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Timing and Foraging: Gibbon's Scalar Expectancy Theory and Optimal Patch Exploitation

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We present a study that links optimal foraging theory (OFT) to behavioral timing. OFT's distinguishing feature is the use of models that compute the most advantageous behavior for a particular foraging problem and compare the optimal solution to empirical data with little reference to psychological processes. The study of behavioral timing, in contrast, emphasizes performance in relation to time, most often without strategic or functional considerations. In three experiments, reinforcer-maximizing behavior and timing performance are identified and related to each other. In all three experiments starlings work in a setting that simulates food patches separated by a flying distance between the two perches. The patches contain a variable and unpredictable number of reinforcers and deplete suddenly without signal. Before depletion, patches deliver food at fixed intervals (FI). Our main dependent variables are the times of occurrence of three behaviors: the ''peak'' in pecking rate (Peak), the time of the last peck before ''giving in'' (GIT), and the time for ''moving on'' to a new patch (MOT). We manipulate travel requirement (Experiment 1), level of deprivation and FI (Experiment 2), and size of reinforcers (Experiment 3). For OFT, Peak should equal the FI in all conditions while GIT and MOT should just exceed it. Behavioral timing and Scalar Expectancy Theory (SET) in particular predict a Peak at around the FI and a longer (unspecified) GIT, and make no prediction for MOT. We found that Peak was close to the FI and GIT was approximately 1.5 times longer, neither being affected by travel, hunger, or reinforcer size manipulations. MOT varied between 1.5 and just over 3 times the FI, was responsive to both travel time and the FI, and did not change when the reinforcer rate was manipulated. These results support the practice of producing models that explicitly separate information available to the subject from strategic use of this information.

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John Gibbon's approach to the study of timing was cognitive and representational: Since his seminal article on scalar timing (Gibbon, 1977) and consistently in subsequent contributions (Gibbon, 1991, 1995; Gibbon & Church, 1984, 1990; Gibbon, Church, Fairhurst, & Kacelnik, 1988; Gibbon, Church, & Meck, 1984), he showed no shyness for following time intervals from the real world into the organism's memory and from there into its decision system and then back out into behavior.

Gibbon's reliance on cognitive constructs such as ''reference memory'' or ''decision system'' contrasts with that of most behavioral ecologists or behavior analysts, who predict behavior either by identifying ecological problems and hypothesizing about the relative advantage of behavioral strategies or by generalizing input–output relations, steering clear of explicit reference to cognitive variables. Since cognitive variables are not directly accessible to observation and measurement, the issue is not their ontological status (does the decision system exist?) but the heuristic benefit of including cognition explicitly in theoretical models. Gibbon clearly was in favor of such inclusion.

Despite our roots in behavioral ecology, we have been won over by Gibbon's approach. It seems to us that, given that ecologically relevant problems do not exist a priori but are created by the animals themselves through their interaction with the ecological setting, cognitive properties, rather than being treated as constraints, are best included in the specification of the problem to be solved. For this notion to be useful, it should be possible to investigate the information a subject possesses separately from how it affects its preferences.

Here we present a set of three experiments aimed at illustrating the distinction between knowledge and decisions with reference to time in foraging problems. The experiments were run under the influence of John Gibbon himself, and, were it not for our reluctance to make him responsible for our interpretation of the outcome, he certainly would be a coauthor. We recognize some limitations in the database: Practical reasons limited the number of subjects and hence the power of some statistical conclusions. The main message we aim to convey, that of a difference between the information the organism has about a problem and its foraging strategy, is—we believe—unaffected by this weakness.

We focus on the classic Optimal Foraging Theory (OFT) problem of a consumer that benefits by maximizing overall feeding rate in an environment where food is distributed in patches (Stephens & Krebs, 1986). Patches are separated by random travel distances and have stochastic properties that are assumed to be fully known to the subject. Typically, patches ''deplete'' within each visit; namely they drop in their potential for yielding reinforcers. The optimality backdrop is given by a model derived from normative economics, the Marginal Value Theorem (MVT; Charnov, 1976b; Samuelson, 1937). This theorem shows that the rate-maximizing strategy is to leave patches when the reinforcer potential of the current patch falls below that expected as an average after departure, taking into account the environment as a whole including typical travel costs.

Here we concentrate on what the forager may infer about patch potential given its ability to measure elapsing time intervals and how these hypothetical inferences translate into the foraging decision of migrating to a new patch. Foraging researchers normally examine the patch ‘‘residence time,’’ i.e., total time between arrival and departure from a patch or the ‘‘giving up time’’ (GUT), namely the time elapsed between the last prey capture and patch departure. We separate three dependent variables by examining the accuracy of the birds’ knowledge about the time of occurrence of reinforcers (through their behavioral production of this time), the point when they cease attempting to obtain food and finally the point at which they start traveling to a new patch (Brunner, Kacelnik, & Gibbon, 1992). Our aim is to find the extent to which changing conditions may modify the timing of patch departure independently of the subject’s ability to locate the time of a reinforcer.

GENERAL METHODS

General Procedure

Starlings (*Sturnus vulgaris*) were used in the laboratory in individual cages that served as both home cages and experimental chambers. Each cage (L × W × H = 120 × 50 × 60 cm) had two perches (1 m apart) with cue lights and a centrally located panel with a pecking key and a food dispenser (see details in Brunner *et al.*, 1992). This panel was located on the floor of the cage. The feeder and key were side to side, with the latter being 2.5 cm off the floor. Drinking water was available at all times. A SPIDER system running in a BBC Master Series computer controlled the schedules and stored the data. Starter turkey crumbs were used as reinforcer. Experimental sessions lasted an unlimited number of cycles, and subjects received all their food within these sessions (except in Experiment 1, in which there was a maximum of 120 cycles and subjects received a food supplement at the end of the day). Each cycle consisted of a ‘‘travel’’ component and a ‘‘patch’’ component (Fig. 1), named because they emulate the foraging problem described above. We refer to the patch component of each cycle as a patch visit.

