

GROWTH SEASON CONSTRAINTS IN CLIMATIC COLD POCKETS: TOLERANCE OF SUBFREEZING TEMPERATURES AND COMPENSATORY GROWTH BY TIGER SWALLOWTAIL BUTTERFLY LARVAE (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT.— The combination of limited seasonal thermal unit accumulations (degree days) and freezing mortality or non-freezing cryoinjury from late spring/early fall freezes in climatically constrained areas has been hypothesized to be major determining factors for geographic range limits and degree of polyphagy in herbivorous insects. We test the hypothesis that cold stress such as from sudden freezes has direct or indirect (delayed) negative impact on egg and larval survival and growth of tiger swallowtail butterflies, *Papilio glaucus* Linnaeus. Nine treatment regimes with three temperatures (-14°C, -8°C, 4°C) and three exposure durations (8h, 24h, or 48h) were tested using 14 different butterfly families. Negative effects were observed for egg viability, 1st instar, 2nd instar, 3rd instar larval survival and growth subsequent to cold treatments, with more serious impact at colder temperatures and longer durations. These results support the hypothesis that, if severe, late spring freezes can select strongly against these vulnerable, non-diapausing stages. However, numerous physiological and ecological adaptations are known to exist for *Papilio* eggs, larvae, and pupae, which maximize successful completion of the generation before winter. A new one reported here is faster subsequent growth rates in surviving larvae which were exposed to the cold stress for the longest duration.

KEY WORDS: freeze tolerance, growth, Nearctic, North America, *Papilio*, physiology, seasonality, thermal constraints.

The seasonal total thermal units (degree days) above the developmental threshold for growth of insect larvae is a fundamental factor determining the voltinism patterns and host plant preferences across latitudinal gradients (Lederhouse and Scriber, 1992; Ayres and Scriber, 1994; Cockrell *et al.*, 1994) as well as in local geographically mosaic "cold pockets" (Scriber, 1996a). For univoltine herbivorous insects in the boreal forest, a number of cold/freezing adaptations may be essential to winter survival (Danks 1987; Kukul *et al.*, 1988, 1991; Lee and Denlinger, 1991; Leather *et al.*, 1993; Storey and Storey, 1996; Strathdee and Bale, 1998). One of these adaptations in ectothermic insects (including *Papilio glaucus* Linnaeus and *P. canadensis* Rothschild & Jordan) is a reduction in pupal/adult size with increased latitude (Scriber, 1994; see also Nylin and Svård, 1991; Mousseau, 1997).

In the Canadian tiger swallowtail, *Papilio canadensis*, a number of adaptations for successful completion of a single generation in thermally constrained areas (e.g., Alaska compared to most of Michigan) each season include the production of larger eggs, shorter larval molting durations, faster larval growth rates at colder temperatures, and pupation at smaller sizes (Ayres and Scriber, 1994), as well as selection of the most nutritious host plants (Scriber and Lederhouse, 1992). In the cold pocket areas of northern Michigan and in the upper peninsula north of Wisconsin, there are also traits in this *P. canadensis* species that suggest an intense selection pressure for rapid completion of the larval stages. These include: photoperiodically insensitive (obligate) diapause (Rockey *et al.*, 1987; Scriber, 1988), smaller female adults (due to pupation at small sizes; Scriber, 1994) and selection of the most nutritious hostplant leaves (*Fraxinus* spp., Oleaceae) in the seasonally coolest areas or areas with the shortest freeze-free summers (Scriber, 1996a). It is presumed that the non-diapausing egg and larval stages of tiger swallowtail butterflies would be particularly vulnerable to freezing injury and/or non-freezing cryoinjury. This is an assumption that is based on the observation that supercooling and cold

acclimation are lowest in the summer for several reasons (Danks, 1978, 1987; Leather *et al.*, 1993), including the fact that larvae with food in their guts have a significantly poorer supercooling point than when gut contents are evacuated (Bale, 1980; Sømme, 1982; Baust and Rojas, 1985).

While both *P. canadensis* and *P. glaucus* can, as diapausing pupae, survive sub-freezing winters under the snow in Alaska (Kukul *et al.*, 1991), to our knowledge, the tolerance of freezing temperatures by eggs and larvae have never been examined. Hard freezes (-2°C) occur late into the spring (late June) and very early in the fall (mid-August) in these cold pockets of Michigan (Eichenlaub *et al.*, 1990). It is possible that eggs, neonate larvae and even larger late instar larvae may be killed or severely damaged by such local weather conditions. If so, this would result in even more protracted (thermally constrained) larval growth season (phenological window) in the cold pockets than predicted by seasonal degree day accumulations (Scriber and Gage, 1995). We address this possibility of cryoinjury or death using laboratory (controlled environment) chambers with eggs and larvae from 14 different tiger swallowtail butterfly mothers.

