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LOCAL ADAPTATION TO REGIONAL CLIMATES IN *PAPILIO CANADENSIS* (LEPIDOPTERA: PAPILIONIDAE)[1]

MATTHEW P. AYRES[2] AND J. MARK SCRIBER
Department of Entomology, Michigan State University, East Lansing, Michigan 48824 USA

Abstract. *Papilio canadensis* encounters shorter, cooler summers in interior Alaska than in northern Michigan: average thermal sums are 583 vs. 985 Celsius degree-days (10°C base); mean daily temperature is 14.4 vs. 18.8°. The temperature physiology of *P. canadensis* could be evolutionarily conserved, or the species may be a composite of regionally adapted populations. We evaluated these hypotheses by comparing the developmental physiology of *P. canadensis* from Alaska and Michigan across a range of temperatures in the laboratory and field.

Higher temperatures generally resulted in more rapid larval development, but the effects varied with insect population and host. At low temperatures (12°), Alaskan larvae grew faster than Michigan larvae (fifth instars doubled their fresh mass in 5.8 vs. 9.1 d), primarily due to 40% higher consumption rates. At high temperatures (30°), Alaskan larvae grew slower, faster, or the same as Michigan larvae, depending upon host. Effects of host quality were greatest at high temperatures. Elevated respiratory expenses in Alaskan larvae (35% higher than Michigan larvae) made them especially sensitive to host quality at high temperatures. Dry matter digestibility and nitrogen use efficiency differed across hosts, but not between populations or across temperatures. Molting accounted for 35–51% of development time. Alaskan larvae completed their fifth molt faster than Michigan larvae at 12° (11.8 vs. 17.8 d), but not at 30° (3.1 vs. 2.9 d). In both populations, molt was more temperature sensitive than growth at low temperatures (Q_{10} of 5.65 vs. 3.04 from 12 to 18°), but less temperature sensitive at high temperatures (Q_{10} of 1.60 vs. 2.06 from 18 to 30°). Survival differed across temperatures, but not between populations.

Under ideal basking conditions, larvae in the field were able to elevate body temperatures ≈10° above ambient, but such conditions were rare in Alaska and larvae were usually near ambient temperature. Alaskan larvae were no better than Michigan larvae at selecting high radiation microsites or converting solar radiation into heat. Growth rates of Alaskan larvae were the same in the field and laboratory when fed the same foliage and exposed to the same mean daily air temperature.

We incorporated *P. canadensis* temperature responses into a life history development model, then used a 48-yr climatic record to evaluate the fitness contributions of apparent adaptations to Alaskan summers. On a good host, at Alaskan temperatures, Alaskan *P. canadensis* had an estimated fitness 3.0 times greater than Michigan *P. canadensis*. Furthermore, the Michigan population was predicted to go extinct in 31 of 48 yr at Alaskan temperatures. Changes in growth temperature responses made the greatest contribution to enhanced fitness in Alaska, followed by increased mass of neonates, enhanced molting abilities at low temperatures, and a reduced size threshold for pupation. Analysis of fitness trade-offs suggested that extreme summers have been more important than average summers in shaping adaptive responses. Regional adaptation to climate allows *P. canadensis* to maintain a broader geographic distribution than would otherwise be possible, but northern distribution limits are probably still constrained by summer temperatures.

Key words: *adaptation; Alaska; basking; climate; consumption; distribution; fitness; growth; herbivory; host quality; molt; respiration;* Papilio; *temperature.*

INTRODUCTION

Why do insect herbivores occur where they do, but not elsewhere? Herbivore distributions are commonly less extensive than that of their host plants (MacLean 1983, McClure 1989), implying that they are not a simple function of host plant distributions. Here we explore the role of abiotic constraints, specifically summer temperatures, in determining the geographic range of the Canadian tiger swallowtail, *Papilio canadensis* R and J (Lepidoptera: Papilionidae).

P. canadensis is a polyphagous tree-feeding insect that occurs throughout much of the boreal forests of North America: from New England and upstate New York, west and north through the Great Lakes states and Canada to interior Alaska (Scriber 1988). Prelim-

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[2] Present address: Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA.

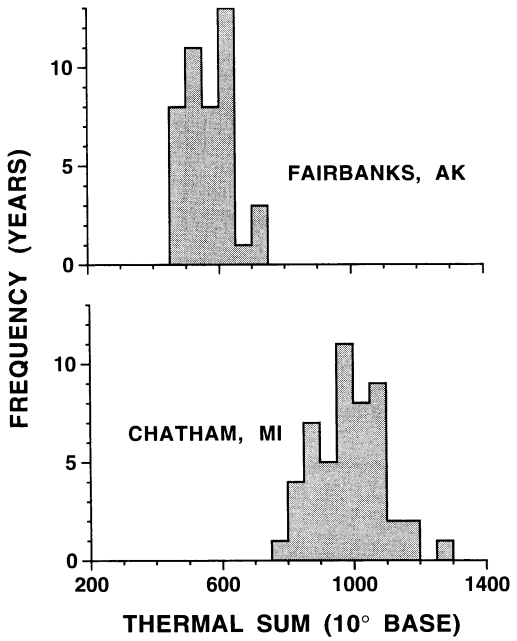

FIG. 1. Frequency distribution of annual thermal sums in Fairbanks, Alaska (48 yr) and Chatham, Michigan (50 yr). Michigan weather records included 1931–1980; Alaska records included 1936–1980 (excluding 1969) and 1987–1990. Annual degree-day accumulations were begun on 1 April and terminated near the time of leaf fall (15 September in Alaska and 1 October in Michigan). Thermal sums were calculated from daily maxima and minima using a sine function recommended by Watanabe (1978).

inary information suggests an important role for temperature in the ecology of *P. canadensis*. Larval development rates are strongly temperature sensitive in swallowtails (Scriber and Lederhouse 1983, Ritland and Scriber 1985), as in most insects (Scriber and Slansky 1981, Taylor 1981). The northern distribution limit of a southern sister species (*Papilio glaucus* L., Hagen et al. 1991) corresponds closely to the 1400 degree-day isotherm (10°C base), which approximates the thermal sum required for completion of its bivoltine life history (Hagen and Lederhouse 1985, Scriber 1988). Thus, the univoltine *P. canadensis* (Hagen and Scriber 1989) would require ≈700 degree-days/yr if the biology of these two taxa were otherwise identical.

As a first step in assessing the importance of summer temperatures for *P. canadensis*, we analyzed the climates they encounter near the southern and northern limits of their distribution. The thermal sums accumulated at Chatham, Michigan (86°50′ W, 46°25′ N) ranged from 760 to 1254 degree-days over 50 yr, with an average of 985 degree-days (Fig. 1). In contrast, the warmest summer in Fairbanks, Alaska (147°30′ W, 64°50′ N) accumulated fewer degree-days than the coldest summer in Chatham: range of 453–747 degree-days over 48 yr, with an average of 583 degree-days (Fig. 1). If 700 degree-days were needed for one *P. canadensis* generation, the upper peninsula of Michigan would always allow one generation, but never two, while interior Alaska would not have allowed even a single generation in 43 yr out of 48. In fact, *P. canadensis* butterflies are abundant in the Fairbanks area.

Summers in interior Alaska are relatively cool as well as short. The average daily mean temperature during the period of *P. canadensis* larval development was 14.4° compared with 18.8° in northern Michigan (Fig. 2). In Alaska, the daily mean temperature was <19.5° on most days (80%), while in Michigan it was ≥21° on nearly half the days (43%).

How does *P. canadensis* complete its life history throughout such a climatically diverse area? The species may be a composite of regionally adapted populations that only collectively maintain a broad distribution (Hypothesis 1). Alternatively, the *P. canadensis* genotype may be evolutionarily conserved, but surprisingly robust in its tolerance of climatic variation (Hypothesis 2). An investigation of host-use abilities in *P. canadensis* supported the conserved genotype model. Populations from Alaska and Michigan did not differ in their ability to feed on various host species, even though there is little overlap in their natural hosts (Ayres 1991). We evaluated these hypotheses with respect to temperature physiology by comparing the lar-

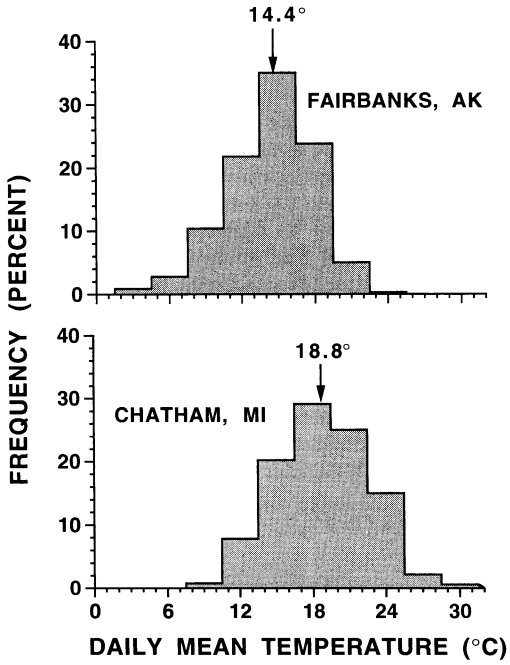

FIG. 2. Average distribution of daily mean temperatures encountered by *Papilio canadensis* larvae during 48 yr in Fairbanks, Alaska (AK) and 50 yr in Chatham, Michigan (MI). The period of *P. canadensis* larval development was defined as 350–700 degree-days in Michigan and 250–550 degree-days in Alaska (truncated at 15 September when necessary). The percentages of days in each temperature class were calculated separately for each year, then averaged across years.

val development of *P. canadensis* from Alaska and Michigan across a range of temperatures in the laboratory and field.

METHODS

Overview

P. canadensis populations were compared with respect to the growth rate of fourth and fifth instars, duration of fourth and fifth molts, consumption rate, assimilation rate, average daily metabolic rate, apparent digestibility, the efficiency of conversion of digested matter, nitrogen use efficiency, pupal mass, and survival to imagoes. Studies included two seasons and three host species. Temperature responses of Alaskan and Michigan larvae were compared on *Populus tremuloides* Michx. (quaking aspen) in 1988 and 1989 and on *Populus balsamifera* L. (balsam poplar) in 1988 (both hosts are used naturally by both populations); 1988 experiments also included Alaskan larvae feeding on *Betula resinifera* Britton (Alaska paper birch, does not occur in Michigan). These experiments were conducted under controlled laboratory temperatures using freshly detached leaves. In addition, we tested the ability of larvae to elevate body temperatures by basking and compared the growth rates of larvae in the field and laboratory.

