TEMPORAL CHARACTERISTICS OF FORAGING MOVEMENTS IN BLACK-CAPPED CHICKADEES

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Abstract.—The present study examined the temporal characteristics of the foraging movements of free-ranging Black-capped Chickadees (*Poecile atricapillus*) in a mixed-coniferous forest in central Maine to investigate how patterns of patch persistence in the wild compared with observations from controlled experiments. Persistence in trees, as measured by the amount of time from the last prey capture attempt in a tree until exit from that tree, was positively correlated with the average amount of time between capture attempts in those trees. These observations agree with the results of controlled experiments showing more patch persistence in the face of unsuccessful search when initial patch quality is low than when it is high. Greater persistence in initially lower quality patches is consistent with the following two hypotheses about patch leaving decision rules: (1) a bird leaves a patch when the estimated interval since the last prey capture reaches some value relative to the estimated mean inter-capture interval in the environment (a flexible giving-up time hypothesis) or (2) a bird leaves a patch when the estimated probability of capturing a prey in the next capture attempt falls below that estimated for the whole environment (a capture-probability hypothesis).

CARACTERÍSTICAS TEMPORALES DE LOS MOVIMIENTOS DE BÚSQUEDA EN *POECILE ATRICAPILLUS*.

Sinopsis.—Este estudio examina las características temporales de los movimientos de búsqueda en individuos de *Poecile atricapillus* libres en un bosque conífero mixto en el centro de Maine para investigar como los patrones de persistencia de parchos en condiciones libres compararon con las observaciones de experimentos controlados. La persistencia en árboles, medida por la cantidad de tiempo fesde el último esfuerzo en capturar presa en un árbol hasta la salida de ese árbol, fué correlacionada positivamente con la cantidad de tiempo promedio entre esfierzo de captura en esos árboles. Estas observaciones coinciden con los resultados de experimentos controlados que muestran mayor persistencia en parchos al enfrentarse con búsquedas poco exitosas cuando la calidad de parcho es baja que cuando es alta. La mayor persistencia en parchos inicialmente de baja calidad es consistente con las siguientes dos hipótesis sobre reglas para determinar si dejar los parchos: (1) un ave deja un parcho si el intérvalo estimado desde su última presa capturada llega a algún valor relativo al intérvalo estimado entre capturas en el ambiente (una hipótesis sobre tiempo flexible para darse por vencido), o (2) un ave deja un parcho cuando la probabilidad estimada de capturar una presa en el próximo intento de captura cae bajo la probabilidad estimada para todo el ambiente (una hipótesis de probabilidad de captura).

Members of the family Paridae foraging in the forest face a spatial matrix of leaves, twigs, branches, limbs, trees, and groups of trees. Local concentrations of prey items (i.e., prey patches) could occur at all levels of this spatial hierarchy. Individuals that possess traits allowing them to locate and concentrate upon locations with higher prey densities may gain an advantage in terms of survivorship and reproductive success (MacArthur and Pianka 1966, Schoener 1971, Stephens and Krebs 1986, Ste-

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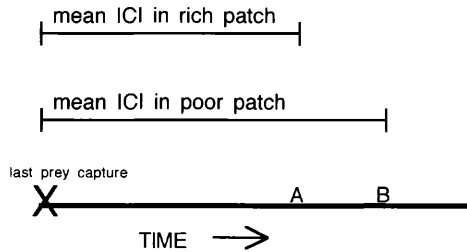
FIGURE 1.   An illustration of the predictions of a flexible giving-up time hypothesis. ICI is the estimated mean inter-capture interval, "A" is the time of patch exit from an initially rich patch, and "B" is the time of patch exit from an initially poor patch.

phens 1990). Because the selection of feeding sites is an important component of parid ecology, information on prey patch-selection decision rules will be valuable in understanding their niches, their interaction with guild members, and their role in the forest community.

One important component of patch selection is the "decision" of how long to remain in one patch before moving on to a new site (Smith 1991, Roche and Glanz 1996). Controlled experiments on patch persistence in parids have observed the following: (1) a tendency to display longer giving-up times (the interval from the last prey capture until patch exit) when the travel time to alternative patches is longer (Cowie 1977), (2) a tendency to display longer giving-up times when the mean quality of patches in the environment is low (Krebs et al. 1974), and (3) a tendency to display longer giving-up times (Roche 1996), or more prey-capture attempts when faced with unsuccessful search (Ydenberg 1984), when the initial prey density in a depleting patch is low.

