

## RELATEDNESS AND GREGARIOUSNESS IN THE ORANGE-STRIPED OAKWORM, *ANISOTA SENATORIA* (SATURNIIDAE)

ADAM H. PORTER<sup>1</sup>, SEAN J. CADARET, SCOTT A. JOHNSON,  
HIDETAKA MIZOHATA, ANDREA I. BENEDETTER<sup>2</sup>,  
CATHLEEN L. BESTER, JENNIFER L. BORASH, SCOTT D. KELLY,  
GRETCHEN S. BUEHNER, AND MARILYN L. SHERMAN

Department of Biological Sciences, Bowling Green State University,  
Bowling Green, Ohio 43403, USA

**ABSTRACT.** Oakworm larvae live in groups and provide a convenient model system for the study of gregarious behaviors of caterpillars. Most caterpillar groups consist largely of related individuals, so the costs and benefits of gregariousness must be considered within the framework of kin selection. In this study, we use allozymes to estimate relatedness within 11 groups of 4th–5th instar larvae. Allozyme diversity was high in four marker loci, with an average heterozygosity of  $H_{exp} = 0.376 \pm 0.029$  (SD) when frequencies were pooled over groups. We found a relatedness of  $r = 0.31 \pm 0.056$ , a relatively low value given that full-siblings show  $r = 0.5$ . The mean nearest-neighbor distance among plants was  $4.34 \pm 3.48$  m, and among groups it was  $5.25 \pm 4.15$  m. Within the framework of a mathematical dispersal model calibrated using observations of larval movement in the field, these values suggest that only about 4% of wandering larvae ever find new hosts, and that exchange is negligible among groups on different plants. Adult behaviors, either multiple mating or aggregation of egg clutches, are therefore probably responsible for the observed relatedness values.

**Additional key words:** caterpillar ecology, Lepidoptera, dispersal, group living.

Oakworm moths (*Anisota senatoria* J. E. Smith) are primarily known by the considerable destruction their gregarious larvae can cause to the foliage of oaks in eastern North America (e.g., Coffelt, Schultz & Wolf 1993). The larvae are brightly colored and easily manipulated in the field, making them excellent models for the study of communal behaviors of caterpillars.

Natural history data relevant to the communal behavior of *A. senatoria* larvae are available from recent studies to assess and control their impact as pests in suburban landscapes (Coffelt & Schultz 1990, 1993). Adults emerge in late June to early July and copulate diurnally (Ferguson 1971), and females lay clutches of 200–700 eggs on the undersides of oak leaves (Coffelt & Schultz 1990). Host plants in other families have been reported in the older literature (compiled in Teitz 1972), but these are probably erroneous (Ferguson 1971). Females are weak fliers and over 90% of the clutches are laid within 5 m of the ground (Coffelt

<sup>1</sup>Corresponding author; current address: Dept. Entomology, University of Massachusetts, Amherst, Massachusetts 01003, USA, email: aporter@ent.umass.edu

<sup>2</sup>Institut für Zoologie, Universität Salzburg, Hellbrunnerstr. 34, A-5020 Salzburg, Austria

& Schultz 1994). The larvae appear to be confined to older leaves (Lawson et al. 1982, Coffelt, Schultz & Banko 1993). The larvae feed gregariously, resting on stems and twigs and relocating to nearby (often higher) branches as defoliation proceeds (Coffelt & Schultz 1994). Mature larvae pupate in the soil beneath their host trees. Most populations are univoltine, but bivoltine populations occur in the southern portion of the range (Ferguson 1971, Coffelt & Schultz 1994).

In most non-eusocial insects studied, group-living is initiated when females lay clutches of eggs (e.g., the eastern tent caterpillar, *Malacosoma americanum* (F.) (Lasiocampidae) (Costa & Ross 1993); the willow leaf beetle, *Plagioderia versicolora* Laicharting (Chrysomelidae) (McCauley et al. 1988)). Group living may subsequently be promoted by larval behaviors that maintain and enhance gregariousness, as in *M. americanum* (Fitzgerald & Peterson 1988) and *Pryeria sinica* Moore (Zygaenidae) (Tsubaki 1981), or it may be maintained simply by the absence of larval dispersal from the oviposition site.

