

Experimental evidence that predation promotes divergence in adaptive radiation

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Adaptive radiation is the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. Recent studies have identified general patterns in adaptive radiation and inferred that resource competition is a primary factor driving phenotypic divergence. The role and importance of other processes, such as predation, remains controversial. Here we use *Timema* stick insects to show that adaptive radiation can be driven by divergent selection from visual predators. Ecotypes using different host-plant species satisfy criteria for the early stages of adaptive radiation and differ in quantitative aspects of color, color pattern, body size, and body shape. A manipulative field experiment demonstrates that the direction and strength of divergent selection on these traits is strongly positively correlated with the direction and magnitude of their population divergence in nature but only when selection is estimated in the presence of predation. Our results indicate that both competition and predation may commonly serve as mechanisms of adaptive radiation.

crypsis | natural selection | *Timema* walking stick | divergent selection | host adaptation

The “ecological theory of adaptive radiation” states that (i) divergent natural selection drives the phenotypic divergence and speciation of lineages and (ii) divergent selection itself stems from ecological differences between environments or from ecological interactions (1–3). A prediction of the theory is that the direction and magnitude of divergent selection in the wild is positively correlated with the direction and magnitude of trait divergence among natural populations (4, 5). Our understanding of adaptive radiation has been greatly increased by studies describing general patterns or documenting the process of divergent selection (6–11). However, such studies do not test the critical prediction of a correlation between selection and trait divergence. With respect to the causes of divergent selection, support for even the best-studied mechanism of interspecific competition is mostly indirect (2). The role of other processes, such as predation, has long been discussed (12–14) but remains controversial (2, 15–18). Part of the controversy stems from the fact that predation is notoriously difficult to study in the wild. Here we demonstrate that divergent selection and trait divergence are strongly correlated in natural populations of walking stick insects, and we elucidate predation as the source of divergent selection by using a manipulative field experiment.

Timema walking sticks are plant-feeding insects distributed throughout southwestern North America (19). The genus as a whole satisfies three of the four criteria for adaptive radiation (2): recent ancestry, environment-phenotype correlations, and rapid bursts of speciation (19, 20). Only experimental tests for trait utility at the among-species level remain to be conducted. By contrast, all four criteria are satisfied for host-associated ecotypes of *Timema cristinae* adapted to feeding on two different host-plant species. Ecotypes are defined by which host-plant species they are found on, *Ceanothus* versus *Adenostoma*. Fig. 1 depicts the insect ecotypes, and Fig. 2 depicts the host-plant species at various spatial scales. The two host-plant species differ strikingly in foliage form, with *Ceanothus* plants being relatively large, tree-like, and broad-leaved, and *Adenostoma* plants being small, bush-like, and exhibiting thin,

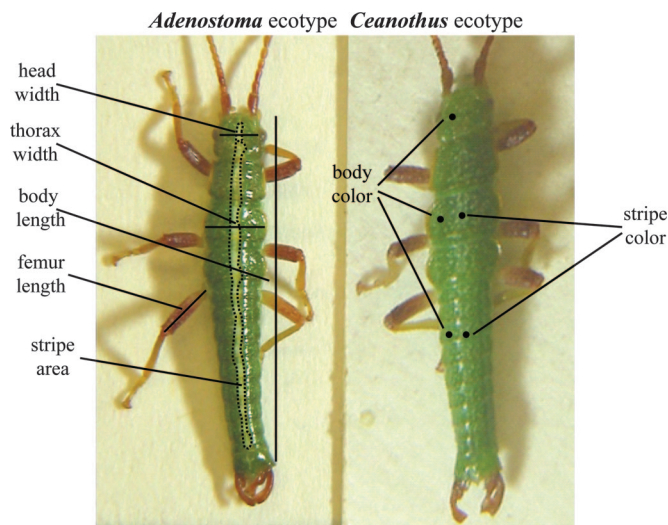


Fig. 1. The traits examined depicted on representative specimens of each host ecotype. Body color and stripe color represent three different variables each (hue, saturation, and brightness). Individuals from *Adenostoma* tend to exhibit larger and brighter stripes, less-bright bodies, and shorter body size than individuals from *Ceanothus* (all traits except stripe hue and all size-corrected traits except stripe hue and thorax width differ significantly between ecotypes; $P < 0.05$, t tests).