Methods

Females of *Papilio glaucus* (collected in Clarke County, Georgia) were set up in standard multi-choice rotating oviposition arenas using the methods of Scriber (1993). Female butterflies were fed honey water and eö we#ected daily. Eggs were stored in standard conditions at 25°C (18:6 photoperiod) for larval eclosion or else used directly in the freezing treatments. *Papilio glaucus* eggs and larvae were obtained from a southern population (Clarke County, Georgia) in order to maximize the probability that potential negative effects of sub-freezing regimes on *Papilio* would be detected. We also did not have any *P. canadensis* concurrently available for a parallel study.

Forty to sixty eggs per female from 6 different isofemale lines (number codes 12555, 12560, 12574, 12577, 12580, and 12606) were exposed for 8, 24 or 48 hours in darkness to constant temperatures of -14°C, -8°C, or 4°C. The number of surviving individuals

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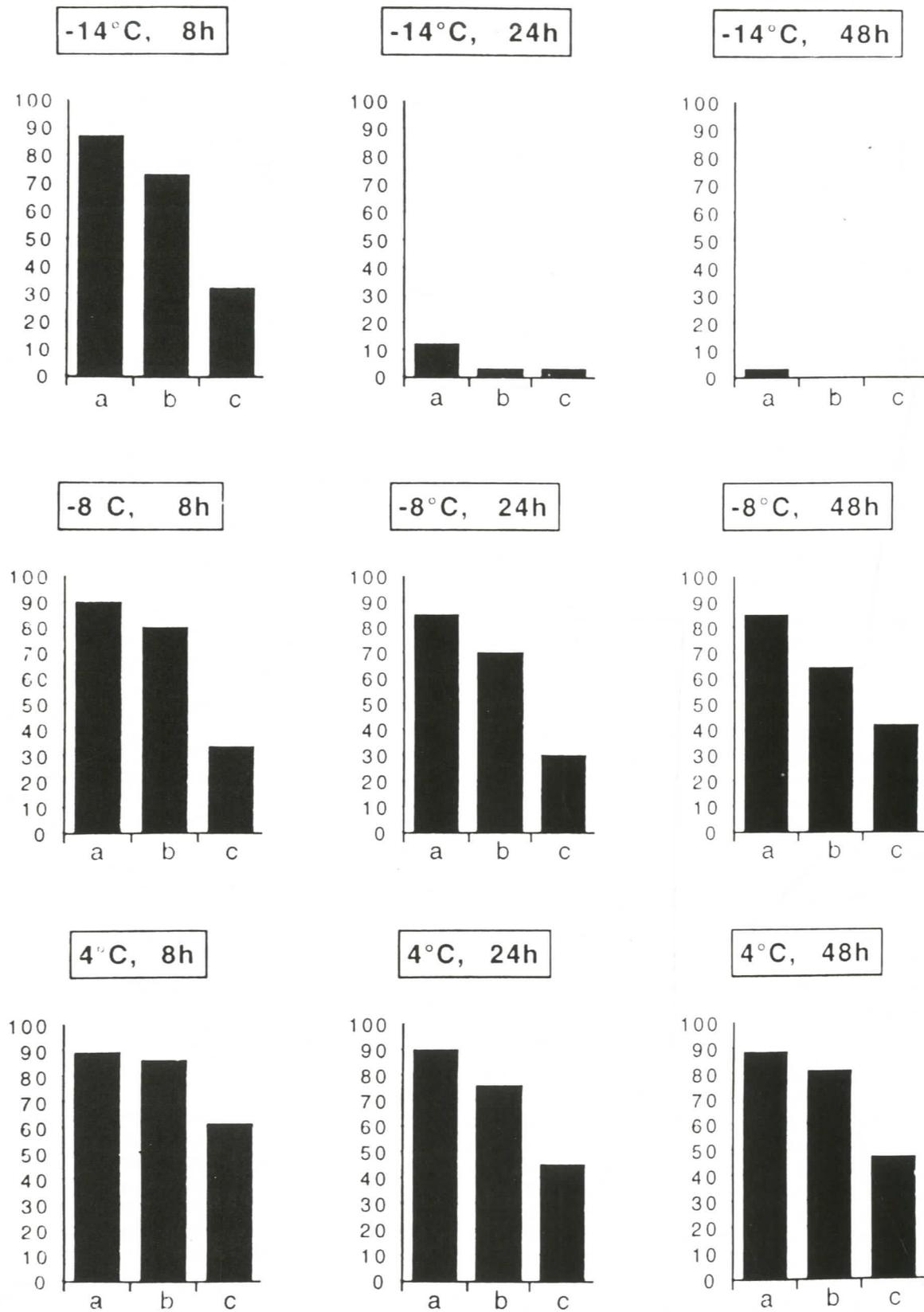


