LEAVING PATCHES: EFFECTS OF TRAVEL REQUIREMENTS

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Five pigeons were trained in an analogue foraging procedure in which, by completing a travel requirement, they entered a "patch" in which a reinforcer might be available after an unpredictable time. They also had the opportunity, by emitting a defined response, to exit the patch and travel to another patch. Prey availability in a patch was not signaled. Data were collected on the length of time that subjects stayed in patches before exiting (residence times) as a function of various travel requirements: travel for a fixed time in blackout, fixed-interval schedule traveling, fixed-time traveling with an added response required to terminate traveling, and fixed-ratio traveling. For each of these conditions, the required amount of travel (time or responses) was varied over a wide range. As previously reported, residence times increased with increases in fixed-time traveling, as they did with increasing fixed-interval or fixed-ratio traveling. There was no evidence that adding response or work requirements systematically affected residence time except via increased travel time, although 3 of the 5 birds stayed longer in a patch under higher fixed-ratio values. A "threshold-maximization" model described the data well with a single parameter that was consistent across subjects, procedures, and experiments.

Key words: patch residence time, travel time, travel requirements, choice, pecking, pigeons

An animal foraging in the wild commonly searches for prey that are not spread randomly throughout the environment; instead they occur in groups or locations called patches (Cowie, 1977). The animal's behavior consists of searching a patch for prey, attacking and handling prey, and traveling between patches. An important survival-related decision facing an animal is when to leave a patch and travel to a new one. Researchers have typically studied this question by measuring the time from entering a patch to the time of exiting a patch (e.g., Kamil, Misthal, & Stephens, in press; Kamil & Yoerg, 1985; Kamil, Yoerg, & Clements, 1988). This has been called the animal's patch residence time (or "moving-on" time; Brunner, Kacelnik, & Gibbon, 1992).

Early laboratory studies of foraging behavior used concurrent variable-interval (VI) schedules to simulate patches, with either obstacles between the keys or changeover delays (CODs) arranged to represent traveling between patches. Baum (1982), for example,

trained pigeons to respond on a two-key concurrent schedule with a physical barrier between the keys. In order to change over between the concurrent alternatives, the animals had to travel around the barrier. The amount of travel between patches was thus controlled by varying the length of the barrier. For one group of birds, the barrier was 20.3 cm (8 in.) in length with an 8.3-cm (3.25-in.) hurdle added to its end. For another group of birds, the barrier was only 10.2 cm (4 in.) in length. Baum showed that birds with the greater travel requirement stayed longer on each alternative (i.e., the frequency of changeovers decreased) as the length of the barrier increased beyond 10.2 cm. In addition, Baum varied the relative frequency of reinforcers obtained from the concurrent alternatives and analyzed the resultant data in terms of the generalized matching law (Baum, 1974). This law states that the ratio of behavior on two concurrent alternatives is a power function of the ratio of the reinforcers obtained from the two alternatives. The exponent of the power function provides a measure of the sensitivity of response allocation to reinforcer frequency allocation. Birds exposed to the longer partition (and, hence, the greater travel requirement) showed unusually high overmatching (sensitivities greater than unity), whereas the birds exposed to the easier travel requirement showed consistent undermatching (sensitivities less than unity). In other words, the increase in the travel requirement

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resulted in a large increase in the sensitivity of behavior allocation to relative reinforcer frequencies.

Davison (1991) trained pigeons on a switching-key concurrent schedule. Rather than a partition between keys, Davison arranged a fixed-interval (FI) changeover requirement. Under this arrangement, the birds were required to complete either an FI 0-s, an FI 10-s, or an FI 20-s schedule on the switching key in order to change between the alternative schedules available on the main key. For each value of the FI schedule, Davison varied the relative frequency of reinforcers available on the two alternatives. A generalized matching law analysis showed that the sensitivity of behavior allocation to the reinforcer distribution was significantly higher on the FI 10-s condition than on the FI 0-s condition, but sensitivities did not differ between the FI 10-s and FI 20-s conditions. Consistent with Baum's (1982) finding, response-allocation sensitivities increased as the travel requirement increased. Davison further found that, as in Baum's study, the rate of changeovers systematically decreased as the travel requirement increased. In other words, patch residence time on an alternative increased with increases in travel requirements.

Other laboratory studies have attempted to use more naturalistic representations than are provided by simple concurrent schedules. Kamil, Lindstrom, and Peters (1985), for example, used a discrete-trials procedure to study the behavior of blue jays searching for a cryptic moth prey in slides of birch bark. The experimental chamber contained two response keys. Slides were projected onto the larger of the keys (the patch key), and the smaller key represented the patch-exit key. Searching was terminated by a peck on either the patch key or the patch-exit key. A peck on the patch key extinguished the patch-exit key for 30 s and simulated handling time, after which time a reinforcer was delivered if a prey item had been present on the slide. Following delivery of the reinforcer, a period of blackout represented travel to a new patch. A patch-exit response immediately produced the travel period in blackout. Kamil *et al.* used the latency of patch-exit responses in patches that did not contain prey as a measure of patch residence time, and showed a systematic increase in res-

idence time as the duration of travel time was increased.

