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NORTHERN ILLINOIS UNIVERSITY

The Foraging Behavior of *Peromyscus leucopus* in a Tallgrass Prairie

A Thesis Submitted to the

University Honors Program

In Partial Fulfillment of the

Requirements of the Baccalaureate Degree

With University Honors

Department of Biology

by

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Abstract. This experiment was conducted to discover what effect predation, food supplementation, microhabitat, season, and lunar light levels had on the foraging behavior of *Peromyscus leucopus* in a tall grass prairie. The research was conducted over four nights in the spring and fall of 1995. The pre-existing site contained four predator exclusion plots and four predator access plots. These were used throughout the experiment and the other variables were manipulated at this site. GUDs (giving up densities) were measured to determine the relative foraging levels for each variable. Live trapping census was conducted monthly for the duration of the experiment. Lunar light levels, microhabitat, and season had a strong affect on the foraging behavior of *Peromyscus leucopus*. The high population in the fall is the most likely explanation for the lower GUDs. GUDs were high during bright nights and on the elevated microhabitat, regardless of predator treatment. These findings raise questions about the motivation for avoidance behaviors in this species. Since they exhibited these behaviors even when predators were not a threat, predation does not completely explain the behaviors. Perhaps they are not a preferred prey, or these behaviors are a fixed aspect of their phenotype that does not change during a short term experiment.

Abstract. This experiment was conducted to discover what effect predation, food supplementation, microhabitat, season, and lunar light levels had on the foraging behavior of *Peromyscus leucopus* in a tall grass prairie. The research was conducted over four nights in the spring and fall of 1995. The pre-existing site contained four predator exclusion plots and four predator access plots. These were used throughout the experiment and the other variables were manipulated at this site. GUDs (giving up densities) were measured to determine the relative foraging levels for each variable. Live trapping census was conducted monthly for the duration of the experiment. Lunar light levels, microhabitat, and season had a strong affect on the foraging behavior of *Peromyscus leucopus*. The high population in the fall is the most likely explanation for the lower GUDs. GUDs were high during bright nights and on the elevated microhabitat, regardless of predator treatment. These findings raise questions about the motivation for avoidance behaviors in this species. Since they exhibited these behaviors even when predators were not a threat, predation does not completely explain the behaviors. Perhaps they are not a preferred prey, or these behaviors are a fixed aspect of their phenotype that does not change during a short term experiment.

INTRODUCTION

Studies have suggested that predation is the major factor influencing the foraging behavior of rodents (Brown et al. 1994; Hughes and Ward 1993; Hughes et al. 1994; Kotler et al. 1993; Kotler et al. 1991; Lima and Dill 1990; Travers et al. 1988). Risk of predation causes rodents to choose safer areas to feed and to reduce their activities on brighter nights due to the higher success rate of predators (Brown et al. 1988; 1994). Predation, lunar light levels, and microhabitat have been shown to have an effect on foraging behavior (Brown et al. 1988; Lima and Dill 1989; Travers et al. 1988). Foraging rates can be determined by what the forager leaves behind when foraging in a particular location. This is the giving up density (GUD), the point at which an individual's risk of being predated, or its metabolic cost of foraging is greater than the energy it will gain from the food gathered or eaten (Brown et al. 1988). Some heteromyid rodents prefer a bush microhabitat; however, bipedal species utilize open habitat more frequently, particularly during a full moon. In the presence of predators, both bipedal and non-bipedal rodents shift their microhabitat utilization to a bush-covered area. Also, regardless of lunar light level (e.g. high or low) bipedal rodents prefer covered habitat over open habitat, because the risk of being predated is lower in a covered area (Brown et al. 1988 and Brown et al. 1994). The presence of owls decreased the GUDs of three species of heteromyid rodents in both covered and open microhabitats; in fact they almost completely avoided the open areas. This response was due to the fact that owl predation rates were higher in the open habitats (Brown et al. 1988).

Other vertebrates have also been shown to alter their foraging strategies to reduce predation risk (e.g., Angradi 1992; Holmes 1991; Moore 1994; Newman and Caraco 1987). Pikas and squirrels have been shown to limit their foraging to areas near cover. In so doing they sacrificed potentially rich food sources for safety (Holmes 1991; Newman and Caraco 1987).

Similar behavior patterns have been observed in fish and birds. Minnows, juvenile rainbow trout, and bluegill sunfish altered their habitat in response to predators. They remained in a more covered habitat where predation was low, and they also reduced their foraging efficiency as a consequence (Angradi 1991; Gillian 1987; Werner and Hall 1988). Finally, several species of tits have been observed retreating to cover in the presence of predators (Suhonen 1993a, 1993b; Todd and Crowie 1990). Todd and Cowie (1990) used GUDs to show that Blue Tits reduced their foraging when predation risk was high.