Travel

Travel consisted of a number of flights between the two perches. Landing on a perch during travel had two effects: to render that perch inoperative, switching off its cue light; and to turn the opposite perch operative, turning the corresponding cue light on. Once the required number of flights was completed, both perches became inoperative and the patch component started.

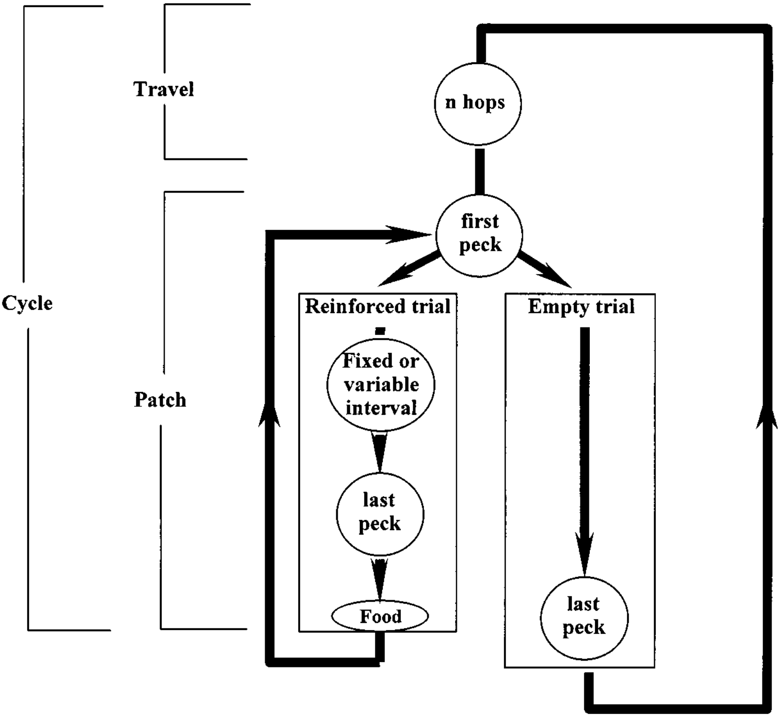

FIG. 1. Flow diagram showing the experimental schedule. Birds must hop on a perch *n* times to enable the patch component. A first peck to a key initiates a chain of trials which can be either reinforced or not. In reinforced trials, the first peck after a fixed interval (FI) elapses is reinforced with access to a hopper. In unreinforced trials, the patch component is terminated and the travel component initiated when the bird hops on a perch.

Patch

The patch component started when the key light in the panel switched on, at the completion of travel. Patches consisted of a variable number of trials (one to five), the last of which was always unreinforced (Fig. 2). The distribution of patches of different number of trials followed an approximation to a truncated geometric distribution, programmed over a pseudorandomized listing of 60 patches of which 30 had one trial and were, therefore, unreinforced; 15 had two trials (one of them reinforced); 8 had three trials (two reinforced); 4 had four trials (three reinforced); and 2 had five (four reinforced). This pattern resulted in an almost constant probability of one-half that a trial being initiated would be reinforced, independently of the number of reinforced trials already experienced in the patch (the fifth trial was predictably unreinforced, but this event occurred very infrequently, as described above).

In both reinforced and unreinforced trials, the key light changed color with

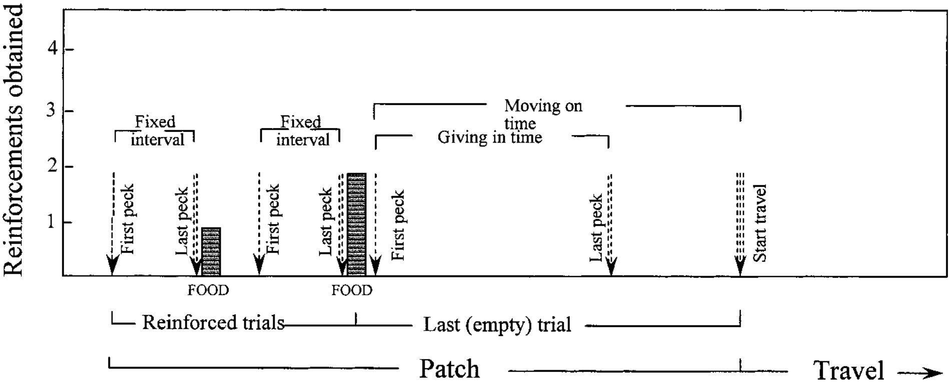

FIG. 2. Chart depicting the different dependent measures. During unreinforced trials, the pecking is recorded until a first hop on the perch occurs (start of travel). Birds earn reinforcements until a reinforced trial is programmed.

the first peck. In reinforced trials, this also started a timer that set reinforcement after a fixed interval (FI). Birds collected reinforcers with the first peck emitted after the FI had elapsed. The key light was off during reinforcement and travel. In unreinforced trials, the key light remained on until the patch was abandoned by starting travel landing on a perch at any moment of the patch component.

General Method and Data Recording

In unreinforced trials, we measured (a) pecking rate in time bins of a fifth of the FI, (b) the time between the first and the last peck (the giving in time, or GIT), and (c) the time between the first peck and the first perch landing (the moving on time, or MOT) (Fig. 2). Both GIT and MOT are equivalent to what is known in patch models as the giving up time, or GUT, the time it takes to abandon the search within a patch to move elsewhere (Brunner *et al.*, 1992; Kacelnik, 1984; Kacelnik & Todd, 1992; Stephens & Krebs, 1986).