Several selection pressures may act simultaneously on group-living behaviors of larval insects. Factors acting against group living in caterpillars include greater risks of detection by predators (Morris 1972, Stamp & Bowers 1988) and parasitoids, increased cannibalism, and greater chances of intragroup competition via defoliation of the host plant (Tsubaki & Shiotsu 1982). Those favoring gregariousness include facilitation of feeding on tough host leaves (Ito et al. 1982; and suggested for early instars of *A. senatoria* by Hitchcock 1961), the sharing of silken trails and nests (Fitzgerald & Peterson 1988), enhanced thermoregulation at low air temperatures (Stamp & Bowers 1990a), and potentially greater effectiveness of defensive behaviors against parasitoid attack (Stamp & Bowers 1990b). Additional benefits of larval gregariousness include enhanced effects of chemical defenses (Tostowaryk 1972 for *Neodiprion* sawfly larvae) and warning coloration (Sillen-Tullberg 1990) for distasteful species, and selfish-herd effects mediated by predation, provided that predation is not too intense (Hamilton 1971). These selection pressures may change with age, influencing the degree of grouping and cooperation that is optimal for larvae of different ages (Cornell et al. 1987, McCauley et al. 1988, Costa & Ross 1993). Inasmuch as individuals in larval groups are likely to be related because of maternal oviposition behavior, the costs and benefits of gregariousness need to be interpreted within a kin-selection framework.

In this study, we use allozymes to assess relatedness within late-instar groups of *A. senatoria* larvae, and present results of a simple experiment on larval dispersal ability to assess its influence on relatedness. Other factors that may influence *A. senatoria*'s gregariousness, outlined above, will be pursued in separate studies.

## MATERIALS AND METHODS

Fourth and fifth instar larvae of *A. senatoria* were observed on individual red oaks (*Quercus rubra* L.; Fagaceae) at the Girdham Road sand dunes in Oak Openings Metropark in Lucas Co., Ohio, on 9 September 1995. The site includes a mixture of mature, sapling, and seedling age classes on a sandy substrate, and larval groups were abundant and easily accessible on the smaller plants. Larvae were identified using the key in Ferguson (1971). Few groups were seen at heights >5 m, in agreement with Coffelt & Schultz (1994).

**Relatedness.** Eleven larval groups were arbitrarily chosen and from each, 15 individuals (or all individuals if <15 were present) were removed and frozen at  $-80^{\circ}\text{C}$ . Tissue was sampled by shaving slices from the abdomens of the still-frozen larvae, taking care not to include gut contents. Starch gels were prepared using standard techniques (Porter & Mattoon 1989). Seven loci were stained: glutamic-oxaloacetic transaminase (GOT-1, GOT-2), malate dehydrogenase (MDH-1, MDH-2), malic enzyme (ME), phosphoglucosmutase (PGM), and phosphoglucose isomerase (PGI). Alleles were scored alphabetically by locus. Individuals with rare alleles were re-run in adjacent lanes to confirm their scoring, and unresolved individuals were re-run as well.

The relatedness statistic,  $r$ , describes the extent to which individuals within groups share alleles, beyond the degree to which alleles are shared with an 'average' individual in the population as a whole. Grafen (1985) provides an excellent discussion of the interpretation of relatedness statistics. Relatedness was calculated using equation 6 of Queller & Goodnight (1989), a method that accounts for sampling bias. All calculations were performed using a population genetic analysis program written by A. H. Porter, which is available upon request.

