The Energetic Costs of Alternative Rate Currencies in the Foraging Starling

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In classical optimal foraging models, it is assumed that organisms maximize a "currency" that acts as a proximate surrogate for fitness. The currency used in many existing foraging models is the average net long-term rate of energy intake (reviewed in Stephens and Krebs 1986). This is equal to the ratio of the expected net energy gained (G) over the expected time spent foraging (T), which is estimated as follows:

Long-term rate, or Ratio of Expectations (RoE)

$$= \frac{\left[\dfrac{\sum_{i=1}^{n} G_i}{n}\right]}{\left[\dfrac{\sum_{i=1}^{n} T_i}{n}\right]} = \frac{\sum_{i=1}^{n} G_i}{\sum_{i=1}^{n} T_i}, \quad (1)$$

where G_i is the energy gained from the ith food item, T_i is the time taken to acquire this item, and n is the total number of food items on which the estimate is based. The choice of this currency has been justified on the grounds that both the survival and the reproduction components of fitness have an obvious relation to the amount of energy obtained per unit of time spent foraging. The more energy available, the more can be channelled into reproduction, and the less time spent feeding, the more is available for other activities, such as predator avoidance and reproductive behavior.

However, an alternative rate currency for combining G and T is supported by a number of recent empirical results from European Starlings (*Sturnus vulgaris*, Bateson and Kacelnik, *in press*), Rock Doves (*Columba livia*, Mazur 1984, 1986), and bumble bees (*Bombus pennsylvanicus*, Harder and Real 1987, Real et al. 1990). The currency in question is the expected ratio of G over T, where, using the same definitions as for Eq. 1,

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$$\text{Expectation of Ratios (EoR)} = \frac{\sum_{i=1}^{n} \left(\dfrac{G_i}{T_i}\right)}{n}. \quad (2)$$

This algorithm is what arises if the rates associated with the capture of each prey item are estimated individually and the average of these rates is computed. The crucial difference between long-term rate (Eq. 1) and EoR (Eq. 2) is that in the latter, the rates at which individual prey items are obtained (i.e., G_i/T_i) are weighted equally when the average rate is computed, rather than being weighted according to the time over which the rate is experienced (T_i). Thus, estimates of EoR are sensitive to variance in T, whereas estimates of RoE are not. This results in the so-called "fallacy of the averages," the fact that the expectation of a function of random variables is not equal to the function of the expectations of the same variables (Templeton and Lawlor 1981, Gilliam et al. 1982, Turelli et al. 1982). In practice, this means that when T is variable, it will be the case that EoR is not equal to long-term rate. It is also true that, for two options of equal long-term rate, the one with the greater variance in T will have the greater EoR (Caraco et al. 1992).

Given that there is no obvious link between maximization of EoR and fitness (Gilliam et al. 1982, Turelli et al. 1982, Possingham et al. 1990), the apparent use of this currency in a number of species has been a source of much discussion in the foraging literature (Harder and Real 1987, Real et al. 1990, Real 1991, Bateson and Kacelnik 1995, Bateson and Kacelnik, *in press*). One partial explanation not tested so far is that in the natural environment there is no energetic difference between maximizing long-term rate and EoR (Bateson and Kacelnik, *in press*). In experiments designed to separate different rate algorithms, the values of T have been chosen so as to have high variance and, therefore, to exaggerate the discrepancy between the predictions of the long-term rate and EoR maximizing. However, these experiments are unlikely to represent accurately the situation in the natural environment where variance in T may be smaller. If there is no variation in T, then long-term rate and EoR are identical. In fact, as long as the variance in T is relatively small, the discrepancy in the rates estimated by an EoR maximizer and by a long-term rate maximizer will be negligible. In this situation, natural selection would be neutral with respect to whether rates are calculated using EoR or long-term rate (as long as the only fitness consequences of the currencies are measured in terms of energetic intake). This would not explain why animals use EoR rather than long-term rate, but it would remove the necessity of explaining why animals have evolved an algorithm that results in suboptimal deci-

sion making. Any explanation for the maximization of EoR would have to depend on something other than the behavioral decisions that arise from maximizing this currency.

