PREDATOR-PREY INTERACTIONS: VULNERABILITY OF ESTROUS MICE TO LEAST WEASELS

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ABSTRACT

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This study addressed the theory that predators can intercept intraspecific reproductive cuees from the prey, specifically if estrous female prairie deer mice (Peromyscus maniculatus bairdi) are more vulnerable to least weasel (Mustela nivalis) The study consisted of four experiments. In the first experiment the behavior and activity patterns of estrous and diestrous mice were observed in out door arenas. Estrous mice became activity earlier, were more active while out of the nest box, more exploratory, and crossed open areas more frequently than diestrous mice. The second and third experiments tested whether the weasels preferred estrous or diestrous urine scents. In the second experiment 12 weasels were tested in a Y-maze. All 12 weasels displayed a selective preference for estrous urine, as all 12 choose the estrous urine on their first trial and all selected estrous urine on the majority of their trials. In the thrid experiment nine weasels were tested in a 3-chambered T-box. In this experiment the weasels sampled the urine only if they entered the compartment that contained either the estrous or diestrous urine. The amount of time the weasel spent in a urine compartment during a two hr. test was recorded and each weasel was tested five times. The weasels spent less than 2.0% of the available time in a urine compartment and displayed no preference. In the fourth experiment the weasels were allowed to hunt a pair of mice. The pair of mice were either an estrous and diestrous mouse or an estrous and a diestrous mouse that had been painted with estrous urine. The results of the hunt with the estrous and normal diestrous mouse demonstrated that the estrous mice were significantly more vulnerable to weasel predation. The results from the the second type of hunt revealed that the scent of the females was the major factor in the weasel's ability to locate the females. Further observations revealed that the estrous female's behavior increased the weasel's abiltiy to capture the females. The results from this study support the theory that intraspecific reproductive cues can be intercepted by predators and used to facilate their predatory success.

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INTRODUCTION

I hypothesize that estrous mammalian prey, in particular rodents, are more susceptible to predation than diestrous females. Estrous cows are disproportionately parasitized by vampire bats, but the reason for this is as yet undetermined, unless their location at the edge of the herds and their increased activity at night makes them more susceptable to nocturnal vampire bat attacks (Turner 1975). Madsion (1978), while studying meadow vole populations in New York, observed four predatory acts by garter snakes, of these two acts were on adult males while the other two were on adult females that had just had litters. He speculated that the scents associated with post-partum estrus resulted in the location of the females voles, whose increased aggressive behavior lead to their capture. These studies suggest that increased vulnerability may be due to the prey's odor, behavior, or a combination of these factors.

Predators are known to use a variety of cues to facilitate the location of prey, including the interception of intraspecific reproductive communications. Predatory bats locate frogs by auditory cues arising from their chorusing (Tuttle & Ryan 1981). Parasitic flies locate and parasitize male crickets while they are chirpping to attract mates (Cade 1976). Predatory fireflies trail and hawk other species of fireflies in response to their flashing visual signals (Lloyd 1965). Finally, polar bears are attracted to the odors of human menstrual blood (Cushing 1983). This attraction is not of a predatory nature, but it does demonstrate that one species can be attracted to odors associated with reproduction in another species.

Along with the use of intraspecific signals to facilitate prey capture predators may also increase their success by preying on individuals that exhibit differential behavior leading to increased vulnerability. Metzgar (1967) working with white-footed mice (_Peromyscus leucopus_), and Ambrose (1975) with meadow voles (_Microtus pennsylvanicus_), found that transients were more susceptible to owl predation than residents. They hypothesized that the increased vulnerability of the transients resulted from increased activity and a lack of familiarity with the terrain. If experienced male rodents can differentiate and prefer the scent of estrous females (Carr et al. 1965, Lydell & Doty 1972), and estrous rodents are more active than diestrous females (Wang 1923, Finger 1961, Richards 1966), then predators can increase their success by intercepting intraspecific signals, and by taking advantage of the increased activity of the estrous mice.

To investigate the possiblity that estrous females are more vulnerable to predation I chose the prairie deer mouse (_Peromyscus maniculatus bairdi_) as the prey and the least weasel (_Mustela nivalis_) as the predator. This particular predator/prey system was selected for several reasons. First, estrous mice display an early onset of activity and an increase in wheel running activity at the initiation of estrus (Stinson 1952). Second, there are indications that males can differentiate and prefer odors of estrous mice (Moore 1962, Doty 1972), suggesting that olfaction is an important component of their reproduction. Finally, these mice are known to be preyed upon by least weasels (Polderboer 1942). Least weasels were used because of their size, the ability to maintain them in the laboratory, and the fact that they are considered to be specialized predators (Rosenzweig 1966). A small specialist, such as the least weasel, would be the most likely candidate to detect estrous mice because their high metabolic rate (Iversen 1972, Moors 1977) might necessitate using all possible cues that could increase their predatory effeciency.

This study investigated three problems with four experiments. The first problem examined was the behavioral patterns and activities of estrous and diestrous mice under natural conditions (Experiment 1). The second problem was to see if least weasels could differentiate between the odors of estrous and diestrous mice and if they could, to determine if the weasels displayed any preference for one odor or the other. In Experiment 2 a Y-maze was used to allowed the weasels to choose between estrous and diestrous odors presented simultaneously at the ends of arms of the maze. Experiment 3 tested the weasels in a 3-compartment T-box, which enabled a weasel to smell estrous and diestrous odors sequentially, rather than simultaneously, and to come into contact with the urine by entering a separate compartment. This was done to determine if the weasels would prefer to remain in the presence of one type of urine once they had entered a compartment, as opposed to selecting between two odors as they moved down the Y-maze. Once the behavioral differences of the mice were established and the predator's response to the two scents was known, then the final problem was to determine if these factors influenced the vulnerability of the mice. In Experiment 4, the weasels were allowed to hunt both estrous and diestrous mice to test if estrous mice were more vulnerable to predation. Also by manipulating the scent of the diestrous mice, i.e. making them smell like estrous females, it should be possible to evaluate the relationship between prey odors and behavior in the predatory success of the weasels.

LITERATURE REVIEW

Mustela nivalis, the least weasel, is the smallest living carnivore, ranging in size from 150 mm to 270 mm (Hall 1951), and is holarctic in distribution (Ellerman & Morrison-Scott 1966, Hall & Kelson 1959). In North America it shares the common name of weasel with two other species, *M. erminea*, the short-tailed weasel or stoat, and *M. frenata*, the long-tailed weasel. The three species are morphologically similar, varying mainly in size, and their ranges widely overlap. All three display a change in coat color from brown to white during the early to late fall and this change is brought about by decreasing day length (Flintoff 1933). Least weasels appear to maintain homeranges (Polderboer 1942, Erlinge 1974, King 1975), with the males having larger ranges than the females (King 1975). Male ranges average 2 ha, while the females average around 1.4 ha. Least weasels usually produce one to two litters a year with an average of 4-5 young per litter (Hall 1951). There is a major difference between the reproduction of least weasel and other mustelids in that most members of the genus *Mustela* display some form of delayed implantation, but least weasels do not (Heidt et al. 1968). It has been suggested that the lack of delayed implantation facilitates the least weasel in reproducing in response to increased prey densities (King 1975, King & Moors 1979, Simms 1979).

Food habits

Eibl-Eibesfeldt (1963) and Gossow (1970) have described the killing technique of least weasels in captivity. The weasel grabs muriod prey with it's mouth and then wraps it's legs and body around the victim. At this point it bites repeatedly at the base of the skull or near the ear. If more than one prey is present then the weasel will attempt to capture as many as possible, by quickly biting one and then moving onto another. Then it will return and finish the ones it has disabled. These laboratory observations are comfirmed by free-ranging weasels, which regularly cache food (Criddle & Criddle 1925). It may be necessary for the animal to obtain food whenever possible in case there should be a prolonged period of scarity as they have very high metabolic demands (Iversen 1972).

