

SPARROWS AND A BRUSHPILE: FORAGING RESPONSES TO DIFFERENT COMBINATIONS OF PREDATION RISK AND ENERGY COST

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Abstract. Our observations of wintering house sparrows (*Passer domesticus*) feeding on cracked corn at feeders placed at different distances from a brushpile and in positions differentially exposed to the wind supported the hypothesis that where food patches are equal in net energy return, foragers use the one furnishing the most protection from predation. Results reinforced the hypothesis that when food sources furnish equal protection from predators, homeotherms below their lower critical temperature use the one providing the largest net energy return. When the sparrows had available both a colder, safer feeding site and a warmer, riskier one, they frequented both over the course of the winter and, as predicted, their use of the colder, safer site was negatively correlated with wind velocity and positively related to temperature and solar radiation. In this last case, it appeared the birds decided where to feed on the basis of some threshold difference between metabolic rates at the colder, safer site and the warmer, riskier location.

Since antipredatory behaviour is frequently incompatible with maximal foraging efficiency (Pulliam 1973; Stein & Magnuson 1976; Milinski & Heller 1978; Sih 1980), compromise solutions to these two selective pressures should exist and should be accessible to natural selection. Here, we explore the feeding responses of house sparrows (*Passer domesticus*) to conflicting demands for energetic efficiency and predation protection.

Suppose there are two food patches which have identical qualities and quantities of food, but one is colder, so an homeothermic animal must spend more energy per unit time there. If foraging efficiency is indexed by net energy accumulation (Pyke et al. 1977), the optimal strategy should be to feed only in the warmer patch (Grubb 1977).

Consider two other patches of identical food properties, but one is located closer to a refuge from predation. Selection should favour animals choosing the patch closer to 'cover'. Schneider (1979) found that the dominant bird in a flock of white-throated sparrows (*Zonotrichia albicollis*) monopolized a source of food closest to a brushpile. She concluded such behaviour is adaptive, as the dominant animal need travel only the minimal distance to safety in the event of a hawk's attack. Caraco (1979) reported that juncos (*Junco phaeonotus*) feeding on the ground would venture no farther than about 3 m from thick bushes, behaviour he interpreted as antipredatory.

Now suppose there are two patches of equal food characteristics. One is close to cover, but

it is cold and imposes high energy costs on a forager. The other is farther from cover, but it is warmer and costs a forager less energy. An animal needing food must choose between the two patches. By creating this pair of patches, we forced house sparrows to decide between predation protection and foraging efficiency.

We constructed a brushpile 2 m high and 3 m in diameter on a mown lawn surrounded by open fields. Near the brushpile we placed pairs of 20-cm diameter trays filled with cracked corn (maize). By placing one tray fully exposed to the wind and the other in the shelter of the brushpile, we established two food patches of differing net energy return to the sparrows. Assuming that vulnerability to hawk predation increases with distance from cover, we could vary predation protection by moving feeders toward or away from the brushpile.

At various times, four feeding stations were used, two exposed to the wind at distances of 1 m and 3 m from the brushpile (E_1 and E_3) and two sheltered by the brushpile at distances of 1 m and 3 m (S_1 and S_3). When only E_1 and E_3 contained food, energy costs were identical at the two sites, and if the sparrows fed near cover for predation protection, they should have always used E_1 , regardless of prevailing weather. When E_1 and S_1 held corn, predation protection at the two sites was the same and if net energy gain determined patch use, the birds should have always used S_1 . With corn at E_1 and S_3 , neither energy cost nor predation protection was the same. Below the lower critical

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temperature, energy cost, or metabolic rate, is a negative function of ambient temperature and radiation flux, and is proportional to the square root of wind velocity (Porter & Gates 1969; Robinson et al. 1976). As these three physical parameters vary, so will the difference in energy cost between E_1 and S_3 . We tested the prediction that over the course of the winter the sparrows would use both the E_1 and S_3 feeders, and that the extent of their foraging at the E_1 site would be positively correlated with temperature and solar radiation, and negatively correlated with wind velocity.

Methods

At the start of each study session during the Ohio winter of 1979–80, feeders were positioned with respect to the wind direction indicated by a weather vane mounted on the brushpile. We then took up station 25 m away and watched events through binoculars. As soon as at least five sparrows were seen feeding at either feeder, we tallied the number of birds at both sites. In some cases more than five birds flew together to a feeder; all were included in our count. After each record, we returned to the brushpile area, flushing the birds into neighbouring fields in the process, recorded weather variables, brushed stray bits of corn back onto the feeders, and realigned the feeders with wind direction if necessary. Ambient temperature was taken in the shade in degrees Celsius. Total shortwave radiation ($W m^{-2}$) was measured with a radiometer ('Solar Meter', Dodge Products, Houston, Texas) aimed at the sun. Wind velocity ($m s^{-1}$ 'Velometer, Jr.', Alnor Instrument Company, Chicago, Illinois) was measured at bird height 5 cm above the E_1 feeder.

Results

Over the course of the study, ambient temperature ranged from -17 to $5^\circ C$, wind velocity from 0.1 to $3.8 m s^{-1}$ and total shortwave radiation from 10 to $1170 W m^{-2}$.

