Published in final edited form as:

Behav Processes. 2012 November ; 91(3): 236–243. doi:10.1016/j.beproc.2012.09.002.

Rats (*Rattus norvegicus*) and pigeons (*Columbia livia*) are sensitive to the distance to food, but only rats request more food when distance increases

Mark P. Reilly, Diana Posadas-Sánchez, Lauren C. Kettle, and Peter R. Killeen
Arizona State University

Abstract

Three experiments investigated foraging by rats and pigeons. In Experiment 1, each response on a manipulandum delivered food to a cup, with the distance between the manipulandum and the cup varying across conditions. The number of responses made before traveling to collect and eat the food increased with distance for rats, but not for pigeons. In Experiment 2, two manipulanda were placed at different distances from a fixed food source; both pigeons and rats preferentially used the manipulandum closest to the food source. Experiment 3 was a systematic replication of Experiment 1 with pigeons. In different conditions, each peck on the left key increased the upcoming hopper duration by 0.5, 1.5 or 2.5 s. Completing a ratio requirement on the right key of 1, 4, 8, 16 or 32 pecks, depending on the condition, then produced the food hopper for a duration that depended on the number of prior left pecks. As the ratio requirement increased on the right key, pigeons responded more on the left key and earned more food. Overall, the results replicate previous research, underlining similarities and differences between these species. The results are discussed in terms of optimal foraging, reinforcer sensitivity and delay discounting.

Keywords

foraging; impulsivity; longbox; pigeons; reinforcer accumulation; rats; travel requirement

1. Introduction

In all foraging decisions two variables are of key importance: the benefits and the costs associated with the alternatives. These are explicitly considered in the optimal foraging framework (OFT; Perry and Pianka 1997; Fantino and Abarca 1985; Stephens and Krebs 1986), but they are implicit in all experiments with animals. Optimal foraging theory requires that animals adjust their behavior to maximize some value function with respect to some cost function. Experiments are aimed not at testing this truism, but rather learning the variables and their transformations that are necessary to achieve such invariance (Smedslund 2002; Kacelnik and Houston 1984). Oftentimes variables such as calories in versus calories out are discussed; but calories provide a poor metric: The basal metabolic rate of most animals adds such a large fixed intercept, that calories expended is an insensitive indicator variable. Time invested (and the opportunity costs it entails) or distance traveled (and the

© 2012 Elsevier B.V. All rights reserved.

Send correspondence about this manuscript to: Peter Killeen, 405 Marcus Dr. Prescott, AZ 86303, 480-967-0560, Killeen@asu.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

predation risk and energetic cost it entails) are more credible dimensions for calculation of cost. The mean rate of reinforcement is often assumed as the benefit, but the average delay to reinforcement is apt to be a much more relevant and powerful controlling variable (Bateson and Kacelnik 1996): 15 years ago, Vázquez and Kacelnik could write of another reviewer “the definition of long-term rate maximization has been questioned so many times on both theoretical and empirical grounds, that we wonder why this definition of optimal behaviour is put forward at this stage” (1998, p. 110). Although the issue of delay to sources of food and their proper mensuration has been thoroughly studied, the effects of amount of food, and physical travel, have received less attention. In most operant experiments the distance between the Manipulandum (M) and the Source of reinforcement (S) is short and fixed; the benefits—access to some kind of reinforcement—and the costs—unrequited responses—are manipulated by varying the schedules of reinforcement on the manipulanda. A few experiments (Aparicio and Baum 1997; Timberlake 1984; Baum 1982) exact much more substantial costs by requiring extensive travel of the animals. Do animals respect economic models, optimizing some function of value with respect to some function of cost, when these are varied? To know that requires that both those benefits and costs be explicitly manipulated.

One way of measuring animals' cost-benefit tradeoff is to evaluate the amount of food just necessary to motivate travel over various distances. Various psychometric procedures permit this determination. One of the simplest is to ask the animal itself to set that value. Imagine a scenario where each response at M produces a food pellet at S, and the distance between M and S is manipulated. OFT must predict that animals will emit more responses before collecting the food as the M-S distance increases. Some research has addressed this inference. Killeen (1974) trained Wistar rats to lever press for food in an eight-foot long operant chamber. Each lever press resulted in one food pellet delivered into a food cup and, across conditions, the distance from the response lever to the food cup was manipulated, with M-S distances of 20, 120, 180 and 240 cm. When the lever was near the food cup, the rats pressed the lever once or twice before collecting the food. When the lever was positioned farther from the food cup, the number of lever presses before collection increased, and did so monotonically with distance, providing a psychological scale of distance in units of rat pellets (“cross-modality matching”: Stevens and Guirao 1963). Similar results were obtained in other experiments (Killeen & Riggsford, 1989), where effort was varied by changing both the distance and the inclination of running to different sites of collection. In two experiments, the travel requirement was instantiated as responses on another manipulandum, whose force threshold could be varied (Killeen, Smith, & Hanson, 1981; McFarland & Lattal, 2001). Orderly increases in provisioning were found as a function of the effort involved in collecting the provisions.

These results were extended to pigeons by Yankelevitz, Bullock, and Hackenberg (2008) who reported very orderly increases in the accumulation of provisions in a token-economy. Tokens were accumulated, at costs of 1, 5 or 10 responses per token, with each exchangeable for 2 s access to food. Earning that exchange required up to 250 responses on an exchange-production FR. The average number of tokens provisioned per exchange increased as an approximately linear function of that FR, with the slopes decreasing with the costs of tokens. The results of these studies are consistent with OFT (Charnov, 1976; Krebs, 1978; Shapiro & Allison, 1978), as the increase in provisioning with distance reduces the total travel time, and thus the effort associated with food procurement and consumption..

