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HARDWOOD FOREST

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VERTICAL STRATIFICATION OF THE SMALL MAMMAL COMMUNITY IN A NORTHERN HARDWOOD FOREST

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ABSTRACT. Small mammal research in forests is typically conducted with traps placed on the ground or affixed to trees at heights up to only 2 meters. In a study conducted in northwestern Massachusetts, USA, we compared these conventional methods with an innovative new technique of trapping high in the forest canopy. Using an adaptation of Malcolm's (1991, 1995) pulley method and a canopy walkway, we compared canopy-trapping to ground-trapping. Total captures per station and total number of individuals captured per station differed between canopy and ground for both dominant small mammal genera: flying squirrels (*Glaucomys volans*) and mice (*Peromyscus* spp.). Ground traps were biased toward *Peromyscus* spp., underestimated the abundance of *G. volans*, and misrepresented the species composition of the small mammal community at the site.

We also compared canopy-trapping with understory-trapping and found that total captures per station and total number of individuals captured per station differed between understory and canopy locations. *Peromyscus* was more abundant in the understory. The small mammal community was represented quite differently according to trap location, and vertical stratification of this temperate forest community was evident. We discuss implications of these results for other species (e.g. gypsy moth).

INTRODUCTION

Forest canopies are inhabited by an extraordinarily diverse assemblage of organisms (reviewed in Wilson 1992). Yet studies of forest ecology have primarily taken place on the forest floor, which has a community of organisms quite different from that of the canopy (Lowman & Moffett 1993). Canopy studies are typically limited by the inherent difficulty of access, but recently the canopy has become more accessible for research through innovative use of cranes (Parker *et al.* 1992), walkways (Lowman & Bouricius 1993), and hot-air balloons (Hallé & Pascal 1992). Even so, despite the obvious importance of canopies to forest animals, little research has been conducted on mammals in the tropical forest canopy and virtually none in the temperate forest canopy (Malcolm 1991, 1995; Emmons 1995).

Techniques used to study small woodland mammals on the forest floor include radio telemetry (Wolff & Hurlbutt 1982, Mikesic & Drickamer 1992), fluorescent powder tracking (Lemen & Freeman 1985, McShea & Gilles 1992, Etheridge *et al.* 1989, Mullican & Baccus 1990), smoked aluminum plates (Raphael *et al.* 1986,

Carey & Witt 1991), plastic-laced bait (Packer & Layne 1991), and live-trapping (Harney & Dueser 1987, Carey *et al.* 1991, Witt 1991, Sonenshine *et al.* 1979, Kaufman *et al.* 1985).

Of these, the two-dimensional, ground-level grid of live traps is the standard setup for assessing temperate small mammal populations, but this technique does not adequately sample populations of arboreal woodland mammals (Witt 1991, Etheridge *et al.* 1989). Researchers in temperate forests have attached traps to tree trunks to account for vertical stratification of mammals in forests (Harney & Dueser 1987, Kaufman *et al.* 1985, Carey *et al.* 1991, Hall 1991), yet their traps have been affixed within human reach, usually 1–2 m above the ground. The fluorescent powder technique (Lemen & Freeman 1985) has also been used to investigate arboreality of small mammals, but the practical difficulties of following a trail through the upper layers of a forest restricted these efforts to heights of only a few meters above ground (McShea & Gilles 1992, Lemen & Freeman 1985, Etheridge *et al.* 1989, Mullican & Baccus 1990).

Recently, Malcolm (1991) designed a system employing pulley mechanisms that enabled him to trap high in the canopy of a neotropical forest. Relative abundance of mammal species differed significantly between 0, 2, and 15 meter trap heights. We hypothesized that a similar pattern exists in temperate forests, although with overall

