White-Crowned Sparrows (Zonotrichia leucophrys):
Foraging Preferences in a Risky Environment

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Summary. White-crowned sparrows were presented with a series of two-choice experiments. Mean rewards were the same in each experiment, but the standard deviations differed. When fed at a rate faster than that minimally required to meet daily costs, the birds most often preferred the reward with the lower standard deviation. However, when the same birds could expect an energy deficiency, they most often preferred the greater standard deviation. For each sparrow and each mean reward level, I attempted to construct a preference ranking based on experimental pairwise comparisons of all elements of a set of reward probability distributions. The birds usually most-preferred the minimal or maximal standard deviation, depending on whether they avoided or favored reward variability. However, in a few cases either an intermediate standard deviation was most-preferred, or a bird exhibited inconsistency in its preferences.

Introduction

Several recent stochastic models of resource utilization assume that foragers will exhibit risk-sensitive behavior. That is, an animal’s preferences are assumed to depend (minimally) on both the mean and variance of the net benefits associated with each available resource (Oster and Wilson 1978; Real 1980; Caraco 1980). Whether or not these models enhance our understanding of behavior will depend, in part, on the appropriateness of the assumption of risk-sensitivity.

We know that foragers respond to differences in mean rewards (Pyke et al. 1977; Krebs 1978), but there is some ecologically oriented evidence that foragers also respond to differences in the variability of rewards. In experimental circumstances granivorous birds display risk-sensitive foraging (Caraco et al. 1980; Caraco 1981a, 1982), as do some nectar-feeding insects (Real 1981; Real et al. 1982; Waddington et al. 1981) and a primate species (Behar 1961). Since foraging is often an inherently stochastic phenomenon (Oaten 1977; Green 1980), it is perhaps not so surprising that animals’ ‘decision-making’ capacities can, at least sometimes, deal with variability both between and within different resources.

Predicting a risk-sensitive forager’s use of resources is sometimes a problem at two levels. We may have to deduce the way selective pressures have molded the organism’s preferences, and then infer a feeding strategy consistent with those preferences (Caraco 1980). However, in a particular simple situation predictions follow directly from a survivorship model (Stephens 1981; Stephens and Charnov 1982; Pulliam and Millikan 1982). Consider a non-breeding forager attempting to minimize its probability of starvation. The animal must obtain at least a required amount of food during the day (or some other finite time interval) to survive; the possibility of starvation during the day is neglected. Suppose the forager must choose between two food rewards providing the same expected amount of food, but differing in their variances. The option providing the lower probability of starvation depends on a comparison of the animal’s total expected food intake with its requirement or, equivalently, a comparison of its average feeding rate with the minimally required rate. If the expected amount of food exceeds the requirement, the animal should choose the reward with the lower standard deviation (hence, lower variance). If the requirement exceeds the expectation, the animal should choose the reward with the greater standard deviation (Caraco et al. 1980; Ste-
phens 1981; Stephens and Charnov 1982; Pulliam and Millikan 1982; McNamara and Houston 1982). The basic idea can be conveyed with an elementary example. Let one option always provide a reward of 3, while the other provides either 0 or 6 with equal probability. Suppose the animal has time for five foraging efforts, all of which (for simplicity) must be committed to one of the options before feeding begins. Choosing the first option provides a total reward of 15, with certainty. If the second option is selected, the possible total rewards are [0 6 12 18 24 30], the probabilities associated with the respective outcomes are [1 5 10 10 5 1]/32. The expected total rewards are equal (15), but variabilities differ between options.

Assume that the animal must acquire a total reward exceeding 12 to survive. If x represents total reward, the probability of starvation is simply Pr (x ≤ 12). For the first option, the probability of starving is 0. For the variable option, the probability of starving is 0.5. Therefore, the animal should be risk-averse and prefer the constant reward when the mean exceeds the minimal foraging requirement.

Now assume that survival requires a total reward exceeding 20, so that the probability of starvation is Pr (x ≤ 20). For the first option, the probability of starving is 1. For the second option, the probability of starving is 13/16. Therefore, the animal should be risk-prone and prefer the variable reward when the minimal foraging requirement exceeds the mean reward.

These simple rules relating foraging requirements to preference for reward variability predicted the foraging behavior of two Junco species (Caraco et al. 1980; Caraco 1981a). One objective of this study is to test the prediction with white-crowned sparrows (Zonotrichia leucophrys), which weigh approximately 10 g more than the juncos.

When mean rewards of n different foraging options (n ≥ 3) are equal, the survivorship model (c.g. Stephens 1981) predicts a ranking where preference either strictly decreases with the standard deviation (risk-aversion) or strictly increases with the standard deviation (risk-proneness). This preference structure is called a monotone ordering. Biologically, a monotone ordering by standard deviation might be most reasonable if the probability of starvation varied strictly monotonically with reward variability.

A monotone preference ordering is a special case of the possible orderings admitted as "rational" under portfolio theory, as described in Coombs (1969), Coombs and Huang (1970, 1976) and van Santen (1978). This theory proceeds from an axiomatic system for decision-making, and was developed (in part) as an alternative to expected utility theory (e.g. DeGroot 1970). In the context of the foraging example, portfolio theory assumes that the decision-maker possesses a single-peaked preference function. The 'optimal' risk (here, the most-preferred standard deviation) corresponds to the function's single peak. By assumption, the optimal risk may be the smallest, largest, or some intermediate standard deviation. If an intermediate risk is preferred over all others, the resulting preference structure is termed a folded ordering. The monotone orderings predicted by the survivorship model are consistent with portfolio theory, but a folded preference ordering is not consistent with the survivorship model. A second objective of this study is to investigate whether foraging sparrows preferences over reward variability are reliably ordered, and if so, whether the ordering is monotone, folded or inconsistent with both models. A monotone ordering (in the right direction) would suggest that minimizing the probability of starvation might be an objective sought by non-breeding foragers in nature.

For a given mean reward (average number of seeds), I constructed a series of two-point probability distributions differing in their standard deviations. Each pair of distributions was presented in choice experiments, and a preference ranking was inferred from each individual's behavior. Previous demonstrations of risk-sensitivity in foraging sparrows involved only choices between a constant and a variable reward, but the ability to discriminate between variable rewards is necessary if risk-sensitivity is to influence foraging in nature.

Materials and Methods

In October 1981 I captured three white-crowned sparrows: an adult male (W1), a juvenile male (W2) and an adult female (W3). Each bird was housed in a separate aviary. A large one-way glass was mounted in one wall of each aviary. Aviaries are equipped with two feeding stations, separated by a large partition. At the feeding stations an experimenter, positioned behind the one-way glass, presented small dishes containing predetermined numbers of millet seeds (Panicum miliaceum). The dishes were attached to sliding trays which were pushed into the aviary through metallic sleeves mounted in the wall. Physical characteristics of the aviaries are otherwise as described in Caraco et al. (1980).

The birds quickly learned to perch at a point on the midline between the two feeding stations in order to obtain food. To properly document preferences for food rewards, one must guard against an animal's position preference for either side of its enclosure. Each sparrow was tested for position preference before the experiments began, and was retested every two weeks thereafter. Caraco et al. (1980) describe the details of this