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Energy Budgets, Risk and Foraging Preferences in Dark-Eyed Juncos (*Junco hyemalis*)

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Summary. Juncos' preferences for constant versus variable food rewards were tested in three series of aviary experiments. Deprivation and feeding rates were varied across the three treatments, but the mean of the variable reward equalled the constant reward in every experiment. When the birds gained energy faster than required to meet all 24-h costs, they preferred the constant reward. When the birds' energy intake was less than the minimally required rate, they preferred the variable reward. When energy intake just balanced average daily costs, the birds preferred the constant reward or were indifferent, and their response depended on the particular mean-variance combination presented.

Introduction

Models of foraging behavior usually assume that animals rank resources from most to least preferred. Recent theory predicts that natural selection molds such preferences so that the rank-order depends on both the mean and variance (of net benefits) associated with each resource (Oster and Wilson 1978; Real 1980a; Caraco 1980). These models of risk-sensitive behavior can predict resource utilization strategies that contrast with predictions based on mean rewards only. Therefore, it is important to ascertain how foraging preferences depend on benefit variance.

Consider an animal with access to only two patches of food. Suppose the average net benefit obtained after a foraging bout is identical for the two statistically independent patches, but the variances differ. If the forager always prefers the smaller variance, its behavior is risk-averse, or tychophobe (Oster and Wilson 1978). If the forager always prefers the larger variance, its behavior is risk-prone, or tychophile (Oster and Wilson 1978). It has been suggested that foragers should avoid risk when they can expect to meet all energetic requirements, but should behave in a risk-prone manner when requirements exceed their average energetic benefit (Caraco 1980; Pulliam and Millikan, in press; Stephens, in press). In each case the predicted behavior maximizes the probability of obtaining enough food to meet energetic costs.

A number of studies indicate that animals are capable of risk-sensitive foraging behavior in situations analogous to this two patch problem. Psychologists often work with severely deprived subjects, and have found that both birds and mammals usually prefer variable rewards (where energy or energy/time varies) over constant rewards (Pubols 1962; Herrnstein 1964; see references cited in Lea 1979). However, in the field Real (in press) showed that two species of nectar-feeding insects prefer constant over variable rewards when copious amounts of nectar are provided. Pimm (1978) observed that aggressively dominant hummingbirds also prefer constant rewards in the field. The contrasting results could be due to differences in the energetic condition of the foragers, if severe deprivation induces risk-prone behavior, while well-fed animals are risk-averse.

The first direct test of the hypothesized relationship between expected energy budgets and risk-sensitivity involved yellow-eyed juncos (*Junco phaeonotus*). The same individuals foraged in a risk-averse, and then in a risk-prone manner, depending on whether they could expect to obtain sufficient daily energy (Caraco et al. 1980). To more fully examine this relationship, preferences for benefit variance were investigated in dark-eyed juncos (*Junco hyemalis*). In all experiments reported here, a bird chose repeatedly between two rewards: one was constant, one was variable, but the mean of the variable reward always equalled the constant reward. The anticipated preferences were: (1) risk-aversion when the birds' rate of energy intake was greater than the rate required for

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24-h energetic balance, (2) risk-prone behavior when requirements exceeded expected energy intake, and (3) either indifference to variance or some pattern of intermediate preferences when energy intake just equalled the minimal rate required to meet all costs.

Materials and Methods

1. Four dark-eyed juncos (*Junco hyemalis*) of the slate-colored variety were captured in February 1980; they were involved in a total of 84 experiments. Each bird was kept in a separate aviary (2 m × 3 m × 2 m). All of the aviaries were equipped with two feeding stations, at which an experimenter presented small dishes containing predetermined numbers of seeds. The physical design of these experimental chambers was otherwise identical to that described in Caraco et al. (1980).

The juncos were trained to perch at a point on the midline between the two feeding stations to obtain food. When conducting experiments involving choices between food rewards, one must guard against an animal's position preference for one side of its enclosure. Each junco was tested before any experiments were performed, and retested every three weeks, to assure that it had no position preference. This control procedure was conducted exactly as detailed in Caraco et al. (1980). During this study one bird developed a position preference. The bird was then released, and all data that might have been biased by its preference were discarded.