Juvenile animals begin to respond to prey at about 35 days of age when they begin to make mock attacks on food provided by the female (Heidt 1972). At 55 days of age juvenile weasels are first capable of killing small prey. Heidt (1972) indicated that while there is no difference in the adult ability to capture prey, learning does appear to play a role in the development of the predatory behavior of the juveniles. Juveniles that are raised by the female and allowed to play with their siblings develop efficient predatory techniques sooner than do juveniles raised alone. As the juveniles mature the animals will stay together as a family unit for several months. In general, the adults are solitary predators, but there is one report of two adult weasels cooperating in an attempt to capture an adult hare (Bullock & Pickering 1982).

M. nivalis is considered to be a specialized predator (Rosenzweig 1966, Day 1968, Moors 1975), feeding predominantly on small rodents. However, their diet is not limited to rodents and Table 1 contains a list of known prey items. This table is compiled from data on weasels in England and Europe, as there are only a few incomplete studies on the diets of least weasels in North America (Polderboer 1942, MacLean et al. 1974). In these areas large numbers of weasels are obtainable because at large English estates weasels are considered to be vermin and are regularly trapped or shot by the grounds keepers, thereby supplying investigators with large numbers of animals. In North America the species known to be eaten by least weasels include Lemmus spp., Peromyscus spp., and Reithrodontomys spp. (Polderboer 1942, Maclean et al. 1974). It is unfortunate that so little is known about the food habits of North American weasels in comparison to its European counterpart because the European is 1.5 to 2 times larger than the North American subspecies and it may therefore be difficult to generalize from the results of English studies. This area of investigation deserves further attention.

Least weasels are not only considered specialists on rodents, but they are also considered to be specialized to fed on Microtus spp., voles. This contention appears to have become fixed in much of the literature, even though evidence to the contrary exists. Numerous articles state or imply that weasels are Microtus specialists (Swenk 1926, Hatt 1940, Criddle 1947, Day 1968,

Table 1. Types of prey consumed by weasels.

Prey	Prey
Rodentia	Insectivora
Apodemus	*Sorex*
Arvicola	*Talpa*
Clethrionomys	Aves
Micromys	Passerine
Microtus	Galliforme
Mus	Ralliforme
Muscardinus	Bird eggs
Rattus	Reptilia
Chiroptera	*Lacerta*
Lagomorpha	Invertebrates

Fitzgerald 1972, King 1975). This contention is so strong that when Walker (1972) discovered that over 50 % of the diet consisted of Apodemus sylvaticus he felt obligated to explain this unlikely result. The basic logic behind this assumption has been that the size and shape of M. nivalis is ideal for moving through tunnels and into the nests of voles, even into subterranean nests. However, their form is basically the the same as other mustelids except they are smaller and the ability to move into nests and underground tunnels would be just as advantageous when hunting other prey. For example, weasels have been observed to use mole tunnels (Ellison 1947). Also, several studies have not found voles to be the predominant prey (Polderboer 1942, Walker 1972) and King (1975) even while saying that they were specialized for voles found, that in certain locals, Apedomus sylvaticus was the predominant prey species. Goszczynski (1977) in an extensive study on the effects of predation on Microtus arvalis correlated the percentage of voles taken by various predators and classified them as to whether or not they specialized on voles. He found that barn owls, foxes, cats, and martins specialized in vole predation, but not Mustela nivalis. Also, an examination of Table 1 indicates that there is substantial variety in the prey of least weasels, but variety alone does not eliminate the possiblity that a predator specializes on one prey.

Instead of considering the least weasel as a Microtus specialist it should be classified as an opportunistic predator with a limited number of potential food items due to its size. Erlinge (1974) found that when the results from live trapping small mammals were compared with weasel fecal and stomach samples, the weasels were consuming prey proportional to the local densities, although he did note that weasels appeared to avoid shrews. He took this one step further and presented weasels in enclosures with a variety of species at various densities and again found that rather than specializing the mammals were captured in the proportions present. Trapper's (1976) study suggests the opportunistic side of these predators because he found that in the early summer when gamebird chicks were present that they made up a large portion of the diet. Dunn (1977) showed that during seasons when rodent populations were low, the weasels would switch and take significantly more tits, *Parus* spp., and Trapper (1979) found this to be true for birds in general. However, least weasels still depend upon rodents and display rapid population declines during low rodent populations, especially when compared to competitors such as *M. erminea* (King & Moors 1979).

Physiological Constraints

The size, shape, and the physiology of the least weasel influence or constrain the habitats in which it can occur, although these limitations are probably not as strict for the English/European weasel because it is substantially larger than the North American version. Due to the elongated shape of mustelids they have a greater rate of heat loss than more compact mammals of the same weight (Moors 1977). The need to be in areas with high densities of prey, such as fields which often support large rodent populations may well be influenced by their high metabolic rates.

Iversen (1972) found that taking size into account that least weasels have a proportionally higher basal metabolic rate than, other mammals, and even higher than other mustelids, such as *M. frenata* and *M. vison*. Therefore, least weasels require proportionally greater amounts of food. This probably explains why such a small animal has a fairly large home range (Polderboer 1942) and only two or three may be found in area with a high density of prey (Golley 1960).

Competition

Rosenzweig (1966) postulated that since all three species of North American weasels can co-exist that this co-existence could only be maintained through differences in the types and variety of prey items. At first this seems questionable if one examines food habit studies, as all three have fairly similar diets (Hamilton 1933, Quick 1944, 1951, Simms 1979). However, in the areas where they overlap there does appear to be some differences in the diet, i. e., stoats (*M. erminea*) eats more lagomorphs when it co-exists with *M. nivalis* (King & Moors 1979). Least weasels are capable of entering nests and runways of small rodents and would therefore appear to be more·effiecent in exploiting these animals. Reproductively the least weasel is adapted to take advantage of annual increases in prey density as in a good year they can produce more litters that year, while delayed implantation prevents the other species of weasels from responding to the sudden increase. However, King and Moors (1979) have suggested that the stoat has the superior edge, because when they examined island populations either both species were present or only stoats were on the islands. Competition may also be reduced through differential use of habitats. The least weasel seems to be restricted to fields and meadows, while the other weasels hunt in fields and forests. If one examines the subspecies of *M. erminea* it suggests that competition between the species may be avoided or reduced in the manner suggested by Rosenzweig. There is a subspecies of short-tailed weasel that is the same size as the least weasel and appears to exploit prey in the same way (Fitzgerald 1972, MacLean et al. 1974, Simms 1979), but this subspecies is found in extreme environments, such as high altitudes or northern latitudes, and does not co-occur with *M nivalis*. When the two species overlap *M. erminea* is always larger.

Predation

As is often the case the predator is prey for other species. The major predators of least weasels appear to be raptors, such as owls and hawks (Handley 1949, Kulczycki 1964, Emmett et al. 1972, Mikkola 1972). Powell (1982) has suggested that avian predation pressure is the reason why least weasels lack a black tip on their tail. He demonstrated using models that a raptor is drawn to the black tip and in being drawn there often missed the models body. The black tip would be disadvantagous to a least weasel because the tail is so short that the raptor would strike the weasels body.

Least weasel are also probably preyed upon by other mustelids and carnivores, but there is little evidence to support this, although there is one finding of least weasel remains in one *M. frenata* scat (Polderboer et al. 1941). Possibly least weasels are restricted to grassy fields because of the amount of cover that they provide as opposed to the openness of many forests. It has also been suggested that predator avoidance is one of the reasons that weasels turn white in the winter to blend in with the snow.

CHAPTER 1

EXPERIMENT 1

INTRODUCTION

Studies in which running wheels were used to monitor activity in female rodents have shown that there is an increase in activity and a phase advance in the circadian rhythm of activity with the onset of estrus. (*Rattus norvegicus*: Wang, 1923; Richter, 1927; *Mesocricetus auratus*: Richards, 1966; Morin et al., 1977; *Peromyscus*: Stinson, 1952). Barnett (1963) criticized the use of running wheels as they may enhance activity. However, using stationary cages Finger (1961) and Schenck et al. (1978) demonstrated that rats still display an increase in activity when in estrus.

