times more often. Likewise, parrots offered only regular pellets removed 47.6 ± 6.4 g (mean \pm SE) pellets from their feeder per day, but removed only 6.5 ± 2.0 of regular pellets, if over-sized pellets were offered concurrently. Finally, the option of manipulating/consuming over-sized pellets strongly affected use of wooden cube enrichment devices. During a 3-day period, parrots offered both regular and over-sized pellets reduced the mass of wooden cubes (through biting/chewing) by approximately 0.13 g; removal of the over-sized pellet option increased this amount 50-fold. These results suggest that parrots offered only regular-size pelleted diets are deprived of an opportunity to engage in foraging behavior. Offering parrots over-sized pellets or enrichment devices that provide foraging-like opportunities can dramatically reduce periods of inactivity and encourage a more naturalistic activity budget, thereby enhancing welfare.

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1. Introduction

During the 1970s, 1980s, and 1990s the popularity of parrots as companion animals in the United States and Europe increased dramatically (Stern and Stern, 1990), fueling the development of such technologies as genetic

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sexing of monomorphic species (Dvorák et al., 1992) and the development of formulated, pelleted diets for parrots (Roudybush et al., 1984). Interest in avian medicine also increased, as reflected in publication of major texts on companion bird species (Altman et al., 1997; Harrison and Harrison, 1986; Ritchie et al., 1994), a journal focused largely on companion bird medicine (*Journal of Avian Medicine and Surgery*), and in 1993 board certification in avian practice (American Board of Veterinary Practitioners, Inc., Nashville, TN, USA). In recognition of the nutritional value of pelleted diets, both veterinarians and nutrition scientists recommended their adoption.

But pelleted diets, while nutritionally desirable, may contribute to a deficient behavioral environment. Individual parrots, particularly of the larger species, often develop behavioral pathologies in captivity, such as stereotyped behaviors and feather-picking. Many believe these maladies derive from austere captive environments (e.g., Garner et al., 2003). In response to this perceived cause, a sizeable market has developed to supply cage enrichment devices to parrot owners, and enrichment is mandated in animal care guidelines for companion birds in the retail pet industry (PIJAC, 2006). The basis of birds' attraction to various enrichment devices, however, is only beginning to be experimentally explored; some studies suggest that certain enrichment devices may mimic food properties and act as surrogate substrates for foraging behavior (e.g., Kim et al., 2009).

Captive parrots often benefit when presented with increased foraging opportunities. For example, providing young Orange-winged Amazon parrots (*Amazona amazonica*) with foraging enrichment devices reduced and/or prevented feather damaging behavior (Meehan et al., 2003). Similarly, feather scores improved when African grey parrots (*Psittacus erithacus*) were provided with foraging enrichment devices (Lumeij and Hommers, 2008). In both of these studies, the devices consisted of assorted receptacles (e.g., pipes, baskets, t-shirt bags) that contained food. However, few studies have attempted to identify properties of enrichment devices that promote foraging behavior but which do not incorporate food as an endpoint. Meehan et al. (2003) suggest that parrots may be highly motivated to locate, acquire, and process food items. However, it remains unclear which design features of enrichment devices might satisfy a captive parrot's foraging needs: behaviors associated with searching for, acquiring and processing an item, or that the item at issue is edible or, perhaps, a combination of the two.

The relatively high metabolizable energy (ME) density of common pelleted (15.6 ± 1.4 MJ ME/kg) and seed (16.4 ± 1.0 MJ ME/kg, 22.4 ± 2.9 MJ ME/kg if dehulled) diets (Werquin et al., 2005), as compared to common alternative foodstuffs (e.g., many fruits and vegetables), may potentially reduce foraging time by permitting energy needs to be consumed in a relatively short time-span. Additionally, daily energy needs of inactive, caged birds may be just a fraction of those of free-living birds, depending on time spent flying, foraging, preening, etc., activities which can vary seasonally for both captive and wild birds (Goldstein, 1988). As a consequence, activity budgets of pellet/seed-fed birds in captivity may differ substantially from conspecifics

foraging on natural foods in the wild, but this point has received little research attention.

A typical pelleted diet (Roudybush low-fat maintenance, small size, Roudybush, Inc., Woodland, CA, USA) is extruded to produce pellets weighing approximately 0.16 g/pellet (modal size). But we noted anecdotally that Orange-winged Amazon parrots interacted extensively with pellets extruded to be 20–30 times larger. These anecdotal observations led us to take a detailed view of the activity budgets of captive Amazon parrots fed pelleted diets and to determine whether their activity budgets were influenced by pellet size, whether parrots exhibited a preference for one pellet size over another, and whether over-sized pellets altered interactions with cage enrichment devices. To these ends, we developed and tested the feasibility of using a computer-monitored data collection system employing interruptible infra-red beams for detecting the presence of parrots at critical cage locations.

