

**DIFFERENCES IN THE UTILIZATION OF TREE SPECIES AS LARVAL HOSTS AND PUPATION SITES BY THE GYPSY MOTH, *LYMANTRIA DISPAR* (LEPIDOPTERA: LYMANTRIIDAE)**

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**Abstract**

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In the summer of 1980, gypsy moth populations were monitored in 13 sparsely infested forests in southwestern Quebec; counts of living and dead larvae and pupae were made on 1,870 trees representing 28 deciduous and one coniferous species. Contrary to our null expectations, the proportionate numbers of pupae compared with larvae on the various host species were not equal. Hosts more preferred by larvae were less preferred by pupae, and *vice versa*. For example, pupae were disproportionately abundant on host species like *Acer pensylvanicum* L., *Carya ovata* (Mill.) K. Koch, and *Juglans cinerea* L. which are not generally favored larval hosts. Conversely, favored larval hosts like *Quercus rubra* L. and *Ostrya virginiana* (Mill.) K. Koch carried lower numbers of pupae than expected from the numbers of larvae feeding on them. Such differential utilization of host trees by larvae versus pupae, which can arise either from host-dependent differences in larval mortality or from late instar migration between hosts, may contribute to maintaining the broad polyphagy of gypsy moth larvae.

**Résumé**

Durant l'été de 1980, des populations de spongieuses ont été inventoriées dans 13 forêts du sud-ouest québécois peu abondamment infestées par cet insecte; les larves vivantes et mortes, et les chrysalides ont été comptées sur 28 décidus et un conifère pour un total de 1870 arbres. Contrairement à notre prédiction, le nombre de chrysalides identifié sur les arbres n'était pas proportionnellement égal au nombre de larves retrouvées sur les différentes essences hôtes. Les hôtes les plus préférés par les larves sont les moins préférés par les chrysalides, et *vice-versa*. Par exemple, les chrysalides étaient plus abondantes d'une façon disproportionnée sur les essences hôtes comme *Acer pensylvanicum* L., *Carya ovata* (Mill.) K. Koch, et *Juglans cinerea* L. qui sont généralement des essences non favorites. En contrepartie, les essences favorites comme *Quercus rubra* L. et *Ostrya virginiana* (Mill.) K. Koch comportaient moins de chrysalides que leur nombre de larves laissait prévoir. Les différences dans l'utilisation de l'essence hôte par les larves versus les chrysalides peuvent être en partie dues à la mortalité larvaire sur une essence en particulier, ou bien à une migration des derniers stades larvaires vers d'autres hôtes, ceci pouvant contribuer à maintenir la diversité du choix de ce polyphage qu'est la spongieuse.

**Introduction**

The gypsy moth, introduced from Europe in 1869, has gradually colonized over 473,000 km<sup>2</sup> of forest in North America (Pritchett 1975). Gypsy moth larvae may consume foliage from over 400 plant species (Forbush and Fernald 1896), but exhibit clear preferences within their wide range of acceptable hosts (Lechowicz and Jobin 1983; Mauffette *et al.* 1983). The early instar larvae, which account for most dispersal in gypsy moth populations, respond selectively to available host foliage (Barbosa *et al.* 1979). Once a host tree is chosen the larvae usually live on, or close to, that tree during their larval development (Lance and Barbosa 1979).

Most early studies emphasized that in sparse populations larvae primarily use the forest litter near the larval host tree or a protected location on the tree itself for pupation (Bess *et al.* 1947; Campbell *et al.* 1975*a,b*; Campbell and Sloan 1977*a,b*). Some between-tree larval migration by late instars does occur, however, and increases with larval pop-

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ulation density (Lance and Barbosa 1981; Wallner 1983). In a study of gypsy moth on five host species, Barbosa (1978) noted an increase of the later instar larvae and the pupae on non-preferred hosts; he postulated a behavior-related selection of a pupation site that differed from host selection behavior by dispersing larvae. Similarly, Rossiter (1981) observed a shift of late instar larvae from oak to pine which resulted in disproportionately high pupal numbers on this less-preferred larval host. She further showed that pupae on pine suffered lower mortality due to viral pathogens. There is then increasing evidence from studies on a few host species for differential utilization of host trees during the larval and pupal phases of the gypsy moth life cycle. To more generally test the idea of differential utilization, especially in sparse populations, we have compared gypsy moth larval and pupal numbers on 29 tree species occurring in a diversity of native forests.

