AN EMPIRICAL DEMONSTRATION OF RISK-SENSITIVE FORAGING PREFERENCES

By THOMAS CARACO*, STEVEN MARTINDALE & THOMAS S. WHITTAM

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721

Abstract. We report laboratory experiments with yellow-eyed juncos (*Junco phaeonotus*) revealing that the birds' foraging preferences for variable rewards respond not only to the mean, but also the variance, of food rewards. The nature of their preferences for variable rewards is related to their expected daily energy budget. We summarize the birds' preferences in utility functions for energetic rewards. Since mean reward size is inadequate to predict their behaviour, we believe that foraging models should consider environmental stochasticity and an animal's response to this variation.

Preferences and Utility

Models of selective resource use assume that animals discriminate food types and possess preferences among available resources (see references in Pyke et al. 1977). Preferences are logically considered as consistent with a ranking by some currency of fitness. We assume that a forager has preferences over the probability distributions of energetic rewards associated with available resources, since it seems reasonable that natural selection has acted on the preference behaviour of those animals faced with environmental variation. Therefore, we expect that preferences will reflect not only the various mean rewards, but also the variances in foraging benefits. This variation may entail the risk of doing very poorly energetically, as well as the possibility of acquiring the greater value of random energetic rewards.

Our investigation of these preferences employs what decision theorists (e.g. Keeney & Raiffa 1976) term 'single attribute cardinal utility theory'. The single attribute of interest here is the size of a food reward. We develop a numerical (cardinal) scaling for the size of a food reward that takes into account a forager's preferences for both mean energetic benefit and the risks resulting from variation in energetic benefits. More specifically, we will summarize an animal's foraging preferences in a utility function, $U(s)$, where s is a well-defined random variable following a known probability function. The units of s in our experiments are the number of seeds obtained at a feeding trial, but other reasonable indices of energetic reward can be used. A utility function has a number of interesting properties that help depict an animal's preferences regarding the statistical characteristics

*Present address: Department of Biology, University of Rochester, Rochester, N.Y. 14627.

of food resources. The function can be evaluated for various probability distributions of energetic rewards, and so provides values that define the animal's numerical preference scaling over those reward distributions. For any probability distribution of energetic rewards, with a finite mean, U allows us to associate an expected value of the utility function, $E[U(s)]$, usually termed the expected utility. Since natural selection should mould preferences for food resources, we assume the 'best decision' maximizes expected utility (Von Neumann & Morgenstern 1948; DeGroot 1970; Bertsekas 1976; Keeney & Raiffa 1976). More generally, the optimal strategy in a stochastic environment should depend a great deal on the forager's response to the risks associated with the use of variable resources (see Real, in press).

An investigation of preference behaviour must, of course, deal with lack of preference. We define indifference as lack of preference between known energetic rewards. When a forager exhibits no preference (is indifferent) with regard to two energetic rewards (one or both of which may be variable), either one may be substituted for the other in a ranking by preference. For example, if a forager prefers resource A over resource B and is indifferent between resources B and C, we assume the forager prefers resource A over resource C. To interpret indifference quantitatively we employ the 'certainty equivalent' concept (as in Keeney & Raiffa 1976). While both certainty equivalents and preferences indicate the nature of a forager's response to the risks imposed by reward variation, certainty equivalents further provide the data for estimating the utility function, $U(s)$. Suppose there is an energetic reward, $\hat{s}$, such that the forager is indifferent between receiving $\hat{s}$ for certain (i.e. obtained with probability 1) or receiving a reward where the value

varies according to a probability distribution $f(s)$. Since the forager has no preference between the two, $\hat{s}$ is termed the certainty equivalent for $f(s)$.

Fitness should increase with energetic rewards, implying that $U(s)$ also must increase with reward size ($U'(s) > 0$). Since the utility function for foraging benefits should increase strictly monotonically, we can assume there will be a unique certainty equivalent for any probability distribution of energetic rewards.

To apply utility theory to animal foraging, we must interrelate probability distributions of energetic rewards, preference behaviour, and responses to variation in foraging benefits. Consider a discrete set of energetic rewards S with elements s_1, s_2, ..., and s_n. Let $s_a < s_{a+1}$ for $a = 1, \ldots, n - 1$. When $s_i < s_j$, we have reasonably assumed that the forager prefers the greater reward. We indicate the preference for s_j over s_i by $s_j P s_i$. Then $U(s_i) < U(s_j)$, since $U' > 0$. The utility of the preferred reward must be greater than the utility of the non-preferred reward. If $s_i = s_j$, assume the forager is indifferent between the two rewards, indicated $s_i I s_j$. Lack of preference between the two rewards implies that $U(s_i) = U(s_j)$.