needle-like leaves. For the insect ecotypes, molecular evidence supports recent ancestry (21), geographic variation in morphology is correlated with host-plant use (such that color and body shape appear cryptically matched to each host plant; see refs. 22 and 23), and experimental evidence confirms trait utility and a higher rate of evolution of reproductive isolation when divergent host-plant adaptation occurs than when it does not (21, 23–25). Adaptive radiation in the classical sense concerns diversification among species. But, by satisfying all of the criteria for adaptive radiation, the ecotypes of *T. cristinae*, like limnetic and benthic ecotypes of sticklebacks (15), can be considered an early stage of radiation that provides a useful model for testing outstanding questions (much like laboratory microorganisms provide useful experimental models for adaptive radiation; 3, 16). Patterns detected between the ecotypes can then be compared with patterns of among-species diversification to connect microevolutionary processes with macroevolutionary patterns.

Testing the prediction that selection has driven divergence requires both quantitative estimates of trait divergence in nature and estimates of divergent selection in the wild. We quantified divergence between *T. cristinae* ecotypes in 11 quantitative traits that differ between them to varying degrees (*Ceanothus*, $n = 283$;

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Abbreviation: PC, principal components.

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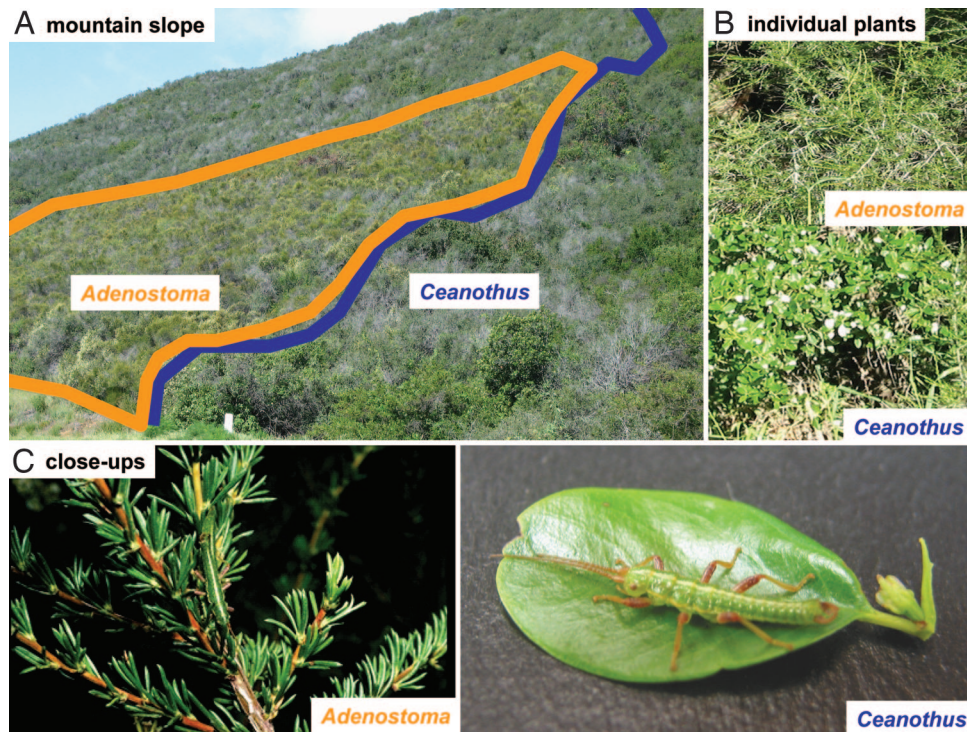


Fig. 2. The two host-plant species used by the ecotypes of *T. cristinae* (*Ceanothus spinosus* and *Adenostoma fasciculatum*). The hosts are depicted at three spatial scales. (A) The scale of a hillside or mountain slope (approximately 20 m × 20 m). (B) Individual plants. (C) Close-ups of each host species. The close-up of *Adenostoma* was taken by C. P. Sandoval. All other photos by P.N.

Adenostoma, $n = 321$). These traits comprise aspects of color, color pattern, body size, and body shape. Fig. 1 depicts the traits measured and typical differences between ecotypes (raw and size-corrected trait means for each host ecotype can be found in Table 2, which is published as supporting information on the PNAS web site). Trait divergence was estimated as mean trait value for individuals from *Ceanothus* minus mean trait value for individuals from *Adenostoma*.

