The effect of host plant on larval survivorship of the Alaskan swallowtail butterfly (*Papilio machaon aliaska*)

Shannon M. Murphy*

Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853-2701, USA

Abstract

The Alaskan swallowtail butterfly, *Papilio machaon aliaska* (Lepidoptera: Papilionidae), uses three plant species as host plants. *Cnidium cnidiifolium* (Turcz.) Schischk. belongs to the family Apiaceae, the ancestral host-plant family of the *P. machaon* group. *Artemisia arctica* Less. and *Petasites frigidus* (L.) Franch, in contrast, belong to the distantly related Asteraceae family and were colonized relatively recently by this group of butterflies. Previous work has shown that larval survival is highest on the novel host plants when natural enemies are present in the field. Here I examine whether *P. m. aliaska* fitness varied when individuals were reared on the three host plants in a common environment, free of environmental and ecological complications such as predation. I collected 12 *P. m. aliaska* females and measured their reproductive success when their progeny were reared on each of the three host plants. I assessed larval fitness on each of the hosts by recording the percentage pupation and percentage emergence as well as by measuring pupal mass. I found that larvae reared on the ancestral host plant, *C. cnidiifolium*, had higher fitness than did larvae reared on either of the novel host plants, *A. arctica* or *P. frigidus*. Larvae reared on *C. cnidiifolium* were more likely to pupate, achieved a greater pupal mass, and had higher emergence rates than larvae reared on the novel hosts. I interpret these results to mean that, in the absence of predation, the ancestral host plant is a better host for *P. m. aliaska* larvae than either novel host and I contend that this result does not appear to support the hypothesis that *P. m. aliaska* populations in central Alaska are divided into host races.

Introduction

Herbivorous insects account for approximately one quarter of the world's biodiversity (Strong et al., 1984; Mitter et al., 1988). Much of this astounding diversification of plant-feeding insects has been driven by host shifts in which an insect population incorporates a novel plant into its diet, eventually abandoning the ancestral host plant. In order for this process to succeed, adult females need to find the novel hosts attractive for oviposition and their offspring must be able to survive and grow on these plants (Ehrlich & Raven, 1964; Thompson, 1988a; Thompson & Pellmyr, 1991; Bernays & Chapman, 1994; Janz & Nylin, 1997). Lepidoptera are the largest radiation of insect herbivores (Schoonhoven et al., 1998) and swallowtail butterflies in particular have become model organisms for studies of the diversification, ecology, and evolution of diet breadth (Wiklund, 1975; Berenbaum, 1983; Feeny, 1991; Scriber et al., 1995; Thompson, 1998).

Swallowtail butterflies from the *Papilio machaon* L. (Lepidoptera: Papilionidae) group use plants of the Apiaceae as their primary hosts (Wiklund, 1981; Feeny et al., 1983; Sperling, 1987; Thompson, 1995). Apart from occasional use of plants in the family Rutaceae, an ancestral host family for the genus *Papilio* (Sperling, 1987), *P. machaon* swallowtails have rarely incorporated non-apiaceous plants into their diet. In Alaska and northwestern Canada, *Papilio machaon aliaska* Scud. oviposits and feeds not only on the local apiaceous host, *Cnidium cnidiifolium* (Turcz.) Schischk., but also on *Artemisia arctica* Less. and *Petasites frigidus* (L.) Franch. (Scott, 1986), which are both in the Asteraceae. This host-range expansion by *P. m. aliaska* appears to represent an intermediate step towards 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* (Sperling, 1987); *Papilio oregonius* Edwards, a close relative of *P. m. aliaska*, has shifted completely to the family Asteraceae and is

*Correspondence and present address: Department of Entomology, 4112 Plant Sciences Building, University of Maryland, College Park, MD 20742-4454, USA. E-mail: smurph@umd.edu

monophagous on *Artemisia dracunculus* L. (Thompson, 1988b). It is unclear, however, whether *P. m. aliaska* and *P. oregonius* represent a single host shift or two independent host shifts to *Artemisia*.