The variable food sources that we employ in our experiments are called 'lotteries'. We designate a lottery by (s_i, q, s_j), meaning that the forager receives a reward of s_j units with probability q and s_i with probability $1 - q$. For any particular lottery, the certainty equivalent, $\hat{s}_{ij}$, is the reward size such that the forager has no preference between receiving s_{ij} with probability 1 or exploiting a food source where reward size follows the lottery's probabilities. We indicate this indifference as $\hat{s}_{ij} I (s_i, q, s_j)$. By definition, the utility of the certainty equivalent equals the expected utility of the probability function, $U(\hat{s}_{ij}) = E[U(s_i, q, s_j)]$ (DeGroot 1970; Keeney & Raiffa 1976). This simply means that the utility of the certainty equivalent is the appropriately weighted average of the utilities of the lottery's rewards. If utility reasonably reflects the action of natural selection on foraging decisions, then the animal's lack of preference should indicate that the certainty equivalent entails the same expected consequences for survivorship and fecundity as does the variable resource. Our assumption that $U' > 0$ necessarily implies that a forager will prefer any invariable reward size greater than the certainty equivalent over the associated variable food source (the lottery), and will prefer the variable food source over any invariable reward size less than the lottery's certainty equivalent.

Utility is a relative measure. Therefore, we may assign numerical values of the utility function for any two unequal elements of S, so long as $U(s_i) < U(s_j)$ when $s_i < s_j$. By selecting different values of s_i and s_j (and the probabilities of their realization, if desired), we can construct a number of lotteries to serve as variable food sources. For each such probability function for energetic benefits, we can locate the reward size where the forager exhibits indifference. We then may calculate the utility of each certainty equivalent relative to the two originally assigned values. These utilities then permit estimation of a continuous $U(s)$, such that its first two derivatives may also be continuous functions.

For any variable food source, suppose the associated constant reward where the forager is indifferent (the certainty equivalent) is less than the average reward obtained from the variable source. Then the forager's preference is termed risk-averse. In the context of our lotteries, risk aversion implies $\hat{s}_{ij} < (1 - q)s_i + qs_j = E[s]$ when $U(s_{ij}) = E[U(s_i, q, s_j)]$. That is, the utility of the certainty equivalent equals the expected utility of the variable food source (because the forager is indifferent between the two), even though the certainty equivalent is less than the probability function's average reward. By a result known as Jensen's inequality, this will be true when the forager's utility function is everywhere concave; $U'(s) > 0$ and $U''(s) < 0$ (see DeGroot 1970 for a proof). Since $U'(s) > 0$, it immediately follows that the forager averting risk prefers to receive a distribution's average reward with certainty over sampling from the distribution itself. Risk aversion means that the forager tends to avoid food sources with relatively high variation. In fact, the animal will probably exploit resources with relatively small variation even if their average reward is less than the means of more variable food sources (Caraco, in press). This implies that avoiding the chance of doing very poorly while feeding, due to the stochastic nature of available resources, is more important than obtaining a relatively large energetic benefit.

Now suppose that for any variable food source, the associated certainty equivalent is greater than the mean reward obtained from the variable resource. In this case the forager's preference is termed risk-prone, implying for our lotteries that $\hat{s}_{ij} > E[s]$ when $U(\hat{s}_{ij}) = E[U(s_i, q, s_j)]$. This is always true when $U(s)$ is every-

where convex; $U'(s) > 0$ and $U''(s) > 0$. The animal now favours exploiting a variable food resource over receiving the average reward of that resource with certainty. By favouring risk the forager accepts the chance of doing poorly, in order to capitalize on the possibility of obtaining relatively large energetic rewards (Caraco, in press; Real, in press).

Most deterministic foraging models assume that animals rank resources according to average rewards. This effectively assumes insensitivity to environmental variation ($U''(s) = 0$), suggesting that a forager has no preference between a variable resource and receiving the average reward of that resource with certainty.

The difference between the mean reward provided by a variable resource and the value of the associated certainty equivalent also has a behavioural implication. Let $Y = E[s] - \hat{s}_{ij}$; Y is termed the 'risk premium' (Keeney & Raiffa 1976) for a given probability distribution. If the forager avoids the risks of resource variation, $Y > 0$, while $Y < 0$ if the forager favours risk. If we present a forager with a series of lotteries where the variance, $E[s^2] - (E[s])^2$, is constant, we can ask if Y varies as the mean reward, $E[s]$, increases. If $Y > 0$ and decreases as the mean increases ($\partial Y/\partial E[s] < 0$), the forager exhibits decreasing risk aversion. This indicates that the animal behaves less conservatively as: (1) the average energetic reward increases while the variance is constant, (2) reward variation decreases about a constant mean reward, and (3) the average energetic reward increases while the variance decreases. Constant risk aversion occurs when $Y > 0$ and independent of the mean reward ($\partial Y/\partial E[s] = 0$). In this case the forager's behavioural conservatism decreases with decreasing variation in energetic rewards, but changing the mean reward alone does not affect the difference between the mean and the certainty equivalent. Decreasing risk proneness implies that the difference between the mean of a variable food source and the associated certainty equivalent increases toward zero whenever the same conditions describing decreasing risk aversion occur.

