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COMPARING LOCOMOTION WITH LEVER-PRESS TRAVEL IN AN OPERANT SIMULATION OF FORAGING

CARLOS F. APARICIO AND WILLIAM M. BAUM

UNIVERSITY OF MISSISSIPPI AND
UNIVERSITY OF NEW HAMPSHIRE

An operant model of foraging was studied. Rats searched for food by pressing on the left lever, the patch, which provided one, two, or eight reinforcers before extinction (i.e., zero reinforcers). Obtaining each reinforcer lowered the probability of receiving another reinforcer, simulating patch depletion. Rats traveled to another patch by pressing the right lever, which restored reinforcer availability to the left lever. Travel requirement changed by varying the probability of reset for presses on the right lever; in one condition, additional locomotion was required. That is, rats ran 260 cm from the left to the right lever, made one response on the right lever, and ran back to a fresh patch on the left lever. Another condition added three hurdles to the 260-cm path. The lever-pressing and simple locomotion conditions generated equivalent travel times. Adding the hurdles produced longer times in patches than did the lever-pressing and simple locomotion requirements. The results contradict some models of optimal foraging but are in keeping with McNair's (1982) optimal giving-up time model and add to the growing body of evidence that different environments may produce different foraging strategies.

Key words: foraging, travel, depletion, operant behavior, locomotion, lever press, rats

Optimal foraging theory maintains that evolutionary events and conditions have shaped the behavior of species over generations. To be effective, however, evolutionary events and conditions must select particular mechanisms that are subject to proximate causation (Mellgren, 1982). Proximal causes are environmental events and conditions in the immediate environment that affect behavior during an individual's lifetime (Mellgren, Misasi, & Brown, 1984). Like any other behavior, foraging must depend on proximal causes.

Although ecologists usually study evolutionary events and conditions and psychologists usually study proximate causes of behavior, ecologists and psychologists have the same purposes: to study and understand behavior. Operant behavior may be viewed as foraging, and foraging may be studied as operant behavior (Shettleworth, 1988). Foraging and operant behavior both involve locomotion, and both are modified by their consequences (Baum, 1982b). As a result of this convergence, operant simulations of foraging have become common (Baum, 1982a, 1982b; Fantino, 1987; Pietrewicz & Kamil, 1977). For example, the methods of operant psychologists have been used to test MacArthur and Pianka's (1966) model of prey selection (Collier & Rovee-Collier, 1981). Because they offer relatively precise tests, operant techniques have gained acceptance as a suitable way to test optimal models of foraging (Kamil & Yoerg, 1985; Pulliam, 1981; Schoener, 1987).

In operant simulations of foraging, the values of a set of parameters are usually held fixed for several (sometimes many) sessions in which food is available under a schedule of reinforcement. The foragers thus gain substantial experience with each set of parameter values. Each condition is considered an environment with which the forager eventually becomes familiar. When enough data have been gathered in one environment, the values of one or more parameters are changed to define a new environment, and the process of familiarizing and data gathering is repeated. A typical experiment includes data from several environments or conditions.

By using optimal models of foraging, researchers try to predict how an animal foraging for food will behave (often described in the foraging literature in terms of decision making) in an environment in which its behavior depletes discrete concentrations of

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Address correspondence and reprint requests to Carlos F. Aparicio, Centro de Estudios e Investigaciones en Comportamiento, Av. 12 de Diciembre 204, Col. Chapalita, Guadalajara, Jalisco, Mexico, A.P. 5-374.

food (patches). That is, researchers try to take account of the depletion of food by the forager within the patch and to identify the variables that determine when the forager will move to a new patch (Redhead & Tyler, 1988). Among the most important variables that determine moving to a new patch are the quality of the patch and the travel cost to other patches.

Optimal models of foraging predict that patch utilization (i.e., the length of time the animal remains in a patch, termed *residence time*) should increase if travel time to other patches increases (Krebs, 1978). This prediction has been corroborated in the field (Anderson, 1978; Zimmerman, 1981), in the laboratory without operant techniques (Cowie, 1977; Hartling & Plowright, 1979), and in experiments in which all elements of the patch were simulated with operant techniques (Fantino & Abarca, 1985; Hanson, 1987; Hanson & Green, 1989a, 1989b; Killeen, Smith, & Hanson, 1981; Lea, 1979). Operant simulations that incorporate two sources of food (patches) have shown that residence time in each patch increases as a function of the travel requirement to the alternative patch (e.g., Abarca & Fantino, 1982; Fantino & Abarca, 1985; Hanson, 1987; Hanson & Green, 1989a, 1989b; Killeen et al., 1981; Lea, 1979).

In operant simulations of foraging, travel has been modeled by requiring rats to press a lever or pigeons to peck a key. Accordingly, foragers "travel" by staying in the same spot and responding on a schedule for a period of time. When no locomotion is involved, the lack of energy expenditure may produce data that deviate quantitatively from optimal models of foraging (Cowie, 1977; Kacelnik & Cuthill, 1987). When this happens, the fault may lie less with the theory than with the simulation.

Skepticism toward using operant models that omit locomotion as a travel requirement also arises from studies showing that in the same experimental situation, different response requirements produce different results. For example, McSweeney (1978) found that pigeons learned more quickly to peck a key than to press a treadle when both responses produced food. Similarly, Dreyfus, DePorto-Callan, and Pesillo (1993) found molar and molecular differences in performance on a concurrent schedule when two different contingencies (a changeover delay and a fixed-ratio changeover requirement) were arranged in different portions of a session. These results raise the possibility that travel simulated by lever pressing might be affected differently than travel requiring locomotion even when the consequence is the same, and other aspects of foraging might be affected differently as well.

Operant conditioning chambers have been modified to incorporate locomotion travel (Krebs, Kacelnik, & Taylor, 1978; Ydenberg, 1984), but no one has directly compared locomotion travel with lever-press or key-peck travel. Nevertheless, some data show that pecking a key has qualitatively similar effects to moving from place to place. Baum (1982a) exposed pigeons to a choice between two patches that provided food according to concurrent variable-interval schedules, and he varied the travel between patches by requiring the pigeons to run around barriers separating the patches. As travel increased, residence times increased and changeovers between patches decreased. These results resembled those obtained with concurrent schedules in which changeover rates decreased when the duration of a changeover delay was extended (Shull & Pliskoff, 1967) or a fixed-ratio changeover requirement was increased (Pliskoff & Fetterman, 1981).

Although Baum's (1982a) data suggest that in choice situations the effects of locomotion travel resemble those of travel simulated with operant responses, operant-simulated travel has never been compared with locomotion travel within the same experimental situation. Thus, the following question remains unanswered: Do locomotion travel and lever-press or key-peck travel affect the forager's residence and giving-up times in an equivalent way? The present experiment addressed this question. Rats searched for food by pressing on the left lever, the patch, which provided one, two, or eight reinforcers before extinction (i.e., zero reinforcers). Residence and giving-up times modulated by locomotion travel were compared with residence and giving-up times modulated by lever-press travel. If the question can be answered "yes," then the results may shed light on the variables that determine patch leaving in the natural environment.

In the present experiment, each condition modeled an environment in which (a) all patches contained one, two, or eight reinforcers, (b) the amount of searching (lever pressing) required to obtain a prey item varied randomly, (c) prey became increasingly difficult to obtain, and (d) random amounts of travel were required to reach a new patch. A rodent might face such an environment, for example, when it hunts under bushes for fallen seeds.