Data Analysis

Otherwise stated, data from the first 60 cycles of each of the last 5 days of each condition were included in the analyses. The subject’s time of maximal expectancy of reinforcement was inferred from the point (Peak) at which pecking rate peaked while waiting for a reinforcer. To calculate this point, in each unreinforced trial we identified the time bins in which responding was maximum for that trial. In trials where response rate was maximal in more than one bin (about 25% of the trials) we took the mean of these high rate bins as the peak time for that particular trial. We then averaged the Peak time across trials.

For GIT and MOT we removed outliers from individual distributions by an iterative method (Brunner *et al.*, 1992; Roberts, 1981). For statistics, otherwise stated, we used medians for each of the last 5 days of each treatment and treated them as five within-individual replicates. For the analyses of variance (ANOVAs), subject was a random factor and all others were fixed. In Experiment 2, the FI was a nested factor.

EXPERIMENT 1: THE EFFECT OF TRAVEL

In this experiment, we examine behavior as a function of changes in travel cost. Travel cost (in our experiment travel ratio) is the most common independent variable in tests of the MVT. (For a recent review see Nonacs, 2001.) Typically, subjects are studied while foraging in a patchy environment, and their patch-leaving behavior is compared across treatments that differ in the time or distance between patches. In contrast to our procedure, in most experiments each patch is programmed so that the interprey interval (or instantaneous probability of capture) starts at some given value for each patch visit and increases (in the case of probability of capture decreases) gradually as the subject exploits the patch. In the MVT analysis, time in each patch competes with time spent elsewhere, and if the environment is made poorer by an increase in travel costs, then the degree of patch exploitation that should be tolerated before departure should increase, and hence patch time should increase even if patches themselves are unmodified.

Because the MVT identifies the optimal (rate-maximizing) policy but does not specify the mechanisms for achieving it, various suggestions have been made for rules that animals may follow to achieve this policy. Direct measurement and comparison of instantaneous rates in the patch and in the environment are excluded as discrete events (prey and patch encounters) make continuous measurement of rates impossible. However, consumers may eschew the assessment of instantaneous rate and simply follow a rule of fixing the time of patch residence or the GUT, adjusting it until the resulting overall reinforcer rate is maximized (McNamara & Houston, 1985). Alternatively, they may use one or more consecutive intercapture intervals to infer instantaneous local rate and compare these estimates against a weighted moving average of overall rate (Ollason, 1980). In our setting, however, the subject is forced to use interval timing, and this makes it easier to evidence time perception and decision criteria.

Given that patches deplete suddenly after an unpredictable number of trials, the unconstrained rate maximizing policy is to leave each patch when the waiting time for a reinforcer precisely exceeds the FI, independently of travel costs. This rule can only be realistic if a subject has error-free time perception. If, instead, the ability to measure time follows Weber's Law (according to which the just noticeable time difference is proportional to the FI) then the giving up time (GUT) should increase linearly with the FI. Brunner *et al.* (1992) have shown through experiment a linear relationship between GUT and FI. Weber's Law, however, makes no prediction about the effect of travel costs. If we now include the fact that the subject's certainty that the FI has elapsed does not follow a step function but increases gradually as time elapses (according to SET, subjective certainty of reaching the end of an interval approximates the cumulative normal distribution centered on the FI, with standard deviation proportional to the FI), then a more complex effect of travel time can be expected (Fig. 3). Under this circumstance, because the reinforcer potential of a patch is the product of its undepleted potential times the subjective certainty that the FI has not elapsed, and certainty decreases gradually, then the effect is similar to gradual depletion and increasing travel costs should lead to increased patch times (Brunner *et al.*, 1992; Kacelnik, Brunner, & Gibbon, 1990). The subject should stay longer in a patch when environmental rate drops, even when the temporal properties of the patch and the subject's expectancy for the reinforcement time are unaffected.

In this experiment, we can examine the accuracy of the birds' temporal

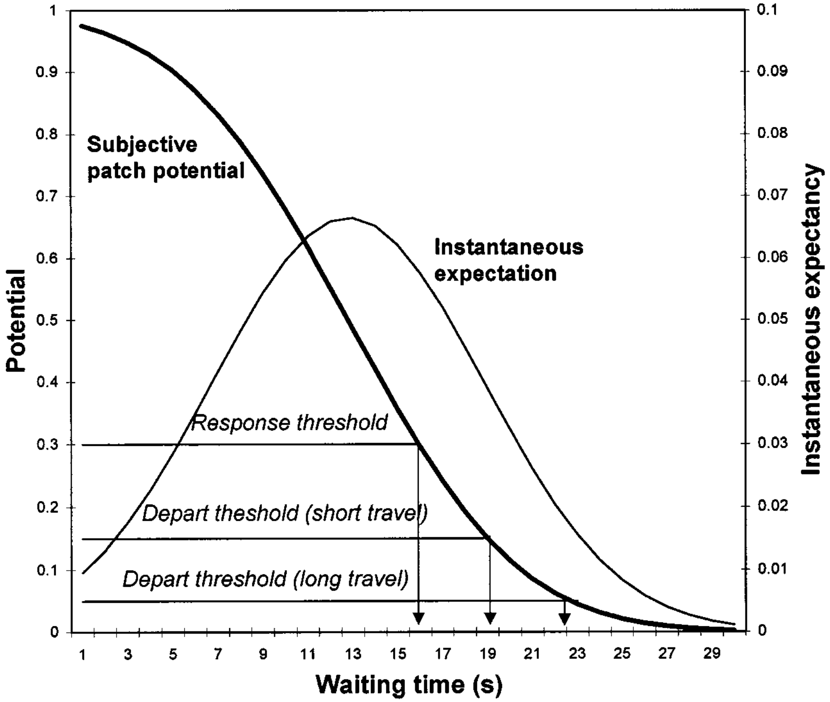

FIG. 3. A model of memory and decision processes. The reinforcement time in reference memory is assumed to be a Gaussian function centered around the FI with standard deviation proportional to the FI. The inverse cumulative function represents the probability that the current trial is reinforced. As time elapses and the probability of reinforcement diminishes, a response threshold is crossed and the subject stops responding. A different threshold governs results in a departure to a new patch (by the initiation of a new travel).

expectation of reinforcers by exploiting the similarity of our within-patch component to the ''peak procedure'' (Catania, 1970; Church, 1984; Roberts, 1981), and at the same time we can investigate the problem in the frame of the MVT by examining two measures of GUT: the end of any attempt to collect a reinforcer (the GIT) and the time at which the subject starts traveling toward a new patch (the MOT). Given the ''lost opportunity'' logic of the MVT, these last two measures should in fact coincide because a rate-maximizing agent would not stay in any patch when its reinforcer potential is nil, as it clearly should be when the bird ceases to respond.