Variable risk aversion (or proneness) is a useful concept since it can depict a forager's degree of sensitivity to environmental variation as average energetic rewards increase or decrease. Decreasing risk sensitivity should be a reasonable behavioural characteristic, since the impact of a given level of environmental variation on survivorship or fecundity should decrease as average energetic rewards grow large (Caraco, in press). Variable risk sensitivity governs the curvature of an individual's utility function and can, therefore, be represented with the derivatives of $U(s)$. Pratt (1964) defines 'local risk aversion' as $r(s) = -U''(s)/U'(s)$. For decreasing risk aversion, $r(s) > 0$ and $dr(s)/ds < 0$.

Many non-breeding foragers appear to feed until their gross energy intake equals or exceeds all daily costs and anticipated overnight expenditures (King & Farner 1966; Wolf & Hainsworth 1977a). Caraco (in press) suggests that such foragers will avoid the risks imposed by environmental variation when food resources are sufficiently abundant so that they expect to meet 24-h energy requirements. Contrastingly, when a forager expects to lose energy during a day, so that its immediate survivorship is imperiled, it may respond to environmental stochasticity by preferring risk. If acquiring relatively large rewards potentially available through the exploitation of highly variable resources is the only way to escape serious energy depletion, then preferences favouring risks are logical. Real (in press) independently reaches a very similar conclusion. If a forager is always risk-prone, it seeks greater average energetic benefits than do risk averters, but it does so at the expense of a greater probability of starvation.

An individual's utility function for random energetic rewards describes observed preference (or lack or it) and can further be employed to predict an animal's foraging decisions. The function transforms distributions of the random variable into a preference scale that incorporates responses to risk. Our laboratory experiments ask whether yellow-eyed juncos (*Junco phaeonotus*) have preferences over probability distributions of food rewards such that $U''(s) \neq 0$. We also test hypotheses linking a forager's expected energy budget and the nature of its response to risk.

Methods

Our experiments involved seven yellow-eyed juncos captured in southeastern Arizona. We kept four or fewer birds at a time in an aviary measuring 4 m × 3 m × 3 m. Temperature in the aviary, which is equipped with one-way mirrors, was maintained 24 h a day at 7 ± 1 C. A timer controlled a 12 h/ 12 h light/dark cycle.

Yellow-eyed juncos feed almost entirely on grass seeds during the winter. When a bird was not involved in an experiment, it was given ad lib commercial millet (*Panicum miliaceum*). Every

three weeks the birds also received ground beef to assure proper nutrition. Water, with vitamins added, and grit were always available.

We used millet seeds of homogeneous size as the food reward in all experiments. We estimated handling time as 2.82 ± 0.22 (SE) s/seed. The energetic cost of husking a seed is small compared to the reward, and the 'search time' (time spent running from the perch to a feeding station) was independent of reward size. Therefore, we take the number of millet seeds as the random variable for which we determined utility functions.

During experiments, all but one bird were removed from the aviary. The perch was located equidistant ($\simeq 3.5$ m) from each of two feeding stations. A wooden partition (1 m high) was placed between the feeding stations, so that the bird was forced to make an unambiguous decision between food sources at each trial (see below).

The two feeding stations were apertures through which the observer slid wooden trays. We glued a petri dish to each tray and attached a small piece of paper to each tray with a string. At every trial we covered each dish with the paper, so the junco could not visually determine reward size. The birds quickly learned to remove the paper with their beaks. During experiments, no food was available other than that provided at the feeding stations. The range of reward sizes used in our experiments was 0 to 12 seeds. In energetic terms, this is approximately equal to the range a junco in a flock of four acquires during a visit to a single patch at 6 to 9 C (Caraco, unpublished data).

We conducted two series of experiments. In the first series we estimated utility functions for five birds. Every preference test (our term for a single experiment which consisted of 40 trials) in this series was begun after 1 h of starvation (0900 to 1000 hours). All trials within these preference tests were delayed 30 s for each seed eaten during the previous trial. In the second series of experiments we estimated utility functions for two of the birds used in the first series and two other birds that had not been exposed to previous experiments. In the second series we starved the birds for 4 h (0900 to 1300 hours), with all trials delayed 1 min for each seed eaten during the previous trial.

The Appendix presents our analyses of the energetic values of the seeds, oxygen consumption of the birds, and other data used to estimate 24-h expected net energy budgets for the two

series of experiments. Calculations in the Appendix indicate that the birds required 1.39 seeds/min in the first series of experiments to balance energy intake and expenditure, while they were fed 2 seeds/min. In the second series, the birds required 2.08 seeds/min to achieve a balanced energy budget, and they were fed an average of 1 seed/min. Therefore, we believe the first series of experiments provided the birds with an expected non-negative net energy budget, but in the second series they could expect a negative net energy budget.

