

RAPID MOVEMENT OF A *HELICONIUS* HYBRID ZONE: EVIDENCE FOR PHASE III OF WRIGHT'S SHIFTING BALANCE THEORY?

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Abstract.—It has been proposed that a moving hybrid zone can be a mechanism for the spread of adaptive traits in phase III of Wright's shifting balance model of evolution. Here I present an example of a moving hybrid zone in warningly colored *Heliconius* butterflies, a system which is considered to be a possible case of shifting balance evolution. Having moved approximately 47 km in 17 years, the hybrid zone shift has led to the *H. erato hydara* color pattern rapidly displacing the adjacent *H. erato petiverana* pattern. The movement is potentially due to dominance drive augmenting a slight selective advantage of *H. erato hydara* over *H. erato petiverana*, which is largely consistent with theoretical conditions favoring the success of phase III.

Key words.—Dominance drive, *Heliconius*, moving hybrid zone, shifting balance.

Received September 20, 2001. Accepted July 16, 2002.

Understanding of hybrid zone genetics has substantially increased over the last decade, but little attention has been paid to one of the most interesting features of hybrid zones—mobility. Zone movement is theoretically possible, but is difficult to document because it requires long-term study of hybrid zone positions (McDonnell et al. 1978; Moore and Buchanan 1985; Kohlman and Shaw 1991; Urbanelli et al. 1997; Hafner et al. 1998; Britch et al. 2001; Dasmahapatra et al. 2002). The relatively few empirical studies documenting positional shifts partly underlies a common assumption that most clines and hybrid zones have reached a migration-selection equilibrium and have been stable for long periods of time (Barton and Hewitt 1985, 1989). Yet such assumptions of long-term stability remain largely untested. Theory suggests that disruption of equilibrium conditions, such as environmental change or genetic asymmetries, may force a hybrid zone to move (Barton 1979; Mallet 1986a; Mallet and Barton 1989a). Hybrid zones acting under exogenous selection are expected to track any underlying ecological changes because differential selection for or against particular genotypes across an ecotone will force clines to settle on the boundary between environments. When under endogenous selection (such as selection against heterozygotes, epistatic selection, or frequency-dependent selection against rare genotypes), the position of the zone becomes arbitrary and may shift in response to any asymmetrical change in migration or selection. Identifying the factors underlying positional shifts may offer key insights into the maintenance and fate of hybrid zones.

Shifting clines and hybrid zones are potentially important forces of evolutionary change as a form of phase III of Sewall Wright's controversial shifting balance hypothesis (Wright 1932; Mallet 1986a, 1993; Rouhani and Barton 1987). Wright (1932) envisioned evolution as a three-step process. After an initial phase of genetic drift (phase I), alternate states of an adaptive trait become prevalent in separate populations (phase II). The third phase occurs when the global adaptive peak of the fitness-enhancing trait spreads from population to population via interdemec selection. Wright (1932) described phase III as the spread of a fitness-enhancing trait

via interdemec selection, and other work showed that cline motion can also result in the spread of such a trait (Rouhani and Barton 1987). A moving hybrid zone represents a mechanism for the spread of an adaptive or fitness-enhancing trait because two adaptive peaks may meet and form a cline stabilized by a migration-selection balance, which then shifts in favor of the fitter peak (Rouhani and Barton 1987). Because there is little evidence for phase III and for all three phases acting in the same system, the shifting balance model of evolution has been largely discounted (Haldane 1959; Coyne et al. 1997, 2000). Evidence for cline mobility, especially in a model system that has been widely considered a potential example of the shifting balance process, may encourage more work to clarify the importance of Wright's hypothesis (Wade and Goodnight 1998, 2000).

In the present study, I demonstrate the existence of cline movement in a system in which the shifting balance has been proposed to be important, warningly colored *Heliconius* butterflies. Mullerian mimicry in *Heliconius* butterflies is considered one of the best examples of natural selection maintaining alternative stable equilibria (Turner and Mallet 1996). Many of these butterflies have evolved similar aposematic wing color patterns under frequency-dependent predation on individuals expressing rare patterns (Mallet and Barton 1989a,b). Evidence for strong selection on wing color pattern helps explain the homogeneous distribution of patterns within species and between Mullerian mimics (Mallet and Barton 1989b; Kapan 2001). However, many *Heliconius* species are subdivided into wing color pattern races, which participate in multiple mimicry rings. The most thoroughly studied example is *H. erato* and *H. melpomene*, which form a mosaic of parapatrically distributed, parallel races that are separated by coincident hybrid zones. Mallet (1986a, 1993) as well as Mallet and Joron (1999) have argued that the races formed through a shifting balance process. This argument has been criticized partly because no study has demonstrated the spread of one wing color pattern at the expense of a competitor (Turner and Mallet 1996; Coyne et al. 1997). By documenting that color pattern cline motion involves the replacement of one pattern over another, this study tacitly sup-

