Enemy-free space maintains swallowtail butterfly host shift

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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 cnidiifolium) 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

S wallowtail 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 cnidiifolium (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 dracunculus 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. cnidiifolium.

Materials and Methods

Study Sites. *C. cnidiifolium* 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. cnidiifolium* 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 hostplant 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, \approx 720 m), Murphy Dome (64°57'N, 148°21'W, \approx 890 m), and Wickersham Dome (65°13'N, 148°3'W, \approx 977 m). Females oviposited in the laboratory, and their larvae were reared in equal numbers on the three host

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Abbreviations: EFS, enemy-free space; Cc, Cnidium cnidiifolium; 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 Hortorium Herbarium at Cornell University (Murphy 418, BH). Insect vouchers were deposited in the Cornell University Insect Collection (lot no. 1250).

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plants. After the third-instar molt, larvae were placed in the field on the plant species on which they had been reared; larvae cannot be switched between host plants (14). Third-instar larvae were used because they are easy to find, not prone to wandering and not as likely to fall off plants as are early instar larvae. Significant effects of site ($F_{5,240} = 7.08, P < 0.01$) and dam ($F_{5,240} = 9.66, P < 0.01$) on initial length, with larvae on *C. cnidiifolium* longer than *A. arctica* or *P. frigidus* larvae, were controlled for in the statistical analyses. Larvae in the laboratory experiment (n =848) were reared under ambient conditions ($\approx 17^{\circ}C/24$ h light). Larvae from each dam were divided equally among the three host plants ($n \approx 280$ larvae per species) for quantification of percent pupation and pupal weights.

Treatments. Larvae were individually placed on haphazardly selected natural host plants and assigned to one of three treatments: bagged (B), control (C), or bagged with holes (H) to control for bagging effects other than protection from predation. Treatment B: Bags were made of green netting (7 holes per cm; Barre Army Navy Store, Barre, VT) and secured with a nylon drawstring. The gap, through which the stem passed, was filled with cotton and sealed with Tanglefoot. Larval presence/ absence was noted on all visits to the site, and larvae were measured on days 1 and 6 of development. This treatment ended on day 6 because C. cnidiifolium larvae had reached the fifth instar; hence, all larvae were removed from the bags to complete their development in the laboratory (8). All sites experienced some mortality because of faulty molting (n = 13) or entrapment in Tanglefoot (n = 2), not predation. Treatment C: If present, larval resting length and instar were measured. If absent, and >1day had elapsed since the previous visit, the date of disappearance was estimated to be the average between those two dates. Fifth-instar larvae were removed from the field to complete development so that the proportion of larvae at each site that had been parasitized by T. l. panzeri could be observed the following spring upon emergence (8). Treatment H: Similar methods were used as for treatment C, but plants were covered with bags that were identical to those used in treatment B, except for the addition of several holes (3- to 15-cm diameter). Neither Tanglefoot nor cotton was used in this treatment. This treatment occurred only at sites Aa2, Cc1, and Pf1.

A total of 306 larvae were used in this study. Offspring from at least four dams were placed at each site and evenly divided between treatments (n = 16-24 larvae per treatment per site). The frequency of visits varied by site. Most, but not all, sites were visited daily because of the considerable distances between them. Never >2 days passed between visits except at site Aa1, which once had a 5-day gap between visits.

EFS Through Host-Plant Chemistry. On July 2–3, 2003, from 11:30 to 13:00 at site Cc1, 15 third-instar larvae from a single dam were used to test whether predators preferred larvae from a specific host plant. For each of five trials, three larvae that did not differ in size (P > 0.9) were selected, one reared on each host plant. The larvae were placed simultaneously onto individual leaves from a nonhost bean plant (*Vicia faba*) and then placed on the ground. Leaves were 7.0 \pm 0.5 cm², and their positions were rotated randomly before each trial. The time elapsed since the start of the trial was recorded for each larva–predator encounter. Trials concluded when all three larvae were removed from their leaves by predators.

EFS Through Host-Plant Dispersion. To test whether there are fewer predators at the novel host-plant sites than at the ancestral host-plant sites, pitfall traps were placed at the five sites (Aa2 and Pf2 were the same) from July 7–9. Cups (118 ml, 7.5-cm diameter, 4 cm deep) were buried with the rim at ground level, and 30 ml of 95% ethanol was added. Ten traps were placed at

each site and left for 24 h. Trap locations spanned the field site; each trap was within 1 m of at least three marked plants and at least 2 m from neighboring traps.

