

The influence of current-visit experience within a prey patch on patch persistence

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Received 6 August 1997; received in revised form 30 September 1997; accepted 2 October 1997

Abstract

A critical component of efficient foraging behavior is leaving a feeding site when prey density in that site declines. If “real time” hypotheses are to explain patch-leaving mechanisms, we will need to examine the influence that moment-to-moment experience within a current prey patch has on persistence in that patch. We used linear regression to investigate how current experience of patch quality influenced homing pigeons’ patch persistence. We did this by examining the amount of variance in persistence that was accounted for by different measures of within-session patch quality. The importance of several measures of the precise sequence of events in individual sessions were assessed with selected averaging algorithms. Mean inter-capture interval and mean number of inter-capture pecks accounted for a significant amount of the variance in giving-up time in three of four, and four of four birds, respectively. Conversely, only one rate measure in one bird showed an influence on patch persistence. In three birds, recent information had a strong influence on giving-up time. Current-visit experience did influence the patch persistence of the pigeons, but the birds’ behavior indicated that different individuals used different measures of patch quality, different mechanisms of assessing those measures, and different patch-exit mechanisms. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Averaging models; Foraging; Patch-leaving hypotheses; Pigeons; Prey patches; Rock doves

1. Introduction

In many environments, prey items are clumped or “patchy” in their distribution. Animals capable

of focusing their foraging efforts on concentrated patches of prey should enjoy advantages in terms of survival and reproductive success (Schoener, 1971; Sullivan, 1988). In support of this prediction, many species of animals have been observed to focus their foraging successfully on rich patches of prey, or on richer schedules of reinforcement in

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operant simulations (see Stephens and Krebs, 1986; Kamil et al., 1987; Stephens, 1990). To concentrate their efforts on rich patches, animals must be able to recognize when an initially rich patch depletes so that they can move to more profitable patches (see Green, 1984; McNamara and Houston, 1985; Stephens and Krebs, 1986; Shettleworth, 1988; Stephens, 1990). Therefore, assessment of patch depletion, and the decision to leave a patch based on this assessment, are critical components of efficient patch utilization and are important topics in behavioral ecology (see Shettleworth, 1988, 1994). The present study examines how homing pigeons (i.e. rock doves, *Columba livia*) assess depletion in a simulated prey patch in an operant procedure and what implications this assessment has for hypotheses about patch leaving.

Several hypotheses have been proposed that predict how an animal decides to leave a patch (Table 1; see Houston et al., 1982; Stephens, 1990; Roche, 1996; Roche and Glanz, 1996). First, an animal could leave the patch after a certain number of prey items have been captured (a “fixed-number-of-prey hypothesis”; see Gibb, 1958, 1962, but see also Krebs, 1973; Krebs et al., 1974). Second, an animal could leave a patch when the ratio between the mean inter-capture interval (or the mean number of capture attempts per capture) and the present run-of-bad-luck (the duration or number of capture attempts since the last prey capture) reaches some threshold (a “run-of-bad-luck hypothesis”; see Kamil et al., 1988; Brunner et al., 1992, 1996; Roche, 1996; Roche et al., 1996). Specific forms of run-of-bad-luck hypotheses are listed in Table 1. (Note that some versions of run-of-bad-luck hypotheses discussed in the literature predict that giving-up time is fixed; in the run-of-bad-luck models that we discuss, the giving-up time, or number of giving-up pecks, flexibly adjusts to changes in recent experience.)

Third, an animal could leave a patch based on its rate of prey capture. The well-known marginal value theorem makes an idealized prediction about how an animal should leave a patch; it predicts that an animal will leave when the instantaneous rate of capture in the depleting patch falls

to the mean rate in the entire environment, adjusted for travel time (see Charnov, 1976; Stephens and Krebs, 1986). A patch-exit hypothesis, or “marginal value rule”, based directly on this theorem assumes that the animal has perfect information about the environment and that the animal does not use information gathered within a patch; neither of these predictions are realistic (see Oaten, 1977; Green, 1980, 1984; Iwasa et al., 1981; McNair, 1982; McNamara, 1982; Stephens and Krebs, 1986, pp. 94–99; McNamara and Houston, 1987a; Stephens, 1993). These limitations can be addressed, however, in an ‘estimated-rate hypothesis’ that predicts that information is based only on experience and that information gathered within a current visit to a patch is used. Specifically, the “estimated-rate hypothesis” predicts that an animal leaves a patch when the *estimated* rate of capture in the current patch falls to that *estimated* for the whole environment, adjusted for travel time (Roche, 1996; Roche et al., 1996).

Fourth, the animal could leave a patch when the estimated capture-probability in that patch falls to that estimated for alternative patches (a “capture-probability hypothesis”; Roche, 1996; Roche et al., 1996; see Appendix A; see also McNamara and Houston, 1980; Stephens and Krebs, 1986; Kacelnik et al., 1987).