The research of Yankelevitz and associates (2008) suggests that the research with rats showing increased provisioning with increased physical distance should be easily replicated with pigeons. Against this is the fact that pigeons are not natural hoarders: Will pigeons, like rats, increase the number of responses per trip for food when the distance between food and

the manipulandum is increased? Pigeons have been shown to be more sensitive to delayed reinforcement than rats (Mazur, 2000; Tobin & Logue, 1994). In choice procedures for example, pigeons have been shown to have steeper delay discounting gradients (Green, Myerson, Holt, Slevin & Estle, 2004). In the foraging paradigm, reducing the travel-per-pellet associated with food procurement (i.e., responding more at the manipulandum before collecting the food) increases the delay to food reinforcement. The procedure therefore is somewhat analogous to the intertemporal choice procedure; pigeons may uniformly opt for the “small-soon” option of minimal provisioning, rather than the “late-large” option of multiple responses on the “earn” manipulandum before the eventual trip to collect the large hoard. Because of their steep delay gradients, pigeons may not show the similar increases in the number of responses per trip because doing so will increase the delay to reinforcement, to which they are more sensitive.

Experiment 1 was a systematic replication of Killeen (1974) in which pigeons and rats were directly compared on a procedure in which each response on a manipulandum delivered food, and the distance between the manipulandum and the food source varied across conditions. Experiment 2 was prompted by the results from Experiment 1 and was designed to assess the animals' sensitivity to the M-S distances used in that experiment. In Experiment 2, manipulanda preference was assessed by providing rats and pigeons choices between two concurrently available levers that differed in their relative distances from a fixed food source. In Experiment 3, pigeons were exposed to a variation of the M-S travel distance manipulation in which M-S distance was simulated with a ratio requirement on another manipulandum. Each peck on one key would increase the duration of food availability for the upcoming reinforcer and the completion of a fixed-ratio requirement on another key resulted in the food delivery.

2. Experiment 1

If each response delivers food at a remote source, will rats and pigeons respond more and accumulate that food before they collect it, relative to a situation where food delivery occurs at a nearer source? An elongated operant chamber or *longbox* was used to address this question. Each response on a manipulandum produced food, and the distance between the manipulandum and a stationary food cup was manipulated across conditions. As the distance increases, it is expected, based upon Killeen (1974), that both pigeons and rats will accumulate more pellets before traveling to collect them—that is, responses per trip to the food source will increase with M-S distance.

2.1. Materials and methods

2.1.1. Subjects—Four male homing pigeons (*Columbia livia*) and four male rats (*Rattus norvegicus*) with extensive experimental histories served as subjects. The pigeons were housed individually with free access to water and grit. The pigeons were maintained at 80% ! 10 g of their free-feeding weights by supplemental feeding with fortified mixed grain. The pigeon colony was illuminated on a 12-hr light/dark cycle, with dawn at 6:30 am. The rats also were housed individually with free access to water in their home cages. The rats were maintained at 85% ! 10 g of their free-feeding weights by supplemental feeding with chow. The rat colony was illuminated on a 12-hr dark/light cycle, with dawn at 6 p.m. For the rats all experimental sessions were conducted during the animals' dark cycle.

2.1.2. Apparatus—An elongated operant chamber (*longbox* hereafter) measuring 121 cm × 37 cm × 27 cm was used. A white house light was positioned in the center of the longbox on the front long wall, 20 cm from the floor and remained illuminated throughout the session. A BRS/LVE¹ PDC/PPD series 45 mg pellet dispenser delivered Milo grain into a food cup which was located 1 cm from the right-side wall of the longbox and 3 cm from the

floor. A photocell positioned slightly above the food cup detected entry into the food cup. A single Gerbrands response key extended 8 cm into the longbox and was positioned horizontally 2 cm from the chamber floor (pigeons had to peck down). A force of 0.34 N was required to activate the microswitch. The key could be positioned along the length of the longbox up to a distance of 107 cm from the food cup. The experiment was controlled with a QuickBasic¹ program, and a PC-XT computer controlled and recorded all experimental events. The same longbox was adapted to use with the rats. A 5-cm wide lever was employed that required 0.15 N of force to register the response, with 45 mg Noyes¹ sucrose pellets used as reinforcers.

2.1.3. Procedure—Shaping was not necessary, as the subjects had been trained to respond in previous studies. For rats, each lever press produced one sucrose Noyes[®] food pellet in the food cup whereas for pigeons, each peck produced one grain of milo in the food cup. There was no maximum to the number that could be accumulated. Four manipulandum positions were investigated: 14, 45, 76 or 107 (cm between the food cup and the manipulandum). The manipulandum positions were counterbalanced between subjects using a Latin Square design and remained at each position for four consecutive sessions. This sequence of positions was repeated for each subject in a second cycle to test for a replication of the conditions. Sessions were conducted 6 days a week and terminated with the delivery of 112 reinforcers.