Although these laboratory studies indicate that a shortened period of circadian rhythm and increased activity do occur with the onset of estrus, there are no studies which attempt to deal with the activity of estrous females under more natural conditions, although Lisk et al. (1983) has described some activities associated with reproduction in golden hamsters under seminatural conditions. Activities or behaviors that may differ between estrous and diestrous mice include emergence times, movement, and/or exploratory behavior. In order to investigate the differences between estrous and diestrous mice I compared activity patterns of estrous and diestrous prairie deer mice, *Peromyscus maniculatus bairdi*, in outdoor arenas.

METHODS

Fifty-five adult female prairie deer mice livetrapped during the summer of 1981 from the Rose Lake Wildlife Research Area in Clinton county Michigan were housed individually, supplied ad lib. with Wayne breeder blocks and water, and maintained on a 15L:9D light cycle. The mice were lavaged daily to obtain vaginal smears to determine the periodicity of individual estrous cycles and the phase of the subject. A total of 46 of these mice was used, 23 were obsevered in estrus and 23 in diestrus and all mice were run within 30 days of capture.

On a test day an estrous and diestrous mouse were selected and tagged with yellow or orange fluorescent eartags. Approximately 5 h before sunset (EDST) a mouse was individually enclosed in a 10.2 x 10.2 x 10.2 cm wooden nest box (with a 3.8 cm diameter entrance). The nest boxes contained bedding from the mouse's cage and a supply of food. Food was supplied in order to eliminate food search as a cause for leaving the nest box. The nest boxes containing the mice were transported, approximately two kilometers south of Michigan State University, to the outdoor testing arenas, and each nest box was placed in the center of one of two adjacent arenas (1.83 x 1.83 m). Water was placed beside the opening to the nest box. The floor of each arena consisted of a natural plant cover approximately 2.54 cm deep and the aluminum walls were 0.76 m high. The walls were marked and numbered at 30.5 cm intervals with fluorescent paint to create a 36 square visual grid. Half an hour before sunset a

Coleman Charger SP lantern equipped with an ultraviolet tube was placed at one corner of each arena. The ultraviolet lights enabled me to use the grid system and see the eartags during the mouse's nocturnal forays. At sunset the nest boxes were manually opened, permitting the mice to leave the nest. Observations were made for a 7-h period after sunset, after which the mice were collected and returned to the laboratory where another vaginal smear was taken to confirm their phase in the estrous cycle. The results of this second lavage confirmed that all mice were in the expected phase.

Data were collected using a time-scan with a record taken every 2 minutes after the mouse emerged. A mouse was considered to have become active only if it remained out for a minimum of two full minutes without re-entering the nest box. Data recorded were: time of emergence, number of emergences before becoming active, location at 2-min intervals, whether or not the subject moved between readings, and the activity of the mouse. Activity was divided into three categories: stationary, active within a single grid, or transitory (moving through a grid or grids). Most data were converted to percentages and arcsin transformed for analysis. Observer reliability was checked twice for activity classification and location, with a correlation of 92% and 95% on the two evenings. Sample sizes varied, because of difficulties experienced with the fluorescent marking technique during the first few runs. However, some data from these tests were obtained and used, but these animals were not tested again.

RESULTS

Emergence

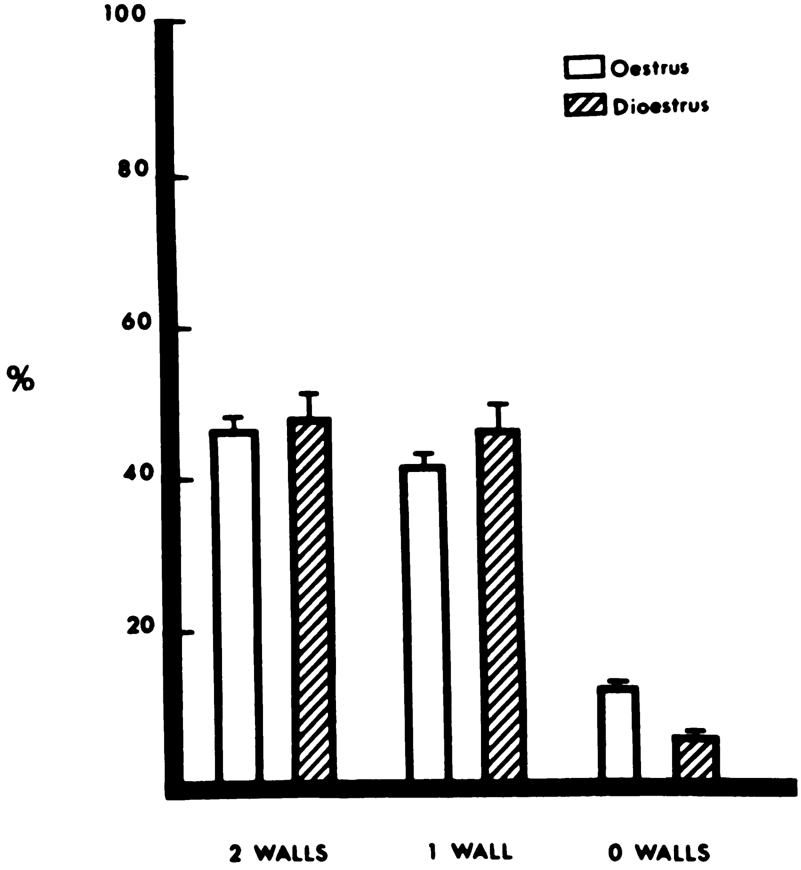
Estrous mice left the nest box first on nine of 19 trials ($P > 0.30$). However, once out, estrous mice were more likely to remain out for at least 2 min (become active) than were diestrous mice. The number of exits before becoming active was 1.1 ± 0.1 ($X \pm SD$, $n = 18$) for estrous mice and 2.5 ± 2.1 ($n = 14$) for diestrous mice (Mann-Whitney, $t = 3.25$, d.f. = 30, $P < 0.01$). (A t statistic is used instead of a U if some of the values are the same, Sokal and Rohlf, 1981). In 13 of 19 tests estrous mice became active first; on one test the mice became active simultaneously (paired Sign test, $P < 0.05$). The mean latency to begin activity was 172 ± 26.9 min ($X \pm SE$, $n = 23$) for estrous mice and 249 ± 28.6 min ($n = 23$) for diestrous mice (Mann-Whitney, $t = 2.32$, d.f. = 44, $P < 0.05$), this suggests that estrous mice were experiencing a phase advance in their circadian rhythm.

Activity Patterns and Space Use

The estrous mice not only emerged sooner, but spent more time in the arena. Estrous mice spent an average of 66.4 min longer out in the arena than the diestrous mice, 187 ± 25.5 min ($X \pm SE$, $n = 19$) versus 121 ± 26.4 min ($n = 20$) ($t = 1.803$, d.f. = 37, $P < 0.05$). Both estrous and diestrous mice often returned to their nest boxes during the 7-h period, possibly to feed and/or rest.

After becoming active the activity patterns of estrous females differed from diestrous females in several respects. Estrous mice moved frequently, remaining in the same grid from one 2-min interval to the next an average of 34.8% of the time as compared to 63.8% for the diestrous animals (Mann-Whitney U, $U = 42$, $P < 0.005$). The diestrous females were stationary 68.1 ± 2.8% (X ± SE, $n = 13$) of the scans, whereas the estrous animals were stationary 39.2 ± 3.9% ($n = 15$) of the scans (arcsin transformation, $t = 6.29$, d.f. = 26, $P < 0.001$). Estrous mice were active within a single grid square 39.4 ± 2.8% ($n = 15$) as compared to 24.6 ± 2.3% ($n = 13$) for diestrous mice ($t = 4.15$, d.f. = 26, $P < 0.001$), and displayed greater mobility and exploratory behavior as they were transitory on 21.3 ± 1.5% ($n = 15$)of scans whereas the diestrous mice were transitory 7.2% ± 1.0% ($n = 13$) of the scans ($t = 7.75$, d.f. = 26, $P < 0.001$). The increased exploratory behavior of the estrous females was indicated by the location of the animals within the arenas (Figure 2) The grids were classified as having two walls (corner), one wall, or no walls. Comparison of the percentage of scans that estrous mice were found in the two walls and one wall categories versus diestrous mice revealed that there was no difference in the use of these areas between the two types of females (Figure 2, arcsin transformation, $t = 0.022$, d.f. = 26, $P > 0.9$ and $t = 0.78$, d.f.= 26, $P > 0.4$ NS). However, estrous mice were located in the no walls grids on 12.1 ± 1.5% (X ± SE, $n = 15$) of the scans whereas the diestrous mice were found there on 5.6 ± 1.3% ($n = 13$) of the scans (Figure 2, $t = 3.15$, d.f.= 26, $P < 0.01$).