**Dispersal.** Larvae were tested to determine their dispersal and re-aggregation capabilities following disturbances. Four plants <2 m in height were found with larval groups ( $n = 22, 4, 5, 6$ ) on them. Concentric circles with 1, 2, and 3 m radii were drawn in the sand around these plants and the branch containing the group was jolted to simulate the arrival of a potential vertebrate predator. The larvae dropped to the ground and their movement distances and directions were monitored at 2 min intervals for 10 min. These were converted to average movement rates to provide a rough estimate of the ability of larvae to move among plants. The circle was divided into four quadrats and movement direction was determined for each larva as the quadrat it occupied after 10 min. Larvae could disperse in any direction so circular statistics (Batschelet 1981) were used on these data to assess whether the larvae tended to move together.

TABLE 1. Allele frequencies (s.e.) of the pooled data. Sample sizes (n) indicate number of stainable individuals for each locus.

allele	GOT-1	MDH-2	PG1	PGM
n	107	153	158	142
A	0.009 (0.001)	0.761 (0.002)	0.066 (0.001)	0.025 (0.001)
B	0.944 (0.001)	0.239 (0.002)	0.025 (0.001)	0.056 (0.001)
C	0.047 (0.001)		0.051 (0.001)	0.486 (0.003)
D			0.725 (0.002)	0.419 (0.003)
E			0.133 (0.001)	0.014 (0.001)

**Distances among hostplants and larval groups.** To estimate the probabilities of larvae moving between plant or to new groups, hostplants and all larval groups within 2 m of the ground were first identified and mapped within a  $50 \times 100$  m area. This area was chosen because it contained sufficient plants and larval groups for a statistical analysis, and it was set apart from other areas with infested plants. The map was constructed by creating a lattice of triangles with sampled plants at the vertices, then measuring the distances between plants; nine missing measurements were estimated from field notes and sketches. Under this system, the coordinates of a third point of a triangle can be found using simple geometry once the first two are established. The lattice was thereby converted to a Euclidean coordinate system by establishing the coordinates of the first two points along a north-south line (the first point is at  $(0, 0)$ , the second is at  $(0, d)$ , where  $d$  is the distance between points) and iterating through the lattice until all coordinates were calculated. The distances between any two lattice points can then be found directly using the Pythagorean relationship. All calculations were performed using a *Mathematica* notebook (v2.2; Wolfram 1991). This convenient method provides an explicit map of all points of interest on the site without the need for erecting a grid. The method readily yields the distributions of interplant and intergroup distances, information that is not obtainable using nearest-neighbor measurements.

We estimated the proportion of wandering larvae that find new plants from the geometry of the plants in the study area. The angle subtended by a plant at distance  $d$  is  $0.2/d$  radians, and the proportion of a search circle that culminates in a plant is  $0.1 \pi^{-1} \Sigma d^{-1}$ . When plant density is low, these proportions are rather small, and to provide a conservative assessment of the role of dispersal, we chose assumptions that overestimated the chances of concluding that a larva would find a new plant. We thus assumed a relatively constant heading for a searching caterpillar, and that any plant within 10 cm of its path would be detected. A constant heading is the best strategy for a searching caterpillar when plant density is low (Jones 1977). As this assumption is relaxed and the