Method

Four starlings experienced with the experimental schedule were kept in a 15L : 9D cycle and retrained with an FI of 12.8 s. At the beginning of each trial, a white key light was switched on, which turned to green after the first peck.

Each bird experienced three conditions depending on travel requirements: 10, 20, or 40 flights in a balanced order between subjects. Treatments lasted for at least 17 days and ended, for each animal, when the travel times and giving in times did not show a trend for 5 consecutive days, as judged by eye. Between conditions, birds had food *ad libitum* for 2 consecutive days.

Results

The timing of reinforcers. The acuity of the birds' timing of reinforcers is expressed in two behavioral measures, the average pecking rate at various times into the trial (number of responses per bin averaged for each subject and then over subjects) and the distribution of the temporal location of the peaks across trials or temporal distribution of peak times (Figs. 4 and 5).

ANOVA on both of these measures did not reveal a tendency for expected interprey interval to increase with longer travel costs. In fact, the observed trend (nonsignificant overall [$F(2, 6) = 4.2$, $P < .071$] but significant for three of the four subjects [$F(2, 48) = 6.0$, $P < .005$; $F(2, 48) = 15.3$, $P < .001$; $F(2, 48) = 14.8$, $P < .001$]) is in the opposite direction: Response rate peaked slightly earlier as travel time increased. This suggests that the birds do not simply respond to a molar measure of reinforcer rate but that they possess precise information about the interprey interval.

The giving in time. The time at which subjects make their last attempt to collect a reinforcer is shown in Fig. 6. An ANOVA showed no discernible effect of travel cost on this variable. As for the previous measure, the implication is that changing travel costs does not modify the information available to the subjects about the temporal properties of the patch.

The moving on time. Figure 7 shows the distribution of times at which subjects initiated travel. As travel times increase, MOT distribution tends to shift to the right and flatten [$F(2, 6) = 3.4$, $P < .1$]. The change was reliable for three subjects and marginal for the fourth [$F(2, 48) = 3.1$, $P < .055$;

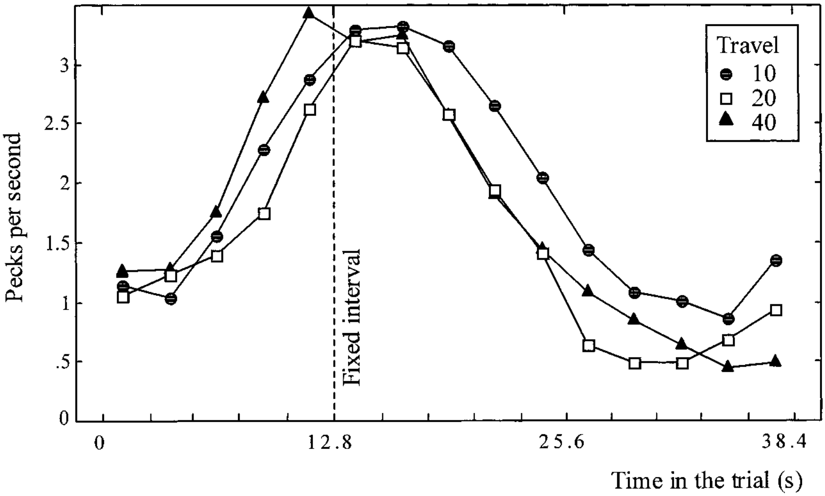

FIG. 4. Experiment 1: Average response rate for three different travel requirements (10, 20, and 40 hops). The vertical dashed line shows the time of reinforcement (FI = 12.8 s).

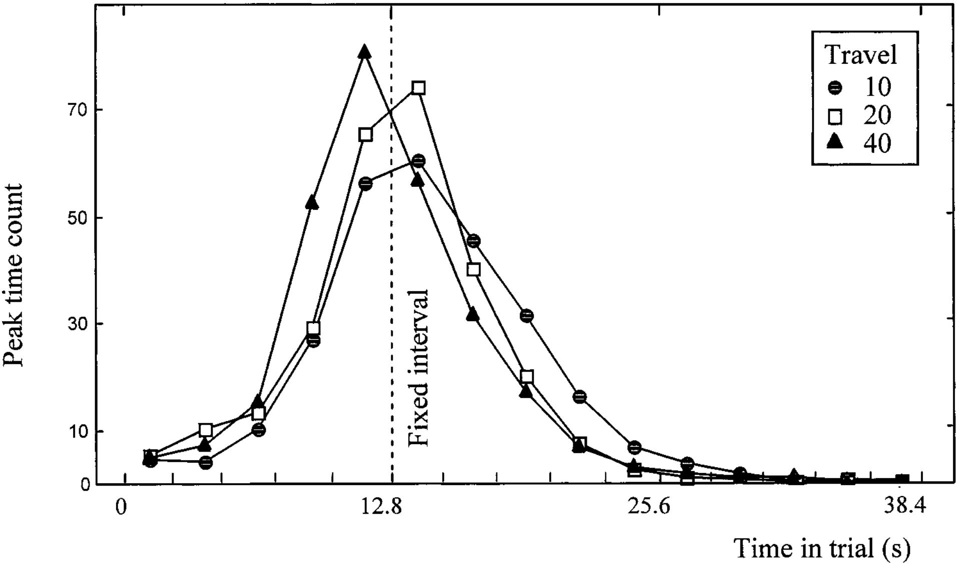

FIG. 5. Experiment 1: Average distribution of peak times (time of the maximal response rate) for three different travel requirements (10, 20, and 40 hops). The vertical dashed line shows the time of reinforcement (FI = 12.8 s).