Which of the above hypotheses can better explain observed avian patch-leaving behavior? This

Table 1
List of several potential patch-exit hypotheses and the variables that those hypotheses predict are assessed

Hypothesis	Variable(s) assessed
Fixed-number of prey	Number of captures since patch entry
Run-of-bad-luck	Mean ICI:mean ROBL (time-based)
Run-of-bad-luck	Mean ICA:mean ROBL (time-based)
Run-of-bad-luck	Mean ICA:mean ROBL (attempt-based)
Estimated-rate	Captures per time or captures per attempt
Capture-probability	Capture probability

Abbreviations: ICI, inter-capture interval; ROBL, run-of-bad-luck; and ICA, number of inter-capture attempts at prey capture.

question is complex. For example, on a qualitative level, different patch-leaving models differ in their predictions about whether the correlation between measures of duration per capture and patch persistence is positive or negative. On a quantitative level, patch-leaving hypotheses differ in their predictions about what measures are assessed by the animal (see Table 1). On an even more precise quantitative level, there are different potential averaging mechanisms with which these measures may be assessed and there are different potential memory windows into the past over which information could be assessed. Therefore, to increase our understanding of patch-leaving mechanisms, it is important to gather information on what variables within the animal's experience show the most pronounced influence on patch persistence, the manner in which these variables influence persistence, how these variables are averaged, and over what memory window into the past these variables are averaged.

Different patch-leaving hypotheses differ in their predictions about whether the correlation between the mean inter-capture interval (or the mean number of capture attempts per capture) and giving-up time is positive or negative. Birds in several studies averaging data across multiple sessions have been observed to show positive correlations between mean inter-capture interval and giving-up time, a trend predicted by run-of-bad-luck and capture-probability hypotheses, but not by an estimated-rate hypothesis (see Section 4; see also Nevin, 1979, 1988; Kacelnik et al., 1987; Roche, 1996; Roche et al., 1996). Therefore, an important component to exploring predictions of patch-leaving hypotheses is to look at the direction of the correlation (if any) between inter-capture interval and measures of persistence.

An elemental component of each patch-leaving hypothesis is the measure that is predicted to be assessed by the animal (see Staddon, 1983; Lea and Dow, 1984; Dow and Lea, 1987; Staddon and Reid, 1987; Gallistel, 1990). The fixed-number-of-prey hypothesis predicts that the animal assesses the sum of prey captures, the estimated-rate hypothesis predicts that it assesses captures per time, run-of-bad-luck hypotheses predict that it assesses runs-of-bad-luck and the mean duration (or num-

ber of capture attempts) between captures, and the capture-probability hypothesis predicts that it assesses capture probability.

There are a variety of types of averaging mechanisms that animals could use to assess patch quality; these mechanisms can be explored by testing the predictions of specific averaging algorithms. Algorithms averaging inter-capture intervals or number of capture attempts per capture include arithmetic mean, harmonic mean, moving-minimum mean, and exponentially-weighted mean or "integrator" algorithms (see Appendix A; also see McNamara and Houston, 1985, 1987a,b; Davis et al., 1993; Brunner et al., 1996; Wynne et al., 1996). Algorithms assessing the rate of prey capture (captures per time or captures per capture attempt) include what are called the ratio of expectations (RoE) and the expectation of ratios (EoR) (see Templeton and Lawlor, 1981; Harder and Real, 1987; Bateson and Kacelnik, 1995a,b; Kacelnik and Bateson, 1996). There are different memory windows over which animals could potentially assess patch quality; the length of animals' memory windows can be explored by testing the predictions of specific averaging algorithms that average different durations into the past.

In the present study, we examined how moment-to-moment experience within a patch visit influenced patch persistence, in order to increase our understanding of patch assessment and patch exit mechanisms. Many studies of patch-choice behavior average results across multiple experimental sessions (see Stephens and Krebs, 1986; Kamil et al., 1987; Hughes, 1990; Stephens, 1990). Yet if students of foraging behavior are to develop realistic, "real time" hypotheses about patch exit, these models must explain the influence that moment-to-moment experience within a patch has on persistence within that patch. We used linear regression to investigate how much of the variance in patch persistence of individual homing pigeons in individual experimental sessions was accounted for by the moment-to-moment sequence of inter-capture intervals (or capture attempts per capture) experienced within those individual sessions (see Fetterman, 1993, for a related technique; see also Wynne et al., 1996).

We did this by presenting the birds with an initially high quality patch that depleted suddenly to a zero probability of reinforcement and a lower quality patch that was unchanging. This “sudden-death” depletion provides a simple and effective probe into an animal’s patch-exiting behavior (Kamil et al., 1988). Patches were simulated by random-ratio schedules of reinforcement in large operant chambers. The data from this procedure shows day to day error that is averaged out in means taken across sessions. But it allows us to examine the actual influence, over short time scales, that experience with a patch visit has on patch persistence. As such, this procedure offers a finer scale of discrimination than studies averaging across sessions. And if significant amounts of the variance in patch persistence is accounted for by within-visit experience, it indicates that short-term experience did influence patch persistence, in spite of the day-to-day noise. The analysis of the influence of within-session experience on behavior may offer a degree of realism, because animals in the wild frequently have only brief exposure to particular sets of conditions and may therefore be expected to react quickly to changes in experienced prey density.

An added advantage of this procedure is that it allows investigators to detect differences among individuals. If the specific averaging mechanisms of individual birds are influenced by differences in experience, or differences in genotype (and there is no reason to expect that individual behavior would not be influenced by experiential and genetic differences) individual differences among animals are not anomalous, but rather expected (see Fetterman, 1993). By examining the influence that moment-to-moment experience has on patch persistence in individual birds, we can examine, on a fine-grained scale, the extent to which individuals differ in their behavior.

