A DETERMINATION OF THE ENERGETIC EQUIVALENCE OF
THE RISK OF PREDATION[1]

MARK V. ABRAHAMS[2] AND LAWRENCE M. DILL
*Behavioural Ecology Research Group, Department of Biological Sciences,
Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada*

Abstract. The influence of predation risk on patch choice was measured by examining the spatial distribution of 10 guppies (*Poecilia reticulata*) between two feeders, at one of which there was a risk of predation. The distribution was assumed to be ideal free. Nine unique situations were examined using all possible combinations of three risk levels and three diet levels, for each sex of guppy separately. Both sex and diet level influenced the effect of predation risk on patch choice. For the females the effect of risk was highest at the intermediate diet level. However, the males exhibited the opposite response: the effect of risk of predation was lowest at the intermediate diet level. A simple equation was then used to predict how much extra food (representing the energetic equivalent of risk) must be added to the risky patch for the guppies to become indifferent to the risk differences between the two types of patches. This manipulation caused a similar number of guppies to use both the risky and safe feeders, reducing or offsetting the influence of risk of predation. However, the male guppies were less influenced by this manipulation than were the females. The different results for the two sexes are consistent with known differences in their life histories, indicating that a knowledge of an animal's life history will often be necessary to understand how it makes trade-offs when choosing where to forage.

Key words: foraging; guppies; habitat selection; ideal free distribution; Poecilia reticulata; *predator–prey; risk of predation; trade-off.*

INTRODUCTION

For over a decade, the approach of assuming that animals decide when, where, and how to forage with the goal of maximizing their net rate of energy intake has enjoyed considerable success in predicting foraging behavior in both the laboratory and the field (Stephens and Krebs 1986). However, recent experiments have demonstrated that exposing foraging animals to risk of predation can profoundly alter their decisions (Sih 1982*a, b*, Mittelbach 1984, Gilliam and Fraser 1987). Several studies reviewed by S. L. Lima and L. M. Dill (*unpublished manuscript*) have demonstrated that both energy intake and risk of predation influence behavior in a manner that appears adaptive, yet few attempts have been made to describe quantitatively the trade-off between energy and risk of predation. To be able to predict how these factors combine to influence behavior, each should be measured as its contribution to the fitness of the animal. For most species, this is difficult. Alternatively, risk of predation can be measured in units of energy, providing a common currency for these two factors. The relationship between energy and fitness will be determined in large part by the animal's life history, and is crucial to predictions concerning the effect of predation risk on foraging behavior.

Behavioral decisions made from strictly energetic concerns would not be affected by the shape of this energy–fitness relationship: so long as there is some increasing relation between energy intake and fitness, animals would be predicted to behave so as to maximize their net rate of energy intake. However, this relationship can profoundly influence the behavior of animals faced with a trade-off between energy intake and predation risk. Consider an animal that must choose between two patches. One patch is free of risk but provides food at a relatively low rate. The other provides food at a greater rate, but with an associated risk of death. The choice of patch will depend upon the relation between energy intake and fitness. If the difference in extra fitness from additional energy more than offsets the fitness cost of predation risk, then the animal should use the risky patch; otherwise, it should use the safe patch. Thus, the adaptiveness of risking death is dependent upon the precise form of the relation between energy and fitness.

We performed a series of experiments using separate groups of 10 male and 10 female guppies (*Poecilia reticulata*) to examine how their foraging behavior was influenced by risk of predation. Female guppies are typical of an animal whose fitness is energy limited. They mate promiscuously and give birth to litters of live young. Litter size is positively correlated with female size and also influenced by the energy content of the diet (Hester 1964). In contrast, male fitness is limited by access to females (Baerends et al. 1955, Farr 1980). However, the ability of males to attract females

is not affected by manipulating the availability of food (M. V. Abrahams and J. D. Reynolds, *unpublished manuscript*).

We measured the energetic equivalence of risk with two series of experiments. In the first series groups of guppies were allowed to choose between two patches providing food at equal rates. One patch was safe, but the other required the guppies to feed in the presence of a predator. As the guppies shared the food equally at both patches, their spatial distribution was used to measure the energetic equivalence of risk, taken to be the difference in intake rate between individuals at the risky feeder and those at the safe feeder. The second series of experiments used these data to determine how much additional food must be added to a patch to offset the effect of risk, i.e., that amount necessary to achieve equal numbers of guppies using the safe and risky patches. Having measured the energetic equivalent of risk, we could also determine the relative influence that risk has on animals with different life histories. Specifically, we could determine whether risk has a relatively greater effect on animals that receive fewer benefits from additional energy (i.e., males).