There are two proposed hypotheses of patch persistence that are consistent with empirical findings. One possibility is that a bird leaves a patch when the estimated interval since the last prey capture reaches some value relative to the estimated mean inter-capture interval in the environment (a flexible giving-up time hypothesis; Brunner et al. 1992; 1996; Roche 1996; Roche et al. 1996, 1998). This hypothesis (Fig. 1) predicts that when a bird is in an initially poorer patch, the mean inter-capture interval estimated for the environment will be longer than it will be in a rich patch (i.e., it will be lengthened by the long inter-capture intervals experienced in the poor patch). The longer mean inter-capture interval will cause the bird to leave the patch less quickly (e.g., at "B") than it would in an initially rich patch (e.g., at "A") (Fig. 1).

Alternatively, a bird may leave a patch when the estimated probability of capturing prey in the next time interval, or in the next capture attempt, falls below that estimated for the environment as a whole (a capture-probability hypothesis; McNamara and Houston 1980, Stephens and Krebs 1986, Kacelnik et al. 1987, Roche 1996, Roche et al. 1996). This hypothesis predicts (Fig. 2) that foraging animals should be more persistent in initially poorer sites because estimated capture probability drops
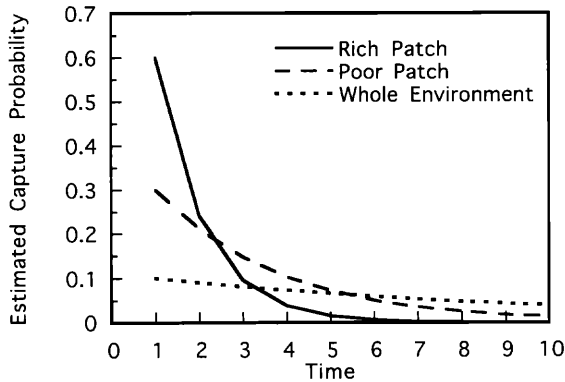
FIGURE 2.   The decline in estimated capture probability predicted by the capture-probability model in a rich patch, a poor patch, and in the environment as a whole, in the face of unsuccessful search (Roche 1996). Note that estimated capture probability in the initially poor patch takes longer to decline to that found in the whole environment than the estimated capture probability in the initially rich patch.

more slowly in initially poor patches than in initially rich patches (see Roche 1996). Both hypotheses predict that it takes longer to discern a decline in capture rate when the rate is initially low than when it is initially high. This information constraint produces greater patch persistence in initially rich patches (Nevin 1979, McNamara and Houston 1980).

Both the flexible giving-up time hypothesis and the capture-probability hypothesis require birds to assess patch quality. The flexible giving-up time hypothesis predicts that quality is assessed by forming an estimate of the mean inter-capture interval. The capture-probability hypothesis predicts that quality is assessed by an estimate of capture probability, based on the estimated capture rate immediately after the last capture and the amount of time since that last capture. Possibilities for how inter-capture intervals could be assessed include an arithmetic mean and a harmonic mean (Killeen 1984, 1991; Dow and Lea 1987; Kacelnik and Bateson 1996). Possibilities for how the rate of prey capture could be assessed include what are called the ratio of expectations and the expectation of ratios (Templeton and Lawlor 1981, Harder and Real 1987, Bateson and Kacelnik 1995, Kacelnik and Bateson 1996, Real 1996). The ratio of expectations averages all energy intake over some memory window (Real 1996) and divides it by the duration of that memory window. The expectation of ratios, on the other hand, averages energy intake divided by handling/consumption time for each capture, and then sums these individual averages (see Methods).