Fig. 1. Mean survival in percent a) at hatch out, b) completion of the 1st larval instar, and c) completion of the 4th (penultimate) larval instar of 6 *Papilio glaucus* families after cold stress to the eggs at 3 temperatures (-14°C, -8°C, and 4°C) and 3 durations (8, 24 and 48 hours) (East Lansing, MI 1996).

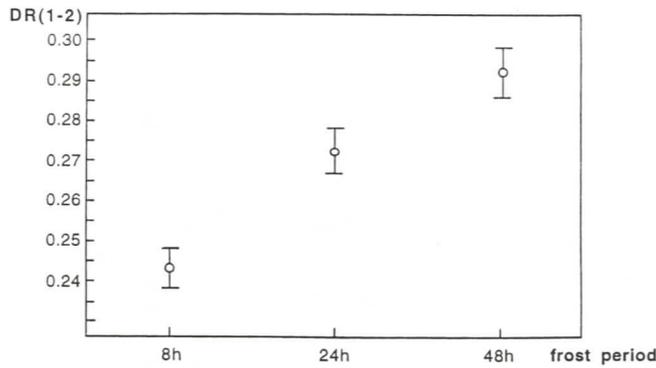


Fig. 2. Developmental rates (mean \pm se) of *Papilio glaucus* first instar larvae after having survived cold stress for 8, 24, or 48 hours at the egg stage (East Lansing, MI, 1996).

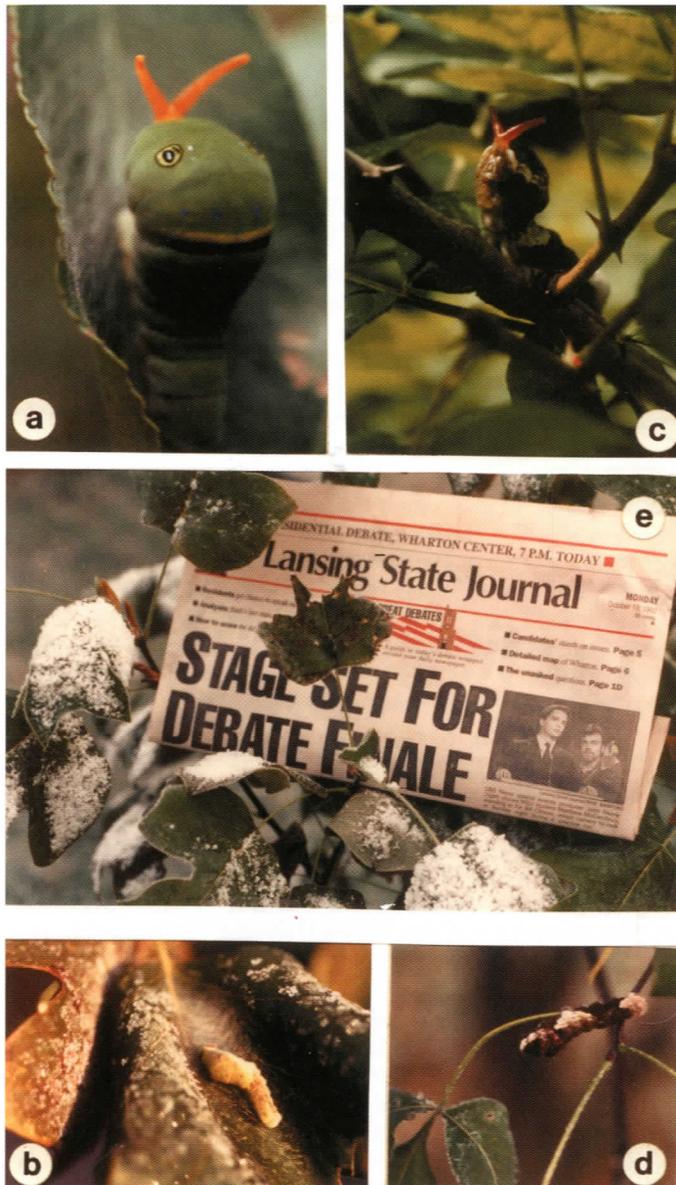


Fig. 3. Natural weather-induced mortality was 100% for all of the 4th and 5th instar tropical, Rutaceae-feeding *Papilio cresphontes* (c and d), however 4th and 5th instar *Papilio glaucus* survived this 8-10 hours at subfreezing temperatures with snow (a and b) on the morning of October 19, 1992 (e, Okemos, MI).

and the duration of the first instar larvae fed black cherry leaves (*Prunus serotina* Ehrh., Rosaceae) were recorded daily for 8 days (at 25°C and 18:6 photoperiod) after exposure as eggs to the 3 temperature regimes. Survival and growth rates through later instars were also carefully monitored for individuals of these females which were subjected to these treatments as eggs.