METHODS

Experiment 1

We used the ideal free distribution (Fretwell and Lucas 1970, Fretwell 1972) as a tool to determine the energetic equivalence of risk. Ideal free distribution (IFD) theory predicts that animals should distribute themselves in a habitat in such a way that all individuals benefit equally from the available resources. This will occur if the animals satisfy two assumptions: they are "ideal," in that they have perfect knowledge of their environment, and "free" to enter and use resources in any patch on an equal basis with residents. In an environment in which there is only one type of resource available, the animals will distribute themselves in such a way that their spatial distribution equals that of the resource (i.e., the proportion of animals in a patch will equal the proportion of total resources available in that patch). This type of distribution is considered to be an example of a spatial evolutionarily stable strategy because no animal could improve its situation by moving to another patch (Parker 1984).

The method by which the IFD can be used to quantify the energy equivalence of risk of predation can best be explained by an example. Consider an environment in which 10 individuals compete for 20 units of food divided evenly between two patches. The IFD predicts that, if food is the only variable, there should be an equal number of individuals in each patch. However, if one patch has an associated risk of predation whereas the other does not, fewer individuals will use the risky patch than the safe patch, and consequently those individuals that risk attack by a predator will receive more food than will individuals in the safe patch. In

such a situation, animals conforming to an IFD will have equal fitness in both the safe and risky patches, but will not necessarily have equal energy intake rates. Therefore, the energetic equivalent of the imposed risk per individual (ER_i) can be calculated as the intake of those individuals in the risky patch in excess of that in the safe patch:

$$ER_i = (F/NR_i) - (F/NS) \qquad (1)$$

where:

F = the amount of food available in either patch
NR_i = the number of foragers in the risky patch at risk level i
NS = the number of foragers in the safe patch.

In our example, if 7 individuals used the safe patch, then ER_i would be $10/3 - 10/7$, or 1.90 food units.

This approach was used to quantify risk with two separate groups of 10 similar-sized male (average live mass of 0.110 g) and female (average live mass of 0.414 g) guppies. Experiments were performed in a 90-L aquarium maintained at 27°C and illuminated at 350 lx. Feeders placed at each end of the aquarium (Fig. 1) provided food (eggs of the onion fly, *Delia antigua*) at a constant rate for 24 min, and distributed it over a large area, making it an indefensible resource. A 1.3-cm mesh plastic screen placed down the middle of the aquarium separated the feeders, and by placing a predator on one side, a risky patch could be created. Square holes (2.5 cm on a side) cut in the plastic mesh allowed the guppies to travel easily between the patches.

When the spatial distribution of food was varied between the two feeders, and no risk was associated with either of them, both male and female guppies adjusted their distribution in conformity with an IFD (i.e., the distribution of fish conformed to the distribution of food, Abrahams 1989). In addition, analysis of videotaped sequences of guppies using the feeders demonstrated that intake rates were not significantly different among individuals at a single feeder (Abrahams 1989). Thus, with this apparatus, the IFD is a valid tool for determining the equivalence between energy and risk of predation.

A 150-g cichlid (*Cichlasoma* sp.) was used as the predator for the females and two 20-g gouramis (*Trichogaster leeri*) for the males. Different predators were used for the females and males because of differences in size and susceptibility to predators between the two sexes. The appropriateness of these fish as predators was determined through a series of pilot studies. The criterion for selecting a predator was that the guppies would tend to avoid it if approached (i.e., they treated it as a threat), yet still would be willing to use the risky feeder. To encourage the predators to stay at the far end of their side of the aquarium we dug a hole in the gravel for the cichlid and provided a flower pot for the gouramis. These different predators represented a sim-

ilar threat to the males and females. The cichlid killed 5 females in 162 experiments and the gouramis killed 3 males in 153 experiments. When a guppy was killed, it was replaced in the next trial by a similar-sized individual.

