

Foraging-efficiency–predation-risk trade-off in the grey squirrel

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Abstract. Many animals must often respond to environmental patterns that simultaneously influence both foraging efficiency and predation risk. We noted that grey squirrels (*Sciurus carolinensis*) sometimes immediately consume food items in areas of relatively great exposure to predators, and at other times carry food items to the safety of a tree prior to consumption. We outlined a hypothesis that the squirrels were somehow trading-off energy intake rate against predation risk. A simple model shows that maximal energetic efficiency is associated with immediate consumption, whereas (under the field conditions studied) carrying items to the safety of trees provides for minimal exposure to predation. Our analysis of the model predicts that the tendency to carry a food item should decrease with distance of food from cover (travel time) and increase with item size (handling time). To test our predictions, we presented free-roaming grey squirrels with patches containing a fixed number of identical food items. We estimated the proportion of items carried to trees before consumption for 12 different combinations of distance to the nearest tree and item size. The results support our hypothesis and indicate that a simple behavioural criterion based solely on foraging rate or time exposed to predators is insufficient to explain the variation in the data.

Optimal foraging theory has stimulated a great deal of research, and many of the theory's predictions have been substantiated, particularly in the laboratory (for an extensive review, see Krebs et al., in press). Taking energy intake rate (or a related currency) as a correlate of fitness, the usefulness of optimal foraging theory lies in its ability to generate quantitative predictions against which observations can be compared. Few who study foraging behaviour, however, would argue that energy intake rate is the only factor likely to influence the fitness of an animal in its natural environment. Factors such as predator avoidance and reproductive needs will also be important determinants of fitness. In short, we must at some point appreciate the fact that fitness is actually an *n*-attribute phenomenon (Oster & Wilson 1978; Caraco 1980) in which foraging is but a single attribute. We agree with the contention of Krebs et al. (in press) that this realization does not invalidate current foraging theory. It does, however, suggest directions for future research that should lead to a more complete view of foraging behaviour and how it interacts with other behaviours to influence fitness. With this goal in mind, we present an analysis of how predation risk and foraging considerations combine to influence the behaviour of feeding grey squirrels (*Sciurus carolinensis*).

As an introduction to the problem investigated in the present paper, consider the following. Impli-

cit in a non-central-place optimal foraging model is the assumption that prey items are eaten where they are encountered. Transporting a food item elsewhere presumably would waste time and energy. But suppose that a forager is itself subject to predation. An animal foraging under the risk of predation might benefit from carrying food items encountered to the safety of protective cover for consumption. Carrying food items to protective cover, however, also involves a cost: energy intake rate is decreased relative to the rate achieved by eating each item where it is encountered. Since the decision to 'carry' or 'stay' influences both exposure to predation and the rate of acquiring energy, we might reasonably expect that the animal would attempt a strategic compromise when these two demands conflict (e.g. Milinski & Heller 1978; Caraco 1979; Sih 1980; Cerri & Fraser 1983).

That such a situation might be important for some animals was suggested by our observations on the foraging behaviour of free-roaming grey squirrels. These squirrels, and forest squirrels in general, make extensive use of trees for both feeding and safety. They must, however, often venture out in the open in order to obtain food, sometimes at a considerable distance from the nearest tree. While observing squirrels foraging in the open, we noticed that smaller food items are usually eaten where they are found, whereas larger items are often carried to the nearest tree before

they are consumed. We suspected that this behaviour represented a response to predation risk, as outlined above, and that the apparent dependence on item size was related to handling time relative to the travel time necessary to reach cover. The simple model we present below incorporates our ideas into a mathematical framework that makes qualitative predictions concerning the tendency to 'stay' or 'carry'. It is, of course, desirable for a model to make detailed, quantitative predictions, but this will probably be an elusive goal in specifying behavioural trade-offs of this sort (see below). For now, we must be satisfied with qualitative predictions.

SIMPLE MODEL OF A COMPLEX INTERACTION

We develop a weak utility model (Luce & Suppes 1965) to predict variation in the probability that a squirrel carries a food item to cover. We will not require a quantitative specification of the way that avoiding predators and feeding efficiency interact to influence fitness. Indeed, in a later section we will argue that such a specification often will be a difficult and complex matter. We reasonably assume, however, that avoiding predators and acquiring energy are the main factors influencing fitness in non-breeding squirrels, and that survivorship and fitness in the sense of McNamara & Houston (1982) increases strictly monotonically with both the probability of avoiding predation and the rate of food intake. For convenience, all variables used in the model developed below are summarized in Table I.