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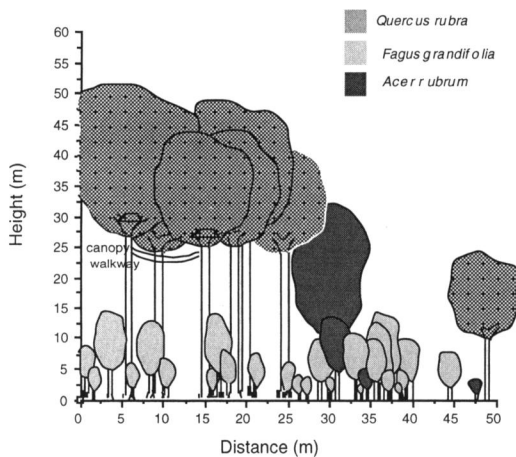


FIGURE 1. Site profile (50 m \times 5 m) representative of site and including one station (canopy walkway). Dominant canopy species was red oak (*Quercus rubra*). Understory was primarily beech (*Fagus grandifolia*).

lower species diversity than in Malcolm's tropical Brazilian forest.

Interest in the vertical distribution of small mammals in temperate oak forests stemmed from our observation that, at the time of our study in northwest Massachusetts, USA, predation on gypsy moth (*Lymantria dispar*) pupae increased with height above ground, reaching a maximum in the canopy. We speculated that this discrepancy was caused by differences in the predator community between ground and canopy. Our preliminary data on predation have since been supplemented, and made more complex, by further experiments, some of which yielded contradictory results. Nonetheless, we were prompted to examine vertical stratification of the small mammal predator community to understand the mechanism causing increased predation with height.

Our study examined the influence of trap height on relative abundance of small mammal species in a temperate forest. By comparing both canopy-trapping with ground-trapping, and canopy-trapping with understory-trapping (1–2 m on tree trunks), we tested the hypothesis that trapping on the ground or in the understory may provide a representation of the small mammal community that is misleading compared to trapping in the canopy.

METHODS

The study was conducted at Williams College in the Hopkins Memorial Forest, a northern hardwood tract covering 2250 acres in NW Massachusetts, USA. Our site was predominantly red oak (*Quercus rubra*) and red maple (*Acer rub-*

rum), with an understory of beech (*Fagus grandifolia*) (FIGURE 1). Trees reached heights of approximately 50 m and were aged at an average of 95 years by increment boring (Maxwell & Collier 1991).

Canopy- Versus Ground-trapping

Five stations were established to compare trapping in the canopy with trapping at ground level. Each station consisted of three Sherman live traps in oak canopy (15–20 m) and three traps on the ground approximately 10 m east of the canopy-trap tree. Stations were approximately 20 m apart. Canopy-trapping at four of the stations was accomplished using an adaptation of Malcolm's (1991) pulley system. Canopy-trapping at the fifth station was accessed by a canopy walkway bridge and platform system constructed as a research station (see Lowman & Bourcius 1993, 1995).

To minimize the possibility of animals present at a station not being captured because of insufficient traps, three traps per location (canopy and ground) were used at each station. (In a pilot study, we repeatedly set out five traps per location; the largest number of animals captured in a single night was three.)

Traps were baited with a mixture of peanut butter, oatmeal, and bacon. They were checked at 0700 hr. Captured animals were identified to species and most were ear-tagged. Trapping was conducted for 9 days during February and March 1992.

Canopy- Versus Understory-trapping

In this experiment, each station consisted of three traps in oak canopy and three traps nailed 1–2 m above the ground on a tree trunk approximately 10 m east of the canopy traps. Trapping was conducted at five stations for 12 days during March and April 1992 using the same protocol as in the previous experiment.

Data Analysis and Statistics

For statistical analysis of trapping data, observations on 'number of *individuals* captured' are preferable as experimental units to observations on 'number of captures' because the former have a greater degree of independence (i.e. 'number of captures' may include recaptures, which likely are influenced by previous captures). However, in both of our experiments some animals were not tagged, and ID numbers of some recaptured animals were not obtainable. Consequently, analysis of the data based on 'number of individuals captured' was hampered.

Therefore, to approach the question of how

TABLE 1. Number of small mammal captures per location (canopy, understory, ground) at each station for (a) canopy vs. ground comparison (9 trap nights) and (b) canopy vs. understory (1–2 m) comparison (12 trap nights).

