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Bluegills continuously update patch giving-up times based on foraging experience

MARK L. WILDHABER*†, RICHARD F. GREEN‡ & LARRY B. CROWDER*

**Department of Zoology, North Carolina State University, Raleigh, NC 27695-7617, U.S.A.*

‡*Mathematics and Statistics, University of Minnesota, Duluth, MN 55812, U.S.A.*

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Abstract. The data from a series of patch-choice experiments with bluegill sunfish, *Lepomis macrochirus*, were analysed within feeding periods to describe the proximal leaving strategy bluegills use when choosing between food patches. The following hypotheses regarding strategies by which these choices are made are considered: (1) a fixed giving-up time; (2) a fixed residence time; (3) a linearly increasing giving-up time; and (4) a linearly increasing residence time. Five experiments, in which the difference in food availability between patches (tank sides) decreased from experiment to experiment, were run with eight different bluegills in each experiment. The bluegills tested did not use the fixed giving-up time rule or the fixed residence time rule to decide when to leave a patch, but did have both a longer average residence time and a longer average giving-up time in poorer environments. Within an environment, both patch residence times and giving-up times increased linearly with increasing prey encounter; the linear giving-up time rule better described bluegill behaviour than the linear residence time rule, however. This giving-up time strategy varies among individuals and yet is still robust enough to allow each individual to effectively sample and use variable food resources.

Over 25 years ago, MacArthur & Pianka (1966) suggested strategies animals may use when exploiting prey in patchy environments. Since that time, many new and more complex theories related to optimal foraging have been described (for recent reviews see Pyke 1984; Stephens & Krebs 1986). More recently, theoretical ecologists have described the more proximal mechanisms animals might use to decide when to leave a patch (e.g. Krebs et al. 1974; Charnov 1976; Oaten 1977; Green 1980, 1984; Iwasa et al. 1981; McNair 1982; McNamara 1982; Lima 1984; Kamil et al. 1987). Unfortunately, many of these theories still have not been tested or compared with each other; which is our intent in this paper.

Charnov's (1976) marginal value theorem has been one of the more widely debated of the patch leaving theories. The assumptions of his model are that the animal knows the average value of patches in the environment and that individual patch values remain constant. Charnov made two major predictions about the optimal foraging strategy an animal

should use in a patchy environment. The first prediction is that with decelerating energy intake (i.e. patch depletion) the optimal strategy is to leave a patch when the rate of food intake falls to the mean rate for the environment as a whole. The second prediction is a lower overall giving-up time, which is the time an animal spends in a patch without encountering a prey item before leaving, in a higher quality environment (i.e. when the average food intake rate per patch within the environment as a whole is higher). If the mean rate of food intake is higher in a richer environment, then the expected time between prey encounters would decrease resulting in a decreased giving-up time.

Both of these predictions are based on a model for continuous food intake, but a discrete case approximation can be made. In the discrete case, there would be one fixed giving-up time for all patches within an environment and it would be shorter in a richer environment (Charnov 1976). Both predictions have generally held for birds (e.g. titmice, *Parus* spp.: Krebs et al. 1974; and downy woodpeckers, *Picoides pubescens*: Lima 1983, 1984) which often feed on relatively sedentary prey that have seasonally stable distributions (Gibb 1966; Simms 1983).

†Present address: United States Department of the Interior, Fish and Wildlife Service, National Fisheries Contaminant Research Center, 4200 New Haven Road, Columbia, Missouri 65201, U.S.A.

McNair (1982) developed an alternative to Charnov's (1976) marginal value theorem. Instead of one fixed giving-up time for an environment, as predicted by Charnov's model, McNair's model predicts longer fixed giving-up times in better quality patches within an environment. Both Charnov's (1976) and McNair's (1982) giving-up time models have limited applicability to real systems because they assume the forager has perfect knowledge of the quality of patches within its environment.

Oaten (1977) incorporated the organism's lack of perfect knowledge into a stochastic foraging model that can be used to predict giving-up times. In Oaten's model, an organism uses its foraging experience in a patch to decide when to leave. From Oaten's model, an organism is predicted to have a longer giving-up time in a better quality patch. An organism should increase its giving-up time for the patch currently occupied if its experience suggests that the patch is of better quality than initially perceived.

Two simple applications of Oaten's (1977) model are that foragers may use a linear giving-up time rule (offered here as a possible alternative patch-leaving mechanism) or a linear residence time rule (residence time is the time an animal will spend in a patch during a visit to that patch, Green 1980). The difference between these rules is that giving-up time is based only on the time spent in a patch after the last prey encounter during a patch visit, whereas residence time is independent of when the last prey was encountered and is based on the entire time spent in a patch during a patch visit. For both the linear giving-up time rule and the linear residence time rule, the forager's decision whether or not to leave a patch depends on how many prey are found and on when prey are found. For both rules, the optimal time (giving-up time or residence time, respectively) the forager uses to decide when to leave a patch takes the approximate form: leave a patch at time $t(k) = a + bk$, if exactly k prey have been found by that time. For our study, a and b are the fitted intercept and slope, respectively, of the relation between the measured patch-leaving times and the number of prey encountered.

A rule like the linear residence time rule has already been well developed and studied (e.g. Green 1980, 1984, 1987). We are suggesting a linear giving-up time rule based on logic and previous research (e.g. Krebs et al. 1974; Charnov 1976; McNair 1982) which suggests that prey encounter

rate may influence the giving-up times used in patch-leaving decisions of animals.

Form of the Foraging Rules Tested

The foraging rules, such as those evaluated in this paper, proposed by optimal foraging theorists are precise, but the behaviour shown by real animals is variable. For example, in an experiment on downy woodpeckers, Lima (1984) offered the birds a number of artificial trees, each having either no prey or a fixed number of prey. Based on the theoretical optimal foraging strategy, it was predicted that the birds would search the same number of sites within each tree; if any prey were found in a tree during this initial search, the birds were expected to remain in the tree, otherwise the birds were expected to leave. To test whether downy woodpeckers used this strategy, Lima (1984) looked at the number of empty sites searched in a tree before the birds decided to leave. For optimal foragers, this number was expected to have a particular fixed value, but Lima found that there was moderate variation from tree to tree in the number of empty sites examined before individual birds decided to leave. However, the average number was close to the particular optimal value. Lima (1984) took the observed variability as evidence that foraging was suboptimal.