Other than belonging to unrelated genera, *P. m. aliaska* host plants are also situated in significantly different environments. *Cnidium cnidiifolium* is found at low elevations, often along river bluffs, whereas *A. arctica* is found at higher elevations in tundra meadows. *Petasites frigidus* grows at both low and high elevations in moist habitats; at high elevations it may co-occur with *A. arctica* plants while at low elevations it is often found in bogs, although it can sometimes be found in the vicinity of *C. cnidiifolium* plants (pers. obs.). Previous work has demonstrated that these host plants are not equal in terms of larval survival in the field (Murphy, 2004). In the absence of predators, *P. m. aliaska* larvae survive best on the ancestral host plant, *C. cnidiifolium*, but in the presence of predators, larval survival is greater on the novel host plants. In the field, *A. arctica* and *P. frigidus* plants seem to offer larvae enemy-free space that is not found on the ancestral host plant *C. cnidiifolium*. This enemy-free space appears to result from the diverse environments in which the novel host plants occur, and is unlikely to result from any particular trait of the plants themselves. The goal of the work presented here is to more fully examine differential *P. m. aliaska* fitness when reared on the three host plants in a common environment, free of environmental and ecological complications such as variation in elevation and the presence of natural enemies.

Materials and methods

Origins of the study populations

Papilio machaon aliaska butterflies are univoltine. My field observations over the past 5 years indicate that *P. m. aliaska* is a typical hill-topping swallowtail butterfly (cf. Lederhouse, 1982). 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 towards larval host-plant sites. Populations from the different larval host-plant sites surrounding a hilltop are supposedly panmictic; females and males from surrounding larval sites arrive at the top of the tundra domes within a few days of each other. Due to the scale of the landscape in the interior of Alaska, it is difficult to collect *P. m. aliaska* individuals other than from hilltops.

Papilio machaon aliaska females were collected during June 10–19, 2003, from three alpine-tundra hilltops (domes) near Fairbanks, AK, USA. Six females were collected from Ester Dome (64°52′N, 148°4′W, ~720 m), one female from Murphy Dome (64°57′N, 148°21′W, ~890 m), and five females from Wickersham Dome (65°13′N, 148°3′W, ~977 m). The females were caught as they arrived at the summit of the domes and were therefore assumed not to have already mated. During a previous field season, females were similarly caught as they arrived at the summit of a dome, but were left unmated; these females never laid fertilized eggs, indicating that they had not mated in the field before capture (SM Murphy, unpubl.). To ensure viable offspring, the females in this study were mated by hand pairing (Carter & Feeny, 1985) in the laboratory with males from the same field site. Hence, each female's offspring are most likely full siblings, but if the females had already mated in the field, the offspring could be half siblings. Females oviposited in the laboratory in clear, plastic boxes ($31 \times 16.5 \times 8$ cm) that were provisioned with sprigs of all three host plants: *C. cnidiifolium*, *A. arctica*, and *P. frigidus*. The sprigs were placed in florist 'aquapiks' to prevent desiccation. Dams were categorized into two groups based on the number of eggs that they laid: low (0–150 eggs) and high (151–395 eggs). Some of the larvae (n = 306) were reared in the field as part of another experiment (Murphy, 2004) and are not included in the results presented here except in the initial egg counts for each dam. Insect vouchers were deposited in the Cornell University Insect Collection (Lot no. 1250).