Food items are located in a patch at a distance d from cover. Food items are discrete and easily found within the patch (no search time). We assume that the forager knows that there are exactly N (identical) items in a patch at the beginning of a foraging bout. The forager can carry only one item at a time: all N items are consumed consecutively during a foraging bout. Let N_s be the number of items consumed at the patch (number of 'stays'), and let N_c be the number of items consumed in cover (number of 'carries'). Since a patch contains a total of N items, $N = N_s + N_c$.

Let t be the one-way travel time from the patch to cover (or the reverse direction). Assume that the forager travels at a constant velocity. Let h be the time required to consume a single food item:

Table I. Definition of symbols

d	distance to cover from patch
t	travel time between cover and patch
h	time to handle (consume) one food item
w	size (weight) of one food item
N_s	number of items consumed at the patch
N_c	number of items carried to cover before consumption
N	total items: $N = N_s + N_c$
T	duration of entire foraging bout, sum of travel and handling times
α	probabilistic rate of death due to predation
π	probability that the forager survives predation over $(0, T)$
R	food intake rate: ratio of total food to total time
ρ	proportion of items carried to cover

(handling time), and let w represent the size (weight) of each identical item within the patch. We assume that handling time increases strictly monotonically with item size, and that handling time is independent of travel time and distance from cover.

T represents the duration of the entire foraging bout, which begins and ends with the forager in cover. T is the sum of travelling and handling times; by definition T begins with the forager travelling to the patch. In partitioning T into a time budget, we use primes (e.g. h') to designate time spent in the safety of cover. At all other times the forager, whether travelling or consuming an item at the patch, is assumed to suffer predation at a constant probabilistic rate α .

Before specifying the time budget, our assumptions yield a simple prediction: the forager should always carry the last item in a patch to cover before consumption. If the forager stays, the last two elements of the time budget will be $t + h$. If it carries, the last two elements are $t + h'$. The time per last item is the same, but carrying leads to lower exposure to predation. Independently of how the forager deals with the first $N - 1$ items, it should carry the last item in the patch back to cover.

Assuming that the last item is carried (i.e. $1 \leq N_c \leq N$),

$$T = t + 2t(N_c - 1) + (N_c - 1)h' + N_s h + t + h' \quad (1)$$

Since $N_s = N - N_c$, (1) simplifies to

$$T = 2tN_c + (N - N_c)h + N_c h' \quad (2)$$

Let π represent the probability that the animal survives predation over the length of T . We note that the first two terms on the right-hand side of (2)

represent the time that a forager is exposed to predation, and thus

$$\pi = \exp[-\alpha(2tN_c + (N - N_c)h)] \quad (3)$$

R represents the food intake rate, expressed simply as the ratio of the total amount of food eaten to the total time T :

$$R = Nw/T = Nw/(2tN_c + Nh) \quad (4)$$

We first consider how π varies with N_c . N_c is a discrete variable and therefore we use finite differences in the analysis of π : $\Delta\pi = \pi(N_c + 1) - \pi(N_c)$. From (3) we have

$$\Delta\pi = \exp(k) [\exp(\alpha(h - 2t)) - 1] \quad (5)$$

where $k = \alpha[N_c(h - 2t) - Nh]$. If $h > 2t$, $\Delta\pi > 0$ for all $N_c \leq N$. Thus carrying all N items to cover before consumption will maximize π . If $h < 2t$, $\Delta\pi < 0$ for all $N_c \leq N$ and therefore carrying only the last item will maximize π . Any combination of N_c and N_s (in any order as long as the last item is carried) provides the same probability of surviving predation if $2t = h$. Notice that the value of N_c which maximizes (3) depends on the value of round-trip travel time ($2t$) relative to handling time. If handling requires more time than travelling back and forth to cover, then it is clear that carrying food items will minimize the amount of time spent away from cover. Conversely, if handling requires less time than travelling, staying to eat at the patch will minimize the time spent away from cover.

We next consider how R , the food intake rate, varies with N_c . With $\Delta R = R(N_c + 1) - R(N_c)$, from (4) we have

$$\Delta R = -2tNw/(ab) \quad (6)$$

where $a = 2t(N_c + 1) + Nh$ and $b = 2tN_c + Nh$. We see that (6) is always negative. In other words, carrying items (other than the last item) decreases the food intake rate. Thus R is maximized when $N_c = 1$.

When the patch is relatively distant from cover and/or items are sufficiently small (i.e. $h < 2t$), there is no conflict in maximizing both π and R : staying to consume the first $N - 1$ food items at the patch maximizes π and R simultaneously. A conflict arises, however, when the patch is relatively close to cover and/or the food items are relatively large, i.e. $h > 2t$. The analysis of (5) and (6) indicates that the forager cannot maximize π and R simultaneously: they are conflicting demands. Specifically,

(a) carrying all items maximizes π , and minimizes R ;

(b) staying to consume the first $N - 1$ items minimizes π and maximizes R ; and

(c) Intermediate combinations of carrying and staying are intermediate with respect to both π and R .