2. Methods

2.1. Subjects, caging, and management

Subjects were captive-bred male and female Orange-winged Amazon parrots (*A. amazonica*), ranging in age from 7 to 8 years. All birds were previously used in novelty and neophobia studies (Fox and Millam, 2004) and studies of cage enrichment devices (Kim et al., 2009; Webb and Millam, 2010). Studies were conducted between May 2008 and August 2009.

Birds were individually housed in white, galvanized steel wire cages (0.84 m wide \times 0.64 m deep \times 1.73 m high). Each cage was equipped with a 4 cm \times 9 cm \times 0.81 m Douglas fir perch placed approximately 1.14 m from the floor, a wide-mouth "L"-shaped feeder (Bass Equipment Co., Healdsburg, CA, USA) and a nipple drinking fount. Birds were held on a 12 h light and 12 h dark (12L:12D) photoperiod with light onset at 08:00 h. A low-fat pelleted diet (Roudybush low-fat maintenance, small size, Roudybush Inc., Woodland, CA, USA) and water were provided *ad libitum*, unless otherwise stated. A sample ($N = 72$) of "regular" sized (Roudybush "small") extruded pellets measured approximately 4.25 mm dia. \times ~5–15 mm in length, with a modal mass of 0.16 g/pellet. A sample ($N = 51$) of experimentally extruded "over-sized" pellets produced a bimodal size-distribution frequency of pellet sizes with peaks at 3 (~15 mm dia. \times 17 mm in length) and 5 g (~17 mm dia. \times 22 mm in length). The process of extrusion is inherently variable; pellets are also subject to breakage during handling. Experimental protocols and standard operating procedures were approved by the University of California's Institutional Animal Care and Use Committee; the University is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care International.

2.2. Experiment 1 – feasibility

A cage (as above) in a test room was equipped with four pairs of infra-red (IR) beam transmitters (employing a light emitting diode [model #TSAL5100, Vishay Semiconductor, Shelton, CT, USA, from Newark, Chicago, IL,

USA, SKU #33C1730] encased in a block of high-density polyethylene plastic [25.4 mm × 76.2 mm × 50.8 mm] for protection) and receivers (employing a photodarlington transistor [model #BPV11F, Vishay Semiconductor, from Newark, SKU #32C9138], similarly encased). Transmitters and receivers were placed along the long axis of the perch, in front of the mouth of the feeder, in front of the water fount, and across the long axis of the peak of the cage; interruption of an IR-beam indicated the location of the bird. A single-board computer (LabJack, Model U-12; LabJack Corp., Lakewood, CO, USA) was connected to a Windows XP-based microcomputer and programmed to interrogate and record the output state (“1” or “0”) of each IR receiver, once per second, into a txt file, using DAQFactory Express software (AzeoTech, Inc., Ashland, OR, USA, bundled with the LabJack). Additionally, a video camera was focused on the cage with a field of view that encompassed the perch, feeder and drinking fount, and the output was recorded on a digital recorder (Model TA-418All four-channel VCR, Fuho Technology, Ltd., Chang Hua City, Taiwan, with PCViewer software, ver. 3.8), allowing up to 8× normal speed-compressed replay. IR-beam data could thus be compared to video recordings. Six consecutive days of data were analyzed to characterize typical durations and activities of the parrot as characterized by the IR-beam switches and video recordings.

2.3. Experiment 2 – activity budget analysis

Two cages, equipped with IR-beam switches, as above, were located in a test room, permitting two birds to be monitored simultaneously. Following re-location of parrots from a larger, holding aviary to the test room, birds were fed regular pellets until behavior was judged to be stabilized on the basis of normal appearing droppings, consistent food use, and time being spent principally on the wooden perch, as opposed to the cage walls (alarmed birds tend to move to the highest possible location within a cage, which was on cage walls). After several days of data were collected, during which time birds were fed regular pellets, over-sized pellets were gradually introduced either in a separate food dish or mixed in with regular pellets. After a variable period of what we judged to be neophobic avoidance (for individual parrots, from a few hours to a few days), birds were uniformly attracted to the over-sized pellets, though it occasionally took several days for birds to learn how to hold them (by one foot) well enough to allow them to chip off pieces with their beaks for eating. We termed this manipulation of the pellet with the synchronous use of beak and/or foot “podo-mandibulation.” After birds gained skill in eating the over-sized pellets, regular pellets were removed. After behavior stabilized, 2–5 days of data were collected for each diet-type for statistical analysis. Three sets of two parrots were tested ($N=6$), unless otherwise indicated. Frequency distributions of off-perch bout lengths were compared using the glimmix procedure and random statement to specify a repeated-measures model: frequency = bird id + pellet size + time bin (SAS, 9.2, Cary, NC, USA). This procedure was used to account for the expected Poisson distribution due to the properties of frequency distribution data. The Tukey–Kramer adjustment

was used to check for differences between means and the Satterthwaite method was used to compute degrees of freedom.