Larvae were reared in equal numbers on the three host plants, under ambient conditions (~17 °C and L24:D0) in the same plastic boxes as described above, with never more than 10 larvae per box after the second-instar molt. Each larval box contained only one host-plant species and fresh foliage was supplied at least twice daily. *Cnidium cnidiifolium* was collected from two sites, both of which were broadleaf woodlands on steep river bluffs (site 1 = 64°42′N, 148°18′W, 185 m; site 2 = 64°57′N, 147°38′W, 220 m). *Artemisia arctica* was collected from two high elevation tundra meadows (site 1 = 64°52′N, 148°4′W, 710 m; site 2 = 64°57′N, 148°21′W, 880 m). *Petasites frigidus* was collected at one of the same sites as *A. arctica* (64°57′N, 148°21′W, 880 m) as well as from a lower elevation, poorly drained bog (64°52′N, 147°50′W, 175 m). Host-plant vouchers were deposited in the L. H. Bailey Hortorium Herbarium (Murphy 418, BH).

After the larvae had pupated, they were taken to Ithaca, NY, USA, and refrigerated (5 °C and L0:D24) for 9–13 months. The sex of all surviving pupae in March 2004 was determined using methods described by Carter & Feeny (1985), and the mass of each pupa was recorded. From May through September 2004, the pupae were removed from refrigeration in batches and adults were allowed to emerge in an environmental growth chamber (Environmental Growth Chambers, Chagrin Falls, OH, USA) set at diapause-breaking conditions (L16:D8 and 21 °C:15 °C).

Statistical analyses

I characterized female reproductive success by analyzing the number of eggs that each female laid, by measuring pupal mass of her offspring, and by recording how many of her offspring successfully emerged. All analyses were done using SAS statistical software (version 8, SAS Institute Inc., Cary, NC, USA). Using Proc Mixed, I tested whether the number of eggs that a female laid was dependent on either her site of origin or her lifetime. Both site of origin and lifetime measured in days were fixed effects. Measurements of pupal mass were analyzed using Proc Mixed with the dam's site of origin, dam's egg-laying level, larval host-plant species, and the pupa's sex as the fixed effects while dam and individual pupa were random factors. Interactions between the fixed effects were also tested. Pupal emergence upon removal from refrigeration was coded as either 1 (adult emerged) or 0 (adult did not emerge). Emergence success was analyzed using Proc Glimmix because individuals from the same dam could not be considered independent samples and the variable emergence has a binomial distribution. Dam's site of origin, dam's egg-laying level, the mean pupal mass of the dam's offspring, larval host-plant species, pupa's sex, and the date on which the pupa was removed from refrigeration were all fixed effects. Dam was a random effect. For all of the analyses, the significance of the random factors in the models was tested with likelihood-ratio tests (Neter et al., 1996) and the t-tests used to test the differences in least squares means were adjusted using Tukey–Kramer.

Results

Number of eggs laid

Both the site from which a female was caught ($F_{1,403} = 241.63$, P<0.0001) and the number of days she lived ($F_{6,403} = 3380.25$, P<0.0001) had significant effects on the number of eggs that she laid. The Murphy Dome site could not be included in the site analysis because only one female was caught there, but females from Wickersham Dome on average laid more eggs per female than did females from Ester Dome ($t_{403} = 15.54$, P<0.0001). The variance, however, was extremely high, with females from Ester Dome laying both the least and most number of eggs. Female lifetime appeared to be a better predictor of how many eggs she would lay (Table 1). Females who lived more than 10 days laid significantly more eggs than did females who lived 9 days or fewer ($t_{408} = 32.14$, P<0.0001). The number of days that females lived did not differ between Ester Dome (8.8 ± 1.6 days) and Wickersham Dome (8.6 ± 1.1 days); the single female from Murphy Dome lived 9 days.