The way in which this conflict is resolved will determine how the proportion of items carried to cover, $\rho(\rho = N_c/N)$, should vary as a function of the distance from cover and/or food item size. As mentioned earlier (see also Discussion), we lack a specific function which maps π and R into a squirrel's fitness; we therefore cannot make quantitative predictions concerning ρ . However, our assumption that fitness increases with both π and R in conjunction with a second-order analysis of (3) and (4) yields the following.

Effect of Increasing Distance to Cover

As the distance to cover (or travel time) increases, it is apparent from (3) and (4) that both π and R decrease for a given N_c . As the distance to cover increases, however, the benefit gained from carrying (in terms of π) decreases, while the cost incurred from carrying (in terms of R) increases. Since the benefit gained decreases and the cost incurred increases, we make the prediction that the proportion of items carried should decrease as the distance to cover increases (item size held constant).

To be more rigorous, we define the quantities $\Delta\pi_m$ and ΔR_m as the difference between the maximum attainable and realized π and R for $1 < N_c < N$. As we have seen, carrying all N items maximizes π ($h > 2t$) and carrying only the last item maximizes R . Therefore, $\Delta\pi_m = \pi(N) - \pi(N_c)$ and $\Delta R_m = R(1) - R(N_c)$: both $\Delta\pi_m$ and $\Delta R_m > 0$. Noting that travel time is equivalent to the distance to cover in our model, we have

$$\begin{aligned} \partial\Delta\pi_m/\partial t = \\ 2\alpha\{N_c \exp[-\alpha(2tN_c + (N - N_c)h)] - N \exp[-\alpha 2tN]\} \end{aligned} \quad (7)$$

which is always negative for $h > 2t$. In other words, there is less to be gained from carrying as the distance to cover increases. Taking the partial derivative of ΔR_m with respect to t yields

$$\partial\Delta R_m/\partial t = 2Nw(N_c - 1)/(uv) \quad (8)$$

where $u = 2t + Nh$ and $v = 2tN_c + Nh$. Since (8) is always positive, there is more to be lost from

carrying as the distance to cover increases. Our prediction therefore follows as outlined above.

Effect of Increasing Item Size

Once again, we see that π decreases for a given N_c as item size (or handling time) increases. For increasing item size, however, the benefit gained from carrying (in terms of π) increases. This follows from (9) as $\partial\Delta\pi_m/\partial h > 0$.

$$\frac{\partial\Delta\pi_m}{\partial h} = \alpha(N - N_c) \exp[-\alpha(2tN_c - (N - N_c)h)] \quad (9)$$

The effect of increasing item size on ΔR_m is more complex, as we must explicitly consider the dependence of h on w . Earlier, we assumed that h is an increasing function of w . A reasonable form to assume for this relationship is a power function, i.e. $h = cw^\beta$ where c and β are constants. Substituting this explicit formulation of h into ΔR_m and taking the partial derivative of ΔR_m with respect to w yields

$$\frac{\partial\Delta R_m}{\partial w} = 2tN(N_c - 1)[uw - \beta Ncw^\beta(u + v)]/(uw)^2 \quad (10)$$

where u and v are as previously defined. The sign of ΔR_m depends upon the sign of the bracketed term in (10), which is negative when

$$uv/[\beta Ncw^\beta(u + v)] < 1 \quad (11)$$

For large N , the criterion given by (11) approaches $\beta > 1/2$. Thus, as β gets larger, handling time tends to dominate (4) and the extra travel time from carrying becomes a less significant detriment to R (i.e. $\partial\Delta R_m/\partial w < 0$). When (11) holds, we can make the prediction that the proportion of items carried should increase with item size (distance to cover held constant). This follows because the benefit gained from carrying (in terms of π) increases with item size and the cost of carrying (in terms of R) becomes less significant with increasing item size.

When (10) is positive, i.e. when β is small ($< 1/2$), the way in which the proportion of items carried will change is less clear because both the benefit gained and the cost incurred (relative to maximal π and R , respectively) become larger with item size. We will note, however, that $\partial R/\partial w > 0$ for $\beta \leq 1$. In other words, R will be higher for any level of carrying as item size increases. Therefore, although the difference between the maximal obtainable R and the realized R increases with w , the cost of carrying will be less important since the overall rate of food intake is increasing. We therefore expect

that the prediction forwarded earlier will hold in general: the proportion of items carried should increase with item size.