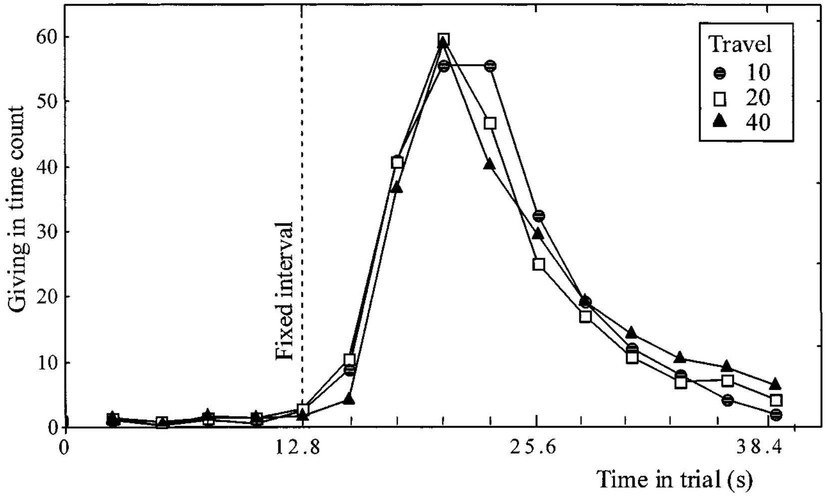

FIG. 6. Experiment 1: Average distribution of giving in times (GIT) for three different travel requirements (10, 20, and 40 hops). The vertical dashed line shows the time of reinforcement (FI = 12.8 s).

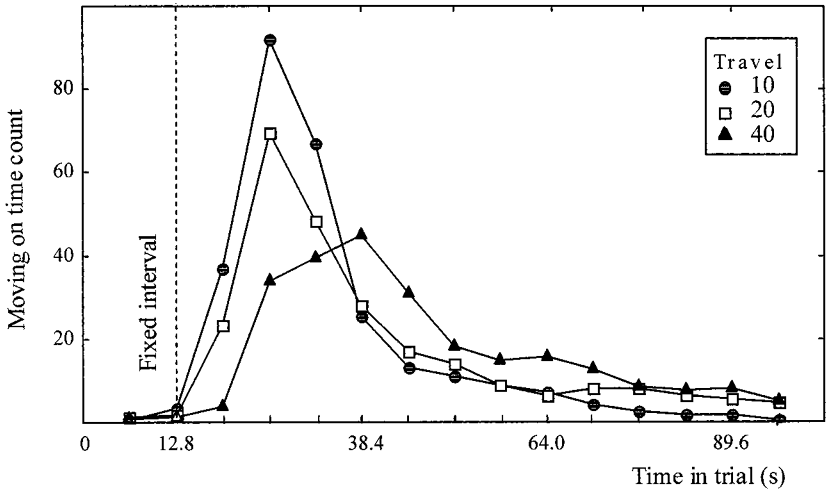

FIG. 7. Experiment 1: Average distribution of moving on times (MOT) for three different travel requirements (10, 20, and 40 hops). The vertical dashed line shows the time of reinforcement (FI = 12.8 s).

$F(2, 48) = 4.3$, $P < .02$; $F(2, 48) = 7.9$, $P < .002$; $F(2, 48) = 34.4$, $P < .001$].

Discussion

The overall results of Experiment 1 are summarized in Figs. 8A and 9A. They show that starlings do adjust total patch times to travel costs as predicted by the MVT, namely they stay longer in patches when the environment becomes poorer because interpatch travel cost increases. Further, longer patch residence times are not mediated through a nonspecific perception of reduced reinforcer rate. (The data do, however, have features that contradict the rate maximizing interpretation, as we discuss below.)

We present a theoretical interpretation of our results in Fig. 3. Following SET, we envisage the subject's instantaneous expectation of reinforcer as a Gaussian probability density function centered on the value of the interreinforcer interval. The standard deviation of this function should increase proportionally to the FI, but this parameter is invariable in this experiment. The subject's assessment of the probability that the patch still has reinforcer potential equals the complement of the cumulative normal distribution. In this scenario, the subject stops attempting to extract reinforcers (it gives in) when its assessment of patch potential drops below some value (perhaps related to the cost of responding). The start of flying toward a new patch (the moving on time) occurs when the assessed potential drops below the expected payoff in the rest of the environment, and this depends on travel costs. The longer the travel to future patches, the lower the benefit of moving on and hence the greater the drop in potential tolerated before flying away. MOT must always exceed GIT (because it contains it), but no rate-maximizing interpretation can account for anything but the briefest difference between them. In particular, no rate-maximizing interpretation can explain why GIT should be insensitive to travel cost while MOT increases with it.

The effect, however, can be incorporated into a psychological description: The decision to start flying appears to be under the control of the contrast between local expectation and the immediately following event (in this case between the reinforcer expectation as a function of time elapsed without a reinforcer in this patch and the cost of the next travel), while the decisions about responding appear to be controlled by the properties of the present patch alone. The gap between GIT and MOT is thus related to the latency to start responding in FI schedules (Wynne & Staddon, 1988) but it differs from a postreinforcement pause because it is not triggered by a reinforcer but rather by the absence of one at the expected time.

