

1573294

DEB/DEB



United States
Department of
Agriculture

Gypsy Moth Handbook

Ag84Ah
Cop. 3

Combined Forest Pest
Research and
Development Program

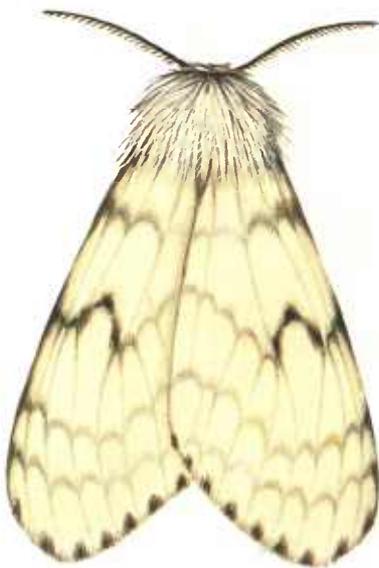
Agriculture Handbook
No. 534

Predators of the Gypsy Moth

U.S. DEPT. OF AGRICULTURE
NAT'L. AGRIC. LIBRARY
RECEIVED

APR 23 '79

PROCUREMENT SECTION
CURRENT SERIAL RECORDS



Contents

In 1974 the U.S. Department of Agriculture initiated the Combined Forest Pest Research and Development Program, an interagency effort that concentrated on the Douglas-fir tussock moth in the West, on the southern pine beetle in the South, and on the gypsy moth in the Northeast. The work reported in this publication was funded in whole or in part by the program. This manual is one in a series on the gypsy moth.

Introduction	2
Understanding Predation	3
Life history of the gypsy moth	3
Gypsy moth behavior and predation	6
Role of predators in gypsy moth control	9
Predation and gypsy moth population stability	10
Why natural control?	10
Predation potential of birds and mammals	12
Factors affecting predator potential	13
Effect of defoliation on gypsy moth predators	16
The Predators	17
Overview	17
Birds	17
Mammals	31
Amphibians, reptiles, and fish	46
Invertebrate predators	51
Reexamining Our Wildlife Perceptions	63
Conclusion	64
References	70

Predators of the Gypsy Moth

by

Harvey R. Smith and R. A.

Lautenschlager ¹

Introduction

An all-out research effort by the U.S. Department of Agriculture is being made to find ways to control the gypsy moth, *Lymantria dispar* (L.), a major pest in the Northeast that has defoliated as much as 2 million acres of forest and shade trees in a year. Since its accidental release in Massachusetts in 1869, the gypsy moth has spread north into Canada, south into West Virginia, and west into Ohio. The insect is most damaging as a larva (caterpillar), when it feeds on leaves from May to early July. Although the gypsy moth prefers oaks, more than 500 plant species are eaten by this insect (Forbush and Fernald 1896, Mosher 1915).

The goal of the Expanded Gypsy Moth Program is to develop and select ecologically sound, practical measures to manage the gypsy moth and reduce its damage. Scientists are currently developing an integrated control system, a program that uses a combination of control measures in a selected area. This system emphasizes the biological control methods of interrupting the gypsy moth's reproductive cycle, spreading its fatal diseases, exploiting its parasites and predators, and using safer, selective pesticides.

¹Respectively, research biologist and consulting wildlife biologist, Forest Service, Northeastern Forest Experiment Station, Hamden, Conn.

Understanding Predation

Life History of the Gypsy Moth

An understanding of predators and the associated components of predation is necessary to develop a successful gypsy moth control program. It is important to know how the predators that kill gypsy moths affect and are affected by the other components of an integrated control management system.

The goals of this booklet are to:

- Provide insight into the variety, number, potential, and impact of gypsy moth predators.
- Aid in the understanding of the components of a predator/prey system.
- Pave the way to understanding the relationship of gypsy moth predation with predation of other northeastern forest insect pests.
- Help to develop an appreciation for the intricacies of the forest ecosystem.

Like all butterflies and moths, the gypsy moth has four distinct life stages: egg, larva, pupa, and adult (figs. 1–3). In the Northeastern United States gypsy moth eggs usually hatch around the first of May. The young larvae grow rapidly; males molt four times and females five times. The stages between these molts are called instars. First-instar larvae climb trees to feed on tender, spring foliage, and to spin silken threads, from which they hang and are then blown by the wind to other areas. Larvae remain on or near foliage until they have molted twice (third instar). In the fourth instar a behavioral change occurs, and the insects descend from the tree crowns each day at dawn to rest in the litter around the base of the host tree or under flaps of loose bark. Larvae leave these resting places at dusk to return to the tree crowns to feed. In sparse populations this daily migration continues for 2 to 3 weeks until the larvae are fully grown (fifth instar for males, sixth for females). Most of the gypsy moth larvae will pupate in this same daytime resting location. However, when gypsy moth densities are high, older larvae remain on the foliage and feed day and night, and pupation occurs mainly on the trunks or under large limbs of the host tree.



Figure 1.—Gypsy moth larva.
Figure 2.—Female (left) and
male gypsy moth pupae.
Figure 3.—Gypsy moth female
adult with egg mass.



3



Female gypsy moth larvae pass through one more instar than males, pupate about 1 week later, and are larger than males. Both female and male adult gypsy moths emerge from their pupal cases in about 2 weeks. The adult female moth has wings but rarely flies. She rests on a tree, emitting a potent chemical

signal called a sex pheromone that attracts male gypsy moths. After mating, the female normally deposits one egg mass containing between 100 and 800 eggs. During egg laying, hairs from the female's abdomen are incorporated into the egg mass to insulate the eggs.

Gypsy Moth Behavior and Predation

The gypsy moth in North America exhibits a defense behavior that evolved in its native European habitat—the migrating of larvae from the tree crown to the litter at the base of the host tree. Campbell and Sloan (1976) suggested that this behavior evolved to enable the gypsy moth to evade natural enemies (birds and parasites) that were active in the canopy. In North America, however, this downward migration increases the insect's vulnerability to mammals and often results in high gypsy moth mortality.

The gypsy moth has other defenses, including stiff, prickly hairs and warning coloration, both apparent in the larval stage. Buckner (1966) pointed out that there are few vertebrate predators of the forest tent caterpillar and the gypsy moth, apparently because of their strong defenses against predation by vertebrate predators.

These defense mechanisms may have limited the number of gypsy moth predators in North America, but many predators do exist. Some appear completely unaffected by these defense mechanisms and others have developed ways of coping with or circumventing them. For instance, small mammals often attack gypsy moth larvae from the underside, removing organs and fluids, while leaving the larval skin and the protective, prickly hairs intact. Some birds that ingest the larvae whole periodically shed and regurgitate their stomach linings that have become embedded with the larval hairs (fig. 4).

The defense behavior of larvae raises some interesting questions about its effectiveness for survival of the species. In this country birds still seem an important regulatory force (Campbell and Sloan 1977), causing the gypsy moth larvae to maintain their pattern of resting in litter at the base of a tree. But is this behavior really protective, since larvae in litter are exposed to small mammals? Are the larvae surviving only to become prey in the pupal stage?

Bess (1961) and Bess et al. (1947) indicated that in moist forests, when gypsy moths rest in the litter, survival is low, and innocuous populations exist. Campbell and Sloan (1976, 1977) verified these observations and presented further evidence that vertebrates are essential in maintaining low populations. They estimated that vertebrates killed 70 percent of the pupae in a series of sparse, stable populations and that white-footed mice (*Peromyscus*) accounted for 40 percent of those removed. They also showed that when birds and small mammals were removed, the insect populations could increase tenfold in 1 year.

Gypsy moth larvae seeking a daytime resting location often select the dark tunnels of small mammals located just below the litter. In a sparse gypsy moth population in Mashpee, Mass., which showed no visible signs of defoliation, gypsy moth larvae apparently favored these small mammal tunnels as a resting location (Paszek 1977). An



Figure 4.—Cuckoo stomach.

Animal and Plant Health Inspection Service field crew collected within a 52-ha area approximately 8,000 female sixth-instar larvae, prepupae, and pupae almost exclusively from small mammal tunnels located at the base of oak trees. Few pupae were found anywhere else. This behavior of resting and pupating in small mammal tunnels is not unique and has been observed in our study area in Connecticut, but the fact that gypsy moths used these tunnels almost exclusively at pupation locations seemed unusual. Small mammal predation was evident in these tunnels by the large number of pupal fragments found (Paszek 1977), raising the question of what is the subsequent effect on survival in these situations.

The role of small mammals as predators of the gypsy moth in Europe is not well known. However, the effectiveness of defense mechanisms that the gypsy moth evolved in Europe may have been lessened in northeastern American forests because the potential predators and habitats are different.

We know of only one study dealing with mammalian predators of the gypsy moth in Europe—Rotschild 1958. He reported that the remains of gypsy moth larvae and pupae were found in the stomachs of *Apodemus flavicollis* and *A. sylvaticus* (Old World wood mice) and *Dyromys nitedula* (the tree dormouse) in the Soviet Union, and that the stomachs of these mammals were often filled exclusively with the remains of these insects. These European rodents, plus the smaller *Micromys* sp. (the harvest mouse), have characteristics that could make them important gypsy moth predators: All eat insects, and the forest dormouse and the harvest mouse are skillful climbers.

It is difficult, however, to draw any conclusion about the role of European mammals in gypsy moth population dynamics. For example, one American scientist who visited the Soviet Union in 1975 was told that *Apodemus* was not important in regulating gypsy moth populations (Lewis 1978).

Although *Apodemus*, *Dyromys*, and *Micromys* may be gypsy moth predators in Europe, only Rotschild's (1958) paper indicates that the first two are. In northeastern American forests, we have two common small mammals that are important gypsy moth predators: The white-footed mouse and the shorttailed shrew (*Blarina*). Both of these mammals readily eat gypsy moths, and the white-footed mouse commonly climbs trees to eat larvae, pupae, and adult moths. Although European forests contain a variety of shrews, including several *Sorex* sp. (longtailed shrews) and *Crocidura* sp. (the white-toothed shrew), there is no equivalent of the North American shorttailed shrew.

Habitat differences also influence predator effectiveness. The long dry summers typical of the south-central European forests where gypsy moths occur cause considerable vegetation competition for the available moisture. This situation often results in forests composed of overstory trees with more grasses and fewer shrubs in the understory (Smith 1978). This condition provides poor habitat for the small mammals that depend on dense shrubs for both food and cover and probably limits both the number and diversity of small mammals that live in these areas. Forests in the Northeastern United States, however, are quite moist and often have well-developed shrub and herb layers that offer both food and cover to small mammals and birds.

Role of Predators in Gypsy Moth Control

In each life stage, the gypsy moth becomes prey and is part of the diet of several animals, but until recently the role of predators in gypsy moth population dynamics was not well documented. The predatory role of birds received most of the attention of early naturalists (Forbush and Fernald 1896), who based their findings on daytime observations. Diurnal (daytime) birds were considered to be the primary predators of forest insects, and these investigators seldom discussed nocturnal mammals or mentioned other vertebrates.

Birds were recognized as being important in gypsy moth population dynamics and as an instrument of control over 80 years ago when Forbush and Fernald (1896) identified several species that ate gypsy moths. The same study also mentions amphibians, spiders, and insects as predators; mammals, however, are ignored (except skunks, which are reported as feeding on adult female moths).

Hamilton and Cook (1940) emphasized that the beneficial role of small mammals in the economy of the forest had received little attention. When Buckner (1966) described the role of vertebrates in biological control of forest insects, the situation still had not changed significantly. Bess et al. (1947) were the first to suggest that small mammals (mice and shrews) were important predators of the gypsy moth. Although more species of birds have been identified as predators of the gypsy moth in this country, mammals may have a more important impact on gypsy moth populations. Gypsy moth populations in Japan (Furuta 1976) appear to be regulated by birds, but in the United States, the roles of birds and mammals appear uniquely to complement each other.

