

USING VIGILANCE BEHAVIOR TO TEST WHETHER PREDATION PROMOTES HABITAT PARTITIONING¹

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Abstract. Predation could be responsible for habitat partitioning by species if different species are safest from predation in different habitats. Alternatively, predation cannot be responsible for habitat partitioning if all species rank the safety of habitats similarly. I developed predictions to test these two hypotheses, using data on the rates at which animals scan the environment for predators while they forage. Preliminary results suggest that predation is unlikely to be responsible for the habitat preferences of sparrow species wintering along an elevational gradient in the Sonoran Desert of southern California, USA.

Two predictions can be tested using vigilance behavior. (1) If species differ in which habitats they are safest from predation, some species will experience increased risk when moved from one habitat to another, whereas other species will experience decreased risk; changes in vigilance levels between habitats will be inconsistent among species. (2) If species are safest in the same habitat, they will experience similar changes in risk between habitats, and should exhibit similar changes in vigilance levels between habitats.

Sage Sparrows (*Amphispiza belli*) and Black-throated Sparrows (*A. bilineata*) spend the winter in different habitats. I recorded vigilance levels in each habitat while birds foraged on naturally occurring seeds in a portable aviary. Sage Sparrows and Black-throated Sparrows exhibited similar changes in vigilance between habitats, suggesting that these two species are safest in the same habitat, and that predation is unlikely to explain their habitat preferences.

Also, I tested and found support for the prediction from vigilance theory that food abundance affects vigilance level. Vigilance declined in response to increased foraging patch profitability, counter to the intuitive prediction that increased food abundance relaxes the threat of starvation, allowing more time for vigilance. This relationship between abundance and vigilance is explained by a simple model of starvation.

Key words: *bird behavior; California; elevational gradient; habitat distribution; predation risk; Sonoran Desert; sparrow; trade-off models; vigilance.*

INTRODUCTION

Seemingly simple factors that shape population abundances and distributions can be difficult to investigate. For example, predation is intimately linked to food supply if animals are at greater risk of predation while foraging than they are during other activities (McNamara and Houston 1986, 1987, 1994, Lima 1987b). Individual animals trade the risk of being killed by predators against the risk of starving. If this trade-off is optimized to maximize survival, changes in food supply may be reflected largely as changes in the level of predation, e.g., decreased food abundance increases the numbers of animals killed by predators (McNamara and Houston 1987). Hence, changes in predation risk cannot be distinguished reliably from changes in food supply by partitioning risks according to the numbers of deaths attributable to individual factors.

One method of distinguishing the extent to which

predation and food supply shape mortality is to study factors that contribute to risk: changes in food abundance, foraging success, energy budgets, and the risk of predation while foraging. An alternative method is to measure behavior that reflects changes in risks. For example, foraging birds frequently scan the environment for predators while they forage, and changes in vigilance levels can be used as a means of assaying the risk of predation while animals forage.

Here, I develop predictions, from changes in levels of vigilance, that might be used to make inferences about predation, and I use the predictions to test hypotheses about how predation shapes the habitat distributions of sparrows. Sage Sparrows (*Amphispiza belli*) and Black-throated Sparrows (*A. bilineata*) spend the winter in different habitats along an elevational gradient in the Sonoran Desert, California, USA (Weathers 1983, Repasky and Schluter 1994). Predation might shape species' habitat distributions in two ways: (1) species differ in which habitats are safest, and occupy different habitats because of predation risk (Mercurio et al. 1985); or (2) species are all safest in the same habitat and should have similar habitat distributions if predation shapes these distributions (e.g.,

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Mittelbach 1984, Longland and Price 1991). Briefly, testable predictions rest on the assumption that birds accurately perceive changes in predation risk as they are experimentally moved between habitats, and that changes in perception are reflected in vigilance levels. If species differ in their perceptions of habitat safety, some species should increase vigilance when moved from one habitat to another, whereas other species should decrease vigilance, as predation risk increases for some species and declines for others. In contrast, if species perceive similar changes in predation risk between habitats, then they should exhibit similar changes in vigilance when experimentally moved between habitats. I measured qualitative changes in vigilance levels of species between habitats, using an experimental enclosure.