2.2. Results and Discussion

The main dependent measure was the number of responses (i.e., lever presses or key pecks) per trip. A trip was defined as a response on the manipulandum followed by the breaking of the photobeam that was located above the food cup. Thus, the number of responses per trip refers to the number of responses emitted prior to collecting and consuming the food. The data were consistent between animals, thus averages will be shown for economy of presentation. Figure 1 shows responses per trip averaged for pigeons (top panels) and rats (bottom panels) in the first (left panels) and second (right panels) cycles. For pigeons, the number of pecks per trip was invariant as the M-S distance increased. A repeated-measures Analysis of Variance (ANOVA) was conducted for both cycles. The *F* value for the linear trend was not statistically significant. The number of pecks per trip actually slightly decreased in Cycle 1 for two pigeons (1 and 24) as the M-S distance increased. For rats, the number of lever presses per trip increased as a function of hopper distance, $F(1, 7) = 75.09$, $p < .01$ (Cycle 1 and 2 combined). All the rats showed an increase in the number of lever presses per trip as the distance from the hopper increased.

Thus for rats, but not pigeons, the number of responses per trip increased with travel distance between the manipulandum and the food source. Rats responded in a way that reduced the amount of travel associated with food procurement, whereas pigeons did not. The results with the rats replicate previous research (Killeen, 1974; Killeen & Riggsford, 1989). That pigeons did not reduce the total distance traveled by responding more and accumulating food before collecting the food is consistent with three hypotheses:

- a. Perhaps the immediacy to food collection has a greater influence over pigeons' behavior than a reduction in travel. Davison and Jones (1997) showed that once delays to food exceed 6 seconds, effects on foraging decisions can become perverse, showing irrational nonmonotonicities.
- b. Perhaps the small increments in food were not sensible to the pigeons—perhaps they were below a threshold of discriminability.
- c. Perhaps the distances studied in the longbox were too short to occasion any change in the behavior of the pigeons. Pilot experiments, in which obstacles were added to

the course, or lead weights to the pigeons' feet, also had no effect on levels of provisioning. All of these manipulations on distance may have been below a threshold for engaging cost evaluations.

The second experiment was designed to more carefully address this question of potential differential sensitivity between rats and pigeons to the distances employed in Experiment 1.

3. Experiment 2

In order to test the third hypothesis, a concurrent schedule with two manipulanda was arranged such that relative distances between the manipulandum and a fixed food source (M_1 -S- M_2) were manipulated across conditions. It is expected that subjects should prefer the manipulandum closest to the food hopper. If behavior of the pigeons is insensitive to the M-S distances employed however, one might not expect to see M-S distance affect manipulanda choice.

3.1. Materials and methods

3.1.1. Subjects and Apparatus—The subjects and apparatus were the same as in Experiment 1 except that the longbox was fitted with two manipulanda and the hopper was moved to the center of the chamber. As in Experiment 1, the apparatus was modified to accommodate each species. Milo and sucrose pellets were used for pigeons and rats, respectively.

3.1.2. Procedure—Subjects were exposed to a non-independent concurrent variable-interval 20-s schedule in which reinforcers were randomly assigned to one of the two manipulanda. Once the sampled time had elapsed, the next response to the assigned manipulandum generated reinforcement. This equated the number of reinforcers earned from each manipulandum and allowed an unbiased measure of preference. The manipulanda were moved to two of six different locations on a daily basis, and preference between manipulanda was assessed. The hopper always was positioned in the middle of the chamber. The manipulanda could be placed on either side of the hopper at distances of 6, 30, and 54 cm from the hopper, measured center to center. Assuming symmetry, there are 9 configurations with the hopper between keys, 3 with the keys on the one side, 3 on the other; these were the conditions programmed, with sides assigned randomly. Sessions ended after 112 reinforcers were delivered. Two sessions were devoted to each of the arrangements, with the data from both sessions averaged for analysis.

3.2. Results and Discussion

Manipulandum preference was analyzed using a one-way repeated measures ANOVA. There were no significant differences in the data when the keys were on the same side of the hopper compared to when they were on different sides. The data were therefore collapsed on the simple relative distance to the hopper. Figure 2 shows relative response ratios (i.e., preference) as a function of the relative distance ratios in logarithmic coordinates. For pigeons ($F(1, 3) = 13.87, p < .05; \eta^2 > 0.95$) and rats ($F(1, 3) = 75.09, p < .01, p_{rep} > 0.99$ (Killeen 2007), the negative slopes of the response-distance functions indicate that the subjects preferred the manipulandum that was closer to the hopper.

Both rats and pigeons responded more on the manipulandum closest to the food hopper and less to the one farthest away, demonstrating a classic pattern conforming to the generalized matching law. According to this law, sensitivity to changes in the independent variable is measured by the slope of the power function (Davison and McCarthy 1988). Figure 2 demonstrates that the choice behavior of pigeons and rats is sensitive to manipulanda-food source distance, distances that were a subset of those used in Experiment 1. Indeed, pigeons

were substantially more sensitive to differences in travel distance than were the rats (slopes of 0.34 vs. 0.19). This was consistent with visual observations of the animals' ambulation: a quick dash for the rats, a more labored strut for the pigeons. Other researchers have reported that pigeons can plan routes to multiple food sources that reduce overall travel distance (Gibson, Wilkinson, and Kelly 2011). By responding more on the closest manipulandum to the food source, it might be inferred that the animals reduced the travel associated with procuring food in the present study. But, because the schedule was programmed to produce the same number of reinforcers on both keys, and the food was available until collected, this preference optimized no global variables in this experiment. The results rule out alternative *c* above, the explanation of the flatline for the pigeons in Experiment 1 as due to insensitivity to M-S distance.