Population sampling

Female butterflies were collected during June 1988 and June 1989 from interior Alaska (vicinity of Fairbanks) and northern Michigan–Wisconsin (Gogebic and Iron counties in Michigan; Vilas, Taylor, and Chippewa counties in Wisconsin). In both cases, butterflies were collected from multiple sites within a region of continuous habitat (≈75 km diameter in Alaska, ≈200 × 75 km in Michigan–Wisconsin). The Michigan–Wisconsin population is subsequently referred to as "Michigan" for simplicity.

After capture, butterflies were transported to the laboratory, fed honey-water daily, and allowed to oviposit on sprigs of *Populus tremuloides* foliage. Resulting larvae from the two populations were reared simultaneously and fed the same foliage until early in the fourth instar, when growth trials began. From the time of egg hatch, larvae were reared on foliage from the host species that they would later be tested on. Maternal parents, eggs, and larvae of both populations were handled with the same protocol, in the same laboratory, and at the same time, presumably precluding any spurious differences between populations due to differing environments.

Experiments during 1988 included progeny from 9 Alaskan females (total of 108 larvae) and 6 Michigan females (96 larvae); 1989 experiments included 10 Alaskan families (76 larvae) and 10 Michigan families (55 larvae). Larvae from each family were allocated evenly across temperatures and hosts, but it was not possible to maintain equal sample sizes of each family in each treatment, and mortality resulted in some families being unrepresented in some treatments.

Larval growth of fourth and fifth instars

Early fourth instars (recently molted but feeding; ≈100 mg fresh mass) were weighed (M_{4i}), offered previously weighed leaves, and allocated to one of four experimental temperatures (12°, 18°, 24°, or 30°C; photocycle of 18 h light, 6 h darkness). Larvae were individually confined to clear plastic vials (355 mL volume) with water-saturated plaster of paris bases that provided a high-humidity atmosphere and maintained leaf turgor near natural levels. Paired control leaves (one sample per larva) were placed in adjacent vials and exposed to the same experimental conditions as the foliage fed to the larvae; the ratio of dry mass to fresh mass of control leaves was used to estimate the initial dry mass of foliage fed to the larvae. When larvae approached the fifth molt (≈380 mg fresh mass; after 1.5 d at 30°, 4–5 d at 12°), they were reweighed (M_{4f}), given fresh foliage, and returned to their respective temperatures. The unconsumed leaf tissue and accumulated frass were dried and weighed. Larval dry mass was estimated from fresh mass as DM = 0.125·FM. (The dry mass : wet mass ratio of *P. canadensis* larvae did not differ between populations and was unaffected by host plant.)

Fourth instar relative growth rates were calculated as:

$$\mathrm{RGR}_4 = [\ln(M_{4f}) - \ln(M_{4i})]/T_{4i-4f},$$

where ln = natural logarithm, and T_{4i-4f} = the elapsed time in days. Relative consumption rate (RCR) and relative assimilation rate (RAR) were calculated following formulae in Gordon (1968), which are similar to those of Waldbauer (1968; produced values within ±5%), but better describe a system of exponential growth. Apparent digestibility (AD) = RAR/RCR. The efficiency of conversion of digested matter (ECD) = RGR/RAR. Average daily metabolic rate (ADMR) was calculated as RAR − RGR. All are expressed in units of dry mass.

When larvae had completed the fourth molt and begun feeding as fifth instars (≈400 mg fresh mass), they were reweighed (M_{5i}), and again offered fresh, weighed foliage. Fifth instar trials encompassed most of the fifth stadium (1.5–5 d depending on temperature) and produced similarly derived estimates of all parameters measured during the fourth stadium. In addition, a subset of the control leaves and frass samples were analyzed for total nitrogen with standard micro-Kjeldahl techniques. Nitrogen use efficiencies (NUE) were calculated as the fraction of ingested nitrogen that did not appear in the frass: $\mathrm{NUE} = (N_{\mathrm{ingested}} - N_{\mathrm{egested}})/N_{\mathrm{ingested}}$.

In 1989, larvae were returned to their experimental temperatures after the fifth instar growth measure-

ments, fed fresh foliage, and monitored daily (12° and 18°) or twice daily (24° and 30°) until they completed the fifth molt and entered the diapausing pupal stage. Four weeks after pupation, pupae were sexed, weighed, and stored at 2° in darkness through the winter. The following spring they were placed outdoors (Fairbanks, Alaska) in screen emergence traps until the adults emerged or the pupae died.

The duration of molts

The process of molting between stadia is not entirely distinct from that of growth within stadia, so its contribution to development time is difficult to measure by simply counting the number of days or hours that an animal appears to be molting (Ayres and MacLean 1987). We estimated the duration of the fourth molt by calculating, based on fourth and fifth instar growth rates, how long it would have taken a larva to grow from its initial fourth instar mass (M_{4i}) to its late fifth instar mass (M_{5f}) in the absence of molt ($T_4 + T_5$) and subtracting this from how long it actually took (T_{4i-5f} = time elapsed between the measurement of fourth instar initial mass and fifth instar final mass). The difference was defined to be the duration of the fourth molt (Molt_4). Calculations follow Ayres and MacLean (1987).

$$\text{Molt}_4 = T_{4i-5f} - (T_4 + T_5).$$

Where:

$$T_4 = [\ln(M_{4\max}) - \ln(M_{4i})]/\text{RGR}_4,$$
$$T_5 = [\ln(M_{5f}) - \ln(M_{5\min})]/\text{RGR}_5,$$
$$M_{5\min} = M_{4\max} - \text{EXUV} - \text{RESP}.$$

The mass of fifth instars when they have first filled their gut after ecdysis ($M_{5\min}$) equals the maximum mass of fourth instars ($M_{4\max}$) minus exuvial losses (EXUV) and respiratory expenses during molt (RESP). For *P. canadensis*, EXUV was estimated as 2.5 mg and RESP as $0.05 \cdot M_{4\max}$. EXUV and RESP are difficult to estimate precisely, but sensitivity analyses show that they have little effect on Molt_4 (Ayres and MacLean 1987). With *P. canadensis*, and other holometabolous insects with which we are familiar (Ayres and MacLean 1987, Matsuki and MacLean 1990, Matsuki et al. 1994), molt durations measured in this way are well-correlated with the number of hours when larvae are not feeding.

The duration of the fifth and final molt (Molt_5; fifth instar to pupa) was calculated similarly to Molt_4, except that it was only based on growth rate in the preceding (fifth) stadium because growth ceases after pupation.

$$\text{Molt}_5 = T_{5i-\text{pupa}} - [\ln(\text{DM}_{\text{pupa}}) - \ln(\text{DM}_{5i})]/\text{RGR}_5.$$

Pupal dry masses (DM_{pupa}) were estimated from pupal fresh masses as $-18.4 + 0.243 \cdot \text{FM}_{\text{pupa}}$ for males and $-56.9 + 0.316 \cdot \text{FM}_{\text{pupa}}$ for females (M. P. Ayres and J. M. Scriber, *unpublished data*). The dry mass of early fifth instars (DM_{5i}) was calculated as before ($0.125 \cdot \text{FM}$) with a correction for indigestible gut contents (−15% fresh mass). For comparison, we also measured the time at which late fifth instars cleared their guts to the completion of ecdysis.

Basking success

During August 1989, fifth instars from Alaska and Michigan (n = 18 and 11) were placed outdoors on *Populus tremuloides* trees where they were allowed to move, feed, and bask naturally. Caterpillar temperatures were measured one to six times daily throughout periods of high insolation using a Sensortek BAT-12 telethermometer (Sensortek, Clifton, New Jersey) with a blunt-tip, fine-gauge copper/constantan sensor (Sensortek model MT-4, needle diameter 0.33 mm, time constant 0.025 s) slid non-invasively into a natural fold dorso-lateral to the first pair of legs. Caterpillar temperature readings stabilized within 5 s and remained stable even when ≥10° above air temperatures. Air and leaf surface temperatures were recorded with each caterpillar observation (≤5 cm from the caterpillar). In addition, we measured "basking potential" as the temperature of a standardized black body exposed to the same insolation as the caterpillar; for this, a black, caterpillar-sized piece of open cell foam rubber (30 × 10 × 10 mm) was suspended next to each caterpillar until its temperature stabilized under the ambient radiation (1–4 min). Our black body cannot be interpreted as a strict mimic of black caterpillars (e.g., thermal conductivity must be different), but it provided a useful standard against which to compare the basking success of real caterpillars.

We measured the relative growth rates of larvae in the field (for comparison with laboratory growth rates) by weighing the Alaskan *P. canadensis* just before placing them outdoors and 3 d later. The daily mean temperatures encountered by field larvae were estimated using a shaded maximum–minimum thermometer (1 m above ground). A matched set of larvae was weighed 1 d later and grown for 3 d in the laboratory at a constant temperature set each day to the mean temperature encountered the previous day by the field caterpillars. Laboratory larvae were fed leaves from the same trees where the field larvae were feeding.