Pupal mass

Pupal mass varied significantly between dams ($\chi^2 = 16.7$, P<0.001); this variation has been controlled for in all subsequent analyses. The host-plant species on which the larvae were reared had a significant effect on pupal mass ($F_{2,298} = 72.0$, P<0.0001; Table 2). Larvae that fed on the ancestral host plant *C. cnidiifolium* had greater pupal mass than did larvae reared on either *A. arctica* ($t_{398} = 4.88$, P<0.0001) or *P. frigidus* ($t_{399} = 11.77$, P<0.0001). Larvae reared on *A. arctica* also had greater pupal mass than did larvae reared on *P. frigidus* ($t_{398} = 8.80$, P<0.0001). In general, female pupae had greater mass than male pupae ($F_{1,392} = 14.88$, P = 0.0003) but there was a significant interaction between pupal sex and larval host plant ($F_{2,399} = 4.03$, P = 0.018). Female pupal mass was greater than male pupal mass when the larvae were reared on *C. cnidiifolium* ($t_{397} = 7.0$, P<0.0001) and *A. arctica* ($t_{398} = 3.66$, P<0.004), but not when reared on *P. frigidus* ($t_{398} = 0.1$, P = 1.0) (Table 2). The number of eggs the dam laid during her lifetime also had a moderate effect on pupal mass ($F_{1,7} = 3.51$, P = 0.1). The offspring of dams that laid few eggs (n = 0–150) had greater pupal mass than did the offspring of dams that laid many eggs (n = 151–395). Neither the dam's site of origin nor any of the other interactions were significant.

Emergence

The random effect 'dam' did not account for a significant portion of the variation in pupal emergence success ($\chi^2 = 0.01$, P>0.8); the site where the dam was caught and the number of eggs that the dam laid also did not affect emergence. However, the mean pupal mass of a dam's offspring (see Table 1) had a moderately significant effect on whether her offspring emerged. Dams whose offspring had a mean mass of 0.86 g or greater had more offspring emerge than did dams whose offspring had a lesser mean mass ($F_{1,395} = 2.73$, P = 0.1).

There was a significant effect of host-plant species ($F_{2,395} = 3.12$, P = 0.045) upon emergence success. Although pupae that had been reared on *C. cnidiifolium* as larvae were the most likely to emerge, followed by those reared on *A. arctica* and *P. frigidus*, respectively, the only difference that was significant was that between *C. cnidiifolium* pupae and *P. frigidus* pupae ($t_{1,395} = 2.47$, P = 0.014). More females than males emerged from their pupae ($F_{1,395} = 6.24$, P = 0.013) and, unlike in the pupal mass analysis, the interaction between pupal sex and larval host plant was not significant. Males emerged an average of 14.5 (± 0.15) days after they were removed from refrigeration while females averaged 16.6 (± 0.17) days to emerge. Once the pupae emerged as adults, I was able to assess that I had correctly identified the sex of 97% of the pupae (257 out of 264) by using the methods described by Carter & Feeny (1985).

Table 1 Reproductive success for *Papilio machaon aliaska* females caught at Ester (E), Murphy (M), and Wickersham (W) Domes in 2003. The number of days that each female lived after she was caught, number of eggs she laid [and how this number was categorized as a low (L) or high (H) level in analyses], number of eggs that hatched (with hatch number as percentage of eggs laid), how many offspring reared per host plant in the laboratory, number of larvae that successfully (and pupated pupation as percentage of number reared), average pupal mass, number of female and male adults that emerged, and the emergence rate expressed as a percentage of the number reared in the laboratory and the number that pupated are given