Two factors were varied in these experiments for each sex: risk and diet level. Risk was varied by moving the "risky" feeder 2, 16, or 32 cm from the dividing screen (corresponding to low, medium, and high risk levels, respectively). Moving the feeder varied risk by changing the distance the guppies had to move to escape predatory attacks. Three diet levels (10, 20, and 40 mg in total for the females; 6, 12, and 24 mg for the males) were provided, divided equally between the two feeders. (Different amounts of food were used for each sex to compensate partially for differences in body size.) Thus, each sex was exposed to nine unique combinations of risk and diet level. During experiments the fish were maintained exclusively on the food provided during experimentation except for a weekly supplement of NutraFin flakes for essential nutrients.

Experiments were first performed using the intermediate diet level, then the lowest, and finally the highest one. Within a diet level, the risk level was randomly chosen and the feeder placed in the appropriate position. Once food began to enter the system, the proportions of guppies using the two feeders was recorded every 30 s for 24 min, providing 48 pairs of observations for each trial. No directional change in the distribution of fish within a trial was observed, so the mean of the 48 observations per feeder was calculated and used to describe the distribution of the guppies. Each risk–diet combination was repeated three times in one day, with at least 3 h separating trials. A different risk level was selected randomly (without replacement) for each day until all three risk levels had been tested for 3 d *each* at a given diet level (nine observations per risk level). After all risk levels had been examined at all diet levels, the entire procedure was repeated as above, except that the predators were removed. This served as a control to determine whether feeder location influenced the results.

Experiment 2

Experiment 1 provided the data necessary to predict how much food must be added to the risky patch to make the guppies indifferent when choosing between the risky and safe patches. The calculation was based upon the IFD prediction that if the two patches are of equal value then an equal number of individuals (five in this case) should be in each patch. We assumed that risk of predation reduces the fitness of each individual by a fixed amount. Thus, the fitness equivalent of risk in experiment 1 (R_i) can be described by the following equation:

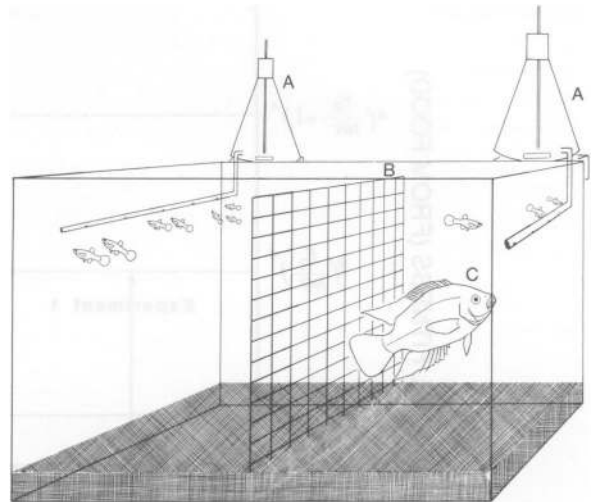$$R_i = a(F_R/NR)^x - a(F_S/NS)^x, \qquad (2)$$

FIG. 1. Apparatus used for experiments 1 and 2. Food is provided by feeders (A) located on either side of the screen (B). The feeder on the right could be placed 2, 16, or 32 cm from the screen. The mesh size of the screen restricted the predator (C) to the right side of the aquarium while allowing the guppies to move freely between sides.

where: $a(F/N)^x =$ a general expression relating individual energy intake (F/N) to fitness, in the safe (F_S) and risky (F_R) patches.

In order to encourage five individuals to use the risky feeder ($NR = 5$), sufficient additional food must be provided to offset the fitness loss due to risk of predation in that patch. From experiment 1 it is known that the energetic equivalent of risk per individual is ER_i. Assuming for now that $x = 1$ in Eq. 2, the total amount of additional food required for five individuals to risk feeding at the risky feeder should thus be $5 \times ER_i$. Consequently, to equalize fish distribution the amounts of food in the two feeders must be related as:

$$F_R = F_S + (5 \times ER_i), \qquad (3)$$

where: $F_R =$ the amount of food in the risky patch,
       $F_S =$ the amount of food in the safe patch.