Each experimental preference test consisted of 20 learning trials followed by 20 preference trials. One feeding station was randomly selected for each bird and used for a certain reward in all preference tests. Learning trials included 10 presentations of a constant number of seeds at this station. At the other feeding station the 10 learning trials offered rewards according to the probability distribution (s_i, 0.5, s_j). Both possible outcomes of the lottery were presented five times. We chose $q = 0.5$ since the apparent deviation between mathematical and subjective (perceived) probabilities in human subjects is relatively small near this value (see Luce & Suppes 1965 for a review). Our interpretations of the data assume that the birds 'know' the reward probabilities at each station. Unless estimation is based strictly on sample statistics, Preston & Baratta (1948) suggest that humans tend to underestimate probabilities near unity and overestimate probabilities near zero. Heuckeroth (1969) discusses situations where humans may overestimate probabilities greater than 0.5 (see DeGroot 1970 for explanation of Bayesian, or subjective, inference). We expect that the effect of any similar biases in the birds would be minimized if lottery outcomes were governed by a simple fair coin toss. Therefore, $q = 0.5$ in all lotteries.

A reward was made available at only one station in each learning trial. This assured that the bird sampled each station 10 times. The order of presentation was randomized among the 20 learning trials.

After the learning trials were completed, we immediately began the 20 preference trials. For these trials, we simultaneously presented the two trays to the bird as it perched equidistant from the feeding stations. At the variable station each of the two possible outcomes of the lottery was offered 10 times, randomly ordered. As soon as the bird moved to one feeding station we removed the other tray.

A given experiment might ask whether the junco prefers two seeds with certainty over the probability distribution (0, 0.5, 4), prefers this lottery over two seeds with certainty, or is indifferent to these two food sources. During the 20 preference trials of this experiment, one station always provided the bird with two seeds, and the other station provided no seeds 10 times and four seeds 10 times.

We recorded the number of times the bird fed at each of the two stations. We assume a significant reward preference whenever the bird's utilization vector differed significantly from (0.5, 0.5). That is, if the proportion of the 20 trials where the bird fed at the certain station differed significantly from 0.5, we assume the bird preferred the reward it chose more often. By the binomial probability function, this occurred when one feeding station was chosen 14 or more times in the 20 preference trials ($\alpha = 0.05$). If neither station was chosen more than 13 times, we assume indifference and use the constant number of seeds as the certainty equivalent for the probability distribution presented at the variable feeding station.

Our use of the binomial distribution requires that each trial be an independent event. Contingency table analysis of the nine data sets reported here indicates that the reward received when the lottery was selected bore no significant relationship to the choice made at the next trial. Since no heterogeneity was detected, we treat each trial as independent.

We estimated utility functions as suggested by Becker et al. (1964). We arbitrarily defined the utility of zero seeds as 0 and the utility of six seeds as 1, i.e. $U(0) = 0$ and $U(6) = 1$. We first located the certainty equivalent (number of seeds where the bird was indifferent) for the lottery (0, 0.5, 6). Recall that the utility of the certainty equivalent equals the expected utility of the associated probability distribution. The number of seeds, $\hat{s}_{0,6}$, for which the bird was indifferent to this lottery was assigned a utility of 0.5, since $U(\hat{s}_{0,6}) = E[U(0, 0.5, 6)] = 0.5[U(0) + U(6)] = 0.5$. We then found utilities for the lotteries (0, 0.5, $\hat{s}_{0,6}$) and ($\hat{s}_{0,6}$, 0.5, 6). The expected utilities of these two probability distributions are, respectively, 0.25 ($= 0.5[0 + 0.5]$) and 0.75 ($= 0.5[0.5 + 1]$). Therefore, the utilities of the respective certainty equivalents are, by definition, 0.25 and 0.75. Proceeding in this manner, we identified utilities for a number of values of s, until we were confident in the estimated $U(s)$ for each bird. Occasionally the experiments yielded

two values for a given number of seeds. In these cases we took the mean as the best estimate.

Experiments revealing significant preferences served as consistency checks on the estimated utility functions. We compared the utility of the certain number of seeds with the expected utility of the variable reward, both calculated with the estimated $U(s)$, and assumed that the bird should prefer the reward with the greater expected utility. If the bird's behaviour was consistent with the expected utility hypothesis, our confidence in the predictive power of the estimated utility function increased. Many consistency checks tested preference between s seeds for certain and either the probability distribution (0, 0.5, 2s) or ($s - k$, 0.5, $s + k$). Note that the mean reward in each of these experiments is the same at both stations, but the variances differ between stations. Apart from assessing the accuracy of a particular form of $U(s)$, such experiments are behaviourally important, since they directly test risk aversion (proneness) versus the deterministic assumption of insensitivity to risk. Other consistency checks tested for decreasing risk aversion (proneness). A series of experiments offering a choice between s seeds for certain and the lottery ($s - k$, 0.5, $s + k$), with s being increased while the variance is held constant, tests for variable responses to risk, as outlined above.