2.3.1. Feeding behavior

To characterize meal patterning, several parameters were measured using 2 consecutive days of data per bird for regular ($N=4$) and over-sized ($N=6$) pellets. Off-perch feeding bouts refer to periods in which a bird moved off the perch solely to retrieve pellets; the duration of a bout consisted of travel to the feeder, one or more feeder IR beam breaks, and travel back to the perch. During a feeder visit, a bird would typically make several discrete “pecks” (English lacks a more accurate word, “grasps” may better describe the behavior) into the feeder to retrieve a pellet or pellets; such pecks were done at a slow enough tempo to interrupt at least one of the once per second interrogations of the feeder IR-beam. Feeder visits tended to be clumped in time into, typically, 3–5 meal clusters per day (see results). Although analysis of off-perch feeding bout lengths were restricted to feeder visits bordered by occupancy on the perch with no other intervening IR-beam interruptions, but pellets were not invariably taken in this manner, sometimes a bird would leave the perch, take a meal and thence drink water or engage in some other non-perch behavior. The latter feeder visits are included in other analyses, but excluded from “off-perch feeding bouts.” Number of feeder visits, the time between feeder visits within a meal cluster, and meal cluster durations were compared using the linear mixed effects model; a blocking factor (pairs) was added to the model to account for the birds being tested in pairs and repeated measures were added for subject, day and pellet type. The model fit was determined via graphical analysis and Shapiro–Wilk value; the data were normally distributed. Meal cluster durations, operationally defined as group of meals with inter-feeder visit intervals of less than 30 min, were defined this way because out of 498 data points, fewer than five deviated from this definition.

To determine podo-mandibulation times, video segments were observed of each parrot after retrieval of 10 regular-size pellet meals and 10 over-sized pellet meals. Mean retrieval times for each pellet type were calculated for each parrot. The resulting means/parrot for each pellet type were compared using a paired two-tailed *t*-test ($N=6$ parrots/pellet type).

2.4. Experiment 3 – pellet preference

Twelve individually housed parrots (six male, six female) in a single test room were used to determine pellet preference. Cage dimensions were as above. Each cage had two Douglas fir perches, located approximately 1.14 m and 1.55 m above the cage floor. Two wide-mouth “L”-shaped feeders mounted adjacently at the center rear of the cage were readily accessible from the lower perch. Feeders, perches and over-sized pellets were introduced to the parrots six weeks before experiments began.

During the experiment, parrots received two pellet treatment regimes: regular pellets in one feeder and over-sized pellets in the other (over-sized present) or regular pellets in one feeder and nothing in the other feeder

(over-sized absent). Pellet type was initially randomly assigned to feeder side and each regime was repeated with the opposite-assigned sides, totaling four test periods, to ensure that potential side preferences were balanced for each pellet type. Side preferences were apparent for some birds, as evidenced by which side of the cage waste tray contained a greater fraction of droppings (by visual estimation). In most instances, these side preferences were obvious and essentially unchanging; they may derive from neighbor preferences and/or the relation to potential stressor sources such as the entrance door to the room.

Each test period was 5 days long; birds received the pellet regime for 2 days (for acclimation) before the 3-day data collection period (days 1–3 for direct behavioral observation and days 2 and 3 for food removal determination). Test periods were separated by 2–5 days to allow for routine husbandry and veterinary visits. On data collection days, all pellets were removed from the feeders 1 h before lights-out the previous night and added 1 h after lights-on in the morning. Pellets were weighed before being added to the feeders in the morning and after removal in the evening. Parrots received 150 g of regular pellets and 400 g of over-sized pellets, enough to fill the trough of the feeder and to last 3 days (more over-sized pellets were provided, because they were frequently dropped). When over-sized pellets were present, pellet choice was recorded by direct observation for the first 30 min after pellet presentation, for 3 consecutive days.

The last 2 days of data from each data collection period were used for the statistical analysis of regime comparisons. The linear mixed effects model was employed (SAS), taking into account repeated measures for regime, day and subject. The model fit was determined via graphical analysis and Shapiro–Wilk value; the data were normally distributed. Means of pellet choices were compared by averaging 3 days of data for each individual and comparing diet regime means by a paired two-tailed *t*-test.