We examined the following specific issues regarding patch assessment: (1) which assessment mechanism correlated more closely with patch persistence, mean inter-capture interval, mean capture attempts per capture, mean captures per time, or mean captures per capture attempt; (2) whether correlations were higher for the predictions of arithmetic mean, harmonic mean, mov-

ing-minimum mean, or exponentially-weighted mean algorithms; (3) whether algorithms averaging over shorter periods of time showed higher correlations with patch persistence than algorithms averaging over longer periods; (4) whether there is a positive or negative correlation between mean inter-capture interval and giving-up time; and (5) whether there are individual differences in how moment-to-moment experience influences patch persistence. We do not assume that homing pigeons assess only one measure, use only one averaging mechanism, or employ only one patch-leaving mechanism; it is likely that they use multiple mechanisms and assess multiple variables. We simply examine which measures and which algorithms have the most pronounced effect on patch persistence. The results of our analyses offer information that will have implications for our understanding of patch-assessment and patch-exit mechanisms.

2. Materials and methods

2.1. Subjects

Four White Carneau homing pigeons served as subjects. The homing pigeons, which were experienced on concurrent random-ratio schedules of reinforcement, were housed in individual stainless-steel cages. They had constant access to grit and water and were maintained at 85% of their free-feeding weights.

2.2. Apparatus

The experimental sessions were conducted in two large operant chambers measuring 58 cm deep by 74 cm wide and 40 cm high. The walls of each chamber consist of light brown particle board, the doors (orientated to the left of the keys and feeder) are made of clear plexiglass covered with dark blue cardboard, and the ceilings are made of translucent plastic. The floors consist of black, plastic mats. Background noise was provided by a fan in each chamber. A 15-W fluorescent house light lit each chamber from above the translucent ceilings. Each chamber had two 2.6-

cm diameter keys, which were 38 cm from each other and were 24.3 cm from the floor. The square feeder bay, the bottom of which began 7.5 cm from the floor, measured 7.7 cm². An IBM-compatible PC, connected to each chamber with homemade interfaces, recorded data and controlled the experimental sessions using “Conman” software (©Gary Lucas).

2.3. Procedure

In each experimental session, a bird was presented with a left key and a right key on which they could peck to receive food. At the beginning of each session both keys were lit with red lights. The bird could then peck on the left key to obtain reinforcers (a 2.5-s access to a hopper filled with mixed grain), or could peck on the right key. The first peck on the right key initiated a changeover delay of 2 s during which both key lights went out. After the 2-s delay, the right key was lit again and the bird could peck on the right key to receive reinforcers. Once a bird had switched to the right key, the red light on the left key remained out and no more reinforcers were available on the left key. Therefore, only one changeover was possible per session. Each peck provided a reinforcer with a predetermined mean probability with a random distribution (a random ratio schedule of reinforcement). Key pecks simulated search behavior, reinforcers simulated prey captures, and the changeover delay, along with the physical movement between the two keys, simulated travel time between patches. The large size of the experimental chambers offered slightly more ecological realism than that provided by smaller operant chambers because the distance between the two keys was greater, and thus the birds had to walk farther to switch between the two keys. The birds also had more room to move about.

Twenty-two sessions on a single-step change procedure were conducted for each bird. One session was conducted per bird per day between 10:00 and 14:00 EST, 6 days per week. Initially, each peck on the left key offered a reinforcement probability of 0.12 (i.e., an average of 8.33 pecks was required to receive a reinforcer); the reinforcement probability of pecks on the left key

then suddenly declined to zero after 30 reinforcers had been received. The right key offered a reinforcement probability of 0.03 throughout each session. Thus the left key represented a depleting patch and the right key represented a non-depleting patch. Each session ended after a homing pigeon had received 60 reinforcers. The number of reinforcers in the depleting patch, the long-term reinforcement rate in the depleting patch, and the long-term reinforcement rate in the non-depleting patch were all kept constant so that we could unambiguously examine the influence, if any, that moment-to-moment changes in patch quality had on patch persistence in individual sessions.

2.4. Algorithms and analysis

For each bird in each session, we calculated the mean inter-capture interval, the mean number of pecks per capture, the mean captures per time, and the mean captures per peck yielded by several averaging algorithms given the exact sequence of inter-capture intervals and inter-capture pecks observed. We chose these measures because of their potential as factors in run-of-bad-luck or capture-probability models. We also calculated the persistence, in number of giving-up pecks, predicted for each session for each bird by a capture probability model that assesses capture probability by captures per peck. In addition, we calculated the mean rate of pecking during each session. We used linear regression to compare all of the above values with the actual observed giving-up times, and also observed numbers of giving-up pecks, in individual sessions. With these regression analyses, we examined the following: (1) the variance in giving-up time accounted for by measures of the estimated inter-capture interval; (2) the variance in giving-up time accounted for by measures of inter-capture pecks; (3) the variance in giving-up time accounted for by measures of captures per time; and (3) the variance in giving-up pecks accounted for by measures of captures per peck. We also determined if the number of giving-up pecks predicted by a capture-probability model accounted for a significant amount of the variance in observed number of giving-up pecks. Data were not used on the days birds left the depleting patch

Table 2
 r^2 values and p values for regressions between the predictions of algorithms averaging time per capture and giving-up time