In the past 10 years considerable knowledge of the predatory role of birds and mammals has been gained, and it is hoped that someday forest managers will accept vertebrates as an important regulatory force and utilize that knowledge in pest management systems.

Predation and Gypsy Moth Population Stability

Predation, although a powerful natural force that operates simultaneously with other physical and biotic forces such as climatic catastrophes, habitat limitations, food shortages, diseases, and parasites, has limitations. Predation does not exert constant pressure and as a suppressive force does not reduce populations to levels as low as those resulting from climatic catastrophes, starvation, and epizootics.

What is the relationship between predation and gypsy moth population stability? This is difficult to answer because the specific causes leading to gypsy moth outbreaks have not yet been determined. We do know, however, that in certain circumstances predators are capable of maintaining gypsy moth populations at harmless levels for an indefinite period (Campbell 1975, Campbell and Sloan 1977), but it would be inaccurate to say that predation can control gypsy moth populations or prevent future outbreaks.

Gypsy moth population densities do respond to predator pressure, but periods of low predatory pressure alone do not necessarily cause an outbreak. When low predatory pressure coincides with other population "releasing" mechanisms, an outbreak is more likely to occur. Furthermore, during an outbreak, predation may seem insignificant when other forces, such as disease, are decimating gypsy moth populations.

Why Natural Control?

The gypsy moth has found an ecological niche in this country and is here to stay. What we must do now is choose how we wish to live with or control this insect:

- Do nothing and let nature take its course.
- Continue to use pesticides on the hot spots.
- Attempt an integrated control management program that may allow us to maintain low gypsy moth populations.

The history of gypsy moth control in this country has three stages. First there was the mechanical era, a seek-and-destroy approach, where armies of men sought to eradicate the insect with fire and creosote. This approach resulted in only local and temporary suppression of the pest.

Then came the chemical era, the pesticide approach, when millions of acres of forest and woodland were aerially sprayed with DDT. Although this direct kill approach provided quick and decisive protection from the insect, it was again only temporary. The money and effort expended on pesticides did not get at the underlying causes of gypsy moth outbreaks and did nothing to prevent outbreaks from reoccurring. Watt (1968) stated that the aerial application of pesticides, if timed correctly, would save the foliage but would not reduce the populations during the following generation. He believed that the main factors determining generation-to-generation density were weather and other density-dependent factors.

Brown (1961) demonstrated that despite extensive spraying of DDT over 600,000 acres in 1950, gypsy moth populations rose in 1951.

The reason pesticides cannot keep pace with forest insect pests involves the basic biology of the pest species. As Watt (1968) said, “. . . through eons of natural selection it has evolved homeostatic capabilities to deal with catastrophes so that insecticidal treatment is merely one of a class of events the species is adapted to withstand.”

The third stage, integrated control, is an ecological approach to the control of a pest insect. An integrated control program combines suitable control techniques—biological agents such as pathogens, parasites, and predators, habitat manipulation, and chemicals—in an ecologically compatible way. A properly executed integrated control system should maintain pest populations below levels of economic injury. Smith (1969) stated that integrated control obtains uniqueness because emphasis is put on the fullest practical utilization of existing mortality and suppressive factors in the environment, and that strategy is one of management and containment rather than one of seek and destroy.

For reasons of economy, and because of concern about chemical contamination, it would be wise to control forest pests through management of suppressive forces,

which are self-limiting and keep pest species at low densities. To successfully accomplish this goal it is necessary to analyze natural mortality factors and determine the influence or impact of each factor on the pest. Predators are one of the most promising natural mortality factors being considered.

The fundamental reasons why biological controls could work have been outlined by Watt (1968):

“The affected, or doomed, individuals are left in the population *after* they have been committed to die, or *after* they have been committed to produce sterile offspring. In this way, individuals who are destined not to do the population any good in the future are still in the population, eating food, taking up space, and in general exerting competition pressure on individuals who will survive the treatment. In this situation, the population of pests has the worst of both worlds: it faces the same, or almost the same, competition pressure that there would be without control, so no anticontrol homeostatic mechanism is elicited, yet at the same time the population is being, or is about to be, controlled.”

Predation Potential of Birds and Mammals

Birds and mammals have been recognized as important predators of the gypsy moth for many years, but it is only recently that we have been able to begin to understand and appreciate their precise roles within sparse gypsy moth populations.

Two major factors are unique to birds and mammals that allow them to achieve such an economically important impact potential: They are warmblooded, and they have a highly developed learning ability. Because they are warmblooded they have a high metabolic rate requiring a tremendous amount of food just to produce the energy necessary to maintain a warm body temperature. Additional food is required by birds and mammals to have enough energy to perform other activities such as running, climbing, flying, and reproduction. Adult birds may eat one-third their weight per day, and young birds often eat more than one-half their weight per day (Chapman 1968). One study of food consumption by birds and mammals in a 1,000-ha virgin forest in Czechoslovakia indicated that the total bird population consumed food equaling about 25 percent of its weight daily, and the mammal community consumed the equivalent of 20 percent of its weight daily (Turcek 1952).

Those mammals most useful as predators of forest insects—mice, shrews, and voles—eat weight equivalents much greater than 20 percent of their own weight every 24 hours. Shrews have ravenous appetites and are alleged to consume their own weight equivalent in food every day.

The other major factor is the degree to which certain functions of the brain are developed in these vertebrates. Both birds and mammals learn to search out places where various foods are found, concentrate their foraging in those places, learn to avoid insect defense mechanisms, and seek insects or parts of insects that are most palatable or desirable. For example, the white-footed mouse prefers the larger female pupae to the smaller male pupae and, after catching moth larvae, eats only a very small portion of the insect. Hoarding, a behavior associated with learning and well developed in mammals, has been demonstrated by shorttail shrews, which often gather pupae and carry them below ground to be eaten later.

By necessity to meet metabolic demands, the activity patterns and the inquisitive and opportunistic behavior of birds and mammals make them particularly adapted for searching out and killing gypsy moths. Although diets will vary among forested areas, and impact potential can be lessened by other prey and food items, both birds and mammals can have a significant impact on gypsy moth populations.

Factors Affecting Predator Potential

Perhaps the key to the effectiveness of bird and small mammal predation on sparse, stable gypsy moth populations lies in the behavior of the gypsy moth. The feeding response of a predator to a prey usually follows this pattern: At low prey densities, a few or no prey are attacked; at moderate prey densities, a steep rise in predation occurs; at high prey densities, predation levels off. This pattern would hold true for the gypsy moth and its predators if the insects did not migrate out of the canopy and aggregate in lower resting locations during the day. This prey behavior creates a unique situation; instead of the predator chasing the prey, the prey (gypsy moth) comes to the predator at dawn and dusk, when the insect is visible and attracting attention simply by moving and when many vertebrate predators are at their peak activity.

By aggregating under loose bark or leaves in the litter, the insect is found in predictable resting sites that predators have learned are rewarding when searched. The predators are thus able to exert much greater predatory pressure on sparse gypsy moth populations, which aggregate, than would be expected on insect prey (at low population densities) with a random resting distribution.

Determining the predator potential for any species is difficult because of the variables involved.

Understanding the following variables will help us to assess predator potential:

- The abundance and availability of the prey (prey density), or at what prey density do predators recognize the prey as a potential food and start to search for it.
- The abundance and availability of alternate foods (including other prey items).
- The density of predators.
- The size of predators.
- The number and the timing of the birth of the predators' young.
- Each predator's period of residency and the size of its feeding area.
- Each predator's willingness to eat the prey and the life stages preferred and eaten.
- Each predator's ability to capture and consume the prey (prey defenses, conspicuousness, size, and palatability, and the same characteristics of the alternative food sources).

Predators normally do not search for or prey on species that are rare because these species are seldom encountered. Even when a preferred prey item becomes available, the amount consumed depends on the abundance and availability of alternative foods (Tinbergen 1960).

Predator density is a major factor to predator potential. For example, a low-density predatory species that eats many gypsy moths will not have as great an impact on the prey population as an abundant predator that eats moderate amounts of the insect. A predator's size is also important. It is energetically inefficient for large predators to feed on small prey, except when the prey populations are dense, but a small predator may use a small prey extensively whenever it is available.

Several experiments have been conducted with caged mammals in order to better understand predator potential. The history of one experiment and two observations from natural situations will help to illustrate several factors that affect predator potential.

In the experiment, six adult male white-footed mice were individually caged with 100 fifth-instar gypsy moth larvae and water. Two of these mice also received mouse chow (a dried laboratory food), and two others received mouse chow and sunflower seeds. Mice given no alternative food ate 98 percent of the larvae, mice with mouse chow ate 57 percent of the larvae, and mice with mouse chow and sunflower seeds ate 23 percent of the larvae. The effect these alternative foods had on the percentage of larvae eaten after 48 hours clearly demonstrates the selective feeding ability of the mice and appears to be similar to what happens in the wild—the number of prey eaten depends on the availability of alternative foods.

A natural situation that illustrates the effects of alternative food, the defense mechanism of stiff hairs, and prey density on gypsy moth survival was recently observed in New Lisbon, N.J. (Garlo 1977). Nest boxes were placed on a 0.7-ha site as part of a small mammal study. In early summer 1976, while checking the nest boxes for small mammals, it became apparent that gypsy moth larvae were using the nest boxes for resting sites and white-footed mice were using the same boxes for nesting. Not only were predator and prey living together, but the gypsy moth larvae had a high survival rate and adults laid egg masses in the boxes.

Although all the nest boxes were being used by mice, mouse density was low (10 mice per hectare). In addition to low mouse density, the key to gypsy moth survival appeared to be the abundance of cankerworms, a hairless larvae whose availability coincided with that of gypsy moth larvae. In laboratory feeding studies mice have demonstrated a definite preference for hairless larvae; mice in the wild also prefer hairless cankerworms to gypsy moths. This preference was a definite factor in the high gypsy moth survival rate.

By 1977, however, the situation in New Jersey had changed. Mouse density had increased to 35 per hectare, and the alternative food, cankerworms, had disappeared. Gypsy moth density remained essentially the same, and the larvae continued to rest in the nest boxes, but few gypsy moth larvae survived. The absence of the cankerworms and the increased mouse density created more competition for food, which resulted in a low gypsy moth survival rate.

Another example of availability and abundance influencing gypsy moth predation occurred in central Pennsylvania in 1975. In early summer gypsy moth larvae began migrating from the tree crown at a time when the litter and ground had dried because of limited precipitation and increased sunlight reaching the forest floor through the partially defoliated canopy. This in turn caused earthworms and other soil invertebrates to move deeper into the soil, making them unavailable as a food source. In this situation robins were forced to change their diet and eat large quantities of gypsy moth larvae when they became available on or near the ground.

Effect of Defoliation on Gypsy Moth Predators

One factor unique to predators of defoliating insects is the effect of defoliation on predators. Each predatory species chooses a habitat that meets its need for food and cover. However, an infestation of gypsy moths that results in near or complete defoliation destroys the protective cover and causes unfavorable changes in the microclimate within the defoliated area. Many species of birds nest near the ground (DeGraaf et al. 1975), and most small mammals live on the ground in a forest. During the day in a severely defoliated forest, the temperature, especially near the ground, increases dramatically, and humidity drops. As species are subjected to extremes in temperature and humidity that they are either unwilling or unable to tolerate, and possibly increased predation because cover has been diminished, they leave the area.

