

# Enemy-free space maintains swallowtail butterfly host shift

Shannon M. Murphy\*

Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14853

Edited by May R. Berenbaum, University of Illinois at Urbana-Champaign, Urbana, IL, and approved November 12, 2004 (received for review September 2, 2004)

**Natural enemies can be significant sources of mortality for herbivorous insects and therefore important agents of natural selection. One might expect selection to favor herbivores that escape from their natural enemies into enemy-free space. Although this is an appealing idea, it has received little empirical support, and no studies have documented enemy-free space as part of a nonagricultural, nonartificial host shift. The Alaskan swallowtail butterfly, *Papilio machaon aliaska*, uses as host plants a species in the family Apiaceae (*Cnidium cniidifolium*) along with two Asteraceae species (*Artemisia arctica* and *Petasites frigidus*). I analyzed growth and survival of *P. m. aliaska* larvae in the field on the three host plants in treatments that either exposed or protected them from predators. I found that, in the presence of predators, larval survival is greater on the novel hosts (Asteraceae) than on the ancestral host (Apiaceae), but that in the absence of predators survival and growth are greater on the ancestral host. These results are a demonstration of enemy-free space as a mechanism for maintaining a naturally occurring host shift.**

*Papilio machaon aliaska* | Lepidoptera | predation | *Formica podzolica*

Swallowtail butterflies from the *Papilio machaon* (Linnaeus) group use plants of the Apiaceae as their primary hosts (1–4). Behavioral and metabolic constraints evidently limit potential opportunities to switch to other co-occurring plant species (5). Apart from the occasional use of plants in the family Rutaceae, an ancestral host family for the genus *Papilio* (2), *P. machaon* swallowtails have rarely incorporated nonapiaceous plants into their diet. In Alaska and northwestern Canada, *P. m. aliaska* Scudder oviposits and feeds not only on the local apiaceous host, *Cnidium cniidifolium* (Turczaninow) Schischkin, but also on *Artemisia arctica* Lessing and *Petasites frigidus* (Linnaeus) Franchet (6) in the distantly related family Asteraceae. This host-range expansion by *P. m. aliaska* appears to represent an intermediate step toward a complete host shift. There is at least one example of a species in the *P. machaon* group that is now restricted to the novel host genus *Artemisia* (2); *Papilio oregonius* Edwards, a close relative of *P. m. aliaska* (2), is monophagous on *Artemisia dracuncululus* Linnaeus (7). It is unclear, however, whether *P. m. aliaska* and *P. oregonius* represent a single host shift or two independent host shifts to *Artemisia*.

The *P. m. aliaska* system presents an ideal opportunity to examine the role of enemy-free space (EFS) in a naturally occurring host shift. Other swallowtail larvae are subject to attack by a range of invertebrate and vertebrate predators (8, 9); my observations over the past 5 years of *P. m. aliaska* near Fairbanks, AK, suggest that the two most important larval predators are *Formica podzolica* Francoeur, an ant species that is widely distributed throughout North America (10), and the ichneumonid parasitoid *Trogus lapidator panzeri* Carlson. Jeffries and Lawton (11) defined EFS as “ways of living that reduce or eliminate a species’ vulnerability to one or more species of natural enemies.” Berdegue *et al.* (12) proposed three falsifiable, null hypotheses that must be rejected to demonstrate the existence of EFS. Support for the alternative hypotheses demon-

strates that enemies have played an important role in the establishment of a novel host association. First, the fitness of the organism in the presence of enemies must be less than in the absence of enemies, demonstrating that enemies have a negative effect on prey fitness. Second, the fitness of the organism in the alternative habitat with natural enemies must be greater than that in the original habitat with natural enemies. This establishes that the alternative behavior, host plant, or habitat provides EFS. Third, the fitness of the organism in an alternative habitat without enemies must be less than in the original habitat without enemies. Thus, when predators are absent in both habitats, there must be a cost to living in the alternative habitat, which suggests that predation is responsible for creating the EFS in the alternative habitat. I designed this study to test whether the novel host plants, *A. arctica* and *P. frigidus*, offer *P. m. aliaska* larvae EFS not found on the ancestral host plant, *C. cniidifolium*.