Algorithm	Bird 1 ($n = 18$)		Bird 2 ($n = 19$)		Bird 3 ($n = 22$)		Bird 4 ($n = 19$)	
	r^2	p	r^2	p	r^2	p	r^2	p
Last 1	0.352	0.009	0.031	0.434	– 0.243	0.032	0.166	0.083
Arith. last 5	0.059	0.35	0.016	0.568	<0.001	0.988	0.046	0.379
Arith. all	0.004	0.792	0.071	0.231	<0.001	0.914	0.108	0.170
Harmonic last 5	0.213	0.054	0.165	0.061	<0.001	0.984	<0.001	0.92
Harmonic all	0.059	0.333	0.069	0.239	0.037	0.43	0.980	0.192
Moving-min.	0.391	0.109	0.691	< 0.001	0.005	0.984	0.104	0.670
Integ. (0.2)	0.080	0.257	0.036	0.398	0.013	0.636	0.038	0.416
Integ. (0.4)	0.238	0.04	0.021	0.519	0.079	0.244	0.006	0.76
Integ. (0.6)	0.36	0.009	0.212	0.511	0.149	0.102	0.006	0.76
Integ. (0.8)	0.377	0.007	0.026	0.47	0.203	0.053	0.014	0.629
Integ. (0.95)	0.359	0.009	0.030	0.443	–0.234	0.036	0.125	0.137

before depletion (this occurred an average of only 2.5 times per bird during the experiment).

We used arithmetic mean, harmonic mean, moving-minimum mean, and exponentially-weighted mean or “integrator” algorithms to average inter-capture intervals and the number of inter-capture pecks (see Appendix A). The measures of mean inter-capture interval, and mean number of inter-capture pecks, were calculated as follows: (1) the duration of, or number of pecks in, the last inter-capture interval; (2) arithmetic and harmonic means of the duration of, or number of pecks in, all inter-capture intervals since patch entry; (3) arithmetic and harmonic means of the duration of, or number of pecks in, the last five inter-capture intervals; (4) the minimum inter-capture interval, or number of inter-capture pecks, in the last five inter-capture intervals (a moving-minimum mean); and (5) the mean inter-capture interval, or mean number of inter-capture pecks, yielded by integrator algorithms with currency parameters ranging from 0.20 to 0.95 (IN 0.2, IN 0.4, IN 0.6, IN 0.8, IN 0.95, respectively). (A currency parameter of 0.20 means that at each iteration, recent information is weighted 20%, past information 80%.)

We used the two most popular measures of rate, the RoE since patch entry, the RoE over the last five inter-capture intervals, the EoR since patch entry, and the EoR over the last five inter-capture intervals to average captures per time and

captures per peck (see Appendix A; see also Templeton and Lawlor, 1981; Bateson and Kacelnik, 1995a,b).

3. Results

The birds consistently began pecking on the key for the initially rich patch at the start of a session, pecked on that key until depletion had been detected, moved over to the key for the undepleting patch, and pecked on that key for the remainder of the session. We have organized the results according to the amount of the variance in patch persistence (giving-up time and number of giving-up pecks) accounted for by different measures of patch quality. The implications these findings have for different patch-exit hypotheses will be discussed in Section 4.

3.1. Regressions of mean inter-capture interval and giving-up time.

Table 2 displays the r^2 values and p values for regressions between the predictions of algorithms averaging time per capture. The duration of the last inter-capture interval accounted for a significant amount of the variance in giving-up time in bird 1. Therefore, as the duration of the last inter-capture interval increased, the duration of the giving-up time tended to increase in this bird.

Table 3
 r^2 values and p values for regressions between the predictions of algorithms averaging pecks per capture and giving-up time

Algorithm	Bird 1 ($n = 18$)		Bird 2 ($n = 19$)		Bird 3 ($n = 22$)		Bird 4 ($n = 19$)	
	r^2	p	r^2	p	r^2	p	r^2	p
Last 1	0.475	0.002	<0.001	0.97	-0.241	0.033	0.436	0.002
Arith. last 5	0.139	0.128	0.003	0.795	<0.001	>984	<0.001	0.907
Arith. all	0.026	0.522	0.004	0.77	0.004	0.79	0.164	0.085
Harmonic last 5	0.026	0.52	0.26	0.015	0.002	0.861	<0.001	0.668
Harmonic all	0.026	0.52	0.227	0.025	0.033	0.455	0.004	0.791
Integ. (0.2)	0.055	0.351	0.001	0.908	<0.001	0.909	<0.001	0.965
Integ. (0.4)	0.006	0.757	<0.001	0.983	0.021	0.555	0.004	0.792
Integ. (0.6)	0.023	0.552	<0.001	0.947	0.04	0.412	0.042	0.397
Integ. (0.8)	0.212	0.055	<0.001	0.956	0.034	0.452	0.150	0.101
Integ. (0.95)	0.345	0.01	<0.001	0.967	0.019	0.574	0.245	0.031
Rate of pecking	0.006	0.751	0.129	0.101	0.066	0.290	0.063	0.300

For bird 1, the predictions of integrator algorithms with currency parameters of 0.40, 0.60, 0.80, and 0.95 accounted for a significant amount of the variance in giving-up time. The highest amount of the variance in giving-up time was accounted for by the predictions of the IN 0.8 algorithm in this bird.

In bird 3, the last inter-capture interval and the predictions of the IN 0.95 algorithm (the integrator with the heaviest weighting of recent information) accounted for a significant amount of the variance in giving-up time. The correlations were negative, however, instead of positive.

For bird 2, a moving-minimum algorithm accounted for a significant amount of the variance in giving-up time. A significant amount of the variance in giving-up time was not accounted for by any of the time-per-capture algorithms in bird 4.

3.2. Regressions of number of inter-capture pecks and giving-up time

Table 3 displays the r^2 values and p values for regressions between the predictions of algorithms averaging pecks per capture and giving-up time. The number of pecks in the last inter-capture interval accounted for a significant amount of the variance in giving-up time in three of four birds. The correlations were positive in birds 1 and 4. The correlation was negative in bird 3, the bird

that displayed negative correlations between giving-up time and both the last inter-capture interval and IN 0.95 algorithms.