In 1975 in central Pennsylvania, the population of yellowthroats, a warbler species that prefers brushy habitats, was approximately seven times greater on the lightly defoliated plots than on plots that were severely defoliated; the population of redback voles, small

mammals that are active day and night, dropped dramatically on severely defoliated plots; the population of white-footed mice continued to increase on all plots (Lautenschlager et al. 1978). The effect of defoliation was clearly less on the nocturnal mice than on the voles, which were forced during the day to cope with increased ground temperatures and/or possibly with avian predation.

Because these conditions occur only at very high gypsy moth densities, a time when predators are having little or no effect, it is doubtful if the loss of some predators would have any effect on subsequent gypsy moth populations. In most cases predators leave the area only for a short time. If refoilation occurs, many predators will return within 2 to 3 months. If major changes occur in stand composition because of defoliation and subsequent tree mortality, and food and cover are affected, significant changes could occur in both the density and the number of predatory species. These changes could last for several years, and the new predator community might be more or less effective than the one present before the changes occurred.

The Predators

Overview

Many species of animals in the Northeast eat forest-defoliating insects, which include the gypsy moth. Some of these predators eat only one life stage of the gypsy moth; others eat two or more. Although the emphasis of research has been on birds and mammals, some observations have been made of predation by amphibians, reptiles, fish, and several invertebrates. Within each predator group are some species that are more important as predators than others. However, every predator is viewed as part of the predator community, with each having a part in the collective impact of predation on sparse gypsy moth populations. It cannot be assumed that all the gypsy moth predators have been identified, and it must be realized that the roles of those identified will change as the factors that affect predator potential change.

Birds

When the total predator community is working together it can maintain gypsy moth populations at harmless levels for an indefinite time. Birds are a major part of the predator community and play an important role in reducing gypsy moth populations.

Birds occur in every habitat type, from nearly open areas to thick brush and mature forests. Within these habitat types they occupy every available stratum, from the forest floor to the top of the canopy. During the breeding season and in good habitats, birds reach population levels of 5–10 pairs per hectare. Our research in central Pennsylvania indicated approximately 7 breeding pairs per hectare; Holmes and Sturges (1975) in New Hampshire showed roughly 10 pairs per hectare; and Hamilton and Cook (1940) in New York State indicated approximately 5 pairs per hectare. Therefore, during the breeding season, a good woodland songbird habitat probably supports between 10 and 20 adult birds per hectare.

Many species of birds move to northern areas to raise their young in the spring and early summer, producing two broods of four to six young each. During the time of mating and raising of the young, most birds need a diet high in protein, and insects are eaten extensively (Welty 1962). Even species that normally do not eat large amounts of insects often become seasonal insectivores.

Unfortunately, most observations of birds eating gypsy moths have been made when gypsy moth populations were near or at outbreak levels, a time when predation has no significant impact on gypsy moth populations. From observation and from what is known of the history, behavior, and predator potential of each species (Forbush and Fernald 1896, Galipeau 1975, Palmer and Fowler 1975), birds can be placed in one of two groups: Those species that eat gypsy moths regardless of the gypsy moth density (these species would be particularly useful in maintaining sparse gypsy moth populations), and those species that are attracted to high-density gypsy moth areas because of the availability of an abundant food source (these species would normally have little or no impact on gypsy moth populations at low densities).

Bird species in the first group include the black-capped chickadee, blue jay, red-eyed vireo, rufous-sided towhee, scarlet tanager, northern oriole, catbird, and robin. These species are common residents and eat gypsy moths when the insect is at low population densities.

Birds species in the second group include the yellow-billed and black-billed cuckoos, common crow, chipping sparrow, starling, common grackle, red-winged blackbird, and cowbird. The species in the first group are more likely to encounter gypsy moths at low population levels and therefore are more likely to eat them, but birds in the second group will eat gypsy moths from sparse populations if the moths are encountered.

Many bird species besides those just listed eat gypsy moths. Forbush and Fernald (1896) listed 38 bird species seen eating one or more life stages of the gypsy moth. Many migrating warblers, which often nest farther north, often pass through gypsy moth infested areas when the larvae are still small. At resting stops during migration these warblers contribute to the collective impact of bird predation on low-density gypsy moth populations.

**Birds Useful in Maintaining Sparse Gypsy
Moth Populations**

Black-Capped Chickadee (*Parus atricapillus*)



The chickadee (fig. 5) is a small (about 11 g), common, wide-ranging species that eats all life stages of the gypsy moth, including the eggs. The chickadee, normally found in forests and along forest edges, has two broods of approximately six young per brood per year. The chickadee is important because of the high population densities it often reaches, its activity pattern (foraging from ground level to the lower canopy), and its willingness to eat all life stages of the gypsy moth. These birds swallow small larvae whole but must tear apart the larger larvae to eat the preferred parts. The chickadee has been seen catching

adult male moths resting on foliage or tree trunks and then flying to a branch with the insect in its mouth, breaking off and discarding the wings, and swallowing the rest of the insect.

Figure 5.—Black-capped chickadee.

Blue Jay (*Cyanocitta cristata*)

6



The blue jay (fig. 6) is a common, large (about 85 g), wide-ranging bird found in woodlands and along forest edges. A pair of blue jays will normally raise two broods of four to six young per brood per year. Both young and adult blue jays eat large quantities of gypsy moth larvae when the insects are available. They have been observed moving from branch to branch eating larvae, pupae, and adults. Blue jays do not eat all the larvae they kill; sometimes larvae are simply killed and then dropped to the ground.

In 1977 on Cape Cod, Mass., blue jays demonstrated an interesting behavior for catching adult male gypsy moths (ODell 1977). Shortly after sunrise the jays would begin to search systematically the lower branches and tree trunks for adult moths resting there. The captured

moths were swallowed whole. By midmorning, the jays would then exhibit a behavioral change—they searched the shrubs for adult moths resting on the underside of the foliage. The blue jays soon learned that these moths could be easily flushed by hitting the shrubs and became quite proficient at flying into the shrubs, flushing the resting moths, and capturing the insects in flight.

Figure 6.—Blue jay.

Rufous-Sided Towhee (*Pipilo erythrophthalmus*)

The towhee (fig. 7) is an important predator of the gypsy moth because of its willingness to eat late-stage larvae and adult moths. The towhee is also important because of its large size (about 40 g) and the high population densities it often reaches—up to two adults per hectare in most early successional forests where there is a large amount of brush cover near the ground. Under ideal conditions the species may reach densities of two to three times that of other bird species in the same area. Towhees normally raise two broods of four to six young per brood per year. Towhees feed mainly on the ground but search for and capture gypsy moths in sparse gypsy moth populations whenever the gypsy moths migrate to the litter. By consistently consuming late-stage larvae, pupae, and adults, the towhee assists in maintaining sparse gypsy moth populations.



Figure 7.—Rufous-sided towhee.

Red-Eyed Vireo (*Vireo olivaceus*)

The red-eyed vireo is seldom seen but often heard singing from the tree tops. It weighs about 18 g and is found in many habitat types in the Northeast, from forests to more open areas. In prime habitats, the red-eyed vireo may reach population densities of two to five per hectare; this bird normally has two broods of four young per brood per year. Red-eyed vireos forage in the canopy and definitely contribute to the mortality of young gypsy moth larvae. They have been observed eating all life stages of the gypsy moth except eggs and, like the chickadee, often swallow smaller larvae whole. The vireo will place a larger larva on a branch, tear it to pieces, and eat selected parts. Because the bird feeds mainly in the canopy and consumes many early-stage gypsy moth larvae, it helps to reduce populations of the gypsy moth before the insects have a chance to cause significant defoliation.

Catbird (*Dumetella carolinensis*)

The catbird is commonly found along shrub edges where these areas meet more open areas. It nests and feeds close to the ground in dense cover and has been seen taking larvae of all sizes and pupae to its young. The catbird weighs approximately 40 g and may have three broods of up to five young per brood per year. The catbird normally forages in areas from the litter to the lower canopy, so its major impact is on late-stage gypsy moth larvae, pupae, and adults.

Scarlet Tanager (*Piranga olivacea*)



The beautiful scarlet tanager (fig. 8) is a useful gypsy moth predator. Although this species never reaches extremely high population densities (approximately one pair per 2 to 8 ha), this bird is found in most forests and along forest edges, including yards which are bordered by woodland. The scarlet tanager may weigh as much as 30 g and normally has one brood of four young per year. It readily takes many gypsy moth larvae from the branches in the canopy. The tanager eats all stages of the gypsy moth except eggs. The majority of the tanager's predation, however, occurs during the early stages of the gypsy moth's life cycle, when larvae remain in the canopy during the day.

The scarlet tanager reduces the amount of defoliation by eating many larvae before they have a chance to eat large amounts of foliage.

Figure 8.—Scarlet tanager.

Northern Oriole (*Icterus galbula*)

9



The northern oriole (fig. 9), commonly called the Baltimore oriole, is useful in combating many forest insect pests. Orioles are found in the canopy along edges of lawns, roads, fields, and ponds wherever the edges blend into more mature forests, including suburban yards. Along these edges hang their intricately woven nests. Orioles weigh approximately 35 g and may have one or two broods of four young per brood per year. The oriole is well known for its ability to kill hairy caterpillars, like the eastern forest tent and gypsy moth caterpillars. This bird also eats gypsy moth pupae and adults. Like other birds that feed in the canopy, the oriole starts to eat gypsy moths when they are small larvae, before they have a chance to consume large amounts of foliage.

Figure 9.—Northern oriole.

Robin (*Turdus migratorius*)

10



The robin (fig. 10) is familiar to almost everyone and is commonly found along forest edges and in urban, suburban, and rural yards. The robin weighs approximately 80 g and often raises two or three broods of four young per brood per year. Although the robin lives in forests, it never reaches high population densities away from natural or manmade openings. The robin eats larvae, pupae, and adult gypsy moths; depending on their abundance, this insect may become an important part of the robin's diet.

Although robins are usually pictured pulling worms from the lawn, they also forage in trees, removing larvae and pupae. They have also been observed picking up gypsy moth larvae from dirt roads in Pennsylvania. The robin probably

has its greatest impact on gypsy moth populations when the ground is dry and earthworms are not readily available, because at that time the bird must search for other food.

Figure 10.—Robin.



Figure 11.—Black-billed cuckoo.

**Birds Attracted to High-Density
Gypsy Moth Populations**

Cuckoos (*Coccyzus* sp.)

The cuckoos (both black-billed, fig. 11, and yellow-billed) are normally the first on a list of bird predators of gypsy moth. However, because they are uncommon away from a gypsy moth outbreak, they have little impact on maintaining sparse populations. Cuckoos live in forests and along forest edges, are large birds (approximately 65 g), and may raise two broods of four young per brood per year. Cuckoos prefer late-stage gypsy moth larvae, which they also feed to their young. As soon as the young can fly, small family groups of cuckoos can be seen eating gypsy moth larvae and pupae in infested areas.

Common Crow (*Corvus brachyrhynchos*)

The crow, although very wary and often hard to observe, is known to eat large amounts of insects, including late-stage gypsy moth larvae, pupae, and adults. Crows have often been observed searching for larvae and pupae in infested areas and removing loose, dead bark from trees to reach larvae aggregated there. Crows search for food in most habitats, have extensive home ranges, and travel a considerable distance to utilize an available food source. Their travels often include visits to areas with a high gypsy moth density, when late-stage larvae and pupae are available. They often return with their young to feed in these areas.