Studies have shown that prey associate increased illumination with increased predation risk; numerous experiments have demonstrated a decrease in foraging activity on bright nights as compared to dark nights (Brown et al. 1988; Kotler et al. 1994; Kotler et al. 1993; Lima and Dill 1990; Travers et al. 1988). There were fewer seeds taken from sample trays and fewer microhabitats utilized on bright nights. The open habitat was the least favored, and the covered habitat was the most favored by heteromyid rodents in arid environments (Brown et al. 1988, II 1994; Hughes et al 1994; Kotler et al. 1993; Kotler et al. 1991; Travers et al. 1988). Brillhart and Kaufman (1991) showed a decrease in non-foraging activity on bright nights, and concluded that the prey did nothing but travel to and from the nest and seed trays, thereby reducing their exposure to predation. Prey also favor covered habitats on brighter nights, staying in the shadows and nearer to the walls of experimental arenas (Travers 1988; Brillhart and Kaufman 1991; Brown et al. 1988). GUDs of some gerbils and heteromyd rodents were lower on nights with a full moon than on dark nights and/or cloudy nights (Brown et al. 1994; Hughes and Ward 1993; Hughes et al. 1994; Kotler et al. 1991; Kotler 1993). GUDs on cloudy nights were correlated with those on new moon nights since light levels were low during both circumstances (Kotler et al. 1993). On dark nights there was intense patch use and low GUDs, but GUD's were higher in open areas than in the covered ones (Brown et al. 1988; Hughes et al. 1994; Kotler et al. 1993; Travers et al. 1988) . For gerbils and other desert rodents, illumination is a very important factor in predation risk; under high illumination gerbils must increase their

foraging rate to compensate for the higher risk of predation. In other words, they must eat faster or gather food faster to avoid predators, but they still gather less than on dark nights (Kotler et al. 1993; 1991).

Microhabitat utilization is affected by illumination and predation risk. All species reviewed, with the exception of large bipedal *Dipodomys* species, switched their activity to a covered microhabitat on bright nights and when exposed to predators. It was assumed that these species have a limited ability to detect and avoid predators and so they reduce risk by remaining under cover (Brown et al. 1988; Hughes et al. 1994; Kotler et al. 1993). The large bipedal species did not seek cover on bright nights except when predators were present. Brown et al. (1988) suggested that the bipedal species have a better ability to detect and avoid predators so they can utilize open habitats as well as the covered ones. GUD's were higher in the open microhabitat for all species of heteromyid rodents in desert habitats regardless of the experimental treatment (Brown et al 1988). This is most likely due to the increased success rate of owl predation in the open (Brown et al 1988; Kotler 1991).

Most of the above studies were done with rodents in arid climates, and predation was not manipulated in a natural setting, with exception of Brown (1988). In Brown's (1988) large enclosures, however, the predator-prey ratio and study areas were not representative of a natural setting. In the following experiments, predation risk, lunar light levels, food availability and microhabitat utilization were examined under a natural setting. GUD's were used to document the foraging activity of the white-footed mouse (*Peromyscus leucopus).* The habitat studied was a tallgrass prairie at Fermi National Accelerator Laboratory (Fermilab), Batavia, Illinois. Food availability was controlled with food supplementation. The microhabitats were studied by use of ground level and elevated platforms to see how *Peromyscus leucopus* utilized the vertical structure of a tallgrass prairie. It has been shown that *Peromyscus leucopus* preferred habitat with complex vertical structure which is usually found in wooded and shrubby areas and lime-stone ledges, and that *Peromyscus maniculatus* preferred the open or recently

burned prairie (Clark et al. 1987). Although *P. maniculatus* was known to be present in the study area it was relatively rare (Yunger 1996).

My hypothesis was that *Peromyscus leucopus* would have lower GUD's in predator exclusion grids. They would utilize the elevated microhabitat more due to the absence of risk from either terrestrial or avian predators. With predators excluded, activity at higher elevations would not increase their risk of being predated. On food supplemented plots, the greater amount of available food could increase the GUD's because the mice would not explore other food sources. This might be most noticeable on the higher elevated trays because the mice were not driven by low food availability to take a greater predation risk. Finally, I predicted that the GUD's would be higher in the control grids on nights with a full moon, and would remain the same, regardless of lunar light levels in exclosure grids due to the absence of predation.

SITE DESCRIPTION

The field site was a 32 ha tallgrass prairie restoration at Fermi National Accelerator Laboratory (Fermilab), Batavia, IL. There were eight 0.60 ha plots. Each plot had a trapping grid arranged in 6 x 6 array with 12 m spacing (Fig. 1). One Sherman live trap was placed at each station and baited with peanut butter and rolled oats. Trapping was conducted for three consecutive nights at monthly intervals. Captured individuals were marked with uniquely numbered ear tags for subsequent identification and data were collected on species, age, sex and reproductive condition. Plots 2, 4, 6 and 8 were terrestrial and avian predator exclusion plots. The exclusion grids were surrounded by 2 m high 2.5 cm mesh chicken wire fencing with an overhang on the top to prevent predators from climbing over. To date, exclusion methods have been observed to be effective for terrestrial predators (pers. observ.). The exclusion plots were also covered with 12.5 cm x 12.5 cm mesh nylon gill netting to prevent avian predation as well. Plots 1, 3, 5 and 7 were control plots surrounded by low 2.5 cm chicken wire fencing 0.25 m high to simulate potential fence effects on mouse movements. There were five stations on each

plot, positioned approximately 6 m in from each outside corner of the plot with one in the middle; each station contained one stand and one petri dish for seeds.