The amount of extra food required was calculated for each of the nine situations previously described, for both sexes. Note that this manipulation will increase the intake rates of *all* individuals by a constant amount (I). We assume that R_i is independent of this manipulation, such that the following relationship must hold:

$$a[(F_R/NR) + I]^x - a[(F_S/NS) + I]^x$$
$$= a(F_R/NR)^x - a(F_S/NS)^x. \qquad (4)$$

Note that the equality in Eq. 4 will only apply if $x = 1$. If the relation between fitness and energy increases at a greater-than-linear rate ($x > 1$), then we will have
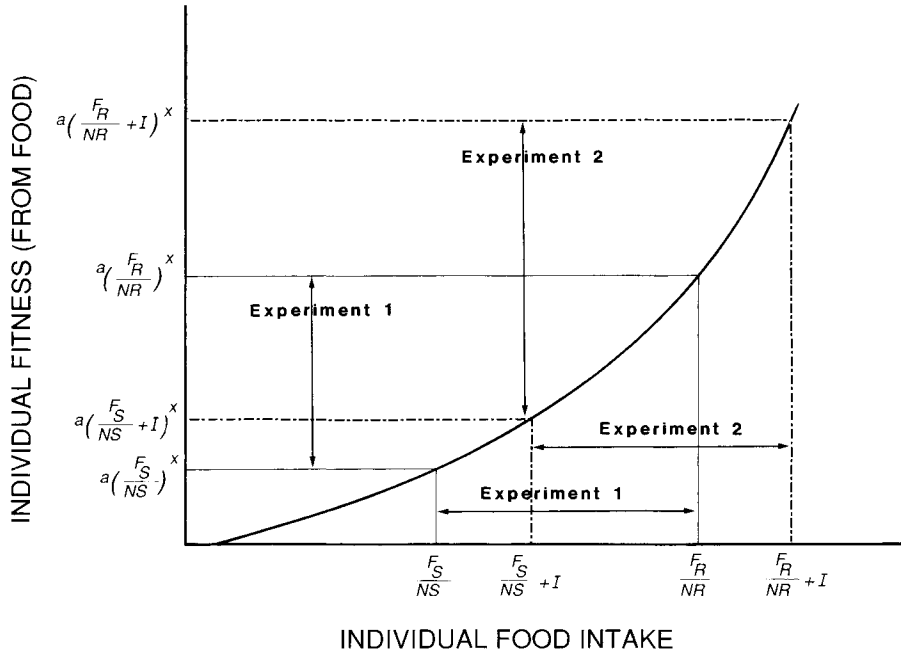
INDIVIDUAL FOOD INTAKE

FIG. 2. An illustration of how a non-linear relation between energy and fitness can cause a characteristic deviation from the predicted result of experiment 2. The —— lines represent a single result from experiment 1 (i.e., one combination of risk and diet level). The energetic equivalent of risk (ER_i) from the horizontal axis is $(F_R/NR) - (F_S/NS)$, where F_R and F_S are the amounts of food in the risky and safe patches, respectively, and NR and NS are the number of foragers in these two patches. This result can be translated into the fitness equivalent of risk from the vertical axis as $a(F_R/NR)^x - a(F_S/NS)^x$. The —·—·— lines represent the situation for experiment 2. The manipulation of experiment 2 should cause all individuals to receive an extra I units of food. Therefore the energetic equivalent of risk will be the same in experiments 1 and 2. In this hypothetical example, an accelerating relationship $(x > 1)$ exists between energy and fitness, resulting in the difference in fitness between individuals in the risky and safe patches increasing between experiment 1 and 2. Thus, individuals choosing the risky patch in experiment 2 would have higher fitness than those in the safe patch, unless the fitness cost of the predator increased as a result of the food manipulation. Since this is unlikely to be the case, the fish will have to adjust their distribution so that all have equal fitness. This will be achieved by more fish than predicted using the risky patch. Conversely, if a decelerating relationship exists $(x < 1)$, then fewer fish than predicted should be observed in the risky patch.

added more food than necessary to offset the fitness loss due to the risk of predation (Fig. 2). Consequently, the risky patch with additional food will be of greater value than the safe patch so more individuals than predicted will use the risky feeder. Conversely, if the true relation between fitness and energy increases at a less-than-linear rate $(x < 1)$, insufficient food will have been added to offset the fitness loss from risk, resulting in too few individuals using the risky feeder. Thus, deviations from an equal distribution of animals can be used to infer the shape of the energy–fitness relationship. Experiments were then run using the calculated amounts of extra food.

The order of these experiments was determined by the same method as the previous experiments. The intermediate diet level was examined first, then the low and finally the high diet level. Within a diet level, risk levels were randomly chosen and each combination was repeated nine times (three times on each of 3 d), except for the males at the high diet level where experiments were repeated only six times (three times on each of 2 d). The same groups of male and female guppies were used as in experiment 1.