2.5. Experiment 4 – over-sized pellets and use of enrichment device

Experiment 4 was conducted as Experiment 3 and consisted of one 3-day test period for each regime. Two unstained 3.8 cm³, 24–28 g wooden cubes made of Douglas fir (see Kim et al., 2009) were attached to cage walls with approximately 2 mm diameter wire (a shower curtain hook), one placed at either end of the upper perch, at foot height. The shower curtain hooks permitted limited mobility of the cubes; they could be moved laterally and vertically over a distance of approximately 5–7 cm by foot and/or beak. Cubes were weighed at the beginning and end of each 3-day test period.

For pellet removal comparisons, regimes from Experiment 4 (wooden cubes present) were paired with like regimes from Experiment 3 (wooden cubes absent) for design balance. Cube weight difference for each bird was determined by totaling the weight differences of both cubes in the cage. Differences in pellet removal and beginning vs. end weights of cubes were analyzed by the linear mixed effects model (SAS). The model fit was determined

via graphical analysis and Shapiro–Wilk value; the data were normally distributed.

3. Results

3.1. Experiment 1 – feasibility

Cumulative time spent in interruptions of IR-beam switches on the perch, at the feeder and at the water fount accounted for over 99.1% of the bird's time, i.e., only 13.3 ± 1.06 min were unaccounted for at places other than these locations. Inspection of video data confirmed that switches reliably characterized the bird's behavior, i.e., there was essentially complete coherence between time spent at each of the three locations as indicated by IR-beam data and as evidenced by video recording.

Eating bouts of the regular pellet diet typically occurred approximately 25 times per day. Each bout consisted of a brief foray to the feeder lasting approximately 10–35 s, during which time video observation showed that approximately one-to-four pellets were consumed in one-to-two individual pecks into the feeder (Fig. 1A). Pellets were held in the beak/mouth as the bird returned to the perch, where they were manipulated with beak and tongue before swallowing. Feeding bouts were somewhat concentrated into morning and afternoon components (Fig. 1B), with the afternoon component being more prominent.

Most off-perch bouts (<5 s/bout, approximately 30–40 per day) were artifactual, resulting from normal postural movements on the perch, e.g., like wing-flapping, which often moved the bird's body out of the IR-beam path, permitting switch closure (Fig. 1A); this remained true in all subsequent experiments except for bird 7, which often visited the feeder, retrieved pellet(s) and returned to the perch in less than 5 s. Drinking bouts were several times longer than feeding bouts, typically lasting 2–3 min, but they occurred less frequently, often only two or three times per day, and often near light-offset.

Time unaccounted for by any of the IR-beams typically increased substantially following significant changes in placement or location of objects in the room. For example, on one occasion a sheet of cellophane was placed over the bird's waste tray in order to retrieve dropped pellets. This alarmed the bird and it spent several hours high in the cage, grasping the vertical bars that form the sides of the cage. Other instances of neophobic alarm, occasioned by such events as visits to the room by unfamiliar service people, also caused the bird to move high in the cage and cling to vertical bars of the cage wall. The amount of time the bird would remain on the cage walls, ranged from minutes to hours, apparently depending on the extent of neophobic alarm; adaptation to the neophobic stimulus could clearly be seen as an increase in time spent on the wooden perch (not shown), a preferred location, albeit lower in the cage.

3.2. Experiment 2 – activity budget analysis

In broad terms, frequency distributions of off-perch bouts for parrots in the activity budget experiment resembled that of the parrot tested in the feasibility experiment: the shortest duration bouts were most numerous, drink-

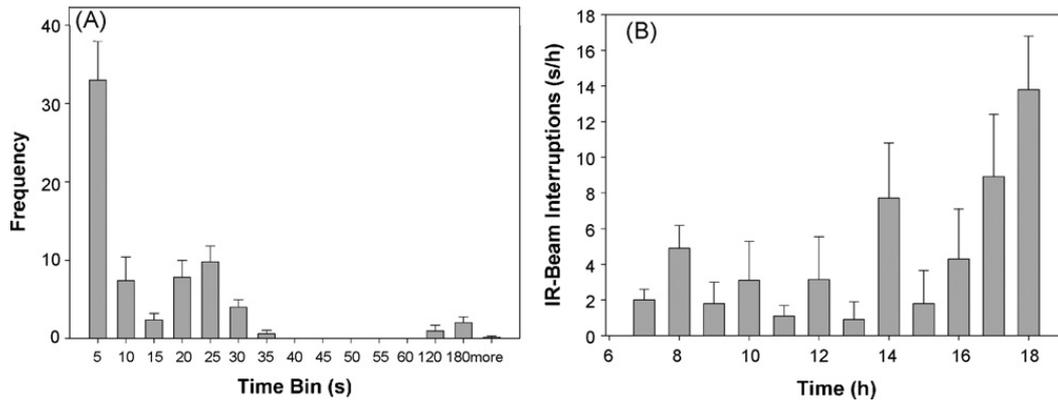


Fig. 1. Daily frequency (mean \pm SE of 6 days of data) of: (A) off-perch bout lengths of the Amazon parrot tested in the feasibility experiment. Video observations and IR-beam data showed the longest bouts were associated with drinking, bouts from 15 s to 35 s were associated with meal-taking, and the shortest bouts were predominantly artifactual, involving normal postural movements that resulted in IR-beam switch closures, but which occurred while the bird was still on the perch. (B) Distribution of feeder IR-beam interruption (s/h; mean \pm SE of 6 days of data).