Green (1990) interpreted Lima's (1984) observations for downy woodpeckers as a mixture of pure strategies. One can evaluate the performance of real, variable behaviour in terms of an average of the performance of certain pure strategies (leave a tree after searching three empty sites, leave only after searching four empty sites, etc.). When the variable behaviour seen by Lima is treated as a mixture of simple, pure strategies, the overall performance of the observed behaviour closely approximates the best pure strategy (Green 1980).

In this paper, we consider these foraging rules to be mixed versions of pure strategies. For example, a giving-up time rule is one in which the decision to leave a patch is based on the time since the last prey was found. For a linear giving-up time rule the decision to leave a patch depends on the number of prey found. One way to visualize such a rule is to imagine an animal that chooses at random a time to remain in the present patch without finding a prey. Each time that another prey is found the animal chooses another waiting time at random. For a linear giving-up time rule, the average of these randomly chosen times increases linearly with the

number of prey found in the present patch. For such a rule, the distribution of the giving-up times would depend on the number of prey found in the patch, but it would not depend on the specific times at which prey were found. On the other hand, if an animal uses a residence time rule, then its decision to leave a patch would depend on the number of prey found in the patch and on the total time spent in a patch, and not when the last prey was found. The question is, what variables are involved in an animal's decision to leave a patch?

The purpose of this paper was to study the proximal patch-leaving rules of the bluegills used by Wildhaber & Crowder (1991) by comparing the observed behaviour of bluegills with the predictions of the numerous patch-leaving rules.

Before presenting these predictions, it is important to note that in all of these patch-leaving rules, except that given by McNair (1982), the forager is assumed to have no knowledge of individual patch qualities within an environment. Also, in this paper, our predictions are based on the assumption of systematic foraging within a patch; the same assumption made by Green (1980) in his study of the linear residence time rule. Systematic foraging is a directed behaviour where the forager, upon entering a patch, begins foraging at one end of a patch and searches its way through a patch without ever re-searching any of the patch.

Systematic foraging may be a good assumption for many animals (Baum 1987) but it is not necessarily appropriate for bluegills (DeVries et al. 1989; Marschall et al. 1989). Even so, in our experiments, there was no patch depletion (see General Materials and Methods), systematic foraging produces a similar effect (i.e. constant food availability). In a natural system, short-term (on the scale of minutes) prey depletion while in a patch may be so small that it is imperceptible to bluegills because of the large number of prey items bluegills often encounter within a patch (Keast 1978). Food availability while in a patch, then, becomes nearly constant. Consequently, even though a constant prey encounter rate was characteristic of our experimental design, our results can still be compared with the predictions of Charnov (1976) and McNair (1982) whose models include patch depletion while foraging in a patch.

Model Predictions

Within an environment of patches, the predictions of these patch-leaving rules are: (1) one fixed

giving-up time for all patches within an environment (prediction similar to that of Charnov 1976); (2) a fixed but higher giving-up time in better quality patches (prediction similar to that of McNair 1982); (3) linearly increasing giving-up time in a patch with increased prey encounter within that patch (our linear giving-up time rule); (4) fixed residence time [i.e. residence time is the same for all patches, giving-up time is unimportant (Marschall et al. 1989)]; (5) linearly increasing residence time with increased prey encounter within that patch (i.e. giving-up time is unimportant, as described by Green 1984).

Among environments with different average food-intake rates among patches, the predictions of these patch-leaving rules are: (1) lower giving-up times in higher quality environments (Charnov 1976; McNair 1982; our linear giving-up time rule); (2) shorter residence time in higher quality environments (i.e. giving-up time is unimportant, Green 1984); (3) equal residence time in all environments (i.e. giving-up time is unimportant, Marschall et al. 1989).

GENERAL MATERIALS AND METHODS

Experimental System

We ran our experiments in an isolation room equipped with fluorescent lights set on a 12:12 h light:dark cycle (lights on from 0700 to 1900 hours). Eight shuttle tanks, built with a design similar to Neill et al. (1972), were placed in the isolation room. Each shuttle tank consisted of a 76-litre aquarium divided in half by an opaque Plexiglas partition (Figure 1 in Wildhaber & Crowder 1991), creating two 'patches'. Each side of a shuttle tank was equipped with a computer-operated feeder (Gerbrands model G5110) which delivered 20-mg fish pellets (P. J. Noyes Inc.). The fish had about 3 s in which to capture a pellet as it dropped through the water column before it entered a collecting funnel and bottle. Temperature in each patch was measured by a thermistor (YSI 44034) and regulated by a submersible heater. The water in each side of the tank was mixed and oxygenated by an airstone. Cover was supplied by an overturned clay pot with a small entrance hole near the top. The entire system was continuously controlled and monitored by computers (Cyborg ISAAC 2000 linked to an IBM PC). This allowed us to collect a

Table I. Treatment for each patch choice experiment

Experiment number	Treatment*
1	100 versus 12.5% C_{\max}
2	100 versus 50% C_{\max}
3	75 versus 50% C_{\max}
4 and 5	62.5 versus 50% C_{\max}

*The percentages represent the portion of maximum daily ration (C_{\max}) that was delivered on opposite tank sides during an experiment.

continuous record of fish location and temperature data for all the shuttle tanks simultaneously. Additional details of the experimental systems are available in Wildhaber & Crowder (1991).

Experimental Protocol

Bluegill sunfish were seined from local ponds and held in the laboratory on pelleted food for at least 2 weeks at 30°C prior to use in any experiments. Before we began any experimental runs, we estimated maximum daily ration (C_{\max}) of a 10 g bluegill feeding on 20-mg pellets so that we could calibrate the food treatments. The result was a C_{\max} of approximately 24, 20-mg pellets (Wildhaber & Crowder 1991). The experimental design used in the experiments was a crossover (Gill 1978) with treatments (feeding levels on each side of a tank) continued for 7 days and then reversed relative to the two tank sides for another 7 days. A main assumption of the crossover design is that residual effects from the first period to the second are minimal. Residual effects were minimized (see Wildhaber & Crowder 1991) by analysing only the data from the last 3 days of each week. The results are from analysis of five experiments (Table I) that were conducted to assess mechanisms underlying overall patch choice behaviour in bluegills (see Wildhaber & Crowder 1991 for general results).

