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Selection of Oviposition Sites by a Lepidopteran Community of a Tropical Forest in Southeastern Brazil¹

Key words: forest edge; leaf size; lepidopteran community; oviposition sites; plant vigor; tropical forest.

PATTERNS OF HERBIVORE PREFERENCE IN RELATION TO PLANT CONDITION have been discussed by several authors in recent years. Various hypotheses have been proposed such as the “plant stress hypothesis” (White 1969, 1984), in which plants become more susceptible to herbivore attack when physiologically stressed, and the “plant vigor hypothesis” (Price 1991a), in which groups of herbivores feed preferentially on more vigorously growing plants. Some insect herbivores are very selective in the individual plants they attack. Females might evaluate plant quality and lay eggs on rapidly growing plant tissues where larvae would probably remain and survive better (Price *et al.* 1990, Price 1991b); in this case, plant vigor would be the best predictor of oviposition (Price *et al.* 1990). Several other factors also may be related to choice of host plant, including leaf age, competition with other related species, the presence of previously laid eggs on the plant, and the presence of predators, like foraging ants (Shapiro 1981, Williams & Gilbert 1981, Pierce & Elgar 1985, Damman 1987, Freitas & Oliveira 1996). In fact, many of the plant discrimination mechanisms used by ovipositing lepidopteran females are still obscure (Chew & Robbins 1984).

In the Neotropics little information is available concerning factors that affect host plant choice by herbivore assemblages. The great diversity of plant and insect species, along with the potential for year-round interactions in tropical communities, may contribute to different patterns from those found in temperate regions (Coley & Aide 1991, Fernandes & Price 1991). To examine the relationship between selection of oviposition sites by lepidopteran females and plant vigor, we addressed the following questions: (1) are immatures more commonly found on new or mature leaves?; (2) does leaf size affect lepidopteran choice?; and (3) are plants with longer internodes more likely to bear immatures than those with shorter internodes in the same patch? Both leaf size and internode length have been assumed as indicative of plant vigor (Price *et al.* 1987).

Data were collected in the Serra do Japi, São Paulo, southeastern Brazil (23°11'S, 46°52'W), a mountain range (700–1300 m elev.) covered by semideciduous mesophytic forest (Leitão-Filho 1992). Fieldwork was carried out in early March at the end of the wet season, when most plants were at the end of their yearly vegetative growth (Morellato 1992). Six 100-m long transects were chosen along forest edges with small shrubs and herbaceous plants. These edges had been created by opening trails through the forest and are in an early successional growth stage. All plants on one side of the trail on each transect were searched carefully for lepidopteran immatures (eggs and/or larvae, but not pupae).

We recorded the location of each immature on the plant (new or mature leaves) and whether the immatures were isolated or grouped. Grouped immatures were defined by their characteristic behavior and/or spatial distribution on the leaves (*sensu* Freitas 1991, 1993), and each group was considered as one record (since they all came from a single oviposition choice by a female). Leaf area and internode length were used as parameters to compare leaves within a plant and among plants along a path, respectively. We determined the size of the leaf in which the immatures were located, and the size of the adjacent leaf with no immatures on the same plant. Leaf area was estimated by multiplying the product of the longest length and longest width by a constant of two-thirds in dicotyledons and three-fourths in monocotyledons (*cf.* Norman & Campbell 1989). We compared leaf size (leaves with the same position on the plants) and length of the third internode from the apex of the nearest conspecific plant without immatures to those of the plant bearing immatures.

In a total 182 records of immatures, we found 76 species of Lepidoptera (51 moth spp.) on 45 plant species. Almost all (90%) were eggs or first instar larvae. The latter were assumed to have low mobility within leaves of the host plant (in several cases, the egg shell was found on the same leaf). With five exceptions, each species of Lepidoptera was found on only one of the six transects. Conspecific plants (with and without immatures) were mostly (98%) < 2 m apart and of the same height.

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Isolated lepidopteran immatures were more frequent than aggregated ones (isolated = 64, aggregated = 18; $X^2 = 25.8$, $df = 1$, $P < 0.0001$). New leaves were apparently preferred compared to mature leaves (new leaf = 107, mature leaf = 69), although mature and old leaves predominated on all plant species checked (70% of all available leaves). The remaining six records were immatures located on leafless new shoots. Leaves bearing immatures were larger ($\bar{x} = 34.3 \text{ cm}^2$, $SD = 3.9$) than leaves with no immatures on the same plant ($\bar{x} = 28.4 \text{ cm}^2$, $SD = 3.1$; $t = 3.723$, $df = 182$, $P < 0.0001$). The pattern of choice for larger leaves was also observed analyzing separately for new ($P < 0.001$) and mature ($P < 0.0001$) leaves (Wilcoxon matched-pairs-signed-rank tests). Leaves bearing immatures were also larger than equivalent leaves on the nearest conspecific plant without lepidopteran immatures ($\bar{x} = 30.1 \text{ cm}^2$, $SD = 3.9$; $t = 2.328$, $df = 182$, $P = 0.021$). The same pattern could be noted when computing both new ($P < 0.0001$) and mature ($P < 0.001$) leaves (Wilcoxon matched-pairs-signed-rank tests); however, leaves without immatures on the plant with immatures were not different from equivalent leaves in the nearest plant without immatures ($t = -0.089$, $df = 182$, $P = 0.93$). In addition, plants bearing immatures had longer third internodes ($\bar{x} = 4.5 \text{ cm}$, $SD = 0.3$) than the nearest conspecific plant without immatures ($\bar{x} = 3.4 \text{ cm}$, $SD = 0.3$; $t = 5.155$, $df = 174$, $P < 0.0001$). These features may have not been those specifically evaluated by the lepidopteran females, but they show a clear pattern of occupation in newer leaves that are larger and on hosts with larger leaves and longer internodes than those not occupied.

