

Host plant adaptation and the evolution of thermal reaction norms

Sarah E. Diamond · Joel G. Kingsolver

Received: 25 July 2011 / Accepted: 8 November 2011 / Published online: 30 November 2011
© Springer-Verlag 2011

Abstract For most ectotherms, increasing the rearing temperature reduces the final (adult) body size, producing a negative slope for the thermal reaction norm. Recent studies show that this relationship may be reversed under conditions of low resource quality, producing a positive slope for the thermal reaction norm. If populations or species differ in the degree of evolutionary adaptation to a resource, how does this differential adaptation alter their thermal reaction norms? We used a common garden experiment with the tobacco hornworm, *Manduca sexta*, to address this question. We examined the thermal reaction norms for body size of two populations of *M. sexta* that differ in their evolutionary exposures to an atypical, low-quality resource (devil's claw; *Proboscidea louisianica*), but have comparable exposures to a typical, high-quality resource (tobacco; *Nicotiana tabacum*). Both populations had increased mean larval mortalities and development times when reared on devil's claw compared with tobacco, but the magnitudes of these increases differed between populations. Both populations had similar, negatively sloped thermal reaction norms on the typical, high-quality resource (tobacco), but had divergent, non-negative thermal reaction norms on the atypical, low-quality resource

(devil's claw): the population with the longer evolutionary history of exposure to the atypical resource exhibited a flat (rather than positive) reaction norm. These results suggest that population differences in host plant adaptation can predictably influence the slopes of thermal reaction norms.

Keywords *Manduca sexta* · Phenotypic plasticity · Temperature · Host plant adaptation · Resource quality

Introduction

A reaction norm describes how the phenotype of an individual or genotype varies with environment, and is a useful way to characterize phenotypic plasticity (reviewed in Gotthard and Nylin 1995). One of the most widely observed patterns of phenotypic plasticity is the temperature–size rule (Atkinson 1994): adult or final body size decreases with increasing rearing temperature such that the thermal reaction norm for size has a negative slope. This pattern has been reported in more than 80% of ectotherms in a wide variety of taxa for nonstressful temperatures (i.e., excluding temperatures near the lower and upper thermal limits).

However, reaction norms are the outcomes of multifarious genetic and environmental factors (Angilletta 2009). In herbivorous insects, thermal reaction norms for growth and size are strongly influenced by nutrition and secondary plant compounds (Stamp 1990; Stamp et al. 1994; Kingsolver et al. 2006). For example, in the tobacco hornworm, *Manduca sexta*, pupal and adult sizes decrease with increasing temperature when reared on its typical solanaceous hosts or on high-quality artificial diets, following the temperature–size rule (Davidowitz and Nijhout 2004; Davidowitz et al. 2004; Diamond and Kingsolver

Communicated by Jérôme Casas.

Present Address:

S. E. Diamond (✉)
Department of Biology, David Clark Labs,
North Carolina State University, Campus Box 7617,
Raleigh, NC 27695-7617, USA
e-mail: sarah_diamond@ncsu.edu

J. G. Kingsolver
The University of North Carolina at Chapel Hill,
Chapel Hill, NC 27599-3280, USA

2010a); on the other hand, when reared on a novel, lower quality host plant, *M. sexta* populations from the southeast US show a reversal of thermal reaction norm slope: final size increases with increasing rearing temperature (Diamond and Kingsolver 2010a). Of course, resource and host plant quality can reflect both intrinsic qualities of the resource and the degree of evolutionary adaptation by the consumer to that resource (e.g., Agrawal 2000). If populations or species differ in their degree of adaptation to a novel resource, how does this alter their thermal reaction norms?

In this paper, we use a population comparative approach to address this question for *M. sexta*. Although *M. sexta* typically feeds exclusively on solanaceous host plants, recent reports indicate *M. sexta* utilizes a nonsolanaceous host plant in two distinct parts of its range—the Southeastern (North Carolina, hereafter the “NC” *M. sexta* population; Diamond and Kingsolver 2010b) and Southwestern (Arizona, hereafter the “AZ” *M. sexta* population; Mechaber and Hildebrand 2000; Mira and Bernays 2002) United States. The nonsolanaceous host plant, devil’s claw (*Proboscidea* spp.), is native to the greater Southwestern US and Northern Mexico, but has been introduced to the Southeastern US within the last 100 years (Small 1903). Although the AZ and NC *M. sexta* both exhibit reduced performance on devil’s claw compared to typical solanaceous host plants (Mira and Bernays 2002; Diamond and Kingsolver 2010b), AZ *M. sexta* have greater evolutionary exposure to devil’s claw compared to NC *M. sexta*, and are therefore potentially better adapted to this host plant.