2. Energy budgets play a central role in these experiments. Several factors are important: ambient temperature, body weight, oxygen (therefore, energy) consumption rate, length of the foraging day, energetic value of the seeds fed to the birds, digestive efficiency, and the rate at which food is provided during an experiment (Caraco et al. 1980). To simplify the discussion, consider the conditions applicable to each experiment reported here. A 19-g junco is kept in an aviary where ambient temperature is maintained at a constant 10° C and the lights are turned on for exactly 10 h (0730–1730 hours) each day. Over 10 h a junco consumes 765 millet seeds (SE = 40.5, n = 14) to meet all 24-h costs and maintain a constant weight. During the first 90 minutes of the foraging day (0730–0900), a junco consumes 163 millet seeds (SE = 6.2, $n=20$). Deprivation is initiated at 0900 hours, so the bird requires an additional 602 seeds during the remaining 8.5 h of the foraging day. Deprivation lasts for d hours. Then the experiment begins, and the bird is fed R seeds/h. If $(8.5-d)\,R>602$, the experimental energy budget exceeds the physiological requirement (positive energy budget). By increasing d (longer deprivation) and decreasing R, the inequality can be reversed, and the bird's energy budget is negative. If $R=602/(8.5-d)$, the bird's energy budget is referred to as balanced. In the experiments $d=1$ and $R=120$ for positive energy budgets, $d=4$ and $R=60$ for negative energy budgets, and $d=2$ and $R=90$ for balanced energy budgets. A balanced energy budget in this context implies that a bird must spend all of its time during daylight hours in feeding, just to meet 24-h costs. Animals in nature surely seek positive energy budgets while foraging, since this reduces the probability of starvation and leaves time for other essential activities (predator detection and reproduction for example).

3. In each experiment a constant reward (x seeds) was presented at one station, and a variable reward was presented at the other station. The variable reward provided either x_1 or x_2 seeds, each with probability 0.5. The expected value of the variable reward always equalled the constant reward; $[x_1+x_2]/2=x$. Since the means were equal, and the variable reward was symmetric about its mean (i.e., no skew), a significant preference for one station should indicate a response to benefit variance.

Each experiment consisted of 24 forced-choice learning trials followed by 25 preference trials. Only one station provided food at each learning trial. The bird visited each station (in a random sequence) 12 times, obtained the same total number of seeds at each station, and learned the differing reward characteristics. Learning trials reduce the impact of sampling behavior (Krebs et al. 1978; Shettleworth 1978) on choices made during the preference test, since 24 trials should allow the bird to discriminate characteristics of the rewards in these simple experiments (Krebs et al. 1978; Lea 1979). The subject also should acquire an estimate of its expected energy budget during learning trials.

The preference test immediately followed learning trials. The two food dishes were presented simultaneously, and the bird selected one at each trial. The time between all trials is controlled so that the junco remains on the appropriate energetic trajectory. Caraco et al. (1980) discuss training and testing procedures in detail.

4. A junco's choice behavior was tested against the null hypothesis of indifference (equal preference), which assumes that choice probabilities do not differ significantly from 0.5. By the cumulative binomial probability function, the null hypothesis is rejected (and a preference is noted) when one station is selected 18 or more times ($\alpha \doteq 0.05$). This test assumes independent trials. Contingency table analysis (see Caraco et al. 1980) of the nine data sets reported here indicate that sequential choices were statistically independent.

Birds C, S, and B were first tested at a positive energy budget. Birds C and S were then tested at a negative energy budget and finally at a balanced energy budget. Bird R was first tested at a balanced energy budget and then at a negative energy budget.

A variety of mean-variance combinations were used at each energy budget, since the variance to mean ratio of the variable reward may secondarily influence choice probabilities in these experiments (Caraco et al. 1980). Each bird experienced a random sequencing of experiments. Data sets for the last treatment administered to birds S and R are slightly smaller than others, since the birds were released when local juncos began spring migration.

Results

Table 1a shows the results of the 34 experiments where the juncos experienced a positive energy budget. The constant reward was preferred significantly in 26 experiments. Indifference occurred six times, and the variable reward was preferred in only two experiments. Two individuals (B and C) preferred the constant reward in every experiment where the variance to mean ratio of the variable reward (designated by θ) exceeds unity. Bird S preferred the constant number of seeds whenever $\theta>1.8$, and in 2 other experiments where $\theta=1$. The juncos clearly favor the less variable reward when their rate of energy intake allows them to meet 24-h requirements easily.