In areas with moderately dense to dense gypsy moth populations in central Pennsylvania, crows started to arrive when gypsy moth larvae were in the fourth instar and were seldom seen after the moths had laid their eggs. Crows often raise two broods of up to six young per brood per year. Nestling crows require large amounts of food and are often fed late-stage gypsy moth larvae, pupae, and adults when abundant. However, even when gypsy moth populations are sparse, they may be eaten if encountered.

Common Grackle (*Quiscalus quiscula*)



12

The grackle (fig. 12) is commonly found along forest edges, especially around farms, where it often flocks with other blackbirds. The grackle eats all life stages of the gypsy moth except the eggs. The grackle is a large bird (about 115 g) and normally raises one brood of five young per year. The grackle's diet consists of about 30 percent animal matter, normally in preparation for and during raising of the young, which coincides with gypsy moth abundance. Grackles have been reported to flock to infested areas to eat gypsy moths (Campbell 1975). These birds may be important predators within sparse gypsy moth populations, when they eat moths

along forest margins, close to open fields, and on farmlands. The grackle does not, however, appear to eat large numbers of gypsy moths at these low densities, when the gypsy moths are not abundant enough to attract its attention.

Figure 12.—Common grackle.

Chipping Sparrow (*Spizella passerina*)

The chipping sparrow normally inhabits forest edges, often nesting in evergreens, and also is very common around suburban homes where there are open country and brush edges. The sparrow may have two broods of four young per brood per year. The chipping sparrow, although it normally feeds on seeds, does eat many insects, including gypsy moth larvae (small and large) and adults. Although it is not big (about 14 g), it may have some impact on gypsy moth populations by feeding on larvae found near the ground.

Starling (*Sturnus vulgaris*)

Since their introduction in 1890, little good has been said about the common starling. These birds are normally found around urban and suburban areas and eat large amounts of gypsy moth larvae, pupae, and adults when they become available. Because starlings are large (about 85 g) and often raise three broods of five young per brood per year, they consume large amounts of food. The starling is an opportunistic feeder and feeds on the ground as well as high in the canopy, depending on where food is available. Although starlings seldom venture far from human habitation, they are probably useful in destroying large numbers of gypsy moths in areas with medium-high densities.

Red-Winged Blackbird (*Agelaius phoeniceus*)

13



The red-winged blackbird (fig. 13) normally nests along swamp edges and marshes but will also live in the high grass along the edges of inland meadows if wet areas are nearby. This blackbird weighs approximately 70 g and may raise two broods of four young per brood per year. When gypsy moths become available, they may form a significant portion of the blackbird's diet because it eats both larvae and adults. During the breeding season, the bird's diet is mainly insects; in areas where the birds are plentiful, or where roving bands of first-year males congregate, they probably have some impact on gypsy moth populations.

Figure 13.—Red-winged blackbird.

Brown-Headed Cowbird (*Molothrus atar*)

Cowbirds lay their eggs in the nests of other birds, leaving the incubation and raising of young to other species. This permits the cowbird to forage wherever food is plentiful. Although associated with open fields and farm animals, this bird is also found in forests, where it eats gypsy moth larvae, pupae, and adults. During the spring in Pennsylvania, groups of cowbirds were observed moving through the forest canopy and consuming large numbers of gypsy moth larvae. The brown-headed cowbird is an opportunistic feeder and takes advantage of any readily available food source, such as the gypsy moth, when it becomes abundant in the environment.

Mammals

Mammals, which live in all types of habitats, have perhaps greater predatory impact on sparse gypsy moth populations than any other group of predators. Because of the numbers, distribution, diets, and agility of mammals, most forest insects probably become available prey to them during some stage of an insect's life. The impact of mammals is essential if the gypsy moth predator community is to have a regulatory effect.

Mammalian predators of the gypsy moth that have been studied include rodents, insectivores, carnivores, and marsupials. Unlike birds, these predators are not very conspicuous nor easily watched because most of them are active only at night. They are less transitory than birds and are more stable residents within an area. They usually have greater population densities than birds, commonly reaching levels four to eight times higher than songbirds occupying the same area. Small

mammals often reach densities of 37 to 100 adults per hectare during the spring and increase to much higher levels later in the year.

Although mammals have the greatest impact on insects that spend part of their development on the ground, they are certainly not restricted to ground level. Squirrels and chipmunks, which eat many insects during certain seasons, are not the only mammals that forage in trees. White-footed mice commonly climb trees to find food, often nesting in abandoned woodpecker holes or bird nests.

In an attempt to gain a better understanding of the predator potential of mammals, 15 common woodland mammal species were observed in the wild and in captivity. Study objectives were to identify the major mammalian predators of the gypsy moth, the life stages of the insect that are eaten by each predator, the quantities eaten, and ways to increase the most important predators' effectiveness through management.

Caged mammals were given gypsy moth larvae, pupae, and adults with and without alternative foods. Observations in the laboratory gave no indication that any mammal tested would eat gypsy moth eggs. This was true even when the mammals were given no alternative foods. In several instances, individual mammals would knock the egg masses apart but were never observed eating them. To verify the observations made on these caged

Rodents

White-Footed Mouse (*Peromyscus leucopus*)

mammals, stomachs were examined from snap-trapped small mammals and road-killed raccoons, skunks, and opossums, all collected from within an area of moderate gypsy moth density. Gypsy moth remains were found in the stomachs of all 15 species, revealing that in the wild the gypsy moth is available food and is eaten by all these species.

After completing analysis of habitats and densities of the mammals and their feeding behavior, it was determined that white-footed mice and shrews have significantly greater predator potential than other species.

White-footed mice have demonstrated their ability to eat large numbers of gypsy moths in the wild. After an intensive study of this species and the many other gypsy moth predators, the white-footed mouse is recognized as the single most important predator of the gypsy moth.

A small mammal food preference study (conducted in the wild with healthy gypsy moth pupae placed in the litter) indicated that shrews (both shorttail and *Sorex* sp.) accounted for approximately one-half of the gypsy moth mortality attributed to small mammals. Remains of gypsy moth larvae and pupae have been found in both stomachs and droppings of shorttail shrews collected within a sparse gypsy moth population.

The white-footed mouse (fig. 14) has received more attention than any other predator of the gypsy moth. Recent studies have emphasized the beneficial impact of this animal in sparse gypsy moth populations (Campbell and Sloan 1976, 1977), their feeding behavior, and even the feasibility of managing this species (Smith 1975) to increase its effectiveness against the gypsy moth.

The white-footed mouse (average weight about 20 g) is the most common and most widely distributed small mammal in the Northeast. It lives in all habitat types, from suburban lawn edges to mature forests, but is most abundant in thick brushy areas. Under ideal conditions, spring breeding densities can reach 13 mice per hectare, with densities later in the year reaching two to three times that number. Each breeding season, adult female mice produce an average of three litters of approximately four young per litter.

White-footed mice have remarkable agility and thoroughly explore and utilize their habitat, nesting and foraging from below the ground to tree tops. Their diet consists of a variety of seeds, nuts, and insects, and their feeding behavior is truly opportunistic. Insects form a substantial part of this mouse's diet, so it is not surprising that the white-footed mouse preys on the exotic gypsy moth when it is available.

The mouse has an interesting way of eating the hairy gypsy moth larvae.



It grasps the insect with its forepaws and pulls back the head capsule with its teeth, discarding it along with the bright-green upper digestive tract. While rolling the insect's skin back, just as a sock might be rolled, the mouse eats the body fluids and some internal membranes. In the woods, larval remains (fig. 15) are most likely to be found at the base of host trees but have been found 30 feet up in trees.

The process of rolling back the larval skin is learned by the mouse to avoid irritation from the gypsy moth larvae's protective hairs. Young mice usually have an unsuccessful first encounter with

larvae. A mouse will sniff a larvae, as it does other foods, but if it gets too close, the larval hairs become embedded in the mouse's nose. The mouse's second approach is more cautious, and soon the larvae is a regular part of its diet.

White-footed mice usually eat pupae by opening one end and eating the contents, but many times they will simply tear apart pupae and eat them. The mice will select female pupae over the smaller males, but both are eaten. Mice do not store

Figure 14.—White-footed mice eating larvae.

pupae, as they do some other foods. Gypsy moth adults (male and female) are also eaten by the white-footed mouse. After capturing a moth, the mouse eats the entire body, normally leaving the wings and legs (fig. 16). It is interesting to note that these mice, which apparently do not eat gypsy moth eggs, do eat the abdomen of the adult female, including the eggs within.

The number of insects eaten by an animal in captivity does not necessarily indicate how many that animal will eat in the wild, but it can provide a rough idea of the maximum number that could be destroyed over a certain time period. In captivity, white-footed mice with alternative foods (apples and mouse chow) have eaten as many as 46 of 50 fifth-instar larvae over 24 hours. Mice without alternative food have eaten 50 of 50 fifth-instar larvae. Mice have eaten as many as 20 of 40 pupae with an alternative food, and 28 of 40 when no alternative food was provided. Overall, mice ate an average of 90 percent of the larvae offered when no alternative food was given and about 60 percent with an alternative food. Alternative foods had no effect on the number of pupae eaten; in both cases mice ate an average of 30 percent of the pupae offered.



15



16

Figure 15.—Larval remains left by white-footed mouse.

Figure 16.—Adult female remains left by white-footed mouse.

Jumping Mice (Woodland, *Napaeozapus insignis*, and Meadow, *Zapus hudsonius*)

17



Jumping mice (fig. 17) are about the same size as white-footed mice (about 20 g) but are easily distinguished from white-footed mice by their long tail and large hind feet. The meadow jumping mouse is normally found in damp, long-grass meadows; the woodland jumping mouse is found in mature or maturing forests, usually along streams or pond edges. These mammals never reach high spring breeding population densities even in ideal habitats but average three to

five per hectare. The jumping mice demonstrated a low predatory potential by eating a few larvae and some pupae. Gypsy moth remains left by jumping mice look similar to those left by white-footed mice.

Figure 17.—Meadow jumping mouse.

Chipmunks and Squirrels

Boreal Redback Vole (*Clethrionomys*)

18



Redback voles (fig. 18) are slightly larger than mice (about 25 g) and may reach fairly high spring population densities (six or more per hectare) in some areas of the Northeast. Redback voles are normally found in thick hardwood forests and moist coniferous forests with decaying logs and stumps. They seem to prefer damp forest situations but are also commonly found in drier areas, if thick cover is available. Redback voles, as are shrews, are active day and night. Like other voles, they feed mainly on vegetation but also eat a variety of insects. In the laboratory redback voles demonstrated little predator potential toward gypsy moth larvae, but often ate pupae. On several occasions they were observed carrying pupae back to their nests in their mouths.

Figure 18.—Boreal redback vole.

Although the bushy-tailed rodents (chipmunks and squirrels) are often considered seed eaters, they do eat a wide variety of foods and are seasonally insectivorous (Burt 1957). They use insects in their diets in the spring and early summer when preferred foods such as stored nuts and acorns are scarce.

The bushy-tailed rodents (chipmunks, gray squirrels, red squirrels, and southern flying squirrels) did not adjust well to captivity, and their feeding behavior was difficult to observe. In captivity all these rodents preferred pupae and larvae. None of the rodents ate many larvae (5 to 10 percent of those offered), and larval remains were often crushed and only partly eaten, or killed but not eaten. Although gray squirrels were observed removing gypsy moth larvae from bark flaps in the forest (Campbell 1975), and chipmunks have been observed climbing trees to capture adult moths (ODell 1977), any impact they might have on gypsy moth populations would most likely come from pupae predation. When eating pupae, these rodents grasp the pupal case with their forepaws and eat it much as they would an acorn. They usually eat the entire pupa, but occasionally large, scattered fragments of the pupal case remain.

