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USING ARTIFICIAL FOOD PATCHES TO EVALUATE HABITAT QUALITY FOR GRANIVOROUS BIRDS: AN APPLICATION OF FORAGING THEORY[1]

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The distribution of food and predators plays an important part in spatial behavior and population dynamics of animals in natural habitats (Stephens and Krebs 1986). However, estimating food availability or predation risk within different habitat types remains a formidable task in ecological studies, largely due to difficulties associated with evaluating habitats "through the eyes" of the organism. Recently, empirical tests of theoretical patch foraging models have been used to assess the relative values of habitats in field experiments (Brown and Alkon 1990, Kotler et al. 1991, 1994, Kohlmann and Risenhoover 1994). Assuming animals favor those resources or habitats providing the greatest net utility, rate-maximizing foragers should abandon a patch when the sum of all foraging costs equals foraging gains incurred in the patch. Because the relationship between harvest rate and resource density in depletable patches is normally asymptotic (i.e., functional response, Holling 1959), the relationship between foraging gains and foraging costs also is nonlinear. As resource density declines, each additional food item becomes more costly to harvest until the net benefit of exploiting a patch is zero and the animal abandons the patch. The harvest rate at this point is termed the "quitting harvest rate" which is functionally linked to the density of resources remaining in the patch or "giving-up-density" (GUD; Brown 1988). Thus, GUD should represent the resource density within a patch at which foraging gains equal foraging costs. Foraging cost in Brown's (1988) model is a cumulative term formalized as:

$$C_i + P_i + MOC_i \qquad (1)$$

where C_i is the energetic cost of exploiting the patch, P_i is the specific cost of predation in a patch, and MOC_i represents the patch specific "missed opportunity cost" (Brown 1988, Brown and Alkon 1990, Brown 1992). All these terms can be expressed in energy as the common currency (Caraco 1979, Stephens and Krebs 1986).

Theoretically, it should be possible to assess foraging costs in natural habitats by creating artificial patches containing a known density of resources and by measuring the GUDs in these patches after animals abandon them. This approach is based on the assumption that the forager balances its harvest rate in the artificial patch with habitat specific foraging costs, thus effectively treating the artificial patch as part of the natural environment. Hence, evaluation of habitat-specific elements of the cost function may be possible either by comparing GUDs among habitats and speculating on the effects of structural or physical differences on foraging costs imposed on the animal (Brown 1988, Abramsky et al. 1990, Brown and Alkon 1990, Brown et al. 1992a, 1992b), or by experimental manipulation of foraging costs (Kotler et al. 1991, 1992).

Here we report on two controlled experiments designed to evaluate the effects of different foraging costs (food abundance and cover from predation) on patch-use patterns of a granivorous bird, the Northern Bobwhite (*Colinus virginianus*). In the first experiment, we tested the hypothesis that exploitation of artificial patches by foraging Bobwhites was related to the availability of resources in the environment. We predicted Bobwhites would abandon artificial food patches at higher food density in rich, supplemented, environments compared to environments where resources were scarce. We also anticipated that GUDs in artificial patches should reflect the amount of augmented food available. In the second experiment, we tested the hypothesis that habitat structure and predation risk perceived by Bobwhites explained foraging decisions. Assuming that Bobwhites are capable of assessing habitat specific risk of predation, which may depend on the

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amount of cover (Klimstra and Roseberry 1975, Lehmann 1989), we predicted that Bobwhites would perceive predation risk to be higher in habitats lacking structural cover, and thus would constitute a foraging cost in equation (1). Consequently, Bobwhites should exploit food patches to lower resource densities in habitats augmented with structural cover (artificial brush piles), and they should abandon patches at higher resource densities in "risky" (open) habitats.