We performed a common garden experiment in which NC and AZ *M. sexta* were reared on devil’s claw (*Proboscidea louisianica*) and a typical solanaceous host plant, tobacco (*Nicotiana tabacum*), at 20 and 30°C. We hypothesized that the slope of the thermal reaction norm for body size would reflect differences in host plant adaptation. In particular, we hypothesized that, for NC *M. sexta* relative to AZ *M. sexta*, less evolutionary exposure to devil’s claw contributes to poor adaptation to this resource; the combination of poor adaptation to devil’s claw and cooler temperatures creates a highly stressful environment (sensu Diamond and Kingsolver 2010a) that alters the typical negative thermal reaction norm for body size. Under this hypothesis, we predict that: (1) when reared on the solanaceous host plant, tobacco, both NC and AZ *M. sexta* will have high survival and rapid development, and will exhibit typical negative thermal reaction norms; (2) when reared on the nonsolanaceous host plant, devil’s claw, NC *M. sexta* will show larger increases in mortality and development time than AZ *M. sexta*; and (3) when reared on the nonsolanaceous host plant, devil’s claw, AZ *M. sexta* will exhibit a more negative slope than NC *M. sexta*.

Materials and methods

Manduca sexta L. (Lepidoptera: Sphingidae), the tobacco hornworm, has distinct egg, larval, pupal, and adult stages. *M. sexta* typically have five larval instars (but may express additional instars; Kingsolver 2007), reaching a maximum size during the “wandering” phase at the end of the final larval instar, when larvae wander off the host plant and burrow under the soil to pupate. Until recently, *M. sexta* larvae were thought to feed exclusively on host plants in the nightshade family (Solanaceae). For example, domesticated tobacco (*Nicotiana tabacum*) and tomato (*Solanum lycopersicum*) are major host plants in the Southeastern US; native tobacco (e.g., *Nicotiana attenuata*) and sacred Datura (*Datura wrightii*) are important hosts in the Southwestern US. However, in the Southwestern and Southeastern US, adult female *M. sexta* oviposit on the nonsolanaceous host plant devil’s claw (*Proboscidea* spp.: Martyniaceae), and the resulting offspring are capable of completing development to maturity feeding on this host plant (Mechaber and Hildebrand 2000; Mira and Bernays 2002; Diamond and Kingsolver 2010b). *Proboscidea* spp. are native to the greater Southwestern US and Northern Mexico (Bretting 1981), but have been introduced to other locations across the US. Devil’s claw was introduced to the Southeast approximately 100 years ago (Small 1903), and while this host plant has since become naturalized to the area, devil’s claw occurs at low frequencies and is sparsely distributed in its introduced range compared with its native range (Radford et al. 1968). This suggests potential further limitations on the adaptation of Southeast *M. sexta* populations to devil’s claw.

We used populations of *M. sexta* from the Southwestern US [the Chiricahua Mountains (near Portal) and the Santa Rita Mountains (near Tucson), both in Arizona; the AZ population], and Southeastern US (Clayton, North Carolina; the NC population), which differ markedly in their evolutionary exposures to the nonsolanaceous host plant devil’s claw, but not to typical solanaceous host plants. In contrast, thermal selective regimes are relatively similar across the AZ and NC populations (representing 32 and 36°N latitude, respectively): *M. sexta* populations experience comparable mean summer temperatures of ~25°C, though with greater diurnal extremes in AZ. In our experiments, we used a species of devil’s claw, *P. louisianica*, common to both the greater Southwestern and Southeastern US, and a low-alkaloid variety of cultivated tobacco, a typical solanaceous host plant (*Nicotiana tabacum*, var. LA Burley 21; National Genetic Resources Program, USDA, ARS; Beltsville, MD, USA). We note that the AZ *M. sexta* used in our experiments typically feed on devil’s claw species other than *P. louisianica* (i.e., *P. althaeifolia* and *P. parviflora*), and as a result, may

perhaps be less adapted to *P. louisianica*. However, if there is differential adaptation of AZ *M. sexta* among these three *Proboscidea* species, the differences are likely to be small, as *P. louisianica* is phylogenetically nested between *P. parviflora* and *P. althaeifolia* (Gutierrez 2008), and *Proboscidea* spp. tend to be similar chemically (Ghosh and Beal 1979). Importantly, because our prediction is that AZ *M. sexta* will perform better than NC *M. sexta* on devil's claw, our experimental design using *P. louisianica* is conservative.