METHODS

All three experiments were conducted under both predator treatments and with high and low microhabitats. Each night the experiment was run, light readings were taken and recorded. Stands were constructed of 0.5 cm diameter bamboo with four platforms for seed containers 25 cm above the ground. These platforms represented the elevated microhabitat. Each container was 2.5 cm in diameter and 2.0 cm deep, approximately the size of a seed bundle on a plant (e.g., cone flower, purple prairie cone flower, black-eyed Susan, rattlesnake master, prairie sunflower). A 10 cm diameter petri dish was filled with sand and placed at the base of each stand in order to mimic natural ground microhabitat. The caps were each filled with one gram of black oil sunflower seeds and the petri dishes had 4 grams of black oil sunflowere seeds mixed in with the sand. The seeds were put out after sunset and picked up before sunrise to prevent birds from foraging on the seeds. When the seeds were removed from the stations, the plot, station and microhabitat of each container was recorded. The seeds remaining were the GUD for the station and microhabitat. The sand was sifted to remove the seeds and then allowed to air dry and return to the same moisture level as the room. After drying, the seeds were weighed.

Experiment 1-- The first part of the experiment was conducted on 2 consecutive nights, April 30 and May 1, in spring 1995. Both nights were cloudy with a new moon. The two nights were treated as blocks to test the repeatability of the results. Grids 1 - 4 were supplemented with 11 kg of rodent chow per week per plot which was hand-broadcast from October 1994 through May 1995. Plots 5-8 were left unsupplemented for controls. Vegetation height and density was observed for comparison with fall vegetation. This resulted in a 2 x 2 factorial split plot nested design . The treatments included predator-no predator, and food supplemented - non-

supplemented. The split plot was represented by the 2 microhabitats; ground and elevated. Each of the 5 stations were nested within plot; this was done to avoid pseudoreplication since the plots were the experimental unit. The results were analyzed using SAS PROC GLM (SAS 1989).

Experiment 2 --Data on GUDs were collected on the night of November 20, 1995 under a new moon and cloudy skies. No food supplementation occurred during this period. Vegetation was again observed for comparison with spring vegetation. The November 20 data was compared with the May 1 GUDs. This compared seasonal effects on GUDs. This again resulted in a 2 x 2 factorial split plot nested design; however, the treatments were predator-no predator and season of spring vs. fall. Analyses were the same as experiment 1.

Experiment 3 -- Data on GUDs were collected on the night of November 2, 1995. There were clear skies and a full moon. The data from November 2 was compared with the GUDs from November 20. This compared the effects of lunar light levels from a new or full moon on *P. leucopus* GUDs. This again resulted in a 2 x 2 factorial split plot nested design; however, the treatments were predator-no predator and lunar light levels (full moon vs. new moon). Again, the data were analyzed using SAS PROC GLM as in experiment 1 (SAS 1989).

RESULTS

Experiment 1-- Neither food supplementation or the food x predator interaction had a statistically significant effect on *Peromyscus leucopus* foraging behavior (Table 1). However, they both exhibited suggestive trends that may have been biologically significant trends. GUDs were lower on food supplemented plots than non-supplemented (Fig. 2a).. When predators were present, GUDs were equal on food supplemented and non-supplemented plots, but when predators were excluded, GUDs were 1 g lower in supplemented plots (Fig. 2c). The food x microhabitat interaction had no statistically significant effects (Table 1). We observed the vegetation to be very low. There was little to no new growth and the old growth

from the year before was mostly trampled to below 0.5 m. There was also a significant block effect; GUDs were approximately 1 g lower for the second night (Fig. 2b).

Experiment 2 -- There was a highly significant seasonal effect on foraging levels (Table 2). GUDs were 1 g lower in the fall than in the spring (Fig. 3a). The season x microhabitat interaction also had a highly significant result (Table 2). GUDs remained the same for both seasons at 1.5 g. On the other hand, the GUDs on the ground microhabitat were 1.3 g lower during the fall experiment (Fig. 3b). There were no statistically significant results for the predator x season or predator x season x microhabitat interactions (Table 2). Vegetation was observed to be very tall, greater than 1.5 m, and dense.

Experiment 3 -- Lunar light levels exhibited a highly significant effect on *P. leucopus* foraging (Table 3). GUDs were 1 g lower under during the new moon (Fig. 4a). The predator x moon interaction had interesting, although non-significant, trends (Table 3). GUDs on nights of a full moon were higher than on nights of a new moon regardless of predator treatment (Fig. 4b). However, during a full moon, GUDs were lower when predators were present. During a new moon, GUDs were higher when predators were present. All other interactions, such as predator x microhabitat, moon x microhabitat, and predator x moon x microhabitat, were not significant suggesting no effect on foraging behavior (Table 3). Vegetation was again very dense and tall, and at times greater than 1.5 m.