Station No.	<i>Glaucomys volans</i>				<i>Peromyscus</i> spp.			
	Canopy		Ground		Canopy		Ground	
	Total captures	Min./Max. No. Indiv.	Total captures	Min./Max. No. Indiv.	Total captures	Min./Max. No. Indiv.	Total captures	Min./Max. No. Indiv.
1	2	2/2	0	0/0	0	0/0	2	1/1
2	6	2/2	1	1/1	0	0/0	1	1/1
3	4	1/2	0	0/0	0	0/0	3	2/3
4	10	7/7	0	0/0	1	1/1	2	1/2
Mean	5.5	3.0/3.25	0.25	0.25/0.25	0.25	0.25/0.25	2.0	1.25/1.75
SD	3.42	2.71/2.5	0.50	0.50/0.50	0.50	0.50/0.50	0.82	0.50/0.96

Station No.	<i>Glaucomys volans</i>				<i>Peromyscus</i> spp.			
	Canopy		Understory		Canopy		Understory	
	Total captures	Min./Max. No. Indiv.	Total captures	Min./Max. No. Indiv.	Total captures	Min./Max. No. Indiv.	Total captures	Min./Max. No. Indiv.
1	4	3/4	0	0/0	0	0/0	1	1/1
2	2	2/2	3	3/3	0	0/0	2	1/2
3	1	0/1	0	0/0	0	0/0	3	1/3
4	4	3/3	2	2/2	1	1/1	1	1/1
Mean	2.75	2.0/2.5	1.25	1.25/1.25	0.25	0.25/0.25	1.75	1.0/1.75
SD	1.5	1.41/1.29	1.5	1.5/1.5	0.5	0.5/0.5	0.96	0/0.96

'number of individuals captured' varied between locations, we made note of recaptures and calculated both the minimum and the maximum possible number of new individuals captured at each station for each experiment. Calculation of minimum possible number of individuals assumed that all untagged animals were subsequently recaptured in the experiment and therefore should not be counted as unique individuals. Calculation of the maximum possible number of individuals assumed that all untagged individuals were not subsequently recaptured and therefore always should be counted as unique individuals. To test for differences between heights we calculated Mann-Whitney U test statistics for a) total number of captures (including recaptures), b) minimum possible number of individuals captured, and c) maximum possible number of individuals captured. However, trapping data are notorious for containing violations of various assumptions of statistical theory, particularly assumptions of independence, and our p-values accordingly should be examined with some caution.

Along with examining variation in small mammal population sizes by height, we also were interested in whether the species composition of the small mammal community as a whole varied between heights. At our site, the community consisted primarily of two genera (*Peromyscus* and *Glaucomys*). This implied one of two possibili-

ties: That the numerically dominant genus at ground-level (*Peromyscus*) could remain dominant at all strata (although overall abundances might change), or that numerical dominance could shift depending on height to the other genus (*Glaucomys*).

Distinguishing between these options could potentially help explain our observed pattern of predation on gypsy moth pupae. Toward this end, we used the G test to consider the hypothesis that the dominant species (as measured by number of captures) was independent of height.

No animals were captured at one of the five stations throughout the duration of both experiments. Therefore, this station was eliminated from analysis because it provided no information on stratification of the small mammal community.

RESULTS

Canopy- vs. Ground-trapping

In the canopy, we captured 1 *Peromyscus leucopus* and 22 *Glaucomys volans*, including 9 *G. volans* recaptures (TABLE 1). The minimum possible number of *G. volans* individuals captured was 12; the maximum was 13.

At ground level, only 1 *G. volans* was captured, while 8 *Peromyscus* captures occurred, including one confirmed recapture. Minimum and maxi-

mum possible numbers of *Peromyscus* individuals captured were 5 and 7, respectively. (The *G. volans* captured at ground level was not tagged and may have been subsequently recaptured in the canopy.)

The Mann-Whitney U test (with Z corrected for ties) showed a significant difference in total *G. volans* captures between canopy and ground level ($p=0.018$). Likewise, the difference in total *Peromyscus* captures between canopy and ground level was significant ($p=0.022$). Results were also significant ($p<0.05$) when minimum and maximum possible numbers of individuals were used instead of total number of captures.