Kamil *et al.* (in press) used a procedure similar to that employed by Kamil *et al.* (1985), and arranged the arrival of prey in a prey patch according to an exponential distribution (Part 1) or a uniform distribution (Part 2). Travel time in blackout was varied from 4 s to 8 s to 16 s in each part. Kamil *et al.* (in press) showed that patch residence time increased with increases in travel time in both parts of the experiment.

Using a similar procedure, Davison and McCarthy (1994) varied the duration of travel in blackout from 0.25 s to 16 s at each of three different probabilities of food per second (.05, .1, and .2) in prey patches. Consistent with previous research, they found that both increasing travel time and decreasing the probability of reinforcers per second increased patch residence time.

The commonality in these different methodological approaches to the study of foraging is that patch residence time consistently and reliably increases with increases in the travel requirement (see also Stephens & Krebs, 1986). The major difference among them, however, is that in the discrete-trials procedure used by Kamil and his associates and by Davison and McCarthy (1994), only the duration of travel in blackout has been varied. By contrast, in the concurrent-schedule studies of Baum (1982) and Davison (1991), a work requirement was imposed during travel. The unanswered question is this: Is the increase in residence time simply a function of the *duration* of travel time, or is the amount of work required during travel an important contributing factor?

The present research sought to answer this question by comparing residence times across four different parts in which both the duration of travel and the work requirement during travel were varied systematically. In Part 1, the duration of travel in blackout was varied across eight fixed-time (FT) values ranging from 0.25 s to 60 s. In Part 2, the animals were required to complete an FI schedule during the travel component. The value of the FI was varied across six values ranging from FI 0.25 s to FI 16 s. In Part 3, travel in blackout was reinstated as in Part 1 but with the added requirement that a fixed-ratio (FR) 1 schedule (chained FT FR 1) be completed before patch

entry was obtained. The FT schedule in blackout was varied from 0.25 s to 50 s across seven experimental conditions. Finally, in Part 4, the animals were required to complete an FR schedule in which the response requirement was varied from 5 to 40 responses across five experimental conditions.

The principal dependent variable was the patch residence time, and the major experimental question posed was whether this measure would vary in any systematic way with variations in travel requirements.

METHOD

Subjects

Five experimentally naive homing pigeons (numbered 131, 133, 134, 135, and 136) served as subjects. They were maintained at $85\% \pm 15$ g of their free-feeding body weights by supplementary feeding with mixed grain in the home cage after each experimental session. Water and grit were freely available in the home cage.

Apparatus

The sound- and light-attenuating chamber was 320 mm high, 310 mm wide, and 340 mm deep. Three response keys (20 mm in diameter, 105 mm apart, and 255 mm above the grid floor) were situated on one wall of the chamber. All three keys could be transilluminated white, red, or green. When illuminated, each key could be operated by a peck exceeding approximately 0.1 N. Pecks on darkened keys had no scheduled consequence. A houselight was located on the rear left ceiling of the chamber. A food magazine (50 mm by 50 mm) was situated beneath the center key, 125 mm above the grid floor. Reinforcement was 3-s access to wheat. During this time, the magazine was raised and illuminated by white light, and the houselight and keylights were extinguished. All experimental events were controlled by an IBM PC-compatible computer running MED-PC® software situated in a room remote from the experimental chamber.

Procedure

Initial training. The subjects were initially trained to eat from the magazine and then to

peck all three keys using an autoshaping procedure (see Brown & Jenkins, 1968). Over 11 sessions, the key on which responses were reinforced and the key color (white, red, or green) were varied. The subjects then received six training sessions on a variable-ratio (VR) 5 schedule, followed by 13 training sessions on a single VI 15-s (three sessions) or 30-s (10 sessions) schedule, again with the key and key color varied across sessions.

Following this, the subjects received preliminary training on a two-key concurrent VI 60-s VI 60-s schedule arranged on the left and right keys with no programmed changeover delay. Each subject received one training session with both the left and right keys lit red, one session with both keys lit white, and two sessions with both keys lit green. They then received five training sessions on a three-key concurrent VI 90-s VI 90-s VI 90-s schedule with all three keys lit green. Finally they received two training sessions on a two-key concurrent VI 60-s VI 60-s schedule with the left key lit white and the right key lit red.