RESULTS

Experiment 1: The energetic equivalence of risk

Effects of a predator. — When food was distributed equally between the two feeders, fewer guppies used the risky feeder when the predator was present than when it was absent. In all but one case this difference was highly significant (t tests of arcsine square-root transformed data for each combination of risk and diet level for each sex, $P < .005$). The one exception occurred with the females at the medium diet level, low risk combination (t test, $P = .049$). We attribute this exception to the unusually large variation in the experimental data at this combination (Fig. 3). The proportion that used the risky feeder decreased significantly as it was moved farther from refuge (Figs. 3 and 4; Table 1). This result is consistent with our assumption that risk increases as the feeder is moved farther from the screen, and demonstrates that both male and female guppies are capable of detecting and responding to a variable risk of predation. Since equal amounts of food were available at both feeders, and the guppies captured virtually all of it, the difference in individual
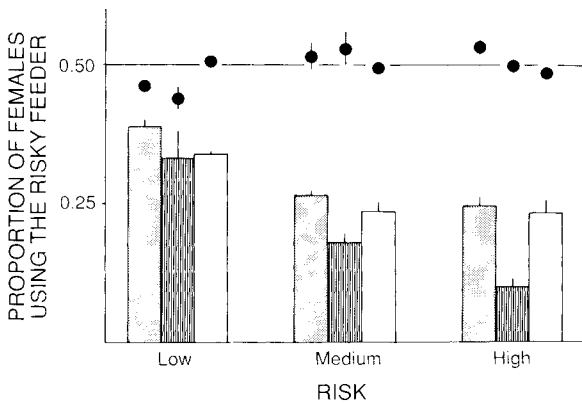
FIG. 3. The proportion of females using the risky feeder as a function of different predator risk and diet levels when equal amounts of food were available at both feeders. Solid circles represent the result in the absence of a predator (controls) and the histogram bars are the result with the predator present. Stippled bars represent the result for the low diet level, striped bars for the intermediate diet level, and open bars for the high diet level. The error bars for both control and treatment data represent one standard error. Where error bars are not visible, the standard errors are too small to be displayed.

intake rates between the two patches also increased as the feeder was moved farther from cover.

Effects of diet levels. — Although equal amounts of food were available at both feeders, diet level significantly influenced the proportion of guppies that used the risky feeder (Table 1). A larger proportion of the females used the risky feeder at the low and high diet levels (Fig. 3) than at the intermediate diet level. At these extreme diet levels, the females appeared to become less sensitive to risk, showing little change in their use of the risky feeder between the medium and high risk levels. There was thus a significant interaction between risk and diet level (Table 1).

There was no significant interaction between risk and diet level for the males (Table 1). They also differed from the females in their response to changes in diet level. The largest proportion of males used the risky feeder at the intermediate diet level, less at the lowest diet level, and almost none at the highest diet level (Fig. 4). At the highest diet level the males completely avoided the risky feeder except for brief visits by one or two individuals.

The difference in response between the male and female guppies at the highest food level may have been due to differences in their ability to consume food. The highest diet level for the males may have provided food at the safe feeder at a rate that exceeded their ability to consume it, a level not experienced by the females. Thus, using the risky feeder would not provide a significant energetic benefit to males. If this explained the males' avoidance of the risky feeder at the highest diet level, then increasing the absolute amount of food available to the females should generate a similar re-

sult. We did this by providing the females with 60 mg of food at each feeder, and placing the risky feeder 32 cm from the screen. Providing food at this rate far exceeded the females' ability to consume it, yet a significant proportion (35%) continued to use the risky feeder. Thus, even if food were provided to the males at a rate in excess of their ability to consume it, their response was different from the females in a comparable situation.

Control experiments. — Repeating these experiments in the absence of a predator revealed that neither the position of the feeder nor diet level significantly altered the distribution of the guppies (Figs. 3 and 4: top; Table 1). However, it should be noted that the feeder position did have a marginally significant effect on the spatial distribution of the females in the absence of predators. This position effect slightly increased their use of the risky feeder as it was moved farther from the screen (Fig. 3: top); this would act to reduce the observed effect of a predator.