The G test for independence with Williams' correction was highly significant ($df=1$, $p<0.05$) for number of captures of each species according to location (canopy vs. ground), indicating that the dominant genus of the small mammal community varied with trap location. *Peromyscus* dominated at ground level, whereas *Glaucomys* dominated in the canopy.

Canopy- vs. Understory-trapping

Over the 12-day period, we captured 11 *G. volans* and 1 *Peromyscus maniculatus* in the canopy (TABLE 1). Minimum and maximum possible numbers of *G. volans* individuals captured were 8 and 10, respectively.

Only 5 *G. volans* captures occurred in the understory traps, whereas 7 *Peromyscus* captures occurred there. None of the *G. volans* captured in the understory went untagged. Possible numbers of captured *Peromyscus* individuals were 4 (minimum) and 7 (maximum).

Captures of *G. volans* in the canopy included one individual that previously had been captured in the understory traps and one individual initially captured in the understory and then recaptured twice in the canopy.

More than twice as many squirrels were captured in the canopy as in understory traps, but the Mann-Whitney U test (with Z corrected for ties) showed no significant difference in *Glaucomys* captures between canopy and understory traps ($p=0.19$). Difference in *Peromyscus* captures between canopy and understory traps was significant ($p=0.034$). The same pattern of significant differences resulted when either the minimum or maximum possible number of individuals was analyzed instead of the total number of captures.

The G test for independence with Williams' correction was significant ($df=1$, $p<0.05$) for number of captures of each species according to location (canopy vs. understory), once again showing that the composition of the small mammal community varied with location.

Spatial Patterns of Flying Squirrel Recaptures

In the entire study, nine individual flying squirrels (*Glaucomys volans*) were captured multiple times. All were captured most frequently in the canopy, including five individuals that were always captured in the canopy. Of these five, two individuals were each captured three times, and the other three were captured twice. The other four recaptured animals were all captured most frequently, but not exclusively, in the canopy. No individuals were repeatedly captured in the low (ground/understory) traps alone.

Five recaptured animals were always captured at the same station. This included 1 individual captured 5 times at the same station, 2 individuals captured 3 times at the same station, and 2 captured twice at the same station. Two other individuals were captured at the same station 2 of the 3 times they were captured. One individual was captured 4 times, 3 at the same station.

DISCUSSION

Our adaptation of Malcolm's (1991) pulley method for canopy-trapping revealed striking differences in the small mammal community across vertical strata of a temperate forest.

The importance of trapping in the canopy was apparent as the relative abundance of small mammals differed dramatically according to trap height. Ground-level traps gave the misleading impression that the small mammal community at the site was dominated by *Peromyscus* spp., with *G. volans* comprising only a minor fraction of the community. Traps located in the canopy showed that flying squirrels were in fact quite abundant. In our canopy- vs. ground-trapping comparison, captures of flying squirrels in the canopy outnumbered those on the ground by a factor of 22. Flying squirrels present in this abundance may play a significant ecological role in the forest. Their importance would have gone undetected with ground traps alone.

The low frequency of flying squirrel captures in our ground traps is consistent with prior research (Witt 1991, Carey *et al.* 1991). A United States Forest Service manual on methods for measuring populations of arboreal rodents recommends that each station consist of one arboreal trap and one ground trap (Carey *et al.* 1991). Yet, it suggests placing the arboreal trap only 1.5 m above ground.

We found that traps placed low on tree trunks did not adequately sample the flying squirrel population. In the comparison between canopy- and understory-trapping, more than twice as many flying squirrel captures occurred in the canopy as in the understory. Furthermore, all re-

captured squirrels were captured more frequently in the canopy than in the understory traps. Five individuals that were recaptured a total of twelve times would not have been captured at all by an experimental design that did not include canopy traps. Thus, in order to achieve comprehensive sampling of arboreal mammal populations, height is a crucial factor. Canopy traps are necessary in addition to ground and understory traps.