In bird 2, the predictions of harmonic mean algorithms going back five captures and going back to patch entry accounted for a significant amount of the variance in giving-up time.

The rate of pecking did not explain a significant amount of the variance in giving-up time in any of the birds.

3.3. Regressions of number of inter-capture pecks and number of giving-up pecks

The r^2 values and p values for regressions between the predictions of algorithms averaging pecks per capture and the number of giving-up pecks are shown in Table 4. None of the algorithms accounted for a significant amount of the variance in the number of giving-up pecks in any of the birds.

3.4. Captures per time, captures per peck, and the predictions of a capture probability model

Table 5 lists the r^2 values and p values of regressions comparing measures of rate, as measured by captures per time, with observed giving-up time. None of the algorithms measuring captures per time accounted for a significant amount of the variance in the number of giving-up time in any of the birds.

Table 4

r^2 values and p values for regressions between the predictions of algorithms averaging pecks per capture and number of giving-up pecks

Algorithm	Bird 1 ($n = 18$)		Bird 2 ($n = 19$)		Bird 3 ($n = 22$)		Bird 4 ($n = 19$)	
	r^2	p	r^2	p	r^2	p	r^2	p
Last 1	0.199	0.064	0.001	0.889	0.204	0.052	0.057	0.324
Arith. last 5	0.021	0.567	0.033	0.416	<0.001	0.984	0.005	0.781
Arith. all	0.064	0.311	<0.001	0.994	>0.05	0.763	0.002	0.849
Harmonic last 5	0.081	0.252	0.162	0.064	<0.001	0.991	0.091	0.209
Harmonic all	0.011	0.68	0.102	0.146	0.114	0.157	0.052	0.35
Integ. (0.2)	0.015	0.626	0.016	0.57	<0.001	0.992	<0.001	0.923
Integ. (0.4)	0.041	0.421	0.004	0.761	0.144	0.109	<0.001	0.910
Integ. (0.6)	0.006	0.763	<0.001	0.913	0.009	0.704	0.003	0.831
Integ. (0.8)	<0.001	0.950	<0.001	0.983	0.008	0.723	0.028	0.498
Integ. (0.95)	0.027	0.512	<0.001	0.913	0.079	0.371	0.083	0.348

The r^2 values and p values of regressions comparing measures of rate, as measured by captures per peck, with the number of giving-up pecks, are displayed in Table 6. For bird 2, the EoR measuring captures per peck five inter-capture intervals back accounted for a significant amount of the variance in the number of giving-up pecks. The correlation between the EoR and the number of giving-up pecks was negative, as would be expected by a run-of-bad-luck (rate is the reciprocal of the number of inter-capture pecks) or a capture-probability hypothesis. None of the other measures of captures per peck accounted for significant amounts of the variance in giving-up pecks.

The measure of captures per peck with the highest median ranking among birds in terms of the amount of variance that it accounted for was the number of captures per peck in the last inter-capture interval. This measure of captures per peck was therefore chosen as the measure to plug into a capture-probability model to examine if the number of giving-up pecks predicted by the capture-probability model accounted for a significant amount of the variance in the number of giving-up pecks observed. The number of giving-up pecks predicted by the capture-probability model did not explain a significant amount of the variance in the number of observed giving-up pecks in any of the birds.

4. General discussion

4.1. Measures assessed

Measures of mean inter-capture interval accounted for a significant amount of the variance in giving-up time in two of four birds, whereas measures of mean number of inter-capture pecks accounted for a significant amount of the variance in giving-up time in three of four birds. Measures of mean number of inter-capture pecks did not explain a significant amount of the variance in giving-up pecks in any of the birds. Therefore, both mean inter-capture interval and mean number of inter-capture pecks showed an influence on giving-up time in some birds, with mean number of inter-capture pecks displaying an influence on giving-up time in one more bird than time per capture.

Predictions of algorithms averaging captures per time did not explain a significant amount of the variance in giving-up time in any of the birds and predictions of algorithms averaging captures per peck accounted for a significant amount of the variance in giving-up pecks in only one bird (bird 2). Therefore, measures of inter-capture interval and number of inter-capture pecks had more of an influence on patch persistence than did rate of capture (captures per time or captures per peck).

Table 5
 r^2 values and p values of regressions comparing measures of captures per time with giving-up time

Algorithm	Bird 1 ($n = 18$)		Bird 2 ($n = 19$)		Bird 3 ($n = 22$)		Bird 4 ($n = 19$)	
	r^2	p	r^2	p	r^2	p	r^2	p
RoE	0.104	0.681	0.209	0.35	0.012	0.961	0.393	0.096
RoE last 5	0.302	0.223	0.017	0.941	0.07	0.777	0.007	0.976
EoR	0.263	0.293	0.243	0.275	0.206	0.398	0.403	0.087
EoR last 5	0.437	0.07	0.398	0.067	0.047	0.85	0.082	0.737

4.2. Implications these measures have for patch-leaving hypotheses

Measures of rate of capture did not explain significant amounts of the variance in patch persistence; this finding does not provide support for an estimated-rate hypothesis. The observed significant amount of variance in giving-up time accounted for by mean inter-capture interval, and mean number of inter-capture pecks, does support run-of-bad-luck hypotheses based on the assessment of these variables. Of potential run-of-bad-luck hypotheses, one predicting that an animal leaves a patch when the ratio between the mean number of inter-capture pecks and the interval since the last prey capture equals some threshold received support in three birds (birds 1, 2, and 4). A run-of-bad-luck hypothesis predicting that an animal leaves a patch when the ratio between the mean inter-capture interval and the interval since the last prey capture equals some threshold received support in only one bird (bird 1). Bird 3 did not support either run-of-bad-luck hypothesis because the correlations displayed were *negative* (run-of-bad-luck models predict that correlations between inter-capture interval, or inter-capture pecks, and patch persistence are positive).