In a parallel study, larvae of different instar (developmental) stages were subjected to the same 3 temperatures for 8 or 24 hours as with the eggs. The offspring of 8 different females (codes 12412, 12442, 12469, 12475, 12508, 12509, 12514, 12577) were distributed evenly across the 3 temperature treatments, but fewer were used at the 8 hour duration. Survival for 7 or 8 days after one of the chill/freeze treatments was recorded for first instar larvae and molting or second instar larvae fed black cherry leaves at 25°C with an 18:6 photoperiod (Fig. 5).

Results

The negative impacts on neonate (1st instar) larvae, molting (1st to 2nd) or 2nd instar larvae, and 3rd instar larvae were clearly evident at -14°C, where none of the larvae exposed for 8 or 24 hours survived the next 7 days (Fig. 5). The same negative impacts were observed for the -8°C treatment where a very low percentage of larvae exposed for 24 hours (-8°C) survived. However, 8 hours of exposure to -8°C had significantly reduced impact on larval survival relative to the 24 and 48 hour exposures at this temperature (Fig. 5).

It was surprising that the non-freezing (chill) treatment 4°C also had some casualties over the 7 days post-treatment. While neonate (1st instar) deaths do normally average 10-20% over a six day period in standard 25°C laboratory rearing temperatures on black cherry (Scriber *et al.*, 1991), the mortality in the 24 hour (4°C) exposure of non-freezing chill temperatures (4°C), may take a significant toll on subsequent larval survival and development (Fig. 5).

To assess the long term damage of chilling/freezing of eggs, we conducted a parallel study of 6 different isofemale broods with the same 9 treatments of temperature and duration of exposure. Egg viability after 4°C chill was excellent at 90%, and not affected by the duration of exposure (bottom histograms of Fig. 1), however there was a progressive decline in embryo survival and hatch with decreased temperatures and increased exposure durations at those temperatures (-8°C and -14°C, Fig. 1).

When the resulting larvae were followed through 8 days of feeding on black cherry leaves at 25°C and 18:6 photoperiod a similar pattern of survival as seen in the eggs of 9 treatments was observed (middle bars in histograms of Fig. 1). Subsequent survival and growth after about 3 weeks, through the 4th instar to the 5th instar, showed an exponential decay type of decline at -14°C for 8, 24, and 48 hour exposures weeks earlier. However, no differences in overall survival (to 5th instar) percentage was observed after -8°C exposures of 8, 24, and 48 hours, which were also only slightly lower than the corresponding 4°C treatment larvae.

One very interesting result was observed in the growth rate of the larvae surviving these egg chill/freeze experimental treatments: the larvae surviving the longest cold stress period grew the fastest (Fig. 2).

Discussion

It seems clear that increased cold stress has increasingly severe effects on survival of *Papilio glaucus* eggs, neonates, and mid-instar larvae. Mortality caused by exposures to -14°C and -8°C for 24 hours was virtually complete (Fig. 5). While this result is not particularly surprising, it is interesting that even at the non-freezing chill treatment (4°C) some neonate mortality appeared (Fig. 5).