Although laboratory and aviary studies have provided important information about the patch persistence of parids in simplified environments, a complete understanding of the patch persistence of parids requires data on their free-ranging foraging behavior and information on how closely their behavior in the wild parallels that in controlled situations. The pres-

ent study had two purposes. The first purpose was to examine temporal characteristics of foraging movements in free-ranging Black-capped Chickadees (*Poecile atricapillus*) to document their residence times on different spatial levels (i.e., on branches and trees) and to see how these residence times compared with residence times in artificial patches in controlled experiments. The second purpose was to investigate whether or not birds in the wild display a pattern of patch persistence observed in controlled situations (i.e., the pattern of shorter giving-up times in initially richer patches).

METHODS

Individual Black-capped Chickadees were observed in mixed-coniferous forest in the University of Maine's University Forest and DeMeritt Forest on Marsh Island in Orono, Maine, an area that exceeded 4.4 km². Observations were made during all months except August. Thirty-two, 3-h observation periods were conducted between June 1992 and May 1995; observation periods were arranged to sample the period 0800–1700 h EST approximately equally. The observer walked in the forest until a chickadee or a group of chickadees was located. The observer then conducted continuous, focal sampling on an individual bird with binoculars, following the behavior of that individual bird for as long as the bird remained in view. The observer made a record of the following events by speaking into a tape recorder: (1) the beginning of an observation of a new individual, (2) the entry of the focal bird onto a new branch, (3) the entry of the focal bird into a new tree, (4) a prey attack movement by the focal bird, (5) the exit from a tree by the focal bird, and (7) the disappearance of the focal bird from direct view. Tape recordings were later transcribed into an event-recorder program.

The observed chickadees generally foraged by gleaning arthropods from the bark and foliage of trees. Prey were often small and identification of prey was difficult (Robinson and Holmes 1982). Nevertheless, we assumed that prey attack movements were precipitated by visual recognition of a prey item within a focal area by a bird (Robinson and Holmes 1982); therefore the number of attack movements per time should be closely related to the birds' estimate of the density of prey in a tree and should be highly correlated with capture rate. Entry of a bird onto the trunk of a tree was recorded as entry onto a branch. Birds flew to the ground rarely; when they did, the event was recorded as exit from a tree. When a bird became lost to view, the observer looked for a different individual chickadee or a different group of chickadees.

From the observations for individual birds we calculated the following: (1) the mean branch residence time per tree for individual birds, (2) the mean tree residence time, (3) the mean rate of attack movements per tree, and (4) the mean interval between attack movements per tree. In addition, we calculated the mean interval between attack movements, the mean rate of attack movements, and the mean giving-up time (the interval from the last attack movement until tree exit) in trees in which three

or more attack movements were observed. Data on foraging in individual trees were only used if the focal bird was observed continuously from tree entry until tree exit. If more than one complete tree residence time was observed for one bird a mean tree residence time was calculated for that bird. In these instances, mean branch residence times, mean intervals between attack movements, and mean rates of attack movements were calculated for each tree; a grand mean of these variables was taken of these within-tree means for the individual bird.

Data used to compare giving-up times from trees with the intervals between attack movements in those trees were only used if a bird made three or more attack movements in the tree. Most observations did not meet this criterion. In addition, if more than one complete tree visit with more than three attack movements was observed for one bird, only the first visit was used in the comparison of giving-up times and mean intervals between attack movements to avoid pseudoreplication.

We recorded 225 total bird observations, 145 observations in which complete tree residence times were observed (37, 43, 38, and 27 for fall, winter, spring and summer, respectively) and 29 bird observations in which more than three attack movements were observed. We avoided pseudoreplication by not watching individual birds more than once at an individual site on an individual day and by sampling many different sites of a large area.

Giving-up times were compared with intervals between attack movements and with rate of attack movements using linear regression. All other comparisons were made with one-way analysis of variance (ANOVA) and Tukey pairwise comparisons (Sokal and Rohlf 1995). To examine how temporal information may have been assessed, we calculated both the arithmetic mean and the harmonic mean of the intervals between attack movements. To examine how rate information may have been assessed, we calculated both the ratio of expectations and the expectation of ratios of the rate of attack movements. The ratio of expectations is calculated as follows:

$$RoE = \Sigma C_i / \Sigma T_i \qquad (1)$$

where C_i is the number of attack movements in interval I (i.e., 1) and T_i is the duration of the intervals between attack movements (interval I) (Bateson and Kacelnik 1995). The expectation of ratios is calculated as follows:

$$EoR = (\Sigma(C_i / T_i)) / n \qquad (2)$$

where n is the number of intervals between attack movements (Bateson and Kacelnik 1995).