ing bouts tended to be several minutes in duration, and duration of bouts for feeding was intermediate in length. These intermediate lengths were impossible to classify as feeding bouts, *per se*, vs. forays off the perch for other purposes: each individual showed its own characteristic pattern and inter-animal variability in duration of feeding bouts obscured the event patterns evident in the feasibility experiment.

3.2.1. Feeding behavior

Time spent interrupting IR-beams at the feeder showed that for birds fed regular pellets feeding did not occur evenly over time, but was concentrated in morning and afternoon periods, with a mid-day period of relative quiescence (Fig. 2A). Also, feeding was not strictly crepuscular, as little feeding behavior occurred during the first hour of light (Fig. 2A). Birds fed over-sized pellets showed a similar, though slightly moderated pattern: morning and evening peaks were evident, though the mid-day quiescent period was less pronounced. (Fig. 2B).

Parrot meals consisted of several events: travel to the feeder, feeder visit, travel to the perch, and podomandibulation. Although meals occurred throughout the day, they were almost always clumped into meal clusters, which occurred approximately 3–6 times/day; rarely did single meal events occur outside of a meal cluster. When fed regular pellets, the time between feeder visits within

each meal cluster was significantly less than when fed over-sized pellets ($F=36.33$, $N=4$, $P=0.0092$); feeder visit intervals had a modal peak of 1–2 min for regular pellets vs. 9 min for over-sized pellets. In addition, the average duration of each meal cluster was about 24 min longer when fed over-sized pellets (20 ± 3.51 min, regular, vs. 44 ± 2.97 min, over-sized; $F=20.55$, $N=4$, $P=0.0201$).

Off-perch feeding bout duration (sum of travel to the feeder, feeder visit, and travel to the perch) ranged from a few seconds to approximately 90 s, with the modal duration between 10 s and 15 s (Fig. 3). Average off-perch feeding bouts for regular and over-sized pellets were strikingly similar, with the majority of bout times devoted to travel and less than 4 s to actual food procurement. Parrots visited the feeder about 25 times/day; there was no significant difference in daily feeder visits between the two pellet types ($F=0.16$, $N=4$, $P=0.7184$).

We noted anecdotally that some birds were often synchronized in their feeding behavior, i.e., if one bird moved off the perch to visit the feeder, the other bird did likewise. Fig. 4 illustrates the synchronous feeding behavior of pairs when fed over-sized pellets; this pattern was also observed when birds were fed regular pellets (not shown). Inspection of Fig. 4 shows that birds often appeared synchronized in their meal clusters, if not individual feeder visits.

In contrast to activity budget estimates from IR-beam data, pellet type exerted a dramatic effect on pod-

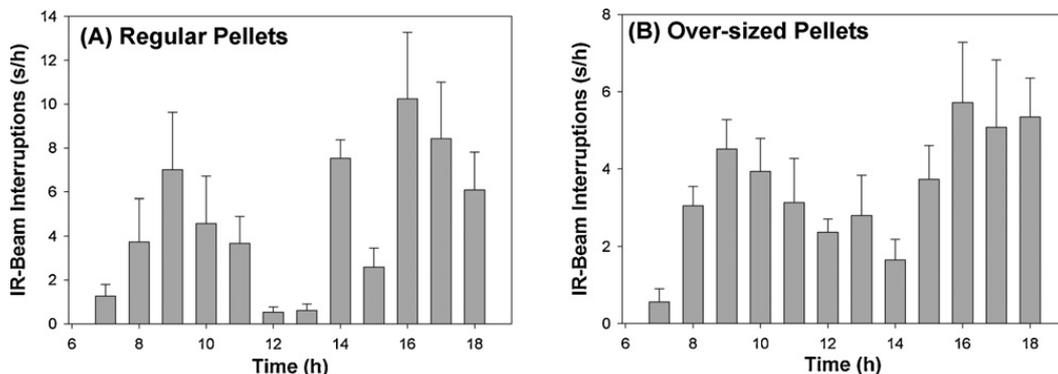


Fig. 2. Distribution of feeder IR-beam interruption (s/h; mean, SE) over daytime h: (A) regular pellets, $N=4$; (B) over-sized pellets, $N=6$.