Full experiments, comprising four treatment groups based on each combination of host plant species (devil's claw, tobacco) and rearing temperature (20, 30°C), were performed on NC population *M. sexta* in late summer 2008 (data from Diamond and Kingsolver 2010a). Full experiments involving AZ population *M. sexta* were performed in late summer 2009. Concurrent with the AZ population *M. sexta*, we reared NC *M. sexta* on devil's claw only ($n = 10$ for each of the two temperature treatments) in order to corroborate results from the 2008 NC devil's claw-reared *M. sexta*. We observed comparable survival rates, body sizes, development times, and thermal reaction norms for body size for NC *M. sexta* reared on devil's claw in the 2008 and 2009 experiments; we therefore pooled data across years for NC *M. sexta*. The NC *M. sexta* (2008 and 2009) were the offspring of adults mated in the laboratory after being reared through one generation in the laboratory on an artificial diet following their initial collection from the field as eggs and early-instar larvae on tobacco. The AZ *M. sexta* were the offspring of adults mated in the laboratory after developing on a typical solanaceous host plant (*Datura* sp.) in the field. Although the parental generations of the AZ and NC *M. sexta* used in our experiments (≥ 40 individuals comprised the parental generation for each population) were reared on different resources (*Datura* and artificial diet, respectively), both are high-quality resources, so nutritionally mediated maternal effects should not greatly influence our results. Indeed, our previous work showed no significant differences in survival, body size, and development time (at/to maturity, i.e., pupation) between tobacco leaf-reared NC *M. sexta* offspring of parents reared on an artificial diet versus tobacco (under comparable conditions: 25°C, 16:8 L:D; $p > 0.05$ for the effect of parental diet on each response; data from Diamond and Kingsolver 2010a and unpubl.).

From each population (AZ and NC), eggs were randomly assigned to tobacco and devil's claw leaves held under two different constant temperature regimes (20 and 30°C) in the laboratory. For the 2008 NC and 2009 AZ *M. sexta*, upon hatching, 20 larvae from each population were transferred to individual tobacco leaves, and 30–40 larvae from each population were transferred to individual devil's claw leaves in each of the two temperature

treatments (the 2009 NC *M. sexta* had ten larvae transferred to individual devil's claw leaves in each of the two temperature treatments). In the full experiments, initial sample sizes were greater on devil's claw in anticipation of higher mortality on this host plant compared with tobacco.

Details of rearing methods are presented elsewhere (Diamond and Kingsolver 2010a); briefly, larvae were fed ad libitum on whole leaves cut from greenhouse-grown plants, and maintained individually in environmental chambers (Percival 36-VL) under a 16L:8D photocycle. Upon reaching the wandering phase, larvae were placed individually in wooden chambers to pupate. At this time, *M. sexta* from both temperature treatments were brought to a constant temperature of 25°C and held at this temperature through adult eclosion.

We measured survival, development time, body mass at the third, fourth, and fifth (sixth in some cases) larval instars, wandering, pupation, and adults (following eclosion). Larval masses were recorded immediately following the molt into a given instar (indicated by slipping of the head capsule). Wandering masses were recorded after completely purging the gut contents. Analyses of growth and development were restricted to individuals that survived to eclosion, though results were qualitatively similar based on analyses of all individuals.

Survival to pupation was considered a binomial variable and modeled using analysis of deviance with population (AZ or NC), host plant species (devil's claw or tobacco), temperature (20 or 30°C), and all two-way interactions between these terms as fixed effects (the three-way interaction between population, host plant species, and temperature could not be estimated, as the number of parameters in such a model would exceed the available degrees of freedom; instead, we perform post hoc tests separately for animals reared on devil's claw and tobacco in which the two-way interactions between population, host plant species and temperature could be estimated; see “Results”). Development time to pupation and body mass at pupation (for individuals surviving to eclosion) were modeled using ANOVA with population, host plant species, temperature, sex, and all two- and three-way interactions between these terms, exclusive of those interactions with sex, as fixed effects. We focused on measurements of pupae because of the stability in body mass at this stage. All statistical analyses were performed using R statistical software (R Development Core Team 2010; version 2.11.1).