In the course of testing the two described hypotheses, I also tested a prediction, stemming from the theory of vigilance, that has not been tested previously in the field. Vigilance for predators is assumed to occur at the expense of food intake, and the amount of vigilance that maximizes survival depends upon both the risk of being killed by predators and the risk of starving (McNamara and Houston 1986, 1987, 1994, Lima 1987*b*). Predictions of the theory of vigilance have been tested by measuring changes in vigilance in response to changes in factors that should affect predation risk (e.g., Lima 1987*a*, Lendrem 1983; see also Lima and Dill 1990). Predictions of how vigilance should respond to changes in food abundance have not been tested.

Predation, starvation, and vigilance

One prediction regarding vigilance is useful for testing hypotheses about how predation shapes the habitat distributions of species. Species are expected to alter their levels of vigilance in similar ways when they are moved between habitats, if they experience similar changes in the risk of predation when moved between habitats. Here, I briefly explain why more detailed predictions are elusive. I also describe how food supply affects vigilance levels and how those effects can be removed from comparisons of vigilance levels between habitats.

Predictions of how changes in predation risk affect vigilance levels are contingent upon which components of predation risk vary. Several components of predation risk probably vary in unknown ways between habitats, hampering exact predictions of vigilance. Factors contributing to predation risk include: the probability of being attacked, the probability of discovering an attack, and the probability of escaping an attack when it has been discovered. The effects of each of these factors on vigilance have been modelled by Lima (1987*b*). Probability of attack is represented by attack rate. Probability of discovering an attack is represented by the amount of time required for an attacking predator to reach its prey: short attack times provide few oppor-

tunities to detect attacks. Finally, the conditional probability of escaping an attack can be represented by distance from escape cover: a bird is less likely to escape the farther it is from cover. Increased probability of attack should result in increased vigilance (Lima 1987*b*: Fig. 3*b*). Decreased probability of detecting a predator should usually result in decreased vigilance (Lima 1987*b*: Fig. 3*a*). Decreased probability of escaping an attack can result in either increased or decreased vigilance, depending on whether the probability of being attacked is high or low (Lima 1987*b*: Fig. 3*b*).

Theoretically, vigilance levels also depend upon food supply. Differences in food abundance between habitats must be taken into account if comparisons of vigilance are to be used to test hypotheses about variation in predation risk between habitats. How might changes in food abundance affect vigilance? Theoretically, vigilance levels are determined by optimizing the trade-off between the risk of predation and the risk of starvation (McNamara and Houston 1987). Both risks can be described as functions of the amount of time spent vigilant: the probability of being killed declines as vigilance increases, whereas the probability of starving increases. The optimal level of vigilance is that at which the decrement in predation risk as vigilance increases is offset by an equal increment in the probability of starving (McNamara and Houston 1987). Changes in food abundance alter the probability of starving at any level of vigilance, and are represented as shifts in the curve describing the risk of starvation as a function of vigilance (Fig. 1). The relationship between vigilance and food supply depends upon how the starvation curve is shifted as food supply changes. No change in vigilance is expected if the new starvation curve is parallel to the old one. A decrease in vigilance is expected if the slope of the starvation curve increases, whereas an increase in vigilance is expected if the slope decreases (Fig. 1).

One method of removing the effects of food supply from comparisons of vigilance levels between habitats is to ask whether or not differences in vigilance between habitats deviate from expectations based on the relationship between vigilance and food supply. This can be accomplished using analyses of covariance. The covariate in the analysis describes the relationship between vigilance and food supply, providing an opportunity to test the prediction from vigilance theory that food abundance affects vigilance level. Differences between intercepts describe changes in vigilance between habitats as the result of changes in predation risks.

