

CHANGES IN FEEDING AND FORAGING PATTERNS AS  
AN ANTIPREDATOR DEFENSIVE STRATEGY: A  
LABORATORY SIMULATION USING AVERSIVE  
STIMULATION IN A CLOSED ECONOMY

MICHAEL S. FANSELOW, LAURIE S. LESTER, AND FRED J. HELMSTETTER

DARTMOUTH COLLEGE

The effects of the risk of electric shock on the meal patterns of rats living in an operant chamber were investigated. Rats could obtain food by working on a response lever that provided reinforcement according to chained fixed-ratio continuous reinforcement schedules that allowed the animals control over meal size. Using a two-compartment operant chamber with a safe nesting area and manipulanda area with a grid floor, shock could be correlated with responding on the schedule. Shocks ( $\leq 1.25$  per hour) were scheduled to occur randomly throughout the day, independent of the rat's behavior. Shock caused a reorganization of meal patterns such that the animals took less frequent but larger meals. This pattern reduced the time the animals spent at risk without compromising caloric balance. Similar changes in feeding pattern were obtained in both hooded and albino rats. Exposure to shock in a separate chamber did not produce these behavioral modifications. The magnitude of shock-induced alterations of meal patterns was greater with chained fixed-ratio 90 continuous reinforcement than with chained fixed-ratio 10 continuous reinforcement. Additionally, the rats seemed to be able to reduce food intake but increase caloric efficiency, such that the reduced food intake did not have deleterious effects on maintenance of body weight. These behavioral modifications reduced the number of shocks received from that which would have been expected if meal pattern changes had not occurred. We suggest that this technique may provide a useful laboratory simulation of the impact that the risk of predation has on foraging behavior.

*Key words:* feeding, foraging, chained fixed-ratio continuous reinforcement, antipredator defense, closed economy, lever press, rats

Bolles (1970) suggested that in aversively motivated situations the range of behaviors available to an animal becomes constricted to a limited number of responses that have a phylogenetic history of protecting individuals of that species from predation. If this assumption is correct, and there is considerable evidence to support it (Bolles, 1975), then a major task in the study of aversive motivation is to specify the environmental conditions that select particular behaviors from an animal's repertoire of species-specific defense reactions (SSDRs). We (Fanselow & Lester, 1988) have proposed a model of defensive responses to predation that suggests that rats are sensitive to the risk of predation and that the topography of their

defensive behavior changes as a function of predatory imminence. Our approach describes three categories of defensive behavior: preencounter, postencounter and circa-strike defensive behaviors. When an animal engages in an activity that has some potential for it to be preyed upon but no predator is currently detected in the vicinity, *preencounter defenses* emerge. If the prey detects a predator in the vicinity, *postencounter defenses*, such as freezing, occur. When the predator is making, or is about to make, a strike at the prey, *circa-strike defenses* (e.g., fighting) are observed. The experiments reported in this paper are concerned with an examination of foraging under the risk of predation, a situation in which preencounter defense might be expected.

In order for most animal species to take in enough energy to reproduce they must first find and ingest food. Foraging for food, however, requires a cost in terms of expenditure of time and energy. The basic premise of optimal foraging theory is that animals strike an optimal balance between the costs (time and energy expenditure) and the benefits (caloric intake)

This research was supported by NIMH Grant MH39786 to M. S. Fanselow. L. S. Lester is now at the Department of the Army, U.S. Army Natick Research, Development and Engineering Center, Natick, Massachusetts 01760. Requests for reprints should be sent to M. S. Fanselow, Department of Psychology, University of California-Los Angeles, 405 Hilgard Ave., Los Angeles, California 90024.

of foraging (MacArthur & Pianka, 1966). Much of the research on foraging has focused on costs directly associated with the food object, such as distance between patches containing food, density of the food object within a patch, and the handling needed to prepare the food object for consumption (e.g., Krebs & Davies, 1981). We can refer to these factors as appetitive costs. However, there are other costs of foraging that are not associated directly with the food object itself, that is, the costs associated with predation (Krebs, 1980; Lima, Valone, & Caraco, 1985). When an animal forages it may have to leave a location of relative safety (home, nest, or burrow) for a location of relative danger because predator and prey may forage in the same location for their respective food objects. Thus, the probability of encountering a predator may increase during foraging. This increase in predatory risk also confers a cost to foraging. Therefore, it might be expected that an animal's pattern of foraging reflects an incorporation of the risk of predation with the appetitive costs associated with a particular food item.

There has been some suggestion that foraging patterns reflect predatory risk. For example, many small mammals are nocturnal feeders; it is generally assumed that this pattern evolved because it minimizes the risks from visually guided predators (Curio, 1976; Daan, 1981; Vilchez & Echave Llanos, 1971). It has also been observed that some herbivores make only a single daily trip to the water hole; it has been suggested that this is because of the increased risk of predation at that location (Collier, Hirsch, & Hamlin, 1972, p. 706). However, without an experimental test, the putative defensive nature of these behavioral patterns remains mere speculation. The present experiments were designed to provide a laboratory analogue capable of examining the effects of predatory risk on foraging. In designing these studies we made the assumption that foraging patterns are plastic and that an animal's foraging behavior may change as a function of predatory risk.

The operant laboratory appears to be an excellent tool for examining changes in foraging behavior as a function of appetitive costs (e.g., Collier & Rovee-Collier, 1981; Mellgren, Misasi, & Brown, 1984; Rashotte & O'Connell, 1986; Snyderman, 1983). In the simulation employed by Collier and colleagues, an

animal (usually a rat) spends 24 hr a day in an operant chamber where it can obtain food by lever pressing on a chained schedule of reinforcement (e.g., Collier, 1983; Collier *et al.*, 1972). The first component of the schedule is referred to as procurement and models the work required to obtain a food source. By executing the procurement requirement the animal can reach the terminal component of the chain (i.e., the meal). During a meal an animal can obtain food by lever pressing. The animal may stay in the meal phase as long as it continues to press the lever. If lever pressing ceases for a fixed time period (e.g., 10 min) the meal is ended and the animal must execute the procurement requirement to obtain more food. Thus, obtaining a meal represents successful procurement of a rich patch of food, because the size of the meal is determined by the animal. The dependent variables most extensively studied by these researchers are the number of meals per day (number of terminal components entered in a 24-hr period) and meal size (mean number of pellets obtained in a terminal component). As procurement cost (number of presses needed to enter the terminal component) increases, daily meal frequency decreases, but there is a compensatory increase in meal size such that daily intake and body weight are maintained. Such changes in meal pattern reduce the net expenditure (in terms of the number of lever presses) the animal makes to obtain food because, by reducing meal frequency, the animal needs to complete fewer procurement requirements. Thus, the animal's meal pattern is plastic in that it is modified in response to environmental variables such as procurement cost. When these environmental variables involve a minimal cost, the meal pattern reflects only the internal costs of digestion that are assumed to increase with meal size (see Collier & Rovee-Collier, 1981, pp. 73-74). Only when external costs outweigh internal costs will the meal pattern shift from this resting point.