Statistical Analyses. Survival analyses were performed with the Kaplan–Meier method using statistical software (JMP V.3.1.6, SAS Institute, Cary, NC). Analyses of initial larval lengths, larval growth rates, percent pupation, and pupal weights used procmixed in SAS V.8 (SAS Institute); treatment, dam, day, and host plant or site were fixed effects, and larva was the random factor. Predator-choice trials were analyzed with the Kruskal–Wallis one-way ANOVA by ranks (15).

Results and Discussion

I tested the first hypothesis, which predicts that the fitness of the organism in the presence of enemies must be less than in the absence of enemies, by comparing survival of *P. m. aliaska* larvae that were exposed to or protected from predators. Larvae protected from predation were significantly more likely to survive than exposed larvae at all sites except one (Fig. 1). This pattern was strongest at sites with the ancestral host plant, *C. cnidiifolium*, where the difference in larval survival between exposed (control) and protected (bagged) larvae was greater than at *A. arctica* and *P. frigidus* sites (Table 1). These results show that natural enemies have a negative impact on the survival of *P. m. aliaska* larvae in the field.

I tested the second hypothesis that in the presence of natural enemies, the fitness of the organism in the alternative habitat must be greater than that in the original habitat by comparing survival of exposed (control) larvae on the ancestral and novel host plants. Survival was greater on the novel host plants, A. arctica and P. frigidus, than on the ancestral host plant, C. cnidiifolium (Fig. 2 and Table 1). Survival on P. frigidus also appeared to depend on the elevation of the host plant (Table 1). During the experiment, larval survival at the high-elevation P. frigidus site was significantly greater than at the C. cnidiifolium sites, whereas no difference existed between survival at the low-elevation *P. frigidus* site and the *C. cnidiifolium* sites. In the second week of the experiment, however, the high-elevation P. frigidus site was partially flooded, and several low-lying larvae were drowned. Thus, the final proportion of larvae to pupate did not differ between the high-elevation P. frigidus site and the C. *cnidiifolium* sites. Upon pupal emergence the following spring, I found that 12 of the exposed larvae (treatments C and H) had been parasitized by T. l. panzeri, and that all of these individuals had been reared in the field at novel host-plant sites (Aa1 = 3, Aa2 = 7, Pf1 = 1, Pf2 = 1). Although none of the larvae at the ancestral host-plant sites were parasitized, T. l. panzeri is not restricted to high elevation sites because one P. m. aliaska larva at the low *P. frigidus* site was parasitized. When treatments C and H are grouped, survival to pupation at the A. arctica sites was 46% but fell to 30% after accounting for parasitism. Similarly, survival to pupation at the *P. frigidus* sites fell from 24% to 21%. Survival to pupation at the *C. cnidiifolium* sites remained at 12%, as none of the pupae were parasitized. Although parasitism decreased survival at the novel host-plant sites, survival was still significantly greater at A. arctica sites ($\chi^2 = 34.10$, df = 1, P < 0.0001) and *P. frigidus* sites ($\chi^2 = 24.76$, df = 1, P < 0.0001) than at the ancestral C. cnidiifolium sites. Despite potentially hazardous weather and the increased presence of T. l. panzeri, higher elevation sites appear to increase the EFS offered by novel host plants. These findings support the hypothesis that the novel host plants A. arctica and P. frigidus provide EFS that is not found on the ancestral host plant C. cnidiifolium.

I tested the third hypothesis, which predicts that the fitness of the organism in an alternative habitat without enemies must be less than in the original habitat without enemies, in both the field and the laboratory. Using growth rate as a correlate for fitness



Fig. 1. Percent survival of *P. m. aliaska* larvae placed in the field within 24 h of the third-instar molt, as part of the C (circles), B (squares), and H (triangles) treatments at two *C. cnidiifolium* sites at low elevation (black = Cc1 and gray = Cc2), two *P. frigidus* sites (black = Pf1, low elevation; and gray = Pf2, high elevation), and two *A. arctica* sites at high elevation (black = Aa2 and gray = Aa1). Pf2 is the only site without significant differences between the treatments. Larvae in the B treatment were removed from the field on day 6, whereas larvae in the C and H treatments were removed from the field once they had reached the fifth instar. The H treatment was included only at the Cc1, Pf1, and Aa2 sites. See Table 1 for comparisons between survival curves.