Dam	Life (days)	Eggs (level)	Hatch (%)	Host plant[1]	Reared (in lab)	Pupated (%)	Mass (g) ± SE	Emerged F	Emerged M	Percentage emergence Reared	Percentage emergence Pupated
E 1	6	14 (L)	7 (50)	Cc	7	7 (100)	0.89 ± 0.05	2	3	71	71
E 2	7	42 (L)	23 (55)	Cc	9	7 (78)	0.82 ± 0.05	4	2	43	71
				Aa	5	4 (80)		0	2		
				Pf	9	3 (33)		0	2		
W 1	5	43 (L)	28 (65)	Cc	10	7 (70)	0.75 ± 0.05	2	2	25	44
				Aa	9	4 (44)		0	2		
				Pf	9	5 (56)		1	0		
E 3	6	63 (L)	63 (100)	Cc	21	17 (81)	0.84 ± 0.02	8	5	35	58
				Aa	21	13 (62)		2	4		
				Pf	21	8 (38)		1	2		
E 4	6	116 (L)	52 (45)	Cc	12	12 (100)	0.83 ± 0.03	1	3	24	44
				Aa	17	5 (29)		1	2		
				Pf	17	8 (47)		2	2		
W 2	7	122 (L)	104 (85)	Cc	35	12 (34)	0.87 ± 0.02	2	7	19	63
				Aa	35	19 (54)		5	6		
				Pf	34	1 (3)		0	0		
W 3	10	150 (L)	128 (85)	Cc	37	12 (32)	0.90 ± 0.03	5	4	19	71
				Aa	37	15 (41)		7	4		
				Pf	34	1 (3)		0	0		
W 4	10	185 (H)	157 (85)	Cc	52	35 (67)	0.82 ± 0.01	14	10	20	53
				Aa	52	22 (42)		7	0		
				Pf	53	1 (2)		0	0		
M1	9	210 (H)	196 (93)	Cc	35	26 (74)	0.88 ± 0.02	10	6	25	60
				Aa	39	16 (41)		6	6		
				Pf	39	5 (13)		0	0		
W 5	11	268 (H)	220 (82)	Cc	69	36 (52)	0.86 ± 0.02	11	2	17	44
				Aa	68	35 (51)		9	9		
				Pf	61	6 (10)		2	1		
E 5	15	268 (H)	199 (74)	Cc	40	25 (63)	0.84 ± 0.02	5	10	23	63
				Aa	36	13 (36)		8	2		
				Pf	39	5 (13)		0	2		
E 6	13	395 (H)	358 (91)	Cc	89	35 (39)	0.74 ± 0.02	13	10	18	64
				Aa	90	34 (38)		9	13		
				Pf	89	8 (9)		1	3		

[1]*Cc*, *Cnidium cnidiifolium*; *Aa*, *Artemisia arctica*; *Pf*, *Petasites frigidus*.

Two males had been mistakenly identified as females and five females were mistaken for males while still in the pupal stage.

Whether pupae were removed from refrigeration in one of the early (May and June; 9–10 months of refrigeration), middle (July and August; 11–12 months of refrigeration), or late (September; 13 months of refrigeration) batches also significantly affected their emergence rate ($F_{2,395} = 7.8$, $P = 0.0005$). Significantly fewer pupae in the late batches emerged than did pupae in either early ($t_{395} = 3.65$, $P = 0.0009$) or middle ($t_{395} = 2.91$, $P = 0.01$) batches. There was no difference in emergence success between pupae in early and middle batches ($t_{395} = 0.82$, $P = 0.7$).

Discussion

Papilio machaon aliaska larvae reared on the ancestral host plant, *C. cnidiifolium*, had higher fitness than did larvae

Table 2 Mean pupal mass for the offspring of *Papilio machaon aliaska* females caught at Ester (E), Murphy (M), and Wickersham (W) domes in 2003. The total number of larvae that pupated is given for each female (repeated from Table 1). Some pupal mortality occurred before the means could be measured. Thus, the number of female and male pupae that were included in the means do not necessarily equal the total number of larvae that successfully pupated. Measurements of pupal mass are given for female and male pupae and are separated by the host plant on which the larvae were reared