### Materials and Methods

We studied 13 different forest sites at three localities near Montreal in southwestern Quebec (Fig. 1). At each site, 15 circular quadrats (each 100 m<sup>2</sup>) were distributed in a stratified random pattern chosen to thoroughly sample a homogeneous forest type. All living trees of 8.0 cm diameter at breast height (DBH) or larger in each quadrat were identified and their DBH tallied. The numbers of tree species present on each site varied from 7 to 17. The total sample consisted of 1,870 trees, among 29 species. Sugar maple (*Acer saccharum* Marsh.), red oak (*Quercus rubra* L.), and basswood (*Tilia americana* L.) were found in all sites except one. Paper birch (*Betula papyrifera* Marsh.), beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), and ironwood (*Ostrya virginiana* (Mill.) K. Koch) were found in 11 sites. The remaining 22 tree species occurred less frequently; a complete summary of the phytosociology of each site can be found in Mauffette (1982). The sites were characteristic of the St-Lawrence Valley forests which are largely dominated by sugar maple (Dansereau 1959).

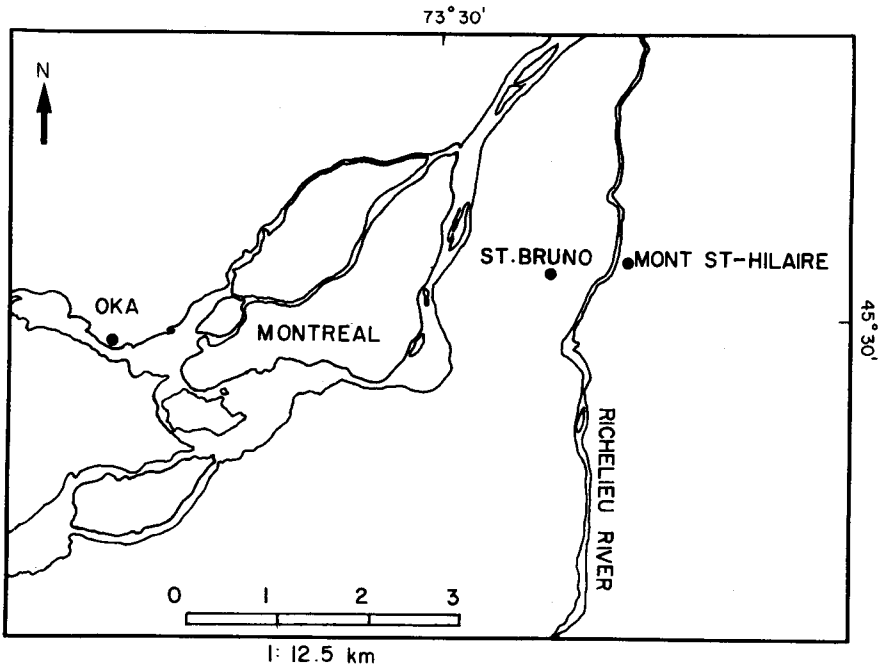


FIG. 1. Location of the three sampling localities.

All sites were infested by gypsy moth (Jobin 1978; pers. commun.) but none had sufficiently dense larval populations in 1980 to cause substantial defoliation. In such relatively low density populations, older larvae (instars IV–VI) typically seek shelter on or near the host tree during daytime (Leonard 1970; Campbell *et al.* 1975a,b). Thus to determine larval numbers we placed a tarpaper skirt that could be used as a larval resting site (Weseloh 1974) at breast height on each sampled tree. Odell and Godwin (1979) reported that 95% of the late instars on a tree used similar artificial bark flaps as resting sites. Using this method, nine larval counts were made on each of the 1,870 trees during the larval feeding season from 9 June to 25 July, and pupae and egg masses were counted in August. Living larvae, dead larvae, and pupae present under the tarpaper were tallied separately during the counts for each tree sampled.