<center>RESULTS</center>

General temporal patterns during all tree visits.—The mean residence time on branches was 5.2 s ($\pm$ 0.5 SE) and the mean residence time in trees was 21.4 s ($\pm$ 1.8 SE). There was a significant difference in the mean
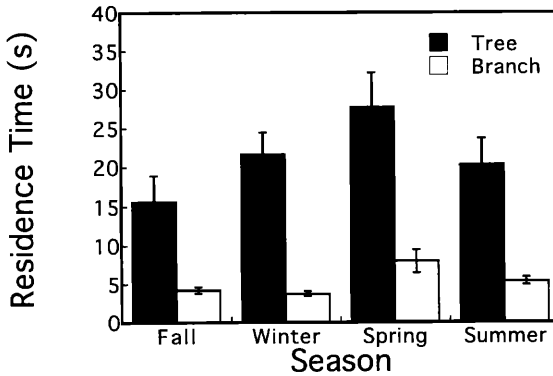
FIGURE 3.   Mean residence time on branches and in trees (± 1 SE) in the four seasons for
    Black-capped Chickadees in Orono, Maine USA.

residence time on branches among seasons (ANOVA; $F_{3,141}$ = 4.743, $P <$ 0.01). Mean residence time on branches in the spring was longer than in the fall (Tukey test; $P < 0.05$) and winter (Tukey test; $P < 0.01$) (Fig. 1). Mean residence times on trees did not differ among seasons (ANOVA; $F_{3,141}$ = 2.028, $P > 0.05$) (Fig. 3). Mean rate of attack movements per tree was 0.053/s (± 0.008 SE). Mean rate of attack movements per tree (as calculated by the ratio of expectations) differed by season (ANOVA; $F_{3,141}$ = 6.852, $P < 0.001$) (Fig. 4). Mean rate of attack movements per tree in the spring (as calculated by the ratio of expectations) was higher than in the fall (Tukey test; $P < 0.01$) and winter (Tukey test; $P < 0.001$).

Persistence in trees during tree visits with three or more attack movements.— The arithmetic mean of the interval between attack movements in trees was 8.2 s (± 1.1 SE) and the arithmetic mean of giving-up times from trees was 8.5 s (± 1.7 SE). Neither giving-up times nor the arithmetic
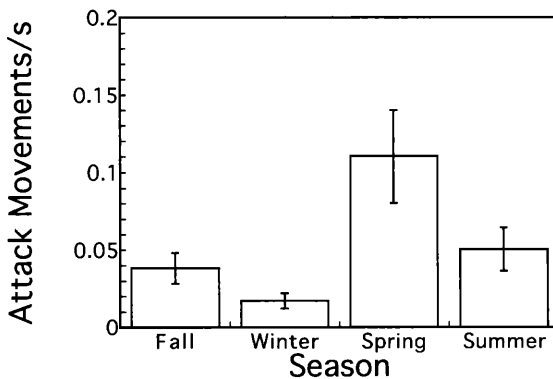

FIGURE 4.   Mean number of attack movements per second per tree (± 1 SE) in the four
    seasons for Black-capped Chickadees in Orono, Maine USA.

TABLE 1. Linear regression analyses comparing observed giving-up times of Black-capped Chickadees from trees with measures of mean interval between attack movements and rate of attack movements experienced in those trees (GUT = giving-up time and IBA = interval between attack movements).

Variables compared	$F_{1,27}$	R^2	P
GUT and arithmetic mean of IBA	12.57	0.32	0.001
GUT and harmonic mean of IBA	28.25	0.51	<0.001
GUT and last IBA	2.87	0.10	>0.05
GUT and ratio of expectations	5.89	0.18	<0.05
GUT and expectation of ratios	3.44	0.11	>0.05

mean of intervals between attack movements showed seasonal differences (ANOVA: $F_{3,25}$ = 0.159, P > 0.05 and $F_{3,25}$ = 0.764, P > 0.05, respectively).