EXPERIMENT 2: THE EFFECT OF HUNGER AND INTERREINFORCER INTERVAL

We interpreted the results of Experiment 1 by arguing that the location of the responding peak and the GIT depend entirely on properties of the

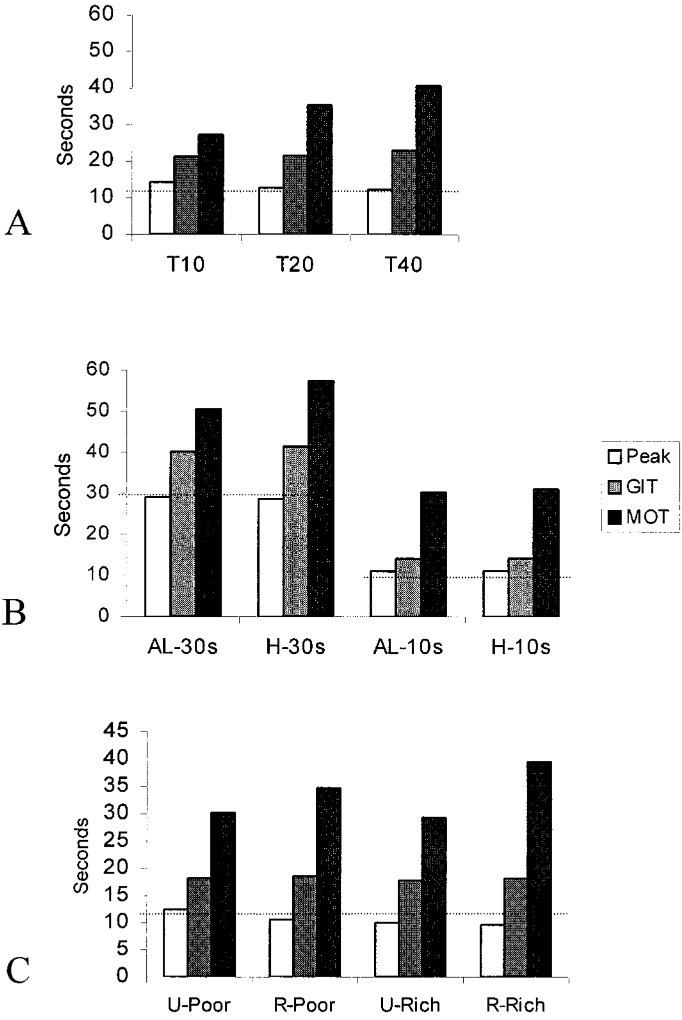

FIG. 8. Experiments 1–3: Average peak time (Peak), giving in time (GIT), and moving on time (MOT) for the three different experiments. (A) Experiment 1: three different travel requirements (T10, T20, and T40). The horizontal line shows the time of reinforcement (FI = 12.8 s). (B) Experiment 2: four different types of trials, *ad libitum* days for those subjects under an FI30 (AL-30 s), hungry days for those subjects under an FI30 (H-30 s), *ad libitum* days for those subjects under an FI10 (AL-10 s), and hungry days for those subjects under an FI10 (H-10 s). The horizontal line shows the time of reinforcement (FI = 10 or 30 s). (C) Experiment 3: four types of trials, patches with no reinforcement and short feeder access (U-Poor), patches with at least one reinforcement and short feeder access (R-Poor), patches with no reinforcement and long feeder access (U-Rich), and patches with at least one reinforcement and long feeder access (R-Rich). The horizontal line shows the time of reinforcement (FI = 12.8 s).

patch, while the MOT is sensitive to the contrast between these and the properties of the environment, a joint function of patch and travel parameters. However, it remains possible to explore if MOT is in fact sensitive to molar properties of the environment; for instance, those mediated through hunger level, which could be higher for longer travel costs. Here we test additional transformations of the foraging scenario to investigate this possibility.

We explore two dimensions that affect hunger in different forms. On one hand, we vary the length of presession deprivation, and, on the other, we vary the interval between reinforcers (trial length). If the increase in hunger at large travel ratios were responsible for the longer MOT observed in Experiment 1, then MOT should also increase with increased food deprivation and longer interreinforcer intervals. If, instead, the SET account is valid, then extra session motivational factors such as longer deprivation should produce no change in temporal foraging parameters, while MOT should increase with greater contrast between patch food density and the environmental rate. If patches are made richer by reducing interreinforcer interval while travel costs are constant, the subject should be less hungry but the contrast between patch potential and the expected payoff of leaving is greater and the subject should be more reluctant to leave the patch; MOT should increase as interreinforcer interval decreases, the opposite of the relation between a putative effect of hunger and MOT found in Experiment 1.

Method

Six starlings experienced with the experimental schedule were kept in a 13L : 11D cycle and retrained to a travel cost of 20 flights. During pretraining all trials started with a yellow light, which turned to green after the first peck. Cumulative individual intake as a function of time of day was recorded for 8 days before the start of the experiment. The experimental schedule was active during the first 12 h of the light period, except on ‘‘normal short days,’’ as explained below.

FIs were set at 10 s for three birds and at 30 s for the other three and remained at those values for the 41 days of the experiment. Data for each individual were recorded on five pairs, or replicates, of ‘‘normal’’ and ‘‘hungry’’ days. On normal days 21, 25, 30, 35, and 40, the experimental session ended after 7.5 h, instead of the normal 12 h, and birds were food deprived for the rest of the day. This period was long enough for all birds to complete 60 cycles, during which ‘‘normal day’’ data were recorded but resulted in the birds being more food deprived the following day. The first 60 cycles on ‘‘hungry days’’ 22, 26, 31, 36, and 41 were used as the ‘‘hungry’’ data set.