## Materials and Methods

**Study Sites.** *C. cniidifolium* sites are broadleaf woodlands on steep river bluffs (Cc1 = 64°42′N, 148°18′W, 185 m; Cc2 = 64°57′N, 147°38′W, 220 m). *C. cniidifolium* does not co-occur with *A. arctica*, which is found at higher elevations in tundra meadows (Aa1 = 64°52′N, 148°4′W, 710 m; Aa2 = 64°57′N, 148°21′W, 880 m). *P. frigidus* grows in moist habitats at “low” and “high” elevations (Pf1 = 64°52′N, 147°50′W, 175 m; Pf2 (same site as Aa2) = 64°57′N, 148°21′W, 880 m). Wild *P. m. aliaska* larvae have been found on all three of the host plants and at all of these sites with one exception. Wild larvae have not been found on *P. frigidus* at the high elevation site (Pf2) even though they have been found on neighboring *A. arctica* plants at this same location (Aa2) as well as on *P. frigidus* at the low elevation site (Pf1).

**Origins of the Study Populations.** Field observations over the past 5 years indicate that *P. m. aliaska* is a typical hilltopping swallowtail butterfly (e.g., ref. 13). Males emerge a few days earlier in the season than do females. Upon emergence, males fly to hilltops, where they defend territories and wait for females to arrive. After mating, females fly downhill toward larval host-plant sites. Populations from the different larval host-plant sites surrounding a hilltop are apparently panmictic (unpublished data). Six *P. m. aliaska* females were collected June 10–19, 2003, from three alpine tundra hilltops (domes) near Fairbanks, AK: Ester Dome (64°52′N, 148°4′W, ≈720 m), Murphy Dome (64°57′N, 148°21′W, ≈890 m), and Wickersham Dome (65°13′N, 148°3′W, ≈977 m). Females oviposited in the laboratory, and their larvae were reared in equal numbers on the three host

This paper was submitted directly (Track II) to the PNAS office.

Abbreviations: EFS, enemy-free space; Cc, *Cnidium cniidifolium*; Aa, *Artemisia arctica*; Pf, *Petasites frigidus*; B, bagged treatment; C, control treatment; H, bagged-with-holes treatment.

Data deposition: Host-plant vouchers were deposited in the L. H. Bailey Herbarium at Cornell University (Murphy 418, BH). Insect vouchers were deposited in the Cornell University Insect Collection (lot no. 1250).

\*E-mail: smm40@cornell.edu.

© 2004 by The National Academy of Sciences of the USA







presumably still important in this system. Shared chemical cues among the three host plants may have provided the opportunity for *P. m. alaska* to incorporate host plants in the Asteraceae as well as the Apiaceae (S.M.M. and P. Feeny, unpublished data). Although similar host-plant chemistry was perhaps an essential first step, EFS may be the force that drives the host shift by *P. m. alaska* to completion.

Why have there been so few studies documenting EFS (12, 18–21)? Only three studies have satisfactorily established the occurrence of EFS, but they have been agricultural systems (22, 23) or artificial host shifts (24). Other studies suggest EFS but did not satisfy all three of the hypotheses proposed by Berdegue *et al.* (12, 18, 25–30). In particular, the third hypothesis is often difficult to test (18) because costs are often difficult to find or may have disappeared if the host shift occurred in the distant past. Costs may be detectable only when investigating an ongoing host shift such as the *P. machaon* system, before herbivores have adapted completely to the novel host(s). Many studies have found ample support for the first two hypotheses and thus suggest that natural enemies have a negative impact on herbivore fitness and that the novel host provides EFS. Without finding a

cost associated with the novel host, however, the possibility that the novel plant is simply a better host cannot be discounted. Strict adherence to the requisite hypotheses will certainly underestimate the occurrence and hence the importance of EFS in structuring plant–insect interactions. Despite its ephemeral nature, EFS is probably not as rare a phenomenon as the literature would suggest.

I thank J. Goodman, P. Bennett, L. Hough, S. Rothman, T. Kast, T. Clausen, M. Walker, T. Hollingsworth, and J. Hollingsworth for assistance in Alaska. I thank P. Feeny, M. Geber and laboratory, A. Renwick, M. Caillaud, N. Stamp, E. Dopman, K. Zamudio, and two anonymous reviewers for helpful comments; F. Vermeylen for statistical advice; P. Ward for ant identifications; R. Hoebeke for parasitoid identification; and J. Murphy for sewing bags. This work was supported by the Andrew W. Mellon Foundation, the American Museum of Natural History Theodore Roosevelt Memorial Fund, the Edna Bailey Sussman Fund, the Explorer's Club Exploration Fund, Sigma Xi, Cornell University Department of Ecology and Evolutionary Biology, a National Science Foundation Doctoral Dissertation Improvement Grant (to S.M.M.), and a National Science Foundation research grant (to P. Feeny).