The capture-probability hypothesis predicts that patch exit is based on a combined assessment of the rate of capture at the time of the last capture and the number of unsuccessful capture attempts since the last capture, which provides an estimate of the probability of capturing a prey item on the next capture attempt (see Roche, 1996). We examined the predictions of this model directly by comparing the predictions of a capture-probability model with the observed number

of giving-up pecks and did not observe any significant correlations in any of the birds.

Roche et al. (1996), in an operant simulation of foraging in pigeons, conducted regressions comparing the mean giving-up times observed in several experimental treatments. The giving-up times were predicted by a capture-probability hypothesis and a run-of-bad-luck hypothesis based on inter-capture interval and time since the last capture. More of the variance in observed giving-up times was accounted for by predictions of the capture-probability model (97.1%) than by a run-of-bad-luck model (87.6%). These differences raise the possibility that different processes are occurring on different temporal scales and emphasize the importance of investigating data from individual sessions as well as data averaged across sessions.

4.3. Averaging algorithms

The algorithm averaging pecks per capture that accounted for a significant amount of the variance in giving-up time in the largest number of birds was the arithmetic mean of the number of pecks in the last inter-capture interval. In addition, integrator (two birds) and harmonic mean (one bird) algorithms averaging pecks per capture accounted for a significant amount of the variance in giving-up time in some birds. Predictions of an arithmetic mean of the last inter-capture interval, integrator algorithms averaging time per capture, and a moving-minimum algorithm averaging time per capture accounted for a significant amount of the variance in giving-up time in some instances. The only rate algorithm that accounted for a significant amount of the variance in patch persistence was the predictions of the EoR algorithm

Table 6
 r^2 values and p values of regressions comparing measures of captures per peck with the number of giving-up pecks

Algorithm	Bird 1 ($n = 18$)		Bird 2 ($n = 19$)		Bird 3 ($n = 22$)		Bird 4 ($n = 19$)	
	r^2	p	r^2	p	r^2	p	r^2	p
RoE	0.081	0.252	0.003	0.796	<0.001	0.922	0.007	0.734
RoE Last 5	0.015	0.626	0.094	0.165	0.004	0.791	0.001	0.895
EoR	0.041	0.421	0.088	0.180	0.144	0.109	0.040	0.415
EoR Last 5	0.015	0.633	-0.194	0.040	0.005	0.769	0.081	0.272

averaging captures per peck over the last five inter-capture intervals, which accounted for a significant amount of the variance in giving-up pecks.

4.4. The role of recent information

Very recent information about the number of inter-capture pecks strongly influenced patch persistence in three of four birds. Interestingly, the bird that displayed negative correlations between giving-up time and interval algorithms also showed a negative correlation between giving-up time and the number of pecks in the last inter-capture interval. The strong influence that recent experience had on the birds in this study agreed with the findings of several other studies. For example, Cuthill et al. (1990) observed that starlings (*Sturnus vulgaris*) displayed patch residence times that correlated with their last experienced travel time. Shettleworth and Plowright (1992) observed that homing pigeons' willingness to accept prey of low quality was strongly influenced by the length of the last interval of search. Roche et al. (1996), employing an operant simulation in which a patch depleted in two steps, observed that the patch persistence of homing pigeons was heavily influenced by events in the last 10, five, and three inter-capture intervals. In addition, Wynne and Staddon (1988) found that the post-reinforcement pause of homing pigeons in operant procedures correlated closely with the duration of the last inter-capture interval, a phenomenon they termed "linear waiting" (see also Innis, 1981; Higa et al., 1991; Staddon et al., 1991; Higa, 1996).

Wynne et al. (1996) further observed that, whereas the last inter-food interval had a pronounced effect on the duration of the post-reinforcement pause, information from before the last inter-food interval also influenced pauses. Specifically, they found evidence that the birds in their study were heavily influenced by the shortest recently experienced inter-food interval. Bird 2 in the present study showed a highly significant correlation between giving-up time and an algorithm based on the shortest recently experienced inter-capture interval, paralleling the results of Wynne et al. (1996). This correlation was not observed in the other three birds, however.

4.5. The influence of patch quality on patch persistence

Studies on several species of birds have yielded a common pattern that provides important information regarding questions about patch-leaving mechanisms. Studies on captive great tits (*Parus major*) (Ydenberg, 1984), captive starlings (*Sturnus vulgaris*) (Kacelnik et al., 1987), captive black-capped chickadees (Roche, 1996), captive homing pigeons (Roche et al., 1996), and wild black-capped chickadees (Roche and Glanz, in press) have observed that birds tend to display significantly less patch persistence when the initial quality of a depleting patch is higher than when it is lower (see also Nevin, 1979).