Foraging procedure. In the preliminary and experimental training with the foraging procedure, each trial consisted of a patch phase followed by a travel phase. Trials began with the illumination of the left white key and the right red key (the patch phase). There was a constant probability of .5 that a patch contained a single reinforcer (a prey patch); otherwise, the patch was empty (a nonprey patch). Responses on the left white key (search responses) when in a prey patch were reinforced with a certain probability per second (see below). The travel phase automatically followed the delivery of a reinforcer. A single response on the right red key during the patch phase (a patch-exit response) produced the travel phase. If the delivery of a reinforcer or a patch-exit response had not occurred after 150 s had elapsed since patch entry, the arranged travel requirement occurred automatically. A new trial (presentation of the white left and red right keys) began immediately after completion of the travel requirement.

Preliminary training. All subjects received several training sessions on the foraging procedure before the main experimental conditions were introduced. In the first 23 training sessions, the probability of reinforcement per second in a prey patch was .2. In subsequent

Table 1

The order of experimental parts and conditions, and the number of training sessions given in each. FT denotes a fixed time in blackout, FI denotes a fixed-interval schedule, and FR denotes a fixed-ratio schedule. All times are in seconds.

Part	Condition	Subject	Travel requirement	Sessions
1	1	all	FT 4	21
	2	all	FT 8	28
	3	all	FT 16	31
	4	all	FT 2	23
	5	all	FT 12	27
	6	all	FT 0.25	22
	7	all	FT 8	23
	8	all	FT 16	21
	9	all	FT 0.25	26
	10	all	FT 12	40
	11	all	FT 2	21
	12	all	FT 4	21
2	13	all	FI 4	21
	14	all	FI 16	24
	15	all	FI 2	24
	16	all	FI 8	30
	17	all	FI 0.25	26
	18	all	FI 12	24
	19	all	FI 4	39
3	20	all	FT 8 FR 1	21
	21	all	FT 2 FR 1	23
	22	all	FT 12 FR 1	24
	23	all	FT 0.25 FR 1	25
	24	all	FT 16 FR 1	26
4	25	all	FT 4 FR 1	21
	26	all	FR 5	18
	27	all	FR 10	21
	28	all	FR 20	23
1	29	all	FR 15	29
	30	all	FT 60	26
	31	all	FT 30	33
4	32	all	FT 8	45
	33	131	FR 40	26
		133	FR 15	26
		134	FR 40	26
		135	FR 30	26
3		136	FR 40	26
	34	all	FT 50 FR 1	28

sessions, this probability was .175 (two sessions), .15 (three sessions), .125 (two sessions), and .1 (two sessions). The duration of travel was 4 s for all training sessions; during this time, all chamber lights were extinguished.

Experimental conditions. The experiment consisted of four parts. The sequence of experimental parts and conditions, and the number of training sessions given in each, are shown in Table 1. In all parts of the experiment, there

was a constant probability of .5 that a patch contained a single reinforcer, and the probability of reinforcement per second within a prey patch was held constant at .075. The travel requirement commenced immediately following the delivery of a reinforcer, or following the emission of a patch-exit response, or after 150 s had been spent in a patch without a food delivery or a patch-exit response.

The four parts of the experiment differed according to the requirements for travel. In Part 1 (Conditions 1 through 12 and 30 through 32), travel was a fixed time in blackout, and the duration of the FT was varied from 0.25 s to 60 s across eight conditions (Table 1). Conditions 7 to 12 constituted replications of Conditions 1 to 6 (with a new order of conditions), and Condition 32 replicated Conditions 2 and 7.

In Part 2 (Conditions 13 through 19), completion of the travel requirement was dependent upon the completion of an FI schedule on the green center key. This key became operative immediately following food delivery, or a patch-exit response, or 150 s had elapsed, and the white and red keys were extinguished during this time. The duration of the FI was varied from 0.25 s to 16 s across six experimental conditions. Condition 19 was a replication of Condition 13.

In Part 3 (Conditions 20 through 25 and 34), the travel requirement was a fixed time in blackout followed by the emission of a single peck on the green center key (a chained FT FR 1 schedule). The duration of the FT was varied from 0.25 s to 50 s across seven experimental conditions.

In Part 4 (Conditions 26 through 29 and 33), the travel requirement was completion of an FR schedule on the green center key. The FR schedule was varied across a range of values (that differed across subjects) from FR 5 to FR 40 (Table 1).

In all parts of the experiment, including preliminary training, a session ended in blackout after the delivery of 40 food reinforcers or, alternatively, after the first patch-exit response, patch end, or reinforcer had occurred once 40 min had elapsed. Experimental sessions were generally conducted 7 days per week, and each experimental condition was in effect until all subjects had satisfied a predetermined stability criterion: Following nine sessions on a condition, the median of the time spent in

nonprey patches divided by the number of nonprey patch entries across three consecutive sessions was calculated. Stability was reached when three consecutive medians did not show a monotonic trend. Conditions were thus in effect for a minimum of 18 sessions, and, on average, 29 sessions (Table 1).