Results

Survival of the AZ and NC populations was consistently high across the two temperature treatments when reared on

tobacco, suggesting comparable adaptation to solanaceous host plants. In contrast, the AZ population had greater survival on devil's claw than the NC population, suggesting that the AZ population is better adapted to using this host plant compared to the NC population (Fig. 1). Analysis of deviance on survival detected significant effects of host plant species ($\chi^2 = 28.4$; $P < 0.0001$), temperature ($\chi^2 = 9.10$; $P = 0.00256$), population ($\chi^2 = 6.65$; $P = 0.00993$), and host plant species \times population ($\chi^2 = 8.99$; $P = 0.00272$). The interactions of temperature \times population ($\chi^2 = 1.83$; $P = 0.176$), and temperature \times host plant species ($\chi^2 = 0.151$; $P = 0.698$) were nonsignificant. Post hoc analyses based on the subset of *M. sexta* reared on devil's claw revealed significant effects of population ($\chi^2 = 10.1$; $P < 0.0001$) and temperature ($\chi^2 = 10.7$; $P = 0.00106$). Survival of the NC population on devil's claw tended to be particularly low at the lower rearing temperature (Fig. 1), though the interaction of population and temperature was not statistically significant ($\chi^2 = 2.33$; $P = 0.126$).

When reared on tobacco, the AZ population had significantly longer development times to pupation ($F_{1,165} = 151$; $P < 0.0001$) and larger pupal masses ($F_{1,165} = 43.6$; $P < 0.0001$) than the NC population (Fig. 2). There was also a significant effect of sex on pupal mass ($F_{1,165} = 94.6$; $P < 0.0001$) but not on development time ($F_{1,165} = 0.205$; $P = 0.652$) (see Madden and Chamberlin 1945).

Rearing on devil's claw significantly increased development times ($F_{1,165} = 18.0$; $P < 0.0001$) and reduced pupal masses ($F_{1,165} = 19.1$; $P < 0.0001$) compared with

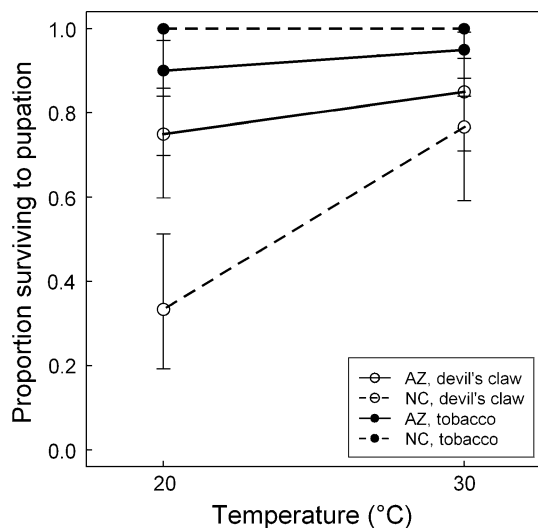


Fig. 1 Mean proportion surviving to pupation (with 95% binomial CI) as a function of temperature for AZ (solid lines) and NC (dashed lines) *Manduca sexta* reared on devil's claw (open symbols) and tobacco (closed symbols)