When the two feeders were equidistant from the brushpile (E_1 and S_1), almost all the sparrows avoided the exposed feeder (Fig. 1A), and their preference for foraging location was not correlated with wind, temperature, or solar radiation. Therefore, when predation protection at the two feeders was equal, most birds used the feeder with the (apparently) lower energy cost.

Our results also reinforced the hypothesis that when two food patches are identical in net energy return, foragers select the alternative

affording greater protection from predators. When given a choice between E_1 and E_3 feeders, sparrows chose E_1 in almost every case (Fig. 1B), and their behaviour was statistically independent of weather variation.

When birds had available a colder, safer feeding site (E_1) and a warmer, riskier one (S_3), they frequented both over the course of the winter (Fig. 1C). As predicted by considering metabolic costs, their reliance on the E_1 site was negatively correlated with wind velocity (Pearson's $r = -0.23$; $P = 0.002$) and positively related to temperature ($r = 0.48$; $P = 0.0001$). The correlation of -0.17 between percentage of use of the E_1 feeder and solar radiation was not only not significant, it was in the direction opposite to that predicted. In the E_1 versus S_3 case, the correlation coefficient between temperature and solar radiation was -0.65 ($P < 0.0001$).

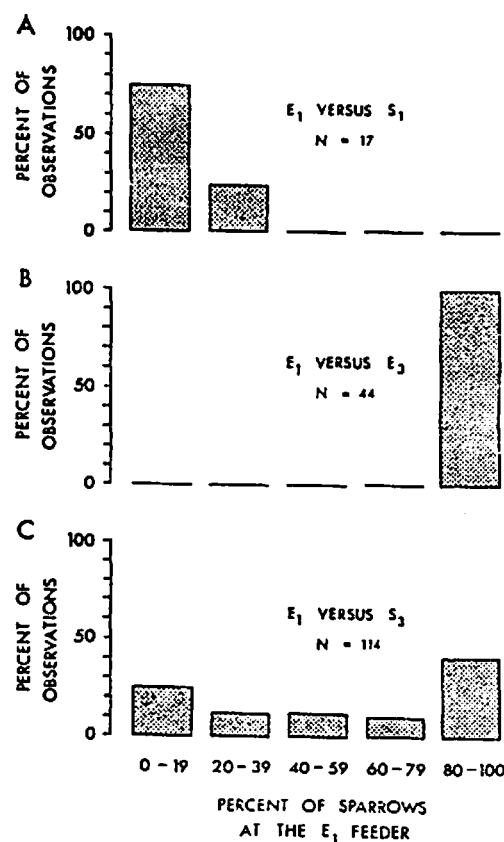


Fig. 1. Use by house sparrows of the E_1 feeder instead of (A) the S_1 feeder, (B) the E_3 feeder, and (C) the S_3 feeder.

Using the method of partial correlation (Steel & Torrie 1960), we found that, as predicted, when the effect of temperature was held constant, the relationship between use of the E_1 site and solar radiation was positive ($r = 0.21$) and significant ($P < 0.05$). None of the other results was complicated by significant autocorrelations.

Discussion

The original models of optimal foraging behaviour (reviewed by Pyke et al. 1977) predict that animals choose where and how to forage, and what to eat, solely by measuring energy (and/or nutrient) return from food per unit energy or time of searching. Studies in the laboratory (Charnov 1976; Krebs et al. 1977) and of wild animals in situations where predation risk was insignificant (Goss-Custard 1977; Heinrich 1979) have supported optimal foraging models. However, it is clear from the review of Stein (1979) and from the recent experiments of Milinski & Heller (1978) and Sih (1980) that many animals reduce their rate of food intake in order to lower predation risk. Our results show that animals may also sacrifice foraging efficiency by raising their energy expenditure to reduce predation risk.

We do not know the precise balance point between predation protection and energy cost. In our third test, birds chose between two feeders, one 3 m and the other 1 m from cover. Figure 1C shows modes at the 0–19 and 80–100% use of the closer (E_1) feeder. There were very few days during which the weather was such that metabolic savings just balanced predation risk. Thus, the birds nearly always made a decision to use one feeder or the other. This is shown by the two modes in Fig. 1C. If the distribution of birds between the two feeders had often been uniform (50% at each feeder), then we would have seen a central mode in the histogram. Our results disproved the null hypothesis that the distribution of birds was uniform ($\chi^2 = 178$; $P < 0.0001$).

Finally, we bring our results to bear on an important concurrent line of inquiry. We defined the preferred site as the one first attracting five birds. By standardizing flock size, we attempted to control the role played by intraspecific behavioural interactions in the sparrows' decision where to forage. In a series of papers, Caraco and his co-workers (Caraco 1979, 1980; Caraco et al. 1980) have explored the relationships among flock size, distance from cover, interference competition and time spent scan-

ning for predators. While examining these variables, they made an effort to control for climatic variation. Our results and theirs should be integrated in future work. On the one hand, as the number of sparrows using the preferred feeder in our study continued to increase beyond five, we might expect intraspecific aggression to drive some birds to the less preferred site. Also, we can now predict, for instance, that the finding in Caraco et al. (1980) that 'Presented with a choice between feeding sites near and far from cover, juncos prefer sites close to cover despite the greater level of aggression', will depend on the difference in energy cost between the sites.

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