Figure 1. The location of estrous and diestrous mice, in percent, within grid types.



Trial vs. Estrous Cycle

Eleven animals were tested in both phases of their estrous cycle, six were in estrus while five were in diestrus on their first trial. A comparison of the females that were observed first in estrus versus those tested when in estrus on their second trial and the same comparison between diestrus first and second should reveal any effects on the mice due to trials, as opposed to phase of the estrous cycle. These comparisons are contained in Table 2. There were no differences in all categories except one. The only apparent effect was on diestrus mice in that on the second trial they spent significantly more time out of their nest box in the arena ($t=2.38$, $df=9$, $P<0.05$). Since there is no difference in the latency to begin activity this difference must be due to the diestrous mice returning to their nests less often or at least spending less time in the nest box when they returned. While the second trial diestrous mice spent more time out in the arena there was no change in the use of the arena nor their activities while they were out. Therefore, it appears that trial experience has little effect on the mouses' behavior or activity while out in the arena, but as has already been demonstrated that a mouse's performance is dependent upon which phase of the estrous cycle it is in. However, when Spearman rank correlation is performed on the results of latency to emerge and activity patterns of the mice that were tested twice in terms of estrus and diestrus, ignoring trial order, there was a significant correlation ($R=0.661$, $n=11$, $P<0.05$ and $R=0.891$, $n=11$, $P<0.01$ respectively for latency and activity patterns). This indicates

Table 2. Comparison of 1st trial estrous females vs. 2nd trial estrous females and 1st trial diestrous mice vs. 2nd trial diestrous females.

	Estrus					Diestrus				
	1st Trial		2nd Trial			1st Trial		2nd Trial		
Activity	N	Mean	N	Mean		N	Mean	N	Mean	
Latency	18	176 min	5	161 min	NS**	17	252 min	6	240.5 min	NS**
Total time	11	41.0 %	4	43.8 %	NS*	9	25.9 %	4	35.9 %	P<0.05
Stationary	11	33.9 %	4	31.9 %	NS*	9	55.2 %	4	57.1 %	NS*
Local	11	39.2 %	4	38.6 %	NS*	9	29.1 %	4	30.2 %	NS*
Transitory	11	26.9 %	4	29.5 %	NS*	9	15.7 %	4	12.7 %	NS*
Location										
2 wall	11	45.9 %	4	47.8 %	NS*	9	49.1 %	4	45.8 %	NS*
1 wall	11	42.8 %	4	37.9 %	NS*	9	45.9 %	4	47.3 %	NS*
0 wall	11	11.3 %	4	14.3 %	NS*	9	5.0 %	4	6.9 %	NS*

* t-test

** Mann-Whitney

that the variation for the total results was due in part to individual variation, in that a more active estrous mouse within the estrous group was also a more active diestrous mouse.

DISCUSSION

The results of this study support previous laboratory studies, using running wheels, that have shown an increase in activity and an early onset of activity associated with estrus (Morin et al., 1977, Fitzgerald and Zucker, 1976, Alleva, et al., 1971, Wang, 1923). Increased activity and phase advance in the circadian rhythm appears to be the result of increased estradiol levels (Morin et al., 1977, Morin, 1980). These effects of estradiol levels combined with the fact that food was provided in sufficient quantities to eliminate food search as a cause of increased activity, the behavior of the mice was most likely associated with reproductive effort. These behavior patterns could serve several functions. The females may be moving about and depositing scent to advertise their condition and attract a mate, as has been observed in golden hamsters (Lisk et al., 1983). This type of condition may exist in meadow voles (*Microtus pennsylvanicus*) where there is an increase in the number of male territories which overlap a female's territory at the time of estrus (Madison, 1980*a*; 1980*b*). Also, Howard (1949) noted that prairie deer mice adults are occasionally found in groups of several males to a female during the breeding season.

Home ranges of male and female Peromyscus overlap, but not with members of the same sex, especially females (Howard, 1949; Terman, 1961; Metzgar, 1971). A female whose home range overlaps several males' home ranges may not only be advertising her condition by depositing pheromones, but may be actively searching for a mate. If Peromyscus displays the same type of localized increase in male per female density, as observed in meadow voles where the males actively move into an estrous female's home range, (Madison, 1980a; 1980 b), then by searching for and encountering males the female could increase the number of potential mates from which to select. Even without a change in spatial organization the female, by her increased time active and her exploratory behavior, could increase her chances of encountering a mate rather than just waiting for the male to detect her.

In conclusion, this study supports the various laboratory studies that showed an increase in activity and a phase advance in the circadian rhythm with the onset of estrus. When in estrus deer mice emerged earlier, spent more time out of their nest box, and showed increased activity and increased movement in open areas. Finally, whether the females are advertising, searching for mates, or a combination of the two the early onset of activity suggests or predicts that males should become active before the females. This should occur if a male is to increase his chances of finding and mating with a receptive female.

CHAPTER 2

EXPERIMENT 2

INTRODUCTION

Some predators are known to locate or identify prey by using auditory, chemical, or visual light cues emitted by the prey (Lloyd 1965; Gove & Burghardt 1975; Tuttle and Ryan 1981). These abilities indicate that predators are able to detect prey by intercepting intraspecific cues. Such cues may even include reproductive condition: male crickets vocalizing for females suffer increased parasitism (Cade 1979) and polar bears (Ursus maritimus) are attracted to human menstrual odors (Cushing 1983). Although the last study does not suggest that the attraction is of a predatory nature it does demonstrate that one species can be attracted to odors associated with another species' reproduction. I investigated the possibility that the sexual odors of prey can be detected by a predator. This question was studied by determining if least weasels (Mustela nivalis) would select estrous urine over diestrous urine from a known prey species, the praire deer mouse (Peromyscus maniculatus bairdi).

METHODS

Twenty-four hours prior to testing a weasel was placed in a 56 x 56 x 23 cm wooden nest box. The end opposite the Plexiglas Y-maze was open and covered with 0.64 cm mesh hardware cloth, this allowed for an air flow from the maze through the nest box. The main tunnel and arms of the Y-maze were each 61 cm long, with internal dimensions of 10.2 x 10.2 x 10.2 cm. At the end of each arm was a small fan with a displacement of 0.71 m^3/min. A gate separated the maze from the nest box.

At the start of a trial the fans were started and followed immediately by the removal of the gate, which permitted the weasel to enter the maze. The weasel was allowed five minutes to chose an arm. A choice was considered to have been made when the weasel reached the end of one of the arms. If the weasel did not choose an arm within the allotted amount of time, then the trial was classified as 'no choice'. Control and treatment trials were the same except that urine was present during treatment trials, whereas the arms were empty during control trials. Estrous urine was obtained from 20 different females that had been implanted with silastic implants of estradiol benzoate. These females were housed individually, but placed in groups of four in a cage over heavy mineral oil for a 20-hr period. At the end of this time the urine was collected and quick frozen for later use and then the females were separated. Silastic implants were used to facilitate the collection of sufficient urine. Diestrous urine was collected from untreated females that were placed in groups of four until all the females were in diestrus, and then their urine was collected. Vaginal lavages were performed on these mice to make sure that they were in the proper phase of their cycle. During a treatment trial 0.1-ml sample of estrous and diestrous urine were placed in separate small petri dishes and then placed at the end of each arm. The arm that the estrous urine was placed in was selected at random and the diestrous urine was placed in the opposite arm. Each weasel participated in eight control and eight treatment trials, which were performed in four sets, each of which consisted of two control and two treatment trials. Each weasel performed only one trial per day, and the Y-maze was broken down and cleaned after each trial. There was a minimum of 10 days between sets for an individual.