METHOD

Subjects

Five experimentally naive male Long-Evans rats from the University of New Hampshire colony that were between 90 and 110 days old participated as subjects. The rats weighed between 280 and 310 g before food deprivation and were maintained at 80% of these free-feeding weights (±8 g). Water was freely available in their home cages, where a 12:12 hr light/dark cycle was maintained.

Apparatus

The experimental space consisted of a rectangular wooden box, 147 cm long and 51 cm wide. A rectangular piece of plywood, 150 cm long and 55 cm wide, attached to the box with latches, formed the roof of the box. The box was divided lengthwise by wire mesh. For lever-press travel conditions, direct passage from one lever to the other (i.e., 33 cm by the most direct route) was permitted. Passage beyond 17 cm from the front wall was blocked with wire mesh. For the locomotion travel conditions, direct passage from the left to the right lever was blocked with wire mesh. Changing from one side of the box to the other required passing around the central partition 130 cm from the front wall. The one-way distance from the left to the right lever was 260 cm. A round trip was 520 cm.

Three 9-V DC lights mounted along each side of the box (at 23 cm, 51 cm, and 117 cm from the front wall) provided the illumination. Two retractable response levers were mounted on the front wall 3 cm from the floor and 33 cm apart and were operated by a force of 0.2 N. A pellet dispenser delivered 45-mg pellets (Noyes Formula A) into a hopper situated on the front wall of the box, 3 cm from the floor and 7.5 cm to the right of the left lever.

Experimental sessions were conducted in a dark room in which extraneous sounds were masked by white noise. Events in the experiment were controlled by a microprocessor (BCC-52; Micromint, Inc.). A Zenith PC computer in an adjoining room was used to collect and analyze the data.

Procedure

At the beginning of a session, the lights on the left side of the box were turned on and the left lever was extended. The first response on the left lever turned off the lights on the left side, extended the right lever, and turned on the lights on the right side, which was correlated with the availability of the reset contingency (i.e., lever-press travel). Consecutive responses on the left lever produced one, two, or eight food pellets, according to a probability of delivering a reinforcer that had been established at the beginning of the session and a depletion schedule. Because food was always obtained by presses on the left lever and collected next to it, this was considered the patch. When the patch provided one pellet, the probability (p) of obtaining the pellet by pressing on the left lever began at .10. This probability dropped to zero (i.e, extinction) after one reinforcer had been obtained. When pressing the left lever produced two or eight pellets, the probability of reinforcer delivery on the left began at 1.0. Each obtained pellet lowered p in steps of .5 (for two pellets) or .125 (for eight pellets) until p reached zero, simulating patch depletion.

In conditions with lever-press travel, a direct route between levers was provided, and the first response on the right lever retracted the left lever, preventing search until the patch was reset. Further responses on the right lever eventually reset p for the patch to .10 or 1.0 according to three reset probabilities (.10, .05, and .025, which corresponded to random-ratio 10, 20, and 40 schedules of reinforcement, respectively) scheduled on the right lever. When reset occurred, the lights on the right were turned off, the right lever was retracted, the lights on the left were turned on, and the left lever was reextended. The first press on the left lever caused the right lever to reextend, and the contingencies of reinforcement on the left lever that existed

at the beginning of a session were reestablished.

In the locomotion travel conditions, a single press on the right lever was required to reset the patch, but only the long route between levers was available. Rats traveled 260 cm from the left to the right lever, made one response on the right lever, and traveled another 260 cm back to a fresh patch on the left lever.

One additional condition was studied in which the patch was depleted in eight pellets, and three hurdles were added to the locomotion travel requirement. These hurdles were 12 cm high and were constructed of wire mesh. Two hurdles were placed one on each side of the box 50 cm from the front wall. The other hurdle was placed at the midpoint of travel, 130 cm from the front wall.

Sessions for all conditions ended when one of three cases was met: (a) 90 visits to the levers (45 to the left lever and 45 to the right lever), (b) no pressing on either lever for more than 300 s, or (c) delivery of 190 pellets.

Each combination of travel requirement and patch type was considered to simulate one environment. Exposure to each environment continued until all rats showed no systematic changes (no increasing or decreasing trends) in travel, residence, and giving-up times for 3 consecutive days. With two exceptions, a minimum of 10 sessions per condition was scheduled. This criterion was adopted from a previous study conducted in the same experimental situation in which it was observed that each environment required no more than 10 days to show stable travel, residence, and giving-up times. However, for seven conditions, more than 10 sessions were conducted because residence and giving-up times changed from day to day (deviated one or more standard deviations from the mean of those times generated the day before). Table 1 summarizes the procedure and the sequence of the experimental conditions in which the travel requirement was varied across each of the three patch-size conditions.

Table 1

Order of the experimental conditions and number of sessions in each. Patches (i.e., reinforcer availability on the left lever) were depleted by decreasing the probability of a pellet (prey) after each pellet delivery. Pressing the right lever reset reinforcer probability on the left lever. The probability that such a press would reset the number of available prey was varied in the lever-press travel condition. The locomotion condition required traversing a longer distance between left and right levers before a single right lever press reset the number of prey.

Reset probability	Order	Sessions
1 prey ($p = .1 \rightarrow 0$)		
Lever-press travel		
.100	1	10
.100[a]	3	19
.050	4	10
.025	5	10
Locomotion travel		
1.000	2	15
2 prey ($p = 1 \rightarrow .5 \rightarrow 0$)		
Lever-press travel		
.100	6	10
.100[a]	7	22
.050	8	15
.025	9	10
.025[a]	18	13
.025[a]	20	9
Locomotion travel		
1.000	17	10
1.000[a]	19	7
8 prey ($p = 1 \rightarrow .125 \rightarrow 0$)		
Lever-press travel		
.100	10	10
.100[a]	12	12
.050	13	10
.025	14	10
Locomotion travel		
1.000	11	10
1.000[a]	15	10
Locomotion with hurdles		
1.000	16	11

[a] Redetermination. The reset probabilities of .1, .05, and .025 corresponded to random-ratio schedule values of 10, 20, and 40, respectively.

Data Analysis

Four dependent variables were measured: travel time, residence time in the patch, giving-up time, and capture success. Travel time was recorded from the last press on the left lever (the patch) to the first press on the left lever after meeting the reset requirement on the right lever. The residence time was recorded for each visit to the patch from the first press on the left lever to the last press on the left lever before travel to the right lever. The giving-up time was recorded for each visit from the last pellet obtained to the last press on the left lever before travel. A value of zero was assigned to giving-up times when

rats departed from the patch immediately after a pellet was obtained. Capture success was the percentage of available pellets (prey) obtained per visit to the patch.

An exploratory data analysis was conducted to examine travel times for possible order effects. Viewed over all five determinations in the experiment, however, no consistent order effects were observed. On the basis of these considerations, the data from all sessions were included in the analysis.

To summarize the data across sessions, we used an alternative measure of central tendency, the biweight mean (BWM). The BWM technique was designed by Mosteller and Tukey (1977; see also Killeen, 1985) to assign less weight to observations that depart from the central tendency of the data set. Although the BWM is sensitive like the mean, it is resistant to outliers (robust) like the median. Accordingly, BWMs of travel time, residence time, giving-up time, and capture success were calculated for each session of each environment. The least squares method, general linear model, was used to fit lines to BWMs of travel, residence, and giving-up times. All data, including redeterminations, were used in the equation.