A manipulative field experiment using enclosures allowed us to then estimate survival selection on these same traits on both host species in the presence versus absence of visual predation ($n = 384$ individuals). Specifically, we estimated standardized directional selection differentials, which measure total selection

on a trait (26). We calculated “divergent selection” as the selection differential on *Ceanothus* minus the selection differential on *Adenostoma* (see Table 3, which is published as supporting information on the PNAS web site, for the raw selection differentials). The association between trait divergence and divergent selection was then evaluated under the two predation scenarios (present versus absent). Our results demonstrate that selection and trait divergence are strongly correlated but only when selection is estimated in the presence of visual predation. Because we were able to manipulate the presence of predation, our findings provide a clear experimental demonstration that predation can drive phenotypic divergence during adaptive radiation.

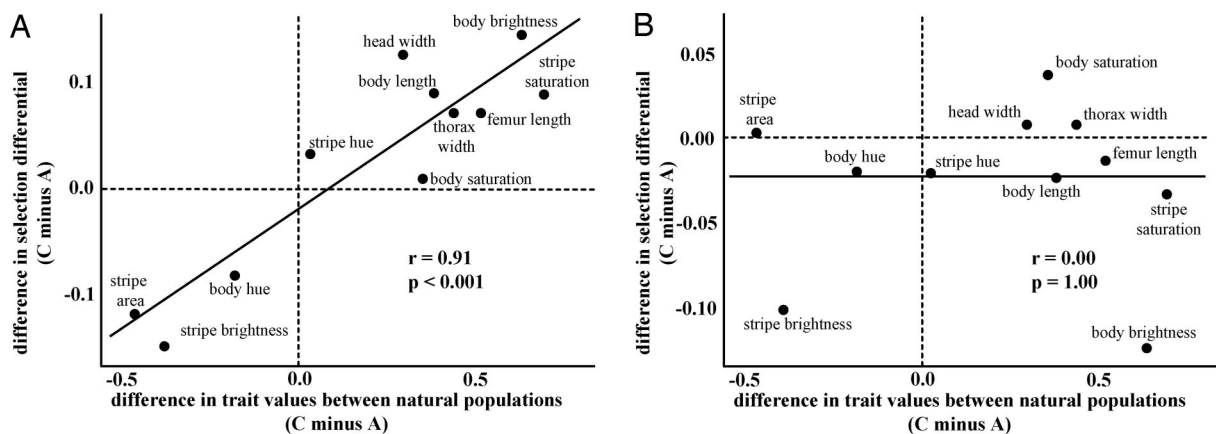


Fig. 3. The direction and magnitude of divergent selection was positively correlated with the direction and magnitude of trait divergence observed between natural populations using different hosts but only when selection was estimated in the presence of visual predation (predation scenario × trait divergence interaction; $P < 0.001$). Moreover, absolute divergent selection was stronger in the presence versus absence of predation for 10 of 11 traits individually ($t_{10} = 4.14$, $P < 0.01$, paired t test). (A) Predation present. (B) Predation absent.

Table 1. The correlation between trait divergence and divergent selection in the presence versus absence of predation, estimated using different methods.

	Predation present				Predation absent			
	Raw values		Size-corrected values		Raw values		Size-corrected values	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Individual traits								
lin, par	0.91	<0.001	0.70	0.016	0.00	0.999	−0.22	0.560
lin, npar	0.75	0.008	0.59	0.056	−0.19	0.474	−0.15	0.670
logit, par	0.89	<0.001	0.68	0.022	−0.25	0.450	−0.50	0.116
logit, npar	0.74	0.010	0.59	0.056	−0.28	0.402	−0.24	0.484
PC axes								
lin, par	0.84	0.16	0.97	0.006	0.31	0.69	−0.05	0.94
lin, npar	0.80	0.20	1.00	<0.001	0.40	0.60	−0.10	0.87
logit, par	0.84	0.16	0.94	0.017	0.26	0.74	0.16	0.80
logit, npar	0.80	0.20	1.00	<0.001	0.40	0.60	0.40	0.51

The different methods included: (i) estimates of selection from linear (lin) versus logistic (logit) regression, (ii) the association between trait divergence and selection analyzed using either parametric (par) or nonparametric (npar) correlation, and (iii) the correlation examined using individual trait values and using uncorrelated principal components (PC) axes in the place of actual trait values. In all cases, results are shown for raw individual trait values, for size-corrected individual trait values, for the four PC axes derived using raw trait values, and for the five PC axes derived using size-corrected trait values. Four and five PC axes were used for raw versus size-corrected traits, respectively, because they were the number of axes required to explain >75% of the variation. Significant results were obtained only in cases where selection was estimated in the presence of predation (denoted in bold), and *r* values were consistently larger in the presence versus absence of predation.