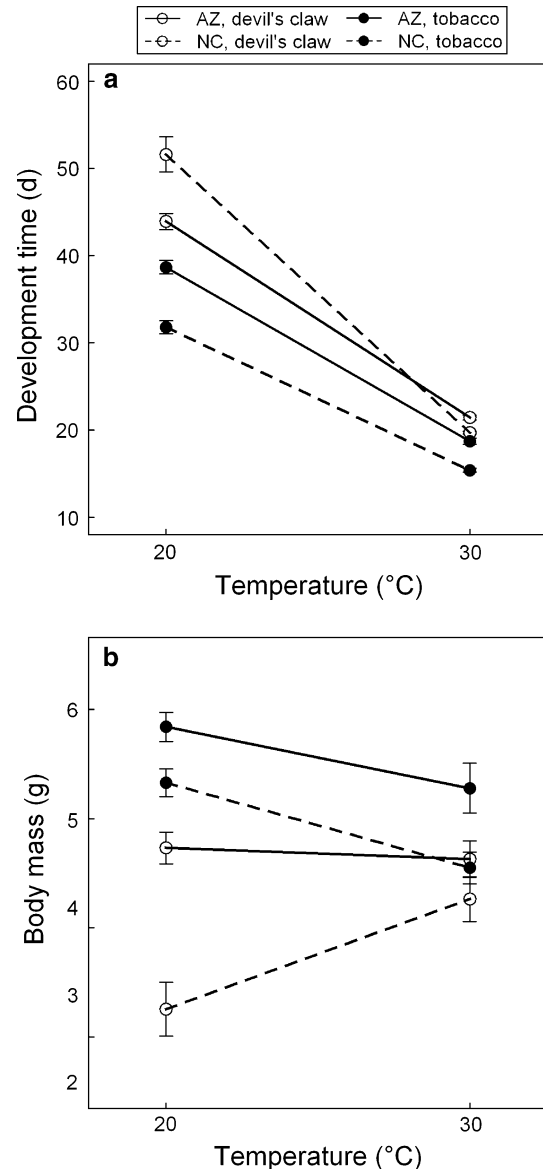
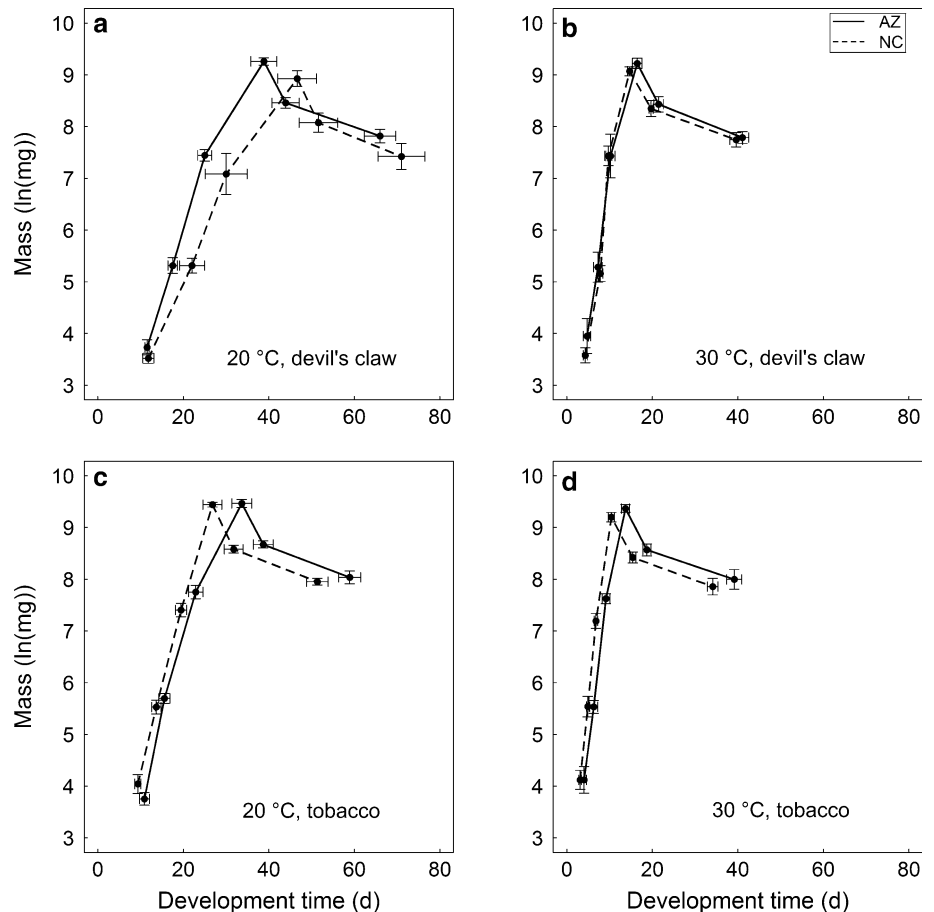


Fig. 2 a Mean development time (± 1 SE) to pupation and b mean pupal body mass (± 1 SE) as a function of temperature for AZ (solid lines) and NC (dashed lines) *Manduca sexta* females reared on devil's claw (open symbols) and tobacco (closed symbols). Results for males (not shown) were qualitatively similar

rearing on tobacco, confirming that devil's claw is a lower quality host plant for *M. sexta*. However, the magnitude and pattern of effects differed between populations and depended strongly on rearing temperature (Figs. 2, 3). For example, on tobacco, mean development times were longer for the AZ than the NC population, whereas on devil's claw, development times were shorter for the AZ than the NC population (host plant species \times population interaction: $F_{1,165} = 179$; $P < 0.0001$) (Fig. 2a). This supports the hypothesis that the NC population is more poorly adapted to devil's claw than the AZ population. The higher

Fig. 3 a–d Mean body mass [± 1 SD; in $\ln(\text{mg})$] as a function of development time (± 1 SD; in days) for AZ (solid lines) and NC (dashed lines) *Manduca sexta* females reared on devil's claw (a, b) and tobacco (c, d) at 20°C (a, c) and 30°C (b, d). Results for males (not shown) were qualitatively similar. Developmental stages shown (points): third, fourth, and fifth larval instars, wandering, pupa, adult. In cases where larvae expressed an additional instar, we present results for body mass and development time to the fifth instar



rearing temperature significantly reduced development times ($F_{1,165} = 1917$; $P = 0.234$), but with a magnitude that depended on host plant and population (temperature \times population: $F_{1,165} = 130$; $P < 0.0001$; temperature \times host plant species: $F_{1,165} = 6.44$; $P = 0.0121$; and host plant species \times population \times temperature: ($F_{1,165} = 125$; $P < 0.0001$).