Experiment 2: offsetting the influence of risk

The combinations of food and risk used in these experiments are summarized in Table 2. The amount of food in the risky feeder was determined using Eq. 3 except for the high diet level (12 mg in the safe feeder) for males. At this diet level the males almost completely avoided the risky feeder; the average number of males using that feeder was less than one. As a result, the amount of food consumed by individuals in the presence of the predator was overestimated. Consequently, the amount of food used for this trial was estimated from the results of the other two diet levels. We observed that, for the males, the ratio of food in the risky feeder (as determined by Eq. 3) to food in the safe feeder approximately doubled with each increase in risk level. Furthermore, the ratios at the low diet were approximately twice those at the intermediate diet level. The amount of food used at the high diet
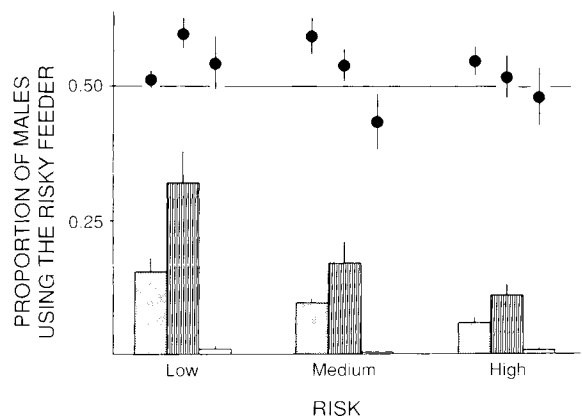

FIG. 4. The proportion of males using the risky feeder as a function of different risk and diet levels when equal amounts of food were available at both feeders. Key as in Fig. 3 legend.

TABLE 1. The influence of feeder position and diet level on the proportion of male and female guppies using the risky feeder in the presence or absence of a predator. Probabilities were calculated by two-way ANOVA using arcsine square-root transformed data.

Sex	Effect	df	Predator absent		Predator present	
			F	P	F	P
Females	Feeder position	2, 72	3.561	.051	80.851	<.001
	Diet level	2, 72	1.365	.283	25.443	<.001
	Interaction	4, 72	2.000	.117	3.671	.014
Males	Feeder position	2, 72	0.786	.400	7.451	.005
	Diet level	2, 72	2.983	.078	110.659	<.001
	Interaction	4, 72	1.504	.223	2.349	.074

level was determined by using ratios that were double those calculated at the low diet level (because the males' avoidance of the risky feeder was most extreme at the high diet level). These ratios were then used to calculate the absolute amount of food to be used in the risky feeder.

The most striking result of this experiment was the difference between the sexes. The additional food resulted in the proportion of females using a feeder returning to or exceeding their control level (Fig. 5 and Table 3). Conversely, the males returned to their control level in only one case, and in all others were below it (Fig. 5 and Table 3). At the high diet level, the males continued to avoid completely the risky feeder.

Diet level appeared to influence the deviation of this result from the control distribution for both the male and female guppies (Table 3). Our manipulation worked well at the intermediate diet level for the females, but exceeded the control distribution at both the low and high diet levels. For the males, deviations from the control distribution increased from the low to high diet levels. Risk level had no obvious influence on these results for either the males or the females (Table 3).

Within both experiments 1 and 2 the intermediate diet level was examined first, then the low, and finally the high diet level. As such, it was possible that the results attributed to diet manipulations could also have been order effects. If order effects were due to habituation or learning, then they should also be present within diet levels. We examined the proportion of fish

TABLE 2. The amounts of food (onion fly eggs) predicted to offset the influence of risk, for the different combinations of risk and diet level. One mg (wet mass) of onion fly eggs contains 8.09 J.

Sex	Food in feeder (mg)			
	Safe	Low risk	Inter-mediate risk	High risk
Females	5	6.1	9.5	10.4
	10	13.8	23.8	50.0
	20	29.7	42.0	42.7
Males	3	9.8	16.1	26.6
	6	10.4	18.4	27.5
	12	81.1	127.2	213.0

(arcsine square-root transformed) which used the risky feeder as a function of order of presentation for each combination of risk and diet level separately. Of the 18 regressions, only 3 had slopes significantly different from zero. All three regressions were for the males and occurred at the high diet level (low risk, slope = −0.035; high risk, slope = −0.023) and the low diet level (medium risk, slope = −0.015). Note that in all cases the slopes were very shallow. Thus, the strong trends observed in the results are unlikely to have been artifacts of order effects. Furthermore, although the order of presentation was identical for the two sexes, they exhibited opposite responses to diet manipulations.