Table 1 also lists the proportion of preference trials where the individual selected the constant reward (designated as P_c). The values of P_c in Table 1a appear to be an upper asymptotic function (Poole 1974) of θ. Averaging the data across the three juncos, the equation obtained was $P_c=0.9-0.81\,(0.34)^{\theta}$. This relationship can be taken only as a general description, however, since the preference data are proportions (see Sokal and Rohlf 1969, p 386).

Table 1. Preference Data. The result of each experiment is recorded as a significant preference or an indifference (i.e., equal preference). $x\ P\ (x_1,\ x_2)$ indicates that a constant reward of x millet seeds is significantly preferred over a variable reward where both x_1 and x_2 seeds occur with probability 0.5. $(x_1,\ x_2)\ P\ x$ indicates a significant preference for the variable reward. $x\ I\ (x_1,\ x_2)$ indicates indifference between constant and variable rewards. θ is the variance to mean ratio of the variable reward. P_c is the proportion of preference trials where the junco chose the constant reward. Table 1a shows the positive energy budget data. The constant reward is preferred in 26 of 34 experiments. Asterisks mark the two P_c values where the variable reward is preferred. Table 1b shows the negative energy budget data. The variable reward is preferred in 19 of 20 experiments. Table 1c shows the balanced energy budget data. Indifference is most common here. Asterisks mark the three P_c values where the variable reward is preferred

a) Positive energy budget

Bird	C			S			B	
Test	θ	P_c	Test	θ	P_c	Test	θ	P_c
2I(1,3)	0.5	0.32	2I(1,3)	0.5	0.32	2P(1,3)	0.5	0.96
5I(3,7)	0.8	0.56	(3,7)P5	0.8	0.16*	(3,7)P5	0.8	0.24*
1P(0,2)	1.0	0.76	1P(0,2)	1.0	0.88	1I(0.2)	1.0	0.40
4I(2,6)	1.0	0.64	4P(2,6)	1.0	0.92	4P(2,6)	1.0	0.76
3P(1,5)	1.3	0.80	3P(1,5)	1.3	0.96	3P(1,5)	1.3	0.88
2P(0.4)	2.0	0.88	5I(2,8)	1.8	0.52	2P(0.4)	2.0	0.84
4P(1,7)	2.3	0.88	2P(0,4)	2.0	0.88	4P(1,7)	2.3	0.96
3P(0,6)	3.0	0.88	4P(1,7)	2.3	0.84	3P(0,6)	3.0	0.88
5P(1,9)	3.2	0.92	3P(0,6)	3.0	0.80	5P(1,9)	3.2	0.72
4P(0,8)	4.0	0.76	5P(1,9)	3.2	0.76	4P(0,8)	4.0	0.92
5P(0,10)	5.0	0.96	4P(0,8)	4.0	0.88	5P(0,10)	5.0	0.76
			5P(0,10)	5.0	0.92			

b) Negative energy budget

Bird	C			S			R	
Test	θ	P_c	Test	θ	P_c	Test	θ	P_c
(1,3)P2	0.5	0.08	(1,3)P2	0.5	0.24	(0,2)P1	1.0	0.08
(0,2)P1	1.0	0.04	(0,2)I1	1.0	0.32	(1,5)P3	1.3	0.04
(2,6)P4	1.0	0.04	(2,6)P4	1.0	0.24	(0,4)P2	2.0	0.12
(1,5)P3	1.3	0.16	(1,5)P3	1.3	0.20	(0,6)P3	3.0	0.08
(0,4)P2	2.0	0.18	(0,4)P2	2.0	0.18			
(1,7)P4	2.3	0	(1,7)P4	2.3	0.24			
(0,6)P3	3.0	0.12	(0,6)P3	3.0	0.12			
(0,8)P4	4.0	0	(0,8)P4	4.0	0.28			