After completion of these tests another experiment was conducted. This time two naturally cycling mice, one estrous and the other diestrous, were enclosed in 10.2 x 10.2 x 10.2 cm nest boxes overnight and removed in the morning. The mice were lavaged before and after removal from the nest box to make sure they were in the appropriate phase of their cycle. Each nest box was then placed at the end of an arm of the Y-maze. Fans were located behind the nest box with the fan blade inside the back end of the nest box. The weasels were then tested as in the first experiment. This experiment was conducted to confirm that weasels would respond the same to natural estrous odors as they did to the estradiol implants.

RESULTS and DISCUSSION

Twelve wild caught least weasels, 7 males and 5 females, were tested in the first experiment, but not all completed 16 trials as three died before the experiment was concluded. A total of 162 trials were observed, 81 controls and 81 treatments. There was no apparent bias as the weasels choose both arms equally (24 right, 26 left) during the 50 control trials where a selection was made. Treatment trials revealed that the weasels displayed a selective preference for estrous urine. All 12 weasels selected the estrous urine on their first trial (Sign test, $P<0.001$). Of the total 81 treatment trials estrous urine was selected 56 times, and diestrous urine 16; no choice was made on nine trials. All 12 weasels selected the estrous urine more often than the diestrous urine (Sign test, $P<0.001$).

The presence of urine influenced the response of the weasels. A comparison of control and treatment trials revealed that the probability of making a choice versus no choice was greater when urine was present. There were 31 instances of no choice during the controls, and 9 during treatments. Using the G statistic (see Sokal and Rohlf 1981) it can be shown that this difference is due to the treatment effect, presence of urine ($G=27.76$, $df=12$, $P<0.01$) and not due to differences in individual performance ($G=27.62$, $df=22$, $P>0.1$, NS).

The results from the second experiment with the nest boxes demonstrated that the odors from nest of a naturally occuring estrous mouse were selected over those from the diestrous mouse; of nine weasels tested, eight chose the estrous nest box and one chose the diestrous nest (Sign test, $\underline{P}<0.05$).

These results demonstrate that least weasels can differentiate between estrous and diestrous odors of their prey and that they select the estrous scents. The fact that weasels do select estrous scents suggests that weasels might be able to intercept the intraspecific signals from their prey. If weasels can differentiate between these physiological states of their prey in nature, then this ability could be used by the weasels when searching for food. Several possible advantages exist for weasels that select estrous females. Estrous mice might be more readily captured than diestrous mice, as they are more active and exploratory (Cushing in press); and Metzgar (1967) suggested an association between activity and predation risk for P. leucopus. An estrous female may also represent a location in which there is an increased prey density. Estrous rodents attract potential mates (Howard 1949; Madison 1980), as the breeding season progresses she may also have a newborn litter, if in post-partum estrus, and finally a litter that has just been weaned. If all these factors were operating at the same time they could represent a substantial increase in the relative prey density in relation to the location of the estrous mouse. It is also possilbe that the weasels are simply responding to reproductive odors in general and not specifically to a predatory cue. Further study is necessary to determine the function of the weasel's preference for estrous odors.

CHAPTER 3

EXPERIMENT 3

INTRODUCTION

Cushing (in press b) established that when presented with a similtaneous choice between estrous and diestrous prairie deer mouse urine in a Y-maze least weasels displayed a selective preference for the estrous urine. The purpose of this experiment is to determine if under different experimental conditions the weasels will display the same preference. In this experiment the weasels will have to actively seek out the estrous and diestrous urine instead of having the odors actively presented to them. This search will be done in such a manner that the weasel will be unable to smell or detect both types of urine at the same time.

METHODS

Nine weasels participated in this experiment. Twenty-four hours prior to testing a weasel was placed in a 3-chambered T-box (Figure 2). The T-box consisted of a large 0.318 cm Plexiglas chamber (45.7 x 45.7 x 25.4 cm) connected to two 20.3 x 12.7 x 25.4 cm Plexiglas compartments, by 15.2 x 3.8 x 3.8 cm Plexiglas tunnels. The floor of the main chamber was covered with pine shavings and the weasel was housed in this area. The weasel was provided with a 10.2 x 10.2 x 10.2 cm wooden nest box. Outside of each tunnel was a pair of photo cells (Figure 2), which were hooked up to a Esterline Angus

Figure 2. 3-Chambered T-box

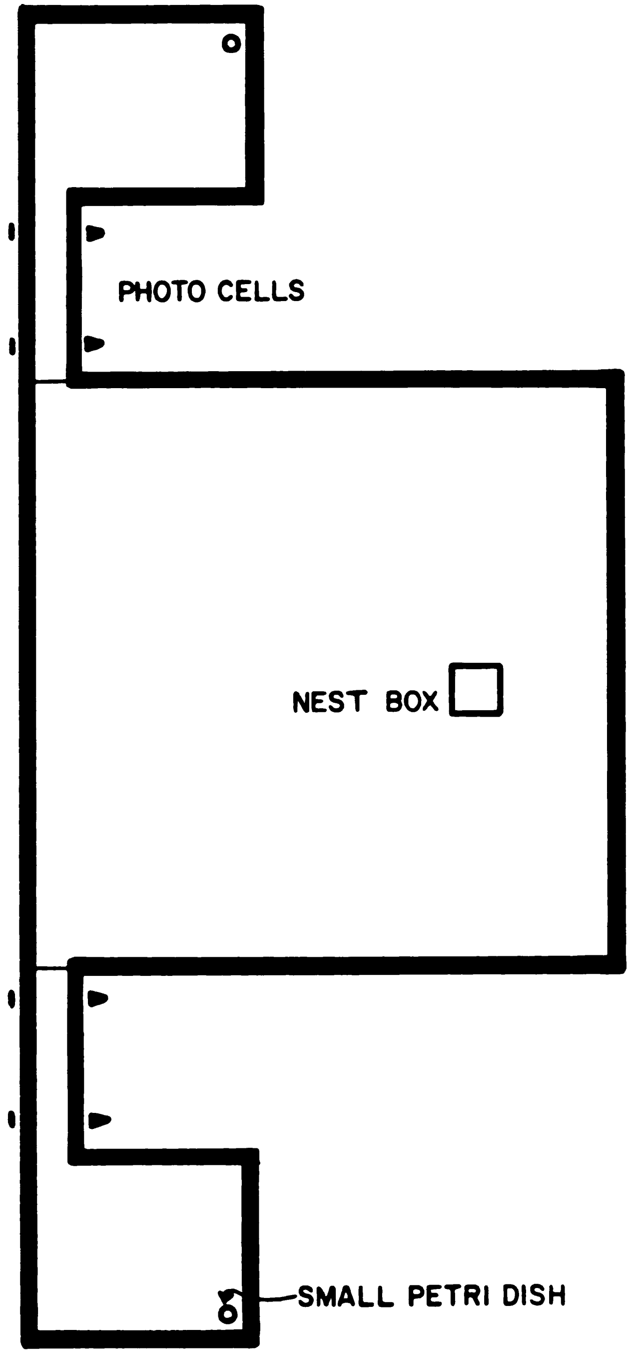


chart recorder. The photo cells and their lights were 10.2 in apart and each one was located 2.54 cm from the ends of the tunnels. Except during a test run these tunnels were closed at their junction with the main chamber. While in the T-box and during captivity the weasels were maintained on a 15L:9D cycle and were fed one mouse every other day beginning on the second day of testing. They were fed after the test for that day had been completed.