METHODS

The experiment was carried out in the Coachella Valley, in the Sonoran Desert of southern California. Detailed descriptions of the study sites and species can be found elsewhere (Zabriskie 1979, Weathers 1983, Repasky and Schluter 1994). Briefly, Sage Sparrows

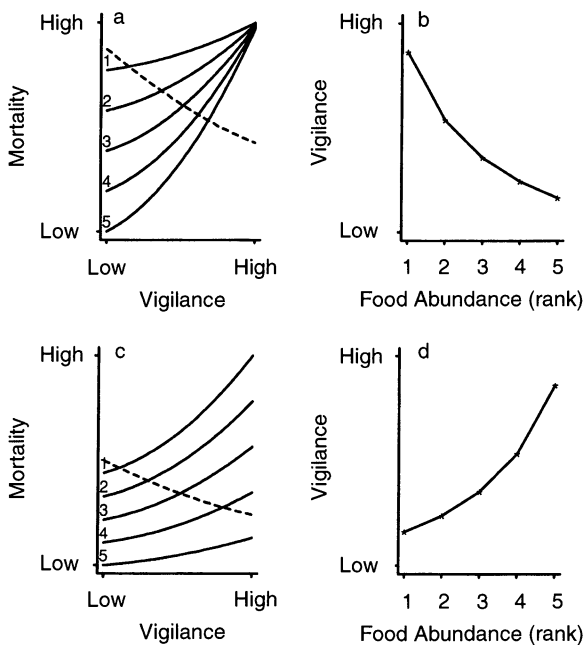


FIG. 1. Hypothetical relationships between level of vigilance and the probability of starving, and the resulting relationship between optimal vigilance level and food supply (after McNamara and Houston 1987). (a, c) Family of solid upward sloping curves represents the probability of starving in habitats differing in food supply. The number to the left of each curve indicates rank of food abundance (1, low food abundance; 5, high food abundance). Dashed downward sloping curve is the probability of being killed by predators. (b, d) Relationship between optimal level of vigilance and food supply resulting from the trade-off depicted in the corresponding left panel. The sign of the slope depends upon whether starvation curves diverge or converge with increasing vigilance.

winter on the floor of the Coachella Valley, and Black-throated Sparrows winter on adjacent mountain slopes and on alluvial fans that form where canyons and smaller valleys open into the valley. The valley floor is flat, hard-packed sediment of an old lake bed, overlaid with sand in some areas. It is sparsely vegetated by shrubs (*Larrea tridentata*, *Atriplex* spp.) and herbs (e.g., *Schismus barbatus*, *Cryptantha* spp.). Alluvial fans are rocky and more densely vegetated with shrubs (e.g., *Larrea tridentata*, *Hymenoclea salsola*, *Bebbia juncea*), herbs (e.g., *Schismus barbatus*, *Cryptantha* spp., *Bromus rubens*), trees (*Cercidium floridum*), and cacti (e.g., *Opuntia* spp.).

Vigilance was observed in a portable aviary placed over natural vegetation in habitats. The aviary measured $4 \times 4 \times 2$ m and was constructed of wooden frames covered with screening that could easily be seen through (further details in Repasky and Schluter 1996). Video tape recordings of solitary birds foraging for naturally occurring seeds were made from a blind, and were used to estimate both vigilance and the foraging

profitability of the patch of ground enclosed by the aviary.

The aviary was an appropriate venue for observing vigilance. Although the enclosure might provide foraging birds with a sense of security from attack, birds of prey attempted to attack sparrows foraging in the aviary. Any effect of the aviary on vigilance should be constant among habitats. Finally, vigilance also serves functions other than predator detection. It might provide warning of attack by dominant conspecifics (e.g., Waite 1987, Roberts 1988) or of attack by other, food-robbing species (e.g., Thompson and Lendrem 1985). Both of these factors were controlled by observing solitary individuals free from either threat. Sage Sparrows and Black-throated Sparrows typically forage in small flocks (Weathers 1983), and vigilance levels generally decline with increasing flock size (e.g., Caraco 1979, Barnard 1980, Elgar and Catterall 1981, Lendrem 1984, Sullivan 1984, Lima 1995). Hence, the experiment rests on the assumption that species experiencing similar changes in predation risk will behave consistently at a given flock size. This assumption is reasonable in the absence of strong differences between species in the slopes of curves describing vigilance as a function of flock size.

Experimental design

The experiment was carried out according to a repeated-measures design. Six individuals of each species were caught 2–7 d before the study began. Birds were housed singly in outdoor cages and maintained on a commercially available mix of seeds for pet finches, meal worms, water, and a vitamin supplement. Food was removed from cages 1 h prior to foraging trials. Each individual was videotaped during one 30-min foraging trial in each habitat. Three species were tested in each of three habitats, but data from only two species are presented here because data from the third species (Dark-eyed Junco, *Junco hyemalis*) were not amenable to analysis. The experiment was carried out in two blocks, each containing three birds of each species. The design controlled any effect that previous experience might have on vigilance by ensuring that equal numbers of birds of equal experience were tested in each habitat. The aviary was moved to a new location each day, and three birds, one of each species, were tested in random order beginning 1 h after sunrise.