Chipmunk (*Tamias striatus*)



19

The eastern chipmunk (fig. 19), which weighs approximately 75 g, often reaches spring populations of eight per hectare and is found in forests, in most thick, brushy habitats, and along forest edges and lawns. Although the chipmunk is active during the day, it is most active at dawn and dusk. The chipmunk normally has two litters of four young per litter per year.

Figure 19.—Chipmunk eating pupa.

20



The gray squirrel (fig. 20), weighing approximately 500 g, is basically arboreal (found in trees) but does spend some time foraging on the ground. The gray squirrel is found in hardwood forests and forest edges, around suburban and urban environments, or wherever there are ample food and nesting holes. Gray squirrels normally have two litters of four young per litter per year. Spring breeding population densities in good habitats often reach 12 per hectare. Like the chipmunk, the gray squirrel is most active at dawn and dusk.

Red squirrels, which weigh approximately 180 g, are usually found in pine, spruce, or mixed forests. Although they reach their highest spring densities (two per hectare) in the preferred conifer forests, they are also found in northeastern hardwood forests. The red squirrel normally has two litters of four young per litter per year. The red squirrel is active throughout the day, from early morning to late evening.

Figure 20.—Gray squirrel.

Insectivores

Southern Flying Squirrel (*Glaucomys volans*)

The southern flying squirrel, approximately 65 g in size, is nocturnal and is found where nest holes are available in maturing hardwood forests and along forest edges. This flying squirrel normally has two litters of four young per litter per year. It often reaches spring breeding densities of two to three per hectare.

Shorttail Shrew (*Blarina brevicauda*)



The shorttail shrew (fig. 21) is the largest North American shrew (average weight about 18 g) and is the most populous insectivore in many areas. These shrews are common in a variety of habitats (forests, grasslands, marshes, and brushy areas) east of the Rocky Mountains. Although abundant (two to three litters of five to eight young per litter per year, with populations reaching 20 per hectare), shorttail shrews are among the least conspicuous of the forest mammals. These shrews are seldom seen but often heard rustling through the litter as they search for food beneath logs, stumps, rocks, and leaf litter, and even in the surface runways of rodents—all places where gypsy moth larvae rest and pupate. In addition to worms, snails, and other small animals, nearly half the shorttail shrew's diet consists of insects.

Figure 21.—Shorttail shrew eating larva.

Masked Shrew (*Sorex cinereus*)

Shrews must spend most of their time in search of food, as their extremely high metabolic rate requires that they eat approximately the equivalent of their own weight each day. To meet their food demands, shrews are active day and night and rest only periodically.

A shorttail shrew eats a gypsy moth larva by grasping the larva with its forepaws, holding the insect against the ground, rolling it over, and biting it near the middle segment on the ventral side. The bite injects a poison secreted from glands in its mouth that helps to subdue the larva. The shrew then eats the head. Seldom will the head capsule remain; this is one way to distinguish larvae eaten by shrews from those eaten by mice. The shrew then eats the larva, including the gut from the ventral side. All that remains is the skin from the back, where the hairs are attached.

Caged shorttail shrews consistently ate at least 65 percent of the larvae offered and nearly all the pupae, even when an alternative food (canned dog food) was available. Shrews eat large numbers of pupae; unlike mice, they have not shown a preference for the larger female pupae over the smaller male pupae. A shrew will usually pick up a pupa and carry it below ground to a nest. One adult shorttailed shrew was seen making 15 separate trips to its nest, carrying one pupa each time in its mouth.



The masked shrew (fig. 22) is one of the smallest mammals in the Northeast, weighing only 3 to 4 g at maturity. Like the shorttail shrews, they are active day and night and spend most of their time foraging in the litter. Females may produce two or three litters of up to seven young per litter per year, and in optimum habitats (maturing hardwood forests) masked shrews may reach spring densities of 20 per hectare.

Masked shrews readily eat larvae and pupae, although they appear to prefer pupae. Capturing a sixth-instar larva that may weigh half as much as the mammal itself is no problem for these shrews. The manner in which they attack and eat gypsy moth larvae and pupae is similar to that of shorttailed shrews. Masked shrews are certainly capable of causing high mortality to both gypsy moth larvae and pupae located in the litter.

Figure 22.—Masked shrew eating pupa.

Smoky Shrew (*Sorex fumeus*)

23



The smoky shrew (fig. 23) is one of the largest (6 to 11 g) of the longtailed shrews and may reach spring population densities of eight per hectare. The smoky shrew normally has two litters a year of five young per litter. The smoky shrew has feeding habits similar to other shrews and is active day and night. These shrews prefer, and are most abundant in, mature northeastern forests where there is a deep layer of leaf mold and litter.

Caged smoky shrews consumed large quantities of both larvae and pupae; when eating larvae they did not appear to be disturbed by larval hairs. Although the feeding behavior of this shrew is similar to that of the shorttailed shrew and the masked shrew, the smoky shrew is less likely to have as great an impact on gypsy moth populations because its densities are lower.

Starnose Mole (*Condylura cristata*)

24



The starnose mole, a relatively large insectivore weighing about 60 g, is easily distinguished from other moles by the fleshy projections, or tentacles, on the end of its nose (fig. 24). This mole commonly inhabits eastern hardwood forests but reaches its greatest densities in moist, swampy areas. Females produce one litter of three to seven young per year. These moles often appear above ground, but unlike the eastern mole they spend a considerable amount of time foraging in the litter. They are active day and night, spending most of their time, like the shrews, trying to satisfy a voracious appetite.

Figure 23.—Smoky shrew eating pupa.

Figure 24.—Starnose mole.

Carnivores

Striped Skunk (*Mephitis mephitis*)

Starnose moles seem to detect food with the sensitive tentacles on their nose, but their sense of smell appears to be poor. This mole eats a variety of foods, but insects comprise about one-third of its diet.

Starnose moles are not considered as important gypsy moth predators as other insectivores. Although caged starnose moles often ate pupae, few larvae were eaten; the stiff protective hairs on the larvae seemed to irritate their tentacles. If, however, larvae are found in the tunnel of the starnose mole, they are attacked and killed by this mammal, which rigorously defends its tunnel against all intruders.



The striped skunk (fig. 25) is one of the best known mammals in the Northeast. Skunks are found in a variety of habitats, including suburban yards, but prefer semi-open country with a mixture of woods and brushland. Skunks have one litter of as many as seven young per year. Spring densities can reach one per 2.4 ha, but more commonly the densities range between 5 and 10 per 2.6 km². Skunks have a varied diet but rely heavily on insects as a food source. It has been estimated that insects comprise approximately one-half their intake. Skunks are chiefly nocturnal, emerging shortly after dusk to begin their search for food.

When a skunk eats a gypsy moth larva, it beats the larva with its forepaws, rolling the larva toward itself as the skunk backs away.

Figure 25.—Striped skunk eating larva.

Raccoon (*Procyon lotor*)

26



When the protective hairs have been broken and the larva has been turned into a pulpy mass, the skunk eats it. Skunks also eat gypsy moth pupae and adults with ease.

In experiments with caged mammals, skunks demonstrated the greatest willingness of all the mid-size mammals to eat gypsy moth larvae and ate large quantities of them. Individual skunks would consistently eat 25 fifth-instar larvae in 2–3 minutes. In one cage containing five young skunks the animals would actually try to take larvae away from each other.

The raccoon (fig. 26), which can weigh 12 kg, is the largest mammal that has been observed eating gypsy moths. They are common along streams and around pond and lake borders if wooded or forested areas are nearby, and in suburban and urban areas where they are often seen at night alongside highways or raiding garbage cans. Raccoons have one litter of approximately four young per year and may reach spring densities of approximately three per square kilometer.

Figure 26.—Raccoon eating larva.

Marsupials

Opossum (*Didelphis marsupialis*)

Although the omnivorous raccoon's natural diet is most often thought to be crayfish, frogs, fruits, nuts, and bird eggs, it also eats large quantities of insects. During the feeding studies, caged raccoons ate more than 90 percent of the larvae and pupae given them. When it ate a larva, a raccoon picked it up in its forepaws and rolled it, or rolled it on the ground or against some object, to break it apart to make it more palatable. The entire larva was then eaten. Raccoons in the wild have been observed picking the flightless gypsy moth females from the base of trees and eating them. All life stages of the gypsy moth, except deposited egg masses, have been identified in the stomachs of wild raccoons.

The opossum (fig. 27) is the only naturally occurring marsupial in the United States. Adult opossums can weigh as much as 6.5 kg and may produce one or two litters of approximately 10 young per litter per year. Opossums prefer farm areas but are also found in forests and wooded areas, especially near water. Opossums eat a variety of food that includes fruits, vegetables, meat, eggs, and insects. They are opportunistic scavengers and reach their greatest densities around human habitation, where they can forage in garbage. When opossums are away from garbage sources, insects form a substantial portion of their diet, so it is not surprising that the gypsy moth is part of this mammal's diet. The opossum is the only mammalian predator of the gypsy moth that appears unaffected by the larval hairs. It simply grasps a larva and eats it whole.

Opossums in captivity ate approximately 80 percent of the larvae offered, missing only those that had crawled out of reach. Movement by a larva increased its probability of being eaten. When attacking a gypsy moth larva, an opossum would hold its head motionless and then quickly strike and grasp the larva in its mouth, chewing and swallowing it in seconds. Pupae were eaten in the same way, but being immobile they did not stimulate attack and were eaten only when encountered.

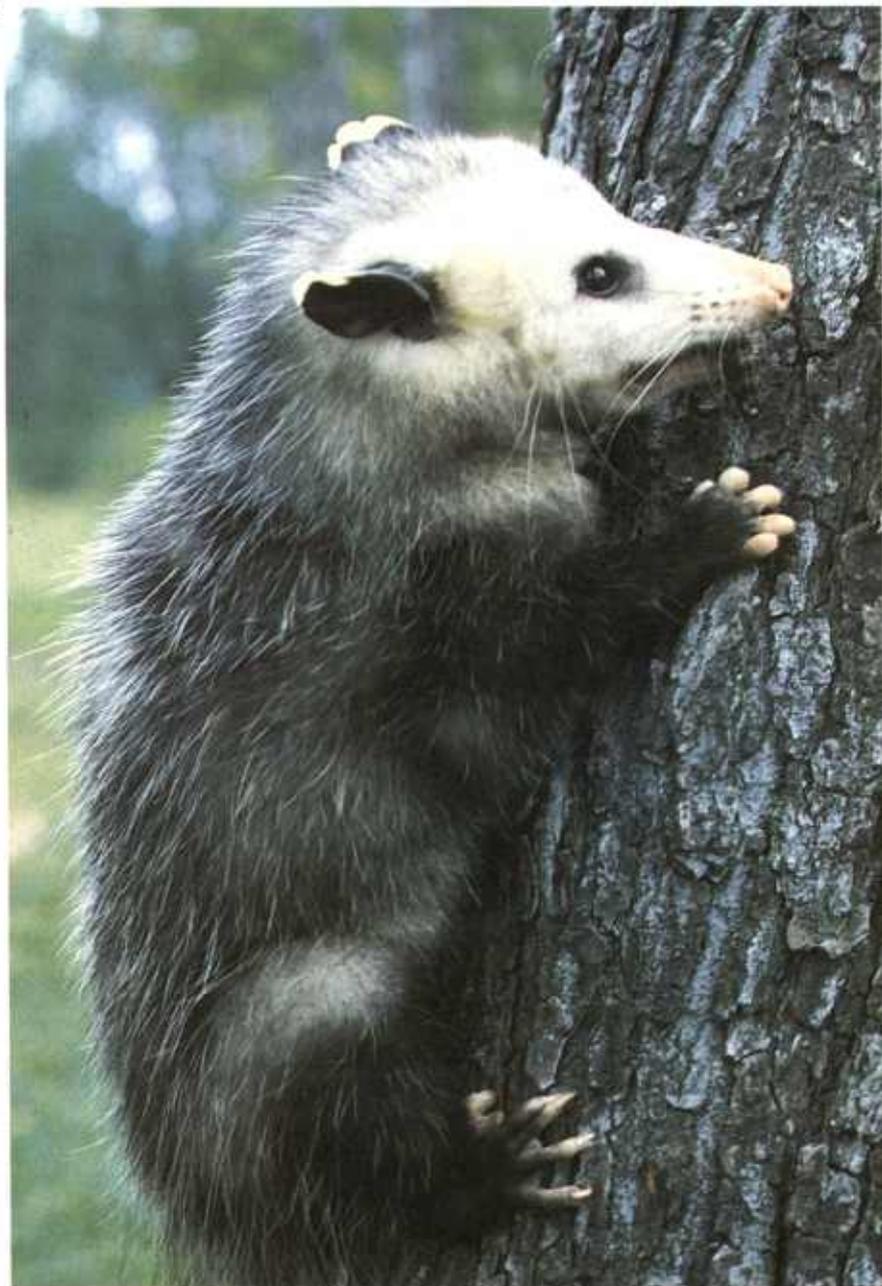


Figure 27.—Opossum eating larva.