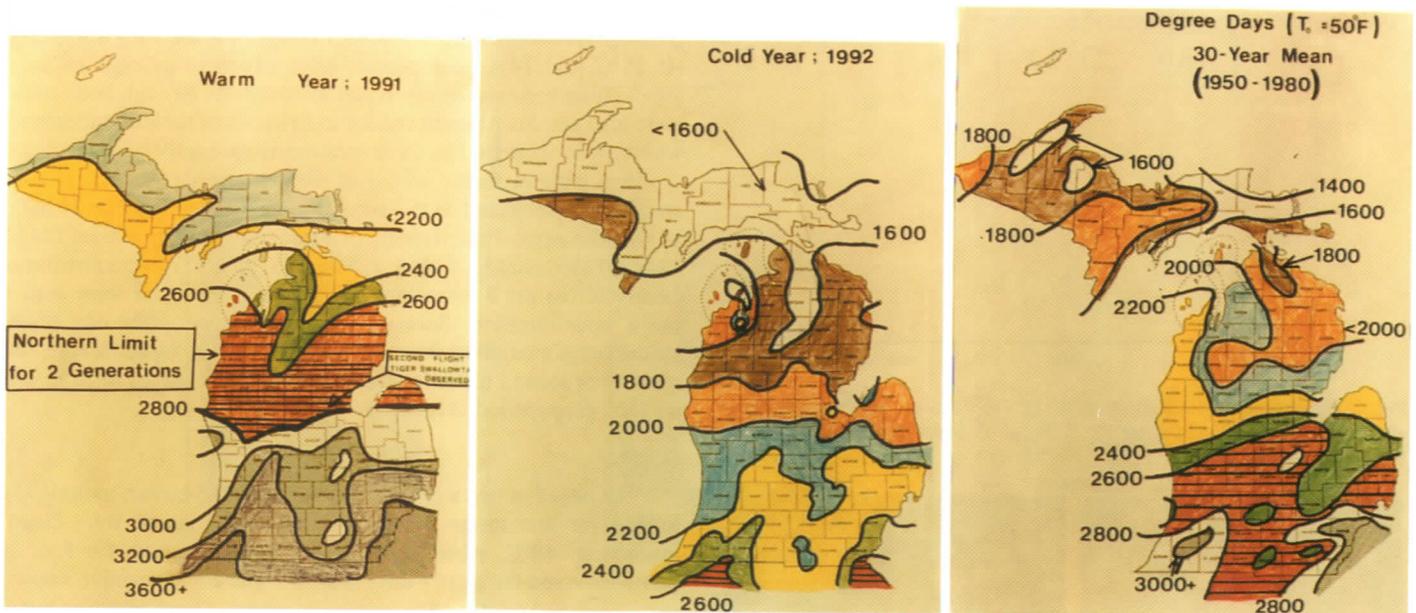


Fig. 4. The total seasonal thermal unit accumulations (Mar 1 to Oct 30 degree days above a base 50°F) for the state of Michigan. The 3-4 years directly preceding the very cold 1992 season had enhanced northern movement/abundance of the bivoltine *P. cressphontes* (giant swallowtail) populations, which were essentially killed out of Michigan by the October 19th freeze in 1992 (see also Fig. 3). The red color indicates the northern limits of 2nd-generations (bivoltinism) on good hostplants.

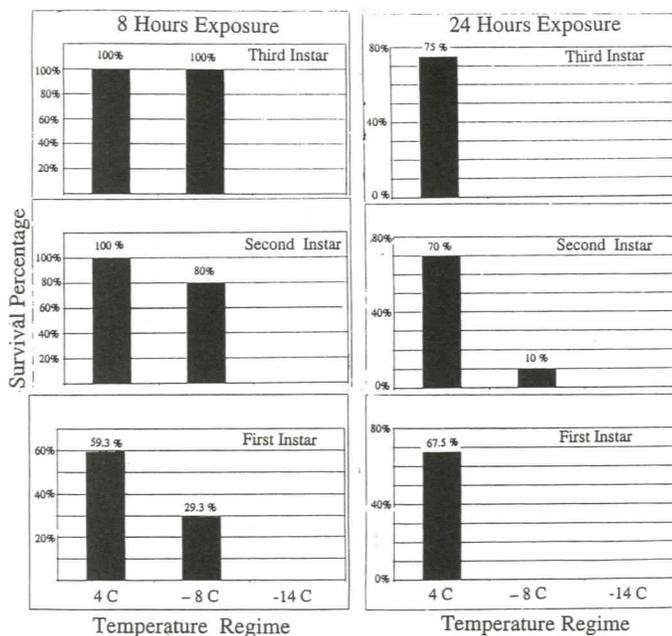


Fig. 5. The mean survival of 5 populations of *P. glaucus* as a function of 3 temperature regimes (4°C, -8°C and -14°C, left to right) and 2 durations (8h and 24h, left to right) for 1st, 2nd and 3rd instar larvae.

Long term survival to 5th instars was increasingly suppressed at -8°C and -14°C for survivors of the egg chill experiment for all 3 durations of exposure (Fig. 1).