Price *et al.* (1990) state that clutch size (among other features) is likely to be influenced by the abundance and quality of oviposition sites. Scarcity in oviposition sites may result in female competition and changed spacing in egg distribution. In early successional environments, as in our study, vigorously growing plant parts are used most (Cates 1981, Price 1991b), and the female's assessment of plant quality may favor laying eggs singly rather than in clusters (Price *et al.* 1990). Although most species do not change from single to cluster oviposition due to phylogenetic constraints, some cases have been reported in which clutch size varies within the species (Vasconcellos-Neto & Monteiro 1993; A. Freitas, pers. obs.). In our study, we found a trend for immatures to be isolated and on new leaves, suggesting that in this lepidopteran community, females could have been selected to use high quality oviposition sites.

A positive relationship between plant vigor and probability of herbivore attack has been documented for various other insects, including Cynipidae, Agromyzidae, Aphididae and Curculionidae (Price *et al.* 1990). Because leaf size and internode length may be considered parameters of plant vigor (Price *et al.* 1987), our results suggest that most of the lepidopteran community in the study site supports this pattern. Other factors that can influence choice by ovipositing females (not evaluated in this study) are leaf shape, secondary plant compounds, and presence of conspecific eggs or ants (Chew & Robbins 1984, Thompson & Pellmyr 1991, Freitas & Oliveira 1996). Many authors (*e.g.*, Whitham 1978, Auerbach & Simberloff 1989) consider leaf size as an important criterion used by herbivores in choosing oviposition sites. Bogacheva (1994) argues that age, more than size, is a criterion used by insects in general, when choosing among several plant leaves (Coley 1983). We found, however, that lepidopteran immatures were on the largest leaves, even among those of the same age class.

A working hypothesis for oviposition behavior is that preference corresponds to larval performance. In some cases, especially in the Lepidoptera, the relationship between oviposition preference and larval performance has not been confirmed (Thompson 1988, Craig *et al.* 1989). Several alternative hypotheses have been proposed for interactions lacking a strong preference-performance relationship (Thompson 1988). In most of the cases, however, the choice was among different plant species, and not among plant parts (*e.g.*, Gilbert 1991). Singer (1986) discussed the factors affecting measurements of oviposition preference, especially egg distribution and relative plant abundance. In other studies with lepidopteran species, plant size structure in natural populations seems to be even more important in determining oviposition preference than plant density (Thompson & Pellmyr 1991). For the lepidopteran community in our study, experiments of performance have not been done, and investigations are needed to determine whether oviposition sites selected by females will result in significantly higher larval survival or faster growth than in comparable sites not used.

We did not investigate all factors involved in plant choice or preference by each lepidopteran species, but some tendencies related to the "plant vigor hypothesis" are clearly noted. The results also would be different if we were to regard each individual in grouped immatures as one record; grouped immatures clearly would be dominant. This study was not designed to answer all of these questions, but was an

initial test of the vigor hypothesis at the community level, showing that it needs testing under several conditions of successional stages and with different insect assemblages.

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Do Tapirs Steal Food from Palm Seed Predators or Give Them a Lift?¹

Key words: Atlantic forest; palms; seed dispersal; seed predation; southeastern Brazil, tapir; *Revena rubiginosa*; *Syagrus romanzoffiana*; *Tapirus terrestris*; weevils.

TAPIRS ARE BROWSER-FRUGIVORES (Salas & Fuller 1996), most species feeding on a wide diversity of fruits (Olmos 1997) that may be an important part of their diet; the diet of the lowland tapir, *Tapirus terrestris* Linnaeus, is 30 percent fruit (Bodmer 1990, 1991). Tapirs chew or ingest seeds of many species, although as hindgut fermenters they have a limited capacity to digest most of them. Because of the relatively long time it takes seeds to pass through their digestive system along with their wide-ranging habits, they may disperse many seeds far from parent trees (Fragoso 1994, Olmos in press).

Although the evidence for tapir-dependent seed dispersal systems is limited (Williams 1984, Bodmer 1990, Fragoso 1997, Downer 1995), dispersal by tapirs appears especially important for some palm species (Bodmer 1990, Fragoso 1997, Brooks *et al.* 1997, Olmos 1997). Tapirs may be important seed dispersers through competition with seed predators such as beetles and rodents (Fragoso 1997, Olmos 1997); seed-boring beetles such as weevils and bruchids are the largest source of palm seed mortality in the Neotropics (Wilson & Janzen 1972, Herrera 1989, Smythe 1989, Wright 1990, Oyama 1991, Fragoso 1997, Johnson *et al.* 1995). Rodents, especially squirrels, are another important source of palm-seed mortality potentially consuming most of an individual's seed crop (Heaney & Thorington 1978, Glanz *et al.* 1982, Galetti *et al.* 1992).

Some palms rely on vertebrates to disperse their seeds (Janzen 1971, Bradford & Smith 1977, Smythe 1989, Fragoso 1997). Although rodents are regarded as important dispersers (as well as predators), they rarely disperse seeds far from the parent trees (Howe & Schupp 1986; Forget 1990, 1991, 1992; Peres & Baidier 1997). Tapirs, on the other hand, have large home ranges, and may move seeds tens of km from parent trees (Williams 1984, Fragoso 1997). Also, tapirs apparently kill some beetle larvae already in the fruits without harming the seeds (Fragoso 1997).

We tested the hypothesis that lowland tapirs reduce seed mortality in the palm, *Syagrus romanzoffiana*

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