Results

The results of this experiment are shown in Fig. 8B. Response peaks do again occur very precisely around the value of the FI, and GIT increases with the FI [$F(1, 4) = 1495.0$, $P < .0001$], maintaining a constant ratio with the value of the FI for the four conditions (Fig. 9B). This value is not far from 50% longer than the FI. MOT is not affected by previous deprivation, but it changes with shorter interreinforcer interval: It shortens marginally in absolute terms [$F(1, 4) = 4.863$, $P < .09$] but almost doubles in relative length as the patch reinforcer density increases.

Discussion

Peak times and GIT in this experiment provide additional evidence that subjects possess accurate information of the temporal properties about the patches, that this information is not distorted by hunger, and that they appear to modify their foraging strategy as a function of local conditions. The use of two values of FI shows that GITs are an approximately constant multiple of the interval and not a constant absolute time after the peak, a feature characteristic of SET that showed in experiment 1 (Fig. 9A) and that we have reported elsewhere (Brunner *et al.*, 1992). Regarding the MOT, the subjects stay longer in absolute terms (compatible with hunger interpretations) but shorter in relative terms when interreinforcer interval increases: MOT was below twice the FI for 30 s and above thrice the FI for 10 s (Fig. 9B).

EXPERIMENT 3: THE EFFECT OF PATCH TYPE IN A HETEROGENEOUS ENVIRONMENT

In Experiments 1 and 2, all comparisons were between homogeneous environments. Here we introduce a between-patch, within-environment manipulation. We use an environment made of a mixture of two equally frequent types of patch, ‘‘rich’’ and ‘‘poor,’’ with almost identical temporal properties but delivering different reinforcer sizes. Patch type (i.e., reinforcer size) is signaled by a cue so that it can in principle be identified on arrival. This sort of mixture has been used in the foraging literature to discuss the problem of patch selection: If travel time is sufficiently small, it may pay for a consumer to abandon all poor patches on identification, specializing on rich patches alone. Although a specialist consumer pays twice as much travel cost per patch exploited, it spends the majority of its time in rich patches, and this may lead to higher overall payoff (Charnov, 1976a). We programmed our protocol so that travel costs were well above the limit at which specializing would pay, as the purpose of this study was to investigate patch departure and not patch selection.

The rationale is as follows. Because rich and poor patches have equal temporal properties but different reinforcer size, certainty of nondepletion is identical for a given waiting time, but the reinforcer potential may differ because it now depends on the kind of patch: a subject leaving a rich patch will, after paying the travel cost, encounter a poor or rich patch with equal probability, and hence on average should expect to lose in patch quality,

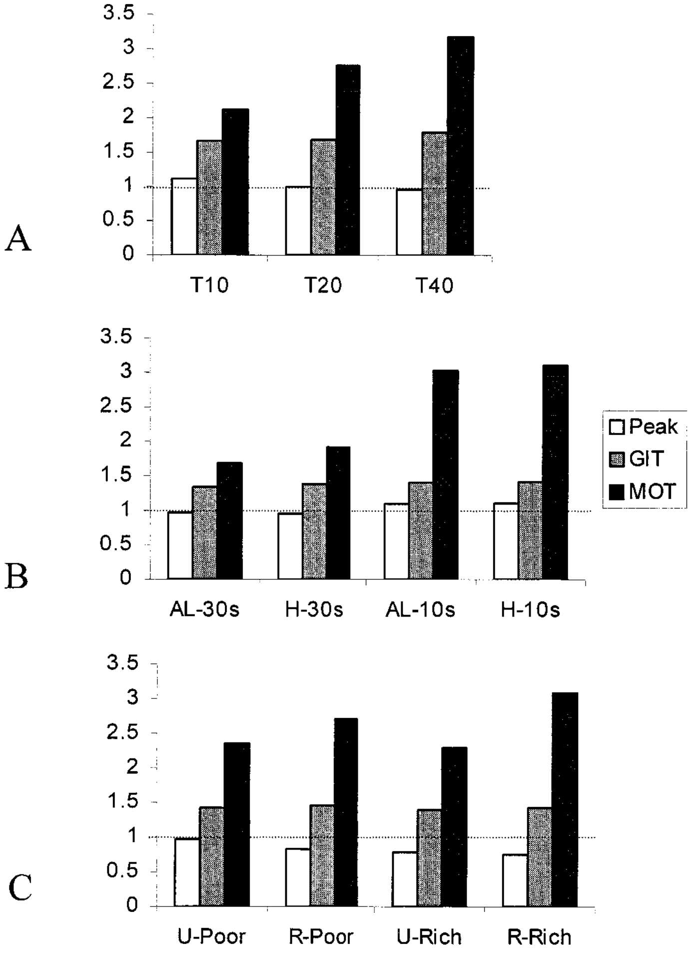

FIG. 9. Experiments 1–3: Average peak time (Peak), giving in time (GIT), and moving on time (MOT) in relative time (divided by the corresponding FI) for the three different experiments. (A) Experiment 1: three different travel requirements (T10, T20, and T40). (B) Experiment 2: four different types of trials, *ad libitum* days for those subjects under an FI30 (AL-30 s), hungry days for those subjects under an FI30 (H-30 s), *ad libitum* days for those subjects under an FI10 (AL-10 s), and hungry days for those subjects under an FI10 (H-10 s). (C) Experiment 3: four types of trials, patches with no reinforcement and short feeder access (U-Poor), patches with at least one reinforcement and short feeder access (R-Poor), patches with no reinforcement and long feeder access (U-Rich), and patches with at least one reinforcement and long feeder access (R-Rich). The horizontal lines show the time of reinforcement in relative time (FI = 1).

while the opposite is true for someone in a poor patch. Although the expected payoff for departing animals in both patch types is identical (as they cannot predict what they will find), for a given chance of depletion having occurred, the relative value of present patch relative to the future is greater in a rich than in a poor patch. The MVT thus predicts that this manipulation should lead to greater conservatism in rich than in poor patches. Based on our previous results, we expected that Peak and GIT should not vary because the temporal properties are unchanged, but MOT should be longer in rich patches [although taxi drivers have been found to do the exact opposite! (Camerer *et al.*, 1997)].