DISCUSSION

Lunar light levels, microhabitat and season appear to strongly affect the foraging behavior of white-footed mice (*Peromyscus leucopus)*. Previous studies with other vertebrate species suggest that predation also has a significant affect (e.g., Angradi 1991; Brown et al. 1988; Holmes 1991; Kotler et al. 1994; Lima and Dill 1990). In this study, *P. leucopus* behaved in a very similar manner to other species mentioned in the introduction; they had increased GUDs during bright nights and in the more open elevated microhabitat. Other studies attribute

this behavior to predator avoidance and perceived predation risk by the prey species (e.g., Brown et al. 1988; Lima and Dill 1990; Kotler et al. 1994). However, in my study, when predation risk was eliminated, mice continued to avoid bright nights and open habitats. It is possible that the mice do not recognize the plots as an area of reduced predation risk and continue to reduce foraging and to utilize fewer microhabitats. However, this seems unlikely due to the absence of scat and/or pellets from the exclosures. Recent studies have also shown that canid and possibly raptor predation do not play important roles in controlling *Peromyscus leucopus* populations (Cooper unpublished data; Randa 1996; Yunger 1996). Randa (1996) showed a low frequency of *P. leucopus* remains in the scat of canid predators and Yunger (1996) found that their populations densities were not greatly affected by predator exclusion. There are two possible explanations for these findings. Either these predator avoidance behaviors are effective and the predators cannot catch many mice, or the predators do not prefer this species as prey. If *P. leucopus* are not preferred prey items, then predation may not be a strong selecting force for this species, so the presence or absence of predators would not affect their foraging behavior. Conversely, if they are not predated upon because they display avoidance behavior there would been strong selection for that trait. Thus, individuals would be less likely to alter their behavior since that component may be genetically fixed. This could explain why these mice do not alter their behavior when predators are absent. Further experiments will have to be conducted to discover why *P. leucopus* exhibit predator avoidance behaviors in the absence of predation.

The only suggestive significant trend involving predation occurred during experiment 1; these results were not statistically significant but seem worthy of comment. GUDs were higher on non-supplemented and predator exclusion plots than on supplemented and predator exclusion plots (Fig. 4b). There is no plausible explanation for this trend. Population densities were nearly equal for all experimental treatments (Fig. 5) so different densities could not have been the cause of these results.

Although GUDs were significantly different in the spring vs. fall, this is probably due to higher densities (Fig. 5) or possible higher energetic demands in fall. When season and microhabitat were considered together (Fig. 3b), GUDs were lower in the fall for the ground only. The elevated GUDs remained nearly unchanged. Interestingly, the GUDs for the elevated microhabitat were lower than the ground microhabitat in the spring session. This contradicted our original hypothesis. It was expected that *P. leucopus* would utilize the upper microhabitat more as the vegetation grew and vegetation was significantly denser and taller in the fall. This hypothesis was suggested by Kaufman et al. (1983), who found that *Peromyscus leucopus* prefer vegetation with complex vertical structure and utilize multiple levels of vegetation. Perhaps mice foraged more in the elevated microhabitat in the spring because that was their preferred habitat and the stands offered the only opportunity to exploit it. However, in the fall, when the vegetation was tall and dense, they utilized it more than the stands because it was more plentiful. The GUDs for the ground microhabitat most likely decreased because population density increased in the fall; there were more individuals foraging at the ground microhabitats, so the GUDs were lower.

In conclusion, predation may not have as great an effect on *Peromyscus leucopus* foraging behavior as previously believed. While they exhibit classic predator avoidance behaviors, such as reduction of foraging in open areas and on bright nights, they do so regardless of the presence or absence of predators. An explanation could be that they do not recognize the exclusion plots as areas of reduced predation risk. However, it seems more likely that the lack of predation on this species is the reason for these results. Either predators do not prefer *Peromyscus leucopus* as prey or prey avoidance behaviors are a relatively fixed aspect of their phenotype which do not change rapidly in short-term experiments.

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FIGURE LEGENDS

Figure 1-- Map of research site Hatched plots are predator exclusion, control plots are predator access. Plots 1-4 were food supplemented and 5-8 were non-supplemented.