This observation is consistent with the predictions of both run-of-bad-luck models and capture-probability models, but not those of fixed-number and estimated-rate hypotheses. For example, when the initial quality of a depleting patch is high, the estimated mean inter-capture

interval is short, and thus the animal will leave quickly in the face of a run-of-bad-luck (producing a short interval from last capture to patch exit, or “giving-up time”). Similarly, if the initial quality of a depleting patch is high, the estimated capture probability will decline more rapidly in the face of a run of bad luck than if the initial quality was low, making the animal leave more quickly. An estimated-rate model, however, would predict that it would take longer for the instantaneous rate of intake to decline in the face of a run of bad luck when the initial quality of the depleting patch was high (producing a longer giving-up time).

The results of the present study were mixed in this regard. In two birds, measures of mean inter-capture interval accounted for a significant amount of the variance in giving-up time. In three birds, measures of the number of pecks per capture accounted for a significant amount of the variance in giving-up time. Therefore, these birds tended to display greater persistence in the face of a run of bad luck when its estimate of mean inter-capture interval over recent intervals was long than when it was short. In one of the birds (bird 3), measures of inter-capture interval (and measures of the number of pecks per capture) accounted for a significant amount of the variance in giving-up time, but the correlations were negative. Therefore, this bird displayed greater patch persistence in the face of a run of bad luck when its estimate of the duration of recent inter-capture intervals was longer, or when its estimate of recent numbers of pecks per capture was higher. This trend runs counter to the observation of greater patch persistence when the inter-capture interval is longer that has been observed in studies that average across sessions. These negative correlations may have resulted because the bird's motivation to remain in the initially rich patch was increased when the estimate of the inter-capture interval was short (that is, when it expected to receive a high rate of prey captures). The pattern of positive correlations being observed in three birds and negative correlations being observed in a fourth bird indicate that short-term experience may have pronouncedly different types of effects on patch persistence in different individuals (see Fetterman, 1993).

4.6. Individual differences

One of the most striking results of the present study was that pronounced individual differences were observed in the measures that accounted for variance in patch persistence (see Fetterman, 1993), and in the direction of the correlations between measures of quality and patch persistence. These differences indicate that different birds may employ different assessment or patch-exit mechanisms, differences that would be masked by averaging across individuals.

4.7. The use of multiple measures

Whereas the present study observed that the number of pecks per capture accounted for significant amounts of the variance in giving-up time in all four birds, this does not mean that capture attempts per capture is the only type of information that influences patch persistence. Gibb (1958, 1962) suggested that blue tits (*Parus caeruleus*) foraging for eucoosmid moth larvae in pine cones left cones after finding a certain number of larvae. Krebs (1973) questioned this conclusion, and both Krebs et al. (1974) and Roche (1996) observed that captive black-capped chickadees did not leave patches after fixed numbers of prey items had been captured. However, a tendency for the sum of the number of prey captures made in a patch to influence patch persistence has been demonstrated in some studies.

Lima (1984) studied patterns of patch utilization of three wild downy woodpeckers (*Picoides pubescens*) foraging on sections of ash saplings (*Fraxinus* spp.) into which 24 holes had been drilled to hold pieces of sunflower seeds. Lima presented the woodpeckers with environments in which patches (sections of sapling) were either ‘full’ (some of the 24 holes contained seeds) or empty (none of the holes contained seeds). There were three environments, presented sequentially over a period of days: one in which full patches contained 24 seeds, one in which full patches contained 12 seeds, and the last in which full patches contained six seeds. Lima discovered that the woodpeckers' persistence within a patch was influenced by the number of prey items recently

experienced per full patch. For example, in the environment in which one quarter of the holes in full patches contained seeds, they sampled an average of 6.3 holes in empty patches before exiting; in the environment in which half of the holes in full patches contained seeds, the birds sampled an average of only 4.5 empty holes in empty patches before exiting. Thus, the birds exhibited a number expectation, but one that flexibly adjusted to recent experience. Lima (1983), in a study of two downy woodpeckers foraging on sections of ash saplings, found evidence that the woodpeckers may have been using both number and time expectations in different situations, as well as an assessment of energy intake within a patch visit.

In a study on captive blue jays (*Cyanocitta cristata*) employing simulated depleting and non-depleting prey patches in an operant chamber, Kamil et al. (1988) also documented that patch persistence can be influenced by the number of prey captured (see also Kamil and Yoerg, 1985). Kamil et al. presented jays with two round keys that the birds could peck in response to slides displayed above these keys on rectangular stimulus panels. The depleting patch had an initially high prey density that declined to zero in a single step and the non-depleting patch had a low, but unvarying prey density. The jays displayed a higher probability of leaving the depleting patch when the number of prey items found in the depleting patch was higher than when it was lower. The patch-leaving behavior of Kamil et al. jays was not solely controlled by the number of prey captured, however. The birds also displayed a higher probability of leaving the depleting patch after long runs-of-bad-luck than after shorter runs. Therefore, both the number of prey items captured, and the duration of periods of unsuccessful search, influenced the birds' patch persistence. Interestingly, these two factors also showed a significant interaction: so, for example, when the number of prey items found in the patch was higher, the birds were more sensitive to runs of bad luck and would leave the patch more readily after experiencing unsuccessful search.

There are other examples of studies showing that birds can assess multiple types of cues simul-

taneously. Fetterman (1993) observed that assessment of the value of alternatives by homing pigeons in an operant simulation of foraging was influenced by both time per capture and the number of pecks per capture. Heinrich and Collins (1983) observed that black-capped chickadees are capable of using a hierarchy of different cues to locate concentrated patches of prey (see also Valone, 1991). That birds can use more than one type of information when assessing patch quality is not surprising evolutionarily. Birds that are able to track different types of information are more likely to forage efficiently in a stochastic environment; i.e. any one type of cue may not always provide reliable information, so the ability to attend to multiple cues provides a redundancy that ensures efficient energy acquisition in a wide variety of circumstances (see also Iwasa et al., 1981; Lima, 1983).