In the present article we ask the following question: If a predatory risk factor is added to appetitive costs during foraging and consumption will the rat modify its meal pattern in such a way as to reduce that risk? Predatory risk was modeled by electric shock associated with the foraging situation. Using a procedure similar to that used by Collier and his colleagues, rats were provided with a safe nesting

area but had to leave this area to obtain access to a lever and food hopper. Unpredictable shock could be delivered to the foraging area. The Fanselow and Lester model predicts that preencounter defense will occur only if the foraging situation were associated with shock densities lower than those necessary to disrupt consumption through elicitation of defensive behaviors such as freezing (Fanselow & Lester, 1988, p. 207). Therefore, we predicted that rats will make changes in feeding behavior that will reduce the risk of electric shock without compromising energy intake. One such strategy is to decrease meal frequency but increase meal size. By reducing meal frequency the number of procurement components entered decreases, reducing the time susceptible to electric shock. By increasing meal size, this strategy could accomplish that reduction in shock receipt without sacrificing caloric intake. We have provided some preliminary data that are supportive of these predictions (Fanselow & Lester, 1988). In that earlier work, a single rat, living in an operant chamber, decreased meal frequency but increased meal size as the probability of shock during foraging increased.

## EXPERIMENT 1

The first experiment attempted to document further whether or not the risk of shock during foraging would alter meal patterning. Meals were obtained on chained fixed-ratio continuous reinforcement (FR:CRF) schedules of reinforcement (Gunn, 1983). In terms of the analogy to foraging, the fixed-ratio (FR) component represents procurement of a meal and the continuous reinforcement (CRF) component represents a meal (Collier et al., 1972).

## METHOD

### *Subjects*

The subjects were three adult (90 to 120 days old) female Sprague-Dawley rats (Subjects CR3, CR5, and CR7). The animals were bred at Dartmouth College from Charles-River stock and were housed under ad-lib food (Agway Prolab) and water conditions until the start of the experiment. Lights were on 14 hr and off 10 hr until 10 days before the experiment began. At that time the animals were placed in standard single cages and brought into the laboratory. Prior to this period the rats were housed in groups of at least two per

cage. The laboratory was on a 12:12 hr light/dark cycle. The animals were also adapted to handling during this 10-day period.

### *Apparatus*

The apparatus consisted of an operant chamber (58.5 by 26 by 20.6 cm) made of clear acrylic plastic. The chamber was divided into two compartments. The rear of the chamber was a nest area that measured 16 by 25 cm. The nest area was filled with 500 mL of sawdust and was separated from the foraging area by a 5.75-cm high hurdle. The foraging area made up the remainder of the chamber. Its floor consisted of 25 brass rods (3 mm diameter) spaced 1.5 cm center-to-center. Each rod of the grid floor was wired to a Grason-Stadler shock generator/scrambler.

The front wall of the chamber contained the operant manipulandum. Centered on the wall was a 3-mm diameter wire response lever shaped like a C bracket, the open end of which was attached to the wall. The lever was 8 cm long and protruded 1.5 cm from the wall. Mounted on the wall, 9 cm above the response lever, was a 1-cm diameter cue light (28V, 1.1W). The center of the food hopper was mounted 9 cm to the left of the center of the response lever. Bio-Serv dustless precision food pellets (45 mg) could be delivered there. A water spout was located 9 cm to the right of the center of the response lever. A 1.5 by 2.5-cm drip receptacle was mounted on the wall just under the drinking spout. This receptacle caught all water spillage, which was drained by an attached tube. A catch tray was underneath the chamber. A drawing of this apparatus can be found in Fanselow and Lester (1988). Electromechanical equipment controlled and recorded all events.

### *Procedure*

A rat lived in the operant chamber from the start of the experiment. It was removed for only a brief period once per day, during the light portion of the cycle, so that the chamber could be serviced. During this servicing, data were collected, the rat was weighed, the bedding material replaced, and the catch tray cleaned. At this time, food and water supplies were checked and replenished if necessary. Also, the food hopper, nest area, and catch tray were inspected for remaining food pellets. Throughout the experiments the animal could

initiate and terminate feeding and drinking bouts at any time, but the only source of these items was that available in the chamber. Thus, the procedure met the definition of a "closed economy" in that "daily consumption [was] solely the result of the subject's behavior in interaction with the schedules of reinforcement" (Hursh, 1984, p. 445; see also Hursh, 1980). In addition to the absence of supplemental feedings, the present situation had the other characteristics typical of a closed economy: Long exposures to the experimental contingencies, sufficient within-session reward density for survival, and deprivation levels determined by within-session food intake (see Timberlake & Peden, 1987, p. 36).

Each subject progressed at its own rate through four experimental phases:

*Acquisition.* The rats were placed in the chamber and allowed to acquire lever pressing under CRF conditions. No shaping procedures were employed. Once a rat was reliably pressing the lever a chained FR:CRF condition was put into effect. If the rat executed the FR component, the cue light turned on and each response resulted in a single food pellet. This CRF component remained in effect as long as the rat continued to respond. If 4 min elapsed without a lever press, the cue light turned off and the rat was required to execute the FR requirement to obtain another meal. Thus meal size, meal frequency, and intermeal interval were directly under the control of the subject.

Initially the FR requirement was set at one response. Once the animal's meal frequency stabilized under a particular response requirement, the FR component was doubled. This progression was continued until the rat reached a 32-response FR requirement. At that point the rat was advanced to the preshock phase.

*Preshock.* The rat remained on FR32:CRF for at least 10 days to allow stabilization of meal patterning and collection of baseline data. The first rat (CR3) stayed under these conditions for 26 days. Because that animal adjusted rapidly to the schedule and showed little fluctuation in meal pattern once adjusted, the time period was reduced to 10 and 13 days for CR5 and CR7, respectively.

*Shock.* During this phase, the FR32:CRF schedule was in effect. Additionally, scrambled grid-shock (1 mA, 1 s) was delivered to the grid floor of the foraging compartment. Using a probability gate that was sampled every 2

min, shocks were programmed to occur randomly in time and independently of the animal's behavior. The total number of shocks delivered per day was limited to 30. However, shock could be avoided if the rat stayed in the nesting area. This method resulted in a minimum intershock interval of 2 min. There was no programmed constraint on the maximum intershock interval.

Because shock scheduling was done on this random time basis, the animals varied somewhat in the number of shocks per day that were delivered to the grid. For CR3, scheduled shock frequency was 18 to 20 shocks per day (24 hr) for 7 days and was then increased to 23 to 25 shocks per day for the remaining 34 days of its shock phase. For CR5, scheduled shock frequency was 13 to 15 shocks per day for 10 days followed by 28 to 30 shocks per day for the next 25 days.