Giving-up times in trees for individual birds were positively correlated with the arithmetic mean of the intervals between attack movements birds experienced in those trees (Table 1). Thus, when intervals between attack movements were longer, chickadees tended to be more persistent in trees after the last attack movement. Giving-up times in trees were also positively correlated with the harmonic mean of the intervals between attack movements and the ratio of expectations experienced in those trees (Table 1). The highest proportion of the variance in the giving-up time was explained by the harmonic mean of the intervals between attack movements (Table 1). Giving-up times in trees were not significantly correlated with the interval between the last two capture attempts, or with the expectation of ratios, experienced in those trees (Table 1). The residence times in trees were positively correlated with the ratio of expectations experienced in those trees (Linear regression: $F_{1,27}$ = 18.407, R^2 = 0.405, P < 0.001, n = 29). Therefore, chickadees tended to remain longer overall, but were less persistent in the face of unsuccessful search, in trees in which the rate of attack movements was higher.

DISCUSSION

Temporal characteristics of foraging in lab and field.—Mean tree residence times that we observed in free-ranging chickadees were shorter than patch residence times in controlled experiments for Black-capped Chickadees (Roche 1996) and Great Tits (Cowie 1977) (Table 2). Thus, free-ranging chickadees tended to spend less time in a feeding site (at the spatial level of the tree) with which they could gather sampling information than captive parids in the studies of Roche (1996) and Cowie (1977). Observed residence times of chickadees on branches averaged only 5.2 s, indicating that little sampling information could be collected from individual branches. Because much more sampling information could be collected on the quality of trees than of branches, the chickadees may respond to patchiness more on the level of the tree than on smaller spatial levels.

Future tests of patch selection in captive parids may benefit from setting

TABLE 2.   Mean residence times and giving-up times in wild chickadees compared with those of captive parids in four experimental studies.

Study (species)	Residence time(s)	Giving-up time(s)
Present study (*P. atricapillus*)		
Branch	5.2	—
Tree	21.4	8.5
Krebs et al. 1974: exp. I (*P. atricapillus*)		
Poor Environment	NA[a]	15.68
Rich Environment	NA	11.07
Krebs et al. 1974: exp. II (*P. atricapillus*)		
Poor Environment	NA	11.38
Rich Environment	NA	7.56
Roche 1996 (*P. atricapillus*)		
Poor Patch	115.8	37.8
Rich Patch	117.6	13.0
Cowie 1977 (*P. major*)		
Poor Environment	73.67	NA
Rich Environment	45.80	NA

[a] NA = not available.

or interpreting residence times in artificial patches in light of the residence times observed in free-ranging parids. In addition, future efforts at modeling patch assessment and patch persistence may benefit from considering the specific temporal movement patterns observed in the wild for specific species.

The mean of 3.18 attack movements per minute in the present study is comparable to the range of 1.4–5.6 attack movements per minute observed in 10 species of insectivorous birds in the Hubbard Brook Experimental Forest in New Hampshire by Robinson and Holmes (1982).

Patch selection and patch assessment.—Chickadees tended to display longer giving-up times when the mean interval between attack movements was longer, and the arithmetic mean of the rate of attack movements was greater, within a tree (Nevin 1979, Kacelnik et al. 1987). This observation agrees with the findings of controlled experiments in which parids displayed greater persistence in patches offering initially lower prey densities (Ydenberg 1984, Roche 1996).

The observed correlation between giving-up times and the mean interval between attack movements (and the mean rate of attack movements) agree with the predictions of both the flexible giving-up time hypothesis and the capture-probability hypothesis. It is difficult to differentiate quantitatively between these two hypotheses with data from the present study because it is not known what the inter-capture intervals experienced in alternative trees were for many of the individual birds. Nevertheless, the observed pattern does not agree with alternative hypotheses predicting that birds leave a patch after a fixed number of prey have been captured

(fixed-number hypothesis), after a fixed residence time has elapsed (fixed-residence-time hypotheses), or after a fixed interval of unsuccessful search (fixed-giving-up-time hypothesis) (Gibb 1958, Stephens 1990, Roche 1996).