Statistical analyses

Statistical comparisons of *P. canadensis* populations from Alaska and Michigan were based on the number of families representing each population and the variance among families. Except as noted, figures and tables show population means and standard errors calculated from family means. RGR_4, RGR_5, and Molt_4 were analyzed separately at each temperature (due to extreme heteroscedasticity among temperatures) with an ANOVA model that included population (Alaska vs. Michigan) and host (*Populus tremuloides* and *P.*

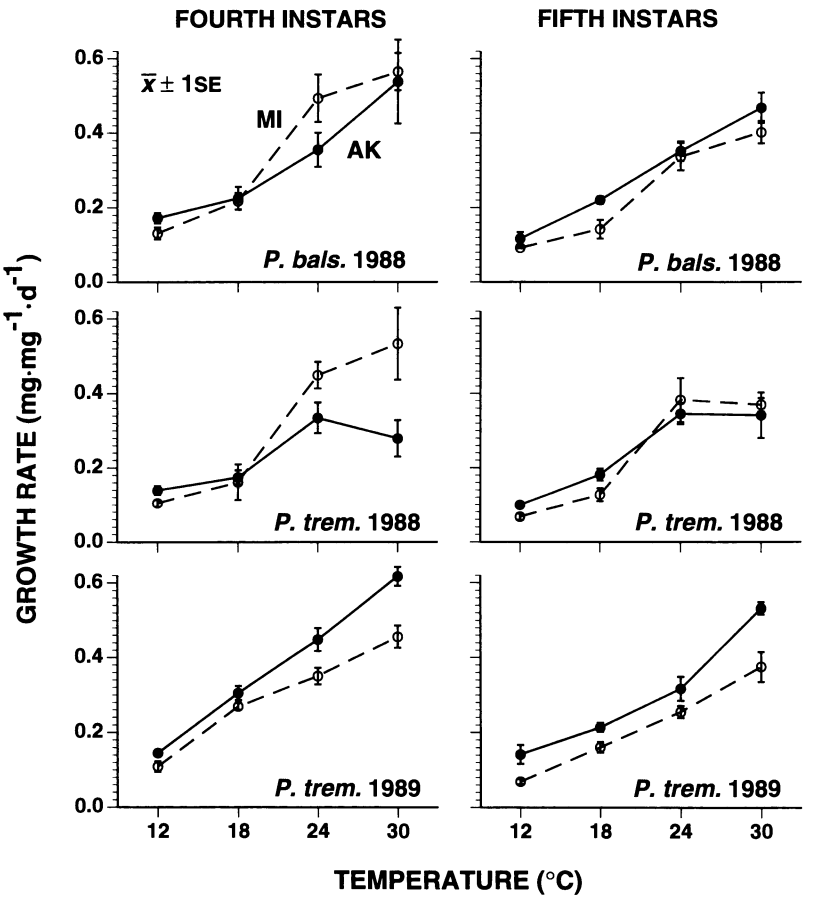

FIG. 3. Relative growth rates of *Papilio canadensis* larvae from Alaska (●) and Michigan (○) as a function of temperature. Experiments included fourth and fifth instars reared on *Populus balsamifera* and *P. tremuloides* in 1988 and *P. tremuloides* in 1989. Some standard errors are obscured by the data point. Table 1 shows corresponding ANOVAs.

balsamifera in 1988 and *P. tremuloides* in 1989) as fixed effects, and families nested within population as a random effect. $Molt_5$ (only measured in 1989) was analyzed with an identical ANOVA model except that temperature was substituted for host. Nitrogen use efficiency (incomplete factorial) was analyzed with two two-way ANOVAs, one comparing two populations across four temperatures on a single host (main effects were population and temperature), and one comparing a single population (Alaska) across three hosts and four temperatures (main effects were host and temperature). Pupal mass was analyzed with a three-way ANOVA that included temperature, population, and sex. Family was not explicitly included in analyses of nitrogen use efficiency and pupal mass because of limited sample sizes and because variance among families contributed only trivially to the other models. $Molt_5$ was square-root transformed to correct for heteroscedasticity (figures show non-transformed data); all other variables satisfied assumptions of normality and equal variance. ANOVAs were calculated using the SAS General Linear Models procedure (SAS 1985). The effects of population and temperature on survival were tested with a two-way contingency analysis (CATMOD procedure, linear model, SAS 1985).

RESULTS

Larval growth rates

As expected, temperature had an enormous effect on larval growth rate, with higher temperatures generally resulting in higher growth rates (Fig. 3). In addition, there were substantial differences between populations and interactions among temperature, population, and host (Table 1). At low temperatures (12°C), Alaskan *P. canadensis* had consistently higher fourth and fifth instar growth rates than Michigan *P. canadensis* (Fig. 3): least square means ± 1 SE = 0.152 ± 0.008 vs. 0.114 ± 0.007 mg·mg^{-1}·d^{-1} for fourth instars and 0.119 ± 0.008 vs. 0.076 ± 0.010 mg·mg^{-1}·d^{-1} for fifth instars ($F_{1,23}$ = 14.10 and $F_{1,19}$ = 11.69, Table 1). Thus, Alaskan fifth instars at 12° doubled their mass in 5.8 d vs. 9.1 d for their Michigan counterparts (doubling time = ln(2)/RGR). At 18°, Alaskan growth rates were higher than Michigan growth rates in six of six comparisons (Fig. 3) and significantly so for fifth instars (Table 1).

TABLE 1. Summary of ANOVAs comparing the relative growth rates of fourth (RGR_4) and fifth (RGR_5) instar *Papilio canadensis* from Alaska and Michigan on three hosts at four temperatures. Corresponds to data in Fig. 3.

		Temperature					
		12°		18°		24°	
Source	df	RGR_4	RGR_5	RGR_4	RGR_5	RGR_4	RGR_5
		F statistics† (mean squares)					
Population	1	14.10*** (0.01364)	11.69** (0.01573)	1.44 (0.00360)	20.58*** (0.03468)	2.10 (0.02156)	0.26 (0.00209)
Host	2	2.40 (0.00307)	2.89 (0.00182)	7.18* (0.03218)	1.02 (0.00467)	0.26 (0.00290)	4.43* (0.02569)
Pop. × Host	2	0.02 (0.00002)	3.00 (0.00188)	0.10 (0.00045)	0.11 (0.00052)	6.10** (0.06876)	1.50 (0.00873)
Family (Pop.)‡	17–28	0.76 (0.00097)	2.14 (0.00134)	0.56 (0.00251)	0.37 (0.00168)	0.91 (0.01027)	1.37 (0.00794)
Error	10–45	(0.00128)	(0.00063)	(0.00448)	(0.00457)	(0.01127)	(0.00580)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
† The *F* test denominator for Population was $MS_{Family\ (Pop)}$; other terms were tested over MS error.
‡ Family nested within population.

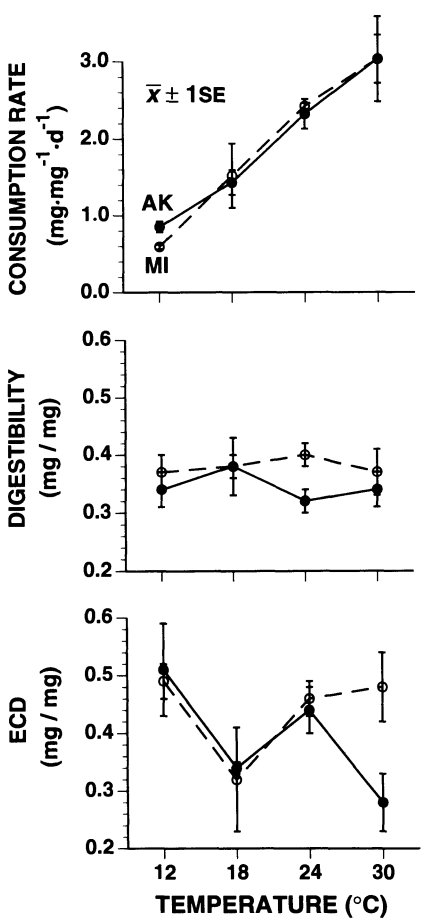

FIG. 4. Dry mass budgets as a function of temperature of *Papilio canadensis* fourth instars feeding on *Populus tremuloides* in 1988. ● and ○ represent *P. canadensis* from Alaska and Michigan, respectively. Corresponding growth rates appear in middle left of Fig. 3. Some standard errors are obscured by the data point.

At high temperatures (24° and 30°), population comparisons differed depending upon the host (Fig. 3; population × host interactions in Table 1). In 1988, growth rates of Alaskan fourth instars feeding on *Populus tremuloides* decreased from 24° to 30°, while the growth rate of Michigan fourth instars increased across the full range of experimental temperatures (Fig. 3, middle left); consequently, Michigan larvae were growing significantly faster than Alaskan larvae at 30° (mean ± 1 SE = 0.533 ± 0.043 vs. 0.279 ± 0.054 $mg \cdot mg^{-1} \cdot d^{-1}$, $P = 0.0009$). Of the remaining five comparisons at 30°, the populations grew at similar rates in two comparisons, and Alaskan larvae tended to grow faster in three comparisons (significantly so in both 1989 comparisons, $P < 0.001$; Fig. 3).

Dry mass and nitrogen budgets

Population comparisons of dry mass consumption rates and conversion efficiencies were summarized through analysis of the two most disparate trials: fourth instars on *Populus tremuloides* in 1988 and fifth instars on *P. tremuloides* in 1989 (middle left and lower right in Fig. 3). At 12° in 1988 (Fig. 4), the high growth rates of Alaskan larvae relative to Michigan larvae were attributable to 44% higher consumption rates (RCR = 0.85 ± 0.07 vs. 0.59 ± 0.03 $mg \cdot mg^{-1} \cdot d^{-1}$ [means ± 1 SE], $P < 0.05$); neither apparent digestibility (AD) nor the efficiency of conversion of digested matter (ECD) differed significantly between populations at 12° (note that RGR = RCR·AD·ECD). At 30°, the reduced growth of Alaskan larvae relative to Michigan larvae was due to elevated respiratory expenses leading to a marked reduction in the efficiency with which digested matter was converted into new larval tissue (ECD = 0.28 ± 0.05 vs. 0.48 ± 0.06 mg/mg for Alaska and Michigan, respectively, $P < 0.05$); in this trial, neither consumption rate nor apparent digestibility differed between populations at 30° (Fig. 4).

In trials where the growth rate of Alaskan larvae

TABLE 1. Continued.

Source	Temperature 30° RGR_4	Temperature 30° RGR_5
	F statistics† (mean squares)	
Population	0.42 (0.01132)	4.67* (0.05400)
Host	5.79** (0.06127)	5.43** (0.03738)
Pop. × Host	13.08*** (0.13841)	4.83* (0.03327)
Family (Pop.)‡	2.58* (0.02726)	1.68 (0.01157)
Error	(0.01058)	(0.00689)

remained higher than Michigan larvae across all temperatures (e.g., fifth instars in 1989), it was due to generally elevated consumption rates (average of 40% higher in Alaskan larvae, $P < 0.001$ at each temperature, Fig. 5). Digestive efficiency (AD) did not differ between populations, so assimilation rates also averaged 40% higher in Alaskan larvae (Fig. 5). Although respiratory expenses (= average daily metabolic rate = assimilation rate − growth rate) averaged 36% higher in Alaskan larvae, the higher assimilation rate was more than sufficient to compensate, and Alaskan larvae maintained higher growth rates at all temperatures (Fig. 5). Because population differences in metabolic rate balanced population differences in assimilation rate, there were no population differences in growth efficiency (= ECD = growth/assimilation; Fig. 5).