For CR7, 26 to 30 shocks per day were delivered by a Coulbourn Instruments (E13-08) shocker for 26 days. At this point the animal was not showing the meal pattern changes characteristic of the other animals. Upon examination of the shock source it was found that the unit was defective and not delivering the current indicated by its amp-meter. Therefore, this unit was replaced with one of the Grason-Stadler shockers used with the other animals, and the animal could have received 27 to 29 scheduled shocks per day for an additional 30 days.

*Postshock.* Following the shock phase, the shock was discontinued and behavior was observed until meal patterns were showing no signs of further change. The postshock phase lasted for 35, 25, and 19 days for CR3, CR5, and CR7, respectively.

#### *Data Analysis*

The data from the last 7 days of each phase were converted into the following three measures: (a) meal frequency (the number of CRF components entered per day), (b) meal size, (the mean number of pellets obtained per CRF component for each of the 7 days), and (c) weight (daily body weight in grams).

#### RESULTS AND DISCUSSION

The means and standard errors, averaged over the last 7 days of each phase, of each of the three measures are presented in Table 1. The pattern of data indicated clearly that the

Table 1  
Means ( $\pm$ SEM) for the three measures for the final 7 days of Experiment 1.

	Rat	Preshock	Shock	Extinction
Meal frequency (meals/day)	CR3	4.0 $\pm$ 0	2.1 $\pm$ 0.3	3.3 $\pm$ 0.2
	CR5	3.9 $\pm$ 0.4	3.3 $\pm$ 0.2	3.4 $\pm$ 0.2
	CR7	6.7 $\pm$ 0.4	3.4 $\pm$ 0.4	5.0 $\pm$ 0.2
Meal size (pellets/meal)	CR3	70.5 $\pm$ 7.3	111.4 $\pm$ 13.1	84.1 $\pm$ 3.9
	CR5	98.9 $\pm$ 14.2	105.5 $\pm$ 7.6	86.4 $\pm$ 5.2
	CR7	55.3 $\pm$ 5.1	98.8 $\pm$ 8.6	65.8 $\pm$ 1.4
Body weight (g)	CR3	266 $\pm$ 1.0	279 $\pm$ 1.7	287 $\pm$ 1.1
	CR5	308 $\pm$ 1.8	344 $\pm$ 1.1	335 $\pm$ 1.9
	CR7	263 $\pm$ 1.4	300 $\pm$ 1.3	310 $\pm$ 0.5

introduction of shock altered feeding/foraging patterns. Compared to the final week of the preshock phase, shock decreased meal frequency by 40% but increased meal size by 40%. Of course, by reducing the number of meals procured, the animals reduced the total number of lever presses they made. Such a reduction in responding is likely to translate into a reduction in the amount of time at risk of receiving shock during the procurement component.

If meal frequency decreased but meal size increased, these two changes should have compensated for each other in terms of total daily intake (i.e., daily intake is the product of meal frequency and meal size). This compensation was not perfect in that total consumption showed a 12% drop from the preshock to the shock phase. However, body weight increased during the shock phase despite the reduction in food intake. Thus there was an inverse relationship between food intake and body weight such that rats ate more during the preshock phase but weighed more during the shock phase. It seems that in response to the risk of shock during foraging the rats became calorically more efficient than they were during the preshock phase. This increased efficiency was not caused by a reduction in spillage between the nonshocked and shocked conditions because inspection for pellets in the litter tray during servicing revealed that spillage never exceeded five pellets, and the amount of spillage was not different across the shock conditions. We do not know the mechanism behind this interesting finding but we can offer several possibilities. First, the rats may have become more efficient in the extraction of calories from the diet. One way this could be

accomplished is by slowing the rate of gastric emptying. Second, they may have altered their metabolism in a way that fostered energy conservation. For example, Rashotte has found that when food is costly in a closed economy, pigeons will lower their body temperature during the inactive period.<sup>1</sup> Third, a greatly reduced level of general activity could result in caloric conservation. Further research will be necessary to distinguish among these alternatives. In addition, it will be necessary to determine whether the change in efficiency is a direct effect of exposure to shock or if it is a response to the meal pattern changes caused by the shock.

During the postshock phase the animals tended to recapture the preshock meal pattern to some extent. All response measures, in all animals, achieved levels between those of the shock and preshock phase measures. The fact that the rats did not completely return to preshock levels suggests that there are persistent effects of shock on meal patterning. Similarly, prolonged effects were observed for the changes in feeding efficiency. This finding is somewhat reminiscent of the great resistance to extinction that has been reported with conventional avoidance procedures (Solomon, Kamin, & Wynne, 1953; Solomon & Wynne, 1953).

<sup>1</sup> Rashotte, M. E. (1985). *A hard day's night: Nocturnal hypothermia in response to high food costs in the 24-hr closed economy*. Paper presented at the 26th meeting of the Psychonomic Society, Boston.

Rashotte, M. E., Rautenberg, W., Henderson, D., & Ostheim, J. (1986). *Thermal, metabolic and feeding reactions of pigeons when food is scarce*. Paper presented at the 27th meeting of the Psychonomic Society, New Orleans.

Table 2  
Means ( $\pm$ SEM) for the four phases of Experiment 2.

	Rat	Preshock	Off-baseline shock	On-baseline shock	Extinction
Meal frequency (meals/day)	L09	6.4 $\pm$ 0.3	6.7 $\pm$ 0.5	2 $\pm$ 0	8.1 $\pm$ 0.6
	L11	5.1 $\pm$ 0.3	4.6 $\pm$ 0.4	1.9 $\pm$ 0.2	4 $\pm$ 0.4
Meal size (pellets/meals)	L09	52 $\pm$ 1.6	34 $\pm$ 3.5	154 $\pm$ 11.6	44 $\pm$ 5.7
	L11	53 $\pm$ 2.7	48 $\pm$ 6.5	130 $\pm$ 18.4	69 $\pm$ 3.3
Body weight (g)	L09	332 $\pm$ 2.2	315 $\pm$ 1.6	311 $\pm$ 3.8	345 $\pm$ 3.5
	L11	315 $\pm$ 1.4	277 $\pm$ 2.6	268 $\pm$ 1.2	298 $\pm$ 0.7

One potential shock-reduction strategy, hoarding, was not used by the rats. It was possible for the rats to store earned pellets, in either the food hopper or nest area for future consumption. During daily servicing food pellets were never found in either location. Additional informal surprise inspections of the laboratory were conducted, and rats' behavior was videotaped for several days. No evidence of any form of hoarding was found. The videotapes permitted observation of the rats' responses to shock. The rat ran rapidly around the perimeter of the box to the nest area, and then made probing movements from the nest area with its nose and forepaws extending over the hurdle and onto the grid.

## EXPERIMENT 2

The purpose of Experiment 2 was to determine whether the meal pattern changes found in the first experiment were nonspecific stress effects. This experiment included a phase during which shock was given in a different situation to investigate whether such off-baseline shock would cause any of the meal pattern changes that occurred when shock was associated with foraging. Additionally, we used Long-Evans (hooded) rats to determine whether the findings of Experiment 1 generalized to a second strain of rat.