METHODS

This study was conducted during June and July 1983 in a large, open area (100×75 m) bordered by a stand of mature oaks (*Quercus* spp.) and hickories (*Carya* spp.) in Highland Park, Rochester, New York. To attract squirrels to the study site, a large number of food-filled patches (see below) were placed at the study site each day, around dawn, for 2 weeks prior to the start of the experimentation. The squirrels in the area quickly began to expect food at the study site, and there would typically be a group of 20–30 squirrels waiting at the site each morning. To further guarantee the reliability of our experimental subjects, experiments (see below) were conducted nearly every day (except when raining) from 0645 to 0800 hours. During experimentation, such a large group of squirrels quickly became unruly if they were all allowed to forage at once. Therefore, before each day's experiment began, sunflower seeds were scattered in an area bordering the study site to divert most squirrels away from the study site itself. Even though most squirrels were sequestered, we seldom lacked subjects at the experimental patches.

The experimental food items were portions of chocolate-chip cookies cut to weigh 1, 2 or 3 g. More natural foods (commercially available nuts) were buried rather than immediately eaten. (One could argue that cookies are not an especially large departure from the normal diet of squirrels inhabiting an urban park.) In any case, the squirrels responded avidly to the cookies and rarely buried them, allowing us to obtain data appropriate to the model's assumptions.

Food items were available to the squirrels in patches which were $28 \times 6 \times 2$ -cm pieces of wood on which we placed seven food items. All patches available at a given time contained the same item size. At the start of each study-day, six patches were placed at the same distance from cover (the edge of the woods) with a constant inter-patch distance of 10 m; exploited patches were replenished to maintain six available patches. Small flags were placed next to each patch to make its location more visible to the squirrels. The patches were available to the

squirrels at one of four possible distances from cover: 3, 6, 9 or 12 m. Distances and item sizes used on successive days followed no set order, with the exception that no combination of item size and distance from cover was available on two consecutive days. In addition, each of the 12 combinations of item size and distance from cover was available on 4 days. Usually, only one item-size-distance combination was available for an entire study-day. On those few occasions when the squirrels depleted our supply of a given item size, we would use another size if time permitted. This did not appear to cause any complication: the squirrels rapidly adjusted their behaviour to the new item size.

Squirrels would begin foraging at patches soon after they became available. Usually, the first squirrel to approach a patch did so alone. The first arrival was termed a 'solitary' forager until it was joined by other squirrels (if any). An aggregation of more than one squirrel foraging at a patch was termed a 'group'. Data from groups of four or more squirrels were discarded since there was much aggression in these groups. Most groups, however, consisted of two or three squirrels foraging in a reasonably orderly fashion. Occasionally, a dominant individual would attempt to monopolize a patch, but complete monopolization was not usually possible.

As defined here, a squirrel 'carried' an item to cover if it actually carried the item greater than half the distance to cover; otherwise, we say a squirrel 'stayed' and consumed an item at the patch. Although our definition of 'stay' versus 'carry' is somewhat arbitrary, food items were usually consumed either close to the patch or carried all the way back to the nearest tree (Fig. 1). A carrying event was considered as such only if the squirrel returned to the patch for another item. This qualifier was necessary because, as the model suggests, if a squirrel intended to eat only one more item, it should always carry it to cover. When possible, handling times for individual prey items were recorded to the nearest 0.1 s with a stopwatch.

Estimating the travel time between patches and cover was somewhat problematic. Squirrels often do not walk directly to a patch from cover. Instead, they often meander and sniff the ground as they go. When carrying a food item back to cover, the squirrels were much more deliberate in their action. Thus, we use travel time back to cover as our estimate of the 'ideal' travel time; but there were problems with determining this travel time as well.

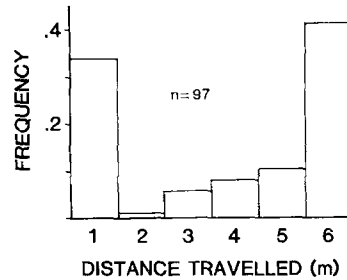


Figure 1. Representative distribution of the distance each food item was actually carried before being consumed (distance travelled). This example is for 3-g items at 6 m from cover. Observations were placed into 1-m intervals (i.e. 1 = 0–1 m, 2 = 1–2 m, etc.). Most items were eaten either close to or at a patch (1 m) or in cover (6 m).

Often, squirrels would not travel all of the way back to a tree and, in addition, they would sometimes briefly stop along the way to take a bite or two of food. The biggest problem, however, was the fact the squirrels seldom carried food items at greater distances from cover. We confined our estimate of travel times to those cases where items were carried all the way back to the nearest tree, without interruption by brief bouts of eating or aggression from other squirrels. As sample sizes were small, we combined all travel times at a given distance to estimate travel time for that distance.