Results and Discussion

We detected strong support for the prediction of the ecological theory of adaptive radiation: The direction and strength of divergent selection under predation was strongly positively correlated with the direction and magnitude of trait divergence between natural populations by using different hosts ($r = 0.91$, $P < 0.001$; Fig. 3). By contrast, there was no correlation between selection in the absence of predation and trait divergence ($r = 0.00$, $P = 1.00$). Thus, there was a highly significant difference between predation scenarios (scenario \times trait divergence interaction; $F_{1,24} = 35.51$, $P < 0.001$), and predation is inferred as the agent of selection driving trait divergence.

The analyses presented above are sufficient and appropriate for evaluating the association between selection and trait divergence, and for assessing the difference between predation scenarios. The results were also highly robust to different analytical methods. The pattern of a strong correlation between selection and trait divergence only in the presence of predation was detected when size-corrected trait values were considered, when nonparametric correlation was used to evaluate the association between selection and trait divergence, when selection was estimated by using logistic rather than linear regression, and when analyses using uncorrelated principal components axes in the place of individual traits were conducted. Table 1 presents the results of all these analyses, and further analytical details can be found in *Supporting Materials*, which is published as supporting information on the PNAS web site. Additionally, our estimates of selection were generally independent from which host the individuals used in the experiment originated from (i.e., ecotype), and they were unaffected by variation among replicates within treatments (i.e., different bushes in the same treatment). Specifically, we conducted selection analyses that considered not only the effect of trait values on survival but also the effects of the interaction between trait value and host of origin and the effects of the interaction between trait value and replicate number. In these analyses, only 5 of 88 interactions were significant at $P < 0.05$, and no interaction retains significance after correction for multiple comparisons (i.e., 11 traits; see Table 4, which is published as supporting information on the PNAS web site, for detailed results). Finally, because insects

could disperse in both predation scenarios, differences between them cannot be explained by differential dispersal. Our findings thus provide robust evidence that phenotypic diversification has been driven by divergent selection from predators.

Further evidence for the central role of predation in population divergence is indicated by stronger absolute divergent selection in the presence versus absence of predation for 10 of 11 traits individually ($P < 0.01$, paired *t* test; Fig. 3). Body brightness and stripe brightness exhibited particularly strong evidence for treatment-dependent selection, with selection differing significantly among treatments [$-2\log$ likelihood ($-2LR$) = 9.45, $P < 0.05$ and $-2LR = 12.14$, $P < 0.01$, respectively]. Under predation, divergent selection on these traits acted in opposite directions (Fig. 3). We simplified visualization and analysis of selection by considering a single “brightness contrast” trait that represents the difference in brightness between the body and the stripe (calculated as body brightness minus stripe brightness). Selection on brightness contrast varied significantly among treatments (Fig. 4; $-2LR = 9.58$, $df = 3$, $P < 0.05$). Thus predation favored bright bodies and dull stripes on *Ceanothus* (i.e., positive brightness contrasts; $P = 0.06$), but the opposite combination of bright stripes and dull bodies was selected on *Adenostoma* (i.e., negative brightness contrasts; $P = 0.01$; combined $P < 0.05$). Conversely, selection was weak and did not approach significance on either host when predation was absent (both $P > 0.35$). Strong selection in the presence of predation apparently favors increased crypsis and has driven adaptive divergence of the ecotypes. Quantitative measures of crypsis were not used and are not required to test the central prediction of a correlation between selection and trait divergence. However, such measurements could provide additional support for a role for crypsis and refine our understanding of color pattern evolution in these insects (13, 27).