Tests were conducted during the light phase of their cycle and a test lasted for two hours. Five minutes prior to a test 0.1 ml of estrous urine was placed in a small fixed petri dish in the corner of one of the smaller compartments, while the same amount of diestrous urine was placed in the other compartment. The placement of the estrous urine was selected at random. (For complete details on the method of urine collection see Chapter 1). After the urine was placed in these compartments the lights activating the photo cells were turned on, and the tunnels were opened. The weasel was then allowed two hours to explore and investigate the compartments. The chart recorder was activated if the weasel broke the second beam while the first was still interrupted and then moved out of the first beam while still interrupting the second beam. The second beam was the one closest to the urine. At this point the weasel was considered to have entered the compartment containing the urine because of the location of the photo cells and the length of the animals, $\geq$15cm, it therefore, had to at least have its head in the compartment. The animal was recorded as being in this area until both beams were again interrupted shutting off the recorder. Data recorded was the amount of time spent in each compartment, in seconds, and the two-hour period was divided into four 30 min blocks. Each weasel was tested once a day for five days and the urine compartments and tunnels were cleaned between tests. The data was analyzed using a mixed model ANOVA.

RESULTS

There were some difficulties experienced with the analysis of the data because the test animal often failed to enter a test compartment during one or more of the 30 min blocks. Therefore, the data could not be analyzed in terms of four 30 min blocks, but had to be compiled and analyzed over the two hour test. This was necessary because of 360 potential data points the weasels only entered a test compartment on 192 of these occassions.

The ANOVA revealed that there was no significant difference in the weasels' response to estrous or diestrous urine. They spent 799.67 ± 582.8 sec (mean ± SD) in the estrous compartment and 538.3 ± 371.97 sec in the diestrous compartment ($F_{(1,8)}=0.683$, NS). There was an overall lack of response by the weasels as out of a total possible time of 648,000 sec they spent 12,447 sec in a test compartment, 1.9% of the total available time.

DISCUSSION

The results from this experiment neither support nor contradict the findings from Cushing (in press b). It appears that when the animals must move about and enter a separate compartment to come in contact with the stimulus urine they display little interest in the stimulus. This effect might be due to the predatory nature of these animals. The subject did not experience any odor until it entered the compartment, and at this point the odor could not be tracked nor could the weasel continue to move towards the source of the odor, as it could in the Y-maze. It was in a dead end as soon as it discovered the odor.

The fact that the weasels spent only a small fraction of the available time in the presence of the urine suggests that the scent of prairie deer mouse urine was not acting as a reward. The lack of response to the estrous urine indicated that the weasels' response in Cushing's Y-maze study was most likely a predatory response and not just a super stimulator or releaser. The idea being that the weasels in that experiment might have been selecting the estrous urine because it functioned as a general releasing stimulus and attracted the weasels. If this were the case then the weasels should have spent more time in the presence of the urine because it in and of itself would be acting as a reward, rather than the potential to locate a prey, and this was not the case. It seems probable that the lack of response by the weasels resulted from habituation or the lack of a potential reward.

CHAPTER 4

EXPERIMENT 4

INTRODUCTION

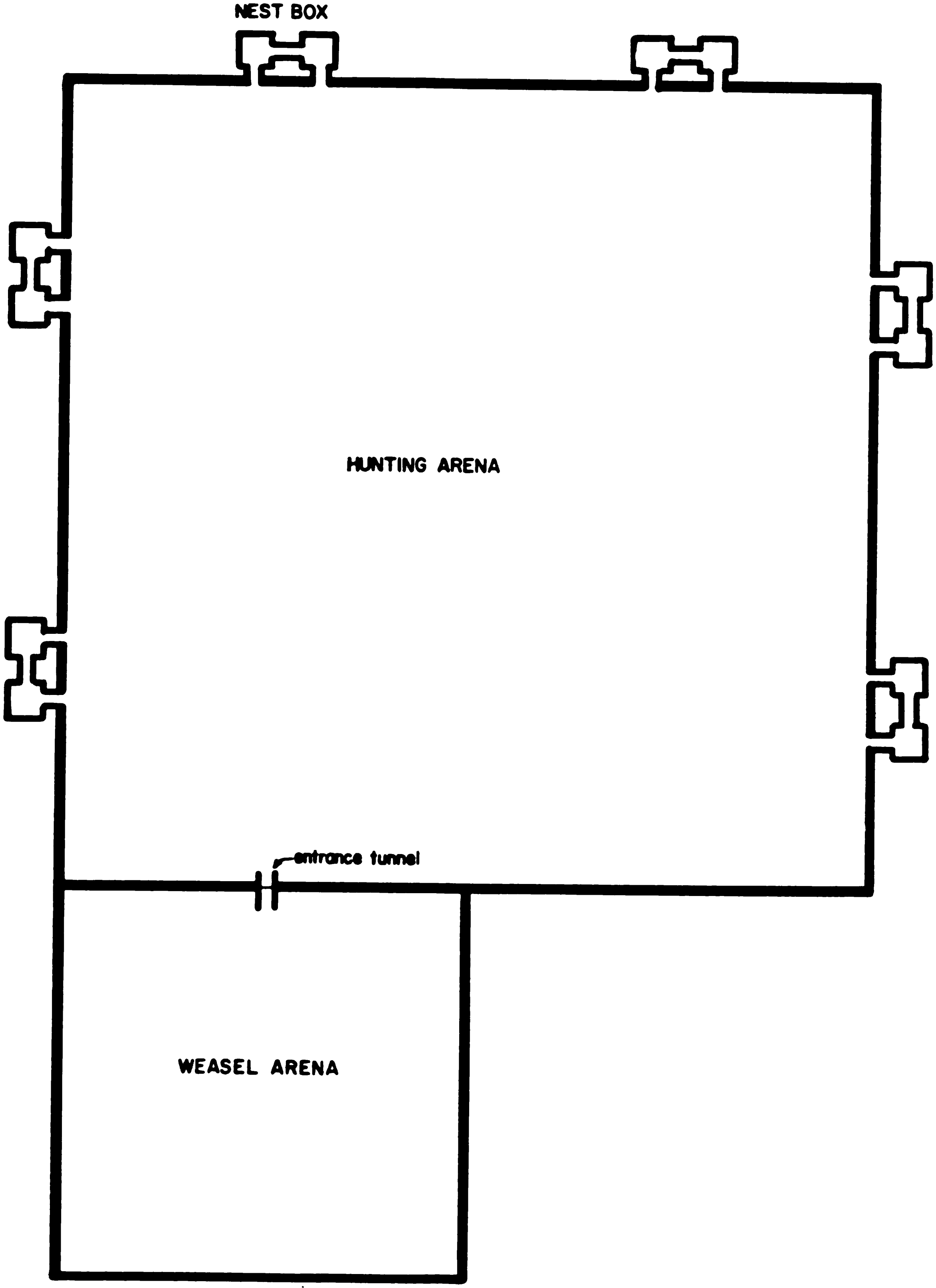
Increased risk of predation has been associated with several conditions related to reproduction. These conditions include: gravid females (Shine 1980), copulation (Valenstein & Crews 1977), and attempts to locate or attract mates (Lloyd 1965, Cade 1979, Tuttle & Ryan 1981). In the latter case the predators often locate or identify their prey by intercepting or decoding intraspecific cues, such as the song of crickets (Cade 1979) or the flash of fireflies (Lloyd 1965). This increased vulnerability while searching for mates mainly affects males, but it has been suggested that estrus might increase the suspectibility of female meadow voles (*Microtus pennsylvanicus*) to predation by snakes (*Coluber constrictor* and *Elaphe obsoleta*) (Madison 1978) and cattle to vampire bat (*Desmodus rotundus*) attacks (Turner 1975). Polar bears (*Ursus maritimus*) are also attracted to human menstrual blood (Cushing 1983), which does not mean that the attraction is of a predatory nature, but does demonstrate that one species can be attracted to the odors associated with another species' reproduction. Since estrous females differ from other females by their scent and behavior, any increased predation on them could be attributable to olfactory or behavioral cues.