## METHOD

### *Subjects and Apparatus*

The subjects were 2 adult female Long-Evans rats bred and raised at Dartmouth College from Blue Spruce Farms stock (Subjects L09 and L11). The primary apparatus was that of Experiment 1. In addition, off-baseline shock was administered in a 23.5 by 29 by 19.5-cm

chamber made of clear plastic and aluminum. The chamber was wired to a Grason-Stadler shock generator/scrambler so that shock could be administered through the grid floor. This chamber was placed in a sound-attenuating chest and was located in a room separate from the closed economy laboratory.

### *Procedure*

Except for the changes detailed below, the procedure was the same as that of the first experiment. Rats were maintained on a pre-shock FR32:CRF schedule for 50 days to obtain baseline data. At that point off-baseline shock began. The animals were removed from the chambers during the daily weighing and equipment servicing period. They were brought into a different room and placed in the off-baseline chambers. One minute after placement in the chambers the rats received 15 shocks (1 mA, 1 s) at a 30-s intershock interval. The rats were removed from the chambers and returned to the closed economy situation 1 min after the final shock. This phase continued for 33 days.

After the completion of off-baseline shock, an on-baseline shock phase was instituted. The rats had 30 shocks scheduled for each day in the same manner as in Experiment 1. This phase lasted for 22 days. The experiment ended with a 22-day postshock phase during which all shock was discontinued.

## RESULTS AND DISCUSSION

Data for each of the four phases are presented in Table 2. The rats were taking about 5.5 meals per day prior to shock; off-baseline shock did not change meal frequency. However, when shock was introduced into the foraging situation, meal frequency showed the reductions characteristic of the first experi-

ment, dropping to about two meals per day. Off-baseline shock actually reduced mean daily meal size relative to the preshock phase. However, meal size showed a dramatic increase during the on-baseline shock phase. During the postshock period, meal frequency and meal size tended to approach their preshock baseline levels.

Thus, when shock was administered during foraging, hooded rats showed a reorganization of meal patterning similar to that found with the albino rats of Experiment 1. However, off-baseline shock did not produce the same pattern of changes. Certainly, the characteristics of off-baseline shock differed from those of on-baseline shock. Off-baseline shock was given in a massed session and, because it was delivered to the entire floor of the chamber, was inescapable. The number of off-baseline shocks was chosen so that the rat probably received slightly more shocks per day during the off-baseline than on-baseline conditions. The off-baseline phase was 11 days longer than the on-baseline phase. Therefore, the off-baseline treatment should have been more, not less, stressful than the on-baseline condition. Although it may be practically impossible to completely equate shock exposure in the on- and off-baseline conditions, it seems reasonable to conclude that the observed changes in meal patterning with on-baseline shock are not non-specific effects of stress. Rather, this control procedure suggests that either a stimulus contingency (foraging area-shock relationship) or a response contingency (foraging response-shock relationship) plays a role in producing the changes in meal patterning.

With off-baseline shock rats tended to decrease meal size but did not show compensatory changes in meal frequency so that total consumption was reduced. This precipitated some weight loss (about 10%) during the off-baseline shock phase. The rats did not regain this weight until the postshock phase.

### EXPERIMENT 3

It was suggested that the meal pattern changes described in the preceding experiments could function to reduce risk. An objective measure of such risk reduction would be if the meal pattern changes reduced shock receipt. Unfortunately, actual shocks received were not recorded in those experiments. For

Experiment 3, switches were installed under the nesting areas so that the animal's location at the time of shock delivery could be determined. The number of shocks received during a shock phase could then be compared to the number of shocks that would have been received during a preshock phase if the same shock schedule had been in effect.

Additionally, the animals in this experiment were maintained on either FR10 or FR90, rather than FR32, during the preshock and shock phase. This was done to ensure the generality of the previous results as well as to allow a comparison of the influence of FR component on the effects of shock.

Because rats' feeding patterns are markedly different during the day than at night the control programming was altered to allow separation of the dependent measures taken during lights-on and lights-off.

### METHOD

#### *Subjects and Apparatus*

Four female Long-Evans rats, about 120 days old at the start of the experiment, served as subjects.

The apparatus of the previous experiments was modified slightly. Weight-activated switches were placed under the nest boxes to allow the position of the rats to be monitored. The wire response levers were replaced by solid oval ones. These levers protruded 1.5 cm into the chamber and were 5 cm wide and 1.3 cm thick. The new levers were positioned like those of the first experiment. Three additional chambers of identical design were added so that 4 rats could be tested simultaneously. Shock for each chamber was produced by a high-voltage, 60-Hz source with a 1-mohm resistor in series with a neon chain that was wired to the floor grid. A computer was used to control and record all events.

#### *Procedure*

Rats were placed in the chamber under conditions like those of the earlier experiment. Initially the rats were on a CRF condition and over 20 days were brought up to an FR10: CRF schedule. They remained on this schedule for 11 days. The rats progressed through FR requirements of 35, 50, and 90 for 7, 5, and 5 days, respectively, to provide the animals with equivalent familiarization with both high

