EFFECT OF SPATIAL DISTRIBUTION AND ALTERNATIVE FOODS ON RISK OF PREDATION BY PEROMYSCUS LEUCOPUS

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Abstract. To explain the persistence of Lymantria dispar (Gypsy moth) in the Northeast American wooded ecosystem, their predator-prey dynamics must be unraveled. Specifically the foraging behavior of one of their predators, *Peromyscus leucopus* (white-footed mouse) was examined to look for the presence of spatially heterogeneous risk for the Lymantria pupae. Field evidence of high and low risk zones for the moth pupae from one of the most significant predators of this life stage can provide insight regarding key habitat features and their influence on the ecosystem. Indeed, the experiment showed a significant decrease in risk on the pupae surrounding a clumped food resource (p < 0.05).

INTRODUCTION

In the deciduous forest of northeast of North America, the oak tree, the gypsy moth, and the white-footed mouse form a three-part predator prey system whose population dynamics and behavior are linked. Moth larvae feed on oak leaves, so high numbers of moths often defoliate oak trees. Defoliated trees produce a reduced yield of acorns the following season. Low acorn output reduces mouse population the next year, so less moth pupae will be eaten. This cycle of effects leads to periodic outbreak levels of moth larvae, which can decimate oak forests during outbreak years (Jones et al. 1998).

The reverse trend would cause great numbers of mice and ever fewer numbers of moths until they would intuitively be eliminated from the local environment. Indeed, past studies on this system that used mathematical models have predicted local extinction of the moth during times of high mouse population. In reality, however, the moths persist even during such mouse booms (Schauber 2000). The discrepancy may be a result of the spatially homogeneous assignment of predation risk on the moths in the model. In nature, risk is not necessarily homogeneous, and often depends on the aggregation of an alternative prey species.

In a study done on big-eyed bugs, pea aphids, and pea plants, which form a similar predator-prey system as previously described, a more dense aggregation of pea plant foliage cause the big-eyed bugs to feed more on foliage and less on aphids (Eubanks and Denno 2000). This suggests that the aphids experienced spatially heterogeneous predation risk, as perhaps the moths do depending on the distribution of the mice's alternative prey. Such an effect would be explained according to the concepts of optimal foraging theory (Stephens 1986), and therefore mice should spend more time foraging on resources that are more aggregated around their source, rather than gypsy moth pupae, which may be more greatly dispersed (Gould et al. 1990).

In the summer, when the pupae are available, mice also have fruits and berries, nesting insects, and nuts to select from, and typically ingest much greater amounts of the latter three food types that lepidopterans (Wolff 1985). Presumably this is partially because of lesser search costs associated with these items than with lepidopterans. If this is so, the foraging behavior of mice may produce refuge areas of low or absent predation risk on the pupae, which are available as prey concurrently with these other food resources.

To investigate this possible explanation of gypsy moth persistence, I performed an alternative prey aggregation experiment testing the hypothesis that clumped food resources will decrease predation on immediately surrounding prey of the same species as well as an alternative species.

METHODS

The clumped food resource consisted of a mass of black oil sunflower seeds sufficient to satiate the local mouse population, and was placed in a feeder made from a two liter soda bottle with an entrance hole approximately an inch in diameter cut into the neck. The feeder was placed on the ground in a plastic crate weighted down with stones to prevent raccoon disturbance (Figure 1). Surrounding the feeder, individual sunflower seeds as well as freeze-dried moth pupae were deployed on the substrate along five annuli to achieve a spatially and density-consistent distribution (0.033 item*m⁻²) over a total 65 prey items (66% seeds and 33% pupae). The annuli had radii of 3, 7, 12, 18, and 25 meters extending from the central feeder (Figure 2).

A random subset of half of the individual prey items, as well as the central feeder, was placed on tracking plates to ensure the identity of the predator. The plates consisted of plastic sheets spread with a mixture of talcum powder and ethanol. The prey items were checked once every two days for eight days (four replacements). Attacked prey was replaced randomly on the same annulus, and the central feeder was replenished.

This 1964 m^2 circular treatment plot described above was replicated three times on the Greenhouse and three times on the Henry Farm experimental trapping grids at IES in Millbrook, New York. Six control plots, identical but lacking food in the central feeders, were also deployed on the two grids. Each of the plot's centers were placed at least 60 meters from one another to prevent the same mice from visiting more than one feeder.

The central feeders were problematic, and were filled with an increasing volume of seeds each replacement, since each time the amount necessary for satiation of the local mice was underestimated. The Greenhouse plots were performed first, and were subject to this problem. The Henry Farm plots were performed the week after, and there the proper estimate (4 liters of seeds) was achieved, as was local satiation.