After completing a series of experiments with each bird, we tested for position preferences, since we sought assurance that the results were not biased by a bird's favouring one side of the aviary. Two seeds were presented at each station during learning and preference trials, so that rewards were certain and equal. A statistically significant position preference was found in only one of nine cases, and it may strengthen our results (see below). This procedure cannot eliminate the possibility that a bird had a position preference during earlier experiments. However, the homogeneity of results among the birds indicates that starvation schedules and food reward characteristics were most important in governing their preferences.

Results
For both series of experiments, we first present the responses to risk. We then provide the calculated utilities and the estimated utility functions.

1-h Starvation, 30-s Delay per Seed
In these experiments the juncos can expect a non-negative net energy budget (see Appendix).

Table I shows individual preferences in all tests where the certain reward either equalled the mean of the variable reward or differed by only 0.5 seed. In 19 of 25 tests the birds avoided risk, since the certain reward was preferred. Moreover, the certain reward was preferred in all 13 tests of the form s versus $(0, 0.5, 2s)$. Indifferences occurred where the lottery had a relatively low variance to mean ratio. This ratio ranged from 0.5 to 6.0, and indifference was never noted when it exceeded 2.0.

Experiments in the first series with two of the birds indicate decreasing risk aversion. For W/W we conducted four preference tests of the form s versus $(s - 3, 0.5, s + 3)$, with $s = 3, 4, 5$, and 7. The mean of the probability distribution increases, but the variance is a constant (9.0). The bird preferred the certain reward for $s = 3$ and 4, but was indifferent at the higher means. Since the risk premium $(E[s] - \hat{s})$ decreased, we interpret this behaviour as decreasing risk aversion. For Y/S there were five experiments of the form s versus $(s - 2, 0.5, s + 2)$, with $s = 2, 3, 4, 5$, and 6. The certain reward was preferred for $s = 2, 4$, and 5, but the bird was indifferent for $s = 3$ and 6.

There are, of course, individual differences in the birds' foraging behaviour (Altmann 1974; Partridge 1976). However, the preferences of all five birds showed aversion to risk, and decreasing risk aversion is apparently a more complete description of their responses to food reward variation when they could expect a non-negative net energy budget.

We found 42 certainty equivalents for the five juncos tested in the first series. Table II presents each bird's utilities calculated from the certainty equivalents as outlined above. In 36 of the 42 indifferences recorded in these experiments, the certainty equivalent is less than the mean of the probability distribution, and no certainty equivalent exceeds the mean of the associated distribution. These indifferences, combined with the preferences noted above, provide strong evidence that the juncos avoided risk while their net energy was increasing. As a utility function, we chose $U(s) = (1/c) \ln(1 + s)$. This function satisfies the criteria for decreasing risk aversion: $U'(s) > 0$, $U''(s) < 0$, and $\partial r(s)/\partial s < 0$. We selected values of c (listed in Table II) to minimize the sum of squared deviations between observed utilities and $\hat{U}(s)$. In each case the estimated $U(s)$ has a lower sum of squared deviations than the best linear regression $(U''(s) = 0)$. Figure 1 graphs the utilities and estimated $U(s)$ for W/W, the bird involved in the greatest number of experiments.

After these experiments we tested each bird to see whether any individual favoured one side of

Table I. Preference Test Results, First Series (1-h Starvation, 30-s Delay per Seed)

Bird	R/O	W/W	Y/S	O/W	W/G
	2 P (0, 0.5, 4)	3 P (0, 0.5, 6)	2 P (0, 0.5, 4)	1 P (0, 0.5, 2)	3 P (0, 0.5, 6)
	3 P (0, 0.5, 6)	4 P (0, 0.5, 8)	3 P (0, 0.5, 6)	3 P (0, 0.5, 6)	3 P (0, 0.5, 7)
	3 P (0, 0.5, 7)	4 P (1, 0.5, 7)	3 I (1, 0.5, 5)	3 P (0, 0.5, 7)	
	4 P (0, 0.5, 8)	5 I (2, 0.5, 8)	4 P (2, 0.5, 6)	4 P (0, 0.5, 8)	
	6 P (0, 0.5, 12)	6 P (0, 0.5, 12)	5 P (3, 0.5, 7)	4 I (3, 0.5, 6)	
		7 I (4, 0.5, 10)	6 I (4, 0.5, 8)		
		8 I (5, 0.5, 12)			

The certain value (± 0.5 seed) equals the probability distribution's expectation, 0.5 $(s_i + s_j)$. Risk aversion is obvious. APB means reward A is preferred to reward B; I indicates indifference.