5. Conclusion

Whereas the precise sequences of events experienced within individual sessions have been investigated in some studies on timing (e.g. Reid et al., 1993; Church et al., 1994) this approach has been less popular in studies on patch selection (but see Brunner et al., 1992, 1996). The examination of the relation between moment-to-moment, within-patch-visit experiences and the behavior of foraging animals offers a potentially powerful tool for understanding fine-scale behavioral patterns, an understanding that can contribute to the refinement of patch-selection hypotheses. Our results indicate that moment-to-moment experience within a session influences patch persistence in homing pigeons in the present procedure. The most consistent effect was that the number of pecks in the last inter-capture interval accounted for a significant amount of the variance in giving-up time. Positive correlations of these variables were observed in three birds, but negative correlations were observed in one bird. The only patch-leaving hypotheses to receive support were run-of-bad-luck hypotheses, but these only received support from the three birds displaying positive correlations. Differences among individu-

als in measures assessed, averaging mechanism, and direction of correlations all indicate that there were pronounced individual differences in how the homing pigeons assessed patch quality. Future research in this area could explore individual differences, and their potential genetic and experiential causes, in large numbers of individuals. In addition to individual differences among individuals, each individual may possess a complex measure/algorithm/decision-mechanism conglomerate that can flexibly adjust to limitations in available information and thus adjust to environmental changes. Thus, further explorations of shifts in the use of specific measures of quality in response to shifts in conditions (e.g., along the lines of Fetterman, 1993) will help us explore the multi-dimensional nature of mechanisms of patch assessment and exit. In addition, comparative studies of the influence of moment-to-moment experience in a range of different species with different ecologies and different foraging repertoires would be extremely useful.

Acknowledgements

Special thanks to John Staddon, Armando Machado, David Boynton, Fran Silva and two anonymous reviewers for their comments on this manuscript. Thanks also to Molly Wright and Jeff Sturgeon for their technical contributions. Support for this study was provided by National Science Foundation grant numbers DIR-9014276, DIR-9413220, and IBN-9408366.

Appendix A

A.1. Capture-probability hypothesis

The capture-probability hypothesis predicts the animal will leave the current patch when the estimated capture probability in that patch reaches some value relative to the estimated capture probability for the whole environment, as follows (Roche, 1996; Roche et al., 1996, see also McNamara and Houston, 1980; Stephens and Krebs, 1986; Kacelnik et al., 1987):

$$\text{leave when } (P_p)(1 - P_p)^n = b(P_E)(1 - P_E)^n \quad (1)$$

where P_p is the estimated probability of prey capture in the current patch at the time of the last capture, n is the number of capture attempts since the last capture, b is a biasing factor that determines how heavily the value of the environment is discounted ($0 < b \leq 1$), and P_E is the estimated probability of prey capture in the entire environment. b decreases with an increase in the travel time to alternative patches. The estimated probability of prey capture at the time of the last prey capture could be assessed as captures per time or captures per capture attempt.

A.2. Averaging algorithms: the harmonic mean

A harmonic mean can be calculated as follows:

$$1/I(t) = (1/n)[(1/x_1) + (1/x_2) + \dots + (1/x_n)] \quad (2)$$

where $I(t)$ is the estimate of the mean inter-capture interval at time t , n is the number of inter-capture intervals assessed, and x_1 is the first inter-capture interval assessed, etc.

A.3. Averaging algorithms: the moving-minimum mean

The moving-minimum mean algorithm appears as follows (see Wynne et al., 1996):

$$I(t) = \text{the minimum ICI in the last } M \text{ ICIs.} \quad (3)$$

where ICI is an inter-capture interval.

A.4. Averaging algorithms: integrator algorithms

An integrator algorithm (Killeen, 1981, 1984; Kacelnik et al., 1987; McNamara and Houston, 1987a,b; Davis et al., 1993) combines an estimate of patch quality in the current iteration with an estimate of past patch quality at each update. There are many different possible versions of integrator algorithms. A version of the integrator that iterates an estimate of the mean inter-capture interval at the time of each prey capture appears as follows:

$$I(t) = \beta Q + (1 - \beta)^{t-1} \quad (4)$$

where $I(t)$ is the estimate of the mean inter-capture interval at capture t , β is the factor determining the influence of recent information (the currency parameter, $0 \leq \beta \leq 1$), Q is an estimate of the current inter-capture interval, $(1 - \beta)$ is the factor weighing past information, and $I(t - 1)$ is the estimate of the mean inter-capture interval at capture $t - 1$. In this version of the algorithm, the larger the value of β , the more that recent information influences the average.

A.5. Averaging algorithms: the ratio of expectations and the expectation of ratios

The ratio of expectations appears as follows:

$$\text{RoE} = \sum C_i / \sum T_i \quad (5)$$

where RoE is the ratio of expectations, C_i is the number of captures in inter-capture interval i (i.e. 1), and T_i is the duration of inter-capture interval i (see Bateson and Kacelnik, 1995a,b). The expectation of ratios appears as follows:

$$\text{EoR} = \left(\sum (C_i / T_i) \right) / n \quad (6)$$

where EoR is the expectation of ratios and n is the number of intervals-between-attack-movements (see Bateson and Kacelnik, 1995a,b, see also Harder and Real, 1987; Templeton and Lawlor, 1981; Kacelnik and Bateson, 1996).

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