Dam	Host plant[1]	Pupated	Females		Males	
			n	Pupal mass (g) ± SE	n	Pupal mass (g) ± SE
E 1	*Cc*	7	2	1.05 ± 0.01	5	0.82 ± 0.04
E 2	*Cc*	7	5	0.99 ± 0.03	2	0.86 ± 0.03
	Aa	4	1	0.56	3	0.73 ± 0.05
	Pf	3	0	`–	2	0.65 ± 0.11
W 1	*Cc*	7	2	0.87 ± 0.05	3	0.83 ± 0.09
	Aa	4	0	–	3	0.70 ± 0.05
	Pf	5	2	0.59 ± 0.06	0	–
E 3	*Cc*	17	10	0.92 ± 0.04	7	0.80 ± 0.04
	Aa	13	2	0.90 ± 0.02	9	0.88 ± 0.03
	Pf	8	2	0.63 ± 0.09	4	0.63 ± 0.05
E 4	*Cc*	12	4	1.04 ± 0.02	8	0.84 ± 0.03
	Aa	5	1	0.70	4	0.77 ± 0.08
	Pf	8	2	0.79 ± 0.19	3	0.62 ± 0.04
W 2	*Cc*	12	2	0.90 ± 0.05	8	0.87 ± 0.05
	Aa	19	9	0.89	6	0.85 ± 0.06
	Pf	1	0	–	0	–
W 3	*Cc*	12	7	1.04 ± 0.03	5	0.78 ± 0.07
	Aa	15	9	0.92 ± 0.05	5	0.86 ± 0.07
	Pf	1	0	–	1	0.61
W 4	*Cc*	35	21	0.85 ± 0.02	13	0.79 ± 0.03
	Aa	22	11	0.85 ± 0.03	6	0.75 ± 0.05
	Pf	1	0	–	0	–
M1	*Cc*	26	11	0.98 ± 0.01	15	0.88 ± 0.03
	Aa	16	7	0.91 ± 0.05	7	0.82 ± 0.04
	Pf	5	0	–	2	0.55 ± 0.08
W 5	*Cc*	36	15	0.91 ± 0.05	13	0.86 ± 0.04
	Aa	35	14	0.92 ± 0.02	18	0.81 ± 0.02
	Pf	6	2	0.60 ± 0.05	2	0.71 ± 0.15
E 5	*Cc*	26	11	0.96 ± 0.03	15	0.86 ± 0.02
	Aa	13	9	0.79 ± 0.02	3	0.74 ± 0.04
	Pf	5	1	0.58	3	0.63 ± 0.02
E 6	*Cc*	35	16	0.87 ± 0.03	18	0.74 ± 0.02
	Aa	34	9	0.73 ± 0.05	21	0.70 ± 0.01
	Pf	8	4	0.53 ± 0.05	4	0.63 ± 0.02

[1]*Cc, Cnidium cnidiifolium; Aa, Artemisia arctica; Pf, Petasites frigidus.*

reared on either of the novel host plants, *A. arctica* or *P. frigidus*. In general, larvae reared on *C. cnidiifolium* were more likely to pupate, achieved a greater pupal mass, and had higher emergence rates than larvae reared on the novel hosts. Pupal mass has previously been demonstrated to be a predictor of lifetime fitness in Lepidoptera (Slansky & Scriber, 1985) and the results presented here lend further support. Groups with greater pupal mass had higher emergence rates; survival, as indicated by successful emergence, is a component of fitness. For instance, pupae reared on the ancestral host had greater mass than pupae reared on novel hosts and were also more likely to emerge. Similarly, female pupae generally had greater mass than male pupae and likewise had higher emergence rates.

Finally, when offspring mass is averaged for each dam, dams with high mean mass also had more offspring emerge as adults indicating higher overall fitness.

An interesting interaction could be shown between the sex of the pupa and the host plant on which it was reared as a larva. Female pupae reared on *C. cnidiifolium* and *A. arctica* had greater mass than male pupae reared on these same species, but the difference between females and males disappeared for pupae reared on *P. frigidus*. Pupal mass, as well as emergence success, was extremely low for all pupae reared on *P. frigidus*. Although the sample sizes were too small to test, there may be differences between sites in how well larvae are adapted to feed on *P. frigidus*; all females from Ester Dome had at least two of their offspring

reared on *P. frigidus* successfully emerge as adults whereas only two females from Wickersham Dome had any of their offspring successfully emerge when reared on *P. frigidus*. Nonetheless, compared to either of the other plant species, *P. frigidus* appears to be a very poor host. So why do *P. m. aliaska* females continue to oviposit on it in the wild? As low as larval fitness is on *P. frigidus* in the laboratory, it appears that many of the surviving larvae in the field are able to escape predation, which may account for its continued use as a host plant (Murphy, 2004).