I investigated a predator's ability to use the behaviors and intraspecific signals of estrous females to detect and capture these animals. The weasel (Mustela nivalis) was selected as the predator and prairie deer mice (Peromyscus maniculatus bairdi) as prey. This predator/prey system was selected because of behavioral patterns displayed by these mice, the fact that there is an olfactory component to reproduction, and because deer mice can make up a significant portion of a weasel's diet (Polderboer 1942). Behaviorally, transient mice and voles are more vulnerable to predation than residents, and Metzgar (1967) and Ambrose (1972) have suggested that this is due to increased activity by the transients. Also Cushing (in press a) has shown that there are significant differences in the exploratory behaviors and activity of estrous and diestrous mice. Olfactorially, Moore (1965) suggested that olfactorial discrimination of estrous is important in Peromyscus, and Doty (1972) found that male prairie deer mice were attracted to female odors, and least weasels select estrous scents over diestrous scents from these mice (Cushing in press b).

METHODS

Predatory behavior was observed in outdoor test arenas, which consisted of a 1.83 x 1.83 m weasel arena connected to a 3.66 x 3.66 m hunting arena with six external mouse nest boxes (Figure 3). The arena floors consisted of a natural vegetation cover approximately 3.8 cm deep and the walls of the arenas were 0.71 m high. Each external nest box consisted of two 10.2 x 10.2 x 10.2 cm wooden

Figure 3. Weasel hunting arena



cubicles connected by a 10.2 cm long, 3.2 cm diameter plastic tube. Another tube of the same dimensions extended from the center of each box into the hunting arena. Food was placed in the one of the two cubicles and water was located in the hunting arena. On the day of a test one estrous and one diestrous prairie deer mouse were placed at random in separate double nest boxes approximately 4 hr before sunset (EDST) and then transported to the test arena. The stage of the estrous cycle was determined by performing a vaginal lavage on the mice prior to placing them in a nest box. The mice were used within one month after being captured in the field. The mice and weasel were fitted with fluorescent ear-tags, permitting nocturnal observation with ultraviolet lights. A weasel was placed in the weasel arena one day before testing. Half an hour before sunset, the weasel arena and mouses' nest boxes were opened to the hunting arena, permitting the animals to emerge at will. Eight weasels were used in five tests each; three "regular" trials, where the prey were an estrous and diestrous mouse, and two "treatment" trials were the prey were an estrous female and a diestrous female that had been painted with 0.1 ml of estrous mouse urine. (A ninth weasel particapated in one regular trial, then escaped). The urine was obtained from females with silastic implants of estradiol. Implantation was used to facilitate the collection of sufficient quantities of estrous urine. (For complete details of urine collection see Cushing (in press b). The treatment groups established similar prey scents, while the behavioral differences should have been unaffected. This allowed for determination of the contribution of odors to predation success.

In both regular and treatment trials, a trial ended when one of the mice was captured. Data recorded and analyzed were emergence time of the mice and weasel, prey type pursued, location of pursuit, type of prey captured, location of capture, and use of the weasel arena by the mice.

RESULTS AND DISCUSSION

Results from the regular trials revealed that estrous females were more susceptible to predation than diestrous mice. All weasels caught the estrous female during their first hunt and they all captured more estrous than diestrous mice (Sign test, $n=9$, $p<.0025$). Over the 25 regular trials estrous females were captured 23 times and the diestrous mice twice, both in their nest box (Table 1) ($X^2=17.64$, $df=1$, $p<.001$).

In the treatment with the diestrous mice painted with estrous urine trials, seven treated diestrous mice and nine estrous mice were captured ($X^2=0.25$, $df=1$, NS). In addition, five of the seven treated mice were captured while in the hunting arena, whereas no regular diestrous females were captured out in the arena ($X^2=9.19$, $df=1$, $p<.001$). This suggests that the differences in the scents were responsible for the high rate of capture and that the estrous odors aided the weasels in locating and capturing the mice in the arena.

Table 3. Location and Type of Mouse Captured during Regular and Treatment Trials.

Location of Capture	Regular Trials		Treatment Trials	
	Estrus	Diestrus	Estrus	Diestrus
Nest box	12	2	4	2
Arena	11	-	5	5
Totals	23	2	9	7

Behavioral Component

Although, prey odors appear to be the major factor in the weasels' detecting and locating the mice, additional observations indicate that the behavior of the estrous females also contributed to their capture. Diestrous females were more likely to escape from a nest box when a weasel entered. In regular and treatment trials combined, diestrous mice escaped 14 out of 18 times (77.8%), whereas estrous mice escaped 7 of 23 attempts (30.4%) (X^2=8.21, df=1, $p<.001$). This difference was most likely due to behavioral differences rather than odor because the presence of estrous mouse urine did not increase the number of treated mice captured in the nest boxes (Table 3). The state of estrus appears to reduce a female's avoidance of potential predators, possibly to increase her chances to find a male and mate, which would increase the probability of her reproduction. An observation that supports this contention, was that both types of mice freely entered the weasel arena, but only estrous mice ever climbed or entered the weasel's nest box. This occurred four times among estrous mice and never for diestrous females (X^2=4.09, df=1, $p<.05$). These results indicate that while estrous odors increase the weasel's ability to locate the female, the behavior of the female once located contributes to the weasel's ability to capture the mouse.

Selective Advantages

The evolution of a predator's ability to cue into the intraspecific signals of its prey cannot be directly addressed, but there are several benefits to a weasel in searching for estrous mice, such as detectability and ease of capture. Other potential advantages are apparent when the habits and ecology of the prey are considered. When in estrus female meadow voles (*M. pennsylvanicus*) attract several males into their territories (Madison 1980) and there is evidence that this may also occur in deer mice (Howard 1949). By attracting males the females are in affect creating an area with a temporary increase in population density. If a weasel locates this area it might be able to capture a male if it failed to capture the female. Also unless the mouse was undergoing the first estrus of the breeding season she is likely to be in post-partum estrus, which would mean that the weasel might locate the new born litter. As the breeding season continues, the female may have a recently weaned litter in addition to a new born litter (Blair 1940, Storer et al. 1944). This would again result in an increased prey density and with the weanlings inexperienced at avoiding predators. Finally, a combination of these situations, with adult males, a weaned litter, and a new born litter, would result in a substantial increase in prey avalability per unit area if an estrous female could be located.

The results from this study have certain implications in regards to current theories on the evolution of predator/prey relationships. This study supports Vermij's (1982) concept that predatory ability may have evolved prior to the prey's avoidance strategy and these abilities may be modifications of existing abilities that were not necessarily originally associated with predation. This view is contradictory to the life dinner principle associated with an arms race between predator and prey (Dawkins & Krebs 1979). The ability of weasels to intercept intraspecific reproductive cues may require only a modification of their ability to recognize their own species' reproductive signals. Finally, the weasels were not performing as "prudent" predators (Slobkin 1968), because they were selecting the prey that would contribute the most to the next generation, which is the opposite of the strategy predicted for a prudent predator.

Prey's Response

There appears to be substantial risks associated with a female's attempt to reproduce. This indicates that these risks should be acting as selective pressures on the females. Since this risk directly affects the female, any change in reproductive strategy should occur in the female. Attracting mates via pheromones is unlikely to change because a female that did not do this would probably fail to reproduce. The most likely alteration is of female behavior. There are two apparent differences in the behavior of estrous and diestrous mice. First estrous mice emerged from their nest boxes before the weasels 36 out of 44 hunts, including three trials when no capture occurred (X^2=17.82, df=1, p<.001), and their mean latency to emerge (± SE) was 66.9± 6.5 min, after sunset, vs 152.5± 12.7 min for weasels (t=5.516, df=76, p<.0005). A female could use this time to locate a mate, copulate, and return to its nest before a weasel emerged, or at least reduce the amount of time it was active while weasels were out. The estrous mouse emerged before the diestrous mouse 26 out of 39 tests (X^2=6.08, df=1, P<.025), and this is consistant with earlier findings by Cushing (in press a). Also there was no difference between the first emergence of weasels and diestrous mice, 18 vs 26 (X^2=.727, df=1, P>.3, NS). These results are consistent with the notion that estrous females could be reducing their predation risk by regulating their nightly emergence time. This theory is testable in that it predicts that scrotal males should be active and out before the estrous females emerge in order to compete for the receptive females. This should occur because otherwise the receptive females would not be reducing the amount of time they were active and would probably further increase their risk of predation by predators other than weasels, such as avian predators.