A powerful interaction between temperature and host quality was revealed by comparing the temperature responses of Alaskan *P. canadensis* across three host species (Fig. 6). On *Populus balsamifera,* fifth instar growth rate increased linearly with temperature from 12° to 30° ($Q_{10} = 2.16$). (Q_{10} is the factor by which a rate increases with a 10° increase in Celsius temperature.) On *Populus tremuloides,* where consumption rates were indistinguishable from *P. balsamifera,* growth rate increased from 12° to 24°, then remained constant from 24° to 30°. The higher growth rates at 30° on *P. balsamifera* compared with *P. tremuloides* were due to lower metabolic rates (ADMR = 0.57 ± 0.08 vs. 0.91

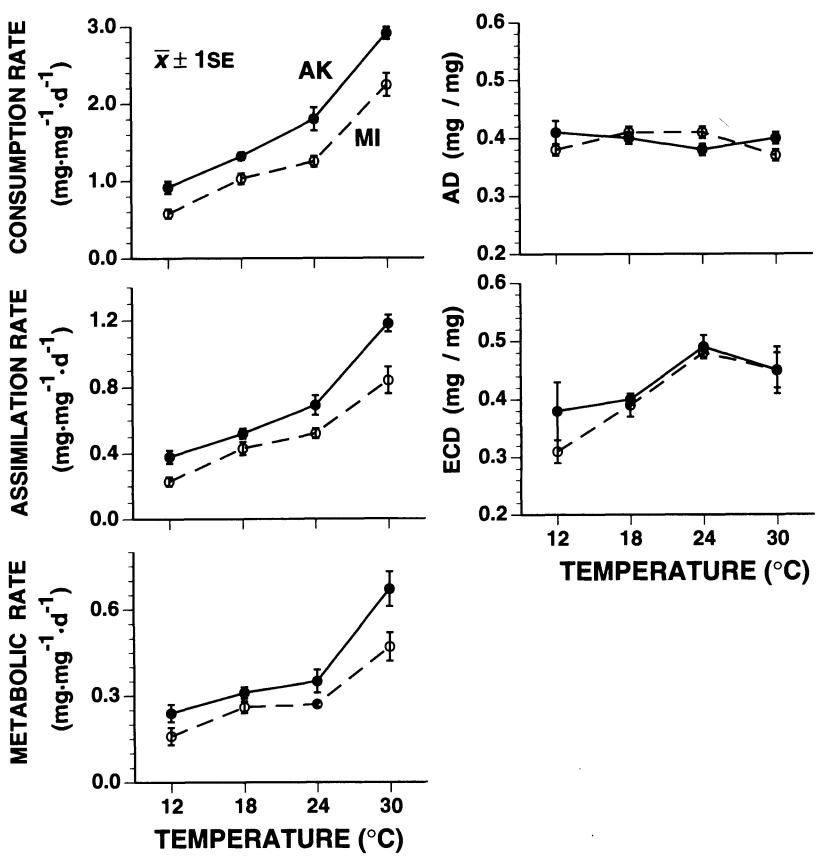

FIG. 5. Dry mass budgets as a function of temperature of *Papilio canadensis* fifth instars feeding on *Populus tremuloides* in 1989. ● and ○ represent *P. canadensis* from Alaska and Michigan, respectively. Corresponding growth rates appear in lower right of Fig. 3.

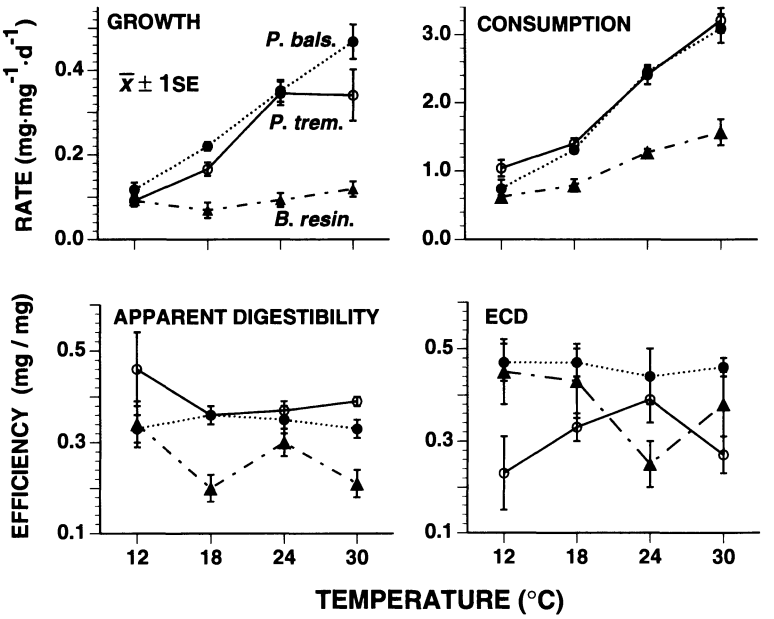

FIG. 6. Dry mass budgets as a function of temperature of Alaskan *Papilio canadensis* fifth instars feeding on three hosts in 1988. Hosts were *Populus balsamifera* (●), *P. tremuloides* (○), and *Betula resinifera* (▲).

± 0.03 mg·mg^{-1}·d^{-1} [means ± 1 SE]). Apparent digestibility, and therefore assimilation rate, was actually lower on *P. balsamifera* than on *P. tremuloides,* but growth efficiency [= ECD = (RAR − ADMR)/RAR] was higher (Fig. 6). On *Betula resinifera,* growth rate was completely insensitive to temperature (Q_{10} = 1.16 from 12° to 30°), even though consumption rate increased steadily with temperature (Q_{10} = 1.68; Fig. 6). Consumption did not, however, increase as steeply with temperature as on the other hosts (compare to RCR Q_{10} of 2.21 on *P. balsamifera*). The apparent digestibility of *Betula* was low (least squares mean ± 1 SE = 0.26 ± 0.02) and relatively insensitive to temperature (Fig. 6). Consequently, assimilation rate on *Betula* was low (RAR at 30° = 0.34 ± 0.06 mg·mg^{-1}·d^{-1}), and the arithmetic difference between assimilation rate and metabolic rate (= growth rate) did not change from 12° to 30° even with a 2.5-fold increase in consumption rate.

There were no apparent differences in the nitrogen use efficiency of *P. canadensis* populations from Alaska and Michigan (Table 2; NUE = 0.67 ± 0.02 vs. 0.69 ± 0.02 mg/mg [least squares means ± 1 SE] for Alaska and Michigan, respectively; $F_{1,28}$ = 1.34, P = 0.26). As with dry mass conversion efficiencies (AD and ECD), nitrogen use efficiency was relatively insensitive to temperature (Table 2; $F_{3,44}$ = 1.94, P = 0.14). However, there were large effects of host species (Table 2; $F_{2,44}$ = 66.71, P < 0.0001). Nitrogen use efficiency may have been somewhat less on *Populus balsamifera* than on *P. tremuloides* (0.61 ± 0.02 vs. 0.67 ± 0.02 mg/mg, P = 0.063), but it was dramatically less on *Betula* (0.36 ± 0.02 mg/mg) than on either *Populus* species (P < 0.0001). Leaf nitrogen content (% dry mass) was lower in *Betula* foliage (2.10 ± 0.13%) than in *P. tremuloides* (2.67 ± 0.11%) or *P. balsamifera* foliage (2.44 ± 0.10%), and larval dry mass consumption rates were also lower (Fig. 6). Consequently, nitrogen consumption rates (NCR) at 30° were 2.3 times higher on *P. balsamifera* than on *Betula* (75.4 vs. 33.0 mg·g^{-1}·d^{-1}), and because

TABLE 2. Nitrogen use efficiency (NUE) of fifth instar *Papilio canadensis* from Alaska (AK) and Michigan (MI) feeding at four temperatures on three hosts. N = 4–5 larvae (3–5 families) in each treatment combination. Data are means ± 1 SE.

	Temperature					
	12°		18°		24°	
Host	AK	MI	AK	MI	AK	MI
	Nitrogen use efficiency					
Populus tremuloides	0.71 ± 0.04	0.78 ± 0.03	0.59 ± 0.05	0.67 ± 0.07	0.67 ± 0.02	0.71 ± 0.03
Populus balsamifera	0.59 ± 0.03		0.61 ± 0.04		0.62 ± 0.04	
Betula resinifera	0.33 ± 0.04		0.31 ± 0.05		0.44 ± 0.04	

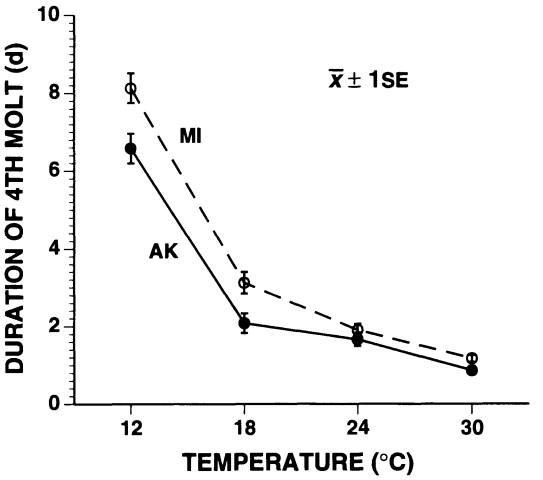

FIG. 7. The duration of the fourth molt in *Papilio canadensis* from Alaska (●) and Michigan (○) as a function of temperature. Experiments included larvae reared on *Populus balsamifera* and *P. tremuloides* in 1988 and *P. tremuloides* in 1989. Some standard errors are obscured by the data point. Table 3 shows corresponding ANOVAs.

of the reduced nitrogen use efficiencies on *Betula*, nitrogen accumulation rate (= NCR·NUE) at 30° was 4.1 times higher than on *Betula* (47.5 vs. 11.6 $mg \cdot g^{-1} \cdot d^{-1}$).

Molting physiology

The fourth molt ($Molt_4$) took 14–50% longer for Michigan larvae than for Alaskan larvae (Fig. 7). Population differences were significant at 12° (least squares means ± 1 SE = 8.13 ± 0.39 vs. 6.58 ± 0.38 d for Michigan and Alaska, respectively), at 18° (3.12 ± 0.28 vs. 2.08 ± 0.25 d), and at 30° (1.18 ± 0.09 vs. 0.86 ± 0.11 d; Table 3). Molt duration was highly sensitive to temperature (required 7.2 times longer at 12° than at 30°, Fig. 7), but relatively insensitive to host (no significant host effects or population × host interactions in Table 3).