Table II. Utilities, First Series (1-h Starvation, 30-s Delay per Seed)

Bird	c	$s = 0$	1	2	3	4	5	6	7	8	9	10	11	12
R/O	2.1	0	0.22	0.39	0.52	0.72	0.78	1	—	1.04	—	—	—	1.4
W/G	1.9	0	0.4	0.5	0.73	0.79	0.95	1	1.05	1.3	—	—	—	—
W/W	1.9	0	0.35	0.54	0.71	0.89	0.95	1	1.05	1.15	—	1.25	—	1.3
Y/S	1.9	0	0.35	0.5	0.7	0.8	0.88	1	—	1.2	—	—	—	1.4
O/W	1.8	0	0.38	0.5	0.75	0.88	0.95	1	—	—	—	—	—	1.5

$U(0)$ and $U(6)$ are arbitrary. The concavity suggests aversion to risk. The column labelled c gives the value used to fit the utility function $U(s) = (1/c) \ln(1 + s)$ to each data set.
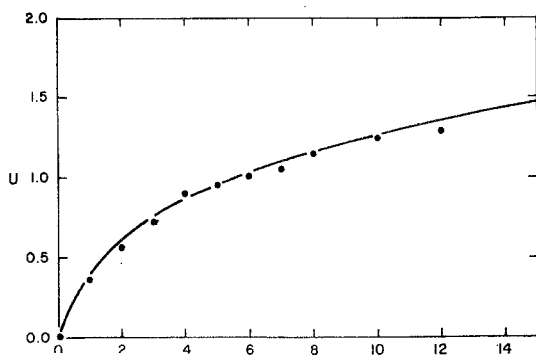
Fig. 1. Utilities and estimated utility function for W/W in first series of experiments. The function is $U(s) = (1/1.9) \ln(1 + s)$. Data for two of the other four birds in the first series are accurately described by the same function. The departure from linearity is obvious, and indicates risk aversion.

the aviary. No bird exhibited a significant position preference.

4-h Starvation, 1-min Delay per seed

Our calculations suggest that under this procedure the juncos can expect a negative net energy budget (see Appendix). Two birds used in the first series (R/O and Y/S) were included in the second series to see whether their responses to risk would change with increased hunger. Two other birds (M/S and S/B) were subjects in only the second series.

Table III shows individual preferences in all tests where both stations offered the same mean, or the difference was only 0.5 seed. In 18 of 29 of these tests, the variable reward was preferred,

and the certain reward was never preferred. In 13 of 15 experiments of the form s versus $(0, 0.5, 2s)$, the variable reward was preferred. These preferences are risk-prone and contrast sharply with the results of the first series (compare Tables I and III).

The data for R/O and Y/S can be taken to suggest decreasing risk proneness. Since we are ultimately interested in the global behaviour of the birds' preferences, rather than just their response over the range of reward sizes used in our experiments, we conservatively assume decreasing, as opposed to constant, risk proneness for all four birds.

A total of 23 certainty equivalents were obtained in the second series. For each bird, Table IV provides the utilities calculated from the observed indifferences. In 17 of the 23 indifferences found in the second series of experiments, the certainty equivalent exceeds the mean of the distribution, and no certainty equivalent is less than the mean of the associated distribution. Both the preferences and indifferences indicate that all four birds responded to variation in a risk-prone manner during the second series of experiments. Note that R/O and Y/S avoided risk while accumulating net energy, but favoured risk when they could expect a negative 24-h net energy budget.

We use a quadratic in s as a decreasingly risk-prone utility function ($U'(s) > 0$, $U''(s) > 0$, and $\partial r(s)/\partial s > 0$). The estimated functions are:

R/O: $U(s) = -0.01 + 0.115s + 0.008s^2$, $R^2 = 0.999$

Y/S: $U(s) = -0.02 + 0.045s + 0.016s^2$, $R^2 = 0.995$

Table III. Preference Tests Results, Second Series (4-h Starvation, 1-m in Delay per Seed)

Bird	R/O	Y/S	M/S	S/B
	$(0, 0.5, 2)\ P\ 1$	$(0, 0.5, 2)\ P\ 1$	$(0, 0.5, 2)\ P\ 1$	$(0, 0.5, 2)\ I\ 1$
	$(0, 0.5, 4)\ P\ 2$	$(0, 0.5, 4)\ P\ 2$	$(0, 0.5, 4)\ P\ 2$	$(0, 0.5, 3)\ I\ 2$
	$(0, 0.5, 5)\ P\ 3$	$(0, 0.5, 6)\ P\ 3$	$(0, 0.5, 3)\ I\ 2$	$(0, 0.5, 4)\ P\ 2$
	$(2, 0.5, 6)\ I\ 4$	$(1, 0.5, 7)\ I\ 4$	$(0, 0.5, 6)\ P\ 3$	$(0, 0.5, 6)\ P\ 3$
	$(0, 0.5, 8)\ P\ 4$	$(4, 0.5, 6)\ I\ 5$	$(0, 0.5, 8)\ P\ 4$	$(0, 0.5, 5)\ I\ 3$
	$(3, 0.5, 7)\ P\ 5$			$(1, 0.5, 5)\ P\ 3$
	$(4, 0.5, 6)\ I\ 5$			$(2, 0.5, 6)\ P\ 4$
	$(3, 0.5, 9)\ I\ 6$			$(1, 0.5, 7)\ I\ 4$
				$(0, 0.5, 8)\ I\ 4$
				$(3, 0.5, 7)\ P\ 5$
				$(0, 0.5, 10)\ P\ 5$

The certain value (± 0.5 seed) equals the probability distribution's expectation, $0.5\ (s_i + s_j)$. Data indicate risk proneness. $A\ P\ B$ means reward A is preferred to reward B; I indicates indifference.