The data were analyzed by a least squares, weighted regression of the mean number of pupae per cm DBH for each tree species on the larval density for that species. The number of trees of each host species was used as the weighting variable (Freund and Littel 1981). The larval density for each tree species was estimated as the mean value of the nine living larval counts divided by the sum of the species DBH in cm. Both variables were log transformed to stabilize the variance. The log transform for pupal number required the addition of 1.0 because a few tree species had no pupae. If the overall patterns of host utilization by larvae and pupae do not differ, the regression of pupal on larval numbers should have a slope of 1. This null expectation assumes that an equal proportion of larvae is lost from all the host species prior to pupation; the possible mechanisms of such losses are not considered in formulating the null hypothesis but are discussed subsequently. We used a *t*-distribution with ( $n - 2$ ) degrees of freedom to test our observed slope against this null hypothesis as described in Kleinbaum and Kupper (1978).

## Results

Table I summarizes the 29 different tree species sampled with the respective maximum numbers of living larvae, dead larvae, and pupae recorded under the tarpaper skirts. The maximum and seasonal mean numbers of living larvae on a host species were highly correlated ( $r = 0.98$ ). Sample sizes ranged from 1 up to 547 individuals for the different tree species; the data presented on larvae and pupae are the sums for all sites recorded for a given host.

The relation of pupal to larval densities across the 29 host species is presented in Fig. 2. Pupal numbers on a host do increase in proportion to larval density, but not as quickly as expected under the null hypothesis. The 0.37 slope of the observed regression is significantly less than 1.0 indicating that hosts more heavily utilized by gypsy moth larvae tend to be less utilized as pupation sites. Trees like *Acer pensylvanicum* L., *Juglans cinerea* L., and *Carya ovata* (Mill.) K. Koch carry unusually many pupae compared with the numbers of larvae feeding on them. Conversely, host plants that are preferred such as *Quercus rubra* L. and *Ostrya virginiana* (Mill.) K. Koch carry fewer pupae than expected from their larval numbers.

## Discussion

Even in sparse gypsy moth populations where food is not limiting, maturing larvae and pupae occur in unexpectedly high numbers on host species generally avoided by early instar larvae. The mechanisms underlying this trend, which appears general across a wide range of hosts in diverse forests, are not clear at present. The trend may rest on either differences in larval mortality among hosts or in a migratory behavior by late instar larvae which is host-dependent.

Migration of gypsy moth larvae away from preferred hosts could be stimulated by high local densities in the available resting sites during the day. Larval densities on individual

Table I. Summary of sampled trees with their numbers of gypsy moth larvae and pupae