Here, we test the hypothesis that maximization of EoR and long-term rate may actually result in similar behavior in a natural environment. We do this by measuring the real distribution of T for European Starlings (*Sturnus vulgaris*) foraging on permanent pasture, and by calculating how the birds would behave if they were maximizing each of the rate currencies. The best estimates of both EoR and long-term rate for a patch are obtained by using as much information as possible (i.e., as high an n as possible). However, since we do not know the memory window used by the starlings we compute each of the algorithms for a range of different memory window sizes. As we have previously pointed out (Bateson and Kacelnik, *in press*), long-term rate and EoR can be seen as two extreme points on a plane of possibilities described by two parameters: n, the total number of prey items remembered by the forager; and f, the size of the frame over which the forager computes the rate. Under this view, both long-term rate and EoR are specific cases of a general expression for rate, where

$$\text{Rate} = \frac{\sum_{j=1}^{n/f} \left(\frac{\sum_{i=1}^{f} G_i}{\sum_{i=1}^{f} T_i} \right)_j}{n/f}. \tag{3}$$

When n is large and $f = n$ this converges on long-term rate; when n is large and $f = 1$, it converges on EoR. Thus we compute the value of Eq. 3 for values of $f = 1$ and $f = n$, and a range of possible values of n.

Data Collection

The subjects were four male and four female starlings caught from the resident population at the University Farm, Wytham, Oxford, UK. The birds were held in outdoor aviaries and were fed on a mixture of turkey starter crumbs, softbill pellets, and mealworms (*Tenebrio molitor*). They were deprived of food from ≈1700 on the day prior to each experimental foraging period. A portable netting enclosure (2 m long × 2 m wide × 1 m high) with no floor was used for recording the birds' foraging behavior in the field. This was designed such that a bird released into the enclosure could forage naturally on the substrate while being recorded with a video camera from a nearby hide. The birds were thoroughly familiarized with this enclosure prior to the observation periods such that, when released into it, they started to forage within 10–15 min. Two permanent pasture fields were selected for the experiment (Fields 1 and 2). A bird was released into the enclosure

TABLE 1. Basic statistics on the first 32 intercapture intervals experienced by starlings (Birds 1–8) foraging in Field 1 and Field 2. All values are in seconds.

| Field	Bird	Intercapture interval				
		Mean	Median	1 SD	Min	Max
1	1	24.91	13.01	27.81	0.16	115.34
1	2	14.29	5.47	24.73	0.61	130.44
1	3	26.06	15.03	31.49	0.38	124.46
1	4	12.36	4.75	16.23	1.05	63.16
1	5	30.53	5.80	52.08	0.88	246.82
1	6	14.40	9.08	14.33	1.04	56.35
1	7	27.57	10.91	37.41	1.09	127.97
1	8	34.90	26.62	35.11	0.72	132.91
2	1	18.16	11.86	17.97	0.17	73.76
2	2	20.93	11.91	20.10	0.82	65.74
2	3	33.20	25.89	32.66	0.33	128.04
2	4	10.66	8.32	7.76	0.05	32.51
2	5	17.00	9.17	18.85	0.94	81.13
2	6	25.29	19.55	21.21	1.20	89.89
2	7	26.12	19.54	27.07	0.93	105.93
2	8	19.60	14.09	21.60	1.48	106.13

and allowed to forage for 20 min before it was recaptured. A bird was only observed in the enclosure once on any one day, and after observation it was returned to the aviary. Each bird was observed foraging in both of the fields, with each session being conducted in a different location. Locations were selected by dividing each field into eight regions of approximately equal area and picking one at random for each observation period. Half of the birds were observed in Field 1 first, and the other half in Field 2 first. The data were collected during March 1992 as part of a larger study of starling winter foraging behavior (see Whitehead et al. 1995).

From the video tapes, it was possible to identify when the bird captured a prey item, and often the nature of the item. A customized event-recording program was used to measure the time period between successive prey captures, or intercapture interval. The first 32 intercapture intervals in each foraging session were used for the subsequent analysis.

Results and Analysis

Table 1 shows basic statistics on each set of 32 intercapture intervals. In all cases, the distribution of intervals is skewed to the left, as would be expected if prey capture by these starlings were a Poisson process. In both fields the majority of prey items were identified as insect larvae, usually leatherjackets (larvae of the crane fly *Tipula paludosa*). For the purposes of the calculations that follow, we made the assumption that all of the prey items had an identical energetic content, arbitrarily assigned a value of 1. Although this is undoubtedly a simplification, the discrepancy between the different rate algorithms is affected only by