Amphibians, Reptiles, and Fish

When the role of vertebrate predators of the gypsy moth is discussed, the emphasis has been on birds and mammals. However, many species of amphibians, reptiles, and fish have been observed eating gypsy moth larvae and adults.

Little is known about this group's role as predators of the gypsy moth or other forest insects. Because these other vertebrates are coldblooded, and their temperature fluctuates to match the temperature around them, their metabolic rate is normally much lower than that of birds and mammals. This lower metabolic rate requires less food and thus these coldblooded vertebrates' potential for consuming prey is low. It is doubtful, therefore, that these vertebrate predators have any significant impact on gypsy moth populations. Nevertheless they do eat gypsy moths and are part of the gypsy moth predator system.

Movement of prey appears to be the key to food selection by the amphibians, reptiles, and fish that have been observed. This selection is largely a random process, with foods taken in proportion to abundance and availability. Unfortunately, when any pest insect becomes abundant enough to represent the major portion of the diet of this group, it is unlikely that predator pressure from even the entire predator community, including birds and mammals, has an impact on the pest population, because there are just too many insects.

Amphibians

American Toad (*Bufo americanus*)

The American toad (fig. 28) is perhaps the most common and most useful amphibian predator of the gypsy moth. The American toad was noted as a predator of the gypsy moth as early as 1896 by Forbush and Fernald, when they reported that these toads ate great numbers of gypsy moth caterpillars in infested brushlands. They examined the stomachs of three toads taken in that area and found them to contain 7, 15, and 65 gypsy moth caterpillars, respectively.

The American toad eats insects, slugs, earthworms, and almost any small invertebrate that moves. It is found in a wide range of habitats that have shallow water (for breeding), moist hiding places, and an abundant supply of insects and other invertebrates (for food).

Observations of captive toads suggest that when a toad is ready to eat and it encounters a gypsy moth larva, the larva will be eaten. Toads actually stalk larvae that are crawling on the litter and then quickly seize them with their sticky tongues.

Fowler's Toad (*Bufo woodhousei fowleri*)

28



29



The Fowler's toad (fig. 29), named after a Massachusetts naturalist, is a common toad of the Atlantic coastal plain; inland distribution is spotty. It is often confused with the American toad. The two species can usually be distinguished from one another by the number of warts in each of the dark spots on their backs—Fowler's toad has three or more; the American toad has one or two.

Fowler's toads have been observed eating gypsy moth larvae (fourth and fifth instar). Their method of stalking and seizing of the insect is similar to that of the American toad.

Figure 28.—American toad eating larva.

Figure 29.—Fowler's toad eating larva.

Wood Frog (*Rana sylvatica*)

30



Wood frogs (fig. 30), which range farther north than any other North American amphibian or reptile, can be found in most moist wooded areas throughout the current gypsy moth infested area. Wood frogs, easily recognized by the black patch behind the eye, are often found considerable distances from water.

Forbush and Fernald (1896) reported wood frogs attacking adult female gypsy moths. Recent observations have confirmed that they also attack gypsy moth larvae.

Figure 30.—Wood frog.

Figure 31.—Gray tree frog.

Gray Tree Frog (*Hyla versicolor* and *Hyla chrysoscelis*)

31



These two species are so similar in appearance they have long masqueraded as one and can only be distinguished from one another in the field by their voices. Figure 31 shows *Hyla chrysoscelis*. Forbush and Fernald (1896) reported tree frogs eating gypsy moth caterpillars. Although they usually forage for food in trees and shrubs near or even in water, tree frogs have been observed in trees at least 200 m from any open water. Although gray tree frogs have not been observed eating gypsy moths, it is probable that the moths are eaten when encountered.

Reptiles

Green Snakes (Genus *Opheodrys*)

Two species of green snakes occur within the gypsy moth's range, the terrestrial smooth green snake and the more arboreal rough green snake. Although sometimes common, both species are difficult to see because they are so well camouflaged. Although green snakes have not been observed eating gypsy moths, it is known that larvae of moths and butterflies form a substantial portion of their diet (Palmer and Fowler 1975). The rough green snake is an excellent climber and often forages for insects in small trees and shrubs.

Other Snakes



Garter snakes (Genus *Thamnophis*) and eastern hognose snakes (*Heterodon platyrhinos*) (fig. 32) may occasionally eat gypsy moth larvae. The diet of young hognose snakes consists mainly of insects; the adult hognose snake eats toads and a variety of other foods but few insects.

Figure 32.—Eastern hognose snake.

Northern Fence Lizard (*Sceloporus undulatus*)

33



The northern fence lizard (fig. 33) is a small, spiny reptile that ranges north into Pennsylvania and New Jersey. Fence lizards are excellent climbers and are often seen in trees as well as on rotten stumps and logs. Fence lizards feed almost exclusively on insects. They have been observed eating gypsy moth larvae and adult males in captivity, and because of this and because fence lizards spend a considerable amount of time where gypsy moth larvae rest, it is assumed that the gypsy moth is part of this lizard's diet. A fence lizard is attracted by

the movement of larvae. It will lunge at the insect with its mouth open, clamp its jaws around the insect, and in successive gulps swallow a larva whole and alive.

Figure 33.—Northern fence lizard.

Fish

It is interesting that forest pest insects are found even in the stomachs of fish. Local fishermen have reported finding gypsy moth larvae in the stomachs of brown and rainbow trout. Although gypsy moth larvae and adults are occasionally eaten by a variety of fish species, including trout, bass, bluegills, and sunfish, it is very doubtful that any real economic importance can be attributed to this predation. Gypsy moth larvae and adult moths often fall or are blown into lakes, ponds, and streams, becoming available food for fish.

Most people who fly-cast realize that the wooly-worm fishing lure is simply an imitation of a hairy caterpillar. Brook trout have been caught in mountain streams in Pennsylvania on both live gypsy moth larvae and adult moths, and bass and bluegills have been observed taking larvae from the water surface at the edge of a small lake.

In comparison to vertebrate predators (birds and mammals), little is known about invertebrate predators of the gypsy moth. Exotic invertebrate predators have been imported, studied, and in some cases released, but very little is known about their impact on gypsy moth populations. Studying the impact and selective feeding behavior of small mammals brought to light that certain native invertebrates, namely ants and harvestmen, had considerable predator potential. Their potential had been overlooked because of the emphasis on small mammals.

Emphasis should be on the vertebrates. Ignoring invertebrates, however, would lead to some loss of appreciation and understanding of the importance of vertebrate predators. It is therefore essential to examine all the components of predation in order to assess the value of any predator or group of predators within a system.

Invertebrate predators are much more important than was generally thought. Campbell and Sloan (1976), when assessing gypsy moth mortality factors, assumed that missing pupae had been carried away or eaten by vertebrates. However, recent field observations indicated that many of the missing pupae classified as killed by vertebrates could actually have been killed and removed by invertebrates.

In a field experiment, ants and harvestmen removed a substantial portion of the pupae (both parasitized and healthy) that were artificially placed under small wooden shelters in the litter or that were allowed to spin up and pupate in those shelters. Pupae attacked by invertebrates had finely serrated edges that easily distinguished them from those attacked by small mammals. A peppering effect caused by pupal case remains left on the boards also indicated invertebrate activity; on litter this peppering would have gone unnoticed. Whether the invertebrates are acting as scavengers or predators is still being studied.

The impact invertebrate predators can have has been demonstrated on several agricultural crop pests within simple systems (monocultures), but within the complex forest ecosystem it is difficult to measure invertebrate predatory impact on gypsy moths. Furthermore, two problems arise when trying to include invertebrate predators in an integrated pest management system: Invertebrates

are not abundant in all areas, and they are often dependent on the density of their prey. Even within these limits, however, they can have a significant impact, as in the case reported by Campbell (1975), when *Calosoma* beetles caused heavy mortality to a gypsy moth population. Again, invertebrates are part of the predatory system and cannot be discounted, even if their predation appears negligible, if an integrated pest management program is to be successful.

To understand the impact of invertebrate predators, it is necessary to consider the total number of species, the density potential, and the diversity of habitats. It is then easy to see that as a group they could have significant economic potential, not only as predators of the gypsy moth but also as predators of other forest pest insects. Many entomologists would agree that most of the invertebrate predators of the gypsy moth have not yet been identified. This section discusses those that have received the most attention and those that are most familiar.

Ground Beetles (Carabidae)

34



This very large family of approximately 2,500 species in North America is believed to be generally beneficial because of the predaceous habits of both larvae and adults. Several species have been reported as predators of the gypsy moth; one species, *Calosoma sycophanta* (fig. 34), has been imported from central Europe and released in New England to help control the gypsy moth. The genus *Calosoma* has the reputation as being a fierce caterpillar hunter; this is reflected in the common names of some of the native species—fiery hunter (*Calosoma calidum*) and fiery searcher (*Calosoma scrutator*).

Ground beetles hide during the day under stones or logs or under the surface of the soil and hunt chiefly at night. The adult beetles of *C. sycophanta*, *C. frigidum* (fig. 35), and *C. scrutator* actively pursue their prey in trees; the larvae of these species forage in the litter. Larvae of the imported *C.*

sycophanta are good climbers and are often seen on trees eating gypsy moth larvae and pupae.

C. sycophanta is the principal beetle that attacks gypsy moth. Although abundant only in certain locales, it is now well established in infested areas. It is usually observed, however, only when there is an abundance of gypsy moths. These beetles were first imported in 1905 and released in 1906. None have been released since 1926.

C. sycophanta is large (sometimes exceeding 3 cm) and can easily be recognized by its brilliant iridescent green wing covers. (Native species are predominantly black.) The adult beetle's life cycle is synchronized with that of the gypsy moth; adults

Figure 34.—Ground beetle (*Calosoma sycophanta*).



emerge in early June when gypsy moth caterpillars are available and go into hibernation soon after egg laying is started. Beetle larvae appear from the end of June to the middle of July.

The predatory potential of ground beetles has been demonstrated in feeding experiments conducted by Burgess (1929). He noted that a single larva of this predator will destroy at least 50 full-grown gypsy moth larvae during its 2 weeks of development and that the adult beetle, which lives from 2 to 4 years, will destroy several hundred larvae. Ground beetles of other genera—*Carabus* sp., *Agonum* sp., and *Harpalus* sp.—have also been observed eating gypsy moths.