Five caveats warrant discussion. First, adaptive radiation requires genetically based population divergence (2). Reciprocal-rearing experiments have shown that population divergence in the linear measurements considered here likely has a strong heritable component (23). Likewise, the presence versus absence of the striped pattern has a simple genetic basis, and population divergence in this trait is unaffected by rearing environment (28). Thus, the more

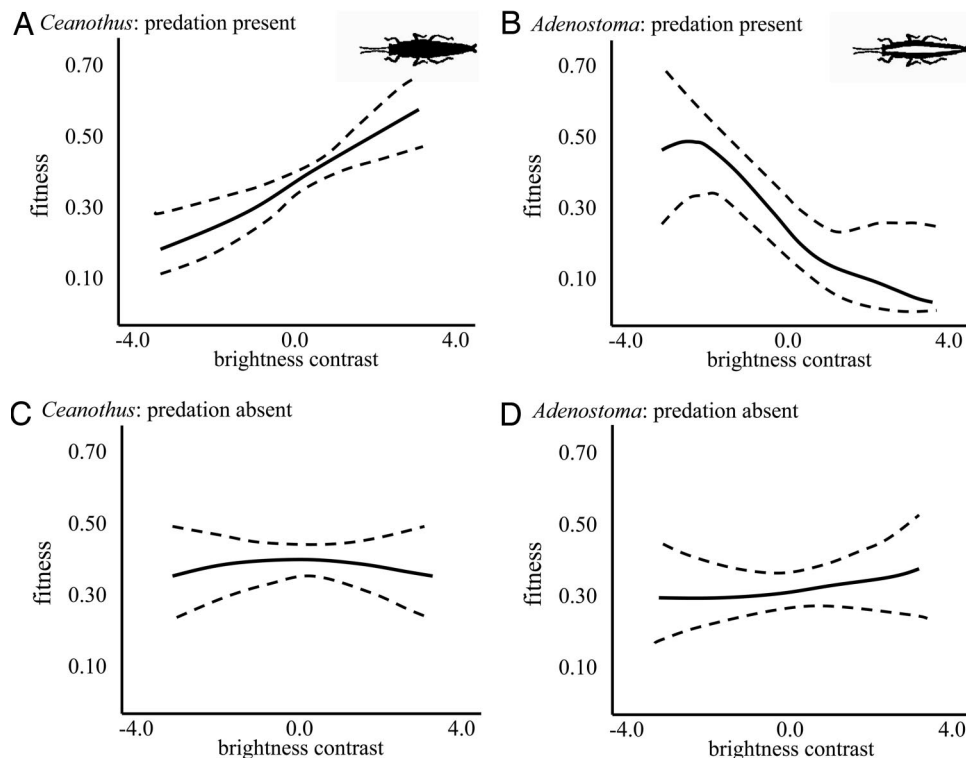


Fig. 4. Fitness functions depicting the relationship between fitness (probability of recapture as a proxy for survival) and brightness contrast (standardized body brightness minus standardized stripe brightness). Selection on brightness contrast varied significantly among treatments ($P < 0.05$). (A) Predation favored bright bodies and dull stripes on *Ceanothus* [B (regression coefficient) = 0.28 (0.16), $P = 0.06$]. (B) Predation favored bright stripes and dull bodies on *Adenostoma* [$B = -0.41$ (0.18), $P = 0.01$] (combined $P < 0.05$). (C and D) Selection was weak and did not approach significance on either hosts when predation was absent [$B = 0.01$ (0.15) and 0.06 (0.16), on *Ceanothus* and *Adenostoma*, respectively; both $P > 0.35$]. The fitness functions are estimated by using the cubic spline (ref. 38; dashed lines represent standard errors from 10,000 bootstrap replicates).

quantitative aspects of color examined here also likely exhibit a strong genetic basis, although further studies are required to confirm this hypothesis. Second, divergent selection in herbivorous insects commonly acts via tradeoffs involving physiological, rather than morphological, traits (29, 30). In *T. cristinae*, physiological tradeoffs in fitness do not occur (31). Third, the traits examined are not completely independent. However, this nonindependence does not affect our general conclusions because intertrait correlations were generally modest (see Table 5, which is published as supporting information on the PNAS web site), and associations between selection and trait divergence are predicted even if selection act on traits indirectly through selection on correlated characters (26). Even more importantly, the general patterns reported earlier persist when analyses are conducted by using principal components (PC) axes, which are uncorrelated (see Table 1 and Table 6, which is published as supporting information on the PNAS web site). Fourth, estimates of selection could be biased downward in traits that are less divergent between ecotypes (because of higher measurement error in such traits). This process did not occur as trait repeatabilities (i.e., error) were uncorrelated with all measures of selection (all $P > 0.35$; bivariate correlation). Fifth, adaptive radiation in a classical sense concerns divergence among species. The patterns detected between ecotypes of *T. cristinae* parallel those observed at the among-species level: In both cases, trait divergence is closely linked to host-plant use, and divergence in cryptic coloration is a central component of diversification (19).