The greater persistence observed in initially poorer patches gives us information about the constraints on behavioral adaptations for efficient foraging behavior. To spend a longer amount of time in a poor patch that has been depleted is inefficient in terms of lost potential captures in other patches. This inefficiency may be particularly costly in the winter when the energetic demands of staying warm are high, food availability is low, and the hours of daylight available for foraging are limited. Yet this inefficiency is unavoidable because animals are constrained to information gathered from experience (Stephens and Krebs 1986).

The two averages of the interval between attack movements (the arithmetic mean and the harmonic mean) explained more of the variance in giving-up time than the capture attempt rate as measured by the ratio of expectations. Therefore, there is more support for the hypothesis that the chickadees were basing their patch-leaving decisions on assessment of intervals between attack movements than on rate of attack movements. More of the variance in giving-up time was explained by the harmonic mean of the interval between capture attempts than by the arithmetic mean of the interval between attack movements. This observation is consistent with the hypothesis that the chickadees' averaging mechanism approximates a harmonic mean more closely than an arithmetic mean (Roche et al. 1998). Note that birds may base patch-leaving decisions on multiple types of information and the degree to which these types of information are weighed could change in different situations (Kamil et al. 1988). Note also that the average that accounted for the highest proportion of the variance in giving-up time still accounted for only 51.1% of the variance. The rest of the variance may have been a result of variation in the quality of recently visited trees and variation in the energy content of individual prey. Factors such as predator avoidance (Lima 1985, Lima and Dill 1990, Suhonen 1993), territorial defense (Ydenberg 1987), and an individual's place in the flock's dominance hierarchy (Glase 1973, Pierce and Grubb 1981, Ekman and Askenmo 1984, Desrochers 1989) could add additional variance to giving-up times (see also Lucas 1987).

Summary.—Most patch-choice models have treated simplified situations in which patches can be easily differentiated and are similar in size. The patchiness faced by bark-gleaning forest birds is more complicated, both because the delineation of spatial levels is often more vague in the forest and because there are many types of potential information available that may give cues about prey density (Lucas 1987). Parids have been observed to use different types of information in their selection of feeding sites, including information provided from sampling (e.g., Krebs et al. 1974, Krebs et al. 1978, Ydenberg 1984, Roche 1996), from visual cues (Heinrich and Collins 1983), from type of tree species (Willson 1970, Morse

1978, Heinrich and Collins 1983), and from type of substrate (Robinson and Holmes 1982). Because patch selection in parids is complex, to develop a complete understanding of their the selection of feeding sites will require the integration of theoretical syntheses, observational and comparative studies, and empirical tests examining how parids assess their environments and how they integrate different types of information.

ACKNOWLEDGMENTS

LITERATURE CITED

BATESON, M., AND A. KACELNIK. 1995. Preferences for fixed and variable food sources: variability in amount and delay. J. Exper. Anal. Behav. 63:313–329.
BRUNER, D., A. KACELNIK, AND J. GIBBON. 1992. Optimal foraging and timing processes in the starling, *Sturnus vulgaris:* effect of inter-capture interval. Anim. Behav. 44:597–613.
———, ———, AND ———. 1996. Memory for inter-reinforcement interval variability and patch departure decisions in the starling, *Sturnus vulgaris.* Anim. Behav. 51:1025–1045.
COWIE, R. J. 1977. Optimal foraging in great tits *(Parus major).* Nature 268:137–139.
DESROCHERS, A. 1989. Sex, dominance and microhabitat use in wintering black-capped chickadees: a field experiment. Ecology 70:636–645.
DOW, S. M., AND S. E. LEA. 1987. Foraging in a changing environment: simulations in the operant laboratory. Pp. 89–113, *in* M. L. Commons, A. Kacelnik, and S. J. Shettleworth, eds. Quantitative analyses of behavior, vol. VI: foraging. Erlbaum, Hillsdale, New Jersey.
EKMAN, J. B., AND C. E. H. ASKENMO. 1984. Social rank and habitat use in willow tit groups. Anim. Behav. 32:508–514.
GIBB, J. A. 1958. Predation by tits and squirrels on the eucomosid *Ernarmonia conicolana* (Heyl.). J. Anim. Ecol. 27:375–396.
GLASE, J. C. 1973. Ecology of social organization in the black-capped chickadee. Living Bird 12:235–267.
HARDER, L., AND L. A. REAL. 1987. Why are bumble bees risk averse? Ecology 68:1104–1108.
HEINRICH, B., AND S. L. COLLINS. 1983. Caterpillar leaf damage and the game of hide-and-seek with birds. Ecology 64:592–602.
KACELNIK, A., AND M. BATESON. 1996. Risky theories: the effects of variance on foraging decisions. Amer. Zool. 36:402–434.
———, J. R. KREBS, AND B. ENS. 1987. Foraging in a changing environment: an experiment with starlings *(Sturnus vulgaris).* Pp. 63–87, *in* M. L. Commons, A. Kacelnik, and S. J. Shettleworth, eds. Quantitative analyses of behavior, vol. VI: foraging Erlbaum, Hillsdale, New Jersey.
KAMIL, A. C., S. I. YOERG, AND K. C. CLEMENTS. 1988. Rules to leave by: patch departure in foraging blue jays. Anim. Behav. 36:843–853.
KILLEEN, P. R. 1984. Incentive theory III: adaptive clocks. Ann. N. Y. Acad. Sci. 423:515–527.
———. 1991. Behavior's time. Psychol. Learn. Motiv. 27:295–334.
KREBS, J. R., J. C. RYAN, AND E. L. CHARNOV. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22:953–964.
———, A. KACELNIK, AND P. J. TAYLOR. 1978. Optimal sampling by foraging birds: an experiment with great tits *(Parus major).* Nature 275:27–31.
LIMA, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. Oecologia 66:60–67.
———, AND L. M. DILL. 1990. Behavioral decisions under the risk of predation: a review and prospectus. Can. J. Zool. 68:619–640.