FIG. 1. Intake rates computed from Eq. 3 for six values of n (the total number of prey items remembered by the forager) and two values of f (the size of the frame over which the forager computes the rate). Each point represents the mean of 16 rates, since each of the eight starlings was tested in both fields. The dotted lines show the best estimates of long-term rate (RoE), which is calculated with $n = 32$ and $f = n$, and EoR, which is calculated with $n = 32$ and $f = 1$.
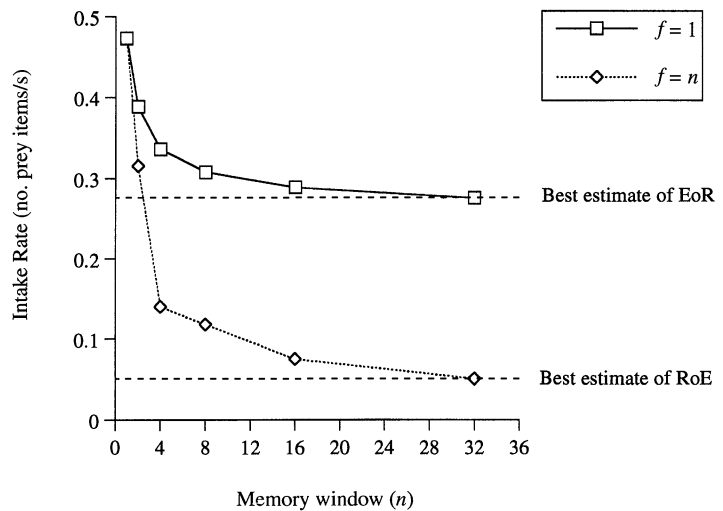
variation in the denominator, T, not by variation in the numerator, G.

Using Eq. 3, we calculated the rates that would be experienced by the birds if they were using different numbers of prey captures (n = the final 1, 2, 4, 8, 16, or 32 captures of the sequence) with two different frame sizes ($f = 1$ or $f = n$, corresponding to the best possible

TABLE 2. The field (either Field 1 or Field 2) offering the higher rate of intake for each of eight starlings, as calculated from Eq. 3, for a range of values of n (total number of prey items remembered) and two values of f (size of the frame over which the rate is computed). The best estimate of long-term rate is given by the rate calculated with $n = 32$ and $f = n$; the best estimate of EoR is given by the rate calculated with $n = 32$ and $f = 1$. The boxes highlight cases where the rate currencies computed with $f = 1$ and $f = n$ conflict in their predictions of which field the bird should choose.

Bird	f	n					
		1	2	4	8	16	32
1	1	1	1	1	1	1	2
	n	1	1	2	1	1	2
2	1	1	1	1	1	1	1
	n	1	1	1	1	1	1
3	1	2	2	2	2	2	1
	n	2	2	1	1	1	1
4	1	1	1	1	1	1	2
	n	1	1	2	1	1	2
5	1	1	1	1	1	1	1
	n	1	1	1	1	1	2
6	1	1	1	2	1	1	1
	n	1	1	1	1	1	1
7	1	2	2	2	2	2	2
	n	2	2	2	2	2	2
8	1	1	1	1	2	1	1
	n	1	1	2	2	2	2

estimates of EoR and long-term rate, respectively, given the amount of information used). Thus, for each of the eight birds, we calculated a total of 12 different rates in each field. The results are shown in Fig. 1. For each foraging session, the best estimate of long-term rate of intake is obtained by using all of the captures (i.e., $n = 32$) and a frame size equal to the number of captures (i.e., $f = n$), whereas the best estimate of EoR is obtained again by using all of the captures (i.e., $n = 32$), but a frame size of one (i.e., $f = 1$). For our data, the best estimate of EoR is 5.44 times the best estimate of long-term rate. As the memory window, n, diminishes, the rates estimated with $f = 1$ and $f = n$ diverge from the best estimate of long-term rate but converge on each other, finally becoming equal when $n = 1$. This result suggests that at memory windows that allow for a reasonable estimate of the environment (i.e., $n = 32$), EoR and long-term rate are far from equivalent. However, for small memory windows ($n < 4$), even if the bird is maximizing Eq. 1, the value obtained will tend to be closer to the EoR for the field than to the long-term rate.