| Species                                     | Common name         | Acronym | Number of trees sampled | Max. number living larvae | Max. number dead larvae | Sum of pupae |
|---|---------------------|---------|-------------------------|---------------------------|-------------------------|--------------|
| <i>Acer negundo</i> L.                      | Box Elder           | An      | 1                       | 7                         | 0                       | 0            |
| <i>A. pensylvanicum</i> L.                  | Striped Maple       | Ap      | 5                       | 2                         | 0                       | 6            |
| <i>A. rubrum</i> L.                         | Red Maple           | Ar      | 42                      | 85                        | 14                      | 64           |
| <i>A. saccharinum</i> L.                    | Silver Maple        | Asm     | 43                      | 96                        | 4                       | 94           |
| <i>A. saccharum</i> Marsh.                  | Sugar Maple         | As      | 547                     | 3640                      | 331                     | 1322         |
| <i>Amelanchier</i> spp.                     | Serviceberry        | Am      | 6                       | 119                       | 12                      | 11           |
| <i>Betula lutea</i> Michx. f.               | Yellow Birch        | B1      | 15                      | 46                        | 2                       | 23           |
| <i>B. papyrifera</i> Marsh.                 | Paper Birch         | Bp      | 148                     | 1248                      | 293                     | 248          |
| <i>B. populifolia</i> Marsh.                | Grey Birch          | Bpo     | 52                      | 244                       | 6                       | 66           |
| <i>Carya cordiformis</i><br>(Wang.) K. Koch | Yellowbud           | Cc      | 75                      | 262                       | 13                      | 53           |
| <i>C. ovata</i><br>(Mill.) K. Koch          | Shagbark Hickory    | Co      | 3                       | 2                         | 1                       | 2            |
| <i>Fagus grandifolia</i> Ehrh.              | Beech               | Fg      | 94                      | 916                       | 100                     | 280          |
| <i>Fraxinus americana</i> L.                | White Ash           | Fa      | 103                     | 153                       | 27                      | 104          |
| <i>F. nigra</i> Marsh.                      | Black Ash           | Fn      | 20                      | 2                         | 0                       | 5            |
| <i>F. pennsylvanica</i><br>Marsh.           | Red Ash             | Fp      | 5                       | 1                         | 1                       | 1            |
| <i>Juglans cinerea</i> L.                   | Butternut           | Jc      | 6                       | 11                        | 0                       | 17           |
| <i>Ostrya virginiana</i><br>(Mill.) K. Koch | Ironwood            | Ov      | 129                     | 3040                      | 233                     | 220          |
| <i>Pinus strobus</i> L.                     | White Pine          | Pst     | 2                       | 12                        | 4                       | 8            |
| <i>Populus deltoides</i><br>Marsh.          | Cottonwood          | Pd      | 7                       | 33                        | 1                       | 6            |
| <i>P. grandidentata</i><br>Michx.           | Large-toothed Aspen | Pg      | 44                      | 886                       | 82                      | 171          |
| <i>P. tremuloides</i> Michx.                | Trembling Aspen     | Pt      | 142                     | 1474                      | 64                      | 165          |
| <i>Prunus pensylvanica</i><br>L. f.         | Pin Cherry          | Pp      | 11                      | 19                        | 1                       | 9            |
| <i>P. serotina</i> Ehrh.                    | Black Cherry        | Ps      | 2                       | 13                        | 4                       | 4            |
| <i>Pyrus malus</i> L.                       | Apple               | Py      | 5                       | 8                         | 0                       | 0            |
| <i>Quercus rubra</i> L.                     | Red Oak             | Qr      | 244                     | 12158                     | 695                     | 1710         |
| <i>Salix</i> sp.                            | Willow              | Sa      | 4                       | 158                       | 11                      | 42           |
| <i>Tilia americana</i> L.                   | Basswood            | Ta      | 67                      | 794                       | 57                      | 217          |
| <i>Ulmus americana</i> L.                   | American Elm        | Ua      | 37                      | 268                       | 5                       | 81           |
| <i>U. rubra</i> Muhl.                       | Slippery Elm        | Ur      | 11                      | 13                        | 1                       | 5            |

trees of preferred hosts often are many-fold greater than on avoided hosts. For example, in our study red oak had 1.71 larvae/cm DBH compared with slippery elm with only 0.03 larva/cm DBH. Rafes and Gninenko (1973) reported that at high densities in local aggregations, frequent contacts between larvae cause a general excitability. Such excitability may induce dispersal of the insects (Lance and Barbosa 1979) thus leading to a decrease in the number of pupating individuals on preferred larval host species. Migratory behavior incurs an increased risk of predation during movement in the litter (Campbell *et al.* 1977 *a, b*) but could potentially reduce the risks of food shortage, infection, or parasitism which are greater for larvae in high density aggregations (Doane and McManus 1981). On the other hand, it may be exactly such mortality factors, which operate most effectively at high local densities, that lead to reduced pupation on preferred larval hosts. Density-dependent mortality could lead to disproportionately high pupal numbers on less preferred larval hosts. Only further investigation can elucidate the relative importance of mortality factors versus migration behavior in determining the observed pattern of larval and pupal distribution across host trees.