Preference might simply be a more sensitive measure of the impact of M-S distance than is the number of responses. There, average travel distance per pellet and delay were inversely related; reducing the travel distance increased the temporal delay to reinforcement. These were largely uncoupled in the choice procedure of Experiment 2: Although more responding on the more proximal manipulandum would in nature likely decrease both the overall travel and the delay to reinforcement, here those were invariant: To collect all the reinforcers, as all pigeons did, they would have to make the trip from each of the manipulanda to the hopper equally often. The most proximate manipulandum was preferred, and preferred even though it did not reduce global time or travel. Animals did, however, show a favoritism to that manipulandum on which the time between the last response on it, and the receipt of food, was minimal. Thus, behavioral rather than economic considerations were paramount in this experiment: responding on the most proximal manipulandum was reinforced with the smallest delay.

It is conceivable that the FR 1 accumulating procedure used in Experiment 1 may have failed to bring the pigeons' behavior into contact with the benefits of accumulating before collecting. Experiment 3 was designed to improve that contact, thereby providing an examination of alternative *b*, the sensitivity to differences in reinforcement as an explanation for the results of Experiment 1.

4. Experiment 3

In Experiment 1, where procuring the food involved traveling various distances, pigeons showed no evidence of increasing the amount of food as a function of increased procurement costs. But the literature shows that rats are also sensitive to a different kind of cost: Killeen, Smith and Hanson (1981) let rats earn a food pellet for each response on a left lever; the pellets were delivered behind a door and could be accessed only after completing a fixed-ratio (FR) requirement on a right lever. Across conditions, completing FRs of 16, 32, 64 and 128 on the right lever opened the door to food. The number of pellets accumulated before they were consumed increased as the FR increased. McFarland & Lattal (2001) conducted experiments with rats that combined features of both ratio requirement and physical distance, and these confirmed and extended the earlier results.

Are pigeons incapable of increasing the benefits requested in anticipation of a more effortful foraging excursion? The purpose of Experiment 3 was designed to move a step closer to the procedures that were successful with rats. To this end, each peck on a left "earn" key increased the duration of food availability obtained when the response requirement on the right "collect" key was satisfied. The ratio requirement on the collect key was manipulated across conditions to simulate the travel distance in the longbox experiments. If pigeons in this experiment forage like rats in the above studies, they will increase the number of earn-key responses before responding on the collect key, as a function of the ratio requirement on

the collect key. If pigeons in this experiment forage like pigeons in Experiment 1, there will be no commensurate change in the number of responses on the earn key.

4.1. Materials and methods

4.1.1. Subjects—Six pigeons (*Columba livia*) served as subjects. The pigeons had various experimental histories, one of them serving in Experiments 1 and 2. Pigeons were housed individually and had free access to water and grit in a colony illuminated on a 12-hr light/dark cycle, dawn at 6:30 am. The pigeons were maintained at 80% of their free-feeding weights by supplemental feeding with fortified mixed grain.

4.1.2. Apparatus—Sessions were conducted in a Lehigh Valley Electronics¹ (Laurel, MD) sound-attenuating operant chamber measuring 34 cm × 31 cm × 35 cm. Three Plexiglas response keys spaced 7 cm apart were located on the work panel 24 cm above the floor. Only the two outside keys were operational and each required a force of approximately 0.2 N to activate the microswitch. A white houselight located 7 cm above the center key provided chamber illumination. A 6 cm × 7 cm hopper aperture was located 9 cm from the floor and 14 cm from the left wall. When raised, the hopper provided access to milo grain, and a white light mounted above the hopper opening was illuminated. White noise was presented through a speaker mounted behind the interface panel to mask extraneous sounds, and a fan mounted on the wall opposite the interface provided continuous circulation. The experiment was programmed using QuickBasic¹, and experimental events were controlled and recorded by a computer located on top of the chamber.

4.1.3. Procedure—Pigeons initially were trained to peck four times on the left key then once on the right key to obtain 2.5 s of hopper access. If a response on the right-side key was emitted prior to the completion of the four required consecutive left key responses, then a 3-s blackout followed. About eight training sessions were given before the experiment proper began.

During the experiment proper, each trial began with the illumination of the houselight and the two keys. The left key was illuminated green, and the right key was illuminated red. Each response on the left “earn” key increased the next hopper presentation duration by a fixed amount, specified by the hopper step size. Once a response occurred on the right “collect” key, the light behind the earn key was extinguished, and reinforcer delivery depended upon completion of the response requirement on the right key. After completing the ratio requirement on the right key, the food hopper was raised for t s; where t was determined by the product of the hopper step size and the number of left key pecks on that trial. In order to earn food, there had to be at least one left key response before completing the ratio on the right key. A right-key response occurring before a left-key response resulted in a 3-s blackout. A 3-s inter-trial interval separated trials during which all lights were extinguished and contingencies suspended. Sessions terminated after 120 s of hopper access time.

The hopper step sizes investigated were: 0.5, 1.5 and 2.5 s. The hopper duration was reset to zero after each reinforcer. During a trial, each peck on the left key (before the right key was pecked) increased the duration of the next hopper presentation by the step size in effect. For example, if three pecks occurred on the left key, the total access time of the next hopper presentation (after the right lever response requirement was satisfied) would last 1.5 s if the 0.5-s condition was in effect (3×0.5) and 7.5 s if the 2.5-s condition was in effect (3×2.5). The FR requirements associated with the right key were 1, 4, 8, 16, or 32. Each combination of hopper step size and ratio requirement was in effect for eight sessions. Pigeons were

exposed to each of the FR requirements in an ascending order before experiencing a new hopper step size. The order of hopper step size was counterbalanced.