Not surprisingly, females that lived longer laid more eggs. However, there was a trend for the offspring of females that laid fewer than 150 eggs to have greater pupal mass than the offspring of females that laid more than 150 eggs. This may suggest a trade-off between the number of eggs and egg provisioning. The advantage of having few siblings, however, did not carry over to emergence success.

Emergence success was also significantly affected by the length of time the pupae were stored. Pupae that were allowed to emerge in May and June, after 9–10 months of enforced diapause, had the greatest success at emergence. This corresponds exactly to the emergence time of *P. m. aliaska* near Fairbanks, Alaska. A group of larvae that were used in another experiment, and not included in the results presented here, were removed from refrigeration in April after 8 months of refrigeration and emerged with similar success as those in the May and June groups. Thus, it appears that emergence success decreases quickly after 10 months of diapause, but the limit for successful emergence has not yet been established for fewer than 8 months of diapause.

When a specialized insect species uses unrelated host plants, the question inevitably arises as to whether the species is divided into host races. Host races are usually invoked in studies of sympatric speciation (Bush, 1969; Feder et al., 1988; Caillaud & Via, 2000; Filchak et al., 2000; Dres & Mallet, 2002). Although I have not investigated the criteria necessary to test the existence of host races, such as measuring genetic differentiation or gene flow between populations, members of different host races are also predicted to have higher fitness on their own host as opposed to the alternative hosts that the species is known to use (Dres & Mallet, 2002). If *P. m. aliaska* populations around tundra domes are not panmictic and host races exist, then the original females caught in this experiment would most likely have been members of either the *A. arctica* or *P. frigidus* host races as these are the plants that may be found on the tops of the domes. This seems unlikely, however, given that many females caught on these domes prefer to oviposit on *C. cnidiifolium* in choice trials (Murphy, in press).

If we assume that host races do exist and that the females caught on the domes specialize on novel hosts, then their offspring would be predicted to fare better on one or the other of these novel host plants as opposed to the ancestral host plant. Yet emergence rates are highest on *C. cnidiifolium* or at least equal between *C. cnidiifolium* and either *A. arctica* or *P. frigidus* (Table 1). The only exception is female W5; more of her offspring emerged when reared on *A. arctica* than *C. cnidiifolium*, yet the percentage to pupate did not differ between these hosts. None of the females' offspring did best on *P. frigidus*.

My sampling was restricted to the interior of Alaska, near Fairbanks. It is possible that there may be host races in other parts of the *P. m. aliaska* range, which extends into northwestern Canada (Northwest Territories, Yukon, and northern British Columbia). It is also possible that had females been caught from the hypothetical *C. cnidiifolium* host race, then their offspring may have fared even worse on the novel host plants than did the larvae in this experiment. It is difficult to imagine, however, how emergence rates could be any lower than those observed on *P. frigidus* in this study; four of 11 females failed to have any offspring emerge as adults when reared on *P. frigidus*. Regardless, it does not appear that the offspring of dams from sites near Fairbanks survive better on the novel host plants than the ancestral host as would be predicted if host races existed. The data presented here do not refute the possibility of *P. m. aliaska* host races, but also do not argue for their existence.

Acknowledgements

References

Berenbaum M (1983) Coumarins and caterpillars: a case for coevolution. Evolution 37: 163–179.

Bernays EA & Chapman RF (1994) Host Plant Selection by Phytophagous Insects. Chapman & Hall, New York, NY, USA.

Bush GL (1969) Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). Evolution 23: 237–251.

Caillaud MC & Via S (2000) Specialized feeding behavior influences both ecological specialization and assortative mating in sympatric host races of pea aphids. American Naturalist 156: 606–621.