Our results support a central prediction of adaptive radiation: a positive correlation between divergent selection and trait divergence. The findings contrast with previous studies demonstrating that the main effect of predation during adaptive radiation is to influence levels of resource competition by

reducing population density through mortality (16, 17). Rather, our findings show that predators can be a critical and direct source of divergent selection during adaptive radiation. A central role for predator-driven selection in adaptive divergence had long been argued in classical studies of crypsis and mimicry (12–14, 18, 13, 27, 32–34), and our results indicate that predation may be a more general mechanism of adaptive radiation than currently appreciated, particularly for many organisms where selection stemming from interspecific competition for resources is weak.

Materials and Methods

T. cristinae were collected near Santa Barbara, CA, from January to June 2003 and 2004 by using sweep nets. All specimens were photographed alive at standard distance by using a Canon (Lake Success, NY) digital camera with external flash in the same room at the University of California, Santa Barbara. Each photo also included a ruler and color standards. To estimate the repeatability of all measurements, 305 individuals were photographed twice. A conservative protocol was used such that each replicate photograph was taken on a separate day, and the specimens were measured twice for each trait (one set of measurements taken from each separate photograph). Previous work on this species has analyzed selection in relation to the presence versus absence of a stripe pattern (22, 25). Selection on quantitative morphology and population divergence in quantitative aspects of color and color pattern was not examined in previous studies.

Quantitative Morphological Divergence. A total of 604 individuals were measured for quantitative morphology by using the digital photographs (*Ceanothus*, $n = 283$; *Adenostoma*, $n = 321$).

Morphological traits were chosen based on functional considerations (i.e., color likely affects crypsis) and previous evidence of host-associated morphological divergence (23). A total of 20 measurements were taken in Photoshop (Adobe Systems, San Jose, CA), which were then collapsed into 11 traits for further analysis as described below (Fig. 1). All 11 traits were highly repeatable, and thus all traits were retained for further analysis (see Table 7, which is published as supporting information on the PNAS web site, for repeatability estimates).

The first set of traits represent quantitative aspects of color and color pattern variation. The hue, saturation, and brightness of different body areas were measured by using the “eyedropper tool” set at “5 by 5 average.” We avoided sampling areas reflecting the glare of the flash or that were poorly lit. The three body color measurements of the same type but from different body areas (e.g., hue measurements from different body areas) were averaged to create three “average” body color variables for further analysis (body hue, body saturation, and body brightness). Likewise, the two stripe measurements of each type were averaged to create three stripe color variables (stripe hue, stripe saturation, and stripe brightness). Additionally, the area of the stripe relative to the entire body area was estimated by outlining both the stripe and the entire body using the “lasso” tool and then using the “histogram” function to calculate relative areas. The second set of traits represents quantitative aspects of body size and shape. The measurements were taken by measuring the length of the trait and of 2 cm on the ruler in the photo by using the “measure tool,” and then scaling to absolute length. These linear traits were chosen based on previous work showing that the ecotypes differed primarily in three traits (overall body size, relative head width, and relative femur length; ref. 23) and by the fact that leaves of the different hosts differ markedly in width such that body width might affect crypsis (thus, the fourth trait was thorax width).

Divergence in quantitative morphology was examined by using both raw and size-corrected values. Size-corrected values are the residual values from a regression of each trait on a PC axis that was a general indicator of overall body size. This PC was the first axis derived from a PC analysis that included all of the linear measurements (linear measurements are *a priori* indicators of size). This PC axis exhibited high and positive loading for all linear traits (trait loadings: head width, 0.82; thorax width, 0.94; femur length, 0.75; body length, 0.89) and is thus appropriate for use in size standardization (35). Analyses using size standardization with body length alone gave congruent results. Mean divergence between ecotypes in each trait was examined after the trait was standardized to a mean zero and variance one (*z* scores; ref. 36).