Method

Five naïve starlings, kept at a 12L : 12D cycle, were trained by autoshaping to collect food from the magazine and to peck at the panel key. The schedule was active for the first 10 h of each day. A travel cost of 20 flights and a FI of 12.8 s were maintained throughout the experiment.

Trials were initiated with a white key light, which turned to either red or green with the first peck. The colors signaled which patch kind (rich or poor) had been encountered and were counterbalanced across subjects. In rich patches, reinforcement (access to the food hopper) lasted for 9 s, and, in poor patches, it lasted 2 s. Patches were self-consistent across trials, so that a bird that arrived at a new patch and saw the white key become a red one could have anticipated that any future reinforcers in that patch would be large (assuming red was associated with rich for that particular bird). The experiment lasted for at least 10 days and ended, for each animal, when the giving in times showed no trend for 5 consecutive days, as judged by eye.

Results

The rationale of this experiment implies that subjects learn that each patch is self-consistent in reinforcer size and that they identify patch type using the colored cue. In analyzing the results, we consider, however, the possibility that subjects do discriminate patch type but need at least one reinforcer to do so. To handle this, we separated the analysis of patches in which at least one reinforcer had been obtained from those in which no reinforcer was available (one trial patches). The results for Peak, GIT, and MOT are shown in Fig. 8C.

Peak times. Peak times were slightly shorter in rich than in poor patches [$F(1, 4) = 7.932$, $P = .048$], but there was no reliable effect of whether a reinforcer had been obtained. This indicates that the subjects did discriminate between the two patch types on the basis of the cue light.

Giving in times. Neither patch type nor presence of at least one reinforcer had any discernible effect on GIT. This result is consistent with the observation in Experiments 1 and 2 that this behavioral measure seems resistant with respect to anything but the temporal properties of the patch.

Moving on times. Here the effects were qualitatively the opposite of those for peak times: Reinforcer size as a main effect did not have a significant effect on MOT, but the experience of at least one reinforcer increased MOT with marginal statistical reliability [$F(1, 4) = 5.64$, $P = .076$], and the interaction between experience of reinforcer and reinforcer size was also close to significance [$F(1, 4) = 6.79$, $P < .06$].

Discussion

In this experiment the travel costs and the interval to reinforcement were kept constant, but the value of the reinforcers varied. The birds seemed to learn that each patch had a characteristic reinforcer size and to identify this from the color of the key. Larger reinforcers caused a slight shortening of the time to peak in response rate, no significant change in the time of cessation of responding (GIT), and a marginally reliable increase in MOT.

CONCLUSIONS

We used a reinforcement schedule that incorporates some features from the study of behavioral timing and others from optimal foraging theory. From the latter, we took the focus on the notion of a foraging strategy and the general structure of the environment, where a consumer faces a resource of diminishing value and decides between investing a cost (travel) in renewal or continuing to exploit the same source (Charnov, 1976b). From research in behavioral timing, we took the basics of the peak procedure, a task in which subjects reproduce a time interval behaviorally, thus offering insights into what they ‘‘know’’ about the environment (Brunner *et al.*, 1997).

We transformed the environment in three experiments in terms of various parameters (travel cost, interreinforcer interval, level of deprivation, and typical reinforcer size of each patch), and we can summarize the results as follows: The subjects acquire a precise notion of the time at which reinforcers are due, as shown by the peak in response rate and the time of cessation of responding, or giving in time. The peak time shows some sensitivity to conditions other than the interval to food: They tend to shorten as travel between patches increases (Experiment 1: Figs. 5 and 8A) and as reinforcer size increases (Experiment 3: Fig. 8C). Giving in time, the time at which subjects cease to work for food in each patch, was insensitive to all our manipulations, tending to settle around 1.5 times the interfood interval (Fig. 9). This value is similar to the patch abandonment time (giving up time) found by Davies in flycatchers in the wild and to the values found by Brunner *et al.* (1992; Davies, 1977) with starlings in the laboratory. The fact that GUT is a relatively stable multiple of interprey interval is strongly suggestive of a multiplicative decision system, as implied in most versions of Scalar Expectancy Theory (Gibbon & Fairhurst, 1994). Although there is some evidence that the peak times are also ruled by a multiplicative process, as both the mean and the standard deviation of the peak times increase proportionally to the reinforcement interval (Brunner *et al.,* 1992), the present article shows that factors other than timing influence peak time. Finally, the time at which the birds left each patch to fly toward a new one (MOT) increased with travel costs (Experiment 1: Figs. 7, 8A, and 9A), increased in absolute terms but dropped in relative terms with the interprey interval (Experiment 2: Figs. 8B and 9B) and tended to increase with expected reinforcer size (Figs. 8C and 9C).

These trends are consistent with postulating that Peak and GIT are under the control of the properties of the present patch while MOT is under the influence of both the present patch and the forthcoming events. There is no single framework that stands on its own. A pure account in terms of rate maximization fails to account for several aspects of the data, of which the most fundamental is that the birds show a long gap between giving in at one patch and moving to the next. In terms of OFT, this is a self-inflicted loss of foraging opportunity. Accounts in terms of timing theories such as SET (to which we referred in detail) or the Behavioral Theory of Timing (Killeen & Fetterman, 1984), in turn, provide a frame in which to discuss the results but yield no a priori predictions for the effects of several of our experimental manipulations.

A representational approach such as that at the heart of SET, informed by the functional considerations of OFT, may lead to a comprehensive theory of foraging involving both function and mechanism. Both the frame of SET and the impulse to hook up mechanism to function belong to the legacy of John Gibbon.

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