METHODS

Experiment 1 was conducted in a bunchgrass-annual forb community on sandy soils at the Rob and Bessie Welder Wildlife Foundation Refuge, near Sinton, Texas in May 1992. Trials were conducted in three portable field enclosures ($3 \times 3 \times 1.5$ m) constructed of a wooden frame and black plastic netting. Each enclosure contained a water source and was stocked with four commercially-raised, flight-conditioned female Bobwhites > 16 weeks of age. Birds were habituated to enclosures and experimental procedures for about 10 days prior to data collection, and the same individuals were kept together as a group for the duration of the experiment (6 days).

Each trial lasted 1 day and consisted of randomly assigning one of three supplementation treatments to each enclosure: no supplementation, low supplementation (200 g of crushed corn) or high supplementation (400 g of crushed corn). The crushed corn supplement was scattered evenly throughout the enclosure. Inside each enclosure, we placed four artificial patches consisting of a metal tray ($22 \times 22 \times 4$ cm) filled with 5 g of milo seeds thoroughly mixed into 400 ml of sand and covered by additional 200 ml sand. Each tray was placed in the center of one quarter of the enclosure. When placing trays, care was taken not to disturb vegetation. Each day before sunrise, we captured birds with a hand held net and moved the enclosures about 10 m to a new location within the meadow. Birds were then released back into the enclosures, and trays and supplemental feed (if any) were placed inside the enclosure. Trays were removed at sunset after 14 hours exposure time, transported to the laboratory, and remaining seeds were weighed to determine GUDs. Although the experiment was designed as a 3×3 factorial design with two replicates, the temporary escape of a group of birds resulted in an unbalanced design. Differences in mean GUD from all four seed trays per enclosure were examined through PROC GLM (SAS Institute 1989) using supplementation, day, enclosure and the interaction between enclosure and day as independent variables. By declaring "day" as a random effect, we obtained Satterthwaite correction for each fixed and random factor.

Experiment 2 investigated the effect of habitat structure on foraging decisions by Bobwhites and was conducted at the Poultry Research Center of Texas A&M University in March 1994. We used four aviaries (12 $\times$ 3 $\times$ 1.8 m) with wire floors 60 cm above ground, and each stocked with four female Bobwhites. Each enclosure was divided in two equal sized halves (6 $\times$ 3 $\times$ 1.8 m) and assigned augmentation with artificial cover patches to one half, while the other half offered no structural cover. The section offering structural cover was reversed in the adjacent aviary. Structural cover

consisted of five 20×20 cm plywood boards, suspended horizontally by strings from the cage ceiling 20 cm above the floor. On these suspended boards we piled cattail (*Typha* spp.), creating cone-shaped cover patches of ca. 80 cm diameter. Cover was distributed equally throughout the section of the aviary. No other vegetation occurred in the experimental enclosures. We placed ten trays (identical to trays used in Experiment 1), each containing 5 g of milo seed, inside each aviary. One tray was located under the center of each cover patch and at each corresponding location in the "open" portion of the enclosure. Trials started at approximately 07:00 and lasted 10 hr. At the end of a trial, trays were removed from aviaries and seeds were sifted and weighed. Thus each trial yielded five samples of GUD for each of the two treatment halves of the four enclosures. The experiment was repeated over six consecutive days. Differences in mean GUDs, calculated from five trays in each treatment ("cover" and "open"), were examined using day and enclosure as independent variables in analysis of variance. Significant differences in GUDs among supplementation levels were established using Tukey's HSD test. All analyses were performed using PROC GLM of SAS (SAS Institute Inc. 1989). We accepted a type-I error probability of 0.05 for all tests.

RESULTS

In Experiment 1, mean GUDs varied significantly with the level of supplementation ($F_{2,2} = 31.7$, $P < 0.001$), but not with day of trial ($F_{5,2} = 8.3$, $P = 0.11$), enclosure ($F_{2,2} = 9.1$, $P = 0.10$) or the interaction between supplementation and day of trial ($F_{6,2} = 8.8$, $P = 0.11$) (Table 1). Mean GUDs differed among supplementation levels, confirming our predictions that birds in supplemented enclosures would abandon patches at a higher density of seeds than birds in unsupplemented enclosures and the amount of food in the environment (0, 200 or 400 g of corn) affected GUDs in artificial patches.