1. Feeny, P., Rosenberry, L. & Carter, M. (1983) in *Herbivorous Insects: Host-Seeking Behavior and Mechanisms*, ed. Ahmad, S. (Academic, New York), pp. 27–76.
2. Sperling, F. A. H. (1987) *Quaestiones Entomologicae* **23**, 198–315.
3. Thompson, J. N. (1995) in *Swallowtail Butterflies: Their Ecology and Evolutionary Biology*, eds. Scriber, J. M., Tsubaki, Y. & Lederhouse, R. C. (Scientific, Gainesville, FL), pp. 195–203.
4. Wiklund, C. (1981) *Oikos* **36**, 163–170.
5. Feeny, P. (1995) in *Swallowtail Butterflies: Their Ecology and Evolutionary Biology*, eds. Scriber, J. M., Tsubaki, Y. & Lederhouse, R. C. (Scientific, Gainesville, FL), pp. 9–15.
6. Scott, J. A. (1986) *The Butterflies of North America: A Natural History and Field Guide* (Stanford Univ. Press, Palo Alto, CA).
7. Thompson, J. N. (1988) *Evolution* **42**, 118–128.
8. Feeny, P., Blau, W. S. & Kareiva, P. M. (1985) *Ecol. Monogr.* **55**, 167–187.
9. Watanabe, M. (1979) *Jpn. J. Ecol.* **29**, 85–93.
10. Francoeur, A. (1973) *Mem. Soc. Ent. Québec* **3**, 1–316.
11. Jeffries, M. J. & Lawton, J. H. (1984) *Biol. J. Linn. Soc.* **23**, 269–286.
12. Berdegue, M., Trumble, J. T., Hare, J. D. & Redak, R. A. (1996) *Ecol. Entomol.* **21**, 203–217.
13. Lederhouse, R. C. (1982) *Behav. Ecol. Sociobiol.* **10**, 109–118.
14. Wiklund, C. (1973) *Entomol. Exp. Appl.* **16**, 232–242.
15. Siegel, S. & Castellan, N. J. J. (1988) *Nonparametric Statistics for the Behavioral Sciences* (McGraw-Hill, New York).
16. Erickson, J. M. & Feeny, P. (1974) *Ecology* **55**, 103–111.
17. Slansky, F. & Scriber, J. M. (1985) in *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*, eds. Kerkut, G. A. & Gilbert, L. I. (Pergamon, Oxford).
18. Stamp, N. (2001) *Oecologia* **128**, 153–163.
19. Zangerl, A. R., Huang, T., McGovern, J. L. & Berenbaum, M. R. (2002) *Oikos* **98**, 431–436.
20. Zvereva, E. L. & Rank, N. E. (2003) *Oecologia* **135**, 258–267.
21. Sipura, M., Ikonen, A., Tahvanainen, J. & Roininen, H. (2002) *Ecology* **83**, 3393–3407.
22. Feder, J. L. (1995) *Ecology* **76**, 801–813.
23. Ohsaki, N. & Sato, Y. (1990) *Ecol. Entomol.* **15**, 169–176.
24. Gratton, C. & Welter, S. C. (1999) *Ecology* **80**, 773–785.
25. Brown, J. M., Abrahamson, W. G., Packer, R. A. & Way, P. A. (1995) *Oecologia* **104**, 52–60.
26. Ballabeni, P., Włodarczyk, M. & Rahier, M. (2001) *Funct. Ecol.* **15**, 318–324.
27. Strohm, E., Laurien-Kehnen, C. & Bordon, S. (2001) *Oecologia* **129**, 50–57.
28. Dopman, E. B., Sword, G. A. & Hillis, D. M. (2002) *Evolution* **56**, 731–740.
29. Mira, A. & Bernays, E. A. (2002) *Oikos* **97**, 387–397.
30. Singer, M. S. & Stireman, J. O. (2003) *Oikos* **100**, 554–562.