4.2. Results and Discussion

Figure 3 shows pecks per trip (the number of responses on the left key before completing the FR requirement on the right key), averaged over the last six sessions of each condition, as a function of the FR requirement. A two-factor repeated-measures ANOVA (hopper step size by FR requirement) revealed a significant main effect of hopper step size and of FR requirement. As the hopper step size decreased, pigeons made significantly more responses on the left key before completing the FR requirement on the right key, $F(2, 10) = 36.26$, $p < .001$. On average, pigeons earned 1.4 s of hopper access time with a hopper step size of 0.5 s, 2.5 s with a hopper step size of 1.5 s, and 4.1 s with a hopper step size of 2.5 s. Post-hoc comparisons, computed using Tukey's Honest Significant Difference test, revealed that significantly more responses were made on the left key with a hopper step size of 0.5 s than for 1.5 or 2.5 s ($p < .001$ for both comparisons). The number of pecks per trip made under the hopper step sizes of 1.5 s and 2.5 s were not different from each other ($p > .05$).

As the FR requirement increased, pigeons pecked the left key more before collecting food, $F(4, 20) = 8.00$, $p < .001$. Tukey's post-hoc test revealed that there was a significant difference between the number of left key pecks for FR 1 and 32 ($p < .001$), 4 and 32 ($p < .003$), and 8 and 32 ($p < .02$). There was no significant interaction between hopper step size and the FR requirement, $F(8, 40) = 1.18$, $p > .05$.

Pigeons in the present experiment behaved consistently with predictions: They pecked the left key more than required (i.e., once) and thereby increased their total access time to food per trip; the number of left key pecks increased as the ratio requirement on the right key increased (i.e., pecks per trip increased). The obtained time of access was twice as great for the 1.5 step size as for the 0.5, and about 3 times as great for the 2.5. The regression slopes found by Killeen and associates (1981) for rats were much steeper (0.13) than found here: 0.04, 0.04, and 0.05 for the 0.5, 1.5 and 2.5-s hopper step size conditions, respectively). The more extensive study by Yankelevitz and associates (2008) found slopes (token responses made per collect response required) of around 0.045 for the comparable condition (FR 1 token production by pigeons), and less in other conditions, and much less when the conditioned reinforcers for the provision responses were removed. These results are therefore consistent with ours.

The 0.5-s hopper step-size condition resulted in a greater number of left key pecks per trip than the 1.5 and 2.5-s conditions. This result may at first appear counterintuitive, because the same number at the larger step sizes would result in considerably more food. However, the 0.5-s hopper step size may have created a different problem: A single response on the left key followed by completion of the fixed-ratio on the right key would result in a hopper activation time of only 0.5 s, probably too short to get to the hopper before it was lowered. The approximately 1 response surplus under this condition remained invariant, tracking the increase in the other conditions at about the same elevation. The number of pecks per collection at the hopper step sizes of 1.5 and 2.5 s was similar across collect requirements, and show a surprising similarity to the data of Yankelevitz and associates, which would lie among them at essentially the same slope. If the marginal utility of extended hopper access is concave, as data suggests it is (Killeen, 1985), the addition gained by extending hopper duration much beyond 6 s may not have been sufficient to sustain provisioning beyond that seen in the bottom lines of Figure 3.

5. General Discussion

Three experiments were conducted for the purpose of comparing the foraging dynamics of rats and pigeons. In Experiment 1, the number of responses per trip to the food source increased for rats but not pigeons as the distance between the manipulandum and the food source (M-S) increased. The finding with rats replicates Killeen's 1974 experiment and extends the results to a different strain of rat; but it failed to generalize across species. In Experiment 2, both species preferred shorter M-S distances; that is, both pigeons and rats responded more on the manipulandum that was closest to the food source even though the schedule of reinforcement and the amount of food were equivalent. In Experiment 3, pigeons had to complete a ratio requirement for food on a second manipulandum, analogous to the travel requirement of Experiment 1. In this situation, pigeons pecked the 'earn' key more as the ratio requirement on the 'collect' key (travel requirement) increased. This result replicates the findings of Yankelevitz and associates (2008).

The reason for the disparity between the rats and pigeons in Experiment 1 remains elusive. Why did the pigeons not increase the number of key pecks per trip as the distance between the manipulandum and food source increased? One possibility was that the distances employed, although metrically equivalent, were not functionally equivalent to the two species. Perhaps the longbox was too short for pigeons and a longer M-S distance would have produced the same effect shown by the rats. This is belied by the results from Experiment 2 in which pigeons favored the manipulandum closest to the food source, showing fine sensitivity to the same M-S distances employed in Experiment 1. This is not to say that absolute measures are likely to be as sensitive as comparative measures (Neuringer, 1967); but in this context pigeons were at least as sensitive as rats to the M-S distance.

It may be that one or a few grains of milo were below the limits of discriminability by pigeons. Given their fine visual acuity, and sensitivity to small differences in grains in a paired-comparison context (Killeen, Cate and Tran, 1993), this is unlikely, but cannot be ruled out. Each peck operated the hopper, whose sound might have constituted a powerful sign of reinforcement that was too compelling to resist (Hearst and Jenkins, 1974).