RESULTS

Capture success was uniformly high. On average, 99.7% of available pellets were obtained per visit in the one-prey patches and 98.8% were obtained in the two-prey patches. All rats showed a small drop in capture success in the eight-prey patches. On average, 90.6% of available pellets were obtained in the eight-prey patches. This drop in capture success suggested that the rats occasionally left these patches before obtaining all eight prey, but this difference was considered too small to be important. Overall, the rats rarely left a patch without obtaining all the prey available: On average, 96.5% of pellets were obtained per visit in all patches.

For each patch size in the lever-press travel conditions, Figure 1 shows travel times as a function of the reset probability on the right lever. Also shown are the best fitting lines and the equations obtained by least squares linear regression. In general, lever-press travel decreased with increasing reset probability. In all three patches, redetermination points fell near the regression lines and close to original determinations. For the one-prey patches, increasing the reset probability caused only small decreases in lever-press travel time, but see the data for Rat 4. Regression slopes ranged from −414.28 to −10.02, showing a negative relation between reset probability and lever-press travel time. For the one-prey patches, the reset probability poorly predicted (mean R^2 = .22) variations in travel time.

Except for Rat 3 in the two-prey patches, Figure 1 shows that for the two-prey and eight-prey patches the reset probability of .025 produced longer lever-press travel times than did the .05 or .10 reset probabilities. Regression slopes ranged from −338.03 to −54.47, which indicated a roughly linear relation between reset probability and travel time that would approximate a power function with an exponent less than 1.0. For the two-prey and the eight-prey patches, variations in lever-press travel time were well predicted (mean R^2 = .70) from the reset probability.

Figures 2, 3, and 4 show travel times, residence times, and giving-up times, respectively, as a function of the number of available reinforcers before patch depletion. Figure 2 shows that every rat's travel times produced by simple locomotion fell within the range of those produced by the lever press. This was the essential requirement for discovering whether lever pressing and simple locomotion produce comparable effects on travel times. For all conditions, redetermination points fell on the regression lines close to original determinations. Travel times for the locomotion condition with hurdles were longer than those for the simple locomotion. Comparison of individual panels across conditions, however, reveals that the locomotion condition with hurdles produced travel times that fell within the range of the lever-press travel times. For lever-press travel, Figure 2 shows little evidence of a relation between the number of available reinforcers before patch depletion and travel time. The regression slopes ranged from −1.55 to 0.94, but because in most of the cases the R^2 is close to zero, the slopes are indistinguishable from zero. Except for Rat 1 and Rat 5, for locomotion travel there was a positive relation between the number of available reinforcers be-

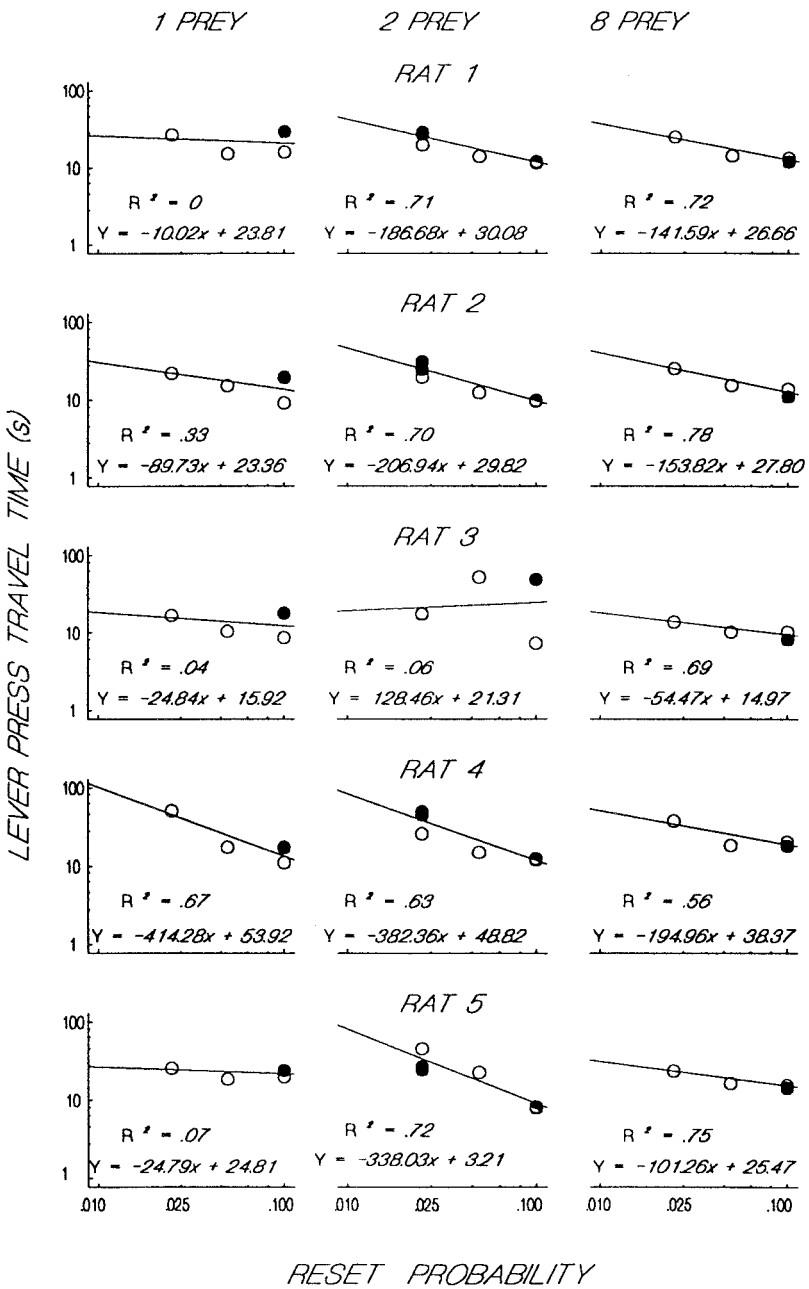

Fig. 1. Travel time (in seconds) as a function of reset probability (.025, .05, or .1) on the right lever for the one-, two-, and eight-prey patch sizes in the lever-press travel conditions. Each point represents the average data from all sessions for one reset probability. The filled circles indicate redeterminations. Lines were fitted to the points by the method of least squares. Equations appear near the lines, along with the values of R^2. Note logarithmic axes.

fore patch depletion and travel time. The regression slopes ranged from −0.31 to 1.17.

Figure 3 shows, for lever-press travel and locomotion conditions, that residence times increased linearly (logarithmic axes) with increasing number of available prey before patch depletion. The regression slopes ranged from 2.97 to 6.97, showing a positive relation between number of available prey before patch depletion and residence time. In