For each experiment, we haphazardly chose eight naive bluegills, ranging in size from 8–12 g (75–95 mm total length), and placed them in an unpartitioned 76-litre aquarium within the isolation room. We fed them ad libitum rations over a 10-h period (0800–1800 hours) for 2 days to familiarize them with the pellet delivery system. Each fish was then deprived of food for 24 h, weighed and placed in a separate shuttle tank; only one fish was used in each tank to control for the

effects of agonistic social behaviour. Thus, these five experiments represent the results from 40 individual fish (i.e. no fish was used in more than one experiment). We then gave each fish free access to both sides of the shuttle tank for 48 h without feeding (i.e. a total of 72 h of food deprivation before the food treatments began). During each experiment the sides of each tank were kept within $\pm 0.1^\circ\text{C}$ of 30.2°C (optimal temperature for growth 30°C, Coutant 1977).

The computerized pellet delivery system made food available from 0800 to 1000 hours each morning; actual pellet delivery times were randomly selected from a uniform distribution each day. The isolation room was opened after 1100 hours and closed by 1400 hours daily to allow for tank cleaning. Except for this maintenance period, we continuously monitored fish activity and side preference. After each 14-day experiment, we again deprived the fish of food for 24 h before taking their final weight.

Variables Under Consideration

In this paper, we refer only to the data from the feeding period (0800–1000 hours) because only giving-up times (in seconds, spent in a patch after the last pellet experienced) and residence times (in seconds, spent in a patch per visit) during the feeding period are appropriate for our purposes. A patch visit was defined as the time the fish entered a tank side to the time it left. Thus, as soon as the fish left a tank side that patch visit ended and a new patch visit began on the opposite tank side. Bluegills spent less than 5% of the total time in the tunnel between patches and this was simply deducted from the total time spent foraging.

We assumed that a fish encountered a pellet if it was in a patch when a pellet was delivered to that patch based on our computer-based monitoring system. Although we did not verify all individual pellet encounters, we are confident that the measure of pellet experience we used was highly representative of the actual number of pellets experienced. From videotapes of individual fish made throughout the experiments to verify the reliability of the computer monitoring system, we observed a number of behavioural patterns associated with the feeding periods that supported our computer estimate of pellet encounter.

The characteristic behaviour of the fish was to orient themselves under the feeding tube. Little, if

any, time was spent in or around the cover in the tank. Except for the few seconds it took to pass through the tunnel, the fish spent little time in the tunnel connecting the two tank sides. The time spent in the tunnel and the pellets delivered while the fish were in the tunnel were not considered in our measure of pellet experience. Thus, it was highly improbable that the fish failed to encounter any pellet delivered to the patch it was occupying.

We also examined the effects of both individual patch quality and overall environmental quality (mean feeding rate among patches) on giving-up times and residence times. We defined patch quality as the per cent maximum ration delivered to a patch (i.e. patch food availability), and environmental quality as the sum of the per cent maximum ration delivered to both patches within a tank (i.e. environmental food availability).

PATCHES WITHIN AN ENVIRONMENT

Fixed Giving-up Times, Fixed Residence Times and Patch Memory

Methods

The purpose of this analysis was to examine whether previous experience of patch food availability ('memory') affected the initial giving-up time or residence time (they are equivalent in this case) that bluegills used each time they visited a patch. Theory predicts one fixed giving-up time (Charnov 1976) or as suggested by previous work (Marschall et al. 1989), one fixed residence time for both patches in a given experiment (i.e. no memory of patch quality from previous visits). Other theory predicts a constant giving-up time for each patch but a larger giving-up time for higher quality patches (McNair 1982). To address this, we first analysed data from each patch separately; only those visits to a patch in which no pellets were experienced were used. These times, then, were related to pellet experiences during previous visits to each patch since no pellets were experienced during the particular patch visits from which these times resulted.

Results

Analysis of variance showed a significantly higher initial giving-up time and/or residence time in the patch with higher food availability only in

Table II. Significance levels for average giving-up times and residence times from analysis of patch visits where no pellets were experienced

Independent variable	<i>P</i> < value for experiment number					
	1	2	3	4	5	4 and 5
Higher food						
Left	0.0005	NS	NS	NS	NS	NS
Right	0.05	NS	NS	0.05	NS	0.05

The analysis and results are the same for giving-up time and residence times. The analyses were done on the average value from the last 3 days of each week of an experiment, with the right- and left-hand tank sides analysed separately. *N* = 16 for experiment 4 *N* = 15; for experiments 4 and 5 combined *N* = 31. NS: Not significant at the *P* < 0.05 level.

experiment 1 (Table II). This implies that, in our system where a patch can be revisited, bluegills set initial giving-up times and/or residence times for patch visits based on their perception of patch quality (i.e. memory), at least when differences in food availability between patches were large (see Wildhaber & Crowder 1991 for more details). Thus, neither one fixed giving-up time (Charnov 1976) nor one fixed residence time (Marschall et al. 1989) can be accepted as an explanation for the bluegill foraging behaviour we observed.

There is other evidence against one fixed giving-up time and/or one fixed residence time for our bluegills. The first is that there were significant differences among giving-up times and residence times of individual fish (Table III). In addition, the overall proportion of time spent in a patch was higher for better quality patches (cf. Wildhaber & Crowder 1991). One fixed residence time would have resulted in no difference in proportional usage between patches under any of the treatments. The longer initial and overall giving-up times (Fig. 1) in higher quality patches support McNair's (1982) prediction.

Giving-up Time, Residence Time, and Experience

Methods

Our purpose here was to examine the hypothesis that giving-up times and/or residence times were related to pellet experience within a patch. We did this by examining the data using crossover design

Table III. Significance levels for average giving-up times and residence times from the analysis of covariance

Dependent variable	Independent variable <i>P</i> < value for experiment number					
	1	2	3	4	5	4 and 5
Giving-up time						
Individual	0.002	NS	0.05	NS	NS	NS
Pellets experienced	0.0001	NS	0.002	0.005	0.0007	0.0001
Residence time						
Individual	0.0001	0.0002	NS	NS	NS	0.009
Pellets experienced	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

Number of pellets experienced during a patch visit was the covariable. These are the results from the analyses done on the average value from the last 3 days of each week of an experiment with both tank sides pooled. NS: Not significant at the $P < 0.05$ level.