The data collected were the total number of search responses (left-key responses) when in a prey patch and when in a nonprey patch, the total number of prey patch entries and nonprey patch entries, the total time spent in prey patches and in nonprey patches, and the total number of reinforcers delivered. In addition, the total number of responses emitted on the green center key during travel was recorded for Parts 2 and 4. The principal dependent variable was patch residence time. This was calculated as the mean time from the commencement of a patch of either type to the time at which the subject emitted a patch-exit response or until the maximum patch residence time of 150 s had elapsed. Note that trials ending in food delivery did not contribute to this measure. Patch-exit responses emitted on prey trials did contribute, as did trials on which the subject did not obtain a reinforcer or emit a patch-exit response. All data reported here are taken from the last five sessions of each experimental condition.

RESULTS

The data for each subject and each experimental condition, summed over the last five training sessions, are shown in the Appendix. These data show that, in all parts of the experiment, the subjects used the patch-exit key consistently and exited patches on most nonprey trials and on some prey trials. The subjects seldom failed either to exit a patch or to obtain a reinforcer, resulting in a trial ending after 150 s had elapsed. In addition, the number of trials completed decreased as the travel requirements were increased.

Part 1

In Part 1, travel was a fixed time in blackout and the duration of travel was varied from 0.25 s to 60 s. Figure 1 (open circles) shows the mean residence time in a patch as a function of the arranged FT travel duration. (With the exception of Bird 131, replicated data points closely approximated the original determina-

tions.) Figure 1 clearly shows that patch residence time increased with increases in travel time. A nonparametric trend test (Ferguson, 1971), using individual-subject data, confirmed that this increase was statistically significant ($N = 5$, $k = 8$, replications averaged, $\Sigma S = 118$; $p < .05$).

Part 2

In Part 2, the subjects were required to complete an FI x -s schedule on the green center key during travel, where x was varied from 0.25 s to 16 s. Figure 2 shows the number of center-key responses emitted, together with response rates, as a function of the arranged FI requirement. First, the number of responses emitted during the FI significantly increased as the duration of the FI was increased (nonparametric trend test, $N = 5$, $k = 6$, replication averaged, $\Sigma S = 73$; $p < .05$). Group means ranged from 1.0 response (FI 0.25 s) to 4.91 responses (FI 16 s). Second, response rates remained roughly constant as the duration of the FI was increased (nonparametric trend test, $N = 5$, $k = 6$, replication averaged, $\Sigma S = -22$; $p > .05$). Response rates, averaged across the six FI values, ranged from 11.7 (Bird 133) to 25.8 (Bird 135) responses per minute.

Figure 1 (filled circles) shows the mean residence times as a function of the mean travel time (i.e., the average time taken to complete the FI requirement). A nonparametric trend test on individual-subject data confirmed that residence times significantly increased as the FI requirement, and hence travel time, increased ($N = 5$, $k = 6$, replication averaged, $\Sigma S = 59$; $p < .05$).

Part 3

In Part 3, the travel requirement was a chained FT FR 1 schedule; that is, a fixed time in blackout was followed by the emission of a single peck on the green center key. The FT in blackout was varied from 0.25 s to 50 s across seven conditions. Figure 1 (open triangles) shows the mean residence time as a function of the obtained travel time (i.e., the time taken to complete the chained FT FR 1 requirement). A nonparametric trend test using individual-subject data confirmed that residence time increased significantly as travel time increased ($N = 5$, $k = 8$; $\Sigma S = 95$; $p < .05$).

Fig. 1. Mean residence times in a patch (measured in seconds) as a function of mean obtained travel times (measured in seconds) for all parts of the experiment. The data are shown for individual subjects and averaged across birds as a group.

Fig. 2. Part 2, FI travel. The number of center-key responses emitted (open circles) and responses per minute (filled circles) as a function of the arranged FI travel requirement. These data are shown for individual birds and averaged across birds as a group.

Part 4

In Part 4, the travel requirement was completion of an FR x schedule on the center key, where x was varied from 5 to 20 (Bird 133), 5 to 30 (Bird 135), and 5 to 40 (Birds 131, 134, and 136). Figure 3 shows response rate as a function of the arranged FR requirement. (Note that no group plot is shown because the arranged FR values were varied across birds; see Table 1.) The individual-subject plots show that response rates generally decreased as the FR requirement was increased ($N = 5$, $k_1 = 5$, $k_2 = 4$, $k_3 = k_4 = k_5 = 5$; $\Sigma S = -24$; $p < .05$). Response rates ranged from 8.1 responses per minute (Bird 135, FR 30) to 78.8 responses per minute (Bird 131, FR 15).

Figure 1 (filled triangles) shows mean residence times as a function of mean obtained travel times (i.e., the average time taken to complete the FR x schedule). Residence times significantly increased as travel time increased ($N = 5$, $k = 5$; $\Sigma S = 40$; $p < .05$).