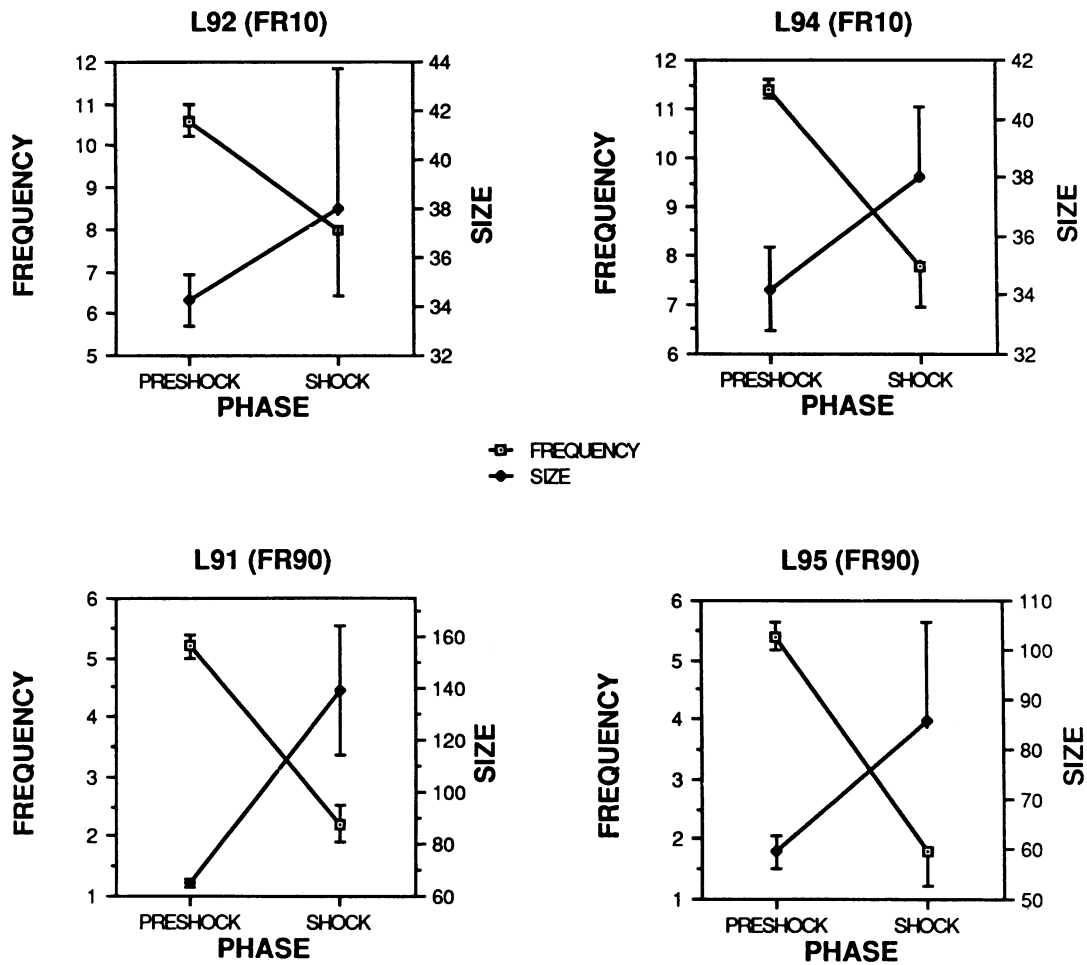


Fig. 1. The mean ( $\pm$ SEM) meal frequency and meal size for rats in Experiment 3 averaged over the last 5 days of each phase.

and low FR requirements. Then, all rats were placed on FR10:CRF for 1 day. At this point the preshock baseline period began. Two rats were moved to FR90:CRF and the other 2 remained on the FR10:CRF schedule. This baseline period lasted for 9 days. During this preshock phase a computer generated shock times on a random basis, so that 25 shocks per 24-hr period were programmed. Shock schedules were generated in the following manner: Each day the computer generated a series of random numbers that were translated into times corresponding to the number of seconds in a day. The computer continued the process until 25 unique times within 24 hr were generated. Thus the minimum possible intershock interval was 1 s, and the maximum possible

interval was 23 hr and 55 s. During the preshock phase the shock generators were disabled. The position of the rats during these random "shock" events was recorded. A 9-day shock phase followed. The shock generators were enabled to deliver a shock intensity of 1 mA (as measured across a 1-kohm resistor substituted for a rat) for 1 s for each of the 25 programmed shocks.

RESULTS AND DISCUSSION

In response to the various FR requirements, rats showed the typical reciprocal relationship between meal frequency and meal size that has been described in detail by Collier *et al.* (1972). Meal pattern data for the last 5 days of the preshock baseline and shock phases are



presented in Figure 1. As in the two earlier experiments, shock decreased meal frequency but increased meal size. The relationship was present on both FR requirements but the effect was greater at FR90. Meal frequency was reduced to 38% of preshock levels by shock in the FR90 animals. The FR10 animals dropped to 72% of preshock meal frequency. A similar differential was found for meal size. Although all animals showed an increase in average meal size during shock, the increase for the FR90 animals was relatively large (74 and 26 pellets per meal) compared to the FR10 rats (four pellets per meal).

The magnitude of the changes for the FR90:CRF animals relative to the FR10:CRF animals does not seem to be because the FR90 animals received more shock. Over the entire 9-day shock period the FR90 rats received 12 and 42 shocks (L91 and L95, respectively), whereas the FR10 rats received 18 and 35 shocks (L92 and L94, respectively). Thus on average the rats received similar amounts of shock on both schedules. The differences obtained between the two FR10 and FR90 components suggest that the effects of shock are dependent on the parameters of the procurement schedule. Certain schedules may enhance or diminish the effects of shock even if they do not affect directly the number of shocks received. This suggests that the rat is responsive to the increased time at risk that is produced by leaner reinforcement schedules. If this observation is extended to naturalistic foraging situations, one might predict that predatory risk has more impact on feeding patterns when patches of food are rare instead of abundant.

All rats showed a reduction in total consumption that did not depend on the FR requirement. As can be seen in Figure 2, despite this relatively large reduction in food intake (averaging 94 pellets per day per animal) body weight was rather well maintained, with 2 rats showing slight increases and 2 showing slight decreases during the shock phase.

To determine the success of the rats' behavioral patterns in avoiding shock, the number of shocks received during the shock phase was compared to the number of shocks that would have been received during the preshock phase had the shock generators been operating. Thus the number of "shocks" received during the preshock phase represents the number of shocks that the rats would be expected to re-

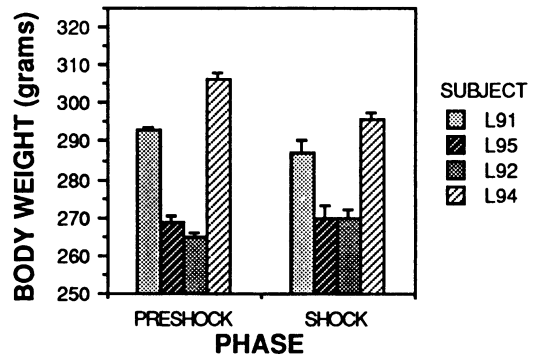


Fig. 2. The mean ( $\pm$ SEM) body weight of rats in Experiment 3 averaged over the last 5 days of each phase.

ceive during the shock phase if they had not changed their behavioral patterns during the shock phase. Additionally, because shock was delivered randomly, shock receipt represents a probabilistic sample of the time the rats were on the grid floor section of the chamber. Figure 3 presents the total number of shocks the rats received during the final 5 preshock and final 5 postshock days. Although 25 shocks per day were programmed, the rats only received, on average, a total of 2.8 shocks per day. The behavioral changes during the shock phase were successful at reducing shock receipt, but this relationship was strong in only 3 of the 4 rats (L95 was the exception). The animals received only 42% of the shocks they would have received without meal pattern changes. With respect to the schedule components the rats' greatest reduction in shock receipt was in the procurement component (33% of preshock). A similar reduction in shock receipt was found for the consumption component (36%). The rats reduced the number of shocks received to 46% of the preshock receipt rate for periods outside of either component. Because the rats spent differing amounts of time in each component, the percentage reduction in shock receipt is not directly comparable across components. It is interesting to note that although all rats reduced total shock receipt, there was great individual variability with respect to the particular component that was most affected. Additionally, the shocks that were avoided did not seem to be systematically related to the light cycle. The rats tended to receive more shocks and to eat more meals during the lights-off portion of the cycle and the animal (L95) that showed only a small reduction in total