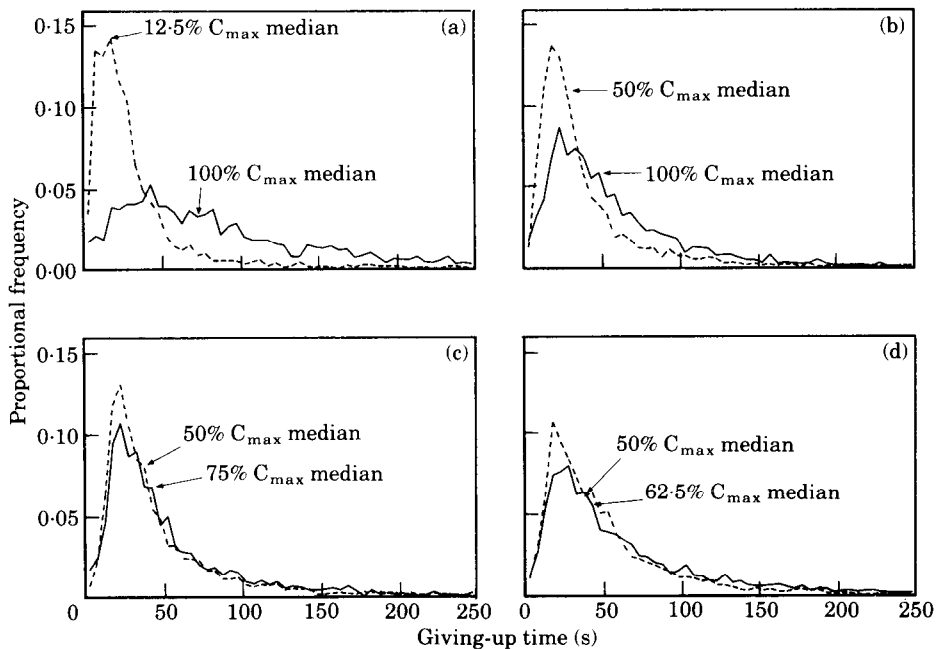


Figure 1. Proportional frequency distribution of giving-up times per patch quality within a treatment. The four graphs represent the four different patch-choice treatments tested: (a) 100 versus 12.5% C_{max} , (b) 100 versus 50% C_{max} , (c) 75 versus 50% C_{max} , (d) 62.5 versus 50% C_{max} . The two patch qualities in a treatment were offered on opposite sides of a 76-litre shuttle tank. Each point on the graphs represents the proportion of the total number of giving-up times observed in a treatment that occurred in a given 5-s range (for ease of graphing).

analysis of covariance for giving-up time and residence time; the number of pellets experienced during a patch visit was the covariable. As before (Wildhaber & Crowder 1991), we used only the

data from the last 3 days of each week during the feeding period. For each fish, the observations for this analysis were generated by averaging all giving-up times and residence times per number of pellets

experienced for each date, and then averaging the daily observations for each number of pellets experienced. In order to examine behaviour patterns as a function of overall environmental quality, we combined visits to both tank sides into one data set before calculating these average responses.

Results

We found significantly longer giving-up times and residence times when larger numbers of pellets were experienced by a bluegill during a patch visit (Table III). The data strongly suggest that pellet experience during a patch visit can modify bluegill foraging behaviour. Thus, we now have evidence against one fixed giving-up time (Charnov 1976), one fixed residence time (Marshall et al. 1989), and one fixed giving-up time for each patch within an environment (McNair 1982).

Linearly Increasing Giving-up Time

Methods

We then examined the hypothesis that there is a linear relationship between the number of pellets experienced during a patch visit and giving-up time (our hypothesis). We calculated the average giving-up time for each level of pellet experience. These averages were calculated for all tank side visits from the last 3 days of each week. These averages were calculated for the number of pellets experienced during a patch visit of zero, one, two and three pellets. We did not consider patch visits where more than three pellets were encountered because the number of observations was very low. We then performed a regression analysis of the average giving-up time versus the number of pellets experienced.

If a linear relationship was observed between giving-up time and the number of pellets experienced during each patch visit, it would be important to know whether giving-up times were randomly chosen for each pellet experience level. To make this evaluation, we compared our results with those of a random-departure time rule (Marshall et al. 1989). If our linear giving-up time rule was no better than random at predicting giving-up times, we would expect to find exponentially distributed giving-up times at each level of pellet experience (Marshall et al. 1989). We used the Kolmogorov type statistic (i.e. W) to test for exponentiality of giving-up times (i.e. Marshall et al. 1989). The details of the calculation of the

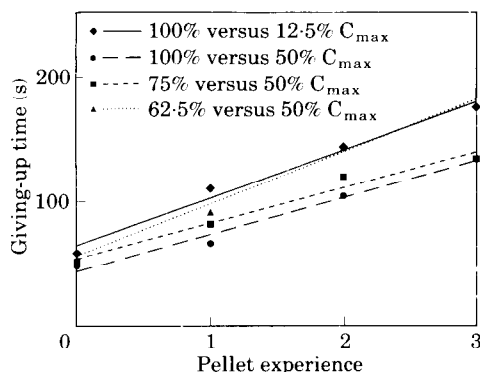


Figure 2. Average giving-up time during 2-h feeding periods plotted against the number of pellets experienced per patch visit. Each point represents the average giving-up time/patch for all fish in each treatment during the last 3 days of each experiment. There is one regression line for each treatment and four observations (three for the 62.5 versus 50% C_{max} treatment) on which each regression is based. Regression equations were: (1) 100 versus 12.5% C_{max} experiment: giving-up time (s) = $64.1 + 38.7 \times$ (number of pellets experienced per patch visit), $F > 120$, $N = 4$, $r^2 > 0.98$, $P < 0.009$; (2) 100 versus 50% C_{max} experiment: giving-up time (s) = $43.2 + 29.9 \times$ (number of pellets experienced per patch visit), $F > 118$, $N = 4$, $r^2 > 0.98$, $P < 0.009$; (3) 75 versus 50% C_{max} experiment: giving-up time (s) = $53.4 + 28.9 \times$ (number of pellets experienced per patch visit), $F > 74$, $N = 4$, $r^2 > 0.97$, $P < 0.014$; (4) 62.5 versus 50% C_{max} experiment: giving-up time (s) = $55.8 + 42.1 \times$ (number of pellets experienced per patch visit), $F > 52$, $N = 3$, $r^2 > 0.98$, $P < 0.087$.

statistic can be found in Seshadri et al. (1969) and Pearson & Stephens (1962). In general, W is a measure of the deviation of the observed distribution of the data from an exponential distribution. The greater the value of W the more the observed distribution deviates from the exponential distribution.