Variables and data collection

Vigilance was defined as any time that a foraging bird held its beak such that the long axis was horizontal to the ground or at an angle above the horizontal. Vigilance ratio was calculated as the amount of time spent vigilant divided by net foraging time (defined as total time spent foraging less time spent vigilant). This measure based on net foraging time ensures that vigilance ratio and peck rate, estimated from the same foraging periods, are independent measures and are not related

to one another simply because they are exclusive activities in a fixed time budget. I attempted to make one estimate of vigilance ratio for each bird based on 2 min of foraging activity, although this was not always possible because of poor visibility or because birds foraged for only short periods of time. Some estimates were made from several short periods of foraging, which amounted to 2 min of cumulative foraging time. Estimates were made from the first segment(s) of video tape in which a bird could be seen well enough to collect data. Foraging time in a segment of video tape was measured using a microcomputer programmed as an event recorder. Vigilance time was determined by counting the number of frames in which the bird assumed a vigilant posture, and dividing the count by the rate at which the camera recorded frames (30 frames/s).

I used the rate at which a bird pecked to pick up seeds as a measure of the profitability of foraging in the patch of ground enclosed by the aviary. To obtain peck rates that birds would achieve in the absence of vigilance, I divided total number of pecks by time actually spent foraging. Net foraging time was difficult to estimate because birds sometimes assume a vigilant posture while handling seeds; it was often impossible to determine whether or not a seed was being handled while a bird was vigilant. Hence, I made two estimates of net foraging time: a minimum estimate under the assumption that no handling time is spent vigilant, and a maximum estimate under the assumption that all handling time is spent vigilant. The minimum estimate was calculated as total foraging time minus observed vigilance time. To calculate the maximum estimate, I added handling time to the minimum estimate. Handling time was estimated as the total number of pecks multiplied by the mean handling time of the seed species being eaten, obtained by observing birds consuming seeds in the lab (Repasky and Schluter 1994). Results were unaffected by the method (minimum or maximum) used to estimate patch profitability. For simplicity, I present results calculated under the assumption that all handling time is spent vigilant, which is probably more realistic.

Analysis

The goal of the analysis was to determine whether or not species exhibit consistent changes in vigilance between habitats after vigilance levels have been adjusted for differences in food supply between habitats. I used an ANCOVA to estimate the difference in vigilance between habitats for each species. The model was:

$$V = \tau_i + \beta X,$$

where V is vigilance ratio, X is patch profitability, β is the slope of the relationship between patch profitability and vigilance, and τ_i is the intercept of habitat i . The difference between intercepts reflects change in vigi-

lance between two habitats. This measure of change is meaningful only if the line describing vigilance in one habitat is consistently above or below that describing vigilance in the other habitat. Hence, β was held constant between habitats, and comparisons were restricted to the two species for which lines were parallel, or nearly so. A statistical test for consistency among species was not possible because the analysis resulted in only one independent observation of change for each species: all of the observations of a species were used to estimate the difference between intercepts. Some degree of confidence in the interpretation of the results can be drawn from the statistical confidence surrounding individual ANCOVAs. Statistically significant differences between habitats strengthen confidence in the rankings.

Analysis was restricted to foraging periods in which seed types common to the two habitats were being eaten, to ensure that any differences in vigilance observed between habitats would result from differences in predation risk between habitats, rather than from differences in seed types. Seeds of different size could result in different levels of vigilance, because they offer different opportunities to scan for predators without cost. I analyzed data from periods in which birds were feeding on small seeds of the grass *Schismus barbatus*, which were common in both habitats and usually constituted the principal food in the diets of sparrows in these habitats. Peck rates estimated from 2 min of video tape reflected peck rates obtained during whole feeding trials by an observer using an event recorder (Repasky and Schluter 1996) (Sage Sparrows: $r = 0.77$, $n = 11$, $P < 0.006$; Black-throated Sparrows: $r = 0.97$, $n = 9$, $P < 0.001$). A few observations were missing from the experimental design because an outlier from a bird that was relatively inactive one day was removed, and because good video tape footage was unavailable in a few instances.