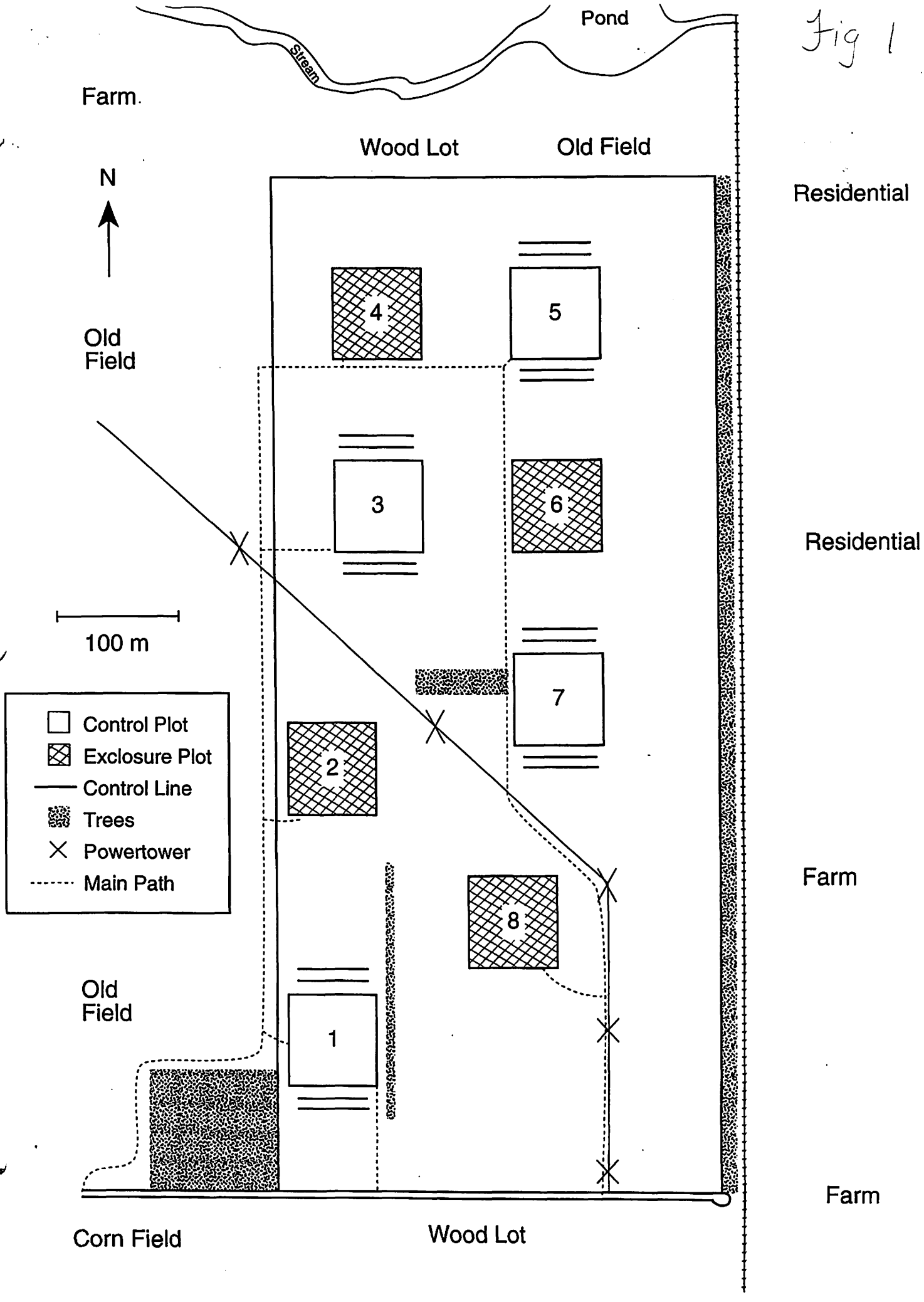
Figure 2-- (a) - GUDs in grams on food supplemented and non supplemented plots; (b) - GUDs in grams for block one and two in experiment one; (c) - GUDs in grams for food x predation interaction

Figure 3 -- (a) - GUDs in grams for spring and fall under a new moon; (b) - GUDs in grams for microhabitat x season interaction

Figure 4 -- (a) - GUDs in grams for full x new moon; (b) -- GUDs in grams for moon x predator interaction

Figure 5 -- Population densities of *Peromyscus leucopus* for the year of 1995, considering predator and food experimental condition