It therefore seems entirely feasible that late spring freezes and early fall freezes could naturally result in significant (if not total) mortality for tiger swallowtail (*Papilio*) larvae at both ends of the growing season in the field. One such hard freeze in the fall (October 21, 1992; Fig. 3) killed all *Papilio cressphontes* Cramer 4th and 5th instar larvae (n=13) on hoptree (*Ptelea trifoliata* L., Rutaceae) in Okemos, Michigan, USA. Since this was the second

coldest growing season on record (Fig. 4), the second generation had not yet pupated and the total mortality from this larvae freezing was likely to have caused the disappearance of this tropical Rutaceae-feeding swallowtail species from the entire southern half of Michigan for the next 3 years (Scriber and Gage, 1995). Warmer years during 1995-99 have brought breeding populations of the giant swallowtail butterfly (*P. cressphontes*) back into southwestern Michigan for the first time in 1998 (J. M. Scriber and M. Watanabe, pers. observ.). In contrast, at the same time, and in the same area, less than 50m from the 1992 *Papilio cressphontes* annihilation, larvae of *P. glaucus* (4th and 5th instars) were also apparently frozen by the October severe freeze (-6°C which lasted for 10-12 hrs). However, unlike the case with the giant swallowtail larvae, some of these tiger swallowtail larvae (3 of 8) survived, and as expected, the normal flights of adults in this area occurred the next summer in 1993 (Scriber and Gage, 1995; Fig. 3 b-d).

There are likely to be local geographic, as well as interspecific differences, in freeze tolerance among swallowtail butterfly populations. Our use of a Georgia population of *P. glaucus* in these experiments was to assure us of observing negative impacts of cold stress if they occur in the species. We hope to follow up these studies with studies of northern *P. glaucus* populations as well as populations of the Canadian swallowtail (*P. canadensis*) from the "cold pockets" of Michigan. It is still possible that these populations are better adapted to cold stress and not affected by late spring freezes or early fall freezes as hypothesized (Scriber, 1994, 1996a).

The observation that survivors of the longer periods of cold stress exposure grew faster than those from shorter exposure periods (Fig. 2) is fascinating. This plasticity could be a compensatory response to enhance the probability of successful completion of the generation. If genetic variation exists, we should expect such increases in metabolic growth rates to be selected for especially in chronically protracted or generally cool climatic regimes. Ayres (1991) and Ayres and Scriber (1994) found a general elevation of metabolic activity in about 36% of *P. canadensis* larvae from Alaska at all temperatures in comparison to conspecifics from Michigan. The mechanisms by which such enhanced growth rates

at cool temperatures, or after cold stress periods as we have observed here, is not understood (Partridge and French, 1996; Van Voorhies, 1997). However, the advantages for successful completion of the generation before serious freezing conditions occur could certainly be very significant. Hybrid vigor of *P. canadensis* and *P. glaucus* in hybrid larvae as expressed in lower development thresholds than either parent may also provide adaptive advantages (Scriber *et al.*, 2001).

The cold pocket regions of northern Michigan experience brief freezes as late into the spring and "summer" as June 30th, in one year out of 4, or July 10th in 1 year out of 10 (Eichenlaub *et al.* 1990). The "fall" freezes begin as early as August 25th in 1 year out of 4 and as early as August 15th in 1 year out of 10. The ability of eggs and larvae to tolerate freezing temperatures would greatly enhance the probability of the thermally constrained generation surviving the growing season. The larval developmental durations of *P. canadensis* from 4th instar to pupae on a single host plant (*Populus tremuloides* Michx., Salicaceae) ranges from 15 days at 30°C to 58 days at 12°C, with the 2 molting durations comprising more than half of this time (Ayres and Scriber, 1994). While not included in the multi-temperature study above, the first 3 instars would also presumably take longer at the 12°C and 18°C temperatures than at 24°C and 30°C, amplifying the differences in total larval durations. Complete larval developmental studies at fixed temperatures simulating the average daily growing season in northern Michigan were previously conducted on various potential hostplant species. The total larval durations (at the thermoperiod of 23:5/19, 5°C during the 16h/8h photo/scotophase) ranged from 32-34 days on black cherry and balsam poplar to more than 40 days on paper birch, white ash and mountain ash (Scriber, 1991). Additional days required for egg hatch may add 4 or 5 days to 15 or 20 days, depending on the temperature. Furthermore, some hostplant species such as Alaskan paper birch, *Betula resinifera* (Betulaceae), are marginally suitable for larval growth due to allelochemicals or nutritional deficiencies, and larval growth rate does not even increase with temperature increases from 12°C to 30°C, whereas others such as balsam poplar, *Populus balsamifera*, increase approximately 500% over that temperature range (Lederhouse *et al.*, 1995). Whether a larva can complete development under severe seasonal thermal constraints depends on an interaction of all of these adaptive traits in egg, larvae, pupae, and adults (Ayres and Scriber, 1994; Scriber, 1994) including choice of the most nutritious hostplants (Scriber, 1996).