DISCUSSION

Using a discrete-trials procedure to simulate a natural foraging situation, the requirements of traveling between two patches were varied. Travel either occurred in blackout (Parts 1 and 3), or the animals were required to complete an FI (Part 2) or an FR (Part 4) schedule during travel. In all parts of the experiment, patch residence times significantly increased as the duration of travel increased (Figure 1). However, no consistent effect of the travel requirement was found. Specifically, when a work requirement was imposed during travel (Parts 2 and 4), mean residence times were not reliably different across subjects from those obtained with no work requirement during travel (Parts 1 and 3; Figure 1), although 3 birds (131, 133, and 135) stayed longer in a patch under higher FR values (Figure 1).

Modeling the Data

A quantitative model for the experimental preparation used here was proposed by McNamara and Houston (1985). They called this situation, "Some patches are empty." Under the assumption that animals would optimize their overall rates of gaining prey items, McNamara and Houston constructed a model to obtain the residence time that demonstrated

this. Because, in the present discussion, we will focus on minimum interreinforcer intervals rather than on overall reinforcer rates, the appropriate equation is:

$$T_i = \frac{\tau + qt + \frac{p}{\lambda}(1 - e^{-\lambda t})}{p(1 - e^{-\lambda t})}, \quad (1)$$

where T_i is the interreinforcer interval that is produced by a residence time of t seconds, τ is the imposed travel time, λ is the probability of prey per second in a prey trial, and p ($= 1 - q$) is the probability of a prey trial.

Kamil *et al.* (in press) showed that this model consistently underpredicted residence times in a variety of situations. Davison and McCarthy (1994) varied p , λ , and τ , and confirmed Kamil *et al.*'s findings. Davison and McCarthy also assessed Mazur and Vaughan's (1987) hyperbolic-delay model and found that although it produced good ordinal predictions, the quantitative predictions were in fact poor. In conclusion, Davison and McCarthy offered a modification of McNamara and Houston's (1985) model, which suggested that residence times may not be accurately controlled by interreinforcer times because of vanishingly small marginal returns around the minimization point. Thus, because of a discrimination failure, the residence time might result from a discrimination threshold in conjunction with the function relating interreinforcer interval to residence time. Specifically, Davison and McCarthy assumed that this temporal threshold was about 1.5 times the value of T_i (from Equation 1), which has the appropriate scalar properties often demonstrated for temporal control (e.g., Gibbon & Church, 1990). Thus, the temporal size of the threshold increases as the residence time increases. Davison and McCarthy assumed that, in the subthreshold area, residence times would be stochastic, and thus that the mean residence time between the points defined above would be an appropriate prediction of residence times. The value of 1.5 for the multiplier, k , produced a reasonably accurate prediction of the obtained residence times, although no fit of this parameter was attempted.

The same "threshold-maximization" model as suggested by Davison and McCarthy (1994) was tested with the present data. In the conditions in which no, or little, work was re-

Fig. 3. Part 4, FR travel. Number of responses emitted per minute as a function of the arranged FR travel requirement.

quired (Parts 1 and 3), we would expect much the same multiplier (k) values as found by Davison and McCarthy. Given that the model assumes a temporal threshold in discrimination, we would expect no effect on k from the addition of a work requirement to a temporal requirement because work should not affect temporal discrimination (except, possibly, as a filled-time vs. empty-time effect). If, on the other hand, the model is better interpreted as a "criterion" model than a "threshold" model, then k would be expected to be a function of the work requirement.

The data from the present experiment were used to determine optimal k values for Parts 1 (FT travel requirement) and 3 (chained FT FR 1 requirement) jointly, and for Parts 2 (FI) and 4 (FR), in Figures 4 and 5. These figures show the residence-time data as a function of the predictions of the threshold (or criterion) interpretation of Equation 1. The FT and chained FT FR 1 residence times (Figure 4) were predicted well by individual-subject k values in the range 1.52 to 1.95, with between 89% and 98% of the variance in the 21 data points accounted for. These k values are reasonably similar to the value of 1.5 reported by Davison and McCarthy (1994).