Results

Our analyses showed a positive, linear relationship between the number of pellets experienced during a patch visit and the average giving-up time (Fig. 2). Analysis of the distribution of giving-up times at the pellet experiences of 1, 2 and 3 suggest that giving-up times were not exponentially distributed, but the results are somewhat equivocal. Only four of the 12 tests gave P -values at or less than 0.10 (Table IV). The plots in Fig. 1 suggest that giving-up times are concentrated around one value, which in the case of each treatment, is related both to patch and environmental qualities. The

Table IV. Test of the exponentiality of giving-up times observed during 2-h feeding periods for each level of pellet experience

Treatment	Pellets experienced/patch visit*		
	1	2	3
100 versus 12.5% C_{max}			
<i>W</i>	0.135	0.790	0.206
<i>P</i> < value	0.50	0.01	0.30
<i>N</i>	349	97	31
100 versus 50% C_{max}			
<i>W</i>	0.310	0.142	0.365
<i>P</i> < value	0.15	0.50	0.10
<i>N</i>	623	85	23
75 versus 50% C_{max}			
<i>W</i>	1.336	0.190	0.126
<i>P</i> < value	0.001	0.30	0.50
<i>N</i>	440	66	15
62.5 versus 50% C_{max}			
<i>W</i>	2.467	0.233	0.065
<i>P</i> < value	0.001	0.30	(> 0.50)
<i>N</i>	810	119	20

W: Kolmogorov statistic value, *P*: associated *P*-value, *N*: number of patch visits analysed.

*Each analysis of pellet-experience level includes all patch visits for all fish observed for the last 3 days of both weeks of an experiment (62.5 versus 50% C_{max} is the combined results of experiments 4 and 5).

distributions of giving-up times appear to be only slightly skewed. From these results we conclude that fish do not use a random-departure time rule (Marschall et al. 1989). Thus, we cannot reject the linear giving-up time rule as a predictor of patch-leaving times for our bluegills.

Linearly Increasing Residence Time

Methods

We next examined the hypothesis that there was a linear relationship between the number of pellets experienced during a patch visit and residence time (Green 1980). We did this by first calculating the average residence time as noted for giving-up times. We then performed a regression analysis of the average residence time versus the number of pellets experienced.

Because pellet delivery times were randomly chosen from a uniform distribution, longer residence times would necessarily be associated with

higher pellet experiences. If bluegills used a linear residence time rule to decide when to end a patch visit, their residence time for that patch visit would not depend on whether or not they encountered prey early or late in the visit. Therefore, to determine whether the linear residence time pattern we observed was an artefact of the experimental design or an actual behavioural mechanism, we needed to test for a negative correlation between the time spent in a patch before and after the last prey was encountered during a patch visit.

The actual steps taken to test the linear residence time rule for bluegills were as follows. First, we obtained the correlation coefficient and associated *P*-value for time spent in a patch before the last pellet was experienced and the giving-up time for that patch visit. This was done separately for one, two, and three pellets experienced during a patch visit because each level of experience may have a different residence time. Because we would be doing multiple tests of correlation significance, we combined all the treatment *P*-values for a given level of experience using Fisher's method (Sokal & Rohlf 1981) to test for overall negative correlation.

Results

The higher usage of better quality patches (see Wildhaber & Crowder 1991) alone indicated bluegills had longer average residence times in better quality patches within an environment as predicted by the linear residence time rule (Green 1980). The regression analysis of residence time versus the number of pellets experienced showed a positive, linear relationship between the number of pellets experienced during a patch visit and the residence time (Fig. 3). These results support Green's (1980) linear residence time rule.

The correlation between the time spent in a patch during a visit before the last pellet was experienced and the giving-up time was actually positive instead of negative in all but one of the 12 tests (Table V). If the linear relationship between residence time and pellet experience were more than just an artefact of the experimental design, we should have seen a negative correlation. The analyses showed correlations that were significantly positive for experience levels of one and two pellets and non-significant for both positive or negative correlations for the experience level of three pellets (Table V). The significant positive correlations observed for experience levels 1 and 2 were mainly due to the large number of

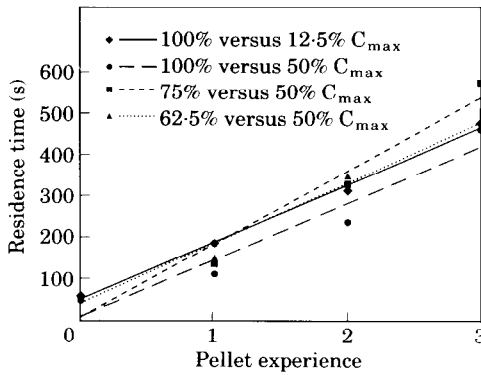


Figure 3. Average residence time during 2-h feeding periods plotted against the number of pellets experienced per patch visit. Each point represents the average residence time/patch for all fish in each treatment during the last 3 days of each experiment. There is one regression line for each treatment and four observations (three for the 62.5 versus 50% C_{max} treatment) on which each regression is based. Regression equations were: (1) 100 versus 12.5% C_{max} experiment: giving-up time (s) = $51.4 + 138.0 \times$ (number of pellets experienced per patch visit), $F > 552$, $N = 4$, $r^2 > 0.99$, $P < 0.002$; (2) 100 versus 50% C_{max} experiment: giving-up time (s) = $9.3 + 136.5 \times$ (number of pellets experienced per patch visit), $F > 28$, $N = 4$, $r^2 > 0.93$, $P < 0.034$; (3) 75 versus 50% C_{max} experiment: giving-up time (s) = $8.3 + 176.3 \times$ (number of pellets experienced per patch visit), $F > 47$, $N = 4$, $r^2 > 0.95$, $P < 0.021$; (4) 62.5 versus 50% C_{max} experiment: giving-up time (s) = $41.3 + 145.2 \times$ (number of pellets experienced per patch visit), $F > 22$, $N = 3$, $r^2 > 0.95$, $P < 0.134$.

observations. The actual r^2 -values were all less than 0.20 with eight of the 12 less than 0.05.