Predators

Since predation risk plays a crucial role in this study, some mention of potential predators should be made. We never saw a squirrel killed or attacked during our observations. The squirrels would, however, rapidly take to the trees with the appearance of a dog, cat or the resident red-tailed hawk (*Buteo jamaicensis*). Squirrels would respond similarly to the alarm calls of other squirrels (Smith 1978), as well as to the alarm calls of chipmunks (*Tamias striatus*) and birds such as chickadees (*Parus atricapillus*). Humans were ignored unless they approached to within a few metres. In general, the appearance of predators interrupted feeding for a short time only, and the squirrels would quickly resume feeding at the patches once the danger clearly had passed. Data from those patches being exploited when a potential predator appeared were discarded.

RESULTS

We can test two of our assumptions concerning handling times. We assumed that handling time increases with food-item size and that handling time is independent of distance to cover. Table II shows the mean handling times for items eaten in cover (carries) and items eaten at a patch (stays) for each combination of item size and distance from cover. Upper and lower entries for each size-distance combination represent carries and stays, respectively. From inspection of Table II, it is immediately clear that handling time increases with item size. We statistically analysed handling times via a randomized-block ANOVA design (Mendenhall 1971, page 343), blocking along distance from cover (items that were carried before being eaten were assigned to a distance of $d=0$). The results are given in Table III. Item size exerted a strong effect on handling time ($P < 0.005$). The variation among blocks was also significant ($P < 0.01$), indicating a significant effect of the distance to cover on handling time. The latter effect is due entirely to the fact that handling time tended to be greater in cover than out in the open at a patch. This difference was not consistently observed for each size-distance combination, nor was there any apparent pattern as to when it occurred (Table II). Excluding items eaten in cover, the handling time for each item size was not correlated with distance from cover (1 g: $r=0.01$, 346 df, NS; 2 g: $r=0.03$, 283 df, NS; 3 g: $r=-0.11$, 132 df, NS).

Why handling times would be greater in cover is not clear. It is probably not related to an interac-

tion of scanning for predators and consuming food. In squirrels, unlike great tits, *Parus major* (Cowie et al., cited in Krebs 1980), scanning and food consumption are not mutually exclusive. A squirrel can simultaneously scan and eat without compromising one or the other. If consuming food was somehow interfering with scanning, we would expect that handling times would be smaller in the safety of cover, not greater. Shorter handling times away from cover may simply represent an attempt by the squirrels to further minimize the time they spend in the open. In any case, our observation of longer handling times in cover does not alter the qualitative predictions put forward earlier.

Our assumption that the squirrels travel to cover at a constant speed was not upheld. The mean travel times to cover for the four distances used were 2.54, 3.98, 5.53 and 6.29 s, for 3, 6, 9 and 12 m, respectively. Including all the data, the associated linear regression is

$$t = 1.3 + 0.44d$$

($r=0.63$, 61 df, $P < 0.01$) and the quadratic regression is

$$t = 0.64 + 0.66d - 0.02 d^2 \quad (12)$$

($R^2=0.94$, $F_{2,60}=49.35$, $P < 0.005$). The quadratic regression yields the better fit to the data. Travel time seems to increase at a slower rate with increasing distance from cover, i.e. the squirrels seem to travel faster while covering greater distances. This effect is slight, however, as indicated by the magnitude of the coefficient of d^2 in (12) and the fact that mean travel time increases at a fairly

Table II. Mean handling times (SE, N), in seconds, for each size-distance combination*

Item size (g)	Distance from cover (m)			
	3	6	9	12
1	41.8 (6.1, 5)	41.4 (5.5, 9)	25.0 (0.71, 2)	27.5 (3.2, 2)
	29.2 (1.4, 74)	27.9 (1.4, 97)	26.4 (1.3, 81)	30.2 (1.0, 96)
2	62.6 (4.7, 21)	82.8 (7.8, 8)	55.8 (5.0, 5)	68.9 (8.5, 9)
	52.7 (2.1, 48)	53.5 (1.7, 52)	57.3 (2.3, 64)	51.3 (1.9, 80)
3	87.9 (5.0, 33)	80.0 (3.5, 22)	111.2 (5.4, 22)	98.6 (8.4, 8)
	89.7 (5.0, 29)	82.1 (4.7, 17)	81.5 (2.8, 37)	83.2 (2.9, 52)

* Upper and lower entries for each size-distance combination represent averages for items eaten in cover (carries) and at patches (stays), respectively.

Table III. Randomized-block ANOVA of mean handling times

Source	df	SS	MS	F
Total	14	8063.4		
Blocks (<i>d</i>)	4	279.8	16.95	8.33 ($P < 0.01$)
Treatments (<i>w</i>)	2	7716.5	3858.3	459.3 ($P < 0.005$)
Error	8	67.1	8.4	

constant increment with increasing distance from cover. The overall increase in speed while travelling greater distances most probably reflects the fact that disproportionately more time is spent both accelerating and decelerating while travelling the shorter distances from cover.