c) Balanced energy budget

Bird	C			S			R	
Test	θ	P_c	Test	θ	P_c	Test	θ	P_c
(1,3)P2	0.5	0.28*	(1,3)P2	0.5	0.24*	2I(1,3)	0.5	0.36
1I(0,2)	1.0	0.44	1I(0,2)	1.0	0.32	1I(0,2)	1.0	0.36
4P(2,6)	1.0	0.84	3I(1,5)	1.3	0.64	4I(2,6)	1.0	0.48
3I(1,5)	1.3	0.32	2P(0,4)	2.0	0.76	3I(1,5)	1.3	0.56
2I(0,4)	2.0	0.56	4P(1,7)	2.3	0.72	2P(0.4)	2.0	0.92
4P(1,7)	2.3	0.72	3P(0,6)	3.0	0.72	4P(1,7)	2.3	0.84
3P(0,6)	3.0	1.00	4I(0,8)	4.0	0.36	3P(0,6)	3.0	0.92
5I(1,9)	3.2	0.48	5I(0,10)	5.0	0.32	5I(1,9)	3.2	0.56
4P(0,8)	4.0	0.88				4P(0,8)	4.0	0.80
5I(0,10)	5.0	0.56				5I(0,10)	5.0	0.48
6I(0,12)	6.0	0.40				(0,12)P6	6.0	0.16*

Most of the experiments indicate significant risk-aversion, and mean P_c values do not vary a great deal when $\theta \geq 2$. Some effort is allocated to the nonpreferred reward in every experiment, and this was interpreted as a sampling constraint on the juncos' behavior (see Discussion).

Table 1b shows the results of the 20 experiments where the juncos experienced a negative energy budget. The variable reward was preferred significantly in 19 experiments. The constant reward was never preferred. The single indifference is found in the data for bird S. Interestingly, this individual allocated less effort to the variable reward than did bird C in all but one experiment. None of the three data sets shows a significant correlation between P_c and θ. The mean P_c value for birds C, S, and R are, respectively, 0.08, 0.23, and 0.08. All but two of the experiments resulting in risk-prone behavior show some utilization of the nonpreferred reward. The important result is that variable rewards are preferred over a constant number of seeds when the birds expect a negative energy budget. Juncos that avoid variance when energy budgets are positive become risk-prone when their intake of energy does not meet the rate required by 24-h physiological costs.

Table 1c shows the results of the 30 experiments where the juncos experienced a balanced energy budget. The constant reward was preferred significantly 11 times. The variable reward was preferred significantly in 3 experiments, and indifference was noted 16 times. The indifferences indicate a lack of risk-sensitivity at certain mean-variance combinations, and indifference occurs much more often in these data than was observed at either positive or negative energy budgets.

The three risk-prone results occur at extreme values of the variance to mean ratio of the variable reward. Birds C and S preferred the variable reward at the minimal value ($\theta = 0.5$), while bird R preferred the variable reward at the maximal value ($\theta = 6$) found in these experiments. Further, preference for the constant reward occurs most consistently at intermediate values of θ. At a balanced energy budget, a junco's response to benefit variance is most strongly dependent on the particular mean and variance of the number of seeds presented.

A pattern in these data can be revealed by considering the P_c values listed in Table 1c. Since most of the choice probabilities fall between 0.3 and 0.7, the data were not transformed (see Sokal and Rohlf

1969). Pooling data for the three birds, one obtains a significant quadratic regression:

$$P_c = 0.15 + 0.39\ \theta - 0.06\ \theta^2;$$
$$R^2 = 0.96,\ F_{1,28} = 50.9,\ P < 0.005.$$

Further, the quadratic regression, $P_c = \sum_{n=0}^{2} b_n \theta^n$, for each individual's data is significant. The regression coefficients (b_n) and associated statistics are presented in Table 2. I have found no simple, yet ecologically relevant, variable which shows a monotonic relationship to these P_c values.

Table 2. Choice Probablity Regressions, Balanced Energy Budget. The quadratic regression, $P_c = \sum_{n=0}^{2} b_n \theta^n$, was calculated for each balanced energy budget data set. P_c is the proportion of preference trials where the junco chose the constant reward. θ is the variance to mean ratio of the variable reward. b_0 is the intercept, b_1 is the coefficient of θ, and b_2 is the coefficient of θ^2. R^2 is the multiple correlation coefficient. The quadratic term significantly increases the explanation of the variance in the dependent variable for each bird

Bird	b_0	b_1	b_2	R^2	F	
C	0.2	0.33	–0.05	0.96	$F_{1,9} = 11.3$,	$P < 0.01$
S	0.03	0.51	–0.09	0.98	$F_{1,6} = 19.3$,	$P < 0.005$
R	0.09	0.48	–0.08	0.98	$F_{1,9} = 34.6$,	$P < 0.005$

For low to medium values ($\theta \leqq 3$) of the variance to mean ratio of the variable reward, these data are roughly similar to the results for positive energy budgets. The allocation of effort to the constant reward increases with θ until each bird is significantly averse to variance. However, at higher values of θ, use of the constant reward decreases when energy budgets are balanced, in sharp contrast to the positive energy budget data.