The residence times in Part 2 (Figure 5) were also well predicted by individual k values ranging from 1.67 to 2.17 (between 98% and 100% of the data variance accounted for). There was no significant difference between the obtained k values between Parts 1 and 3 (conjointly) and Part 2 on a sign test at $\alpha = .05$. On the other hand, although the residence times for 3 subjects (131, 133, and 134) in Part 4 (FR travel; Figure 5) were well predicted with k values between 1.47 and 1.97 (93% to 99% of the variance accounted for), the residence times for Birds 135 and 136 were poorly described. These poor fits were due to residence times for high FR values (not shown in Figure 5) being overpredicted (i.e., the obtained residence times were much shorter than the predicted times). Indeed, the predicted residence times for the greatest FR requirement were both greater than 150 s, the maximum allowed

time in patches in this experiment. Thus, these failures in prediction were, in fact, partly due to the truncation of residence times by the procedure that we used. In order to overcome this problem, the fits for Birds 135 and 136 in the FR travel conditions were reassessed without the data from the highest FR requirement. For Birds 135 and 136, the predictions, and parameter values, from these more limited fits are shown in Figure 5. The predictions were considerably improved, with k values of 2.17 and 2.30, respectively, and percentages of variance accounted for of 100% and 99% (although with only four data points, high percentages would be expected). On a sign test, there was no statistically significant difference between the obtained k values for the FI and FR travel procedures, and no significant difference between the composite FT and FT FR 1 and the FR conditions, at $\alpha = .05$.

This analysis demonstrates two results. First, the threshold-maximization model, as suggested by Davison and McCarthy (1994), can account for the obtained residence times with k parameter values that are consistent across subjects and conditions, and even across experiments and subjects. The model, therefore, is clearly preferable to the simple optimization model suggested by McNamara and Houston (1985). Second, there was again only meager evidence from this analysis that the addition of an explicit work requirement, as an FI or an FR travel requirement, affected the parameter of the model. Researchers have often reported that explicit work requirements do not affect choice (Davison, 1991; Davison, Alsop, & Denison, 1988; Neuringer, 1969). However, the generality of this finding may be influenced by the possibility that the pigeon's peck is probably a very low work requirement.

A further, more tentative, conclusion may be formed. One difference between, on the one hand, FT, or FT FR 1, or FI travel requirements, and FR requirements on the other, is that the former have very little variation from trial to trial, whereas the latter are likely to have more. Because we found no significant difference in k between these conditions, it may

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Fig. 4. Parts 1 and 3, FT and chained FT FR 1 travel requirements. Obtained residence times as a function of residence times predicted by Equation 1 with the k value as shown for each individual subject. The diagonal line shows the locus of perfect prediction, and the percentage of the data variance accounted for by the predictions is also shown for each individual subject.

be that the operation of the threshold-maximization model is independent of variability in travel time. This suggestion, however, requires a more systematic manipulation of travel-time variability to be carried out before it can be accepted.

As Davison and McCarthy (1994) noted, "threshold" models are not supported by modern psychophysical theory, and models couched in terms of the discriminability of various stimuli (temporal durations) are more acceptable. We reiterate here that the fixed-threshold model that we are using should be seen as only an approximation to such a discriminability model, which remains to be developed.

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Fig. 5. Parts 2 and 4, FI and FR travel requirement. Obtained residence times as a function of residence times predicted by Equation 1 with the k value as shown for each individual subject. The diagonal line shows the locus of perfect prediction, and the percentage of the data variance accounted for by the predictions is also shown for each individual subject. For Birds 135 and 136, the model was fitted to only four of the five data points for FR travel, and the k values and fits are indicated with an asterisk. See text for more details. One data point from Birds 135 and 136 fell off the graphs.

APPENDIX

The data for each subject summed over the last five sessions of each condition.