M/S: $U(s) = -0.01 - 0.001s + 0.028s^2$,
        $R^2 = 0.998$
S/B: $U(s) = 0.01 - 0.009s + 0.026s^2$,
        $R^2 = 0.994$

Since the minima of the last two functions occur so close to $s = 0$, we need not worry about the negative coefficients of s. In all cases the term in s^2 significantly increases the explanation of the variance in the data of Table IV (R/O: $F_{1,5} = 36.7$, $P < 0.005$; Y/S: $F_{1,5} = 18.0$, $P < 0.001$; M/S: $F_{1,3} = 26.3$, $P < 0.025$; S/B; $F_{1,7} = 21.6$, $P < 0.005$).

Figure 2 graphs the utilities and estimated $U(s)$ for S/B, the bird involved in the greatest number of experiments. After the second series we found that one of the four juncos (R/O) had developed a significant position preference. However, the bird favoured the side where the constant reward had been presented. Therefore, if its side preference biased these results at all, we may be underestimating its risk proneness.

Discussion

Our laboratory results indicate that yellow-eyed juncos are sensitive to variation in energetic rewards, and that their response to risk depends on a comparison of energetic intake with energetic requirements. The dichotomy between positive and negative net energy budgets is probably an oversimplification, but the birds' behaviour in the two series of experiments certainly contrasts.

Characterizing resources by the expectations alone may be adequate for some dietary problems (e.g. Davies 1977). However, variation in energetic rewards may be important in such diverse problems as patch use (Charnov 1973; Gill & Wolf 1977; Oaten 1977), avian flock formation (Thompson et al. 1974), and parental feeding strategies in birds (Krebs 1974). Utility theory, particularly the concepts of risk aversion and risk proneness, may be a helpful diagnostic tool in understanding the way animals exploit variable environments.

When they avoided risks, the juncos reduced their mean reward in order to reduce reward variation. When risk-prone, the birds favoured variable rewards, so the mean was again insufficient to characterize their preferences. There probably are starvation–trial delay schedules that would produce results consistent with deterministic theory, but we suspect that juncos in nature will generally avoid risk unless they face difficult energetic stress (see Real, in press).

It is tempting to view our results by considering energy/time as the random variable of interest. If the juncos avoid risk when energy/time is greater than the value required for daily energy balance and favour risk when energy/time is less than required, then U has an inflection point (U'' changes sign). Schaffer (1978) suggests that this is the form of an individual's fitness function for energy, and an interesting parallel has been suggested for the global behaviour of utility functions in human economics (Friedman & Savage 1962).

In experiments with laboratory rats, Pubols (1962) shows that subjects increased their preference for rewards with greater variation in energy/time as their mean feeding rate decreased. Logan (1965) treats reward size and time as separate attributes in experiments with rats, and his data indicate slight risk aversion. Since these studies do not comment on energy budgets versus requirements, it is difficult to compare the data to our results, but risk-sensitivity in decision-making is apparent in each case.

Even under controlled conditions, assessing and checking an individual's utility function may take a long time. This function is required before one can ask whether a forager maximizes expected utility. Additionally, Von Neumann & Morgenstern's (1948) utility theory assumes that the organism knows the reward probability distribution for each available resource. This is not particularly different from the assumptions of most foraging models, but see Krebs et al. (1978).

Table IV. Utilities, Second Series (4-h Starvation, 1-m in Delay per Seed)

Bird	$s = 0$	1	2	3	4	5	6	7	8	9	10
R/O	0	—	0.25	0.38	0.56	0.75	1	—	—	1.63	—
Y/S	0	—	0.13	0.25	0.3	0.5	1	—	—	—	2.0
M/S	0	—	0.1	0.2	0.5	—	1	—	—	—	—
S/B	0	0.05	0.09	0.18	0.5	0.55	1	1.05	1.7	—	—