Despite this high attack potential, which was demonstrated with an ad libitum gypsy moth diet, it remains questionable what impact these beetles have within low-density gypsy moth populations. However, this beetle's predator potential is increased because it is long lived (2–4 years), can suffer hunger for a long time, and is unaffected by unfavorable climate conditions.

Figure 35.—Ground beetle (*Calosoma frigidum*).

Stink Bugs (Pentatomidae)

36



Although most members of this family are plant feeders, some predators do exist. Both nymphs (fig. 36) and adults of the native spined soldier bug (*Podisus maculiventris*) have been observed killing gypsy moth larvae and pupae. This insect is said to be “the most useful of the American predaceous Hemiptera” (Swan and Papp 1972).

Figure 36.—Pentatomid nymph eating pupa.



An exotic pentatomid, *Dinorhynchus dybowskyi* (fig. 37), a predator of gypsy moth larvae, pupae, and adults in Japan, has been imported to study the feasibility of establishing it in this country. The insect is currently in quarantine.

Figure 37.—Pentatomid adult eating arctiid larva.

Ants (*Formicidae*)

38



Ants have long been recognized as important predators of some insects. In many countries, ant hills are protected by law and have also been moved and fenced in (for their own protection) to help control pest insects.

In this country ants have been observed eating or tearing apart and removing gypsy moth eggs, larvae, pupae, and adults. Black carpenter ant workers (*Camponotus pennsylvanicus*, fig. 38) have been observed attacking adult female gypsy moths in the process of depositing egg masses. These adult moths were torn apart and carried away. Both black and red carpenter ant workers (*C. ferrugineus*) attack healthy male and female gypsy moth pupae.

Along with chickadees, ants have been the only observed predators of gypsy moth eggs. Campbell (1975) reported that ants, by removing one egg at a time, were successful in destroying several egg masses within a sparse gypsy moth population.

The significance of ant predation on sparse gypsy moth populations may be greater than previously realized, and the impact of ant predation on gypsy moth pupae located in the litter is currently being studied.

Figure 38.—Black carpenter ant eating pupa.

Harvestmen (*Phalangidae*)

Often called daddy longlegs (fig. 39), these invertebrates are familiar to all. Although these invertebrates are arachnids and look like spiders, they belong to the order Phalangida. Harvestmen have been thought of as scavengers of little economic importance. Actually, little is known about their food habits, and scientists disagree about what foods are selected. A few hours spent observing them will demonstrate their ability to capture and kill a wide variety of insects and other invertebrates. In a Connecticut area study, two common northeastern species of harvestmen, *Leiobunum longipes* and *L. politum*, were seen feeding daily on both healthy and parasitized gypsy moth pupae. On several occasions two or three harvestmen attacked and fed on the same gypsy moth pupa. Because harvestmen feed on both healthy and parasitized pupae, it is difficult to determine whether they act more as scavengers or as predators.

Harvestmen live in a variety of places; some species are active during the day and others are active at night. In the Connecticut study after a warm summer rain one



39

evening, harvestmen appeared to be everywhere. That night 30 trees of varying sizes and species were examined at random for 60 seconds with flashlights. On each tree, from the ground to 2.4 m up, was at least one harvestman, and some trees had as many as 12. Because harvestmen are so abundant, utilize a wide variety of foods, and forage on trees and in the litter, it is probable that even in sparse gypsy moth populations they will remove some pupae. It would certainly be wise to investigate further their predator and impact potential.

Figure 39.—Harvestmen eating pupa.

Spiders (*Araneida*)

40



Figure 40.—Wolf spider.

Spiders live everywhere and eat almost any living invertebrate provided it can be overpowered. Spiders are known to be beneficial because they destroy a large number of insects, but they are rarely mentioned as predators of forest pest insects. Forbush and Fernald (1896) listed 11 species of spiders from six families that they had seen attacking gypsy moth eggs, larvae, pupae, or adults.

During the summer, spiders become abundant throughout woodlots and forests, inhabiting the ground as well as plants of all kinds, from grasses to trees. Spiders are divided into two groups, on the basis of the way they capture their prey: Hunting spiders, which run on the ground or



on plants, catching insects wherever they find them, and cobweb spiders, which capture their prey in webs.

Lycosids (fig. 40) are hunting spiders known to eat gypsy moth larvae. They are keen-sighted, swift, long-legged running spiders. Lycosids are often called wolf spiders because they run down their prey. Attids, or jumping spiders (fig. 41), are also a type of hunting spider known to eat gypsy moth larvae. They are usually short and stout, often brightly colored, and quick in their movements. Forbush and Fernald (1896) wrote about

Phidippus tripunctatus, a jumping spider: “. . . it was brought into the insectary and supplied with gypsy moth caterpillars, which it readily destroyed.” This species is very common, and because it lives under sticks and stones it is certain to encounter gypsy moth larvae that search for daytime resting locations in the litter.

Figure 41.—Jumping spider.

42



Figure 42.—Theridid spider with larva caught in web.

Spiders that construct cobwebs are often successful in trapping gypsy moth larvae and occasionally adults. The theridid spider in figure 42 has captured a gypsy moth larva in its web. Theridids build loose and irregular-shaped webs between leaves and branches of low trees and bushes.

Spiders could have some potential impact on sparse gypsy moth populations. Unfortunately, necessary priorities toward the more important gypsy moth predators have prevented study of these interesting animals.

Other Invertebrate Predators



43

There are other invertebrates known to eat gypsy moths: The spined assassin bug, flower fly, green lacewing, baldfaced hornet, and European mantid (fig. 43) are a few. Even mites are known to destroy gypsy moth eggs. The point is that each of these invertebrates, in what often appears to be an insignificant way, adds to the collective importance of predation as an often-regulatory force.

Figure 43.—European mantid eating larva.

Reexamining Our Wildlife Perceptions

The factors of predator potential, predator impact, alternative foods, prey and predator density, and food availability remind us that we are dealing with nature's normal, effective, and continually operating mechanisms, which are subject to change at any time.

In the 1976 New Lisbon, N.J., example, the abundance of cankerworms for all practical purposes had negated the impact of white-footed mice on the gypsy moth. It has already been mentioned that when small mammals are experimentally removed from places where gypsy moth populations are sparse and stable, the moth populations *may* increase by greater than tenfold in just 1 year. However, in the New Lisbon population, although mouse density was very low, no apparent increase in the gypsy moth population occurred the second year. Certainly the potential for an increase was there, and users of predator/prey systems in pest management programs must think in terms of what will happen to the target (pest) insect if any one of the many variables occurs.

Just as important as understanding the effects of these variables are the perceptions of wildlife that most people develop throughout their lives. The word "predator" conjures up images of large animals—wolves, coyotes, and mountain lions, or eagles, hawks, and owls; small animals such as mice, shrews,

warblers, robins, and even insects are seldom thought of as predators. A chipmunk is thought of with an acorn in its mouth rather than an insect pupa; a shrew, searching for worms rather than for gypsy moth caterpillars; or an ant, carrying away picnic crumbs rather than gypsy moth eggs.

These perceptions can be difficult to change and often prevent us from seeing what is really happening. Campbell (1975) reported that shrews seldom come in contact with gypsy moths in the natural state. We have now learned that shrews not only come in contact with gypsy moths but also that they often eat them in significant amounts.

It is possible that our observations of amphibians, reptiles, and even fish as predators of the gypsy moth may be just as incomplete. This report, therefore, stresses that *all* predators must be considered as having an impact on gypsy moth populations. It took half a century from the time Forbush and Fernald discussed bird predation until mammals were mentioned as an important part of gypsy moth population dynamics. Another 25 years passed before researchers began to quantify the predatory potential and impact of mammals on sparse gypsy moth populations.

Conclusion

It should no longer be assumed that other groups of animals are insignificant as predators of forest insects. Given certain circumstances or conditions, they may be important. They are all members of the predator community, and within that context they and their role in gypsy moth population dynamics have been discussed. It is the collective impact from this complex predator community that we should try to understand and utilize in future management programs. To successfully accomplish this, we must start by reexamining and adjusting our wildlife perceptions.

A principal objective throughout the gypsy moth research program has been to develop an understanding of the role and importance of predation in the population dynamics of the gypsy moth. Over the last few years a great deal has been learned about the gypsy moth predator complex, and several characteristics that make predators a major suppressive force well suited for a specialized role in an integrated pest management system have been discussed. However, further information is needed before we can successfully integrate our knowledge of gypsy moth predator/prey theory with biologically and economically feasible practice so that forest managers can use predators in an effective and practical control program.

Particular emphasis in future studies should be placed on understanding the foods and feeding habits of the predators so that they can be used effectively in an integrated pest management program. Also, because predator impact is closely associated with alternative foods, we need a better understanding of annual food production, variety, quantity, and variability within northeastern hardwood forests.

The predator/prey system discussed in this booklet is complex, being composed of many predator species that eat a variety of foods. These predators are all opportunistic and select food largely as a function of availability and abundance. Although a preferred food may be eaten in great quantity, these

predators attempt to vary their diets and are always testing other potential food sources; in this process gypsy moths are eaten by many predators. It is the collective impact of all these predators that leads to their importance in maintaining certain sparse gypsy moth populations.

If the gypsy moth predator system were simple, with one or a few predators dependent upon a particular pest insect for food, the impact and precise role of predation would be easier to predict and determine. On the other hand, the complexity of the gypsy moth predator community may actually give greater year-to-year stability and be a major reason why some gypsy moth populations remain sparse and stable for several years.

Certain aspects of the role of gypsy moth predators are fairly well understood, while many others have not yet been determined. This is probably best exemplified by research experience. The available information in the early 1970's led to the belief that when significant predation of gypsy moth pupae in sparse populations occurred, it was contingent upon white-footed mouse activity. It was then hypothesized that through management to increase populations this important predator might be made even more effective. In one study, white-footed

mouse populations were managed by providing supplemental food and nest boxes from 1973-76, which resulted in a significant annual increase in mouse density. However, the real significance of this study was not realized until after a second study. It seemed that the next logical step was to measure the impact of the increased mouse density on the survival of gypsy moths. A study was therefore designed to determine the feeding behavior of white-footed mice in relation to healthy and parasitized male and female pupae placed in the litter.

In retrospect it was probably overly optimistic to believe that the precise impact of the mice on the pupae could be determined. By the end of the field season it was not readily apparent, without the aid of a computer to assist in analysis, whether mice, shrews, or even invertebrates (ants and harvestmen) had eaten more pupae. Mice may well be the most important predator of gypsy moths, but it was found that they were getting a lot of help.

During that study came the realization of how little was known about the components and interactions within the total gypsy moth predator community. Perhaps most surprising was the abundance of activity of the invertebrates as they scavenged the parasitized pupae and attacked healthy pupae.

The high susceptibility of parasitized pupae to attack by all of these predators certainly warrants further investigations. High parasite mortality related either directly or indirectly to vertebrate and invertebrate predatory behavior may be a significant factor contributing to the ineffectiveness of parasites in this country (Reardon 1976, Campbell and Sloan 1977). An appreciation of the complexity of this predator/prey system comes forth when it is remembered that the study focused only on one life stage (the pupa), in one location (the litter) in one forest.

Buckner (1966), in discussing the role of predators in the biological control of forest insects, stated “particular emphasis should be placed on the factors governing the abundance of the various predators so that advantage may be gained from the large groups of potentially important predators whose members are not related closely to the abundance of the prey.” Human activity and land use practices often govern the abundance and distribution of a large number of predators and can have tremendous impact on species that are important predators of forest pest insects. It seems appropriate, therefore, to make a few comments about the concept of managing these predators and their basic needs.