Fig 1


Pond
Stream
Farm
Wood Lot
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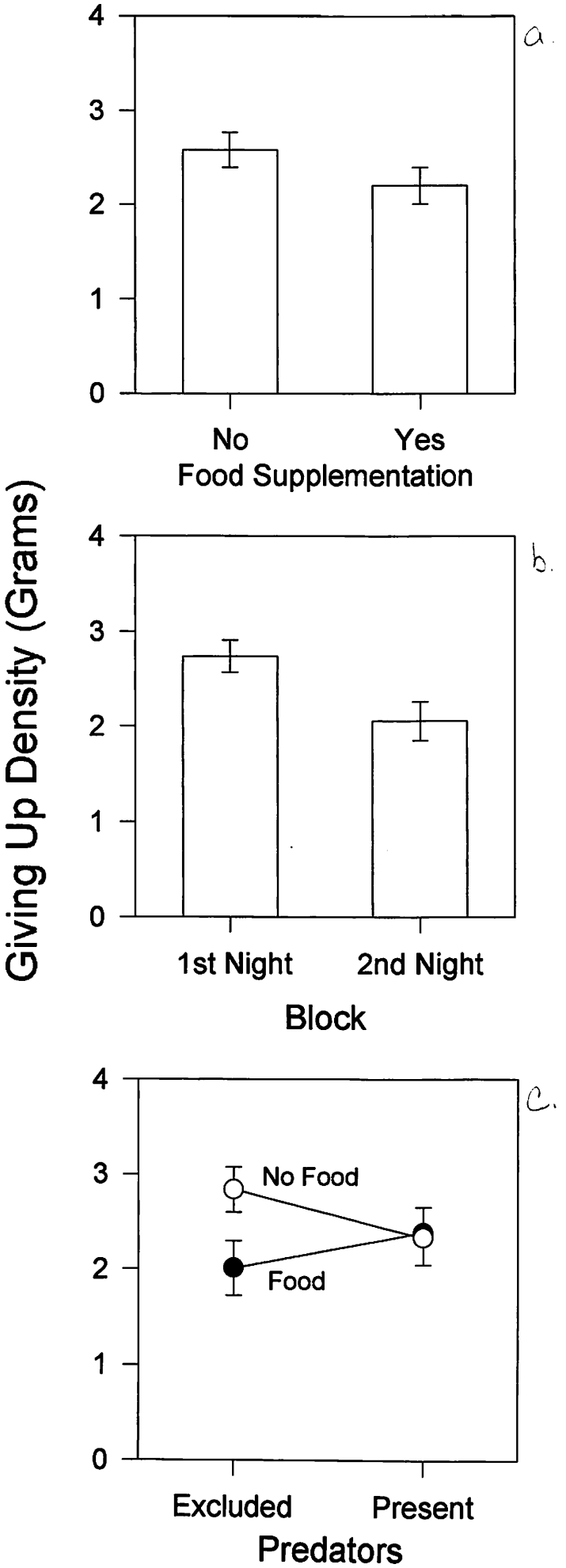
Control Line
Trees
Powertower
Main Path
2
Farm
8
Old Field
1
Farm
Corn Field
Wood Lot

Figure 2


a.
4
3
2
1
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No
Yes
Food Supplementation
Giving Up Density (Grams)
b.
4
3
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1
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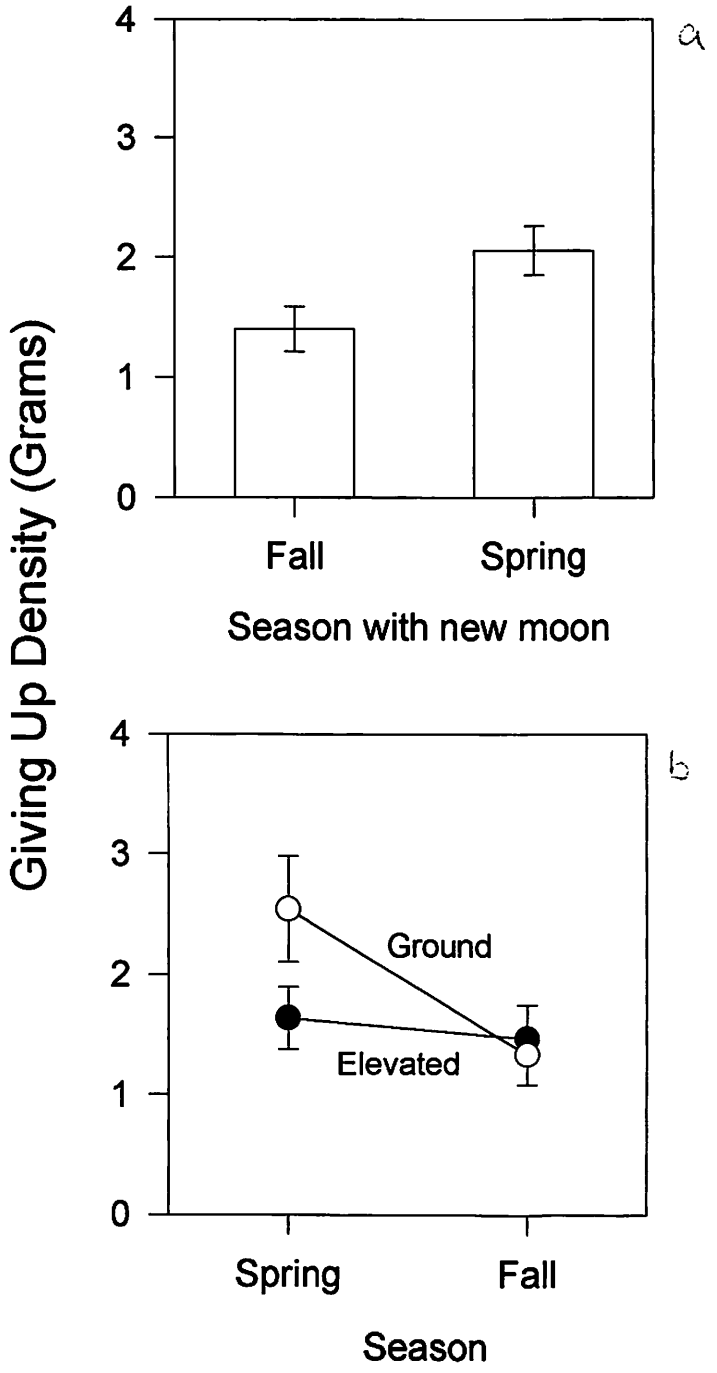
1st Night
2nd Night
Block
c.
4
3
2
1
0
No Food
Food
Excluded
Present
Predators