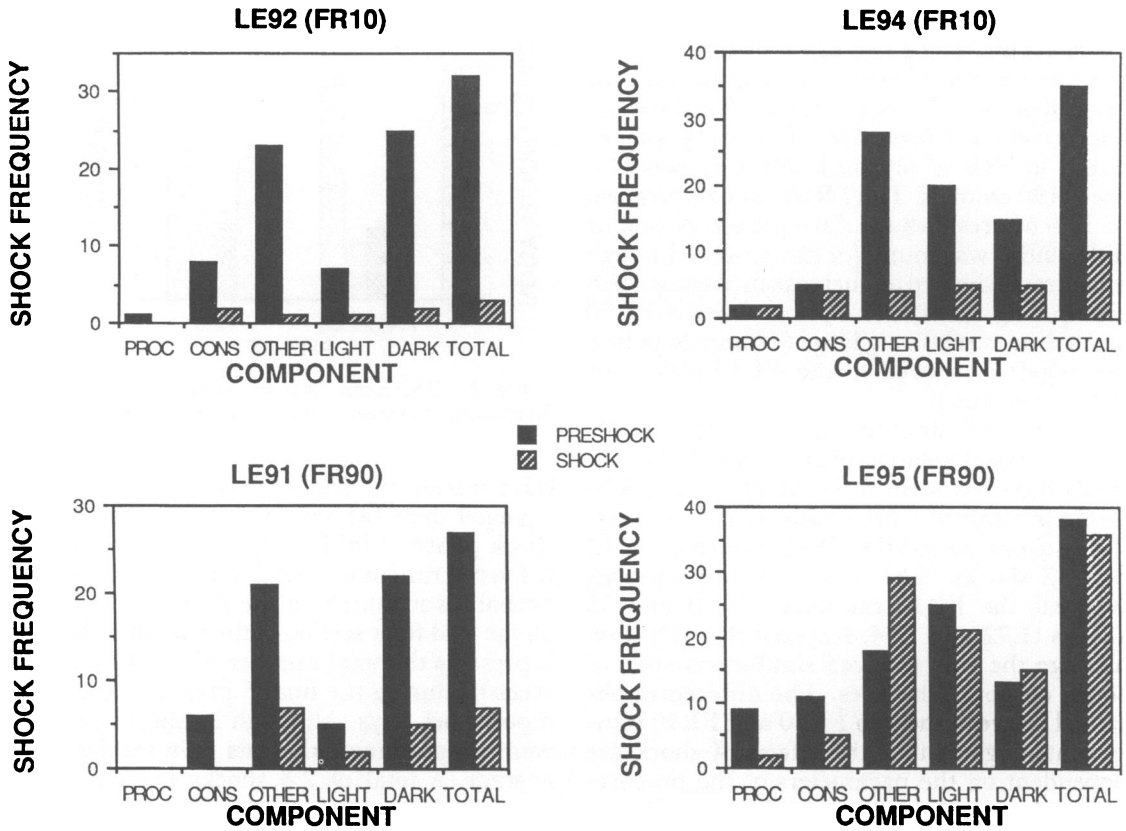


Fig. 3. The total number of shocks received (shock frequency) during the last 5 days of Experiment 3 for each rat. Preshock refers to the number of shocks the rat would have received had the shock generators been connected during the preshock phase. The data are presented separately for the procurement (proc) and consumption (cons) schedule components, as well as for shocks occurring outside of either schedule component (other). Shock frequency data, collapsed over schedule component but separated for light versus dark phase, are also presented.

shock frequency was the one that did not show a strongly nocturnal feeding and shock receipt pattern.

## GENERAL DISCUSSION

When rats were placed at risk of receiving an aversive stimulus during foraging for food, they modified their meal patterns in response to this risk. These meal pattern changes were not a simple suppression of food intake or a simple disruption in meal patterns. Nor were they nonspecific responses to stress. Rather, they seemed to reflect a reorganization of feeding patterns toward less frequent but larger meals. These changes in meal patterns were such that they reduced risk with little sacrifice of homeostatic balance, and they occurred only when shock was administered during foraging.

These meal pattern changes caused by increased risk bear a striking resemblance to the meal pattern changes caused by increasing the work requirement to obtain food (see Collier *et al.*, 1972). Optimal foraging theorists have suggested that the risk of predation may impose a "cost" on foraging (Krebs, 1980; Lima *et al.*, 1985). One difficulty for such analyses is a lack of a common currency or metric for respective scaling of appetitive to aversive costs. With the present procedures both types of costs (amount of work for a meal and the risk of shock associated with a meal) produce similar effects on meal patterns. Therefore, this "closed economy" procedure may be useful for the development of such a common currency. This could be done by determining the shock values that produce changes in meal patterning that are equivalent to specified amounts of work.

Such a quantitative analysis would be facilitated by the fact that all the relevant environmental events (shock, lever pressing, and food pellets) can easily be given quantitative values. The scaling of aversive events relative to appetitive events obtained in this manner could be compared to similar scales based on the use of alternative approaches such as the matching law (Farley & Fantino, 1978).

In addition to these meal pattern changes, food utilization seems to have become more efficient. This allowed the animal to reduce total daily food consumption without much of a compromise in body weight. The effect was most dramatic in Experiment 1, in which the rats ate less but gained weight during the shock phase. In Experiments 2 and 3, when shock was delivered during foraging weight remained stable despite reduced food intake. One way of expressing this efficiency difference is in terms of grams of food consumed per gram of body weight. Here, the means were .052 and .043 g consumed per gram body weight during the preshock and shock phases, respectively. A within-subject *t* test indicated that this was a reliable difference,  $t(8) = 3.5$ ,  $p < .005$ . Eight of the 9 animals examined showed a reduction in this quotient from the preshock to shock phase. A more meaningful impression for this .009-g effect is that on average the 9 rats gained 2 g from the preshock to shock phase while consuming about 2.6 g less per day during shock.

One may question whether these changes are truly adaptive. The results of Experiment 3 indicate that the cumulative changes in meal patterns and total consumption reduce shock receipt to 42% of what it would have been without these meal pattern changes. Most important, the pattern of changes allowed this reduction of risk without compromising body weight. Because the animals avoided shock it seems appropriate to consider the mechanism supporting this avoidance response. Decreasing meal frequency while concurrently increasing meal size is not simply avoidance of the grid floor; rather it is a redistribution of time between procurement and consumption. Additionally, it is difficult to see how simple punishment during consumption (see Figure 3) could result in longer meals. In choosing a larger meal, the rat is choosing to stay at risk immediately so that total time at risk is reduced. This suggests that the rat's behavior is

sensitive to the total duration of exposure to risk. Similarly, Hineline (1984) has suggested that both the "work requirements" and the "long-term" distribution of aversive events in a situation are determinants of avoidance behavior in that situation. In support of this argument, Mellitz, Hineline, Whitehouse, and Laurence (1983) found that rats preferred a response lever that both postponed shock and shortened an avoidance session over one that only postponed shock. In both the present experiment and the one conducted by Mellitz et al. (1983), the rat's behavior was controlled by the reduction in aversive consequences temporally discontinuous with shock.