The differential adaptation to devil's claw across populations was also reflected in differences in their thermal reaction norms for body size (Fig. 2b). ANOVA showed that the main effect of temperature on pupal mass ($F_{1,165} = 1.43$; $P = 0.234$) was nonsignificant, but temperature contributed significantly to body mass through its interactions with host plant species and population. For example, the NC population had markedly greater body size on devil's claw when reared at warmer temperatures (positive thermal reaction norm), whereas the AZ population had comparable body sizes on devil's claw across the two temperature treatments (flat thermal reaction norm) (Fig. 2b). These interactions were reflected in the significant effects of host plant species \times population ($F_{1,165} = 22.8$; $P < 0.0001$), temperature \times population ($F_{1,165} = 28.7$; $P < 0.0001$), temperature \times host plant species ($F_{1,165} = 7.63$; $P = 0.00639$), and host plant

species \times population \times temperature ($F_{1,165} = 20.5$; $P < 0.0001$). These patterns support the hypothesis that both host plant species and herbivore adaptation to host plant quality can influence thermal reaction norms for body size.

Discussion

The main goal of our study was to explore how variation in resource adaptation, particularly among different populations, alters thermal reaction norms for body size. Previous research in this area has demonstrated the importance of both resource quality (Stamp et al. 1994; Kingsolver et al. 2006) and population differences (Kingsolver et al. 2007) in shaping thermal reaction norms. Here we integrate these components to explore how population differences in host plant adaptation alter thermal reaction norms for body size in the tobacco hornworm, *Manduca sexta*. Specifically, we compare thermal reaction norms for two populations of *M. sexta* reared on an atypical, low-quality host plant (devil's claw), to which these populations are differentially adapted; as a control, we compare thermal reaction norms

for *M. sexta* reared on a typical, high-quality host plant (tobacco), to which *M. sexta* populations are well adapted.

Our results confirm previous studies (Mira and Bernays 2002; Diamond et al. 2010) suggesting that both the AZ and NC *M. sexta* populations examined in this study are well adapted to tobacco, a typical solanaceous host plant, compared with devil's claw, an atypical nonsolanaceous host plant: survival, development time, and body mass were all superior on tobacco compared with devil's claw (Figs. 1, 2). Similarly, both populations exhibited the typical negative-slope thermal reaction norm for body size on tobacco, but not on devil's claw (Fig. 2b). Note that the AZ population performed well on domesticated tobacco, although it does not typically encounter this particular solanaceous host plant in the field (see "Methods").

A key result of our study is that AZ and NC populations exhibited quite different thermal reaction norms for body size on devil's claw, in a manner consistent with the evolutionary exposure of these populations to this atypical, nonsolanaceous host plant. The NC population, for which devil's claw is relatively new (Small 1903), exhibited a steep positive reaction norm, whereas the AZ population, which has a much longer history of exposure to devil's claw, exhibited a relatively flat reaction norm, i.e., a slope more similar to the typical negative thermal reaction norm. We interpret this result as a lesser degree of evolutionary exposure to devil's claw contributing to poor adaptation to this resource: adaptation to devil's claw combined with cooler temperatures creates a highly stressful environment (sensu Diamond and Kingsolver 2010a), altering the typical negative thermal reaction norm for body size. These results suggest that population differences in host plant adaptation can strongly and predictably influence the slope of thermal reaction norms.

Developmental and survival data support this interpretation. On devil's claw, the AZ population exhibited a higher mean survival (Fig. 1) and a shorter mean development time (Fig. 2a) than did the NC population. Both results suggest superior adaptation of the AZ population to devil's claw. Importantly, the magnitude of these population differences in survival and development on devil's claw tended to be greater at the cooler temperature. The negative effects of some allelochemicals (e.g., the phenolic compound rutin) have been shown to be magnified under cooler thermal regimes for *M. sexta* (Stamp 1990; Stamp and Horwath 1992; Yang and Stamp 1996; Yang et al. 1996). Although the temperatures used in our experiments (20–30°) are typically nonstressful for *M. sexta*, the combination of cool temperature (~20°C) and low resource quality of devil's claw appears to create a stressful environment for *M. sexta* (Diamond and Kingsolver 2010a). Apart from cool temperatures potentially amplifying the effects of the devil's claw allelochemicals, cool

temperatures might also alter external physical properties of devil's claw. For example, the exudate produced by the glandular trichomes may become more viscous at cooler temperatures, and may be particularly difficult to navigate for the comparatively smaller NC *M. sexta*. Regardless of the mechanism, the combination of the devil's claw resource and cool temperatures creates an environment to which AZ *M. sexta* are comparatively better adapted than the NC *M. sexta*.