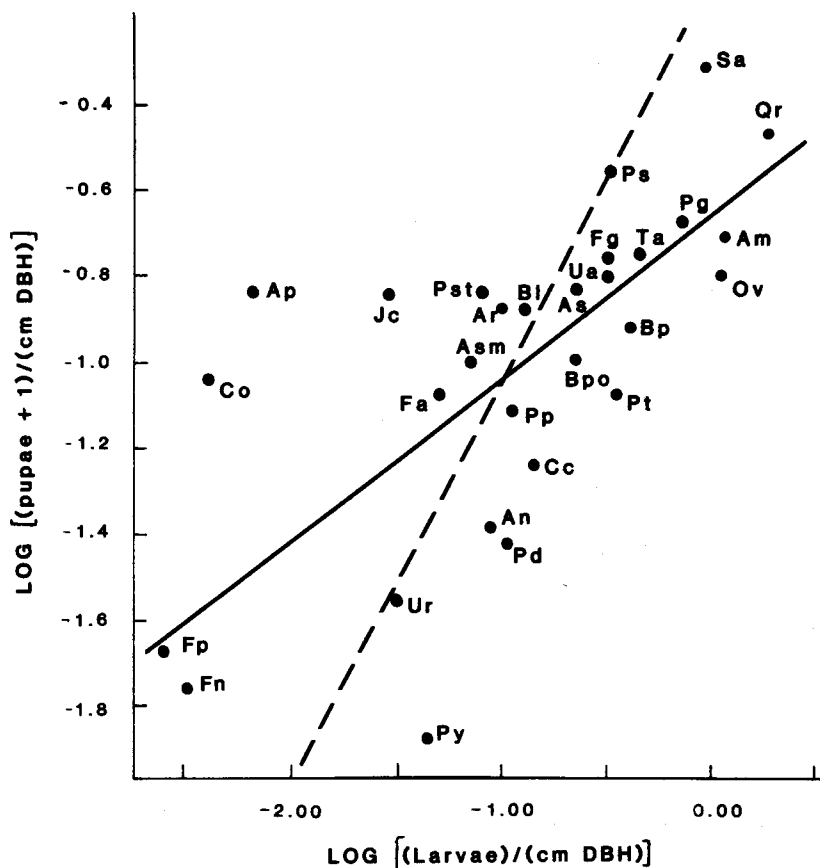


FIG. 2. Weighted regression of log transformed pupal numbers on mean larval density for all the host species; host acronyms appear in Table I. The broken line has slope equal to 1 after the null hypothesis that pupal numbers are directly proportional to larval numbers on a host species. The solid line is the observed regression which differs significantly from the null expectation ( $p < 0.005$ ).

The generally converse relation between larval and pupal host preferences observed here across many tree species in diverse forests may serve to maintain the polyphagous feeding habit of the gypsy moth. Female gypsy moths do not fly, and typically deposit their eggs in close proximity to their pupation site (Doane and McManus 1981). After eclosion not all larvae disperse, and those that do, often travel only a short distance (Doane and McManus 1981). Thus the tendency to pupate away from preferred larval hosts can lead to the maintenance of polyphagy by favoring genotypes able to feed on suboptimal larval hosts favorable for pupal success. Rossiter (1981) has suggested that such differential utilization of hosts by larvae and pupae may also contribute to host range expansion for the gypsy moth. Elucidation of the mechanisms underlying the differential utilization which apparently prevails across all host tree species will help decide the importance of this phenomenon in the evolution of gypsy moth feeding biology.