We suggest that these behavioral responses to the risk of aversive stimulation represent an antipredator defensive response of the animal (see Fanselow & Lester, 1988). That is, we view our experiments as a model for the type of changes we might see if a potential prey's foraging area is associated with an increased risk of predation. Immediately, one question that may come to mind with regard to this laboratory simulation is the use of electric shock as a model of predation. Is there reason to believe that rats would treat such an artificial and arbitrary stimulus as they would a predator? We believe that there is support for this assumption on several grounds. For example, if we examine the rat's responses to innately recognized predators (e.g., a cat) we find a striking similarity of these responses to those generated by stimuli associated with electric shock. Rats will freeze to both cats (e.g., Blanchard & Blanchard, 1971; Bronstein & Hirsch, 1976; Satinder, 1976) and to stimuli associated with shock (e.g., Blanchard & Blanchard, 1969; Bolles & Collier, 1976; Fanselow, 1980). They will react with an endogenous opioid-mediated analgesic state to both cats (Lester & Fanselow, 1985) and shock-associated stimuli (e.g., Fanselow, 1984). Another line of supporting evidence is that certain brain lesions eliminate defensive behaviors to both cats and shock-associated stimuli (Blanchard & Blanchard, 1972), suggesting common underlying physiological mechanisms. Why should these disparate stimuli trigger a common mechanism? Perhaps it is because the animal's phylogenetic development provided it with a mechanism to deal with natural threats such as predators but no mechanism to deal with arbitrary threats. The animal, without a mechanism to deal with

such artificial situations, is limited to the mechanisms provided by its evolutionary history. This argument should be recognized as the basic assumption that underlies SSDR theory's account of laboratory avoidance tasks (Bolles, 1970).

The results of this laboratory simulation support suggestions based on field observations that foraging and meal patterns reflect predatory risk factors (e.g., Lima *et al.*, 1985). We make the assumption that if meal patterns reflect, in part, a strategy that evolved to minimize the risk of predation, then they should be plastic with respect to the level of risk factors. This plasticity assumption allows suggestions based on speculation about evolutionary function to be placed under empirical test. In general, the plasticity assumption states that if a given behavior evolved because it enhanced biological fitness in the face of a particular environmental factor, then that behavior is likely to be plastic in response to actual (or simulated) variations in that environmental factor. This is not to say that behavior must be plastic in response to manipulation of the environmental factors from which its evolutionary benefit derives. However, without such plasticity it may be impossible to subject such functional suggestions to empirical evaluation.

In this shock-associated foraging context we observed a rather subtle form of defensive behavior, a modification or reorganization of the animal's feeding pattern. However, in other shock-associated contexts much more dramatic forms of defensive behavior (e.g., freezing) are observed (e.g., Fanselow, 1980). One important consideration that arises from these observations is the determination of the environmental factor(s) that select between these different forms of defensive behavior. Knowledge of such factors would point to the response selection rules that govern species-specific defensive behaviors (see Fanselow, 1986, and Fanselow, Sigmundi, & Williams, 1987, for discussions of this issue). Elsewhere, we have proposed a predatory imminence model of response selection that argues that the rat's perception of the likelihood of a predatory encounter determines the topography of the SSDRs observed in a given situation (Fanselow & Lester, 1988). This model suggests that in shock-associated situations, shock density determines the rat's perception of predatory imminence and therefore the SSDR topogra-

phy that is observed. Under the conditions of the present experiments shock density was low ( $\leq 1.25$  per hour) and the subtle meal pattern reorganization that we call preencounter defense was observed. When shock density is greater (e.g., four to six per hour) the rat's behavior is dominated by the freezing response (e.g., Bolles & Riley, 1973) a behavior that we refer to as postencounter defense. Even greater shock densities are necessary to observe the types of behavior that are temporally proximal to physical contact with the predator (circa-strike defense). According to this view, the rat's position in a predator-prey sequence can be modeled by manipulations of shock density; through such manipulations we can learn about the performance rules that determine the selection of SSDRs. This view also suggests that different procedures will vary in their sensitivity in detecting behavioral changes to different densities of shock. The closed economy situation may be more sensitive to the very low shock densities ( $\leq 1.25$  per hour maximum) used here than the more common aversive control procedures that typically use higher shock densities (see Sidman, 1966, for a review).

Our separation of antipredator defenses into preencounter, postencounter, and circa-strike defenses may be contrasted with the primary versus secondary defense distinction that is made in the ethological literature on defense (e.g., Edmunds, 1974; Kruuk, 1972). According to Edmunds, primary defenses are those "which operate regardless of whether or not there is a predator in the vicinity" (p. 1). For example, a cryptically colored animal is cryptic regardless of whether or not a predator is there to detect it. Primary defense is considered to be passive; that is, the animal is either cryptic or not, and it expends no energy for crypsis. On the other hand, secondary defenses "operate during an encounter with a predator" (Edmunds, 1974, p. 136). Secondary defenses may be passive (e.g., the shell of a lobster) or they may be active (e.g., defensive fighting). Although the primary-secondary distinction is successful in describing the morphological adaptations that Edmunds was primarily concerned with, the distinction faces some problems in dealing with behavior. For example, it is not clear if one should classify the meal pattern reorganization reported here as a primary or secondary defense. These meal pattern changes operate to reduce the probability of a

predatory encounter but would be detrimental if a predator was actually in the vicinity (i.e., taking a prolonged meal in the face of a predator would not be functional). Therefore, they do not fit the definition of primary defenses that supposedly operate "regardless" of the presence of a predator. Nor do they fit the definition of secondary defenses that supposedly operate "during" a predatory encounter. It seems that a description of defensive behavior must take into account both the stimulus conditions necessary to produce the behavior (whether the predator is present or absent) and whether or not that behavior is functional in the presence of a predator. Both meal pattern reorganization and nest building are types of behaviors that the rat engages in when a predator is not present, whereas freezing occurs in the presence of a predator. Both freezing and nest building function during an encounter with a predator, whereas meal pattern changes reduce the likelihood of encountering a predator. Nest building and meal pattern changes seem to be active responses, but freezing may be a more passive response. Although all three types of behavior may serve a defensive function, it is difficult to classify any of them as primary or secondary with any absolute certainty. The great flexibility and range offered by defensive behavior cause problems for the simple categorization offered by the primary-secondary distinction. The predatory imminence model, by focusing on the stimulus conditions controlling particular defensive patterns and the way those behavior patterns interact with momentary predatory potential, offers a way of dealing with these issues.