These results force us to reject the linear residence time rule as the best descriptor of the observed proximal patch-choice behaviour of our bluegills. Furthermore, the lack of any strong correlation, positive or negative, lends support to the linear giving-up time rule. If pellet experience was the main factor affecting giving-up times, lack of correlation between the time before the last pellet delivered and the giving-up time would be expected.

AMONG ENVIRONMENTS

Giving-up Times

The prediction of lower giving-up times in richer environments made by Charnov (1976) and McNair (1982) is supported by our observed data. The average giving-up times decreased with

Table V. Correlation analyses test of linear residence time rule

Treatment	Pellets experienced/patch visit		
	1	2	3
100 versus 12.5% C_{max}			
Correlation	+	+	-
r^2	0.0273	0.0202	0.0039
P -value	0.0020	0.1653	0.7388
N	349	97	31
100 versus 50% C_{max}			
Correlation	+	+	+
r^2	0.0138	0.0426	0.1246
P -value	0.0033	0.0581	0.0985
N	623	85	23
75 versus 50% C_{max}			
Correlation	+	+	+
r^2	0.1927	0.0565	0.0079
P -value	0.0001	0.0546	0.7527
N	440	66	15
62.5 versus 50% C_{max}			
Correlation	+	+	+
r^2	0.0448	0.0354	0.0035
P -value	0.0001	0.0404	0.8048
N	810	119	20
Negative Correlation			
$-2 \ln(P)$	0.01	0.68	6.87
$P < \text{value}$	1.0	1.0	0.56
Positive Correlation			
$-2 \ln(P)$	69.91	21.52	8.32
$P < \text{value}$	0.0001	0.0059	0.41

The test examines the correlation between the time before the last pellet was experienced during a patch visit and the giving-up time for that patch visit, using data from the 2-h feeding periods for each level of pellet experience. Each analysis includes all patch visits observed for all fish in a treatment during the last 3 days of each experiment (both weeks combined).

increased quality for the environment (Spearman rank correlation $P < 0.05$, Daniel 1978, experiments 4 and 5 were combined because they had the same treatment; Fig. 4).

This pattern of decreased giving-up times with increased environmental quality also held for patches of the same quality among environmental qualities. For experiments 2, 3 and 4, where the overall environmental quality decreased from experiment 2 to experiment 4 (i.e. total C_{max} delivered to a shuttle tank decreased from 150% to

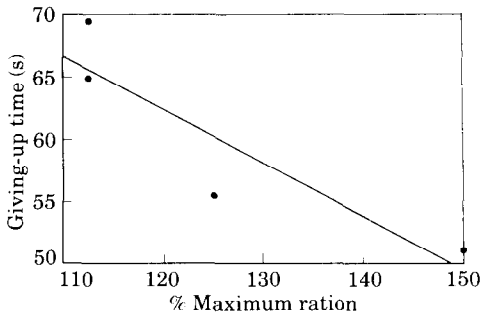


Figure 4. Average giving-up time during 2-h feeding periods plotted against the overall quality of an environment. Each point represents the average giving-up time/patch for all fish in each treatment during the last 3 days of each week of an experiment (combined) (regression equation: giving-up time (s) = $114.0 - 0.43 \times$ (total per cent C_{max} delivered to a tank), $r^2 = 0.81$, $N = 4$, $P < 0.10$).

125% to 112.5%), the giving-up times for the 50% C_{max} patch (12, 20-mg pellets) increased from 41.8 to 51.4 to 58.0 s, respectively. For experiments 1 and 2, where environmental quality increased from experiment 1 to 2, the giving-up time for the 100% C_{max} patch decreased from 100.4 to 60.2 s, respectively.

Also, comparison of the regression lines among treatments for the linear giving-up time rule analyses produced no significantly different slopes between any pair of lines (Table VI). This suggests that the relationship between giving-up times and pellet experience during a patch visit (Fig. 2) could be characterized by one set of linear functions. These linear functions are characterized by a common slope; the intercept decreases with increased environmental quality. The difference in intercepts is further demonstrated by the fact that at zero pellet experience giving-up time decreased with increased environmental quality (Fig. 2) as did overall giving-up time (Fig. 4).

Residence Times

As predicted by the linear residence time rule (Green 1980), average residence times for patch visits within an environment decreased with increased quality of the environment (experiments 4 and 5 were combined because they had the same treatment) (Spearman rank correlation $P < 0.05$, Daniel 1978; Fig. 5). Again, there was no evidence of one fixed residence time (Marschall et al. 1989).

Table VI. Test of differences in regression slopes among treatments for giving-up time versus pellet experience regression equations

Treatment	100 versus 50% C_{max}	75 versus 50% C_{max}	62.5 versus 50% C_{max}
100 versus 12.5% C_{max}			
<i>t</i> -value	1.95	2.00	-0.52
<i>df</i>	4	4	3
<i>P</i> < value	0.13	0.12	0.64
100 versus 50% C_{max}			
<i>t</i> -value	—	0.23	-2.11
<i>df</i>	—	4	3
<i>P</i> < value	—	0.84	0.13
75 versus 50% C_{max}			
<i>t</i> -value	—	—	-2.04
<i>df</i>	—	—	3
<i>P</i> < value	—	—	0.14

The regression equations tested are those described in Fig. 3.

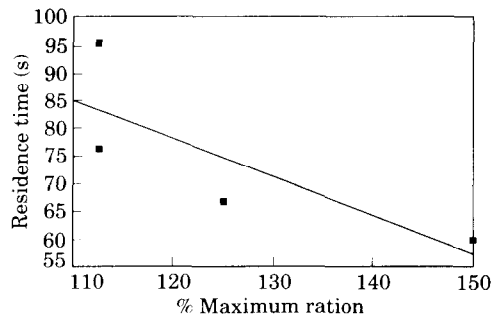


Figure 5. Average residence time during 2-h feeding periods plotted against the overall quality of an environment. Each point represents the average residence time/patch visit for all fish in each treatment during the last 3 days of each week of an experiment (combined) (regression equation: residence time (s) = $160.8 - 0.69 \times$ (total per cent C_{max} delivered to a tank), $r^2 = 0.63$, $N = 4$, $P < 0.21$).