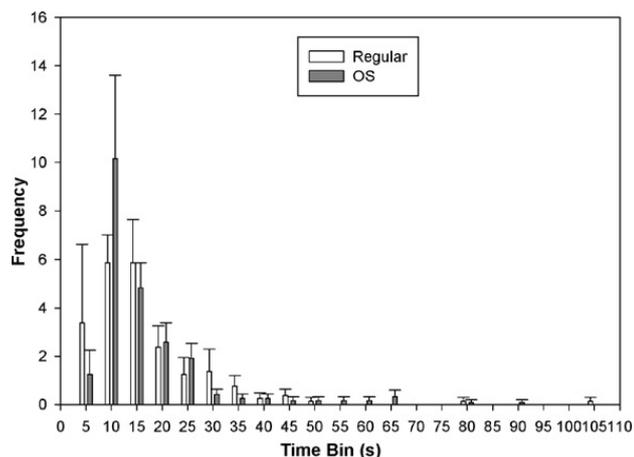


Fig. 3. Frequency distribution of off-perch feeding bouts from Amazons fed regular ($N=4$) and over-sized ($N=6$) pellets; average of 2 consecutive days/bird/pellet type.

mandibulation time as observed by video. Over-sized pellets, which were typically held with a preferred foot and rotated with foot and beak in a coordinated fashion as bite-sized pieces were removed, chewed and swallowed, increased podo-mandibulation time approximately five-fold over regular sized pellets, which were mandibulated much less and whose manipulation rarely involved a foot ($t=5.36$, $N=6$, $P=0.003$). Also, although not quantified, it was anecdotally noted that while over-size pellets were very commonly dropped and rarely, if ever, completely consumed, regular pellets were only rarely dropped, if ever.

3.3. Experiment 3 – pellet preference

When like pellet regimes with opposite-assigned sides were compared there was no evidence of parrot side preference influencing pellet preference (over-sized present: $F=1.58$, $N=12$, $P=0.2448$; over-sized absent: $F=0.18$, $N=12$, $P=0.6800$); this allowed for the combination of both test periods of each regime for further analysis. There was a significant difference and large effect between the two regimes ($F=52.23$, $N=12$, $P<0.0001$): parrots removed an estimated 41.1 g more regular pellets when over-sized pellets were absent than present. Parrots clearly preferred over-sized pellets: during the first 30 min after pellet pre-

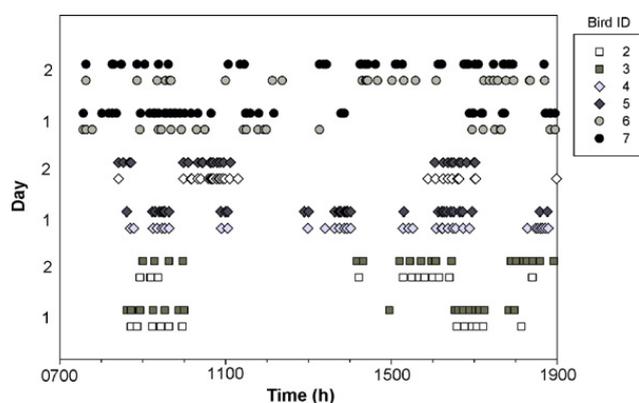


Fig. 4. Feeding behavior of birds fed over-sized pellets ($N=6$) for 2 consecutive days/bird, with each data point representing a feeder visit.

sentation, parrots chose over-sized pellets over regular pellets more than seven-fold ($t=4.79$, $N=12$, $P=0.0006$). There was no significant effect of sex influencing pellet preference ($F=0.16$, $N=12$, $P=0.6991$).

Throughout the study, some birds showed great dexterity and attention in manipulating over-sized pellets, removing fewer over-sized pellets from their feeder daily than birds which appeared less deft (e.g., bird #L6, 80.4 ± 17 g/day vs. bird #R1, 243.5 ± 41 g/day). Several other birds also showed consistency in amount of pellets removed over time.

3.4. Experiment 4 – over-sized pellets and use of enrichment device

There was a significant difference in wooden cube destruction in the presence and absence of over-sized pellets ($F=17.82$, $N=12$, $P=0.0018$). The absence of the over-sized pellet option increased enrichment device destruction. Birds removed 25.8% of the total weight of the cubes when over-sized pellets were absent vs. only 0.5% when over-sized pellets were present, an absolute difference of 6.59 g wood removed in these two conditions.

While enrichment device destruction correlated highly with available pellet type, the presence or absence of wooden cubes did not affect the amount of pellets birds removed from the feeder. There was no significant difference in regular pellet removal ($F=1.49$, $N=12$, $P=0.2492$) or over-sized pellet removal ($F=2.00$, $N=12$, $P=0.2009$), when regimes with and without wooden cubes were compared.