We should point out that handling time was considerably greater than round-trip travel time (i.e. $h > 2t$) for all item-size-distance combinations used. Thus our results apply only to the case where a conflict exists in simultaneously maximizing both the food intake rate and the probability of avoiding predation. The size of the study site and problems with reliably producing food items smaller than 1 g effectively prohibited examining the case where no conflict exists ($h < 2t$). Also, recall that our argument concerning how the proportion of items carried should change as a function of item size depends upon the criterion given in (11), which is a function of c and β , among other variables. A log-log regression of handling time against item size yields estimates of 27.1 and 0.985 for c and β , respectively: the value of β is statistically indistinguishable from 1 (t -test, $P > 0.05$). With these values of c and β , the handling times in Table II and the above travel times, the criterion in (11) holds for all item-size combinations over all possible values of N_c . In addition the food intake rate is increasing with w for all N_c (i.e. $\partial R / \partial w > 0$). Therefore, as outlined earlier (see model), we expect the proportion of items carried to increase with item size.

For solitary foragers, Fig. 2 shows the overall proportion of food items carried back to cover for each of the size-distance combinations. The figure suggests that the proportion carried decreases with distance to cover and increases with item size, as predicted. To evaluate these trends statistically, we conducted a two-way ANOVA. For each estimated proportion p , we took the arcsine transformation of its square root to homogenize variances. There were four entries per cell, corresponding to the 4

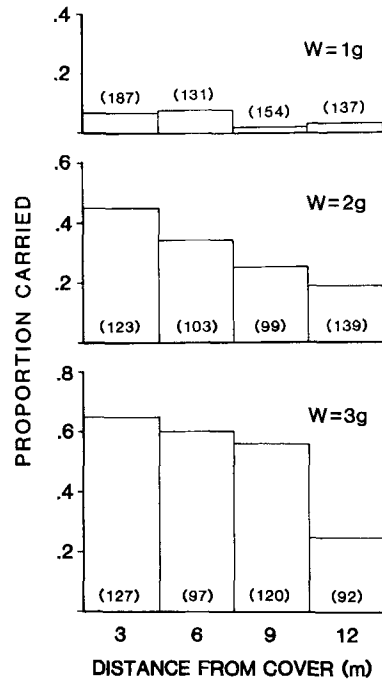


Figure 2. Histograms for the proportion of items carried by solitary foragers for each size-distance combination. Values in parentheses represent sample sizes.

days when each size-distance combination was available. Unweighted proportions were used in the two-way ANOVA; Table IVa shows the (unweighted) mean of the four entries for each size-distance combination. Table IVb shows the results of the two-way ANOVA. Both item size and distance to cover exert a highly significant effect, but their interaction is not significant. Thus the proportion of items carried decreases significantly as the distance to cover increases, and increases significantly as item size increases.

Although the model is not directly concerned with groups of foragers, the effects of groups are interesting. Figure 3 shows the overall proportion of items carried by grouped foragers. In general, the trends observed are the same as those seen for solitary foragers (Fig. 2), but for every size-distance combination, grouped foragers tend to carry more often. This was due mainly to aggression. Upon being chased a metre or two by a more dominant individual, most squirrels would eat their item just far enough away from a patch in order to avoid the dominant: others would often just continue all the way to cover before consuming their

Table IV. Proportion of items carried by solitary foragers

(a) Mean for each cell in two-way ANOVA*

Item size (g)	Distance from cover (m)			
	3	6	9	12
1	0.062	0.073	0.020	0.036
2	0.427	0.244	0.210	0.138
3	0.645	0.645	0.565	0.262

* Values are unweighted means of the four entries in each cell.

(b) Two-way ANOVA

Source	df	SS	MS	F
Total	48	59058.1		
Mean	1	42735.1		
Size (<i>w</i>)	2	10333.1	5166.5	58.6 ($P < 0.005$)
Distance (<i>d</i>)	3	1688.7	562.9	6.38 ($P < 0.005$)
<i>w</i> × <i>d</i>	6	1127.2	187.9	2.18 (ns)
Error	36	3174.1	88.2	

Table V. Proportion of last items carried by solitary foragers

Item size (g)	Distance from cover (m)			
	3	6	9	12
1	0.05	0.21	0.18	0.0
2	0.50	0.73	0.17	0.08
3	0.82	0.67	0.64	0.33

item. The reason why a subordinate squirrel would tend to carry more after a short chase is not clear.