$U(0)$ and $U(6)$ are arbitrary. The convexity indicates risk proneness.
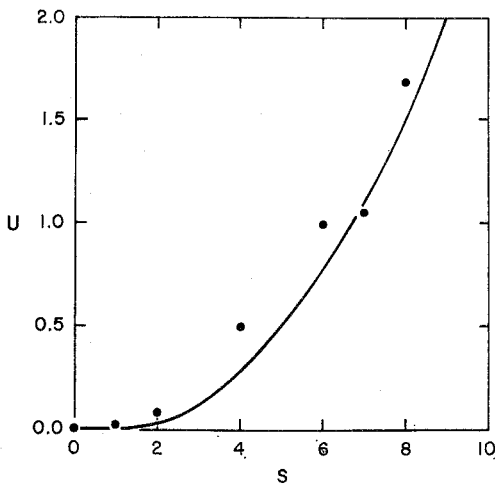
Fig. 2. Utilities and estimated utility function for S/B in second series of experiments. The function is $U(s) = 0.01 - 0.009s + 0.026s^2$, $R^2 = 0.994$. The departure from linearity suggests risk proneness.

However, under a wide variety of conditions, predictions assuming risk aversion often differ from those assuming risk proneness (Derman et al. 1975; Caraco, in press). These differences may prove useful to workers in the field.

Utility theory is but one of many ways to view choice, measurement, and optimal decisions under stochasticity. Generalizations of its assumptions and preference axioms include, for example, consideration of subjective probability (Luce & Suppes 1965), indifference based on inability to discriminate reward differences (Fishburn 1972), and extensions of 'rational preferences' (Coombs & Huang 1976; van Santen 1978). It may be that the accurate description of preference axioms will reveal variation with cognitive abilities of different phylogenetic groups.

In nature organisms face variation in a number of ecological factors that influence survivorship and/or fecundity. Multiattribute utility theory (Keeney & Raiffa 1976) may offer a means to investigate an organism's decisions concerning trade-offs among the components of fitness in a stochastic environment. In any case, we are convinced that our study organisms are attuned to variability in their food resources and we believe that various aspects of utility theory will provide an informative characterization of their foraging strategies.

Appendix

We measured the resting oxygen consumption for three juncos to estimate daily energetic requirements. As in our experiments, the environmental chamber (a cylinder with a height of approximately 15 cm and a radius of 10 cm) was controlled at 7 ± 1 C. Each bird was provided millet seed, a light source, and outside air at a flow rate of 500 ml/min. The percentage decrease in oxygen was continuously recorded for at least 2 h (1500 to 1700 hours) with a Beckman F-3 oxygen analyser. Water vapour pressure was not controlled during the data collection.

After the system reached a steady state, we took the resting oxygen consumption measured during the next 30 min and calculated the bird's average metabolic rate. For the three individuals tested, the resting oxygen consumption averaged 0.52 % (range 0.4 to 0.61 %) atmospheric oxygen, which at 500 ml/min $\times$ 19.87 J/ml of oxygen (F. R. Hainsworth, personal communication) yields 51.662 J/min resting metabolism.

Since the birds were active during the preference tests, we used 1.1 $\times$ lab metabolism (Kontogiannis 1967) as the estimated costs for an active junco at 7 C. The anticipated 24-h requirement (Wolf & Hainsworth 1977a) was 81.833 kJ. On a per gram body weight basis, this is close to published estimates for a related species, *Junco hyemalis* (King & Farner 1961). We assume this value is the minimum target that an individual junco attempts to achieve in a foraging day.

Before the starvation period (beginning at 0900 hours) of the preference tests, an individual was fed millet ad lib. The energy gain during the morning from the moment the lights were turned on until we initiated the starvation period (0700 to 0900 hours) was estimated by recording the food consumption of one of the birds (Y/S) on three different days. The times when feeding bouts were initiated, bout durations, and number of seeds consumed were recorded for each 2-h period. The average number of seeds consumed was 229 (range 175 to 289). Using a Parr Adiabatic Calorimeter, we found the energetic content of millet to be 89.96 J/husked seed (range 86.1 to 96.2 J/seed). These values are

quite close to those given in Willson (1971) on a per gram, but not a per seed, basis. Converting the mean number of seeds eaten to joules, the bird's average energy intake in the morning was 14.42 kJ, assuming 70% digestion efficiency (Wolf & Hainsworth 1977b). Since no energy was ingested during the starvation period, a junco needed about 67.412 kJ to meet 24-h requirements after the morning foraging. To acquire 67.412 kJ after a 1-h starvation (0900 to 1000 hours), the junco required an intake rate of about 124.84 j/min (= 1.39 millet seeds/min) for the remaining 9 h of feeding time. Similarly, after 4 h of starvation (0900 to 1300 hours), it needed a rate of 187.26 j/min (= 2.08 millet seeds/min) to attain the 24-h requirement during the remaining 6 h of the foraging day.

After the 1-h starvation we delayed trials 30 s for each seed eaten at the previous trial. This amounts to 2 seeds/min, which is 1.44 times the rate required for energy balance. After the 4-h starvation we delayed trials 1 min per seed eaten at the previous trial. One seed per min is half the rate required to meet daily costs under these circumstances, so the birds could expect a negative net energy budget.

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