Bird	Condition	Travel requirement	Prey trials	Nonprey trials	Exits by bird	Reinforcers	Exits by clock	Residence time (s)	Responses per travel
131	1	FT 4	219	219	255	179	4	30.83	
	2	FT 8	119	110	90	107	32	72.97	
	3	FT 16	105	133	133	101	4	53.76	
	4	FT 2	253	251	303	200	1	23.93	
	5	FT 12	131	130	130	129	2	55.44	
	6	FT 0.25	161	166	173	144	10	57.32	
	7	FT 8	171	178	188	161	0	39.83	
	8	FT 16	127	125	129	122	1	52.12	
	9	FT 0.25	316	315	431	200	0	17.66	
	10	FT 12	164	142	152	154	0	45.26	
	11	FT 2	300	305	405	200	0	16.25	
	12	FT 4	229	201	230	200	0	29.89	
	13	FI 4	212	220	253	179	0	29.24	1.90
	14	FI 16	110	125	129	105	1	53.39	4.96
	15	FI 2	235	211	246	200	0	26.95	1.45
	16	FI 8	160	190	203	147	0	36.14	3.61
	17	FI 0.25	272	278	350	200	0	23.01	1.00
	18	FI 12	160	130	137	153	0	44.78	3.90
	19	FI 4	233	223	263	193	0	25.11	1.90
	20	FT 8 FR 1	167	180	196	151	0	37.85	
	21	FT 2 FR 1	240	264	316	188	0	22.05	
	22	FT 12 FR 1	148	139	145	142	0	46.25	
	23	FT 0.25 FR 1	239	241	281	199	0	26.01	
	24	FT 16 FR 1	130	126	128	128	0	47.44	
	25	FT 4 FR 1	240	232	283	188	0	25.00	
	26	FR 5	225	211	243	193	0	28.16	5
	27	FR 10	169	161	168	158	1	41.83	10
	28	FR 20	97	100	96	94	4	65.08	20
	29	FR 15	170	151	156	160	1	39.54	15
	30	FT 60	70	60	60	68	1	63.24	
	31	FT 30	92	108	107	90	0	48.36	
	32	FT 8	180	201	220	159	0	32.83	
	33	FR 40	43	43	9	42	32	137.85	40
	34	FT 50 FR 1	71	76	76	67	0	54.18	
133	1	FT 4	203	184	204	174	9	40.32	
	2	FT 8	180	159	180	159	0	42.85	
	3	FT 16	119	124	127	114	2	54.79	
	4	FT 2	293	300	393	199	1	16.66	
	5	FT 12	143	147	161	122	7	44.13	
	6	FT 0.25	324	268	391	200	1	18.06	
	7	FT 8	222	186	244	164	0	29.16	
	8	FT 16	141	159	180	120	0	34.39	
	9	FT 0.25	288	242	338	190	2	23.22	
	10	FT 12	161	163	173	149	2	38.21	
	11	FT 2	233	231	267	197	0	26.89	
	12	FT 4	226	220	247	199	0	30.10	
	13	FI 4	155	169	179	145	0	44.04	1.11
	14	FI 16	88	86	73	87	14	75.68	4.33
	15	FI 2	210	205	230	185	0	32.38	1.14
	16	FI 8	147	142	146	143	0	47.52	1.81
	17	FI 0.25	202	220	240	182	0	33.28	1.00
	18	FI 12	114	120	122	108	4	54.33	4.15
	19	FI 4	176	147	160	163	0	46.05	1.21
	20	FT 8 FR 1	125	113	120	118	0	47.82	
	21	FT 2 FR 1	180	184	195	169	0	39.12	
	22	FT 12 FR 1	114	112	115	110	1	54.19	
	23	FT 0.25 FR 1	191	194	220	165	0	34.33	
	24	FT 16 FR 1	107	104	108	99	1	48.35	

APPENDIX

(Continued)

Bird	Condition	Travel requirement	Prey trials	Nonprey trials	Exits by bird	Reinforcers	Exits by clock	Residence time (s)	Responses per travel
	25	FT 4 FR 1	160	163	173	147	0	36.96	
	26	FR 5	167	159	174	149	2	41.08	5
	27	FR 10	90	76	70	87	7	68.44	10
	28	FR 20	45	56	39	44	17	97.60	20
	29	FR 15	63	52	52	54	8	66.67	15
	30	FT 60	69	62	64	62	5	57.61	
	31	FT 30	99	100	108	86	3	49.73	
	32	FT 8	179	186	212	151	0	35.73	
	33	FR 40	45	26	25	42	4	78.46	15
	34	FT 50 FR 1	67	63	59	67	2	63.39	
134	1	FT 4	234	222	257	199	0	29.17	
	2	FT 8	173	162	174	161	0	42.59	
	3	FT 16	112	108	103	103	14	66.17	
	4	FT 2	223	231	252	200	2	33.02	
	5	FT 12	102	113	96	98	21	73.66	
	6	FT 0.25	239	232	270	196	5	30.49	
	7	FT 8	183	162	176	169	0	40.70	
	8	FT 16	122	118	118	119	3	57.32	
	9	FT 0.25	274	233	306	200	1	21.16	
	10	FT 12	146	125	125	143	3	56.00	
	11	FT 2	239	236	280	195	0	25.63	
	12	FT 4	214	215	244	185	0	28.33	
	13	FI 4	201	192	206	187	0	35.96	2.17
	14	FI 16	106	110	110	105	1	65.87	3.77
	15	FI 2	222	248	285	185	0	28.68	1.21
	16	FI 8	182	179	191	170	0	36.20	3.22
	17	FI 0.25	208	241	266	183	0	30.04	1.00
	18	FI 12	135	124	129	129	1	47.29	4.10
	19	FI 4	197	193	207	182	1	37.91	1.53
	20	FT 8 FR 1	201	132	146	186	1	43.75	
	21	FT 2 FR 1	207	214	235	186	0	31.94	
	22	FT 12 FR 1	116	132	131	115	2	57.32	
	23	FT 0.25 FR 1	225	210	239	196	0	28.32	
	24	FT 16 FR 1	95	99	91	93	8	70.04	
	25	FT 4 FR 1	215	186	207	194	0	31.97	
	26	FR 5	177	175	189	162	0	42.23	5
	27	FR 10	161	166	171	155	0	43.21	10
	28	FR 20	85	66	60	84	6	78.59	20
	29	FR 15	116	107	105	113	2	67.29	15
	30	FT 60	35	54	28	34	24	122.74	
	31	FT 30	96	94	93	91	2	56.87	
	32	FT 8	173	175	189	156	0	39.91	
	33	FR 40	36	30	16	36	13	124.32	40
	34	FT 50 FR 1	57	57	48	57	8	92.25	
135	1	FT 4	146	155	152	133	16	56.21	
	2	FT 8	125	112	94	114	29	74.90	
	3	FT 16	89	125	116	82	16	60.98	
	4	FT 2	188	221	246	160	3	38.03	
	5	FT 12	104	128	118	98	16	64.13	
	6	FT 0.25	277	249	326	200	0	19.85	
	7	FT 8	139	132	129	135	7	60.58	
	8	FT 16	98	114	104	94	14	68.22	
	9	FT 0.25	266	224	289	200	1	24.54	
	10	FT 12	124	137	141	115	5	52.83	
	11	FT 2	207	186	207	182	4	37.78	
	12	FT 4	205	181	201	183	2	39.64	
	13	FI 4	167	180	189	155	3	45.95	3.43