DISCUSSION

These results demonstrate that risk of predation can be measured in units of energy, and therefore that sufficient food can offset the effect of risk. By determining the energetic equivalence of risk, we quantitatively described its influence on foraging behavior at different diet levels. For females, risk had its greatest measured energetic equivalent at the intermediate diet level. For males, the greatest energetic equivalent of risk occurred at the highest diet level. At this diet level, males continued to avoid the risky feeder even when >17 times as much food was available there than at the other feeder. In addition, the measured value of risk was less for females than for males, consistent with the prediction that risk should have a greater influence on animals that receive relatively less fitness advantage from equivalent additional amounts of energy.

When we calculated how much food was necessary to offset risk, we assumed that the amount of energy delivered to guppies was equal to the amount of food they consumed. However, the net intake rate may be affected by risk. When animals are in the presence of a predator, it is possible that the threat increases their metabolic rate. Furthermore, foraging efficiency in the presence of a predator may be reduced owing to the need for vigilance (Milinski and Heller 1978, Caraco et al. 1980). Thus, the absolute energetic value of risk determined in these experiments probably overestimates somewhat the true energetic equivalent of risk. Male guppies may also obtain non-energetic benefits from foraging: If they consume food that contains car-
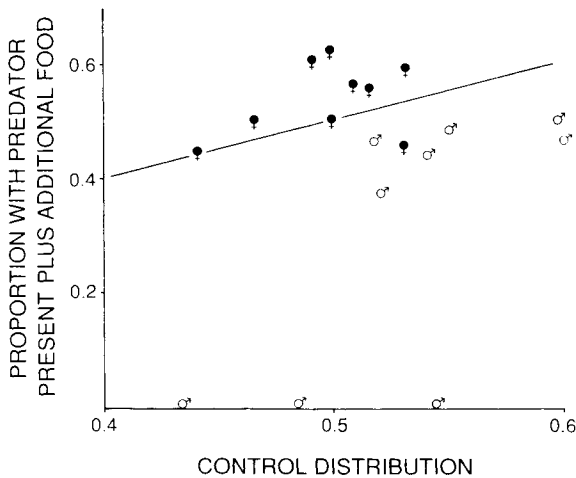
FIG. 5. Summary of the results of the experiment to offset the influence of risk. The abscissa represents the mean proportion of fish using the "risky" feeder in the absence of a predator (experiment 1, control). The ordinate is the mean proportion of fish using the risky feeder in the presence of a predator and with additional food (experiment 2). If the additional food offsets the risk, then the results of experiment 2 should return to the control distribution of experiment 1, i.e., fall along the diagonal. Symbols denote results for the two sexes. Statistical tests of differences between the plotted means are in Table 3.

otenes, this may alter body coloration, providing a mating advantage (Endler 1982). However, the onion fly eggs used in these experiments do not contain carotene (Richards and Davies 1977), so this should not have affected the results of the experiments.

Eq. 3 assumes a linear relation between energy intake and fitness. Violations of this assumption generate a characteristic result: An accelerating relation will result in additional food exceeding the influence of risk so that more guppies than predicted will use the risky feeder. Conversely, a decelerating relation will result in the additional food being insufficient to offset risk, and fewer guppies than predicted will use the risky feeder. Thus, the value of additional food gained by taking a risk depends on the absolute amount of food that can be obtained in safety (see Sih 1982b for a further discussion of this idea). When male and female guppies are placed on identical controlled-energy diets, females always grow more rapidly than males; they also change their growth rate more rapidly than males when their diet is changed (M. V. Abrahams and J. D. Reynolds, unpublished manuscript). These results suggest that the relation between energy intake and fitness is different between the sexes: females appear to benefit more than males from increased energy, a difference consistent with their responses to extra food in experiment 2.

Since single groups of males and females were used, the influence of sex on these results cannot be statistically tested. It is possible that behavioral differences between the two groups resulted from uncontrolled in-

dividual variation within the guppy population. However, we believe it more likely that these differences reflect biological differences between the sexes.

Previous studies have found other factors to be important in determining the response of animals to risk of predation. Sih (1982a, b) found that notonectids (Notonecta hoffmani) were more willing to risk exposure to their predator (larger instars) when they had been starved than when they were well fed. Dill and Fraser (1984) also observed this phenomenon with juvenile coho salmon (Oncorhynchus kisutch). House Sparrows (Passer domesticus) were also more likely to exploit riskier habitats in cold weather because of their increased energy requirements (Elgar 1986). Thus, animals appear to be more willing to risk exposure to a predator when the immediate benefits of energy (e.g., minimizing the probability of starvation) are increased. This present study suggests that the response of animals to a risk of predation was a function of the potential benefits that can be derived from additional food—a characteristic of the animal's life history.