## REFERENCES

- Blanchard, D. C., & Blanchard, R. J. (1972). Innate and conditioned reactions to threat in rats with amygdaloid lesions. *Journal of Comparative and Physiological Psychology*, **81**, 281-290.
- Blanchard, R. J., & Blanchard, D. C. (1969). Crouching as an index of fear. *Journal of Comparative and Physiological Psychology*, **67**, 370-375.
- Blanchard, R. J., & Blanchard, D. C. (1971). Defensive reactions in the albino rat. *Learning and Motivation*, **2**, 351-362.
- Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, **77**, 32-48.
- Bolles, R. C. (1975). *Theory of motivation* (2nd ed.). New York: Harper & Row.
- Bolles, R. C., & Collier, A. C. (1976). The effect of predictive cues on freezing in rats. *Animal Learning & Behavior*, **4**, 6-8.
- Bolles, R. C., & Riley, A. L. (1973). Freezing as an avoidance response: Another look at the operant-responder distinction. *Learning and Motivation*, **4**, 268-275.
- Bronstein, P. M., & Hirsch, S. M. (1976). Ontogeny of defensive reactions in Norway rats. *Journal of Comparative and Physiological Psychology*, **90**, 620-629.
- Collier, G. H. (1983). Life in a closed economy: The ecology of learning and motivation. In M. D. Zeiler & P. Harzem (Eds.), *Advances in analysis of behavior: Vol. 3. Biological factors in learning* (pp. 223-274). Chichester, England: Wiley.
- Collier, G. H., Hirsch, E., & Hamlin, P. H. (1972). The ecological determinants of reinforcement in the rat. *Physiology & Behavior*, **9**, 705-716.
- Collier, G. H., & Rovee-Collier, C. K. (1981). A comparative analysis of optimal foraging behavior: Laboratory simulations. In A. C. Kamil & T. D. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches* (pp. 39-76). New York: Garland STPM Press.
- Curio, E. (1976). *The ethology of predation*. Berlin: Springer-Verlag.
- Daan, S. (1981). Adaptive daily strategies in behavior. In J. Aschoff (Ed.), *Handbook of behavioral neurobiology: Vol. 4. Biological rhythms* (pp. 275-298). New York: Plenum Press.
- Edmunds, M. (1974). *Defence in animals: A survey of anti-predator defences*. Burnt Mills, England: Longman.
- Fanselow, M. S. (1980). Conditional and unconditional components of post-shock freezing. *Pavlovian Journal of Biological Sciences*, **15**, 177-182.
- Fanselow, M. S. (1984). Shock-induced analgesia on the formalin test: Effects of shock severity, naloxone, hypophysectomy, and associative variables. *Behavioral Neuroscience*, **98**, 79-95.
- Fanselow, M. S. (1986). Associative vs topographical accounts of the immediate shock-freezing deficit in rats: Implications for the response selection rules governing species-specific defensive reactions. *Learning and Motivation*, **17**, 16-39.
- Fanselow, M. S., & Lester, L. S. (1988). A functional behavioristic approach to aversively motivated behavior: Predatory imminence as a determinant of the topography of defensive behavior. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning* (pp. 185-211). Hillsdale, NJ: Erlbaum.
- Fanselow, M. S., Sigmundi, R. A., & Williams, J. L. (1987). Response selection and the hierarchical organization of species-specific defense reactions: The relationship between freezing, flight, and defensive burying. *Psychological Record*, **37**, 381-386.
- Farley, J., & Fantino, E. (1978). The symmetrical law of effect and the matching relation in choice behavior. *Journal of the Experimental Analysis of Behavior*, **29**, 37-60.
- Gunn, K. P. (1983). Quantification of rats' behavior during reinforcement periods. *Journal of the Experimental Analysis of Behavior*, **39**, 457-464.
- Hineline, P. H. (1984). Aversive control: A separate domain? *Journal of the Experimental Analysis of Behavior*, **42**, 495-509.
- Hursh, S. R. (1980). Economic concepts for the analysis

- of behavior. *Journal of the Experimental Analysis of Behavior*, **34**, 219–238.
- Hursh, S. R. (1984). Behavioral economics. *Journal of the Experimental Analysis of Behavior*, **42**, 435–452.
- Krebs, J. R. (1980). Optimal foraging, predation risk and territory defence. *Ardea*, **68**, 83–90.
- Krebs, J. R., & Davies, N. B. (Eds.). (1981). *Behavioural ecology*. Sunderland, MA: Sinauer.
- Kruuk, H. (1972). *The spotted hyena: A study of predation and social behavior*. Chicago: University of Chicago Press.
- Lester, L. S., & Fanselow, M. S. (1985). Exposure to a cat produces opioid analgesia in rats. *Behavioral Neuroscience*, **99**, 756–759.
- Lima, S. L., Valone, T. J., & Caraco, T. (1985). Foraging-efficiency—predation-risk trade-off in the grey squirrel. *Animal Behaviour*, **33**, 155–165.
- MacArthur, R. H., & Pianka, E. R. (1966). On the optimum use of a patchy environment. *American Naturalist*, **100**, 603–609.
- Mellgren, R. L., Misasi, L., & Brown, S. W. (1984). Optimal foraging theory: Prey density and travel requirements in *Rattus norvegicus*. *Journal of Comparative Psychology*, **98**, 142–153.
- Mellitz, M., Hineline, P. N., Whitehouse, W. G., & Laurence, M. T. (1983). Duration-reduction of avoidance sessions as negative reinforcement. *Journal of the Experimental Analysis of Behavior*, **40**, 57–67.
- Rashotte, M. E., & O'Connell, J. M. (1986). Pigeons' reactivity to food and to Pavlovian signals for food in a closed economy: Effects of feeding time and signal reliability. *Journal of Experimental Psychology: Animal Behavior Processes*, **12**, 235–247.
- Satinder, K. P. (1976). Reactions of selectively bred strains of rats to a cat. *Animal Learning & Behavior*, **4**, 172–176.
- Sidman, M. (1966). Avoidance behavior. In W. K. Honig (Ed.), *Operant behavior: Areas of research and application* (pp. 448–498). New York: Appleton-Century-Crofts.
- Snyderman, M. (1983). Optimal prey selection: Partial selection, delay of reinforcement and self control. *Behaviour Analysis Letters*, **3**, 131–147.
- Solomon, R. L., Kamin, L. J., & Wynne, L. C. (1953). Traumatic avoidance learning: The outcomes with several extinction procedures with dogs. *Journal of Abnormal and Social Psychology*, **48**, 291–302.
- Solomon, R. L., & Wynne, L. C. (1953). Traumatic avoidance learning: Acquisition in normal dogs. *Psychological Monographs*, **67** (4, Whole No. 354), 1–19.
- Timberlake, W., & Peden, B. F. (1987). On the distinction between open and closed economies. *Journal of the Experimental Analysis of Behavior*, **48**, 35–60.
- Vilchez, C. A., & Echave Llanos, J. M. (1971). Circadian rhythm in the feeding activity of *Oxymycterus rutilans*: Role played by light and food availability. *Journal of Interdisciplinary Cycle Research*, **2**, 73–77.

Received January 4, 1988

Final acceptance July 13, 1988