In Experiment 2, we investigated mean GUDs in covered and open sections of each cage. We found no significant interaction between trial and individual aviary, hence we pooled all data and tested for GUD differences between covered and open habitats using a two-sample t-test. In all trials, mean GUDs were higher in "open" patches than in covered trays ($t = 8.06$, df = 102.5, $P < 0.001$; unequal variance: $F_{79,79} = 6.6$, $P < 0.001$, Table 2), indicating that birds abandoned patches without cover earlier and at higher seed densities than those offering cover.

DISCUSSION

These experiments showed that Northern Bobwhites responded to both food abundance and availability of structural cover. Birds abandoned patches earlier when supplementation offered increased quality of alternative foraging opportunities, or when lack of structural cover increased risk of predation. Previous experiments with Bobwhites foraging in these patches showed that harvest rates decline steeply when seed density falls below 1.5–2 g (authors' unpubl. data). The fact that most GUDs in both experiments were below this threshold suggests that birds were likely to experience rapidly declining harvest rates at the point of patch

TABLE 1. Effects of supplementation level (Experiment 1) on the mean ($\pm$ SE) giving-up density (GUD) by Northern Bobwhites foraging in artificial food patches. Different letters indicate significantly different means (Tukey test, $P < 0.05$).

Trial	Supplementation level		
	0 g	200 g	400 g
1	0.11 $\pm$ 0.01	0.28 $\pm$ 0.15	2.05 $\pm$ 1.48
2	0.61 $\pm$ 0.60	0.72 $\pm$ 0.69	2.21 $\pm$ 0.18
3	0.73 $\pm$ 0.65	1.67 $\pm$ 0.46	3.70 $\pm$ 0.23
4	0.18 $\pm$ 0.11	1.22 $\pm$ 0.32	4.10 $\pm$ 0.86
5	0.11 $\pm$ 0.11	0.60 $\pm$ 0.07	—
6	0.07 $\pm$ 0.03	1.65 $\pm$ 0.96	1.78 $\pm$ 0.93
Total	0.32[a] $\pm$ 0.10	1.23[b] $\pm$ 0.24	2.97[c] $\pm$ 0.36

abandonment. This is a critical requisite of Brown's (1988) model and optimality approaches to patch foraging theory in general (Charnov 1978). Consequently, type of patches (natural or artificial) or the number of foragers exploiting them does not affect the relevance of our results.

In Experiment 1, differences in GUDs represent the cost of "missed opportunity" of foraging elsewhere. A similar relationship between elevated GUDs and habitat augmentation has been found in several studies of mammalian foragers (Brown et al. 1992a, 1992b, Murden and Risenhoover 1993). Although birds foraged less in seed trays when supplementation offered alternative food resources, GUDs in artificial patches did not correlate linearly with the level of supplementation. However, because the marginal valuation of food depends heavily on the nonlinear relationship of harvest rate and resource density (functional response curve), the quantitative effect of MOC on quitting harvest rate is nonlinear.

In Experiment 2, birds responded to the presence of structural cover by exploiting patches to lower densities. Apparently, birds associated the presence of cover with reduced foraging costs compared to "open" patches. Had birds not perceived different foraging costs, GUDs should not have differed. Because seed densities in patches without cover were identical to those in covered patches, missed opportunity costs did not differ among covered and open patches. Thus, differences in foraging costs may be either due to different energetic costs of patch exploitation (C_i) or due to different predation risk (P_i). Energetic costs may include temperature or shade effects in covered patches. Daytime temperatures during the trials did not exceed thermal comfort limits for Bobwhites (Lehman 1989) and birds were occasionally observed basking in the sun at the edge of the cover, suggesting that cover was not preferred for thermo-regulatory reasons. In contrast, differences in foraging costs may have been related to differences in patch-specific predation risk perceived by Bobwhites. These findings parallel those from many studies of foraging decisions under predation (reviewed by Lima and Dill 1990) including field experiments (Holmes 1984, Brown and Alkon 1990, Brown et al. 1992, Kotler et al. 1994) and studies in aviaries (Kotler et al. 1991, Kotler et al. 1992). Although it may be