I used generalized least squares regression to analyze the results (see Rawlings 1988). This method allows the assumption of independent observations to be relaxed to incorporate repeat observations on individuals without estimating large numbers of parameters. A weight matrix is included in the least squares equation that describes the variance-covariance structure of the data: 1's lay down the diagonal, and off-diagonal elements representing paired observations on individual animals were set to the correlation coefficient between the residuals of repeat observations. The average correlation between paired residuals from separate analyses was -0.53 . A negative correlation may result from changes in vigilance associated with previous experience in the aviary. A bird may be more vigilant on the first trial than on the second because it is less familiar with the aviary on the first trial. Vigilance levels may increase again by the third trial if birds become less willing to follow a daily regimen of fasting and feeding. Indeed, some individuals were reluctant to forage by

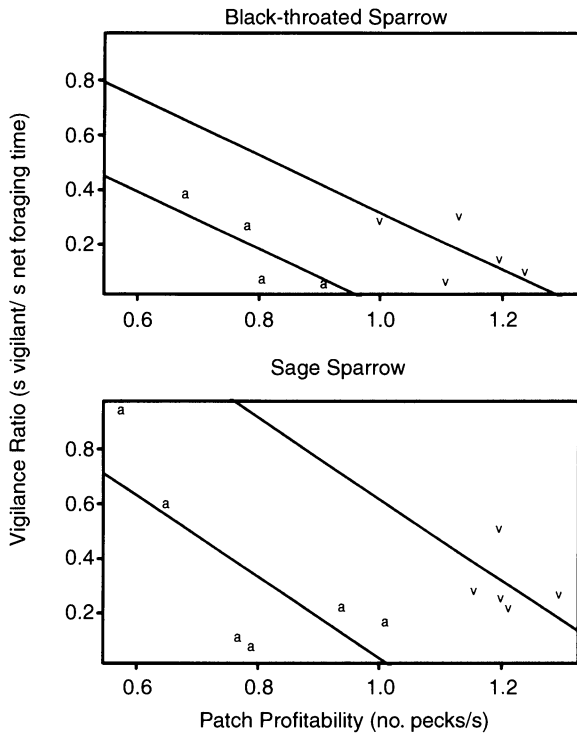


FIG. 2. Relationship between vigilance and food abundance for sparrows consuming similar seed types in pairs of habitats: v, valley floor; a, alluvial fan. Solid parallel lines spanning the entire range of the abscissa were fit by generalized least squares analysis of covariance (see *Methods*). Results of statistical inferences are in Table 1.

their final trial. I used the mean correlation among analyses, rather than using separate estimates for each analysis, for two reasons. First, a single-parameter estimate should be applicable to all of the analyses because the same set of individuals is used in all analyses. Second, generalized least squares is sensitive to error in the estimation of weights, and a combined estimate of correlation should be more robust than individual estimates.

RESULTS

Food supply affects vigilance

Plots of vigilance against food supply suggest that vigilance varied with food supply (Fig. 2). Vigilance declined significantly as foraging patch profitability increased (Table 1).

A decline in vigilance with increasing foraging patch profitability is counter to the intuitive reasoning that increased patch profitability lessens the threat of starvation, allowing more time for vigilance. A negative relationship between vigilance and patch profitability could be an artifact if both vigilance ratio and peck rate are calculated from total time spent foraging, because time is constrained and the number of pecks must decline as vigilance increases. However, this is an unsatisfactory explanation of the present results, because

I calculated vigilance ratio and peck rate from net foraging time. The negative relationship is consistent with theory if the slope of the curve describing the risk of starvation increases with increased food abundance (Fig. 1a).

Comparisons of vigilance levels between habitats

Comparisons of vigilance ratios between habitats were made to test the hypothesis that species exhibit similar changes in vigilance between habitats. Relative to food abundance, both Sage Sparrows and Black-throated Sparrows were more vigilant on the valley floor than on the alluvial fan (Fig. 2). This result is preliminary, because vigilance was observed over a smaller range of food intake rates on the valley floor than on the alluvial fan. The inference would be stronger if the ranges of values of peck rates over which vigilance was observed in the two habitats overlapped broadly, rather than abutting. Nevertheless, the result suggests that species perceive similar changes in predation risk between habitats, and that they are both likely to be safest in the same habitat and at greater risk in the other. Hence, difference in predation risk between habitats is unlikely to be responsible for habitat partitioning between these two species.