As was the case for giving-up times, comparison of the regression lines among treatments of residence times produced no significantly different slopes between any pair of lines (Table VII). This suggests that the relationship between residence times and pellet experience during a patch visit (Fig. 3) would be characterized by one set of linear functions. These linear functions were characterized

Table VII. Test of differences in regression slopes among treatments for residence time versus pellet experience regression equations

Treatment	100 versus 50% C_{\max}	75 versus 50% C_{\max}	62.5 versus 50% C_{\max}
100 versus 12.5% C_{\max}			
<i>t</i> -value	0.06	-1.46	-0.31
<i>df</i>	4	4	4
<i>P</i> < value	0.96	0.22	0.78
100 versus 50% C_{\max}			
<i>t</i> -value	—	-1.10	-0.20
<i>df</i>	—	4	3
<i>P</i> < value	—	0.34	0.86
75 versus 50% C_{\max}			
<i>t</i> -value	—	—	0.70
<i>df</i>	—	—	3
<i>P</i> < value	—	—	0.54

The regression equations tested are those described in Fig. 5.

by a common slope while the intercept decreased with increasing environmental quality. The difference in intercepts is further demonstrated by the fact that at zero pellet experience residence time decreased with decreased environmental quality (Fig. 3) as did overall residence time (Fig. 5).

DISCUSSION

The bluegills in our experiments continuously updated their giving-up times with information both from their present experience and from their overall perception of the quality of patches within their environment. Bluegills tended to decrease their average giving-up times for both patches when the overall quality of their environment increased. Variation in the ability of individual fish to incorporate new information into their patch choices does not seem to strongly affect their response.

In our experiments, bluegills distributed their foraging time between two food patches within their environment. The maximum time bluegills would remain in a food patch without prey encounter (i.e. giving-up time) linearly increased with overall prey encounter during a patch visit. Once time since prey encounter reached the current maximum limit, bluegills left the patch. Of the five models of patch-leaving strategies discussed

(Charnov 1976; Green 1980; McNair 1982; Marschall et al. 1989 and our linear giving-up time rule), the one that best describes the observed bluegill behaviour in our study is the linear giving-up time rule. Unlike the Charnov (1976) and McNair (1982) models, our model incorporates a constant prey encounter rate (i.e. the organism does not experience patch depletion), and the foraging organism's lack of complete knowledge of its environment.

The assumption of complete knowledge of the environment is, perhaps, reasonable for birds, such as great tits (Krebs et al. 1974) and downy woodpeckers (Lima 1983), feeding on patches of relatively immobile prey whose distribution is fairly stable (Gibb 1966; Simms 1983). Thus, it is not surprising that the results of such studies have agreed with Charnov's (1976) model. But for generalist foragers such as bluegill sunfish (Carlander 1977), this assumption may be unreasonable. Studies of bluegills and their prey show that bluegills feed on a large variety of mobile prey which are highly variable both spatially and temporally (Keast 1978; Hall et al. 1979). So the assumption of complete knowledge of patch qualities is inappropriate for bluegills.

The general strategy of increased giving-up time with increased prey encounter in a patch was common throughout our experiments. Even when environmental quality and patch differences changed from experiment to experiment, the general pattern of increasing giving-up time with increased prey encounter persisted. The consistency of this general pattern is supported by the fact that this pattern seems to be accounted for by one basic linear relation.

Some of the conclusions from this study resemble those of Haccou et al. (1991), whose descriptive study of parasitic wasps searching for hosts in artificial arenas showed that the distribution of giving-up times depends on the number of hosts encountered in the patch. The foraging behaviour of parasitic wasps is complicated because wasps may sense the presence of hosts that they have not found, they attack but do not (generally) consume hosts, and they may recognize hosts that have been attacked and marked. Experiments by Waage (1979) have shown that foraging parasitic wasps are affected by the number of hosts they encounter and times at which the hosts are found. Even though the situation seems simpler for bluegills (i.e. bluegills have fewer variables to confuse them) bluegills still

behave in a manner similar to that of parasitic wasps.

The only difference between our observed results and predictions of the linear giving-up time rule is that of the initial giving-up time for visits to particular patches within an environment. Bluegills in our experiments seemed to prefer the patch of higher quality and they used a longer initial giving-up time when visiting that patch. Thus, the bluegill's memory of the quality of individual patches seems to affect its initial giving-up time, a factor which the linear giving-up time rule does not take into account.

Simulation runs of Green's linear residence time rule (Green 1984) show that even if the rule an organism uses in a particular environment may not be the best, often the rule may not significantly decrease the organism's prey intake below that which the best linear rule would produce. Thus, one general residence time rule seems to be very effective when environmental quality varies (Green 1984). Particular linear giving-up time rules are quite robust and they also would be effective in highly variable environments where food patch and/or environmental food qualities may sometimes change faster than they can be assessed (Keast 1978; Hall et al. 1979).

The final observed result of such a giving-up time rule, combined with memory of patch quality, is that the amount of time bluegills spend in a patch is roughly proportional to the patch's quality relative to overall environmental quality (i.e. matching, Wildhaber & Crowder 1991). It seems that approximate matching of overall patch usage and food availability is fairly insensitive to details of the foraging rule fish use, as long as it resembles a linear giving-up time rule. Even with significant differences in individual behaviour relative to overall giving-up times, the same patterns of increased giving-up time with increased food encounter and matching occur. The variation in individual giving-up times and the lack of individual variation in overall patch usage (Wildhaber & Crowder 1991) suggest some evolutionary flexibility. In our experiments, where resources were variable, matching of patch use to patch quality seems to be a good descriptor of overall time allocation among patches for foraging bluegills. More proximally, bluegills seem to use a flexible decision rule (e.g. a linear giving-up time rule), from which matching results.

In conclusion, the patterns of foraging behaviour we observed suggest bluegills have the ability to

continuously incorporate new information into their patch-leaving decisions. In natural systems, bluegills have been observed to change not only patch choice but also prey choice when other patches and/or prey types became more profitable (Werner & Mittlebach 1981; Werner et al. 1983). Thus, a linear giving-up time rule and the use of past information seems to give bluegills the ability to effectively exploit resources that vary both spatially and temporally using a simple decision rule.