The effect of vertical stratification is equally true for species such as *Peromyscus* spp., which are generally thought of as semi-arboreal rather than arboreal. To our knowledge, our observations of 2 *Peromyscus* spp. individuals at approximately 20 m high in the forest canopy are the first published accounts of *Peromyscus* occurring in the canopy, although their climbing ability is well-known (Horner 1954).

Our research showed that, as expected, more *Peromyscus* were captured on the ground and in the understory than in the canopy, but it is clear that to adequately study habits and populations of even a "semi-arboreal" small mammal such as *Peromyscus*, the full extent of forest strata must be considered, from ground-level to canopy. This is especially true for *P. leucopus* and *P. maniculatus*, because they nest above ground (Stah 1980, Wolff & Hurlbutt 1982) and much of their traveling distances may be in trees (Etheridge *et al.* 1989).

Beyond simply censusing small mammal populations, the pulley method facilitates study of animal behavior as well. For example, with further use of this method, and without having to overcome limitations of the fluorescent powder or plastic-laced bait techniques, it would be possible to determine whether *Peromyscus* travel regularly between ground and canopy or tend to remain in a particular stratum. The pulley method would also be extremely useful for studying the relative arboreality of various species. As expected, our experiments established that *Glaucomys volans* was far more arboreal than *Peromyscus*, but the pulley technique could also be used to distinguish differences in the arboreality of sympatric *Peromyscus* species. Other methods have been used for this purpose, but none has extended more than a few meters above the ground (Stah 1980, Harney & Dueser 1987, Packer & Layne 1991). Our captures of 2 *Peromyscus* (believed to be 1 *P. leucopus* and 1 *P. maniculatus*) in the forest canopy indicate that it would be possible to determine which species uses the upper strata more frequently.

Finally, along with population censuses and behavioral studies, the pulley method may prove useful for exploring ecological interactions within the forest community. Our previous research, for example, suggested that the flying squirrel,

known to consume gypsy moths and other insects (Smith & Lautenschlager 1978, Harlow & Doyle 1990), may have been an important predator on gypsy moth pupae experimentally placed at the site. Predation is believed to be an important factor affecting dynamics of sparse gypsy moth populations (Bess 1961, Bess *et al.* 1947, Campbell & Sloan 1977a, 1977b). *Peromyscus* has been widely implicated as the most important predator of gypsy moth pupae, but this is based on indirect evidence such as (1) scraps of dead pupae purported to have been killed by *Peromyscus* (Campbell & Sloan 1976) and (2) abundance of *Peromyscus leucopus* as assessed by conventional ground-level grids of live traps (e.g. Elkinton *et al.* 1988). Our research indicates that acceptance of *Peromyscus* as the most important gypsy moth predator may be premature, however, because scraps of dead pupae may have been left by *G. volans*, not *Peromyscus*. Ground-level trapping provides misleading information on the composition of the woodland small mammal predator community, meaning that large relative abundances of *Peromyscus* at ground-level may not necessarily implicate it as the most important small mammal predator of the gypsy moth.

Often it is suggested that predation on gypsy moths by birds in the canopy is much more common in Europe than in North America. Campbell & Sloan (1976) invoked this as an explanation for evolution of ground-level pupation by gypsy moths in their native Europe and proposed that the same behavior in North American forests exposes individuals to higher mortality than if they remained in the canopy. Campbell & Sloan (1976) suggested that, rather than acting as a refuge from canopy predation, this behavior is a counterproductive evolutionary relict. Yet, our data show that density of flying squirrels, a potential gypsy moth predator, and amount of predation may, in fact, be greatest in the canopy, making ground-level pupation an effective strategy for gypsy moth survival even in North America.

Our adaptation of Malcolm's (1991) pulley system was a valuable means for studying arboreal small mammals in a temperate forest. More appropriate for the study of climbing animals than either ground or trunk traps and more practical than non-trapping methods such as fluorescent dye trails and plastic-laced bait, canopy-trapping may reveal behavioral characteristics and ecological interactions currently unknown.

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