The fifth molt ($Molt_5$, Fig. 8) was 50% longer for Michigan larvae than for Alaskan larvae at 12° ($P < 0.0025$), 42% longer at 18° ($P = 0.02$), 32% longer at 24° ($P < 0.0025$), and actually required slightly less time at 30° ($P = 0.18$; ANOVA population effect: $F_{1,17} = 20.60$, $P < 0.0001$; ANOVA temperature × population interaction: $F_{3,64} = 8.21$, $P < 0.001$). Duration of the fifth molt was very temperature sensitive between 12° and 18° (Q_{10} of $1/Molt_5$ = 5.38 and 5.92 for Alaska and Michigan, respectively), temperature insensitive from 18° to 24° (Q_{10} = 1.02 and 1.21), and moderately temperature sensitive from 24° to 30° (Q_{10} = 1.70 and 2.92). The fifth molt required a surprisingly long time (up to 18 d for Michigan larvae at 12°), and this did not appear to be an artifact of the way it was estimated. The interval from the time at which late fifth instars cleared their gut to when they completed ecdysis to enter the pupal stage averaged 55% as long as $Molt_5$ (range 41–69% in eight treatments). This interval must be an underestimate of the contribution of the fifth molt to total development time. In other experiments (at 24°), repeated weighings of larvae throughout the fifth stadium indicated nearly exponential growth for the first several days. This period was followed by 1–2 d when larvae continued to feed but grew very little (M. P. Ayres and J. M. Scriber, *unpublished data*). Our estimates of $Molt_5$ (Fig. 8) attribute this dramatic slowing of growth late in the stadium to the early physiological demands of molt and preparations for metamorphosis.

Pupal mass

Michigan caterpillars produced larger pupae than Alaskan caterpillars (Fig. 9; $F_{1,88} = 11.89$, Table 4). There were also strong main effects of temperature and sex on pupal mass (Table 4). Overall, pupal mass averaged 25% less at 12° than at 18°, and female pupae averaged 9% larger than male pupae (Fig. 9). Population differences were less pronounced in males and at low temperatures.

TABLE 2. Continued.

Host	Temperature 30° AK	Temperature 30° MI
	Nitrogen use efficiency	
Populus tremuloides	0.70 ± 0.03	0.64 ± 0.04
Populus balsamifera	0.63 ± 0.04	
Betula resinifera	0.35 ± 0.04	

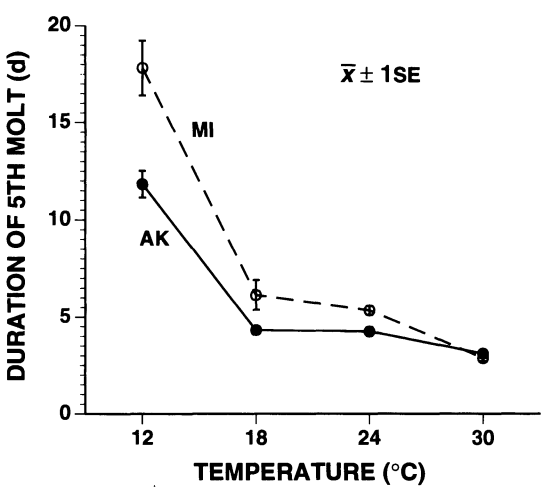

FIG. 8. The duration of the fifth molt (fifth instar to pupa) in *P. canadensis* from Alaska (●) and Michigan (○) as a function of temperature. Some standard errors are obscured by the data point.

TABLE 3. Summary of ANOVAs comparing the duration of the fourth molt in *Papilio canadensis* from Alaska and Michigan on three hosts at four temperatures. Corresponds to data in Fig. 7.

Source	df	12°	18°	24°	30°
			F statistics† (mean squares)		
Population	1	7.53*	7.81**	1.23	4.62*
		(20.536)	(9.054)	(0.538)	(0.874)
Host	2	0.18	1.55	0.70	2.51
		(1.379)	(3.411)	(0.320)	(0.314)
Pop. × Host	2	2.03	0.12	0.25	1.46
		(15.690)	(0.265)	(0.112)	(0.183)
Family (Pop.)‡	19–25	0.35	0.53	0.96	1.51
		(2.727)	(1.160)	(0.438)	(0.189)
Error	10–37	(7.734)	(2.198)	(0.457)	(0.125)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
† The *F* test denominator for Population was $MS_{Family\ (Pop)}$; other terms were tested over MS_{error}.
‡ Family nested within population.

Survival

Populations did not differ in their survival across temperatures or at any one temperature (Table 5; chi-square for population effects in total survival = 0.12, $P = 0.73$, df = 1; chi-square for population × temperature interaction = 2.28, df = 3, $P = 0.52$). However, survival was influenced by temperature (chi-square = 39.77, df = 3, $P = 0.0001$). At 12°, survival to the reproductive adult stage was only ≈25%, primarily due to low pupal survival (Table 5). Survival was highest at 18° (91%) and intermediate at 24° and 30° (60%).

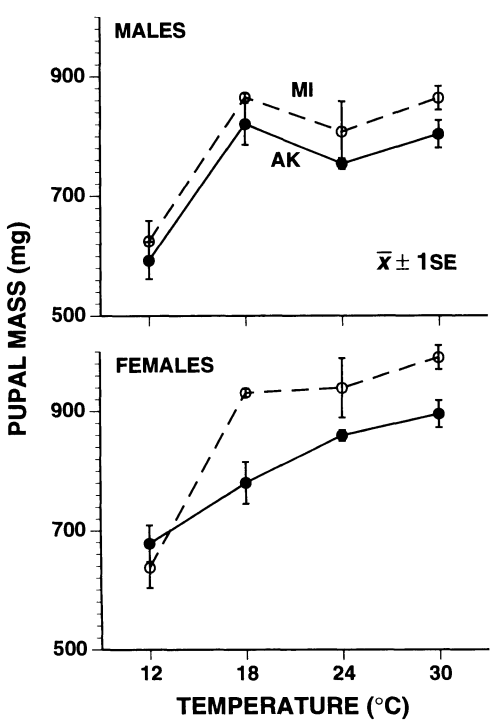

FIG. 9. Pupal mass of male and female *Papilio canadensis* from Alaska (●) and Michigan (○) as a function of temperature. Larvae were reared on *Populus tremuloides* in 1989. Table 4 shows corresponding ANOVA.

Development time

To develop from early fourth instars to pupae, *P. canadensis* in 1989 required 9.5–58 d depending on temperature and genotype (Fig. 10). Michigan larvae required 4.9 times longer at 12° than at 30° (means ± 1 SE = 57.5 ± 2.4 vs. 11.7 ± 0.6 d). Alaskan larvae were somewhat less temperature sensitive (required 4.0 times longer at 12° than at 30°: 37.7 ± 2.6 vs. 9.5 ± 0.3 d) and required 19–34% less time than Michigan larvae (percentage differences were greatest at low temperatures; Fig. 10). The temperature sensitivity of development time would have been even more pronounced except that caterpillars at 12° did not grow as large as at warmer temperatures (Fig. 9). The fourth and fifth molts together accounted for 35–51% of development time; molt made up the largest fraction of development time at 12° (Fig. 10). The fourth stadium required less time for Alaskan larvae than Michigan larvae partly because of higher relative growth rates (Fig. 10) and partly because they began the stadium at a slightly larger size ($M_{4i} = 112 \pm 54$ vs. 86 ± 42 mg; $P = 0.006$; estimated time as fourth instars assumes that larvae began the stadium at 90% of M_{4i}). Larval mass at the start of the fifth stadium did not differ between populations ($M_{5i} = 449 \pm 151$ vs. 492 ± 170 mg for Alaska and Michigan, respectively; $P = 0.21$), and only modestly, if at all, across temperatures ($F_{3,94}$

TABLE 4. ANOVA comparing the pupal mass of male and female *Papilio canadensis* from Alaska and Michigan reared at four temperatures. Corresponds to data in Fig. 9.

Source	df	MS	*F*
Temperature	3	193 720	36.12***
Population	1	63 750	11.89***
Sex	1	92 130	17.18***
Temp. × Pop.	3	6660	1.24
Temp. × Sex	3	11 400	2.13
Pop. × Sex	1	2500	0.47
Temp. × Pop. × Sex	3	4580	0.85
Error	88	5360	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 5. Survival of *Papilio canadensis* from Alaska (AK) and Michigan (MI) reared at four temperatures in 1989. Larval survival is the percentage of early fourth instars that successfully pupated. Pupal survival is the percentage of pupae that survived 9 mo of diapause and emerged as adults the following spring. Total survival is the product of larval and pupal survival.

	Temperature							
	12°		18°		24°		30°	
	AK	MI	AK	MI	AK	MI	AK	MI
Initial number (*n*)	13	9	15	10	21	14	27	22
Larval survival (%)	77	67	93	90	81	86	81	95
Pupal survival (%)	33	40	100	100	83	63	63	75
Total survival (%)	25	27	93	90	63	54	51	71

= 2.54, $P = 0.061$, maximum difference among four temperatures = 14%).

Basking success

We found only rare circumstances that allowed *P. canadensis* larvae in Alaska to elevate their body temperature much above ambient. Larvae were deliberately placed in high radiation microsites (maximally exposed south-facing branches) within a high radiation site (a south-facing forest edge on a south-facing slope), yet in 145 caterpillar observations on eight sunny days (7–12 August and 18–20 August 1989), we never found a larva >4.5° above ambient air temperature (mean ± 1 SD = 0.9 ± 1.3°). Generally, the basking potential (measured by black body temperatures) was not very high because of breezes and/or shading from nearby leaves (2.7 ± 2.5°, maximum 11.0°) . Larvae seldom moved. Most larvae remained within 20 cm of where we placed them throughout the experiment (3–5 d). We did not observe larvae moving to high radiation microsites even though such sites were often within 10 cm. On 22–23 August, in an attempt to maximize basking potential, we placed larvae individually on freshly cut branches (≈50 cm in length) positioned upright on a lawn in full sunlight and protected from breezes. Under these conditions, larvae were able to elevate body temperatures as much as 10°–14° above air temperatures. Across a range of environmental conditions, the basking success of larvae was ≈50% of basking potential as measured by black body temperatures (regression slope = 0.53 in Fig. 11). There were no population differences in basking success (Fig. 11). The body temperatures of Alaskan larvae did not differ from that of Michigan larvae when exposed to the same field conditions (Fig. 12).