Though the model predicts the qualitative trends in the proportion of items carried, the secondary prediction that the last item in a patch should always be carried is not upheld. Table V shows, for each size-distance combination, the proportion of the last items that were carried by solitary foragers. The majority of the estimates are considerably less than the prediction of 1. This prediction often failed in a way not envisioned in the model. After handling the last item within a patch, some foragers would continue to search locally for another food item before returning to cover. Other foragers would sometimes move to another patch rather than return to cover. Hence, the last item was not always recognized as such, nor was it always treated as such. Therefore (and not surprisingly), variation in these proportions tends to follow the pattern observed for the overall proportions plotted in Fig. 2.

DISCUSSION

At a given distance from cover, a squirrel was more likely to carry larger items back to cover before consumption. For any given item size, a squirrel was less likely to carry with increasing distance to cover. This somewhat counter-intuitive result is in accord with the prediction put forward earlier. The squirrels appeared to be trading-off energetic considerations against the risk of predation while foraging away from the safety of trees. If the squirrels were attempting solely to minimize their risk of being preyed upon, we would have seen them carry all of the items eaten for all of the size-distance combinations, as for all combinations, handling time was considerably greater than round-trip travel time. If energy intake rate was their sole concern, we would not have seen any

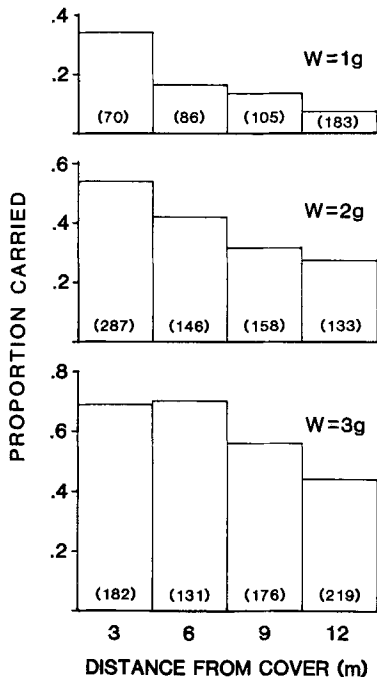


Figure 3. Histograms for the proportion of items carried by grouped foragers for each size-distance combination. Values in parentheses represent sample sizes.

carrying at all. Instead, we found that squirrels would seek the safety of cover if this did not detract greatly from their food intake rate. The greater the cost of carrying, in terms of food intake rate, the less likely a squirrel was to carry food to cover.

For simplicity, our model excludes some factors which may influence such a trade-off. We now consider two factors related to the distance from cover. First, our formulation of (4) implies that the energetic cost of travelling and handling food items is insignificant. Including energetic costs in our analysis would leave our predictions unchanged. Significant energetic costs of travelling, however, would lead to a greater tendency to stay at a patch. Secondly, we assumed that the distance from cover was important because a greater distance from cover leads to a greater time spent exposed to predators. The distance from cover, however, probably has a two-fold effect, one related to exposure time and the other related to the conditional probability of escape given an attack. This latter effect would probably lead to a greater tendency to stay as patches are moved closer to cover. As patches are moved farther from cover, the probability of escaping given an attack tends to zero and thus the risk of predation will be more closely related to exposure time as we simply assumed. We suspect that this effect may have suppressed carrying at the shorter distances to cover. A consideration of the conditional probability of escape given an attack may also provide some insight into 'partial' carries (see Fig. 1).

We also excluded the effects of scramble and interference competition from our model. Scramble competition probably decreases the expected future food gain of a squirrel foraging at a patch: a solitary squirrel could at any time be joined by another, competing squirrel. This possibility would probably increase the tendency to stay at a patch, as this might allow more items to be consumed before a competitor appears. The extent to which this effect operated is not known, but we do not expect that it would alter our qualitative predictions. Interference competition via social dominance could potentially lead to different trade-offs for subordinate and dominant squirrels. For example, the extent to which competitors reduce the future expectations of a currently solitary squirrel may depend upon its dominance rank. We might expect that dominant squirrels would be more likely than subordinates to stay at a patch. We have already seen that the carrying behaviour

of grouped squirrels differs from that of solitary squirrels and that this is probably related to a dominant–subordinate interaction. We do not, however, know whether this represents evidence that dominants and subordinates are trading-off feeding efficiency and predation risk differently. In any case, even if subordinates and dominants employ quantitatively different trade-offs, our qualitative predictions should be the same for both.

A criticism that may be levelled at this study is the lack of an experimental demonstration that predation risk is the impetus behind carrying items to cover. Our interpretation of the results would perhaps be more convincing if we had tested predictions concerning the effects of experimental manipulations of predation risk. Unfortunately, we were unable to perform such a test. We cannot, however, devise a reasonable alternative hypothesis as to why squirrels would choose to carry food items to the nearest tree before consumption. Our assumption that time spent away from the safety of trees is time at risk to predation seems very reasonable and well-founded for squirrels. We therefore conclude that the observed behaviour indeed represents a trade-off between energetic considerations and predation risk.