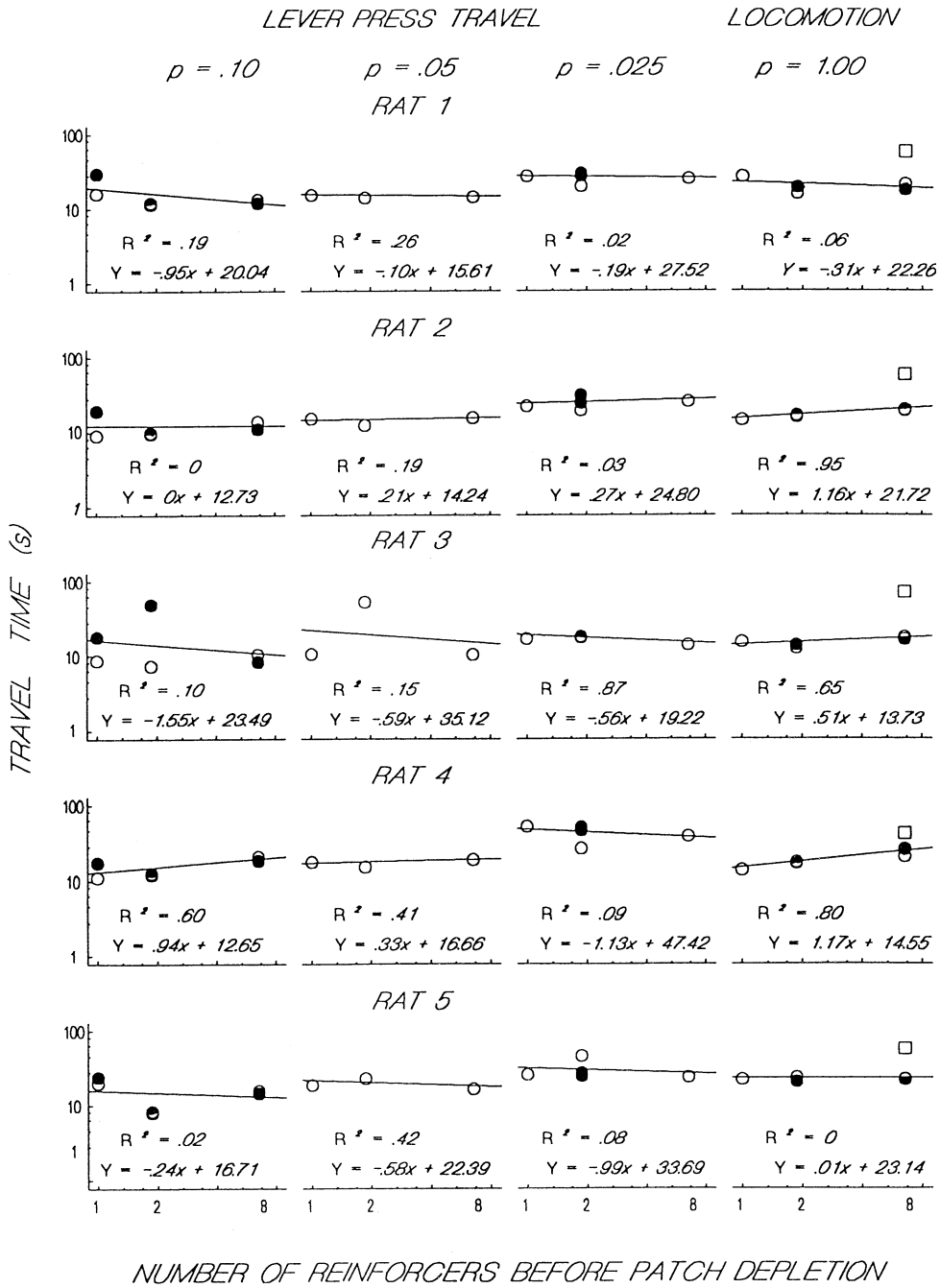

Fig. 2. Travel time (in seconds) as a function of the number of reinforcers (prey) before patch depletion in the lever-press travel and locomotion conditions. The probability that a lever press on the right lever would restore the patch was varied (p = .1, .05, or .025) in the lever-press travel condition. In the locomotion condition the route between levers was longer, but the probability that a right lever press would restore the patch was 1.0. The filled circles indicate redeterminations. The square symbols in the panels in the locomotion column indicate the locomotion condition with hurdles added. Other details as for Figure 1, except that data from the locomotion condition with hurdles were not included in the linear equation.

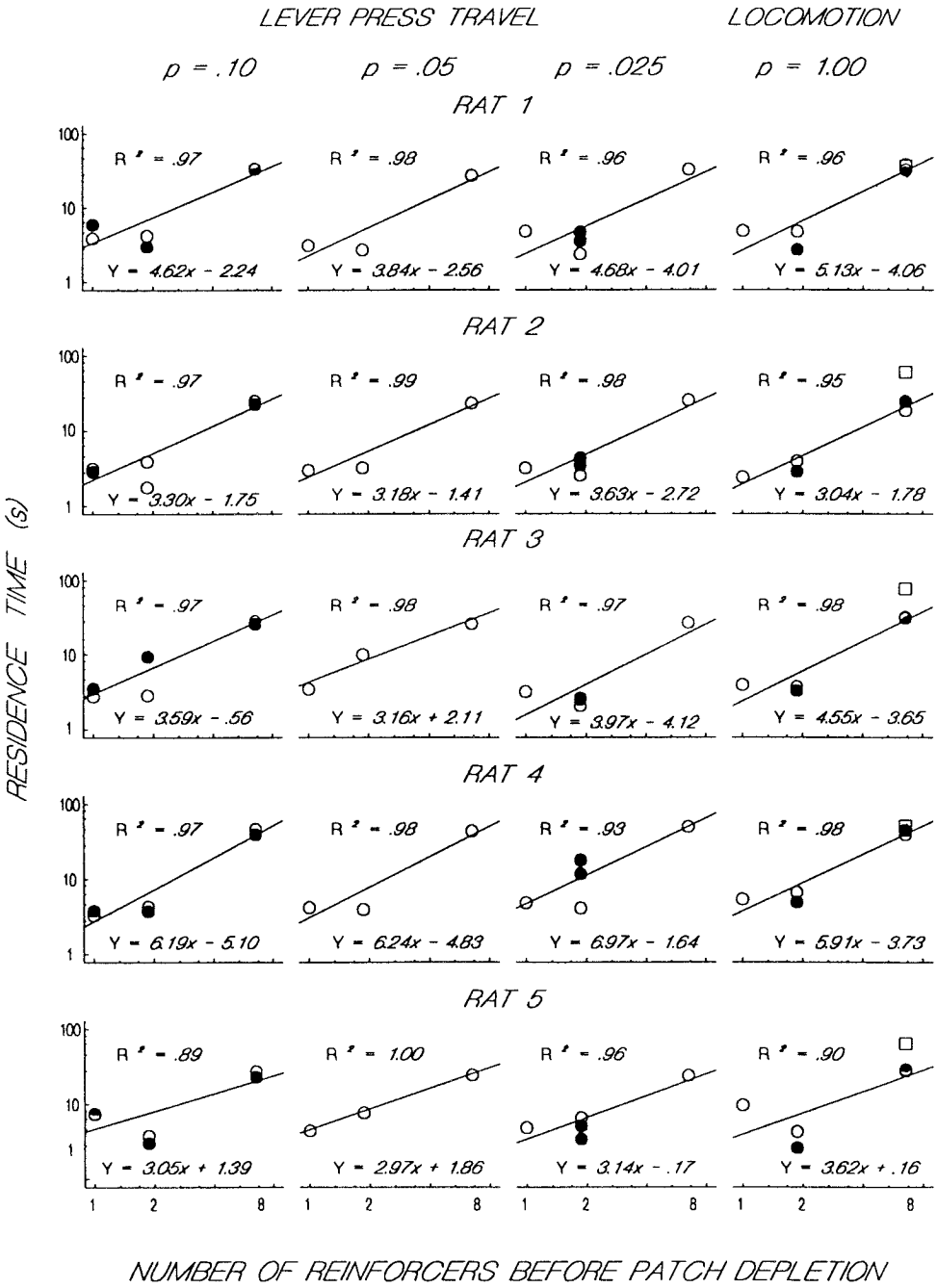

Fig. 3. Residence time (in seconds) as a function of the number of reinforcers (prey) before patch depletion. For a detailed description see the caption of Figure 2.