Growth rates of larvae in the field and laboratory were indistinguishable when the larvae were fed the same foliage and subjected to the same mean daily air temperature (RGR = 0.157 ± 0.006 vs. 0.143 ± 0.014 $mg \cdot mg^{-1} \cdot d^{-1}$ [means ± 1 SE] for field and laboratory larvae, respectively; $t_{12} = 0.79$, $P > 0.20$). On the 3 d of this experiment, daily minimum and maximum air temperatures in the field were, respectively, 10.5° and 24°, 10° and 20°, and 8° and 17°. Larvae in the laboratory were held at constant temperatures of 17°, 15°, and 12.5° on days 1, 2, and 3, respectively.

DISCUSSION

Adaptive modifications of temperature physiology

P. canadensis populations from Alaska and Michigan have diverged in their larval temperature physiology (Figs. 3–5 and 7–8). Alaskan larvae are capable of growing and molting more rapidly at the low temperatures they typically encounter (Figs. 1 and 2). Intraspecific differentiation in insect temperature re-

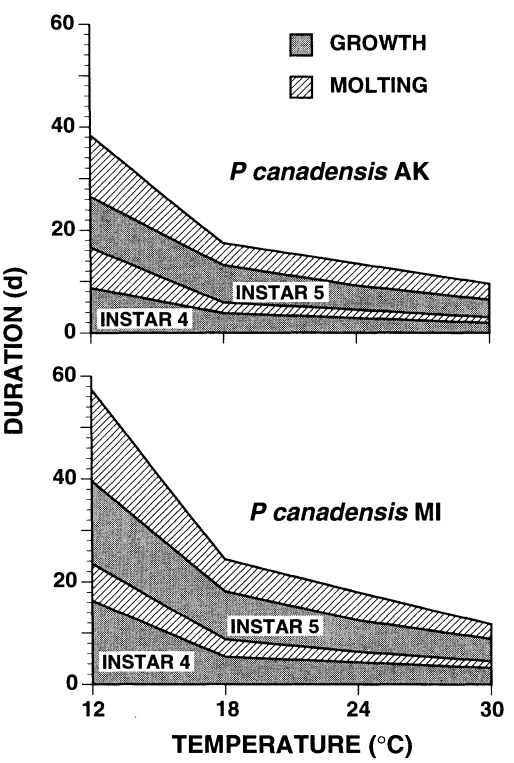

FIG. 10. Development time from early fourth instars to pupae of *Papilio canadensis* from Alaska (upper) and Michigan (lower) as a function of temperature. Durations of the fourth instar, the fourth molt, the fifth instar, and the fifth molt are indicated.

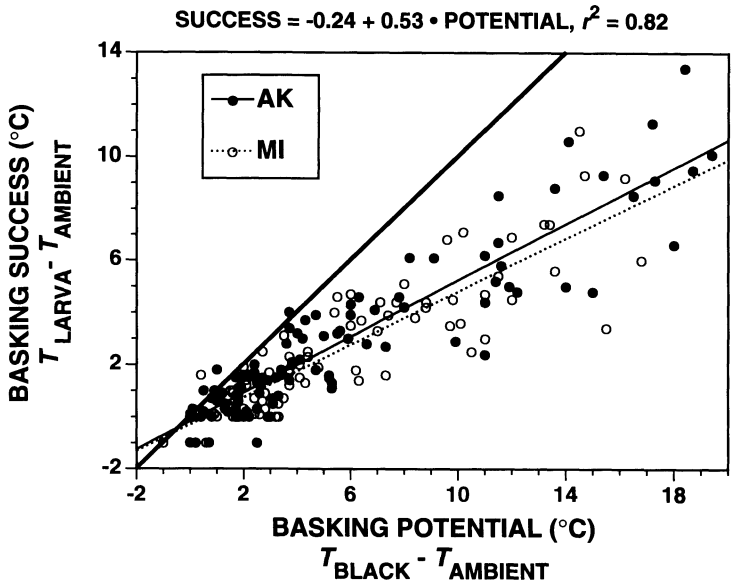

FIG. 11. Basking success as a function of basking potential in fifth instar *Papilio canadensis* from Alaska (●) and Michigan (○). Basking success equals the difference between larval temperature and ambient air temperature; basking potential equals the difference between the temperature of a high absorption black body and ambient air temperature. Heavy solid line shows the points of equality between success and potential. Regressions fit to each population separately did not differ ($F_{2, 112}$ = 1.12, $P > 0.20$). Most points to the right of 6°C on the x axis represent larvae on detached branches placed in full sunlight and protected from the wind.

sponses has also been reported in milkweed bugs (Baldwin and Dingle 1986), *Drosophila* larvae (Barnes et al. 1989), and Colorado potato beetles (Tauber et al. 1988). No such differences were found in the diamondback moth (Sarnthoy et al. 1989).

Adaptation of *P. canadensis* to short cool summers has been accomplished in part through a general elevation of metabolic activity at all temperatures. Average daily metabolic rates of Alaskan larvae were 36% higher than Michigan larvae (Fig. 5). Consequently, Alaskan larvae had very similar metabolic rates at their average environmental temperature (0.268 $mg \cdot mg^{-1} \cdot d^{-1}$ at 14.4°C) as did Michigan larvae at theirs (0.261 $mg \cdot mg^{-1} \cdot d^{-1}$ at 18.8°; linear interpolation of ADMR data in Fig. 5). Probably as a result of this "metabolic compensation" (Scholander et al. 1953), Alaskan caterpillars were able to consume more, grow faster, and molt more quickly at low temperatures than Michigan caterpillars. The metabolic rates of diapausing pupae were similarly elevated in Alaskan *P. canadensis* (35% higher than Michigan *P. canadensis*; Kukal et al. 1991).

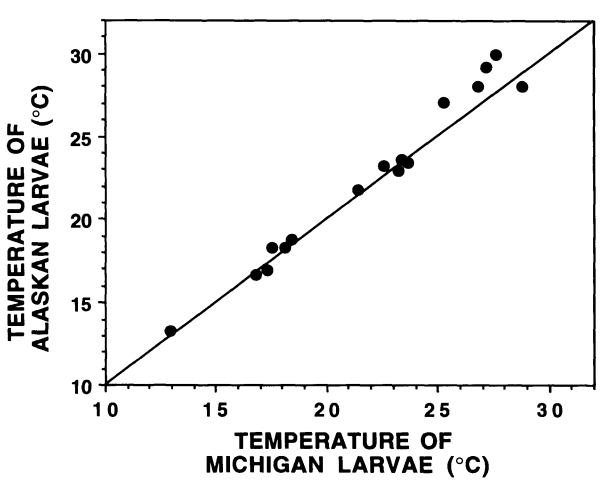

FIG. 12. The temperatures of Alaskan and Michigan *Papilio* larvae when allowed to move and bask naturally under field conditions in Alaska. Each point is the mean of 5–10 larvae from each population. Standard deviations ranged from 0.5°C at low temperatures to 4°C at high temperatures. The line of equality is indicated.

There was limited evidence for concomitant reductions in larval growth performance at high temperatures. Alaskan fourth instars feeding on *Populus tremuloides* in 1988 grew only half as fast at 30° as Michigan fourth instars, even though they grew 34% faster at 12° (Fig. 3). The low growth rate of Alaskan larvae at 30° was due to high respiratory expenses (Fig. 4), suggesting an energetic trade-off between adaptation to low temperatures and performance at high temperatures. However, such trade-offs were far less apparent than we expected.

In 1989, Alaskan larvae grew faster (Fig. 3) and survived as well (Table 5) at 30° as Michigan larvae, even though the Alaskan population never encounters sustained temperatures that warm (Fig. 2). The apparent "cost" of low temperature adaptation (high metabolic

rates) was still evident in these trials (Fig. 5), but high consumption rates with equivalent digestive efficiency allowed the Alaskan larvae to grow faster, nonetheless. Presumably because of their high maintenance metabolism, Alaskan larvae were more sensitive to host quality than Michigan larvae, especially at high temperatures. The variance around relative growth rate means at 30° was 10–33 times greater for Alaskan than for Michigan larvae (fourth instar SD = 0.177 vs. 0.056 for Alaska and Michigan, respectively, $F_{2,2} = 9.99$, $P < 0.10$; fifth instar SD = 0.097 vs. 0.017, $F_{2,2} = 32.56$, $P < 0.05$; each SD calculated from three treatment means in Fig. 3). Yet this represents only a limited spectrum within generally high quality hosts; *Populus balsamifera* and *P. tremuloides* ranked first and second in a comparison of fifth instar growth rates across nine host species (Ayres 1991). Alaskan caterpillars, as a result of their elevated metabolism, may be less able to exploit hosts of low nutritional quality. Shallow growth temperature responses, such as on *Betula resinifera* (Fig. 6), should be more common as a consequence of low temperature adaptation. Even on high quality hosts, the growth rates of Alaskan larvae were less temperature sensitive than those of Michigan larvae: fifth instar Q_{10}s of 1.99–2.16 vs. 2.27–2.58 (Fig. 3, 12°–30°).

In general, biochemical adaptation to low temperatures can occur through two routes (Hochachka and Somero 1973): (1) increased concentrations of enzymes, which increase reaction rates at all temperatures, or (2) qualitative changes in enzyme structure that result in higher substrate affinity at low temperatures (changes in the response of K_m to temperature). Changes in enzyme structure that enhance performance at low temperatures are expected to compromise performance at high temperatures (Powers 1987). The temperature × population interaction in the duration of the fifth molt (Fig. 8) suggests such a change in enzymes associated with pupation. But overall, there was little evidence for shifts in the temperature optima of physiological systems. Consumption rates, assimilation efficiencies, molting rates, survival, and, usually, growth rates remained as high or higher in the Alaskan population, even at the ecologically extreme temperature of 30°. Distinct temperature optima in these same processes are often apparent over only a few degrees Celsius in aquatic insects (Sweeney and Vannote 1978, Grafius and Anderson 1979, Vannote and Sweeney 1980), perhaps because their thermal environment is less variable. Qualitative changes in enzyme structure may be less important in the thermal adaptation of terrestrial insects than aquatic insects.