Table 1. *Papilio machaon aliaska* larval survival in bagged, control, and bagged-with-holes treatments

Comparison	χ^2 value	df	P value
Between treatments B and C ⁺			
Site Cc2	19.12	1	<0.0001**
Site Pf2	1.51	1	0.22
Site Aa1	7.11	1	<0.01*
Between treatments B and C $+$ H ⁺			
Site Cc1	36.76	2	<0.0001**
Site Pf1	17.90	2	0.0001**
Site Aa2	8.64	2	0.01*
Between treatments C and H			
Site Cc1	2.59	1	0.11
Site Pf1	3.37	1	0.07
Site Aa2	3.24	1	0.07
Between all sites			
Treatment B	3.63	5	0.60
Between dams [‡]			
Treatment B	3.10	4	0.54
Treatment C	2.09	4	0.72
Treatment H	6.60	4	0.16
Between sites (treatment C)			
Cc1 and Cc2	0.04	1	0.84
Aa1 and Aa2	0.26	1	0.61
Between elevations (treatment C)			
Pf1 (low) and Pf2 (high)	4.99	1	0.03
Between plant species (treatment C)			
C. cnidiifolium and A. arctica	16.21	1	<0.0001**
C. cnidiifolium and P. frigidus	11.43	1	0.0007**
P. frigidus (high elevation)			
and C. cnidiifolium	13.82	1	<0.0001**
and A. arctica	< 0.01	1	0.99
P. frigidus (low elevation)			
and C. cnidiifolium	3.33	1	0.07
and A. arctica	3.47	1	0.06

*Remains significant ($\alpha\!<\!$ 0.05) after Bonferroni adjustment to correct for type I error.

**Remains significant ($\alpha < 0.01$) after Bonferroni adjustment to correct for type I error.

^tFor comparisons among the bagged (B) treatment and the control (C) and bagged-with-holes (H) treatments, all larvae were censored in sAs v.8 at day 6, because that is when larvae in treatment B were removed from the field. Treatments C and H were combined at the sites with H because there were no significant differences between these treatments.

[‡]Does not include one dam that appeared only at site Cc1.

(16) in the field, I found that site ($F_{5,322} = 5.25, P = 0.0001$), day $(F_{1,229} = 139.17, P < 0.0001)$, and dam $(F_{5,309} = 9.14, P < 0.0001)$ 0.0001), but not treatment ($F_{2,329} = 1.29$, P = 0.28), had significant effects on larval growth. Differences among sites were due to variation in growth rate on the three host-plant species and slower growth rates at higher elevation sites (Fig. 3). In the laboratory, significantly more larvae pupated when reared on C. cnidiifolium than when reared on either A. arctica or P. *frigidus* ($F_{2,10} = 11.72$, P = 0.002; Fig. 4); percent pupation did not differ among dams ($F_{5,10} = 1.67$, P = 0.23). Finally, fitness of larvae reared in the field as well as the laboratory also differed significantly among the three host plants in terms of pupal weight, a predictor of lifetime fitness in Lepidoptera (17) (Fig. 4). Larvae reared on C. cnidiifolium attained greater pupal weights than did larvae reared on A. arctica or P. frigidus (lab: $F_{2,374} = 61.39, P = 0.0001$; field: $F_{2,89} = 18.95, P = 0.0001$). Pupal weights also differed significantly among dams ($F_{11,374} = 2.95$, P = 0.0009) and female pupae weighed more than male pupae $(F_{1,374} = 8.91, P = 0.003)$. Therefore, when natural enemies are absent, larvae on the novel host plants show reduced growth and



Fig. 2. Percent survival of *P. m. aliaska* larvae in the control treatment that were placed in the field on *C. cnidiifolium* (circles, n = 42), *A. arctica* (squares, n = 41), *P. frigidus* at high elevation (filled triangles, n = 21), and *P. frigidus* at low elevation (open triangles, n = 24). The ultimate percent survival for each curve is equal to the proportion of larvae in the control treatment that survived to the fifth instar on that host plant. See Table 1 for comparisons between survival curves.

survival, compared with larvae on the ancestral host plant; this pattern is indicative of a significant cost associated with the transition to EFS.