the two-prey patches, redetermination points sometimes deviated from the regression lines, but not in a systematic way. Residence times produced by simple locomotion travel fell within the range of those produced by lever-press travel. For Rats 2, 3, and 5, locomotion travel with hurdles produced longer residence times than those produced by the lever-press travel or simple locomotion conditions. Overall, the regression lines provided

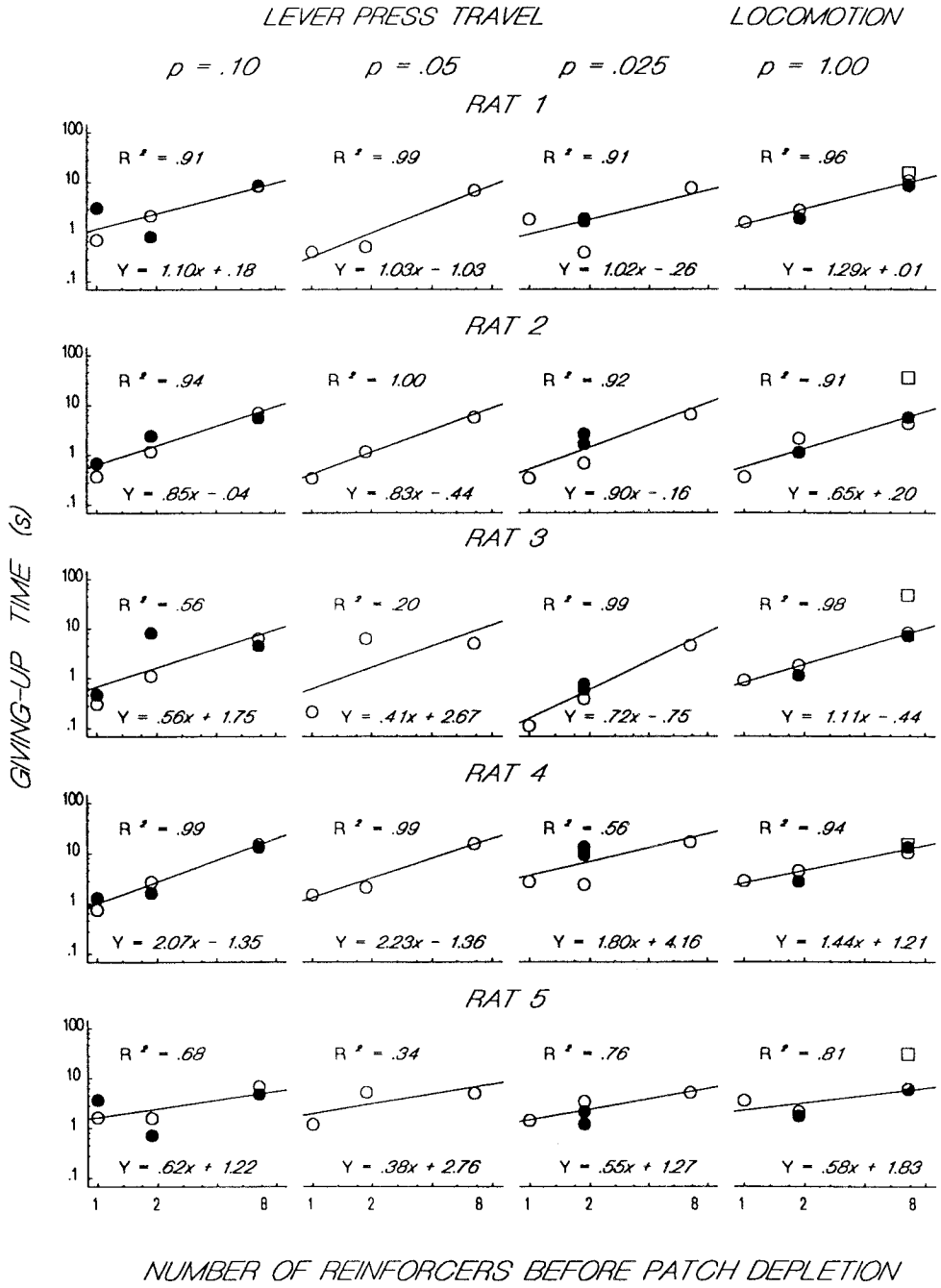

Fig. 4. Giving-up time (in seconds) as a function of the number of reinforcers (prey) before patch depletion. For a detailed description see the caption of Figure 2.

good fits to the data, accounting for most of the variability in residence times (mean R^2 = .96).

Figure 4 shows, for lever-press travel and locomotion conditions, that giving-up time increased as a function of the number of available reinforcers before patch depletion. All conditions show a positive relation between the number of reinforcers before patch depletion and giving-up time. The re-

gression slopes ranged from 0.38 to 1.80. Occasionally, redetermination points in the one-prey and two-prey patches deviated from the regression lines, but not in a systematic way. Giving-up times produced by simple locomotion were similar to those produced by lever-press travel conditions. For Rats 2, 3, and 5, locomotion travel with hurdles produced giving-up times that were longer than those produced by lever-press travel or simple locomotion conditions. Overall, the regression lines fit the data, accounting for most of the variability in giving-up times (mean R^2 = .82).

To find out whether locomotion travel and lever-press travel produced similar effects on residence and giving-up times at equal travel times, we plotted residence and giving-up times as a function of travel time. Figure 5 reveals that in all three patches, residence time generally increased with increasing travel time. Residence times for lever-press travel and the simple locomotion conditions were similar: All fell near the regression lines. No systematic differences in residence times occurred between the one-prey and the two-prey patches. Regression slopes ranged from 0 to 0.31, showing a positive relation between travel time and residence time. In the eight-prey patches, the residence times varied little as a function of travel time, but they were consistently longer than those obtained in the one-prey and two-prey patches. Regression slopes ranged from 0.10 to 0.96, which indicated a positive relation between travel time and residence time. Except for Rat 4, the locomotion travel with hurdles condition produced longer residence times than did the lever-press travel or simple locomotion conditions.

Figure 6 shows that in all three patches, giving-up times increased with increasing travel times. Simple locomotion travel produced giving-up times that were similar to those produced by lever-press travel; all points fell close to the regression lines. There were no systematic differences in giving-up times between the one-prey and the two-prey patches. Regression slopes ranged from 0.01 to 0.27, showing a positive relation between travel times and giving-up times. In the eight-prey patches, rats had longer giving-up times than in the one-prey and two-prey patches. The regression slopes ranged from 0.12 to 0.75, and there was a positive relation between travel times and giving-up times. Except for Rat 4, the giving-up times for the locomotion travel with hurdles condition were longer than those for the lever-press travel or the simple locomotion condition.

DISCUSSION

The results of this experiment supported the use of operant techniques in the study of foraging in the laboratory. The response requirements scheduled on the right lever controlled travel time. As the reset probability increased, lever-press travel time decreased. Put another way, lever-press travel time increased according to a power function of the number of presses required on the right lever. From a practical viewpoint, this means not only that interval schedules serve to control travel time but also that random-ratio schedules can be used to vary lever-press travel time (Baum, 1982b, 1987).

For every rat, travel times produced by locomotion conditions fell within the range of those produced by lever-press conditions, which is the essential requirement for concluding that both activities produce similar effects at equal travel times. Two issues will be discussed: the functional equivalence between locomotion and lever-press travel and its relation to optimal foraging theory.