argued that captive-raised birds are perhaps naive compared to their wild conspecifics, one may still expect the fundamental nature of the relationship between marginal value of food items and environmental conditions to be similar. This experiment showed that neither previous exposure to predators nor the actual presence of a predator was necessary to elicit changes in patch use behavior. Although birds in these experiments were safe from predation and perhaps inexperienced about potential predation risks, they behaved in the predicted manner (i.e., they abandoned patches in the open earlier than those in cover).

Studies of patch use decisions of birds are rare compared with studies using mammalian foragers (Valone and Brown 1989, Valone 1991). Our experiments showed that the concept of a "quitting-harvest rate" and its correspondent GUD in artificial patches can elucidate foraging costs incurred by granivorous birds in natural habitats. By providing (energy) estimates of habitat specific foraging costs, it can serve as a independent test of habitat values derived from observation of habitat selection or population distribution. In order to apply this concept to experiments involving natural habitats and wild foragers, several points seem noteworthy: First, exploitation of artificial patches should not alter the relationship between foraging gains and foraging costs encountered in the habitat. Obviously, if foragers were more visible to predators inside trays or suffered other adverse effects from patches, then GUDs would reflect patch specific costs rather than habitat values. Birds in these experiments had ample experience with trays and foods and were presented with real alternatives from which birds made foraging decisions. This may not be the case for wild birds, which may react differently to artificial patches compared to native patches offering similar rewards. Furthermore, if only the most nutritionally stressed and vulnerable foragers in a wild population made use of

TABLE 2. Effects of structural cover (Experiment 2) on mean ($\pm$ SE) giving-up density (GUD) of Northern Bobwhites foraging in artificial food patches.

Trial	Aviary	n	GUD (open)	GUD (cover)
1	1	5	1.60 $\pm$ 0.18	0.46 $\pm$ 0.13
	2	5	1.07 $\pm$ 0.11	0.13 $\pm$ 0.08
	3	5	1.29 $\pm$ 0.07	0.19 $\pm$ 0.14
	4	5	1.92 $\pm$ 0.33	0.03 $\pm$ 0.01
2	1	5	0.21 $\pm$ 0.08	0.07 $\pm$ 0.02
	2	5	0.33 $\pm$ 0.09	0.25 $\pm$ 0.19
	3	5	0.77 $\pm$ 0.13	0.15 $\pm$ 0.05
	4	5	1.83 $\pm$ 0.17	0.27 $\pm$ 0.07
3	1	5	0.37 $\pm$ 0.07	0.09 $\pm$ 0.02
	2	5	0.35 $\pm$ 0.07	0.15 $\pm$ 0.07
	3	5	0.43 $\pm$ 0.13	0.08 $\pm$ 0.01
	4	5	0.61 $\pm$ 0.12	0.26 $\pm$ 0.16
4	1	5	0.38 $\pm$ 0.15	0.21 $\pm$ 0.07
	2	5	1.56 $\pm$ 0.23	0.66 $\pm$ 0.14
	3	5	0.51 $\pm$ 0.20	0.19 $\pm$ 0.14
	4	5	0.43 $\pm$ 0.05	0.29 $\pm$ 0.07
All trials			0.67 $\pm$ 0.12	0.27 $\pm$ 0.09

artificial patches, then GUDs would only represent the marginal valuation of artificial patches for this segment of the population and any systematic bias associated with that cohort's vulnerability will be reflected. Observation of marked animals could assist in evaluating such biases.

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