Even with successful achievement of the diapausing pupal stage, severe winter conditions combined with lack of snow cover could result in freezing death or significant non-freezing cryoinjuries (Bale 1994) since neither *P. canadensis* nor *P. glaucus* are freeze tolerant (Kukal *et al.*, 1991). While they lack glycerol, other cryoprotectants may explain the ability of some acclimatized pupae of both species to survive an Alaskan winter with 7 consecutive days at -20°C and 19 consecutive days at -15°C (Kukal *et al.*, 1991).

Our severe temperature treatments for eggs and larvae in this study (-14°C, -8°C, and 4°C) were not accompanied by an acclimatizing period prior to the immersion into the experimental cold stress conditions. It is possible that physiological adjustments induced by natural acclimatization could moderate the larval mortality results observed in our laboratory studies. Nonetheless, it seems that direct freezing mortality and non-freezing cryoinjury observed in these studies confirms the possibility that sudden, late spring freezes could provide a significant natural selection pressure against exposed populations of *P. glaucus*, and probably *P. canadensis*, as well.

The northern distribution of *P. glaucus* may be determined largely by limited ability to survive an Arctic winter compared to *P.*

canadensis (Kukal *et al.*, 1991) combined with the need for longer growing seasons. This thermal constraint may be related to fewer seasonal thermal unit accumulations and/or a limited number of freeze-free days between the last spring and first fall freezes (Scriber, 1996a). Such short growing seasons and freezes, interacting with differential hostplant quality, may explain the local cold pocket adaptations (Scriber, 1994, 1996a) as well as the northern distribution limits of both species of tiger swallowtail butterflies (Scriber, 1996b). Such stress at species range boundaries provides unique opportunities to assess adaptations and ecological trade-offs that affect evolutionary change (Hoffman and Parsons, 1997).

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LITERATURE CITED

- Ayres, M. P.
1991. Adaptation and constraint in *Papilio canadensis*: Geographic variation in nutritional physiology and temperature responses. Ph.D. Diss. East Lansing: Dept. Entomology, Michigan State Univ. 107pp.
- Ayres, M. P., and J. M. Scriber
1994. Local adaptations to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecol. Monog.* (Tempe), 64:465-482.
- Bale, J. S.
1980. Seasonal variation in cold hardiness of the adult beech leaf mining weevil, *Rhynchaenus fagi* L. in Great Britain. *Cryo Lett.* (Cambridge), 1:372-383.
1994. Indices of cold tolerance in an era of climate change. In S. R. Leather, K. F. A. Walters, N. J. Mills, and A. D. Watt (eds.), *Individuals, Populations and Patterns in Ecology*, 45-60. London: Intercept. 491pp.
- Baust, J. G., and R. R. Rojas.
1985. Review-insect cold hardiness: facts and fancy. *J. Ins. Physiol.* (Oxford), 31:755-759.
- Cockrell, B. J., S. B. Malcolm, and L. P. Brower
1994. Time, temperature, and latitudinal constraints on the annual colonization of eastern North America by the monarch butterfly. In S. B. Malcolm and M. P. Zalucki (eds.), *Biology and Conservation of the Monarch Butterfly*, 233-251. Los Angeles: Nat. Hist. Mus. Los Angeles Co.
- Danks, H. V.
1978. Modes of seasonal adaptation in insects. 1. Winter survival. *Can. Ent.* (Ottawa), 110:1167-1205.
1987. Insect dormancy: An ecological perspective. In *Biological Survey of Canada (Terrestrial Arthropods)*. Ottawa. 439pp.
- Eichenlaub, V. L., J. R. Harman, F. V. Nurnberger, and H. J. Stolle
1990. *The Climatic Atlas of Michigan*. Notre Dame: Univ. Notre Dame Pr. 165pp.
- Hoffman, A. A., and P. A. Parsons
1997. *Extreme Environmental Change and Evolution*. Cambridge: Cambridge Univ. Press. 259pp.
- Kukal, O., A. S. Serianni, and J. G. Duman
1988. Glycerol metabolism in a freeze-tolerant Arctic insect: an in vivo ¹³C NMR study. *J. Comp. Physiol.* (London), (B) 158:175-183.
- Kukal, O., M. P. Ayres, and J. M. Scriber
1991. Cold tolerance of pupae in relation to the distribution of tiger swallow tails. *Can. J. Zool.* (Ottawa), 69:3028-3037.
- Leather, S. R., K. F. A. Walters, and J. S. Bale
1993. *The Ecology of Insect Overwintering*. Cambridge: Cambridge Univ. Pr. 255pp.