Along with a change in emergence time there appears to be a change in response to the presence of a predator. In lizards gravid females freeze when they spot a potential predator and flee only as a last resort, which is the opposite stratgey from that employed by males and non-gravid females (Bauwens & Theon 1981). Estrous mice appear to employ a strategy opposite from that of gravid lizards, which tended to flee at first opportunity, while diestrous mice froze. This may be related to the weasel's ability to detect estrous scents, making flight the optimal strategy. This concept was supported by the capture of mice while frozen out in the grassy arena, which were either estrous females or diestrous females that had been painted with estrous urine. Finally, predation pressure on an estrous female may be reduced by the fact that an individual female is in estrus at the most every 4th or 5th day (Clark 1936), and a weasel would have to encounter the female during estrus to take advantage of its increased vulnerability.

Conclusion

This study indicates that the state of estrus has potential cost associated with it in terms of predation, because estrous mice are more vulnerable to predation than diestrous mice. The weasel appears to be intercepting the intraspecific odors from the females to assist in locating their prey. While these scents seem to be the major component of the weasels increased success in capturing estrous females the behavior of estrous females also contributes to their ease in capture. Finally, the females may be reducing their risk of predation by emerging earlier than the weasels.

DISCUSSION

The study of predator/prey relations is a field of investigation that is still largely undeveloped, and this is especially true when it involves mammalian predators, with the exception of lions and wolves (Schaller 1972, Mech 1970). Most studies examine the responses or activities of the predator without taking into account the strategies or responses of the prey (Curio 1976). This approach is inadequate, because it addresses only half of the issue, the predator. The difficulty with this approach becomes even more apparent when the results are related to current theories, such as optimal foraging or the co-evolution of predators and their prey. For example a predator may not appear to be foraging in an optimal manner if the value of the prey is analyzed only in terms of caloric content, but a difference in the prey's avoidance or defense strategies might alter the interpretation of the predator's foraging strategy. Therefore, it is essential to examine the interactions of both the predator and prey. This may sound like a major undertaking, but this does not have to be the case. The aspects of the organisms that are of interest are their interactions during predation and their activies that influence predation, so that not all aspects of the animals must be studied.

This study, which dealt with the potential risks associated with reproduction in prairie deer mice, utilized the approach of studying the predator and its prey in concert, and in doing so, revealed several aspects of the least weasel and prairie deer mouse predator/prey system. The first dealt with the comparison of the behaviors and activity patterns of estrous and diestrous mice. Semi-natural field studies supported laboratory studies using running wheels that have demonstrated either increased activity or an early onset of activity associated with estrus (Wang 1923, Richards 1966, Morin et al. 1977). Further contributions were made to these activity studies by including new information on space utilization and activity patterns of females in a natural enclosure. Estrous females spent less time in walled areas and crossed open grids more frequently than the diestrous mice, which spent almost all of their time close to the walls of the arena.

Also, this study demonstrated a potential risk associated with estrus and reproduction, as estrous mice are more vulnerable to predation than diestrous mice. This increased vulnerablitiy has two components to it. First, weasels are able to detect and intercept the intraspecific odors of estrous mice. When presented with a choice in a Y-maze between the two types of urine, the weasels were able to detect the urine and preferred the estrous urine. When allowed to hunt the two types of mice, estrous mice were almost always captured, but when diestrous mice were painted with estrous urine the probablity of capture of the two types of females was equal. Second, the physiological changes associated with estrus significantly alter the behavior patterns of the mice leading to ease of capture by the weasels. Estrous females were less likely to escape from a nest box when a weasel entered and they were observed climbing and entering the weasel's nest box.

While this study did examine the responses of both the predator and its prey, it addressed a very specific question and only one class of prey was tested. In order to obtain a complete understanding of the interactions of least weasels and mice, or any predator/prey system, it is essential to study as many aspects of the interactions of these animals as possible. Controlled experimentation should be used whenever possible to investigate predator prey systems. Experiments should be designed that attempt to address specific questions, as with the weasels and estrous mice, and not just try to take in all aspects of the animals at once. The overall picture can be obtained by putting the pieces together. Another techinque that has provided insight into predator/prey interactions is that of simple field observations, such as has been done with lions, wolves, hyenas, and mongoose (Schaller 1972, Mech 1970, Kruuk 1972, Rasa 1983). These types of studies have been informative, but usually require enormous resources and time and they are not directed at dissecting the phenomenon of predation, but tend more to be good discriptive accounts. Also, these observations of the overall system have been effective for some social predators, but they are less successful with solitary predators. Although the larger carnivores may necessarily be studied in the field, it should still be possible to set up controlled experiments, albiet, they may be limited in scope.

The results from this study suggest other types of investigations that should be undertaken to provide the necessary intergrated view of the predator/prey relations between weasels and mice. In order to do this several aspects must be examined and these should include the social interactions of prairie deer mice, the interactions of the weasels and the mice, and the possible influence of other predators upon the system. By determining how weasel predation affects other classes of deer mice, such as pregnant females, males, and juveniles, it should be possible to actually assess the weasel in terms of such theories as prudent predation. This information would include a complete list of types of prey taken, their relative vulnerability, and their relative abundance and location. For example, in terms of social interactions, it is important to understand the role that adult males play in the overall system, especially if they are out and highly active during the weasel's hunting. Perhaps their activity diverts some of the weasel's attention from the female. Is the pair more vulnerable to predation? Does the pair remain in one location while mating, and if so does this behavior reduce the weasel's ability to locate the female or the pair? Also, what does the female do after mating, does she remain active and increase her chances of encountering a predator or does she return to her burrow?

It is, also necessary to understand the influence of other predators upon the system. With this system the influence of raptors, such as owls, could be very important. First, the increased activity of the female mice could attract avian predators, as suggested by Metzgar (1967) and Ambrose (1972). If this is true, what affect does the early onset of activity and possible mating strategies have upon the mouse's ability to reduce the risk of predation? For example, does the early emergence of the mice also decrease the risk of exposure to owls, as suggested for weasels, or does it increase vulnerability to diurnal raptors. Second, what influence do owls have on weasels where they function both as potential competitors and predators? Owl predation on the weasels may well influence or restrict the predatory strategy of the weasels.

The results of the study of the social interaction of the prey, the predatory success of the predator on the various classes of prey, and the possible influence of other predators should provide an intergrated view of a predator/prey system. However, it is still a simplistic representation, because while providing a detailed understanding of a particular system it assumes that the system consists of one prey and at most a couple of predators. It does not address the question of predator/prey interactions in a complex community of organisms, where there would be several prey species involved. This brings up some different problems to the understanding of complex predator/prey systems and how they interact. Does the predator display a preference for a particular prey species? Do predators exploit different prey dependent upon varibles, such as prey population densities or extrinsic factors like habitat conditions? This may be particularly important when the prey are animals, such as small rodents, that often undergo dramatic population cycles. When examining predator responses to various prey species it may also be necessary to attempt to determine how predators differentiate prey types, or if they do, and how they "learn" to recognize potential prey. Community level questions can also be investigated through the use of controlled experimentation, such as Erlinge (1975) did when he presented short-tailed weasels in an enclosure with various prey species and manipulated prey densities.

Any attempt to address current theories on predator/prey interactions or to determine if predators forage in an optimal manner necessitates a comprehensive understanding of the interactions involved in the predator/prey system. This can only be accomplished if the interactions of a complex variety of factors are studied in concert. Studies that examine only a small portion of the total picture can and do provide pieces of the puzzle, if they examine both the predator and they prey, but they can only indicate direction and ideas for future research. The results from any single piece should not be extended to the point where it is used to explain the interactions of the system as a whole. In the end the approach of building an integrated picture of predator/prey systems step by step from controlled experimentation should provide an understanding of how these complex interactions work, and possibly shed light on the evolution or co-evolution of predator/prey systems.

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