Equivalence of Locomotion and Lever Press

Functional equivalence means that lever-press and locomotion travel produce equivalent effects on important dependent variables, such as residence time and giving-up time. That is, residence and giving-up times for locomotion travel should lie on the functions relating residence and giving-up time to lever-press travel time. Because locomotion conditions produced travel times that were similar to those produced by lever-press travel, assessing whether locomotion effects stand out from lever-press travel effects was possible.

For all prey patches, residence and giving-up times associated with locomotion travel were similar to those associated with lever-press travel. The one possible exception was the locomotion travel with hurdles in the eight-prey patches, for which 3 rats exhibited longer residence and giving-up times than

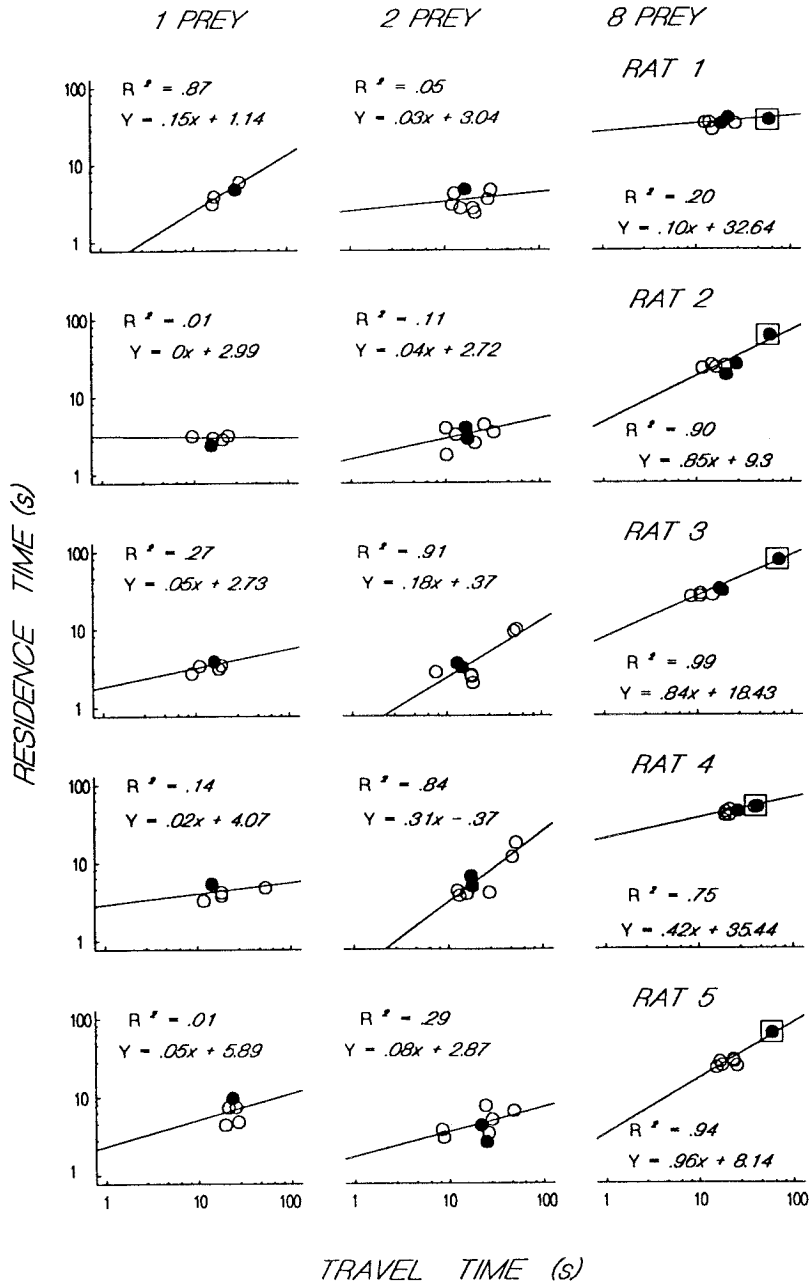

Fig. 5. Residence time (in seconds) as a function of travel time (in seconds). Each point represents the average data from all sessions for each condition studied. The open circles represent lever-press travel, and the filled circles represent locomotion travel. The times produced by the locomotion condition with hurdles are enclosed in small boxes. Some conditions were studied more than once. Added lines were fitted by least squares to the points for lever-press travel and locomotion travel; however, data from the locomotion condition with hurdles were not included in the linear equation. Equations appear near to the lines, along with values of R^2. Note logarithmic axes.

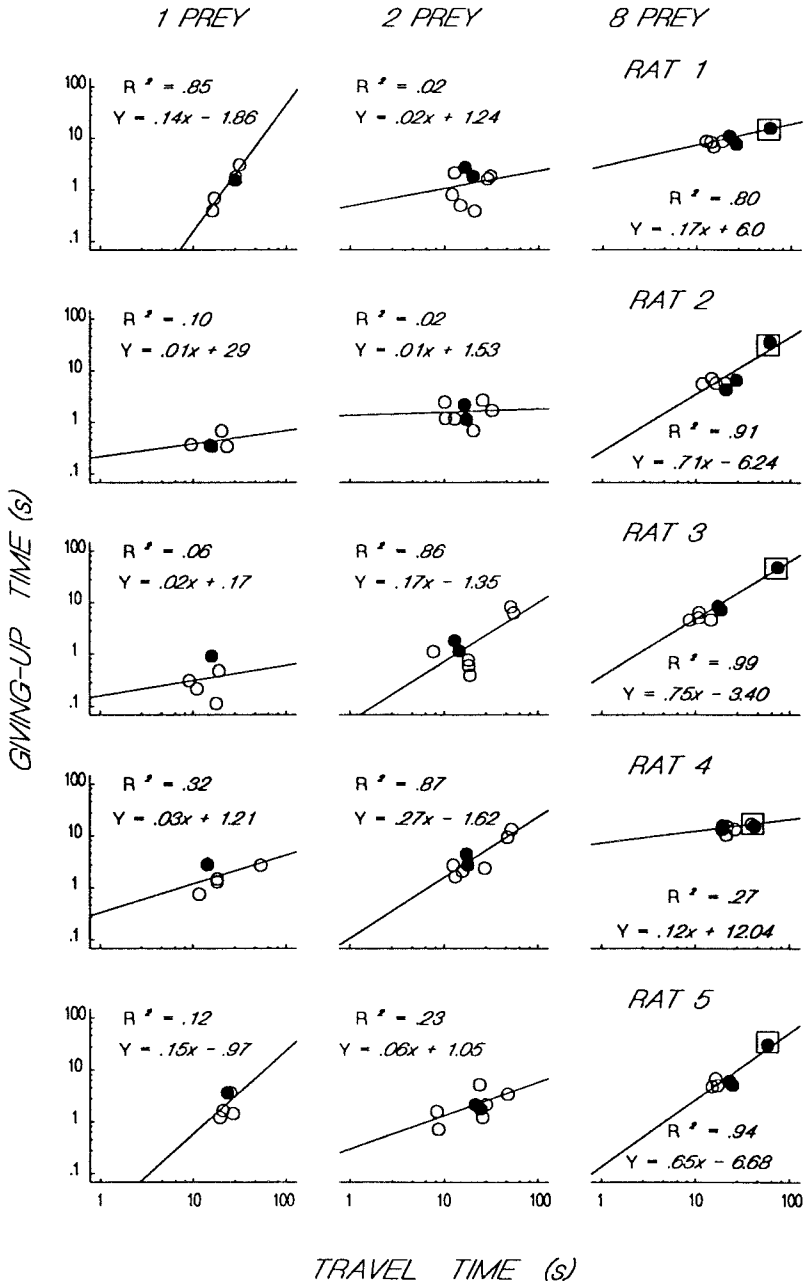

Fig. 6. Giving-up time (in seconds) as a function of travel time (in seconds). For a detailed description see the caption of Figure 5.

those for the lever-press travel conditions or the simple locomotion condition. Nevertheless, this effect was not consistent across animals: For 2 rats, the residence and giving-up times produced by locomotion travel with hurdles were similar to those produced by lever-press travel or simple locomotion conditions.

