Dropping from Host Plants in Response to Predators by a Polyphagous Caterpillar

Authors: Castellanos, Ignacio, and Barbosa, Pedro

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DROPPING FROM HOST PLANTS IN RESPONSE TO PREDATORS BY A POLYPHAGOUS CATERPILLAR

Additional key words: defensive behavior, Lepidoptera, anti-predator defense, *Orgyia leucostigma*, predation risk

Induced behavioral responses to predation risk have been viewed as a consequence of a decision-making process juxtaposing the benefits of escaping predation and the costs of this anti-predator defensive response (Lima & Dill 1990). A large number of studies have shown that caterpillars can reduce mortality from predation by a diverse array of induced behaviors, including hitting (Awan 1985), biting (Soares et al. 2009), regurgitating (Gentry & Dyer 2002), performing defensive displays (Evans 1986) such as aposematic sounds (Brown et al. 2007), thrashing (Iwao & Wellington 1970), ceasing movement (Castellanos et al. 2010), hiding (Rota & Wagner 2008), crawling away (Stamp & Bowers 1988), changing feeding schedules (Stamp & Bowers 1993), dropping on silk threads (Castellanos & Barbosa 2006), and dropping off the plant (Castellanos et al. 2011). However, studies addressing the potential costs of these induced anti-predator behaviors are relatively rare (but see Stamp & Bowers 1988, 1991).

Among the potential behavioral responses of prey, dropping provides an effective adaptation in that it eliminates, or reduces the risk of predation, although it can expose caterpillars to starvation and predation on the ground (Cain et al. 1985; Weseloh 1988; Mathews et al. 2004). Any assessment of ecological costs and benefits of dropping would require a complete understanding of larval post-dropping behavior. One important component of the determination of costs and benefits is the behavior involved in returning to a host plant. After dropping, individuals may land on host foliage underneath the leaf from which they drop or they may fall to the ground where they can either move randomly until a host plant is found or efficiently locate hosts, reducing the likelihood of on-ground mortality (Bierzychudek et al. 2009). Thus, in this study we conducted a series of experiments in order to determine whether *Orgyia leucostigma* (J. E. Smith) (Lymantriidae) caterpillars that drop in response to predatory wasps are able to grasp a leaf or branch underneath the leaf from which they drop, and whether larvae that fall to the ground exhibit orientation behavior that is likely to return them to a tree host.

Orgyia leucostigma caterpillars are polyphagous and external solitary feeders primarily on the foliage of deciduous trees (Raffa & Powell 2004). Larvae used in the experiments originated from a laboratory colony established using larvae collected from *Acer negundo* L. (Aceraceae) (box elder) trees in Patuxent Research Refuge (PRR), Laurel, Maryland, USA. Larvae eclosing from egg masses were reared individually in 437-ml plastic containers, and fed box elder foliage. *Polistes fuscatus* (Fabricius) (Vespidae) is a major predator of caterpillars, which they capture and process to feed their larvae (Gould & Jeanne 1984), and has been observed attacking and consuming larvae of *O. leucostigma* in the PRR (J. Kemper, Dept. of Entomology, University of Maryland; pers. com.). Wasps used in this experiment belonged to a laboratory colony started with individuals collected from the same PRR site.

Predation experiments with wasps. Individual third instar *O. leucostigma* caterpillars were placed on a central apical leaf of potted 2.5 m box elder trees and exposed to a single *P. fuscatus* wasp, which flew from its nest to the experimental trees. Before a wasp was allowed to forage on the experimental tree, the caterpillar was allowed to acclimate for one hour; during this period, caterpillars often selected a different leaf from the one it was placed on. For each encounter, the behavioral responses of surviving caterpillars were recorded; if caterpillars dropped, we also recorded whether they landed on a leaf or branch underneath the leaf from which they dropped, or on the ground. A total of 30 trials were conducted in 2.8 m x 1.5 m x 1.5 m plexiglas cages inside a greenhouse using six box elder trees and different predator and prey individuals.

Orientation behavior of caterpillars. Since several species of caterpillars are known to orient to vertical objects such as tree trunks (Lance & Barbosa 1982; Harris et al. 1995; Rieske & Townsend 2005), we conducted an experiment to study the orientation behavior of third instar *O. leucostigma* to vertical silhouettes of various widths (representing "tree trunks" of various sizes). From this experiment we determined the narrowest tree silhouette that the caterpillars were able to discern. We also determined if caterpillars that drop and fall on the ground in the field exhibit orientation behavior that is likely to return them to a host tree.

TABLE 1. Orientation of *Orgyia leucostigma* caterpillars to black bands of various widths. Band = caterpillars climbing the band. Side with band = caterpillars climbing the half side of the arena with the band. Opposite side = caterpillars climbing the half side of the arena on the opposite side of the band (band-less side). The numbers between parentheses represent percentages.