4. Discussion

To our knowledge, these data are the first to complement direct observation with the use of an automated, unbiased data collection system for characterizing activity budgets of captive parrots. The system provided a temporally detailed characterization of where parrots did (when they were interrupting an IR-beam) – and did not (when they were elsewhere) – spend time. In some instances, positioning IR-beams at only three locations, primary perch, feeder and drinking fount, captured a remarkable amount of the activity budget information: in the feasibility experiment, for example, only 13.3 ± 1.1 min/day were not accounted for by IR-beam interruption at these locations. Anecdotally, we routinely observed that time off the primary perch correlated with neophobic alarm; at these times, birds would climb higher in the cage and cling to cage walls. We anticipated capturing this behavior by placing an IR-beam at the highest point in the peaked cage, but alarmed birds would also often cling to cage walls at slightly lower elevations, thereby not breaking the IR-beam. When validated and combined with video and direct observation, the system provided a useful and untiring tool for characterizing aspects of activity budgets at a detailed level. However, IR-beam interruption did not detect behaviors not involving locomotion, e.g., differences in podo-mandibulation time.

A surprising finding was the extent of inactivity observed in the parrots in this study and the limited

amount of time spent feeding, which stands in stark contrast to reports from wild parrots. The parrots in this study left their perches for only about 30 min/day (~6% of their activity budget); most of this time was accounted for with trips to the feeder and water fount. In contrast, foraging comprises a substantial share of the activity budgets of wild parrots: Galahs (*Cacatua roseicapilla*) spend approximately 50% of their time foraging; red-rumped parrots (*Psephotus haematonotus*) forage 40–75% of daytime (Westcott and Cockburn, 1988); canary-winged parakeets (*Brotogeris versicolourus*) visit a single plant species 31 times/day and feed on many plant species, with each visit lasting 20 s to 42 min (Francisco et al., 2002); lilac-crowned Amazons (*Amazona finschi*) forage during a 4-h morning period and a 3-h late afternoon period (Renton, 2001); crimson rosellas (*Platycercus elegans*) spend 45–55% of their day foraging, climbing and flying, with foraging comprising the bulk of these activities (Magrath and Lill, 1983). Captive parrots, on the other hand, do not need to travel extensively, visit multiple food sources or consume large quantities to meet their nutritional needs when a balanced energy-dense pelleted diet is continuously available, nor would the energy demand of a captive animal be comparable to a wild one. It may be that the ease with which captive parrots can meet their nutritional needs contributes to a substantial behavioral difference between captive birds and their wild counterparts.

Time off the perch did not include time spent manipulating and consuming pellets once a bird had returned to the perch. Assuming an estimated 25 feeder visits per day, regular pellets elicited approximately 36.0 min of podo-mandibulation time. In contrast, the same number of over-sized pellet retrievals elicited approximately 178 min. In addition, because of the difference in podo-mandibulation time, the interval between feeder visits was longer when parrots were fed over-sized pellets; this extended the average duration of meal clusters more than 2.5 times over the meal cluster durations of regular pellets. The summation of all feeding behaviors (travel to and from the feeder, feeder visit, and podo-mandibulation times) comprised an estimated 5.9% of light-phase activity when regular pellets were fed and 25.7% of activity when over-sized pellets were fed; the latter more closely approximating foraging activity budgets of wild parrots.

Activity budget analysis revealed two concentrated feeding periods, similar to that of wild neotropical parrots. In a survey of psittacines at Manu National Park, Peru, approximately 95% of the studied species showed diel variation in activity, with peaks in the morning and late afternoon (Gilardi and Munn, 1998). The same feeding pattern was observed in the Puerto Rican Amazon (Snyder et al., 1987). Several factors may drive such patterns: daily temperature fluctuations, predator avoidance, and the abundance of food in tropical forests have all been suggested (Westcott and Cockburn, 1988; Gilardi and Munn, 1998). The food abundance factor directly relates to captive birds with *ad libitum* diets. Gilardi and Munn (1998) cite unpublished data and personal communications supporting the idea that most captive birds show a similar pattern to wild birds feeding in the tropics: eating to repletion in the morning, resting for several hours, and feeding

again in the late afternoon. This pattern persisted in our study, even in the absence of transitional light cues at dawn and dusk, temperature changes, and predators.

Another evident pattern was the often synchronous feeding behavior of test pairs. Inspection of Fig. 4 shows that pairs were often synchronous within meal clusters, if not individual feeder visits. Extent of behavioral synchrony between pair-bonded cockatiels (*Nymphicus hollandicus*), including feeding behavior, predicts pairbond strength and reproductive success (Spoon et al., 2006). It is possible that the extent of synchronous feeding behavior between test pairs similarly reflects inter-bird affinity.