Residence and giving-up times increased with increasing travel times. Simple locomotion travel produced residence and giving-up times that were similar to those produced by

lever-press travel. The results under the one condition that included hurdles appeared to have a strong effect on the rats' residence and giving-up times. The conditions that arranged locomotion with hurdles generally produced longer residence and giving-up times than did the simple locomotion or lever-press travel conditions. This result resembles the effects of hurdles between the two response alternatives in Baum's (1982a) experiment on choice in pigeons. In that experiment, the addition of a hurdle produced large increments in residence times for both the rich-reinforcement and lean-reinforcement sides of the chamber. If part or all of the cost of travel lies in energy expenditure, then larger effects of climbing over hurdles might be expected. Although the present study found that locomotion with hurdles had a large effect on residence and giving-up times, above that of simple locomotion or lever-press travel requirements, the results of this one condition cannot decide the matter. Unfortunately, the present study did not manipulate travel distance in the locomotion condition, although it did manipulate an analogue of travel distance in the lever-press travel condition. More research on different types of travel with different energy requirements will be required. For the time being, the safest conclusion appears to be that lever-press travel has effects that are equivalent only to simple locomotion, such as running.

Optimal Foraging Theory

Charnov's (1976) marginal value theorem assumes that the quality of a patch is based on a forager's instantaneous rate of intake. It predicts that the forager will leave a patch when the rate of intake falls below the average provided by the habitat and that this final capture rate will be the same for all patches within the habitat (Krebs, Ryan, & Charnov, 1974; McNamara, 1982).

One possible patch-leaving rule, then, is the marginal value rule (Stephens & Krebs, 1986): Leave when the instantaneous capture rate falls to the average rate provided by the habitat. Uncertainty arises, however, because it is unclear how to measure the instantaneous capture rate. Krebs et al. (1974) suggested that giving-up time might be an indicator of the final capture rate in a patch. If so, the giving-up time should be the same for all patches within a habitat, even if these patches differ in quality. In addition, Krebs et al. suggested that in habitats with higher average capture rates, giving-up times should be shorter. Accordingly, the giving-up time should be inversely related to the average capture rate for the environment. Because average rates of capture necessarily decrease as travel time increases, giving-up time should increase with travel time, as we found for the one-prey, two-prey, and eight-prey patches.

Other rules besides the marginal value rule might determine patch leaving, and these might be more effective rules in some environments (Stephens & Krebs, 1986; Ydenberg, 1984). In particular, some simple rule of thumb might apply, such as a fixed time, a fixed number of prey, a fixed giving-up time, or a run of bad luck (Ydenberg, 1984).

Our results partly support the giving-up time rule. The giving-up times increased with increasing travel time for the one-prey, two-prey, and eight-prey patches. However, if giving-up time reflected a final capture rate, one would predict different results than those observed. In the one-prey patch, probability of obtaining the prey (p) was .10; in the two-prey patch, p finished at .5; and in the eight-prey patch, p finished at .125. So, the giving-up time should be shorter for the two-prey condition and about the same for the one-prey and eight-prey conditions. Our results revealed, however, that giving-up time was much longer in the eight-prey patches than in the one-prey patches. By a parallel argument, the results are seen to conflict with a run-of-bad-luck strategy.

Because the number of prey available in an environment was fixed, the rats might have adopted a strategy of obtaining a fixed number of prey and then leaving the patch. But the rats did not do this, particularly in the one-prey patches, where one might expect the giving-up time to be zero.

The more prey in the patch, the longer the rats persisted in the patch. When the patch provided eight pellets per visit, rats produced the longest residence and giving-up times. Thus, the overall rate of reinforcement (capture rate including travel) was highest for the environment with eight-prey patches. This result is consistent with Nevin's (1979) concept of behavioral momentum: Richer schedules of reinforcement produce greater persistence

of responding than leaner ones. Agreement with behavioral momentum holds only across environments, however, because the present data show that giving-up time increased with increasing travel time, and as travel time increased, the overall rate of reinforcement decreased.

Most theories of foraging predict that residence time should increase with travel length (or duration), as the marginal value theorem predicts. This result has been corroborated both in the field (e.g., Anderson, 1978; Zimmerman, 1981) and in the laboratory (e.g., Cowie, 1977; Killeen et al., 1981; Lea, 1979; Mellgren et al., 1984). Not all theories make predictions about giving-up time, and those that do generally make predictions contradicted by the present results. For example, the reasoning of Krebs et al. (1974) would predict an increase in giving-up time in the one- and two-prey patches as the travel requirement increased, but would also predict that, instead of increasing, giving-up time should decrease in the richer environments of the eight-prey patches.

One model that appears to accommodate the present results, at least qualitatively, was developed by McNair (1982). McNair pointed out that the marginal value theorem (Charnov, 1976) has nothing to say about giving-up time, because the model on which it is based refers only to residence time. To incorporate giving-up time, McNair treats it not as a dependent variable but as a theoretical parameter. In his model, giving-up time is the time since the last prey capture that, when exceeded, results in leaving the patch. Measured giving-up time might be an estimate of this parameter. Thought of this way, both residence time and yield (number of prey captured) depend on the giving-up time. McNair showed that there is an optimal giving-up time for each patch type in any habitat and that longer giving-up times should be used in better quality patches. Given the right assumptions, McNair's model appears to predict that in habitats like the ones in this experiment with only one patch type, giving-up time for the one-prey and two-prey patches should be similar, whereas giving-up time for the eight-prey patch should be longer. These are exactly the results we found. Like other models, McNair's model also predicts that increased travel between patches will result in longer residence times and longer giving-up times, and the data from the present study are consistent with that model.

McNair (1982) also suggested that under different environmental conditions different sorts of strategies might be optimal (see also Stephens & Krebs, 1986). The best strategy in one environment might be a giving-up-time strategy; in another, a residence-time strategy (e.g., the marginal value rule); in another, a fixed time or yield (e.g., Gibb, 1962; Iwasa, Higashi, & Yamamura, 1981). The absence of any significant variation in residence or giving-up time in the eight-prey patches in this experiment might indicate such a shift in strategy. It seems clear that conditions can be arranged so that rats use other strategies than they did in this experiment. Redhead and Tyler (1988), for example, trained rats to press one lever to obtain food according to a progressive variable-interval schedule of reinforcement that simulated patch depletion. The schedule was reset by pressing another lever. To model travel time, Redhead and Tyler increased the time between pressing the reset lever and obtaining a reinforcer from the patch lever. They found (Experiment 2), in accordance with the marginal value theorem, that when travel time increased, residence times increased. However, they reported that the rats "appeared to dispense with the giving-up time after the first few trials" (p. 92). Redhead and Tyler suggested that the determinant of patch leaving was the interreinforcement interval.