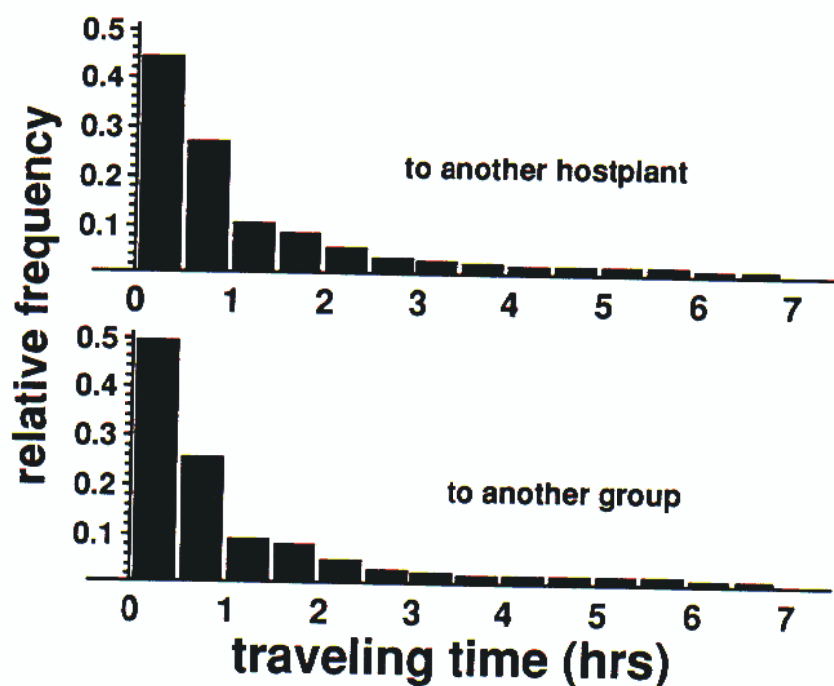


FIG. 1. Estimated distributions of traveling times for larvae successfully dispersing between plants, and between groups on separate plants. An additional 96% of larvae would not find plants at all.

propensity increases for larvae to change their heading during their search, they will wander along increasingly longer average paths before reaching new hosts. This is equivalent to increasing the distances between plants under a constant-heading search, and results in a somewhat lower probability of finding a new host. Dethier (1989) found that dispersing caterpillars tend to maintain relatively straight paths unless perturbed by obstacles. Our study plants were chosen for the relatively few obstacles in the sandy substrate around them, and this too may yield relatively generous estimates of dispersal capabilities. The value of 10 cm for the radius of detection was also chosen to be generous. When unaided by silken trails of conspecifics, other caterpillars species tested rarely showed orientation to hosts beyond 5 cm distance (Dethier 1959, Saxena & Khattar 1977, Saxena et al. 1977), though vertical stems (host or not) induced orientation in some species at 50 cm, even as far as 3 m (Doane & Leonard 1975, Roden et al. 1992). We did not adopt these higher values for three reasons. First, few larvae in our dispersal experiments returned to the source plant despite its close proximity, suggesting that such orientation capabilities are negligible in *Anisota senatoria*.

Second, plants of several non-host species were present in the study area in addition to young oaks, and orientation to these would tend to confound the search for appropriate hosts. Third, these higher values are based on orientation on a smooth substrate, and Dethier (1989) showed that as the substrate becomes more complex, search paths become more convoluted and larvae are increasingly apt to be influenced by encounters with obstacles at close range.

## RESULTS

**Genetic diversity and relatedness.** The ME locus showed clear polymorphism, but because several alleles were difficult to resolve in heterozygotes, this locus was dropped from the analyses. MDH-1, the anodal locus, showed patterns that appeared to indicate polymorphism, but these were not repeatable and this locus was also omitted. GOT-2, the cathodal locus, showed no polymorphism. The remaining loci, GOT-1, MDH-2, PGI and PGM, showed sufficient polymorphism for use in the relatedness analysis. Allele frequencies of the pooled groups are shown in Table 1. The observed heterozygosity (s.e.) of the pooled groups was  $H_{obs} = 0.386$  (0.022), with expected heterozygosity of  $H_{exp} = 0.376$  (0.029). All groups showed polymorphism at >1 locus. Taken together, these results indicate that there was sufficient polymorphism available for a robust relatedness analysis.

The relatedness (SD) among late-instar *A. senatoria* group-mates was  $r = 0.31$  (0.056), where the standard deviation is assessed by jackknifing over loci. This standard deviation drops to 0.033 if the variation is assessed over groups.

**Larval dispersal capabilities.** Oak plants at our site were separated by a mean (s.d.) nearest-neighbor distance of 4.34 (3.48) m. We found nearest-neighbor larval groups in our site to be separated by 5.25 (4.15) m ( $n = 18$  groups), with the closest groups being on plants less than 1 m apart.