LUCAS, J. R. 1987. The influence of time constraints on diet choice of the great tit, *Parus major*. Anim. Behav. 35:1538–1548.

MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. Am. Nat. 100:603–609.

MCNAMARA, J., AND A. I. HOUSTON. 1980. The application of statistical decision theory to animal behavior. J. Theor. Biol. 85:673–690.

MORSE, D. H. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. Ibis 120:298–312.

NEVIN, J. A. 1979. Reinforcement schedules and response strength. Pp. 117–158, *in* M. D. Zeiler and P. Harzem, eds. Advances in the analysis of behavior, vol. I: reinforcement and the organization of behavior. Wiley, New York.

PIERCE, V., AND T. C. GRUBB, JR. 1981. Laboratory studies of foraging in four bird species in deciduous woodland. Auk 98:307–49.

REAL, L. A. 1996. Paradox, performance, and the architecture of decision-making in animals. Amer. Zool. 36:518–529.

ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among several tactics, diet, and habitat structure. Ecology 63:1918–1931.

ROCHE, J. P. 1996. Patch-leaving decisions in black-capped chickadees. Anim. Behav. 52:289–298.

———, AND W. E. GLANZ. 1996. Prey patch selection in titmice. Conn. Warbler: J. Conn. Ornith. 16:111–117.

———, D. A. STUBBS, AND W. E. GLANZ. 1996. Assessment and choice: an operant simulation of foraging in patches. J. Exper. Anal. Behav. 66:327–347.

———, W. TIMBERLAKE, W. E. GLANZ, AND D. A. STUBBS. 1998. The influence of current-visit experience within a prey patch on patch persistence. Behav. Proc. 43:11–25.

SCHOENER, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

SMITH, S. M. 1991. The Black-capped Chickadee. Cornell Univ. Press, Ithaca, New York.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. W. H. Freeman, New York.

STEPHENS, D. W. 1990. Foraging theory: up, down, and sideways. Stud. in Avian Biol. 13:444–454.

———, AND J. R. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, New Jersey.

SUHONEN, J. 1993. Predation risk influences the use of foraging sites by tits. Ecology 74:1197–1203.

TEMPLETON, A. R., AND L. R. LAWLOR. 1981. The fallacy of the averages in ecological optimization theory. Am. Nat. 117:390–393.

WILLSON, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169–174.

YDENBERG, R. C. 1984. Great tits and giving-up times: decision rules for leaving patches. Behaviour 90:1–24.

———. 1987. Foraging vs. territorial vigilance: the selection of feeding sites by male great tits. (*Parus major* L.). Ethology 74:33–38.