Conclusions

The results of the present experiment supported the use of lever-press travel to model simple locomotion between patches, but suggested that more costly (in terms of energy expended) locomotion travel (i.e., with hurdles) might not be equivalent to lever-press travel. The conclusion that ratio schedules of reinforcement can be used to model travel in the laboratory (Baum, 1982a, 1987) may be accepted, but with that note of caution. The experiment also demonstrated the feasibility of these methods for studying foraging in rats. Although the effects observed were generally orderly, they appeared to be complex enough to challenge existing theories.

REFERENCES

Abarca, N., & Fantino, E. (1982). Choice and foraging. *Journal of the Experimental Analysis of Behavior, 38,* 117–123.

Anderson, M. (1978). Optimal foraging area: Size and location of search effort. *Theoretical Population Biology, 13,* 397–409.

Baum, W. M. (1982a). Choice, changeover, and travel. *Journal of the Experimental Analysis of Behavior, 38,* 35–49.

Baum, W. M. (1982b). Instrumental behavior and foraging in the wild. In M. L. Commons, R. J. Herrnstein, & H. Rachlin (Eds.), *Quantitative analyses of behavior: Vol. 2. Matching and maximizing accounts* (pp. 227–240). Cambridge, MA: Ballinger.

Baum, W. M. (1987). Random and systematic foraging, experimental studies of depletion, and schedules of reinforcement. In A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), *Foraging behavior* (pp. 587–607). New York: Plenum.

Charnov, E. L. (1976). Optimal foraging: The marginal value theorem. *Theoretical Population Biology, 9,* 129–136.

Collier, G. H., & Rovee-Collier, C. K. (1981). A comparative analysis of optimal foraging behavior: Laboratory simulations. In A. C. Kamil & T. D. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches* (pp. 39–76). New York: Garland STPM Press.

Cowie, R. J. (1977). Optimal foraging in great tits (*Parus major*). *Nature, 268,* 137–139.

Dreyfus, L. R., DePorto-Callan, D., & Pesillo, S. A. (1993). Changeover contingencies and choice on concurrent schedules. *Animal Learning & Behavior, 21,* 203–213.

Fantino, E. (1987). Operant conditioning simulations of foraging and the delay-reduction hypothesis. In A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), *Foraging behavior* (pp. 193–214). New York: Plenum.

Fantino, E., & Abarca, N. (1985). Choice, optimal foraging, and the delay-reduction hypothesis. *Behavioral and Brain Sciences, 8,* 315–330.

Gibb, J. A. (1962). L. Tinbergen's hypothesis of the role of specific search images. *Ibis, 104,* 106–111.

Hanson, J. (1987). Test of optimal foraging using an operant analogue. In A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), *Foraging behavior* (pp. 335–362). New York: Plenum.

Hanson, J., & Green, L. (1989a). Foraging decisions: Patch choice and exploitation by pigeons. *Animal Behaviour, 37,* 968–986.

Hanson, J., & Green, L. (1989b). Foraging decisions: Prey choice by pigeons. *Animal Behaviour, 37,* 429–443.

Hartling, L. K., & Plowright, R. C. (1979). Foraging by bumblebees on patches of artificial flowers: A laboratory study. *Canadian Journal of Zoology, 57,* 1866–1870.

Iwasa, Y., Higashi, M., & Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist, 117,* 710–723.

Kacelnik, A., & Cuthill, I. C. (1987). Starlings and optimal foraging theory: Modeling in a practical world. In A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), *Foraging behavior* (pp. 303–333). New York: Plenum.

Kamil, A. C., & Yoerg, S. I. (1985). The effects of prey depletion on the patch choice of foraging blue jays (*Cyanocitta cristata*). *Animal Behaviour, 33,* 1089–1095.

Killeen, P. R. (1985). The bimean: A measure of central tendency that accommodates outliers. *Behavior Research Methods, Instruments, & Computers, 17,* 526–528.

Killeen, P. R., Smith, J. P., & Hanson, S. L. (1981). Central place foraging in *Rattus norvegicus. Animal Behaviour, 29,* 64–70.

Krebs, J. R. (1978). Optimal foraging: Decision rules for predators. In J. R. Krebs & N. B. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (pp. 23–63). Sunderland, MA: Sinauer.

Krebs, J. R., Kacelnik, A., & Taylor, P. (1978). Test of optimal sampling by foraging great tits. *Nature, 275,* 27–31.

Krebs, J. R., Ryan, J. C., & Charnov, E. L. (1974). Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Animal Behaviour, 22,* 953–964.

Lea, S. E. G. (1979). Foraging and reinforcement schedules in the pigeon: Optimal and non-optimal aspects of choice. *Animal Behaviour, 27,* 875–886.

MacArthur, R. H., & Pianka, E. R. (1966). On the optimal use of a patchy environment. *American Naturalist, 100,* 603–609.

McNair, N. J. (1982). Optimal giving-up times and the marginal value theorem. *American Naturalist, 119,* 511–529.

McNamara, J. M. (1982). Optimal patch use in a stochastic environment. *Theoretical Population Biology, 21,* 269–288.

McSweeney, F. K. (1978). Negative behavioral contrast on multiple treadle-press schedules. *Journal of the Experimental Analysis of Behavior, 29,* 463–473.

Mellgren, R. L. (1982). Foraging in a simulated natural environment: There's a rat loose in the lab. *Journal of the Experimental Analysis of Behavior, 38,* 93–100.

Mellgren, R., Misasi, L., & Brown, S. W. (1984). Optimal foraging theory: Prey density and travel requirements and *Rattus norvegicus. Journal of Comparative Psychology, 98,* 142–153.

Mosteller, F., & Tukey, J. W. (1977). *Data analysis and regression: A second course in statistics.* Reading, MA: Addison-Wesley.

Nevin, J. A. (1979). Reinforcement schedules and response strength. In M. Zeiler & P. Harzem (Eds.), *Reinforcement and the organization of behavior* (pp. 117–158). New York: Wiley.

Pietrewicz, A. T., & Kamil, A. C. (1977). Visual detection of cryptic prey by blue jays (*Cyanocitta cristata*). *Science, 195,* 580–582.

Pliskoff, S. S., & Fetterman, J. G. (1981). Undermatching and overmatching: The fixed-ratio changeover requirement. *Journal of the Experimental Analysis of Behavior, 36,* 21–27.

Pulliam, H. R. (1981). Learning to forage optimally. In A. C. Kamil & T. D. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches* (pp. 379–388). New York: Garland STPM.

Redhead, E., & Tyler, P. A. (1988). An experimental analysis of optimal foraging behavior in patchy environments. *The Quarterly Journal of Experimental Psychology, 40B,* 83–102.

Schoener, T. W. (1987). A brief history of optimal foraging ecology. In A. C. Kamil, J. R. Krebs, & H. R.

Pulliam (Eds.), *Foraging behavior* (pp. 5–67). New York: Plenum.

Shettleworth, S. J. (1988). Foraging as operant behavior and operant behavior as foraging: What have we learned? In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 22, pp. 1–49). New York: Academic Press.

Shull, R. L., & Pliskoff, S. (1967). Changeover delay and concurrent schedules: Some effects on relative performance measures. *Journal of the Experimental Analysis of Behavior, 10,* 517–527.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory.* Princeton, NJ: Princeton University Press.

Ydenberg, R. C. (1984). Great tits and giving-up times: Decision rules for leaving patches. *Behaviour, 90,* 1–24.

Zimmerman, M. (1981). Optimal foraging, plant density and the marginal value theorem. *Oecologia, 49,* 148–153.

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