Conserved attributes

Although Alaskan larvae had higher development rates at 12° than their Michigan counterparts, there was little evidence for changes in developmental thresholds. The minimum temperature at which a biological process occurs (T_0) can be estimated by linear extrapolation from the temperature response of developmental rate (Arnold 1959). In four experiments, the temperature response of growth rate was sufficiently linear to allow reasonable extrapolation (fourth and fifth instars on *Populus balsamifera* in 1988 and *P. tremuloides* in 1989; Fig. 3). Estimates of T_0 were 6.8 ± 0.5 and 7.6 ± 1.9°C (means ± 1 SD) for Alaskan and Michigan caterpillars, respectively ($t_7 = 0.80$, $P > 0.20$, paired t test). Developmental thresholds for molting were also similar between populations ($Molt_4$ $T_0 = 9.6°$ and 9.5° for Alaska and Michigan; $Molt_5$ rates were too nonlinear for extrapolation), but tended to be higher than thresholds for growth (see also Ayres and MacLean 1987). Estimates of T_0 for *Papilio glaucus*, a southern sister species, range from 8° to 12° (Scriber and Lederhouse 1983, Grossmueller and Lederhouse 1985, Ritland and Scriber 1985). Developmental thresholds of swallowtail caterpillars do not differ very much from Florida to Alaska, even across species.

The probability of *P. canadensis* successfully completing development in Alaska would be enhanced if larvae could regularly elevate body temperatures through basking. Lepidopteran larvae can attain temperatures 5°–20° above ambient by adjusting posture and orientation, exploiting thermal heterogeneity within the environment, and minimizing convective heat losses (Casey 1976, Rawlins and Lederhouse 1981, Casey et al. 1988, Kukal et al. 1988, Weiss et al. 1988). *P. canadensis* and *P. glaucus* spend most of their time sitting on silken mats that they construct on the adaxial surface of individual leaves. Besides providing a secure footing, these mats can retard convective heat loss and contribute to radiant energy gain by turning the leaf into a parabolic reflector (Grossmueller and Lederhouse 1985). *P. glaucus* larvae also exhibit positive phototaxy within the host canopy which tends to put them in high radiation microsites. We hypothesized that these behaviors would be particularly well-developed in Alaskan caterpillars, but in fact, basking efficiency (temperature elevation as a fraction of basking potential) and average caterpillar temperatures were no different in the two populations (Figs. 11 and 12). The opportunities for basking seem to be rare for Alaskan swallowtails under natural conditions, apparently because of the low angle, low intensity sunlight.

Egg size and adult size

As a consequence of different provisioning strategies by their mothers, Alaskan caterpillars begin larval development 36% larger than Michigan caterpillars (neonate fresh mass = 1.33 vs. 0.98 mg), and because larval growth is nearly exponential, this proportional advantage is retained throughout larval development (Ayres 1991). Given equal growth rates, Alaskan *P. canadensis* could attain the same pupal mass with less development time solely as a result of differences in hatching mass.

Alaskan *P. canadensis* further shorten development

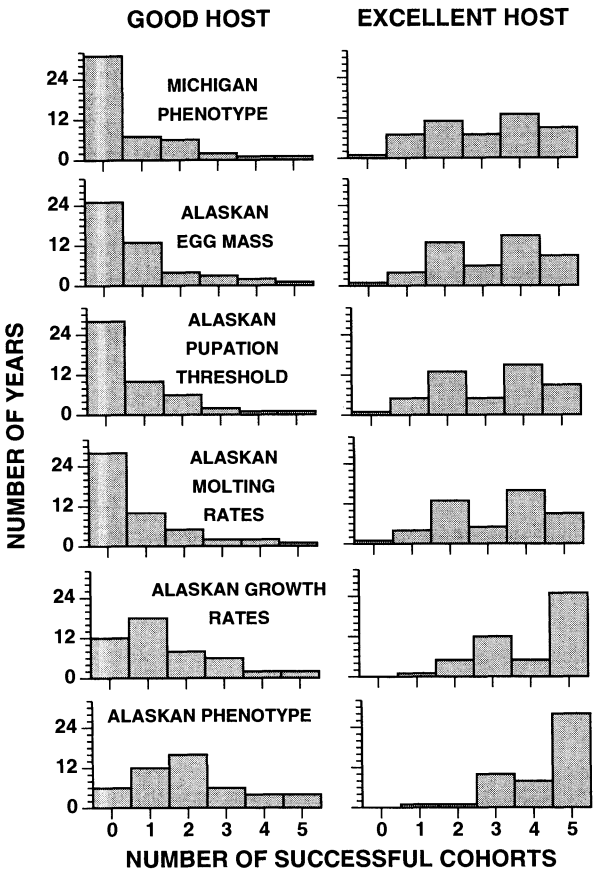

FIG. 13. The predicted developmental success of various *Papilio canadensis* phenotypes under two scenarios of host quality during 48 seasons in interior Alaska. Possible developmental success in each year ranged from zero successful cohorts (extinction) to five successful cohorts (no mortality due to incomplete development). Under two scenarios of host quality, we began with the Michigan phenotype (top), then changed egg mass, pupation threshold, molting rates, and growth rates (one at a time) to the condition of the Alaskan phenotype. Bottom figures show results with the four Alaskan adaptations combined.

time by terminating feeding and initiating pupation at a smaller mass. If we disregard the 12° treatment, where pupae were small and survival low, female Alaskan pupae averaged 814 mg fresh mass compared with 899 mg fresh mass for Michigan pupae (9% difference; Fig. 9). In a different experiment (Ayres 1991), Alaskan pupae were an average of 8% smaller than Michigan pupae. Field-captured butterflies demonstrated the same pattern. Female forewing length averaged 43.7 ± 0.80 mm in three summers in Alaska and 46.6 ± 0.88 mm in seven summers in Michigan (means ± 1 SD of yearly means, n = 10–20 butterflies per sample). Pupal mass is related to forewing length as $M_{pupa} = -528 + 31.05 \cdot \text{WING}$ ($r^2 = 0.55$; M. P. Ayres and J. M. Scriber, *unpublished data*), which indicates that the fresh mass of wild female pupae averaged 829 mg in Alaska vs. 919 mg in Michigan (10% smaller in Alaska).

Comparing the ecological worth of temperature adaptations

Four differences between Alaskan and Michigan populations of *P. canadensis* are interpretable as adaptations to short, cool subarctic summers: increased egg mass, reduced adult size, enhanced molting abilities at low temperatures, and enhanced growth rates at low temperatures. To evaluate the contribution of these hypothesized adaptations, individually and in toto, to swallowtail fitness in an Alaskan environment, we incorporated them into a temperature-driven development model that input 48 yr of daily temperature records from Fairbanks, Alaska and predicted the proportion of swallowtails that would successfully complete development each year.

The model evaluated five cohorts in each year, corresponding to phenologically early, intermediate, and late eggs. Each cohort in each year was represented by hypothetical neonates that hatched at a specified number of degree-days in that year, then developed at rates dictated by prevailing temperatures and stage-specific temperature responses until they reached the overwintering pupal stage or the season ended. The models incorporated two scenarios of host quality: a "good host" and an "excellent host" (based on *P. tremuloides* in 1988 and 1989, respectively; Fig. 3). The model is fully specified in Appendices 1 and 2.

The development model appeared to accurately mimic caterpillars in nature. During 1987–1992, the predicted dates of cohort initiation overlapped and followed the actual times of butterfly flight and matched the times when eggs were hatching in the field. In 1988, two wild larvae with known hatching dates (4 July and 8 July) survived until they were collected as fifth instars on 3 August (fresh mass of 936 and 696 mg, respectively). The actual development of both larvae fell between model predictions under the good host and excellent host scenarios. Careful validation requires more such comparisons, but few larvae survive that long in the field. Inaccuracies could arise if larval temperatures are typically higher than ambient due to basking (Lamb and Gerber 1985), if foraging larvae tend to select high quality leaves (Schultz 1983), or if growth at naturally fluctuating temperatures differs from growth at a constant temperature (Taylor and Shields 1990). Congruence between field and laboratory growth rates (see *Results: Basking success*) suggest that none of these introduce serious errors for *P. canadensis* in interior Alaska. Some parameter estimates, particularly early instar temperature responses (Stage 1), are not as robust as would be desirable, but this has little effect on comparisons among phenotypes.

Under a good host scenario, the Michigan phenotype was predicted to go extinct (no cohorts completed development) in 31 of 48 yr at Alaskan temperatures (Fig. 13). Changing egg size to that of the Alaskan phenotype eliminated 6 extinctions, changes in molting physiology and pupation threshold each eliminated 3 extinc-

TABLE 6. The value, in enhanced developmental success, of apparent adaptations in Alaskan *Papilio canadensis*. Percentage larval success indicates the average proportion of larvae predicted to complete development during 48 seasons in Alaska (based on results in Fig. 13 assuming relative sizes of 12, 32, 27, 18, and 11% for cohorts 1–5*). Alaskan (AK) attributes were introduced into the Michigan (MI) phenotype one at a time (egg size, pupation size, molting rates, and growth rates) and then simultaneously (Alaskan phenotype).

	Good host			Excellent host		
Phenotype	Percentage larval success	Number of extinctions†	Fitness relative to MI‡	Percentage larval success	Number of extinctions†	Fitness relative to MI‡
Michigan	14	31	1.00	65	1	1.00
MI with AK egg size	17	25	1.21	68	1	1.05
MI with AK pupation size	15	28	1.06	67	1	1.03
MI with AK molting rates	16	28	1.12	69	1	1.06
MI with AK growth rates	29	12	2.03	84	0	1.29
Alaskan	42	6	3.00	89	0	1.37

* Cohort sizes based on the emergence phenology of female butterflies in Alaska (median = 164 and 167 degree-days in 2 yr, 10–90% cumulative emergence = 137–209 degree-days), and assuming: a butterfly mortality rate of 11%/10 degree-days; constant egg production per degree-day among living butterflies; and 90 degree-days from oviposition to hatch (M. P. Ayres and J. M. Scriber, *unpublished data*).

† Number of times in 48 yr when even the earliest cohort failed to complete development.

‡ Larval success relative to the Michigan phenotype.

tions, and changes in fourth and fifth instar growth rates eliminated 19 extinctions. The Alaskan phenotype, which incorporates all these changes, was predicted to go extinct in only 6 of 48 yr. Under the excellent host scenario, extinctions were rare, but even the Alaskan phenotype still had failed cohorts in 20 of 48 yr (Fig. 13). This indicates that climate continues to exert hard selection (sensu Wallace 1968) even on the adapted phenotype feeding on the best host. Estimating the relative size of cohorts allowed a more precise assessment of this selection (Table 6).