fig 3


Giving Up Density (Grams)
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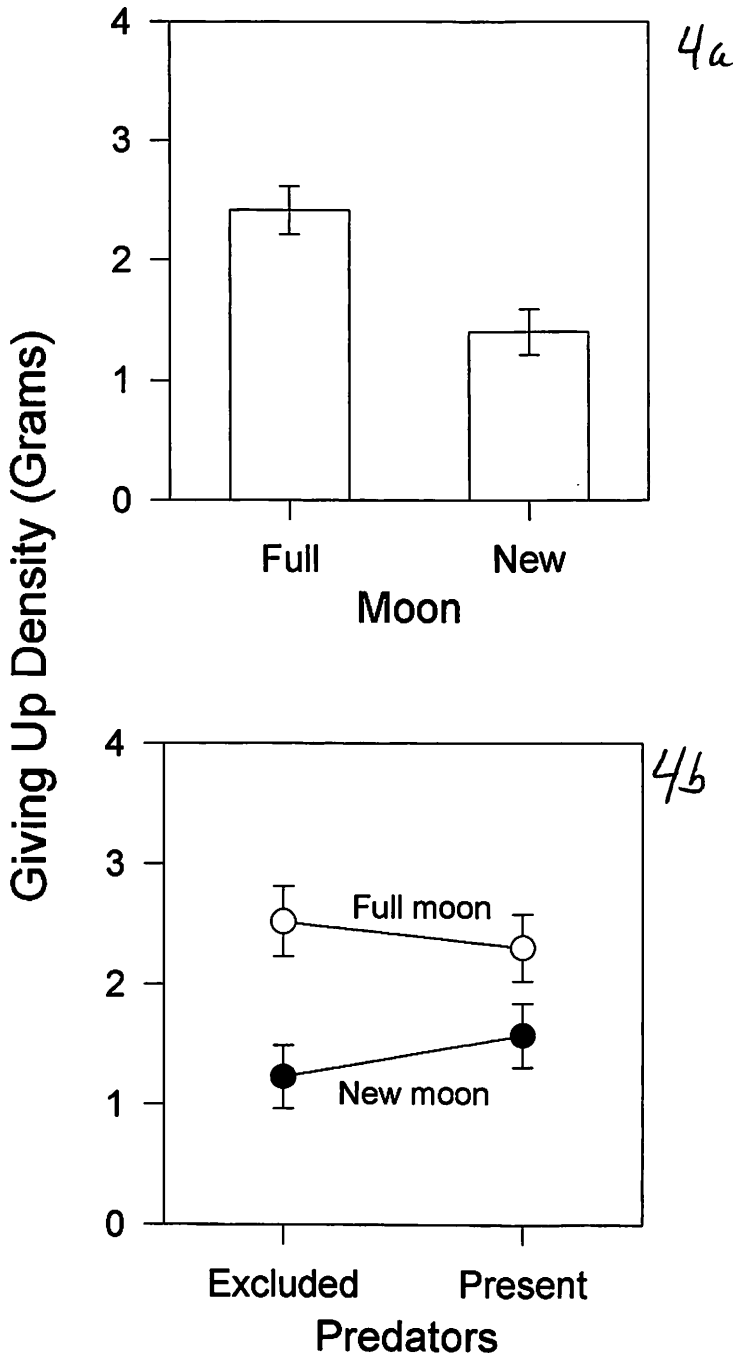
Fall
Spring
Season with new moon
b
Ground
Elevated
Spring
Fall
Season