Greenhouse Results

Using repeated measures analysis of variance to analyze the resulting data, a merely suggestive (not conclusive) effect of the central feeders as inexhaustible clumped food resources producing diminished predation risk on the surrounding prey was discovered (p = 0.074). This suggestive result for [treatment x distance] applies for both seeds and pupae, and was most likely inconclusive because of the afore-mentioned lack of complete satiation, although it appears a partial satiation was still possibly achieved. There was also a strong result (p < 0.01) of the tracking plates affecting a reduced predation risk for both seeds and pupae. No other statistically significant results were observed.

Henry Farm Results

For the Henry farm trial, there was significant statistical evidence that the clumped food resource in the center reduced the risk of predation on pupae only on the surrounding annuli (p = 0.015). Besides this originally hypothesized outcome, there were also strong effects for treatment versus control plots, distance from center, and tracked versus non-tracked prey in general. These effects were only produced for the pupae, however.

DISCUSSION

Presumably the predation risk was reduced for the pupal prey in a negative slope as distance from the central feeder increased because the mice spent a greater amount of their foraging time and energy on the largest clump of resources. Upon first discovery of the feeder, they probably ingested and stored their maximum amount before returning to their burrow. Since the location most likely stayed below average foraging cost of the surrounding environment, the mice likely tended to behave according to optimal foraging theory and returned repeatedly to the feeder, where cost remained minimal (Stephens 1985). This would probably entail less random foraging than normal, and thus more overlook of most of the disperse prey they would have otherwise attacked. Attacks that did occur on the annuli may have occurred before a particular mouse found the feeder, or because they happened to lie closer to the burrow relative to the path mice typically traveled. Such a factor could be understood by recreating a similar experiment in which mouse burrow locations were known (or placed in the case of a lab study), and the central feeder stocked several days before the annuli (giving the mice a chance to learn its location ahead of time).

Prey that were on the tracking plates may have been attacked less frequently because the unfamiliar odors of the talc and traces of human caused hesitation. The discrepancy between the attack rates on sunflowers versus pupae cannot be assuredly explained from this study, but some further hypothesis could be made. The mice may forage according to division of purpose, in which case they may have been satiated for the protein the pupae more efficiently provide before they were ever satiated for the carbohydrates and fats the seeds more efficiently provide (Ivan and Swihart 2000). Alternatively, the pupae may be a lower quality food source in general and may be less preferred in any situation.

Further studies that would elucidate the foraging behavior of *Peromyscus leucopus* include the general preference for seeds against pupae, any preference for fresh against freeze-dried pupae, and of course the repetition of this experiment with greater sample size and fewer procedural difficulties.

CONCLUSION

The hypothesis was confirmed, in part, by the data. The predation risk on an alternative pry was indeed reduced as a result of a larger clumped resource. The predation risk on the same prey, however, was not reduced. The confirmation is based only on one trial, since the other's prerequisite was not met. The clumped food resources were not sufficiently inexhaustible to produce a valid inference. The results of the other trial as well, though they do support the hypothesis, are at best suggestively valid, since the sample size was small. They do provide a quite plausible explanation for the persistence of *Lymantria dispar*, namely that plant-based food resources effectively shield the pupae from intensive predation by virtue of their aggregation and its creation of heterogeneous predation risk on the moths.

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LITERATURE CITED

Eubanks, M. D., and R. F. Denno. 2000. Host plants mediate omnivore herbivore interactions and influence prey suppression. Ecology **81(4)**:936-947.

- Gould, J. R., J. S. Elkinton, W. E. Wallner. 1990. Density Dependant suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies. Journal of Animal Ecology 59(1):213-233.
- Ivan, J. S., and R. K. Swihart. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. Journal of Mammalogy **81(2)**: 549-562.
- Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279:1023-1026.
- May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. Journal of Animal Ecology **47**:833-843.
- Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton, NJ. pp. 13-35.
- Schauber, E. M. 2000 (a). Modeling the indirect effects of acorn masting on gypsy moth population dynamics. Unpublished.
- Wolff, J. O., R. D. Dueser, and K. S. Berry. 1985. Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammology **66(4)**:795-798.





FIGURE 1. Feeder was placed on the ground in a plastic crate weighted down with stones to prevent raccoon disturbance.



FIGURE 2. Sunflower seeds as well as freeze-dried moth pupae were deployed on the substrate along five annuli to achieve a spatially and density-consistent distribution $(0.033 \text{ item}*\text{m}^{-2})$ over a total 65 prey items (66% seeds and 33% pupae).