The majority of psittacines are prehensile-footed and employ their feet when feeding on larger food items; those parrots that do not usually feed on the ground or eat small seeds or seeds of fruits rather than the fruit itself (among other commonalities; Smith, 1971). Coordinated use of beak and foot interaction has been described as an active manipulation involving the outer digits of the foot, which rotate the food, while the beak and tongue access the item (Harris, 1989). It has been argued that the beak is the main source of manipulation, analogous to the right hand of humans, while the foot simply acts as a positioning tool (Peters, 1988). Podo-mandibulation is highly developed in parrots and is remarkable considering the food is lifted directly to the beak for access, whereas other avian species, including some parrots, lower their heads to the food source itself, possibly increasing the risk of predation (Smith, 1971, 1972; Harris, 1989).

Because Amazon parrots are arboreal feeders that regularly use their beak and feet for feeding in the wild, their preference for over-sized pellets may reflect an appetite to manipulate food in this manner. Orange-winged Amazon parrots in the Trinidadian wild feed almost exclusively on *Mauritia* and *Roystonea* palm fruits, with non-palm fruit comprising only 15.57% of their diet; non-palm fruit is only consumed during the dry season, when palm fruit is not available (Bonadie and Bacon, 2000). The fruit of the *Mauritia* palm trees is approximately 30–55 mm in length and 40–70 mm in diameter, while the fruit of the *Roystonea* is smaller, at 12–17 mm in length and about 10 mm in diameter (food and fruit-bearing forest species, 1986; Zona, 1996). Similarly, three other *Amazona* species regularly consume ebony, strangler fig and coma fruits/seeds, which have a comparable size variation to palm fruits (Enkerlin-Hoeflich, 1995). The preference for over-sized pellets may thus reflect their resemblance to native foods: over-sized pellets are intermediate in size between *Mauritia* and *Roystonea* fruits, while regular pellets are much smaller than the smallest fruit typically consumed in the wild. However, birds may also select over-sized pellets based on amount of food. Although the two pellet types were extruded from the same formula, one over-sized pellet is dramatically larger than a typical selection of one to four regular pellets. In choice trials, African grey parrots (*P. erithacus*) were able to discriminate quantities of food (both discrete and continuous) and select the larger amount (Al Ain et al., 2009). Finally, it must be noted that as the preference trials were conducted over only a 2-month period, it must be considered that the preferences we observed may be transient.

The size of the over-sized pellets required the birds to learn new manipulation skills in order to consume them. The rotation of the pellet with beak and foot routinely resulted in the bird dropping some, or all, of the pellet, especially during skill acquisition. Anecdotally, more dexterous birds, which removed fewer over-sized pellets per day, dropped fewer whole pellets.

Several studies have shown the usage, behavioral changes, and positive welfare effects associated with providing captive parrots with foraging enrichment devices (Coulton et al., 1997; Lumeij and Hommers, 2008; Meehan et al., 2004). However, there is a lack of research investigating which characteristics of food create satisfactory foraging opportunities and whether enrichment device use and/or destruction correlates with time spent foraging. The birds in our study interacted with wooden cubes much more when over-sized pellets were not available. This suggests an appetite for podo-mandibulation, *per se*, that is not met when parrots are fed only regular sized pellets. The destruction of the wooden cubes in the absence of over-sized pellets may allow birds to search for, acquire and process an item, satisfying the appetite for podo-mandibulation, even though food is not the endpoint of the interaction; the wooden cubes may thus have acted as a non-food foraging enrichment device.

5. Conclusion

Captive Orange-winged Amazon parrots spent approximately 5.9% of daytime hours foraging in a crepuscular pattern on a conventional pelleted diet. Offering birds over-sized pellets, which they dramatically preferred to regular pellets in choice preference trials, increased their foraging time-budget to approximately 25.7%, a figure more closely resembling activity budgets of wild parrots. The increase in foraging time was primarily spent manipulating over-sized pellets with beak and foot and nibbling off pieces for chewing and swallowing, i.e., podo-mandibulation. Offering over-sized pellets also dramatically reduced destruction of wooden cube enrichment devices, the latter presumably meeting an appetite for podo-mandibulation in the absence of over-sized pellets. Taken together, these findings suggest that parrot appetites are motivated not only by nutrition, but by food form. Food forms that provide the opportunity to manipulate with beak and foot (podo-mandibulation) may meet a native appetite separate from nutrient content. Providing such food forms (or surrogate enrichment devices) promotes more naturalistic foraging behavior by captive parrots and may enhance welfare.

Acknowledgement

This research was supported, in part, by the Department of Animal Science's Winn Endowment for Parrot Research.

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