The potential strategies available to a squirrel ranged from minimal carrying to carrying all items. Presumably, at least one of the possible strategies led to maximum fitness. How closely the observed behaviour corresponded to this optimum is an open question. Our qualitative modelling approach cannot directly address this point: more precise predictions of behaviour would be needed. As we mentioned earlier, deriving such predictions concerning trade-offs of this sort is likely to be an elusive goal in the study of animal behaviour. The main obstacle is the fact that the benefits of energy intake rate and the costs due to predation cannot usually be combined into an easily measureable, common currency to act as a surrogate of fitness (Mittelbach 1981; Werner et al. 1983): one must work more directly with fitness itself. Assuming that such a common surrogate currency could be found, or that fitness itself could be measured, it would still be necessary to specify an exact function mapping all potential trade-offs into lifetime fitness, and it would be necessary to determine the parameter values therein. Using a time-budgeting approach, Caraco (1979) and Caraco et al. (1980) have managed to incorporate feeding benefits and the cost of predation risk into the common cur-

rency of time, but lacking the exact trade-off function, they could only make qualitative predictions. Similar results were reported by Milinski & Heller (1978), although a common currency was not specified. Recently, Gilliam (1982) has developed an optimal control model in an attempt to overcome some of these difficulties (see also Werner et al. 1983).

Although the theoretical problem may be formidable, the empirical evidence presented here and elsewhere suggests that such a task may well be worth the effort. Stein & Magnuson (1976) showed that crayfish (*Orconectes propinquus*) may alter many aspects of their feeding behaviour in the presence of a predator. Cowie et al. (cited in Krebs 1980) suggest that prey handling times in the great tit (*Parus major*) may reflect a trade-off between the need to feed and the need to be vigilant for predators. House wrens (*Troglodytes aedon*) feeding young show a marked decrease in prey selectivity after an experimentally induced increase in predation risk to the nest (Freed 1981). Heinrich & Collins (1983) present evidence indicating that palatable lepidopteran larvae eat plant leaves in such a way as to make their presence less obvious to foraging birds, apparently incurring significant costs in doing so. In an experiment not designed to investigate a potential predation-risk-foraging-efficiency trade-off, Bellman & Krasne (1983) have found that feeding crayfish (*Procambarus clarkii*), when threatened, will tend to carry their food item when they flee only if it is relatively small: large, presumably cumbersome items are dropped before fleeing. This is somewhat analogous to the results of the present study.

The studies mentioned so far are in the minority in that they analyse foraging decisions at the level of individual prey items. The influence of predation risk has usually been assessed at the patch or habitat level. Work with arthropods (Stein & Magnuson 1976; Peckarsky 1980; Peckarsky & Dodson 1980; Sih 1980, 1982; Ohman et al. 1983), fish (Milinski & Heller 1978; Mittelbach 1981; Cerri & Fraser 1983; Fraser 1983; Werner et al. 1983), birds (Howe 1979; Martindale 1982) and mammals (Lockard & Owings 1974; Underwood 1982; Edwards 1983; Leger et al. 1983) has shown that areas of higher feeding efficiency may be partially or totally avoided if their use entails greater predation risks. Many have also suggested that a behavioural response to the risk of predation may mediate a predator's influence upon com-

munity structure independently of prey mortality (Sih 1979, 1982; Peckarsky & Dodson 1980; Mittelbach 1981; Werner et al. 1983). Social systems may also be strongly influenced by behavioural responses to predation risk. Many studies have suggested that a trade-off between foraging efficiency and predation risk is a major factor in shaping patterns of non-breeding sociality, particularly in higher vertebrates (for a review, see Pulliam & Caraco 1984).

In conclusion, many animals will forage under some risk of being preyed upon, and it is likely that foraging considerations and predator avoidance will be conflicting demands. Behavioural responses to this conflict may be expressed from the level of individual prey items to the level of habitat selection, and patterns of sociality may also be affected. In modelling the conflict between foraging and avoiding predation, we may often find that easily measurable quantities such as time or energy are inadequate as currencies of fitness. While this realization may inhibit the development of precise mathematical models, it should not preclude an attempt to understand how these two factors might interact to influence behaviour.

ACKNOWLEDGMENTS

This work was supported by NSF Grant BNS80-20717 and a University of Rochester deKiewiet Summer Fellowship to T.J.V.

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(Received 13 October 1983; revised 8 March 1984;
MS. number: A4178)