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## References

- Barbosa, P. 1978. Distribution of an endemic larval gypsy moth population among various tree species. *Environ. Ent.* 7: 526-527.
- Barbosa, P., J. Greenblatt, W. Withers, W. Cranshaw, and E. A. Harrington. 1979. Host-plant preferences and their induction in larvae of the gypsy moth, *Lymantria dispar*. *Entomologia exp. appl.* 26: 180-188.
- Bess, H. A., S. H. Spurr, and E. W. Littlefield. 1947. Forest site conditions and gypsy moth. *Harvard Forest Bull.* 22. 56 pp.
- Campbell, R. W., D. L. Hubbard, and R. J. Sloan. 1975a. Location of gypsy moth pupae and subsequent pupal survival in sparse, stable populations. *Environ. Ent.* 4: 597-600.
- 1975b. Patterns of gypsy moth occurrence within a sparse and numerically stable population. *Environ. Ent.* 4: 535-542.
- Campbell, R. W. and R. J. Sloan. 1977a. Forest stand responses to defoliation by the gypsy moth. *Forest Sci. Monogr.* 19: 1-34.
- 1977b. Natural regulation of innocuous gypsy moth populations. *Environ. Ent.* 6: 315-322.
- Dansereau, P. 1959. Phytogeographia Laurentiana II. The principal plant associations of the St-Lawrence Valley. *Contrib. Inst. Bot. Univ. Montreal* 75.
- Doane, C. C. and M. L. McManus (Eds.). 1981. The gypsy moth: Research toward integrated pest management. *Forest Serv. Tech. Bull.* 1584. U.S. Dept. of Agriculture, Washington, D.C.
- Forbush, E. H. and C. H. Fernald. 1896. The Gypsy Moth. Wright and Potter, Boston.
- Freund, R. J. and R. C. Littell. 1981. SAS for linear models. SAS Institute, Cary, North Carolina.
- Jobin, L. 1978. Historique et situation actuelle de la spongieuse au Mont St-Hilaire. Internal Report, Laurentian Forest Research Centre, Ste-Foy, Quebec.
- Kleinbaun, D. G. and L. L. Kupper. 1978. Applied Regression Analysis and Other Multivariable Methods. Duxbury Press, Mass.
- Lance, D. and P. Barbosa. 1979. Dispersal of larval lepidoptera with special reference to forest defoliators. *Biologist* 61: 90-110.
- 1981. Host plant influences on the dispersal of late instar gypsy moths, *Lymantria dispar*. *Oikos* 38: 1-7.
- Lechowicz, M. J. and L. Jobin. 1983. Estimating the susceptibility of tree species to attack by the gypsy moth, *Lymantria dispar*. *Ecol. Ent.* 8: 171-183.
- Leonard, D. E. 1970. Feeding rhythm in larvae of the gypsy moth. *J. econ. Ent.* 63: 1454-1457.
- Mauffette, Y. 1982. Larval feeding preferences and their consequences for gypsy moth in southern Quebec. M.Sc. Thesis, McGill University, Montreal, Quebec.
- Mauffette, Y., M. J. Lechowicz, and L. Jobin. 1983. Spatial variation in the feeding preferences of the gypsy moth (*Lymantria dispar* L.) in southern Quebec. *Can. J. Forest Res.* 13: 53-60.
- Odell, T. M. and P. A. Godwin. 1979. Attack behavior of *Parasetigena silvestris* in relation to host density and behavior. *Ann. ent. Soc. Am.* 72: 281-286.
- Pritchett, G. R. 1975. The potential geographic diffusion of the gypsy moth (*Porthetria dispar*) into southern forests. *Southeastern Geographer* 14: 47-55.
- Rafes, P. M. and Y. I. Gninenko. 1973. The survival of leaf eating caterpillars (Lepidoptera) as related to their behavior. *Ent. Rev.* 52: 204-211.
- Rossiter, M. C. 1981. Factors contributing to host range extension in the gypsy moth, *Lymantria dispar*. Ph.D. Thesis, State University of New York, Stony Brook.
- Wallner, W. E. 1983. Gypsy moth host interactions: a concept of room and board. In R. L. Talerico (Ed.), Forest Defoliator-Host Interaction: A Comparison between Spruce Budworm and Gypsy Moth. USDA Forest Service, Washington, D.C.
- Weseloh, R. M. 1974. Relationships between different sampling procedures for the gypsy moth, *Porthetria dispar* (Lepidoptera: Lymantriidae), and its natural enemies. *Can. Ent.* 106: 225-231.

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