On a good host, only 14% of the Michigan phenotypes, compared with 42% of the Alaskan phenotypes, were predicted to reach pupation in the time available (Table 6). Thus, the estimated fitness of the Alaskan phenotype was ≈3.0 times higher (42/14). On an excellent host, larval success was higher (65% and 89% for Michigan and Alaskan phenotypes), but selection against the Michigan phenotype would still have been very strong (relative fitness of the Alaskan population = 1.37). Under both host quality scenarios, changes in growth rate made the largest contribution to improved fitness. Changes in egg mass made the second largest contribution (on a good host, increased egg mass gave a fitness of 1.21 relative to the Michigan phenotype). Changes in the size at pupation had the smallest effect on fitness. All four hypothesized adaptations of the Alaskan population contributed to successful development during Alaskan summers.

Trade-offs

Because smaller pupae produce smaller, less fecund adults, there is a trade-off between the probability of completing development and fitness given successful development. Two days after adult eclosion, an Alaskan butterfly with 814 mg fresh mass as a pupa matured 21 eggs, while a butterfly from a pupa of 899 mg fresh mass matured 26 eggs (R. C. Lederhouse, *unpublished data*). Thus, the fitness cost for *P. canadensis* of pupating 9% smaller is ≈20%, compared with an apparent benefit of only 3–6% from Table 6. Actual benefits of pupating smaller are greater if there is larval mortality due to predation risks. In Alaska, fifth instar field predation rates averaged 27%/d in 1989, 2%/d in 1990, and 5%/d in 1991 (M. P. Ayres and J. M. Scriber, *unpublished data*). Under 1989 temperatures, lowering the pupation threshold shortened the fifth stadium of the middle cohort from 14.2 to 13.4 d. Given predation rates of 5%/d, the probability of surviving is only 4% higher with the lower pupation threshold—still insufficient to balance the costs of reduced fecundity. However, predation rates of 27%/d confer a 29% fitness advantage to fifth instars pupating 0.8 d sooner. Unusual extreme conditions, such as the outbreak of predatory wasps in 1988–1989 and a sequence of three cold summers during 1947–1949, have probably exerted disproportionately strong selection on Alaskan populations of *P. canadensis*. Occasional catastrophes may be more relevant than average conditions in the evolution of many species (Wigley 1985), especially those with annual (univoltine) life histories.

Assuming an equal investment of biomass in reproduction, Alaskan butterflies produce 36% fewer eggs than equal-sized Michigan butterflies. Compare this cost to an estimated benefit of 21% for the advantage of producing larger neonates (Table 6). The actual costs of producing larger eggs may not be as great if cool summer temperatures limit flight more than they limit vitellogenesis (if oviposition rate is not limited by egg production). Nonetheless, this discrepancy between costs and benefits again argues for the importance of occasional severe selection. Note that increased egg size eliminated six extinctions in 48 yr on good hosts (Table 6).

Northern distribution limits of P. canadensis

There was a dramatic effect of host quality on developmental success in Alaska: average larval success of 42% vs. 89% for Alaskan larvae under good host vs. excellent host scenarios (Table 6). Most potential hosts are worse than our good host scenario, and few are better. Fifth instar growth rates on *Populus tremuloides* in 1988 (the basis for the good host scenario) were second highest of nine host species tested (within 7% of the highest growth rates, Ayres 1991). Foliage as suitable for rapid growth as *P. tremuloides* in 1989 (the basis for the excellent host scenario) may not be available in all seasons. Interior Alaska contains many tree species on which *P. canadensis* can potentially produce viable adults (Ayres 1991), but on which growth rates are too low to allow successful development of any but the earliest larvae in the warmest years. Consequently, climate should select for more discriminating oviposition behavior in Alaskan populations of *P. canadensis* (Scriber and Lederhouse 1992). Species of *Salix* and *Betula* that would be suitable hosts for *P. canadensis* given a longer summer extend throughout the circumpolar regions, well beyond the occurrence of *P. canadensis*. We hypothesize that northern distribution limits are a joint function of climate and host quality. As summers become shorter, the number of potential hosts that can be realized becomes increasingly restricted until even the best hosts no longer allow development. If this is a general scenario, insect distributions may respond to climate change (Schneider 1993) almost immediately, without requiring changes in host distribution (Ayres 1993).

Regional specialization allows *P. canadensis* to maintain a broader distribution than would otherwise be possible. It is unlikely that a population with Michigan attributes could be sustained in the Fairbanks area (Fig. 13, Table 6). Yet even with geographic differentiation, many larvae apparently still fail to complete development during the short subarctic summers (estimated failure of 58% on a good host, Table 6). Evolutionary divergence in the thermal physiology of *P. canadensis* is substantial, but Alaskan swallowtails still do not approach the low temperature capabilities of other northern herbivores such as the tenthredinid sawfly, *Dineura virididorsata* (Matsuki and MacLean 1990), or the geometrid caterpillar, *Epirrita autumnata* (Ayres and MacLean 1987), which are capable of feeding, growing, and molting at temperatures just above 0°. Further adaptation in *P. canadensis* may be limited by gene flow from southern regions, or by older constraints dating from their tropical ancestry (Scriber 1973, Kukal et al. 1991, Scriber et al. 1991).

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APPENDIX 1

P. canadensis Development Model

Following hatch, the mass of non-molting larvae was incremented daily as $M_{t+1} = M_t \cdot e^{RGR \cdot t}$, where M_t equals mass at the start of the day and relative growth rate (RGR) was estimated as a function of temperature. When the average daily temperature was less than the developmental threshold, but the maximum was not, development was based on proportion of the day when temperatures were above the threshold (sine function follows Watanabe 1978). Larvae grew from their hatching mass to 99 mg fresh mass (Stage 1), then to 369 mg fresh mass at fourth instar growth rates (Stage 2).

Then growth ceased until completion of the fourth molt (Stage 3). With their mass depreciated by exuvial and respiratory losses during molt, larvae resumed growth at fifth instar rates until they reached a size threshold for pupation (Stage 4). Successful cohorts completed feeding prior to leaf senescence (15 September) and became cold-tolerant diapausing pupae (completed Stage 5) before the onset of winter (1 October).

The fresh mass of hatching neonates was set at 0.98 or 1.33 mg representing Michigan and Alaskan phenotypes, respectively (Ayres 1991). Relative growth rates during the penultimate (RGR_4) and final instars (RGR_5) were calculated for each population as a function of temperature, using linear interpolation between measured temperatures and from 12°C to a developmental threshold of 7.25° (based on *Populus tremuloides* data in Fig. 3). Molting rates for the penultimate and final molt were calculated for each population as a function of temperature, using linear interpolation between measured temperatures and from 12° to a developmental threshold of 9.5° (based on data in Figs. 7 and 8). The size threshold for female pupation was set at 899 or 814 mg fresh pupal mass (Fig. 9).

Growth rates during stadia 1–3 (Stage 1) were modeled using the same functions for all swallowtail phenotypes. Growth rate at 24° during stadia 1–3 was set at 0.270 $mg \cdot mg^{-1} \cdot d^{-1}$ for the good host scenario (= growth rate for this stage on *Populus tremuloides* in 1988; Ayres 1991) and 0.310 $mg \cdot mg^{-1} \cdot d^{-1}$ for the excellent host scenario (= highest growth rate among nine hosts in 1988; Ayres 1991). Stage 1 temperature responses assume the same Q_{10}s as fourth instars feeding on *Populus tremuloides* in 1988 (good host) or 1989 (excellent host).

APPENDIX 2

Summary of Model Parameters

A. Phenology
First day of season to begin accumulating thermal sums: 1 April.
Degree-days (10°C base) of neonate hatch for cohorts 1–5: 240, 280, 320, 360, 400.
Last day of permissible growth (Stages 1–4): 14 September.
Last day of permissible prepupation (Stage 5): 30 September.

B. Fresh mass of hatching neonates
Michigan phenotype: 0.98 mg.
Alaska phenotype: 1.33 mg.

C. Stage 1, Instars 1–3
Relative growth rates at 12°, 18°, 24°, and 30°C:
Good host: 0.083, 0.116, 0.270, 0.280 $mg \cdot mg^{-1} \cdot d^{-1}$.
Excellent host: 0.099, 0.223, 0.310, 0.416 $mg \cdot mg^{-1} \cdot d^{-1}$.

D. Stage 2, Instar 4
Initial mass: 99 mg.
Relative growth rates at 12°, 18°, 24°, and 30°C:
Michigan phenotype, good host: 0.104, 0.161, 0.449, 0.533 $mg \cdot mg^{-1} \cdot d^{-1}$.
Alaska phenotype, good host: 0.139, 0.174, 0.334, 0.279 $mg \cdot mg^{-1} \cdot d^{-1}$.
Michigan phenotype, excellent host: 0.109, 0.268, 0.350, 0.456 $mg \cdot mg^{-1} \cdot d^{-1}$.
Alaska phenotype, excellent host: 0.146, 0.305, 0.448, 0.617 $mg \cdot mg^{-1} \cdot d^{-1}$.
Final mass: 369 mg.

E. Stage 3, Molt 4 (Instar 4 to Instar 5)
Molting rates at 12°, 18°, 24°, and 30°C:
Michigan phenotype: 12.3, 32.1, 52.6, 84.8%/d.
Alaska phenotype: 15.2, 48.1, 60.2, 116.3%/d.

F. Stage 4, Instar 5
Initial mass: 348 mg.
Relative growth rates at 12°, 18°, 24°, and 30°C:
Michigan phenotype, good host: 0.067, 0.127, 0.382, 0.369 $mg \cdot mg^{-1} \cdot d^{-1}$.
Alaska phenotype, good host: 0.099, 0.181, 0.345, 0.341 $mg \cdot mg^{-1} \cdot d^{-1}$.
Michigan phenotype, excellent host: 0.069, 0.161, 0.255, 0.375 $mg \cdot mg^{-1} \cdot d^{-1}$.
Alaska phenotype, excellent host: 0.142, 0.214, 0.317, 0.532 $mg \cdot mg^{-1} \cdot d^{-1}$.
Final mass
Michigan phenotype: 1798 mg (corresponds to female pupal mass of 899 mg).
Alaska phenotype: 1628 mg (corresponds to female pupal mass of 814 mg).

G. Stage 5, Molt 5 (Instar 5 to Pupa)
Molting rates at 12°, 18°, 24°, and 30°C:
Michigan phenotype: 5.61, 16.3, 18.3, 34.8%/d.
Alaska phenotype: 8.45, 23.2, 23.5, 32.3%/d.

H. Minimum developmental thresholds
Growth (Stages 1, 2, and 4): 7.25°C.
Molting (Stages 3 and 5): 9.50°C.