DISCUSSION

Behavioral ecology has provided insight into how populations are affected by decisions made by individual animals. For example, the habitat distribution of a species reflects choices made by individuals weighing the trade-off between the risk of predation and foraging profitabilities of habitats (e.g., Milinski and Heller 1978, Werner and Gilliam 1984, Gilliam and Fraser 1987, Todd and Cowie 1990). I analyzed a defense behavior, vigilance, to detect perceived changes in predation risk between habitats and to test two hypotheses

TABLE 1. Levels of statistical significance associated with tests of analysis of covariance models describing the relationship between vigilance and peck rate of sparrows in a pair of habitats, valley floor and alluvial fan (Fig. 2). The alternative hypotheses tested were: either slope differs from zero, or mean vigilance ratio differs between habitats (overall ANCOVA), pooled slope differs from zero, the intercepts of the parallel lines are unequal, and the slopes of independent linear regression lines fit to each habitat are unequal.

Species	Overall ANCOVA	Pooled slope	Unequal intercepts	Unequal slopes
Black-throated Sparrow				
<i>F</i>	8.1	15.7	7.9	0.85
<i>df</i>	2, 6	1, 6	1, 6	1, 5
<i>P</i>	0.02	0.01	0.03	0.40
Sage Sparrow				
<i>F</i>	7.2	14.4	8.5	0.02
<i>df</i>	2, 8	1, 8	1, 8	1, 7
<i>P</i>	0.02	0.01	0.02	0.89

of how predation might influence the distributions of wintering sparrow species. The first hypothesis was that sparrow species are distributed one per habitat because different species are safest from predators in different habitats. The alternative was that the species are all safest in the same habitat, and that predation is not responsible for habitat partitioning. Defense behavior itself is subject to a trade-off between predation and starvation. Therefore, it was necessary to adjust for variation in food abundance before comparing levels of defense between habitats.

Vigilance and the trade-off between food and predation

This study supports the previously untested prediction from vigilance theory that vigilance level is affected by food abundance (McNamara and Houston 1987, 1994, Lima 1987*b*; Fig. 1). Vigilance declined as food patch profitability increased.

A negative relationship between vigilance level and food patch profitability is consistent with theory (McNamara and Houston 1987, 1994; Fig. 1), but inconsistent with the intuitive expectation that increased food supply alleviates the threat of starvation, allowing more time for vigilance. Theoretically, a negative relationship between vigilance level and food supply is predicted when gains in food intake rate and fitness accelerate as food supply is increased (McNamara and Houston 1994). Intuitively, the benefit of increased food availability is so great that survival is maximized by sacrificing vigilance time to take advantage of it. A positive relationship between vigilance and food supply is predicted when gains in food intake rate and fitness diminish as food supply increases (McNamara and Houston 1994).

Wintering birds near starvation may experience increasing returns from increased food supplies, but those returns should eventually diminish, because birds need only to avoid starvation. Indeed, McNamara and Houston's (1987) model of the trade-off between starvation and predation results in a family of starvation curves that could yield either a positive or a negative relationship between vigilance and foraging patch profitability. In the model, daily food intake is assumed to be normally distributed with a mean and a variance, and the probability of starvation is the probability that food intake will fall below some threshold. Increased vigilance reduces mean food intake, and thereby increases the probability of starving. If habitats are assumed to differ in mean food intake, a family of starvation curves results that both diverges and converges (Fig. 3), regardless of whether increasing vigilance reduces food intake linearly or curvilinearly, and regardless of whether variance in food intake is assumed to be constant or allowed to be proportional to net food intake. Solutions to the trade-off between vigilance and starvation that lie in the area where curves diverge yield a positive relationship between vigilance and food