Figure 4


4a
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Giving Up Density (Grams)
4b
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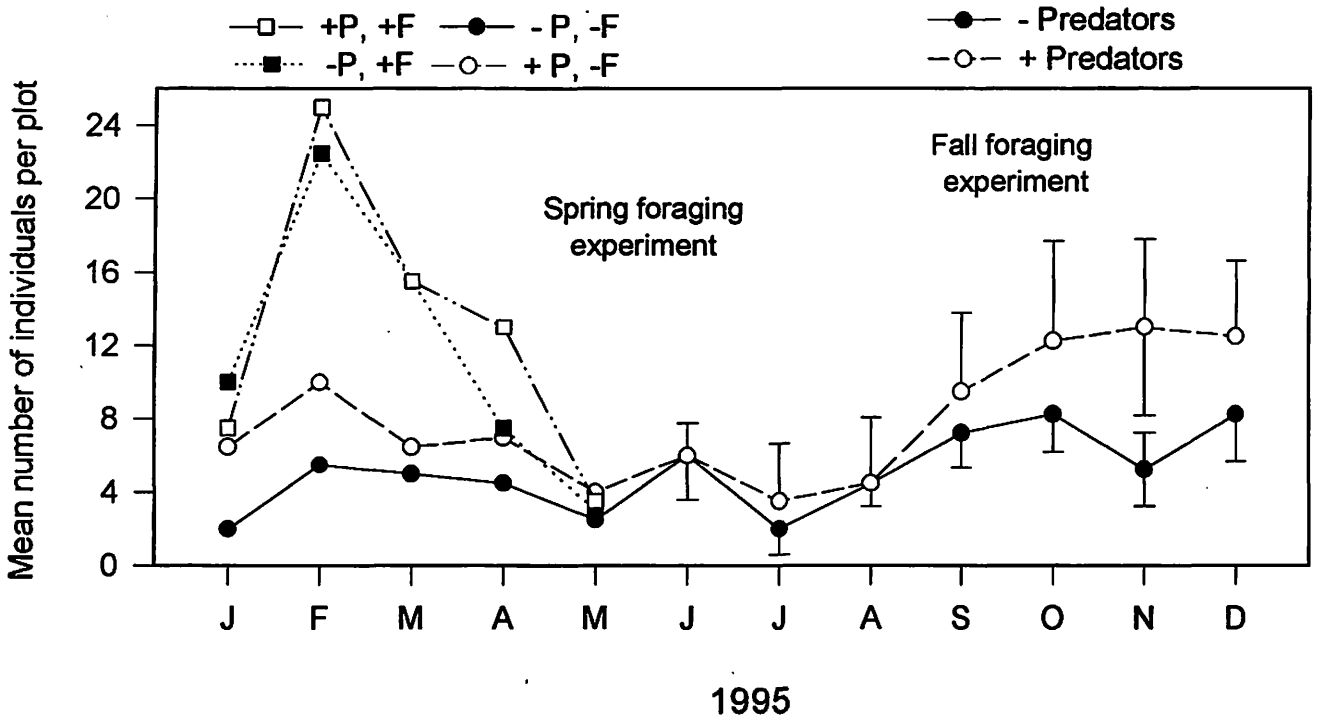
Full moon
New moon
Excluded
Present
Predators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- P, -F
-P, +F
+ P, -F
- Predators
+ Predators
Mean number of individuals per plot
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16
20
24
Spring foraging experiment
Fall foraging experiment
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Fig. 5

Table 1.-- Analysis of variance table for the giving up densities (GUD) of *Peromyscus leucopus* on food supplemented vs. unsupplemented plots and predator excluded vs. predator access plots blocked over two nights.

Source	df	Mean Square	F Value	P > F
Food	1	6.441	3.51	0.0640
Pred	1	0.543	0.30	0.5876
Pred*Food	1	7.066	3.85	0.0526
Plot(Pred*Food)	4	19.004	10.35	0.0001
Stat(Pred*Food*Plot)	32	2.743	1.49	0.0684
Block	1	15.326	8.34	0.0047
Pred*Microhabitat	1	0.160	0.09	0.7683
Food*Microhabitat	1	2.307	1.26	0.2651
Food*Block	1	0.126	0.07	0.7937
Pred*Block	1	2.029	1.10	0.2957
Height*Block	1	1.362	0.74	0.3911

Table 2.-- Analysis of variance table for the giving up densities of *Peromyscus leucopus* on spring vs. fall and predator excluded vs. predator access plots under a new moon.

Source	df	Mean Square	Value	P > F
Pred	1	1.797	0.95	0.3328
Plot(Pred)	6	23.476	12.36	0.0001
Station(Pred*Plot)	32	2.460	1.30	0.1645
Season	1	15.906	8.37	0.0046
Microhabitat	1	3.383	1.78	0.1848
Pred*Season	1	1.097	0.58	0.4489
Pred*Microhabitat	1	0.180	0.10	0.7582
Season*Microhabitat	1	8.670	4.56	0.0349
Pred*Season*Microhabitat	1	1.489	0.78	0.3778

Table 3.-- Analysis of variance table for the giving up densities of *Peromyscus leucopus* on full moon vs. new moon and predator excluded vs. predator access plots.

Source	df	Mean Square	F Value	P > F
Pred	1	0.124	0.07	0.7973
Plot(Pred)	6	12.160	6.45	0.0001
Station(Pred*Plot)	32	4.536	2.41	0.0004
Moon	1	36.734	19.49	0.0001
Height	1	0.275	0.15	0.7029
Pred*Moon	1	4.299	2.28	0.1340
Pred*Microhabitat	1	0.301	0.16	0.6903
Moon*Microhabitat	1	0.369	0.20	0.6591
Pred*Moon*Microhabitat	1	1.287	0.68	0.4104

Table 4 -- Number of between plot movements (predator [+P] vs. no predator [+P]) for *Preomyscus leucopus* during pre- and postmanipulation periods

	Treatment			
Treatmant period	+P → +P	+P → -P	-P → +P	-P → -P
Pre	3	11	12	0
Post	2	12	10	7