To test whether larvae reared on the three host plants were differentially susceptible to predation. I conducted predatorchoice trials in the field by using the only observed predator of P. m. aliaska larvae, F. podzolica. F. podzolica did not demonstrate a preference for larvae reared on any of the three host plants; neither the number of predator encounters $(3.8 \pm 0.15,$ P > 0.1) nor the number of minutes that elapsed before the larva was killed (18.1 \pm 0.68, P > 0.9) varied among larvae reared on the three host plants. Thus, there is no evidence to support the hypothesis that larvae sequester defensive chemical compounds from their novel host plants as an antipredator mechanism. It could be, however, that larvae on the novel host plants are protected from predation, because predators are deterred from approaching the novel host plants. Although this was not directly tested, it seems unlikely to be the case. I observed F. podzolica at both C. cnidiifolium sites not just on C. cnidiifolium plants but also on all of the surrounding vegetation, including another Artemisia species.

An alternative explanation is that larvae are protected from predation not because of the host plants themselves but because of the distinct environments in which the host plants are established. I surveyed the number of predaceous ants at each site to test whether there are fewer predators at the novel host-plant sites than at the ancestral host-plant sites. All five ant species that I collected (Camponotus herculeanus, Formica aserva, Formica neorufibarbis, F. podzolica, and Myrmica alaskensis) are omnivorous and opportunistic predators that are common and widespread species in Alaska (P. Ward, personal communication). All but two of the ants collected at the C. cnidiifolium sites were F. podzolica individuals (total number of ants: Cc1 = 381; Cc2 = 133), whereas F. podzolica was absent from A. arctica and P. frigidus sites (total number of ants: Pf1 =22; Aa1 = 26; Aa2/Pf2 = 1). Thus, the more compelling explanation for why P. m. aliaska larvae are protected from predators on the novel host plants is that there are fewer predaceous ants at these sites.



Fig. 3. Growth rates of *P. m.* aliaska in the field. (A) Mean growth rate (black) and mean instar attained (gray) for *P. m. aliaska* larvae in treatment B (protected from predators) on day 6. Means (±SE) are for larvae on the host plants *C. cridiifolium* (Cc, n = 36), *P. frigidus* (Pf, n = 37), and *A. arctica* (Aa, n = 37). Larvae at the *C. cridiifolium* sites grew (P < 0.01) and attained a later instar (P < 0.001) faster than did larvae at *A. arctica* or *P. frigidus* sites. (B) Mean growth rate (black) and mean instar attained (gray) for all *P. m. aliaska* larvae that survived to day 6. Means (±SE) are for larvae on the host plants *C. cridiifolium* (Cc, n = 47), *P. frigidus* (Pf, low elevation, n = 37; Pf, high elevation, n = 35), and *A. arctica* (Aa, n = 73). The growth rate of larvae at *C. cridiifolium* sites was higher than at *A. arctica* or *P. frigidus* sites (P = 0.02). Larval instar at *C. cridiifolium* sites was higher than at *A. arctica* sites or either *P. frigidus* site (P < 0.0001). Larval instar at the low-elevation *P. frigidus* site was higher than at either the high-elevation *P. frigidus* site or the *A. arctica* sites (P < 0.0001).

This study experimentally demonstrates that EFS can play an important role in maintaining a host expansion or shift in a natural system. *P. m. aliaska* larvae find refuge from their natural enemies by feeding on novel host plants; this appears to be an example of EFS through host-plant dispersion rather than through host-plant chemistry. Host-plant chemistry, however, is



Fig. 4. Percent pupation (squares) and pupal weights (black circles) for *P. m. aliaska* larvae reared in the laboratory from egg-hatch to pupation on *C. cnidiifolium* (Cc), *A. arctica* (Aa), and *P. frigidus* (Pf). Pupal weights also are given for the larvae that were reared in the field (gray circles) from the third-instar molt until just before pupation. Means are given \pm SE.

presumably still important in this system. Shared chemical cues among the three host plants may have provided the opportunity for *P. m. aliaska* 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. aliaska* 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

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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.

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