“The general needs of all animals are much alike in that each must have a sufficient quantity and variety of food and protective cover to meet its physiological needs for

maintenance, growth and reproduction throughout its life” (Trippensee 1948). In all habitats there is a limitation on the number of animals of each species that an area can maintain or support; this is referred to as the carrying capacity. The population of each species adjusts to the carrying capacity for each area. Every time a significant habitat change occurs in an area, the animal populations, given proper time, readjust to the new carrying capacity. Depending on the actual change that took place, wildlife number and diversity can increase, decrease, or remain the same. Generally, however, if food and cover are increased, wildlife populations increase. (Each species does have certain limits beyond which their populations cannot increase. These limits are often referred to as tolerance density, a point where intraspecific competition and crowding take place and become the population’s controlling mechanism.)

Forest managers wishing to employ predator management for insect control can either increase native predator populations, release exotic predator species, or do both. The release of exotic predators is not and should not be an attempt to release a large number of predators available for immediate control—this will not work. Rather, it should be an attempt to establish a breeding population of a particular predator where it previously did not exist.



44

The introduction of the masked shrew from mainland Canada into Newfoundland to control larch sawfly is one example of a successful attempt to establish a breeding population of a vertebrate predator to control a forest pest insect.

Figure 44.—Forest “cleaned up.”

The idea of managing a particular predator or predators to combat a forest pest insect is not new. Buckner (1966) described a successful attempt by Hamilton and Cook in the 1930's to protect a plantation of larch in New York State from an outbreak of the larch sawfly. They supplied nest boxes and brush piles that provided a significant habitat change that

produced an abundance of deer mice, redback voles, and masked shrews. Each of these mammals has a relatively high insectivorous diet, and the increase in their numbers led to a reduction in the number of sawflies in the managed plantations. In the unmanaged control areas, sawflies remained at outbreak levels for years.

Providing and/or improving food and cover for wildlife can increase the density of wildlife. Populations of birds and mammals can often be raised simply by increasing the food supply. Feeding has the advantage of being easily turned on and off; with proper manipulation a manager could change at will a species from eating the feed back to a natural diet, including insects. However, feeding has the disadvantage of being expensive, nonselective, and effective for only a short term.

A more reasonable way to increase population densities of useful vertebrates is through silvicultural habitat manipulation, encouraging plant species that have the capacity of supplying both food and cover. To manage a species through habitat manipulation, it is necessary to understand the habitat requirements for each species and whether those requirements can be manipulated in an economically and ecologically feasible manner to achieve the management objectives. In each case, it must be determined if the habitat can be manipulated in a way to increase the abundance of the vertebrates that eat gypsy moths.

Fortunately, many species of birds and small mammals respond favorably to relatively simple habitat changes. Creating dense ground cover, one of the most important requirements of forest-dwelling small mammals, can effectively increase small-mammal populations. Its importance for large populations of small mammals cannot be overemphasized.

Populations of hole-nesting birds have been successfully increased by providing them with nest boxes. In parts of the Soviet Union, nest boxes have been used to increase bird numbers in an integrated management system for a complex of forest-defoliating insects, including the gypsy moth.

What can forest managers and homeowners do to help increase, maintain, and create a more diverse predator community? Homeowners, unfortunately, often seem compelled to clean up their property and turn natural brushy areas into lawn (fig. 44), thereby removing the food and cover needed by birds and mammals. Foresters also are often involved in similar large-scale cleaning operations, which lead to the elimination of the brush competing with the trees. These cleaning operations often drastically reduce both vertebrate species diversity and the total number of birds and small mammals in the area. The elimination of brush

removes the cover necessary for bird species, which occur from the ground to the lower canopy, and eliminates much of the cover necessary for small mammals.

Few people will manage their land strictly for small mammals and birds, but many foresters and homeowners unknowingly turn good wildlife habitat into unsuitable habitat simply by removing the brush. By understanding the requirements of these predators, one can actually manage for them by not destroying their habitat, or at least by trying to minimize the impact of human activities on the habitats of these animals.

It is hoped that the information presented in this booklet has increased the awareness of the value and importance of predation in maintaining population stability of forest insect pests. It is known that predation is a regulatory factor in certain gypsy moth populations and in populations of some other forest pest insects. However, it must also be realized that predation is only one of the forces suppressing insect population growth in a forest ecosystem. Although at times predators may regulate gypsy moth populations, they cannot regulate them forever and they do not regulate them alone.

Predators have in the past and will continue in the future to be important in the population dynamics of the gypsy moth. Gypsy moth populations in this country usually appear to be at either harmless or outbreak levels. One of the keys to the harmless level is the naturally occurring predation by the predator community. Since the best way to cope with a problem is to prevent it, it would be wise to use predators in future attempts at managing the gypsy moth.

As more is learned about predation and other processes within the forest ecosystem, an appreciation must grow of the importance of slowly and patiently gathering the facts from which conclusions are drawn. Objectivity must be maintained in order to put early preconceptions in their proper perspective and to gather scientifically acceptable evidence from which new research goals are made and future pest management programs are developed. The success of future gypsy moth management systems lies in our ability to appreciate, understand, and wisely use all the natural suppressive mortality factors operating within the forest ecosystem.

Acknowledgments

Special appreciation is given to Roger Zerillo for the many hours spent on the difficult and sometimes frustrating job of photographing most of the wildlife in this booklet.

We would like to thank the following for their outstanding contributions to this report. For research assistance: Dan Arcieri, Joel Bigelow, Paul Castelli, Nancy DePalma, Paul Galipeau, Jean Germe, Pat Goertz, Dan Holland, Candy Hutchinson, Craig Scharf, and Ron Sloan. For reviews and comments of early drafts of this report: Drs. Noble Proctor, Southern Connecticut State College, and Steve Berwick, Yale University. For photographs: Harold Eno (fig. 14), Lt. Col. Murray Cragin, USAF (figs. 40 and 41), Paul Schaefer (fig. 37), and Bob Neely (fig. 42).

We also thank the Encyclopaedia Britannica Educational Corporation for kindly allowing the use of figures 5–13, which were copyrighted 1962–64.

The quotes on page 11 are from *Ecology and Resource Management*, by Kenneth E. F. Watt. Copyright 1968 by McGraw-Hill. Used with permission of McGraw-Hill Book Company.

References

- Bess, H. A.** 1961. Population ecology of the gypsy moth, *Porthetria dispar* (L.) (Lepidoptera:Lymantriidae). Conn. Agric. Exp. Stn. Bull. 646.
- Bess, H. A., S. H. Spurr, and E. W. Littlefield.** 1947. Forest site conditions and the gypsy moth. Harvard For. Bull. 22.
- Brown, W. L.** 1961. Mass insect control programs: Four case histories. *Psyche* 68:75–111.
- Buckner, C. H.** 1966. The role of vertebrate predators in the biological control of forest insects. *Ann. Rev. Entomol.* 11:449–470.
- Burgess, A. F.** 1929. Imported insect enemies of the gypsy moth and the brown-tail moth. U.S. Dep. Agric., Tech. Bull. 86.
- Burt, W. H.** 1957. Mammals of the Great Lakes Region. Univ. Mich. Press, Ann Arbor, Mich.
- Campbell, R. W.** 1975. The gypsy moth and its natural enemies. U.S. Dep. Agric., Agric. Info. Bull. 381.
- Campbell, R. W., and R. J. Sloan.** 1976. Influence of behavioral evolution on gypsy moth pupal survival in sparse populations. *Environ. Entomol.* 5:1211–17.
- Campbell, R. W., and R. J. Sloan,** 1977. Natural regulation of innocuous gypsy moth populations. *Environ. Entomol.* 6:315–322.
- Chapman, F. M.** 1968. The warblers of North America. Dover Publishing Co., New York.
- DeGraaf, R. M, H. R. Pywell, and J. W. Thomas.** 1975. Relationships between nest height, vegetation, and housing density in New England suburbs. *Trans. Northeast Sect. Wildl. Soc.* 32:130–139.

- Forbush, E. H., and C. H. Fernald.** 1896. The gypsy moth. Wright and Potter, Boston.
- Furuta, K.** 1976. Studies on the dynamics of the low density population of gypsy moth and toda-fir aphid (in Japanese, English summary). Jap. Gov. For. Exp. Stn. Bull. 279. Tokyo.
- Galipeau, P. R.** 1975. Avian predators of the gypsy moth. Unpublished report. U.S. Dep. Agric. For. Serv., Northeast. For. Exp. Stn., Hamden, Conn.
- Garlo, A. S.** 1977. Personal communication. U.S. Dep. Agric. For. Serv., Northeast. For. Exp. Stn., Hamden, Conn.
- Hamilton, W. J., and D. B. Cook.** 1940. Small mammals and the forest. J. For. 38:468-473.
- Holmes, R. T., and F. W. Sturges.** 1975. Bird community dynamics and energetics in a northern hardwood ecosystem. J. Anim. Ecol. 44:175-200.
- Lautenschlager, R. A., H. Rothenbacher, and J. D. Podgwaite.** 1978. The response of small mammals to aerial applications of the nucleopolyhedrosis virus of the gypsy moth, *Lymantria dispar*. Environ. Entomol. (In press.)
- Lewis, F. B.** 1978. Personal correspondence. U.S. Dep. Agric. For. Serv., Hamden, Conn.
- Mosher, F. H.** 1915. Food plants of the gypsy moth in America. U.S. Dep. Agric., Bull. No. 250.
- ODell, T. M.** 1977. Personal communication. U.S. Dep. Agric. For. Serv., Hamden, Conn.
- Palmer, E. L., and H. S. Fowler.** 1975. Fieldbook of natural history. McGraw-Hill, New York.
- Paszek, E. C.** 1977. Personal communication. U.S. Dep. Agric. Anim. Plant Health Insp. Serv., Otis AFB, Mass.
- Reardon, R. C.** 1976. Parasite incidence and ecological relationships in field populations of gypsy moth larvae and pupae. Environ. Entomol. 5:981-987.
- Rotschild, E. V.** 1958. Extermination by rodents of the gypsy moth in an area of mass reproduction. (Trans. from Russian.) Byull. Mosk. O-VA. Ispyt. Prir. Otd. Biol. 63:129-130.
- Smith, D. M.** 1978. Personal communication. Yale Univ. Sch. For. Environ. Stud., New Haven, Conn.
- Smith, H. R.** 1975. Management of *Peromyscus leucopus* as part of an integrated program to control the gypsy moth. Trans. Northeast Sect. Wildl. Soc. 32:111-130.
- Smith, R. F.** 1969. Integrated control of insects—challenge for scientists. Agr. Sci. Rev. 7(1):1-5.
- Swan, L. A., and C. S. Papp.** 1972. The common insects of North America. Harper and Row, New York.

Tinbergen, L. 1960. Dynamics of insect and bird populations in pine woods. *Arch. Neth. Zoo.* 13:265–343.

Trippensee, R. E. 1948. *Wildlife management: Upland game and general principles*, vol. 1. McGraw-Hill Book Co., New York.

Turcek, F. J. 1952. An ecological analysis of the bird and mammalian population of a primeval forest on the Polona-mountain (Slovakia). *Bull. Int. de l'Acad. tcheque Sci.* 53:1–25.

Watt, K. E. F. 1968. *Ecology and resource management*. McGraw-Hill Book Co., New York.

Welty, J. C. 1962. *The life of birds*. W. B. Saunders Co., Philadelphia.

Issued December 1978
Available from the Superintendent of
Documents
U.S. Government Printing Office
Washington, D.C. 20402
Stock No. 001-000-03851-6