Fallen larvae rarely went back to the same plant. Upon falling, they moved at variable rates at relatively constant headings, averaging 1.5 (2.2) cm/sec. 32% of the larvae moved only little and thus did not leave the inner circle. There was no evidence that caterpillars took similar headings (Rayleigh tests,  $P > 0.05$ ), indicating that they do not travel in groups once disturbed in this manner.

Based on our dispersal model, only 4% of the larvae that began searching (i.e., the 68% of larvae that traveled at least 1 m in the first 10 min) would ever encounter another host plant. This does not account for movement to plants off the grid, but these were mostly far enough away that the chances of a dispersing larva encountering them could be considered negligible. As noted in the Methods, this estimate is based

on assumptions that are already somewhat generous, and though it is low, it is still probably an overestimate. The low probability of finding a new host should therefore impose a strong limit on the exchange among larval groups on different plants.

We estimated the expected distribution of traveling times between plants by dividing each movement rate estimate by each distance between plants on the grid. Most of the fallen larvae that do find new plants (Fig. 1) would arrive there within the first hour (mean =  $62 \pm 78$  min), and almost all successful larvae would find a new plant within 4 hr. Because of the spatial relationships among plants with and without larvae, approximately 65% of these new plants would already have larval groups, so the distribution of traveling times among groups (mean =  $57 \pm 75$  min) is similar to that among plants (Fig. 1). Traveling time to new plants thus does not appear to be limiting exchange among groups, at least for the 4th and 5th instar larvae we studied. Larvae may also disperse of their own accord (Coffelt & Schultz 1993), whereupon they could expect to find suitable plants, and possibly join other groups, with similar probabilities and within similar time frames.

#### DISCUSSION

The degree of relatedness is moderate, well below the  $r = 0.5$  value expected if larvae were always full siblings, but above the  $r = 0.25$  level expected from half-sibs. This relatedness value is high enough to have strong effects on the realized costs and benefits of the gregarious behaviors of the larvae (Hamilton 1964). There are several ways that this level of relatedness could be realized, and these may be divided among behaviors of the ovipositing females and the subsequent behaviors of their larvae.

Larval behaviors that may reduce intragroup relatedness include active wandering to new groups during foraging bouts, as seen in *Malacosoma americanum* (Costa & Ross 1993), and inadvertent dispersal to new groups after falling off the host plant, as seen in *Hemileuca lucina* (Stamp & Bowers 1987). At Oak Openings, smaller plants with larval groups were often badly defoliated, and some had been abandoned by larvae. In some cases, we found small groups on plants with no evidence of the usual molt skins left by earlier instars, and these groups were adjacent to abandoned, defoliated plants. Even though host plants were relatively close together by human standards (4.34 m nearest neighbor distance), the distances remain formidable for wandering caterpillars, and only about 4% were likely to encounter new hosts. Plants with larval groups were still further apart, at 5.25 m, and we expect only a negligible proportion of larvae to be exchanged among them. This implies that the reduction in relatedness below  $r = 0.5$  on the small,

isolated plants in our study is attributable more to the behaviors of adult parents, rather than to wandering by the larvae. However, intergroup exchange and coalescence in *A. senatoria* may be much more likely among clutches laid on the same plant, as seen in *Malacosoma* (Costa & Ross 1993). We would also expect it to be more pronounced at high density and later instars, when the defoliation rate is highest and larvae are forced to wander, and when larvae are big enough to travel at the rates we observed.

Adult behaviors that would reduce relatedness, not addressed in this study, include multiple mating with sperm-mixing that would result in broods of mixed full- and half-sibs (Wade 1982, 1985, McCauley & O'Donnell 1984), and the aggregation of egg clutches onto the same plant by different females (Wade 1985). These behaviors would be less effective in reducing relatedness to the extent that related adults mated or aggregated their clutches (Wade 1985). Of course, parental behaviors would influence the degree of relatedness and gregariousness initially displayed by larvae, but should not create subsequent changes in gregariousness associated with larval age.

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