Is it also possible that these experiments tapped species differences in delay discounting? Rats have long temporal horizons for the control of their present behavior by forthcoming reinforcers (Shettleworth 1988; Timberlake, Gawley, and Lucas 1987). Perhaps the species differences observed in Experiment 1 reflect species differences in delay of reinforcement gradients (Anslie, 1975; Killeen 2011). Pigeons tend to be more impulsive than rats—that is, they discount future reinforcers more steeply (Green et al., 2004). Experiments 1 and 3 were intertemporal choice/titration procedures, in which smaller, more immediate, or larger, more delayed reinforcers are available to the animal. In Experiment 1 food was always available after the first response. Each additional response resulted in more food accumulated at the food source; however, each additional response took time, and delayed the receipt of reinforcement by that time. Thus emitting one response, then traveling to collect and eat the grain, is tantamount to a choice of the smaller, more immediate reinforcer (McFarland & Lattal, 2001). Emitting several responses before travelling to collect and eat the reinforcer is opting for a larger, more delayed reinforcer. The pigeons in Experiment 1 were more likely to travel to and collect and eat the food as soon as it was available, regardless of the M-S distance, even if this pattern resulted in greater overall average distances travelled per gram consumed.

The results from Experiment 3, where pigeons increased the number of responses on the left key before completing the FR requirement on the right key, run counter to the preceding argument. After all, these additional responses lengthened the delays to reinforcement just as

they did in Experiment 1. So why did the pigeons behave less impulsively in Experiment 3 than in Experiment 1? There were many procedural differences between the experiments. One important difference concerned the timing of the reinforcer delivery. In Experiment 1, each response immediately produced a food pellet at the (remote) food source and signaled as such by the operation of the dispenser. In Experiment 3, however, each response increased the future access to food without a correlated immediate signal of that, and the pigeons were more effective in increasing their relative efficiency of foraging. Research has shown that the presence of a reinforcer increases impulsivity (Grosch & Neuringer, 1981; Killeen & Snowberry, 1982; Mischel & Ebbesen, 1970), and may well have done that in Experiment 1 for the pigeons.

Pigeons and rats are phylogenetically distant, evolving in different ecological niches with different environmental demands (Armitage, 1984; Levi 1957). That considered, the behavioral similarities between the rats and pigeons in Experiment 2; and the similarity between the pigeons in Experiment 3, those reported in Yankelevitz and associates (2008), and the rats in the various provisioning studies cited are noteworthy. Although costs and benefits are relevant to all species, it would be reasonable to expect that certain behavior would be more sensitive to certain experimental arrangements as a result of phylogeny than other behavior (Smith and Reichman 1984). Studies of hoarding show wide disparities between foraging strategies in rodents and avian species (DiBattista & Bedard, 1987; Guerra & Ades, 2002; Smith et al., 1979; Vander Wall, 1990). Pigeons are not among those commonly thought of as caching, but Wakita, Kawamura, and Watanabe (1994) did report pigeons provisioning as a function of forthcoming predictable periods of shortage.

The absence of effort-sensitive provisioning in pigeons in Experiment 1, and the small effects seen in Experiment 3, indicates that they are less prudential than rats. Perhaps this should not be surprising, given pigeons' lack of foresight in other respects (Roberts et al. 2009; but see Zentall and Stagner 2010), and their sub-optimal foraging patterns in others (Killeen et al. 1996). Experiment 2 showed that this apparent failure to optimize was not due to insensitivity to distance, which loomed even more important for pigeons than for rats. In Experiment 1, the reinforcer was one or more pieces of grain. It may well be that a meal for a pigeon consists of several beaks-worth of grain, and differences in one or two grains were not salient—that it was insensitivity to amount, not distance, that flatlined the first panel of Figure 1. Against that argument is pigeons' acute sensitivity to the size of grains (Killeen et al, 1993)(Radtke 2011). A similar hypothesis was part of economic models recruited to fit the data of Experiment 3. To make them work, it was necessary to assume that any operation of the hopper provided a fixed unit of value, beyond which the growth in value with amount was shallow. This model fit the data from Experiment 1 (trivial) and approximated the data from Experiment 3. The approximation was not satisfactory, however, because any model that permitted provisioning to increase with distance, as it did under all 3 hopper conditions, also required that the number of earn responses on the 1.5 condition should lie above those for the 2.5 condition. This is because if larger amounts of food are valued more, as the significant slopes attest, then any model assuming a threshold amount to justify the collect requirement would be satisfied with fewer pecks under the 2.5 condition. This was clearly not the case. Instead, some kind of satisficing strategy was at work. More extensive data using token reinforcers and number of hopper operations, not their duration (Yankelevitz, Bullock, and Hackenberg 2008), returned essentially the same data (see Figure 3).

It is possible that the prospect of the trip increased the pigeons' appreciation of the food in an amount just sufficient to balance the negative aspects of having to make the trip: There is surprising evidence of just such an effect for pigeons (Friedrich, and Zentall, 2004; Zentall, 2007). It is our hypothesis, however, that the sound of the hopper in Experiment 1 undermined the pigeons' self control, and precipitated their movement to it. This is

consistent with the elegant analysis of stimulus control by Zentall and Stagner, showing that conditioned reinforcers may overwhelm more ‘rational’ optimal foraging—extending to a plausible analysis of the allure of gambling (2011). Additional experiments will address this hypothesis, and hopefully integrate this paradigm with others such as Cole (1990), and with delay reduction theory used so effectively by Fantino and associates to study foraging (e.g., Abarca and Fantino, 1982; Fantino and Abarca, 1985; Ito and Fantino, 1986). The conclusion of Johnson and Collier (1999), after a series of seminal experiments on the meal patterns of rats, can serve equally well as ours: “the patterns we observed represent a compromise between minimizing foraging cost, minimizing physiological costs and maintaining total intake and body weight (p. 418)”—even if, in some cases, the compromise seemed short-sighted.