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REFERENCES

- Baum, W. M. 1987. Random and systematic foraging, experimental studies of depletion, and schedules of reinforcement. In: *Foraging Behavior* (Ed. by A. C. Kamil, J. R. Krebs & H. R. Pulliam), pp. 587-607. New York: Plenum Press.
- Carlander, K. D. 1977. *Handbook of Freshwater Fishery Biology*. Ames: The Iowa State University Press.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.*, **9**, 129-136.
- Coutant, C. C. 1977. Compilation of temperature preference data. *J. Fish. Res. Bd Can.*, **34**, 739-745.
- Daniel, W. W. 1978. *Applied Nonparametric Statistics*. Boston: Houghton Mifflin.
- DeVries, D. R., Stein, R. A. & Chesson, P. L. 1989. Sunfish foraging among patches: the patch-departure decision. *Anim. Behav.*, **37**, 455-464.
- Gibb, J. A. 1966. Tit predation and the abundance of *Ernarmonia conicolana* (Heyl.) on Weeting Heather, Norfolk, 1962-1963. *J. Anim. Ecol.*, **35**, 43-54.
- Gill, J. L. 1978. *Design and Analysis of Experiments in the Animal and Medical Sciences. Vol. 2*. Ames: The Iowa State University Press.
- Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theor. Pop. Biol.*, **18**, 244-256.
- Green, R. F. 1984. Stopping rules for optimal foragers. *Am. Nat.*, **123**, 30-43.
- Green, R. F. 1987. Stochastic models of optimal foraging. In: *Foraging Behavior* (Ed. by A. C. Kamil, J. R. Krebs

- & H. R. Pulliam), pp. 273–302. New York: Plenum Press.
- Green, R. F. 1990. Putting ecology back into optimal foraging theory. *Comments Theor. Ecol.*, **1990**, 387–410.
- Haccou, P., de Vlas, S. J., van Alphen, J. J. M. & Visser, M. E. 1991. Information processing by foragers: effects on intra-patch experience on the leaving tendency of *Leptopilina heterotoma*. *J. Anim. Ecol.*, **60**, 93–106.
- Hall, D. J., Werner, E. E., Gilliam, J. F., Mittelbach, G. G., Howard, D., Doner, C. G., Dickerman, J. A. & Stewart, A. J. 1979. Diel foraging behaviour and prey selection in the golden shiner (*Notemigonus crysoleucas*). *J. Fish. Res. Bd Can.*, **36**, 1029–1039.
- Iwasa, Y., Higashi, M. & Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *Am. Nat.*, **117**, 710–723.
- Kamil, A. C., Krebs, J. R. & Pulliam, R. H. (Eds). 1987. *Foraging Behavior*. New York: Plenum Press.
- Keast, A. 1978. Feeding interrelation between age groups of pumpkinseed sunfish (*Lepomis gibbosus*) and comparisons with the bluegill sunfish (*L. macrochirus*). *J. Fish. Res. Bd Can.*, **35**, 12–17.
- Krebs, J. R., Ryan, J. C. & Charnov, E. L. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Anim. Behav.*, **22**, 953–964.
- Lima, S. L. 1983. Down woodpecker foraging behavior: foraging by expectation and energy intake rate. *Oecologia (Berl.)*, **58**, 232–237.
- Lima, S. L. 1984. Downy woodpecker foraging behavior: efficient sampling in simple stochastic environments. *Ecology*, **65**, 166–174.
- MacArthur, R. H. & Pianka, E. R. 1966. On optimal use of a patchy environment. *Am. Nat.*, **100**, 603–609.
- McNair, J. N. 1982. Optimal giving-up times and the marginal value theorem. *Am. Nat.*, **119**, 511–529.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theor. Pop. Biol.*, **21**, 269–288.
- Marschall, E. A., Chesson, P. L. & Stein, R. A. 1989. Foraging in a patchy environment: prey-encounter rate and residence time distributions. *Anim. Behav.*, **37**, 444–454.
- Neill, W. H., Magnuson, J. J. & Chipman, G. D. 1972. Behavioral thermoregulation by fishes: a new experimental approach. *Science*, **176**, 1443–1445.
- Oaten, A. 1977. Optimal foraging in patches: a case for stochasticity. *Theor. Pop. Biol.*, **12**, 263–285.
- Pearson, E. S. & Stephens, M. A. 1962. The goodness-of-fit tests based on W^2_N and U^2_N . *Biometrika*, **49**, 397–402.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *A. Rev. Ecol. Syst.*, **15**, 523–575.
- Seshadri, V., Csorgo, M. & Stephens, M. A. 1969. Tests for the exponential distribution using kolmogorov-type statistics. *J. R. Statist. Soc.*, **31**, 499–509.
- Simms, E. 1983. *A Natural History of British Birds*. London: J. M. Dent.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. New York: W. H. Freeman.
- Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Waage, J. K. 1979. Foraging for patchily distributed hosts by the parasitoid, *Nemeritis canescens*. *J. Anim. Ecol.*, **48**, 353–371.
- Werner, E. E. & Mittelbach, G. G. 1981. Optimal foraging: field test of diet choice and habitat switching. *Am. Zool.*, **21**, 813–829.
- Werner, E. E., Mittelbach, G. G., Hall, D. J. & Gilliam, J. F. 1983. Experimental test of optimal habitat use in fish: the role of relative habitat profitability. *Ecology*, **64**, 1525–1539.
- Wildhaber, M. L. & Crowder, L. B. 1991. Mechanisms of patch choice by bluegills (*Lepomis macrochirus*) foraging in a variable environment. *Copeia*, **1991**, 445–460.

Errata

Anim. Behav., 1990, **39**, 63–69

There is a mistake in expression (11) in Appendix 1 of Sibly et al., which should read:

$$\{(1 - e^{-\lambda_s t_0})[(1 - e^{-\lambda_s t_0})s_{N_s}^2 + 2N_s t_0 e^{-\lambda_s t_0} s_{N_s} s_{\lambda_s} C_{N_s \lambda_s}] + N_s^2 t_0^2 e^{-2\lambda_s t_0} s_{\lambda_s}^2\}^{1/2}$$

Anim. Behav., 1994, **47**, 501–513

In Table II of Wildhaber et al. the footnote should read 'N=16 (for experiment 4 N=15; for experiments 4 and 5 combined N=31)'.

In Fig. 3 caption 'giving-up' time should be replaced with 'residence' time.

In Table VI the footnote should read 'The regression equations tested are those described in Fig. 2' and Table VII footnote should read 'The regression equations tested are those described in Fig. 3'.