The AZ population had a larger mean body size than the NC population for both host plants at both rearing temperatures. The greater size of AZ *M. sexta* relative to NC *M. sexta* has been previously detected (Kingsolver and Woods, unpubl.), and is unlikely to reflect dietary variation in the parental generations across the two populations; see "Methods"). This suggests an alternative interpretation that the AZ population is simply better or more robust than the NC population, as evidenced by their larger body size within each temperature × host plant treatment group (van Noordwijk and de Jong 1986; Stearns 1992; Reznick et al. 2000). The flat thermal reaction norm for body size in the AZ population reared on devil's claw could therefore be interpreted as being due to their intrinsic robustness, rather than their evolutionary exposure and adaptation to devil's claw. However, when reared on the high-quality host plant, tobacco, the NC population had more rapid development times than the AZ population at both rearing temperatures (Fig. 2): mean growth rates (mass/development times) were in fact similar for the two populations on this host. In addition, survival on tobacco was comparable for the AZ and NC populations. These observations are inconsistent with the notion that the AZ population is generally "better" or more robust, independent of resource quality.

We are careful here to note two important caveats of our study. First, while the AZ population has had a longer history of exposure to devil's claw compared with the NC population, rapid evolution to alternative resources can proceed relatively quickly (e.g., Singer et al. 1993), potentially on timescales comparable to the NC population's exposure to devil's claw. Although the point at which sufficient adaptation to devil's claw could result in flat or even negative thermal reaction norms for the NC population is unclear, the relatively short timeframe of exposure of this population and low frequency of occurrence of devil's claw in this region appear to limit adaptation considerably, as evidenced by the poor performance of current NC populations. Secondly, we acknowledge the limitations of our experimental design. As not all treatment groups (population × temperature × host plant) were examined concurrently (see "Methods"), our study does not represent a common garden experiment in the strictest sense; importantly, however, nonconcurrent responses were similar for replicated treatments (e.g., for NC

M. sexta reared on devil's claw in 2008 and 2009), suggesting that environmental conditions and results are comparable across nonconcurrent experiments. In addition, without further population-level replication, we cannot fully exclude the possibility that our data reflect idiosyncratic rather than generalizable patterns in how thermal reaction norms may be altered by host plant adaptation. However, given the strong viability selection we observed (Fig. 1), coupled with the fact that our results for survival, development time, and body size (Figs. 2 and 3) all indicate local adaptation of the AZ *M. sexta* to devil's claw, we are reasonably confident in our interpretation.

Thermal reaction norms for body size with negative slope—a pattern termed the temperature–size rule—are common in ectotherms (Atkinson 1994). The prevalence of this pattern has prompted the development of both mechanistic and adaptive hypotheses, though whether the temperature–size rule is produced by natural selection or by shared physiological and thermodynamic constraints remains unclear (Berrigan and Charnov 1994; van der Have and de Jong 1996; Davidowitz et al. 2004; reviewed in Kingsolver and Huey 2008). The results of our study indicate that both resource quality and evolutionary adaptation to those resources can strongly influence the slope of thermal reaction norms. It would be interesting to revisit exceptions to the temperature–size rule (~20% of reported studies: Atkinson 1994; Angilletta 2009) in terms of resource quality and resource adaptation in those cases. More generally, our analyses suggest that the evolution of thermal reaction norms must be viewed in the context of evolutionary adaptation to resources, and perhaps other environmental factors.

Acknowledgments We thank K. Potter and A. Woods for kindly providing *Manduca sexta* from Arizona, and C. Sorenson for access to the North Carolina State Research Station at Clayton for collecting *M. sexta* from North Carolina. C. Angell, S. Sheline, and M. Smith helped with the experiments. G. Davidowitz, R. Martin, K. Potter, A. Woods, and two anonymous reviewers provided helpful comments on a previous version of the manuscript. The National Science Foundation provided funding (grant IOS-0641179 to J.G.K.).