The results indicate that both energy budgets and reward statistics govern preferences. Juncos avoid variance in these two-choice experiments whenever their energy budget is positive and the variance of the variable reward exceeds its mean; extremely small variance produces indifference. Negative energy budgets induce preference for variance at all levels of θ examined. Juncos are indifferent to variance when their energy budget is balanced and either variation is very small or the mean number of seeds is relatively large; otherwise they prefer the constant reward. Essentially, preference for the constant reward is strong at a positive energy budget, intermediate at a balanced energy budget, and disappears at a negative energy budget.

Discussion

Environmental stochasticity no doubt influences a variety of ecological and evolutionary strategies (Southwood 1977). Responses to variation in benefits and costs may govern phenomena as diverse as schedules of reproduction (e.g., Schaffer 1974; Templeton and Rothman 1974; Gillespie 1977; Istock 1978), the organization of social insects' colonies (Oster and Wilson 1978) and avian flock formation (Thompson et al. 1974; Pulliam and Millikan, in press; Caraco 1980). Fedding preferences clearly can depend on net benefit variation (Pimm 1978; Caraco et al. 1980; Real, in press).

The dark-eyed juncos' response to reward variance is quite labile, but is reasonably predictable. The results are consistent with preferences of yellow-eyed juncos (Caraco et al. 1980). The logic of a variable response to risk has been discussed elsewhere (Caraco 1980; Real 1980b; Pulliam and Millikan, in press). For those interested, roughly parallel phenomena can be found in psychology (Tversky 1967) and economics (Friedman and Savage 1962).

A reviewer has suggested that the relationship between energy budgets and risk-sensitivity noted here may not generally hold in nature. The experiments mimic a very good environment where conditions temporarily decay to different levels of energy availability. The reviewer proposes that an animal constrained to forage in a chronically poor environment might respond differently than did juncos suddenly faced with an expected negative energy budget. In nature foragers obviously have a wider array of strategic options when responding to reduced food availability than these experiments allow (e.g., MacArthur and Pianka 1966; Pulliam 1974; Gill and Wolf 1975). Survivorship might be better enhanced by reducing energetic requirements (if possible) and maintaining risk-aversion, rather than adopting a long-term risk-prone strategy in a poor environment. Furthermore, a strict association of risk-averse and risk-prone preferences with positive and negative energy budgets, respectively, may be an oversimplification. In any case, the results reported here do suggest that responses to benefit variances are not fixed, and are likely to vary with a forager's energetic state (Caraco 1980) or its probability of starvation (Taylor 1976; Pulliam and Millikan, in press).

Perhaps the most interesting step toward increased realism would be achieved by integrating risk-sensitivity into dynamic (i.e., time dependent) foraging models (Oaten 1977; Green, in press). Models for harvesting renewable resources in stochastic environments (Beddington and May 1977; Gleit 1978) employ a conceptual framework which might enhance our ability to predict interactions between foragers and their resources.

One other aspect of the juncos' preferences deserves comment. Though the vast majority of positive and negative energy budget results indicate significant risk-sensitivity, some effort is allocated to the nonpreferred reward in almost all of these experiments. Food resource characteristics often change through time in nature. A currently nonpreferred resource should be sampled occasionally, so that the forager can monitor temporal patterns in resource profitability. I suspect that a sampling requirement constrains the P_c values, whether the birds avoid or favor benefit variance (Pyke et al. 1977; Shettleworth 1978; Caraco 1980). However, the data cannot reject the hypothesis that the juncos use the two rewards to achieve a most preferred level of risk (Coombs 1969; Coombs and Huang 1976).

In nature successful foragers gather sufficient energy while feeding to meet physiological costs and still have time for other essential activities. Their foraging should avoid excessive variation in benefits and costs. However, when a forager is severely stressed, its utilization of more variable resources is likely to increase. I suspect that response to variation is a fundamental aspect of many organisms' behavioral biology and deserves greater attention in both theoretical and empirical work.

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