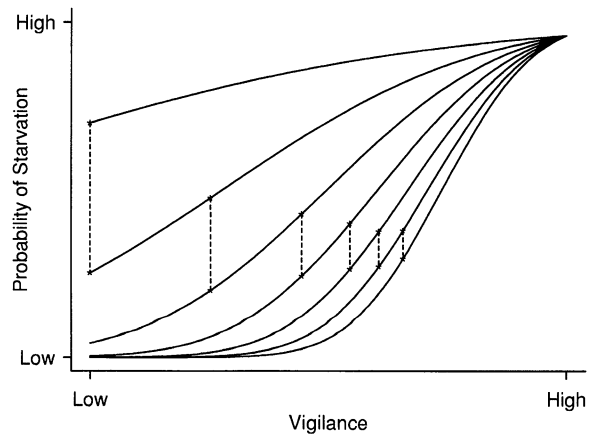


FIG. 3. A family of hypothetical starvation curves derived from the model of McNamara and Houston (1987). Food intake is assumed to be normally distributed, and the probability of starving is the probability of obtaining less than some threshold of food. Mean food intake in the absence of vigilance differs between the curves. Adjacent curves diverge with increasing vigilance to the left of the dashed vertical lines, and they converge to the right.

abundance, whereas those in the area where curves converge yield a negative relationship, as in Fig. 1.

More complex models of vigilance also predict a negative relationship between vigilance level and food intake rate. McNamara and Houston (1992) used game theory to study the effects of group size on vigilance level. Their model incorporated other factors that might affect evolutionarily stable levels of vigilance, including energy reserves and food abundance. McNamara and Houston found that, under conditions of high predation risk, birds should forage only when their energy reserves are low, a situation in which birds are near starvation and gains in survival that result from increased food intake rates are greater than gains that result from increased vigilance levels.

Predation and the habitat distributions of species

In this experiment, Sage Sparrows and Black-throated Sparrows exhibited similar changes in vigilance between habitats. Although this result is preliminary because vigilance was observed over a relatively narrow range of food supply in one of the habitats, it suggests that species rank the danger of predation in habitats similarly, and that predation is unlikely to shape their habitat distributions. If predation were to strongly affect species' distributions, species would have similar habitat distributions.

My result is consistent with previous work on these two sparrow species in the study area. The species use similar methods to escape from avian predators, and they forage closer to woody vegetation than expected from the distribution of available food, suggesting that they should be safest in the habitat with the greatest

amount of cover (Repasky and Schluter 1994). Interestingly, a similar conclusion was recently drawn regarding the risk of predation and microhabitat use by desert rodents (Longland and Price 1991). Heteromyids tend to forage farther from cover than other rodent species, yet despite their remarkable adaptations for feeding far from cover (bipedal locomotion and large auditory bullae for hearing), these rodents are safest close to cover. Perhaps the predation hypothesis will explain the habitat distributions of a group of species differing markedly in their response to predators, such as species that use different methods of escaping from predators (e.g., species observed by Pulliam and Mills 1977, Lima 1990).

If differential predation risk is not responsible, what might account for the habitat distributions of these sparrows? There is another way in which predation might restrict species to different habitats. Species might segregate if they experience greater predation rates when species occur together than when they occur separately (Holt 1977, 1984, Schmitt 1987). This possibility remains to be tested. Food is an unlikely candidate. First, species are not distributed among habitats as predicted from food availability: some species are absent from habitats in which food is at least as abundant as those in which they occur (Repasky and Schluter 1994). Also, transplant experiments suggest that species exhibit only small differences in foraging ability between habitats, and that species might be predicted to have broader habitat distributions than they do if food were to govern distributions (Repasky and Schluter 1996). Habitat partitioning could result from interspecific competition (Lack 1944, Svårdson 1949, Noon 1981, Pimm and Rosenzweig 1981, Rosenzweig and Abramsky 1986, Price 1991). This hypothesis is supported indirectly by the failure of the alternatives, food and predation, to account for species' habitat distributions. Direct tests of the competition hypothesis remain to be done.

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ERRATUM

- In the article by Miguel A. Pascual and Peter M. Kareiva entitled, "Predicting the outcome of competition using experimental data: maximum likelihood and Bayesian approaches," published in *Ecology* **77**(2):337–349, the two species of *Paramecium* in Gause's experiment are mislabeled throughout the paper. Throughout, *Paramecium caudatum* should read *Paramecium aurelia*, and vice versa.