	Width of band (cm)			
	15	7.5	3.5	1.75
Band	17 (60.7)	15 (68.2)	12 (46.1)	9 (27.3)
Side with band	8 (28.6)	6 (27.3)	14 (53.8)	15 (45.4)
Opposite side	3 (10.7)	1 (4.5)	0 (0)	9 (27.3)

Cylindrical arenas were constructed with white cardboard sheets measuring 70 cm in height and forming a ring 90 cm in diameter. A single silhouette consisting of a black paper rectangular band of 15, 7.5, 3.5, or 1.75 cm wide and 70 cm high (representing the silhouettes of trees) was attached to the interior wall of the arenas. The black bands were rotated to eliminate any position effects. Different individual third instars were stimulated to drop from a box elder leaf by bending their hairs to simulate a predator attack (Castellanos et al. 2011), and the path of the larva was observed until it reached the edge of the arena and climbed up its side. The orientation of a caterpillar was recorded as either climbing the band of black paper, the half side of the arena with bands (but not the band itself), or the opposite half (i.e., the band-less) side. If a caterpillar did not reach the edge of the arena within a period of one hour, it was not included in the analysis. Sample size for the 15, 7.5, 3.5, and 1.75 cm wide bands was 28, 22, 26, and 33, respectively. The orientation behavior to the different rectangular silhouettes was analyzed with Chi-square tests for independence (SAS Institute 1990).

Field experiment. At the PRR field site, trees within two 10 m x 10 m quadrats were identified to species. Within the quadrats, six *A. negundo* trees with trunk diameters between 25.5 and 58.6 cm at a height of 70 cm from the ground were chosen as probable hosts from which a caterpillar could fall on the ground. Twelve caterpillars were stimulated to drop from a randomly selected box elder leaf from the canopy of the selected trees. Caterpillar movement after dropping was visually observed and the time it took larvae to reach the trunk of a tree was measured.

All caterpillars that escaped predation from wasps did so by dropping; twelve (71%) landed on the ground and five (29%), on a branch underneath the leaf from which they dropped. All dropping larvae that had subtending vegetation below were able to avoid landing on the ground. Thus, dropping is a primary response to predatory wasps, but dropping did not always result in caterpillars landing on the ground. Some caterpillars actively grasped the foliage under the leaf from which they dropped (I. Castellanos personal observation). Landing on plant foliage after escaping predation risk by dropping may reduce the risk of mortality in the leaf litter.

The presence of black bands in experimental arenas had a significant effect on caterpillar orientation ($P < 0.05$), except when the band was 1.75 cm wide ($P = 0.058$) (chi-square test: $\chi^2 = 10.22$, 11.46, 17.32, and 3.59 for the 15, 7.5, 3.5, and 1.75 cm wide bands, respectively) (Table 1). Thus, the 3.5 cm band was the smallest silhouette that had a significant effect on caterpillar orientation. A band width of 3.5 cm seen from a distance of 45 cm (the radius of the arena) corresponds to a visual acuity of 4.45°. Five percent of the caterpillars did not reach the edge of the arena within one hour and were not included in the analyses.

All twelve caterpillars that landed on the ground under the canopy of box elder trees in the field oriented to and reached the trunk of the same tree from which they were stimulated to drop. It took caterpillars 70.08 min ± 14.31 (mean ± SEM), ranging from 9.1 to 145.5 min to reach the tree.

Our results show that *O. leucostigma* caterpillars exhibit orientation behavior that is likely to return them to a host, which should reduce the likelihood of on-ground mortality. However, larvae could spend more than two hours in the leaf litter before reaching a tree, which could represent a cost in terms of exposure to ground predators. Without data on the rate of encounter with predators in the litter it is not possible to affirm that the travel time required to reach a host tree subjects the larva to significant predation, therefore it becomes difficult to determine costs. However, the data provided in this study do indicate that dislodged larvae of *O. leucostigma* that land on the ground are likely to find a host tree. Since all tree individuals mapped in the quadrants, except one (*Poplar* sp.), were host-plants for *O. leucostigma* (I. Castellanos, unpublished), there is a high probability that any tree reached after crawling in the leaf litter will be an adequate food source for a polyphagous species such as *O. leucostigma*. Specialist

herbivorous insect species that drop will be in a disadvantage in stands where there is a mixture of plant species. However, specialist species may possess other mechanisms that may allow reducing the costs associated with dropping in response to predators. For example, larvae of *Macaria aemulataria* (Walker) (Geometridae), which are specialists on *Acer* species in the PRR, dislodge from plant surfaces in response to predators, but do not reach the ground because they suspend themselves from a silk thread (Castellanos & Barbosa, 2006). An exciting area for further studies would be to compare the propensity to drop for other free-feeder caterpillars that vary in host range.

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IGNACIO CASTELLANOS *(Corresponding author), Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, A.P. 69-1, Pachuca, Hidalgo, 42001, México; email: ignacioe@uaeh.edu.mx,* PEDRO BARBOSA, *Department of Entomology, Plant Sciences Building, University of Maryland, College Park, Maryland, 20742, USA, and Astrid Caldas, Defenders of Wildlife, 1130 17th Street N.W. Washington DC, 20036, USA.*

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