Manipulative Field Experiment. Survival estimates stem from a previous mark-recapture experiment, where experimental details can be found (25). In summary, a replicated, random blocks design with four treatment levels was used (*Ceanothus* versus *Adenostoma*, with avian predators present versus absent). A schematic figure of the experimental set-up can be found in Fig. 5, which is published as supporting information on the PNAS web site. Avian predators were excluded by using chicken-wire enclosures (3-cm mesh), which were molded to surround an entire bush. Each of the four treatments were represented twice within each of two study sites with 24 individuals released onto each bush ($n = 96$ individuals for each of four treatments; each bush previously cleared of all *Timema*). Upon release, sex ratios were equal and morph frequencies were similar among bushes. Sample bushes were separated from all other suitable host plants by a minimum distance of 5 m (12 m is the per-generation dispersal distance; ref. 29). Recapture surveys were conducted 3, 10, 17, and 24 days after release (no individuals recaptured on the final recapture session). At both sites, insectivorous bird species were observed foraging on or near the experimental bushes. The previous study (25) did not quantify or analyze selection on quantitative traits in any way.

This study uses recapture in the experiment (recaptured or not) as a proxy for survival (survived or died). This methodology is highly appropriate and effective because (i) highly congruent results regarding survival were obtained for analyses based on raw recapture probabilities versus results obtained when recapture and survival probabilities were estimated separately (25); (ii) it adds simplicity, yet tends to yield results similar to more complicated survival analyses when recapture bouts are few (as in our experiment); and (iii) it is common procedure in selection analyses because it allows estimation of standardized selection differentials in regression analysis (26). We note that sex had no effect on survival (25), and that sex ratios in the samples used to estimate divergence in morphology are comparable between hosts (*Ceanothus*, 95 females and 188 males; *Adenostoma*, 75 females and 246 males). Thus, the effects of trait values, host-plant, or predation scenario on survival are not confounded by sex. Individuals used in the experiment originate from several populations on each host species (the majority from a contact zone between the host forms where variation is extreme). This approach increases the variation available for selection to act on and thus facilitates detection of selection (15, 17). Individuals were assigned randomly to treatment, such that use of individuals from both hosts increases the power of our experiment while being highly unlikely to confound our results. Finally, we stress that the effects of host of origin on survival are considered explicitly in our selection analyses (see *Selection Analyses*).

Selection Analyses. Standardized linear selection differentials were estimated within each of the four treatments (survival as the binary dependent variable) by using regression techniques (26). According to standard procedures, each trait was standardized to mean zero and variance one. All analyses were conducted by using both linear and logistic regression, and the robustness of the results to method of analysis was evaluated. We note that our primary goal was parameter estimation rather than significance testing of individual differentials such that selection estimates from linear regression are likely appropriate (26, 37). Whether selection differed significantly among treatments for individual traits was evaluated by using data from all treatments and then testing the significance of interaction between trait value (continuous covariate) and treatment (categorical covariate) in a selection analysis with survival as the dependent variable. Significance levels from logistic regression analyses were assessed by using the change in $-2\log$ likelihood (-2LR) when a term was removed from the model. Finally, the effects of host of origin and replicate on our selection estimates were considered as described in *Results* and Table 4.

Correlation Between Divergent Selection and Trait Divergence. Our central analysis tests for a correlation between the direction and magnitude of divergent selection and the direction and magnitude of trait divergence. The correlation reported in *Results* stems from a parametric correlation analysis of the relationship between the difference in selection differentials on different hosts (i.e., divergent selection estimated by using linear regression) and divergence in raw trait values between ecotypes. This correlation is sufficient and appropriate for evaluating the association between selection and trait divergence. However, to evaluate the robustness of this association, we also report this association by using both raw and size-corrected trait values, by using selection estimates from both linear and logistic regression, and by using parametric and nonparametric rank correlation of trait values against divergent selection. Results from all these analyses were congruent. Table 1 presents the results of all these analyses, and details can be found in *Supporting Materials*.

We conducted an explicit test for statistical differences be-

tween predation scenarios in the association between divergent selection and trait divergence by analyzing the interaction between predation scenario (present versus absent) and trait divergence. The analysis used repeated-measures ANOVA because selection was estimated on the same sets of traits in the presence versus absence of predation such that a paired design is most appropriate (36). Divergent selection is the within-subject factor, with predation present versus absent as factor levels. Trait divergence is included as a continuous covariate.

Analyses on Uncorrelated Principal Components Analyses. Intertrait correlations among the 11 traits examined were relatively low (see

Table 5), but the traits are not completely independent. We thus also estimated the relationship between selection and trait divergence by using PC axes, which are completely uncorrelated. The analyses supported the analysis by using individual trait values, thereby confirming a strong association between selection and trait divergence but only in the presence of predation (Table 1; and see Table 6, for detailed results of the PC analyses).

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