- Lee, R. E., and D. L. Denlinger
1991. *Insects at Low Temperature*. London: Chapman and Hall. 513pp.
- Lederhouse, R. C., M. P. Ayres and J. M. Scriber
1995. Physiological and behavioral adaptations to variable thermal environments in North American swallowtail butterflies. In J. M. Scriber, Y. Tsubaki, and R. C. Lederhouse (eds.), *Swallowtail Butterflies: their Ecological and Evolutionary Biology*, 71-82. Gainesville: Scientific Publ.
- Mousseau, T.
1997. Ectotherms follow the converse to Bergman's rule. *Evol.* (London), 51: 630-32.
- Nylin, S. and L. Svård
1991. Latitudinal patterns in size of European butterflies. *Holarc. Ecol.* (Copenhagen), 14:192-202.
- Partridge, L., and V. French
1996. Thermal evolution of ectotherm body size: why get big in the cold? In I. A. Johnston and A. F. Bennett (eds.), *Animals and Temperature: Phenotypic and Evolutionary Adaptation*, 265-292. Cambridge: Cambridge Univ. Pr. 419pp.
- Rockey, S. J., J. H. Hainze, and J. M. Scriber
1987a. Evidence of a sex-linked diapause response in three subspecies of the eastern tiger swallowtail, *Papilio glaucus* (Lepidoptera: Papilionidae). *Physiol. Ent.* (London), 12:181-184.
1987b. A latitudinal and obligatory diapause response in three subspecies of the eastern tiger swallowtail, *Papilio glaucus* (Lepidoptera: Papilionidae). *Amer. Midl. Nat.* (Notre Dame), 118:162-168.
- Scriber, J. M.
1988a. Tale of the tiger: Beringial biogeography, binomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies. In K. C. Spencer (ed.), *Chemical Mediation of Coevolution*, 241-301. New York: Academic Pr.
1991. Differential suitability of 12 Great Lakes tree species for *Papilio canadensis* (Lepidoptera: Papilionidae) larval survival and growth. *Gt. Lakes Ent.* (East Lansing), 24:239-252.
1993. Absence of behavioral induction in multi-choice oviposition preference studies with a generalist butterfly species, *Papilio glaucus*. *Gt. Lakes Ent.* (East Lansing), 28:81-95.
1994. Climatic legacies and sex chromosomes: latitudinal patterns of voltinism, diapause size and host-plant selection in 2 species of swallowtail butterflies at their hybrid zone. In H. V. Danks (ed.), *Insect Life-cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control*, 133-171. Dordrecht: Kluwer Acad. Publ.
1996a. A new cold pocket hypothesis to explain local host preference shifts in *Papilio canadensis*. In 9th Intern. Symp. Insects and Host Plants. *Ent. Exp. Appl.* (Amsterdam), 80:315-319.
1996b. Tiger tales: natural history of native North American swallowtails. *Amer. Ent.* (Lanham), 42:19-32.
- Scriber, J. M., M. D. Deering, and A. Stump
2001. Hybrid zone ecology: geographic and genetic distances influence behavioral, biochemical and ecological trait clines. In C. Boggs, P. Brakefield, and W. Watt (eds.), *Butterfly Evolutionary Ecology*. New Haven: Yale Univ. Pr.
- Scriber, J. M., and S. Gage.
1995. Pollution and global climate change: Plant ecotones, butterfly hybrid zones, and biodiversity. In J. M. Scriber, Y. Tsubaki, and R. C. Lederhouse (eds.), *Swallowtail Butterflies: their Ecology and Evolutionary Biology*, 319-344. Gainesville: Scientific Publ.
- Scriber, J. M., and R. C. Lederhouse
1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores. In M. R. Hunter, T. Ohgushi, and P. W. Price (eds.), *Effects of Resource Distribution on Animal-Plant Interactions*, 429-466. New York: Academic Pr.
- Scriber, J. M., R. C. Lederhouse, and R. Hagen
1991. Foodplants and evolution within the *Papilio glaucus* and *Papilio troilus* species groups (Lepidoptera: Papilionidae). In P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson (eds.), *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, 341-373. New York: John Wiley.
- Sømme, L.
1982. Supercooling and winter survival in terrestrial arthropods. *Comp. Biochem. Physiol.* (Oxford), 73A:519-543.
- Strathdee, A. T., and J. S. Bale
1998. Insect ecology in arctic environments. *Ann. Rev. Ent.* (Palo Alto), 43: 85-106.
- Storey, K. B., and J. M. Storey
1996. Natural freezing survival in animals. *Ann. Rev. Ent.* (Palo Alto), 27: 365-386.
- Van Voorhies, W. A.
1997. On the adaptive nature of Bergman size clines: a reply to Mousseau, Partridge and Coyne. *Evol.* (London), 51:635-641.