References

- Agrawal AA (2000) Host-range evolution: adaptation and trade-offs in fitness of mites on alternative hosts. *Ecology* 81:500–508
- Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford
- Atkinson D (1994) Temperature and organism size—a biological law for ectotherms? *Adv Ecol Res* 3:1–58
- Berrigan D, Charnov EL (1994) Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos* 70:474–478
- Bretting PK (1981) A systematic and ethnobotanical survey of *Probooscidea* and allied genera of the Martyniaceae (PhD dissertation). Indiana University, Bloomington
- Davidowitz G, Nijhout HF (2004) The physiological basis of reaction norms: the interaction among growth rate, the duration of growth and body size. *Integ Comp Biol* 44:443–449
- Davidowitz G, D'Amico LJ, Nijhout HF (2004) The effects of environmental variation on a mechanism that controls insect body size. *Evol Ecol Res* 6:49–62
- Diamond SE, Kingsolver JG (2010a) Environmental dependence of thermal reaction norms: host plant quality can reverse the temperature–size rule. *Am Nat* 175:1–10
- Diamond SE, Kingsolver JG (2010b) Fitness consequences of host plant choice: a field experiment. *Oikos* 119:542–550
- Diamond SE, Hawkins SD, Nijhout HF, Kingsolver JG (2010) Evolutionary divergence of field and laboratory populations of *Manduca sexta* in response to host plant quality. *Ecol Entomol* 35:166–174
- Ghosh A, Beal JL (1979) Seed lipid constituents of three species of *Probooscidea*. *J Natural Prod* 42:287–292
- Gotthard K, Nylin S (1995) Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74:3–17
- Gutierrez R (2008) Preliminary chloroplast DNA studies in the flowering plant family Martyniaceae (order Lamiales). *J Arizona-Nevada Acad Sci* 40:105–110
- Kingsolver JG (2007) Variation in growth and instar number in field and laboratory *Manduca sexta*. *Proc Roy Soc B* 274:977–981
- Kingsolver JG, Huey RB (2008) Size, temperature, and fitness: three rules. *Evol Ecol Res* 10:251–268
- Kingsolver JG, Shlichta JG, Ragland GJ, Massie KR (2006) Thermal reaction norms for caterpillar growth depend on diet. *Evol Ecol Res* 8:703–715
- Kingsolver JG, Massie KR, Ragland GJ, Smith MH (2007) Rapid population divergence in thermal reaction norms for an invading species: breaking the temperature–size rule. *J Evol Biol* 20:892–900
- Madden AH, Chamberlin FS (1945) Biology of the tobacco hornworm in the southern cigar-tobacco district (USDA Tech Bull no. 896). US Department of Agriculture, Washington, DC
- Mechaber WL, Hildebrand JG (2000) Novel, non-solanaceous hostplant record for *Manduca sexta* (Lepidoptera: Sphingidae) in the southwestern United States. *Ann Entomol Soc Amer* 93:447–451
- Mira A, Bernays EA (2002) Trade-offs in host use by *Manduca sexta*: plant characters vs natural enemies. *Oikos* 97:387–397
- R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. <http://www.R-project.org/>
- Radford AE, Ahles HE, Bell CR (1968) Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill
- Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol Evol* 15:421–425
- Singer MC, Thomas CD, Parmesan C (1993) Rapid human-induced evolution of insect–host associations. *Nature* 366:681–683
- Small JK (1903) Flora of the Southeastern United States. JK Small, New York
- Stamp NE (1990) Growth versus molting time of caterpillars as a function of temperature nutrient concentration and the phenolic rutin. *Oecologia* 82:107–113
- Stamp NE, Horwath KL (1992) Interactive effects of temperature and concentration of the flavonol rutin on growth, molt and food utilization of *Manduca sexta* caterpillars. *Entomol Exp Appl* 64:135–150
- Stamp NE, Temple MP, Traugott MS, Wilkens RT (1994) Temperature-allelochemical interactive effects on performance of *Manduca sexta* caterpillars. *Entomol Exp Appl* 72:199–210
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

- Van der Have TM, de Jong G (1996) Adult size in ectotherms: temperature effects on growth and differentiation. *J Theor Biol* 183:329–340
- Van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *Am Nat* 128:137–142
- Yang Y, Stamp NE (1996) Simultaneous effects of temperature and multiple allelochemicals on the performance of a Solanaceae specialist caterpillar (*Manduca sexta*). *Ecoscience* 3:81–92
- Yang Y, Stamp NE, Osier TL (1996) Effects of temperature, multiple allelochemicals and larval age on the performance of a specialist caterpillar. *Entomol Exp Appl* 79:335–344