In a similar study, Gilliam and Fraser (1987) were able to predict successfully how much additional food was necessary to induce juvenile creek chub (Semotilus atromaculatus) to forage in areas of greater risk. They developed a model which predicted that, in the presence of an absolute refuge containing no food, animals should use the refuge and forage in the habitat that has the minimum ratio of mortality rate to feeding rate (see also Werner and Gilliam 1984). The major difference between their experiments and ours was the meth-

TABLE 3. Summary of t tests comparing the distribution of guppies between control experiments and experiments with additional food added to offset the effect of predator risk* (data in Fig. 5). = denotes no significant difference, + denotes (treatment > control), − denotes (treatment < control). Significant P-values are given in parentheses.

	Food in safe feeder	Low	Medium	High
		Risk level		
Females	5	+ (0.006)	=	+ (0.020)
	10	=	=	=
	20	+ (0.004)	+ (<0.001)	+ (<0.001)
Males	3	− (0.016)	=	− (0.030)
	6	− (0.001)	− (0.016)	− (0.008)
	12	− (<0.001)	− (<0.001)	− (<0.001)

* No statistical difference would occur if the additional food completely offset the risk, i.e., returned the animals to the control distribution of experiment 1. Data were arcsine square-root transformed before analysis. The results for each cell are based upon nine observations except for the results for the males at the high diet (12 mg of food in the safe feeder), which were based on six observations.

od by which risk was incorporated into foraging de-
cisions. We assumed that habitat quality is determined
by the additive effects of energy and risk, whereas Gil-
liam and Fraser (1987) assumed that it is determined
by the *ratio* of mortality rate to feeding rate under
certain conditions they specified. These models can be
distinguished experimentally. The ratio approach of
Gilliam and Fraser predicts that habitat use decisions
are affected only by relative differences in habitat qual-
ity. Manipulating an environment in such a way that
intake rates in all habitats are multiplied by a constant
factor should not alter the habitat chosen in addition
to the refuge, unless foraging rates are reduced suffi-
ciently to cause the refuge to be eliminated from the
optimal time budget. Our model predicts that multi-
plication of foraging rates should alter which habitats
are chosen, since habitat quality is measured by the
absolute difference between the benefits of food and
the costs of risk.

Risk of predation is not only an important factor
influencing foraging behavior, but also a potentially
important determinant of community structure (Dill
1987). Kotler (1984), for example, demonstrated that
species of desert rodents least vulnerable to predators
tend to forage in open areas, whereas the most vul-
nerable species are restricted to areas under bushes.
Thus, risk of predation can influence community struc-
ture by allowing animals specializing in predator es-
cape to exploit risky environments, reducing their in-
teractions with superior competitors. Mittelbach (1984)
and Werner et al. (1983) have suggested that predation
risk is important in structuring aquatic communities.
Development of models to describe adequately the in-
fluence of risk of predation on habitat choice therefore
would not only benefit foraging theory, but contribute
to our understanding of community structure as well.

Given that animals choose patches on the basis of
trade-offs between the availability of food and the as-
sociated risk of predation, the following scenario can
be imagined. Animals will find a range of habitats in
which food availability and risk are positively corre-
lated. (Any patches that are relatively safe and have
readily available food will be used preferentially, low-
ering food availability to conform to the correlation;
any patches that are very risky and have low food
availability will be ignored, and predators will be ex-
pected to move to more profitable patches as a con-
sequence.) Faced with this situation, there are a num-
ber of potential strategies that foragers could adopt.
Animals could avoid patches that risk exposure to a
predator, spending their lives in energetically poor hab-
itats. There they would grow slowly, and produce off-
spring at a slow rate, but live a long time. Or, animals
could use the richest habitats, grow and reproduce rap-
idly, but live a relatively short life. If these two alter-
native strategies (and perhaps others that involve time
spent in a range of habitats) produce the same number
of offspring over their lifetimes, they should have equal

fitness and persist in the population. Since individuals
were not marked in our experiments, the possibility of
alternative strategies could not be tested. However, it
could be an important consideration in the develop-
ment of habitat use models that incorporate risk of
predation.

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