Carter M & Feeny P (1985) Techniques for maintaining a culture of the black swallowtail butterfly, *Papilio polyxenes asterius* Stoll (Papilionidae). Journal of the Lepidopterists' Society 39: 125–133.

Dres M & Mallet J (2002) Host races in plant-feeding insects and their importance in sympatric speciation. Philosophical Transactions of the Royal Society of London B 357: 471–492.

Ehrlich PR & Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18: 586–608.

Feder JL, Chilocote CA & Bush GL (1988) Genetic differentiation between sympatric host races of *Rhagoletis pomonella*. Nature 336: 61–64.

Feeny P (1991) Chemical constraints on the evolution of swallowtail butterflies. Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions (ed. by PW Price, TM Lewinsohn, GW Fernandes & WW Benson), pp. 315–340. John Wiley & Sons, Inc, New York, NY, USA.

Feeny P, Rosenberry L & Carter M (1983) Chemical aspects of oviposition behavior in butterflies. Herbivorous Insects: Host-Seeking Behavior and Mechanisms (ed. by S Ahmad), pp. 27–76. Academic Press, New York, NY, USA.

Filchak KE, Roethele JB & Feder JL (2000) Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. Nature 407: 739–742.

Janz N & Nylin S (1997) The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. Proceedings of the Royal Society of London, Series B 264: 701–707.

Lederhouse RC (1982) Territorial defense and lek behavior of the black swallowtail butterfly *Papilio polyxenes*. Behavioral Ecology and Sociobiology 10: 109–118.

Mitter C, Farrell B & Wiegemann B (1988) The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? American Naturalist 132: 107–128.

Murphy SM (2004) Enemy-free space maintains swallowtail butterfly host shift. Proceedings of the National Academy of Sciences, USA 101: 18048–18052.

Murphy SM (in press) Inconsistent use of host plants by the Alaskan swallowtail butterfly: Adult preference experiments suggest labile oviposition strategy. Ecological Entomology.

Neter J, Kutner MH, Bachtsheim CJ & Wasserman W (1996) Applied Linear Statistical Models, 4th edn. Irwin, Chicago, IL, USA.

Schoonhoven LM, Jermy T & van Loon JJA (1998) Insect-Plant Biology: From Physiology to Evolution. Chapman & Hall, London, UK.

Scott JA (1986) The Butterflies of North America: A Natural History and Field Guide. Stanford University Press, Palo Alto, CA, USA.

Scriber JM, Tsubaki Y & Lederhouse RC (1995) Swallowtail Butterflies: Their Ecology and Evolutionary Biology. Scientific Publishers, Inc, Gainesville, FL, USA.

Slansky F & Scriber JM (1985) Food Consumption and Utilization. Comprehensive Insect Physiology, Biochemistry and Pharmacology (ed. by GA Kerkut & LI Gilbert), pp. 87–163. Pergamon Press, Oxford, UK.

Sperling FAH (1987) Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae). Quaestiones Entomologicae 23: 198–315.

Strong DR, Lawton JH & Southwood R (1984) Insects on Plants. Harvard University Press, Cambridge, MA, USA.

Thompson JN (1988a) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomologia Experimentalis et Applicata 47: 3–14.

Thompson JN (1988b) Variation in preference and specificity in monophagous and oligophagous swallowtail butterflies. Evolution 42: 118–128.

Thompson JN (1995) The origins of host shifts in swallowtail butterflies versus other insects. Swallowtail Butterflies: Their Ecology and Evolutionary Biology (ed. by JM Scriber, Y Tsubaki & RC Lederhouse), pp. 195–203. Scientific Publishers, Gainesville, FL, USA.

Thompson JN (1998) The evolution of diet breadth: monophagy and polyphagy in swallowtail butterflies. Journal of Evolutionary Biology 11: 563–578.

Thompson JN & Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. Annual Review of Entomology 36: 65–89.

Wiklund C (1975) The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. Oecologia 18: 185–197.

Wiklund C (1981) Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. Oikos 36: 163–170.