The importance of this discrepancy for decision making lies in the type of foraging problem with which a bird is faced. In patch problems such as those addressed by the marginal-value theorem (Charnov 1976), a quantitative estimate of intake rate is needed in order to compute the optimal point at which to leave a patch. However, in prey- or patch-choice problems, a quantitative discrepancy between long-term rate and EoR will be irrelevant to foraging decisions, since all that is required for the best patch to be chosen is a method of ordering patches by rank. We therefore investigated whether or not rates computed with $f = n$ and $f = 1$ agree on the ranking of Fields 1 and 2 (Table 2). For

TABLE 3. Costs of choosing the field with the lower long-term rate. The second column shows the difference in the number of prey items gained/1 h of foraging by eight starlings in each of two fields. The third column shows the prey capture rate in the bad field relative to that in the good field, where good and bad refer to the relative long-term rates of intake available in the two fields, as estimated by Eq. 3 with $n = 32$ and $f = n$.

Bird	Difference (no. prey items)	Relative difference (%)
1	53.71	72.91
2	79.88	68.29
3	29.72	78.49
4	46.46	86.24
5	93.82	55.69
6	107.69	56.93
7	7.26	94.73
8	80.57	56.15

all values of n, apart from 1 (where the currencies are formally identical) and 2, discrepancies in rank order sometimes occur. In 10 of the 40 possible cases (eight birds times five values of n) that we analyzed, a bird maximizing rate with $f = 1$ would have chosen a different field from a bird maximizing rate with $f = n$. Although six of these 10 cases are contributed by only two birds (numbers 3 and 8), it is still the case that, for any value of n where a discrepancy could occur (i.e., $n = 2, 4, 8, 16$, and 32), a mean of two birds (i.e., 25%) would show one. For example, with $n = 32$, two of the eight birds (numbers 5 and 8) would have chosen the less profitable patch had they been maximizing EoR. In order to assess the effect on fitness of choosing the less profitable patch 25% of the time, it is necessary to compute how much energy a bird would lose through such suboptimal behavior.

McNamara and Houston (1986) introduced the canonical cost as a measure of the cost of deviating from an optimal policy. The cost is measured as the fitness decrement that results from performing some specified action, as opposed to the optimal action. In an attempt to estimate the canonical cost of choosing the field with the lower long-term rate of intake, we computed the number of prey items lost per hour spent foraging in the less profitable field vs. the more profitable field, where the profitabilities of the fields were provided by the best estimate of the long-term rate for each field, i.e., Eq. 3 with $n = 32$ and $f = n$ (Table 3). It is not unrealistic to assume that a starling spends 1 h foraging in a field; at the time that the data in this paper were collected the mean residence time of the flock of starlings in a field was often ≥ 1 h. The mean residence time (± 1 SE) was 53.34 ± 7.86 min in Field 1 and 30.00 ± 13.20 min in Field 2 (S. C. Whitehead, *personal observation*).

In order to get some idea of the impact on fitness of the numbers given in Table 3, we need to ascertain what proportion of a starling's daily requirement these losses represent. For the purposes of this calculation, we shall assume that all of the prey items consumed were leatherjackets. Taitt (1973) has estimated that a starling fed on insect larvae (in this case, mealworms) requires 209.34 kJ/d for survival. Given that a single leatherjacket provides a mean of 1.297 kJ of energy (Whitehead 1994), a starling needs to consume ≈ 161.37 leatherjackets each day to meet its energetic requirements. Thus, the losses recorded in Table 3 amount to a mean 32.47% of the starling's daily requirement (range 4.5–66.7%).

Conclusions

We have shown that, in a natural foraging environment, a starling maximizing EoR would overestimate the long-term rate of gain in a patch by over fivefold, and would choose the less profitable of two fields 25% of the time, resulting in a substantial impact on its food intake rate. Given these results, it is hard to believe that natural selection can be blind to the rate algorithm used by the starling, as has previously been suggested (Bateson and Kacelnik, *in press*). Therefore, animals' use of the EoR currency presents a true functional conundrum.

Our results do lead to the interesting observation that if the starlings were basing their decisions on a maximum of the last four prey captures, then even if they were using Eq. 1, their estimates of rate would tend to be closer to EoR than to long-term rate. Thus, if starlings use short memory windows, either because of some memory constraint or because it is adaptive, as would be the case in very patchy environments, this could explain why they appear to be maximizing EoR. Although this explanation is possible in bumble bees (Real et al. 1990), other data from starlings suggest that they remember more than the last four prey captures (Bateson and Kacelnik, *in press*). In trying to find a general explanation for why animals use EoR, we are left with two broad possibilities: either the use of this currency is adaptive in some way that has not yet been identified, or animals are forced to use this currency because of some constraint in their ability to process information. Further research is needed to resolve which of these explanations is correct.

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