Acknowledgments

This research was supported by NIDA Grant KO1 DA00485.

References

- Abarca N, Fantino E. Choice and foraging. *J Exp Anal Behav.* 1982; 38:117. [PubMed: 16812290]
- Ainslie G. Specious reward: A behavioral theory of impulsiveness and impulse control. *Psych Bull.* 1975; 82:463–496.
- Aparicio CF, Baum WM. Comparing locomotion with lever-press travel in an operant simulation of foraging. *J Exp Anal Behav.* 1997; 68:177–192. [PubMed: 16812854]
- Armitage, D. Animal Diversity Web. University of Michigan Museum of Zoology; Ann Arbor: 2004. *Rattus norvegicus* (On-line). <http://is.gd/LuUSEK>
- Bateson M, Kacelnik A. Rate currencies and the foraging starling - the fallacy of the averages revisited. *Behav Ecol.* 1996; 7:341–352.
- Baum WM. Choice, changeover, and travel. *J Exp Anal Behav.* 1982; 38:35–49. [PubMed: 16812283]
- Charnov EL. Optimal foraging: the marginal value theorem. *Theor Popul Biol.* 1976; 9:129–136. [PubMed: 1273796]
- Cole MR. Operant hoarding: a new paradigm for the study of self-control. *J Exp Anal Behav.* 1990; 53:247. [PubMed: 2324665]
- Davison M, Jones BM. Residence time in concurrent foraging with fixed times to prey arrival. *J Exp Anal Behav.* 1997; 67:161–179. [PubMed: 16812832]
- Davison, M.; McCarthy, D. The matching law: A research review. Erlbaum; Hillsdale, NJ: 1988.
- DiBattista D, Bedard M. Effects of food deprivation on hunger motivation in golden hamsters (*Mesocricetus auratus*). *J Comp Psychol.* 1987; 101:183–189.
- Fantino E, Abarca N. Choice, optimal foraging, and the delay-reduction hypothesis. *Behav Brain Sci.* 1985; 8:315–362.
- Friedrich AM, Zentall TR. Pigeons shift their preference toward locations of food that take more effort to obtain. *Behav Proc.* 2004; 67:405–415.
- Gibson B, Wilkinson M, Kelly D. Let the pigeon drive the bus: pigeons can plan future routes in a room. *Animal Cognition.* 2011:1–13.
- Green L, Myerson J, Holt DD, Slevin JR, Estle SJ. Discounting of delayed food rewards in pigeons and rats: Is there a magnitude effect? *J Exper Anal Behav.* 2004; 81:39–50. [PubMed: 15113132]
- Grosch J, Neuringer A, Armitage. Self-control in pigeons under the Mischel paradigm. *J Exper Anal Behav.* 35:3–21. [PubMed: 16812197]
- Guerra RF, Ades C. An analysis of travel costs on transport of load and nest building in golden hamster. *Behav Proc.* 2002; 57:7–28.
- Ito M, Fantino E. Choice, foraging, and reinforcer duration. *J Exp Anal Behav.* 1986; 46:93. [PubMed: 3746190]
- Hearst, E.; Jenkins, HM. Sign-tracking: The stimulus-reinforcer relation and directed action. The Psychonomic Society; Austin, TX: 1974.