APPENDIX

(Continued)

Bird	Condi- tion	Travel requirement	Prey trials	Nonprey trials	Exits by bird	Rein- forcers	Exits by clock	Residence time (s)	Responses per travel
136	14	FI 16	89	97	89	87	10	80.70	6.20
	15	FI 2	210	203	226	187	0	38.13	1.87
	16	FI 8	175	174	189	160	0	37.55	3.06
	17	FI 0.25	211	179	197	189	4	40.87	1.00
	18	FI 12	115	134	135	113	1	57.84	5.75
	19	FI 4	191	166	174	183	0	42.53	1.96
	20	FT 8 FR 1	163	138	147	154	0	49.41	
	21	FT 2 FR 1	195	207	220	182	0	39.30	
	22	FT 12 FR 1	112	129	133	108	0	57.24	
	23	FT 0.25 FR 1	185	203	223	165	0	39.67	
	24	FT 16 FR 1	81	110	104	81	3	70.95	
	25	FT 4 FR 1	196	171	181	185	0	42.99	
	26	FR 5	173	147	153	162	4	53.00	5
	27	FR 10	137	123	128	130	0	59.86	10
	28	FR 20	58	39	20	58	19	120.60	20
	29	FR 15	49	47	26	49	20	112.65	15
	30	FT 60	64	61	62	60	1	67.45	
	31	FT 30	89	98	97	86	1	59.20	
	32	FT 8	180	155	168	163	0	43.77	
	33	FR 40	2	12	4	2	8	135.32	30
	34	FT 50 FR 1	60	74	74	57	2	57.60	
	1	FT 4	206	216	242	180	0	34.08	
	2	FT 8	152	177	186	141	2	43.26	
	3	FT 16	106	127	131	101	1	56.20	
	4	FT 2	229	205	234	200	0	26.80	
	5	FT 12	144	136	142	138	0	51.05	
	6	FT 0.25	270	251	324	197	0	24.51	
	7	FT 8	183	174	183	174	0	38.60	
	8	FT 16	130	132	135	125	2	48.86	
	9	FT 0.25	228	247	285	189	1	28.00	
	10	FT 12	153	138	145	145	1	46.56	
	11	FT 2	278	270	349	199	0	18.36	
	12	FT 4	234	221	255	200	0	25.14	
	13	FI 4	183	218	239	162	0	33.65	1.89
	14	FI 16	131	119	121	127	2	52.90	5.27
	15	FI 2	211	249	282	177	1	28.27	1.05
	16	FI 8	155	180	193	142	0	38.61	3.33
	17	FI 0.25	225	210	235	200	0	28.37	1.00
	18	FI 12	138	138	144	132	0	48.25	3.41
	19	FI 4	181	201	227	155	0	35.17	1.84
	20	FT 8 FR 1	167	163	171	159	0	40.63	
	21	FT 2 FR 1	228	197	225	200	0	29.95	
	22	FT 12 FR 1	149	140	145	144	0	46.78	
	23	FT 0.25 FR 1	253	269	331	191	0	23.42	
	24	FT 16 FR 1	107	113	113	104	1	61.32	
	25	FT 4 FR 1	203	201	221	181	1	31.94	
	26	FR 5	184	189	206	166	0	38.87	5
	27	FR 10	110	142	138	107	5	57.58	10
	28	FR 20	70	82	56	70	24	93.76	20
	29	FR 15	124	111	108	120	4	63.66	15
	30	FT 60	51	46	18	49	27	134.52	
	31	FT 30	81	71	60	80	9	94.48	
	32	FT 8	188	186	197	173	0	35.73	
	33	FR 40	25	21	1	25	19	147.58	40
	34	FT 50 FR 1	51	53	33	47	22	101.39	