- Johnson DF, Collier G. Prey size and prey density affect meal patterns of rats in depleting and nondepleting patches. *Anim Behav.* 1999; 58:409–419. [PubMed: 10458892]
- Kacelnik A, Houston AI. Some effects of energy costs on foraging strategies. *Anim Behav.* 1984; 32:609–614.
- Killeen PR. Psychophysical distance functions for hooded rats. *The Psych Record.* 1974; 24:229–235.
- Killeen PR. Incentive theory IV: Magnitude of reward. *J Exp Anal Behav.* 1985; 43:407–417. [PubMed: 16812421]
- Killeen, PR. Replication statistics. In: Osborne, JW., editor. *Best practices in quantitative methods.* Sage; Thousand Oaks, CA: 2007.
- Killeen PR. Models of trace decay, eligibility for reinforcement, and delay of reinforcement gradients, from exponential to hyperboloid. *Behav Processes.* 2011; 8:57–63. [PubMed: 21215304]
- Killeen PR, Cate H, Tran T. Scaling pigeons' choice of feeds: Bigger is better. *J Exp Anal Behav.* 1993; 60:203–217. [PubMed: 8354967]
- Killeen PR, Palombo GM, Gottlob LR, Beam JJ. Bayesian analysis of foraging by pigeons (*Columba livia*). *J Exp Psychol Anim Behav Process.* 1996; 22:480–496. [PubMed: 8865614]
- Killeen PR, Smith JP, Hanson SJ. Central place foraging in *Rattus norvegicus*. *Anim Behav.* 1981; 29:64–70.
- Killeen PR, Snowberry K. Information and cooperative behavior. *Behav Anal Let.* 1982; 2:353–360.
- Killeen PR, Riggsford M. Foraging by rats: Intuitions, models, data. *Behav Proc.* 1989; 19:95–105.
- Killeen PR, Snowberry K. Information and cooperative behavior. *Behaviour Analysis Letters.* 1982; 2:353–360.
- Levi, WM. *The Pigeon.* Levi Publishing Co; Sumter, SC: 1957.
- Krebs, JR.; Davies, NB. *Behavioural ecology.* Oxford, England: Blackwell Scientific Publications; 1984.
- Mazur JE. Tradeoffs among delay, rate, and amount of reinforcement. *Behav Proc.* 2000; 49:1–10.
- McFarland JM, Lattal KA. Determinants of reinforcer accumulation during an operant task. *J Exper Anal Behav.* 2001; 76:321–338. [PubMed: 11768714]
- Mischel W, Ebbesen EB. Attention in delay of gratification. *J Per Soc Psychol.* 1970; 16:329–337.
- Neuringer AJ. Effects of reinforcement magnitude on choice and rate of responding. *J Exper Anal Behav.* 1967; 10:417–424. [PubMed: 6050053]
- Perry G, Pianka ER. Animal foraging: past, present and future. *Trends Ecol Evol.* 1997; 12:360–364. [PubMed: 21238109]
- Radtke TM. Granivore seed-size preferences. *Seed Science Research.* 2011; 21:81–83.
- Roberts WA. Distance and magnitude effects in sequential number discrimination by pigeons. *J Exp Psychol: Anim Behav Proc.* 2010; 36:206–216.
- Shapiro N, Allison J. Conservation, choice, and the concurrent fixed-ratio schedule. *J Exper Anal Behav.* 1978; 29:211–223. [PubMed: 16812049]
- Shettleworth, S. Foraging as operant behavior and operant behavior as foraging: What have we learned. In: Bower, GH., editor. *The Psychology of Learning and Motivation: Advances in Research and Theory.* Vol. 22. Academic Press; New York: 1988. p. 1–49.
- Smedslund J. From hypothesis-testing psychology to procedure-testing psychology. *Rev Gen Psychol.* 2002; 6:51–72.
- Smith CC, Reichman OJ. The evolution of food caching by birds and mammals. *Ann Rev Ecol Syst.* 1984; 15:329–351.
- Smith JP, Maybee JS, Maybee FM. The effects of increasing distance to food and deprivation level on food-hoarding behavior in *Rattus norvegicus*. *Behav Neur Biol.* 1979; 27:302–318.
- Stephens, DW.; Krebs, JR. *Foraging theory.* Princeton University Press; Princeton, NJ: 1986.
- Stevens SS, Guirao M. Subjective scaling of length and area and the matching of length to loudness and brightness. *J Exp Psychol: Appl.* 1963; 66:177–186.
- Timberlake W. A temporal limit on the effect of future food on current performance in an analogue of foraging and welfare. *J Exp Anal Behav.* 1984; 41:117–124. [PubMed: 16812361]

- Timberlake W. Behavior systems and reinforcement: an integrative approach. *J Exper Anal Behav.* 1993; 60:105–28. [PubMed: 8354963]
- Timberlake W, Gawley DJ, Lucas GA. Time horizons in rats foraging for food in temporally separated patches. *J Exp Psychol: Anim Behav Proc.* 1987; 13:302–309.
- Tobin H, Logue AW. Self-control across species (*Columba livia*, *Homo sapiens*, and *Rattus norvegicus*). *J Comp Psychol.* 1994; 108:126–33. [PubMed: 8026163]
- Vander Wall, SB. Food hoarding in animals. University of Chicago Press; 1990.
- Vasquez RA, Kacelnik A. Animal foraging: more than met the eye. *Trends Ecol Evol.* 1998; 13:110–111. [PubMed: 21238223]
- Wakita M, Kawamura H, Watanabe S. Hoarding behavior in the pigeon (*Columba livia*): Performance under the restriction of food availability. *Behav Proc.* 1994; 31:167–176.
- Yankelevitz RL, Bullock CE, Hackenberg TD. Reinforcer accumulation in a token-reinforcement context with pigeons. *J Exp Anal Behav.* 2008; 90:283–299. [PubMed: 19070337]
- Zentall TR. Reinforcers Following Greater Effort are Preferred: A Within-Trial Contrast Effect. *Behav Anal Today.* 2007; 8:512–527.
- Zentall TR, Stagner JP. Pigeons prefer conditional stimuli over their absence: A Comment on Roberts et al (2009). *Journal of Experimental Psychology Animal Behavior Processes.* 2010; 36:506–509. [PubMed: 20718554]
- Zentall TR, Stagner JP. Maladaptive choice behaviour by pigeons: an animal analogue and possible mechanism for gambling (sub-optimal human decision-making behaviour). *Proc Royal Soc B: Biol Sci.* 2011; 278:1203–1208.

Highlights

Rats adjust the amount they will receive before travel to a distant patch as a function of the distance; pigeons do not

Both rats and pigeons prefer to work close to the source of food, and that preference is a power function of the relative distance

Pigeons will differentially increment the size of a deferred reinforcer as a function of the number of key pecks required to obtain it

\$watermark-text

\$watermark-text

\$watermark-text

Figure 1. Responses per trip for pigeons (top panels) and rats (bottom panels) in the first (left panels) and second (right panels) cycles. Error bars represent the standard error of the mean.

Figure 2.

Relative response ratios as a function of the relative manipulanda-food source distances (M-S distances; log-log coordinates) for pigeons (left panel) and rats (right panel). Each data point represents the average response ratios pooled across animals. R_1 refers to the right manipulandum, and D_1 its M-S distance; R_2 refers to the left manipulandum, and D_2 to its M-S distance. Error bars represent the standard error of the mean.

Figure 3. Pecks per trip on the provisioning key as a function of the FR value on the collect key. Circles, triangles, and squares represent the hopper step sizes of 0.5, 1.5, and 2.5 s, respectively; error bars represent the standard error around the mean.