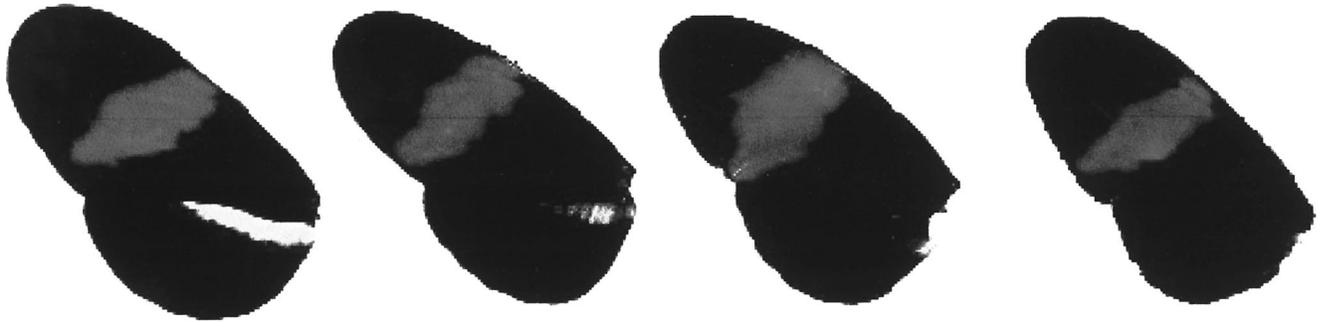


FIG. 1. Dorsal wing color patterns of *Heliconius erato petiverana* (far left) and *H. erato hydara* (far right). Hybrids (middle two) express a gradient of intermediate states—the abundance of yellow scales can range between nearly complete to only a shadow of lightened black on the ventral hindwing.

ports the shifting balance model of *Heliconius* evolution (Mallet 1986a, 1993). Although it is unclear whether the documented cline motion represents an example of phase III acting in nature, this study nonetheless suggests that wing color patterns are labile traits that may rapidly respond to changes in adaptive conditions.

MATERIALS AND METHODS

Mallet (1986a) first characterized the *H. erato petiverana* and *H. erato hydara* Panamanian hybrid zone in 1982. Located at Cañazas on the border between Panamá and the Darién Provinces, it was located in the same region as the *H. melpomene rosina* and *H. melpomene melpomene* hybrid zone. Mallet's 1982 transect paralleled the Pan-American Highway, and included sites between El Copé in Coclé and Yaviza, Darién. He also included sites located farther into eastern Darién forests. Mallet's sampling across the Cañazas zone was more extensive for *H. erato* than for *H. melpomene* because *H. erato* was more abundant during the sampling period. My choice to focus on the *H. erato* races reflects similar sampling conditions. Further work on the *H. melpomene* races and the interactions between *H. erato* and *H. melpomene* is in progress.

The *H. erato petiverana*–*H. erato hydara* zone has three notable characteristics: (1) it is wider than most other *H. erato* zones; (2) it does not correspond to any obvious underlying ecotone; and (3) the two hybridizing races are distinguished by the expression of only one major wing color pattern locus, Y/y_{ca} (Mallet 1986a), more appropriately termed Cr/cr_{ca} (Sheppard et al. 1985; Mallet et al. 1990). In 1982, the zone was a gentle cline 80 km wide, whereas many other *H. erato* hybrid zones have been documented to be only 10–20 km wide (Benson 1982; Mallet and Barton 1989a; Mallet et al. 1990; Mallet 1993). The zone's center, located at Cañazas, did not correspond to a distinctive habitat change. The road to the region had been recently built, and at the time, deforestation was only partially complete near the road (J. Mallet, pers. comm.). Mallet (1986a) also determined that the hindwing yellow bar expressed in *H. erato petiverana*, which is absent in *H. erato hydara*, is the recessive expression of a single locus, cr_{ca} , with standard Mendelian inheritance. Heterozygous hybrids (Cr/cr_{ca}) express an intermediate pattern of either a broken bar or a lightened shadow of a bar (Fig. 1). The genetic control of color pattern elements be-

tween other hybridizing *H. erato* races typically involves more loci and more complex inheritance (Sheppard et al. 1985; Mallet 1989; Jiggins and McMillan 1997).

Crosses between *H. erato petiverana* and *H. erato hydara* showed no evidence of hybrid sterility, inviability or breakdown. Mallet's (1986a) results also showed that populations did not deviate from expected Hardy-Weinberg equilibrium ratios, suggesting that no premating preferences or assortative mating occurs between the two races. Although these results are consistent with early interracial hybridization studies, recent work nonetheless indicates that some *Heliconius* races do show assortative mating (Mallet 1986a; Jiggins et al. 2001). Studies also indicate that *Heliconius* hybrids suffer lower fitness because of frequency dependent predation against individuals expressing rare wing color patterns (Mallet and Barton 1989b; Mallet et al. 1998; Kapan 2001). The selection against hybrids can be strong enough to stabilize both the position and shape of the hybrid zones (Mallet and Barton 1989b). However, Mallet (1986a) suggested that the hybrid zone in Panama may prove more mobile than other *Heliconius* zones because the color pattern differences between the races are minor (Fig. 1) and the zone does not correspond to an ecotonal boundary. He proposed that westward cline movement due to dominance might occur at a considerably high rate if the dominant black hindwing allele spreads and replaces the recessive yellow bar allele. This process, termed "dominance drive," occurs when selection on phenotypes is equal, but selection on genotypes or alleles is asymmetric (Mallet 1986a; Mallet and Barton 1989b).

I revisited the Cañazas zone in November and December of 1999 to determine whether the position or width of the zone had changed in the intervening 17 years. I extended Mallet's (1986a) original transect to include samples between Boquete in Chiriquí Province and El Copé in Coclé Province (Fig. 2; Table 1). Additional samples were taken at sites removed from the transect for other research on the genetic differentiation of *H. erato* populations across Panama. I completed the transect by visiting the sites listed in Mallet (1986a) between Panama City and Yaviza in Darién Province. Samples were not taken at some sites because of localized deforestation and because of access problems due to guerilla activity, no samples were taken east of Yaviza. Individual butterflies were typically sighted visiting adult food plants, chased, and caught with an aerial net. Table 1 lists site lo-

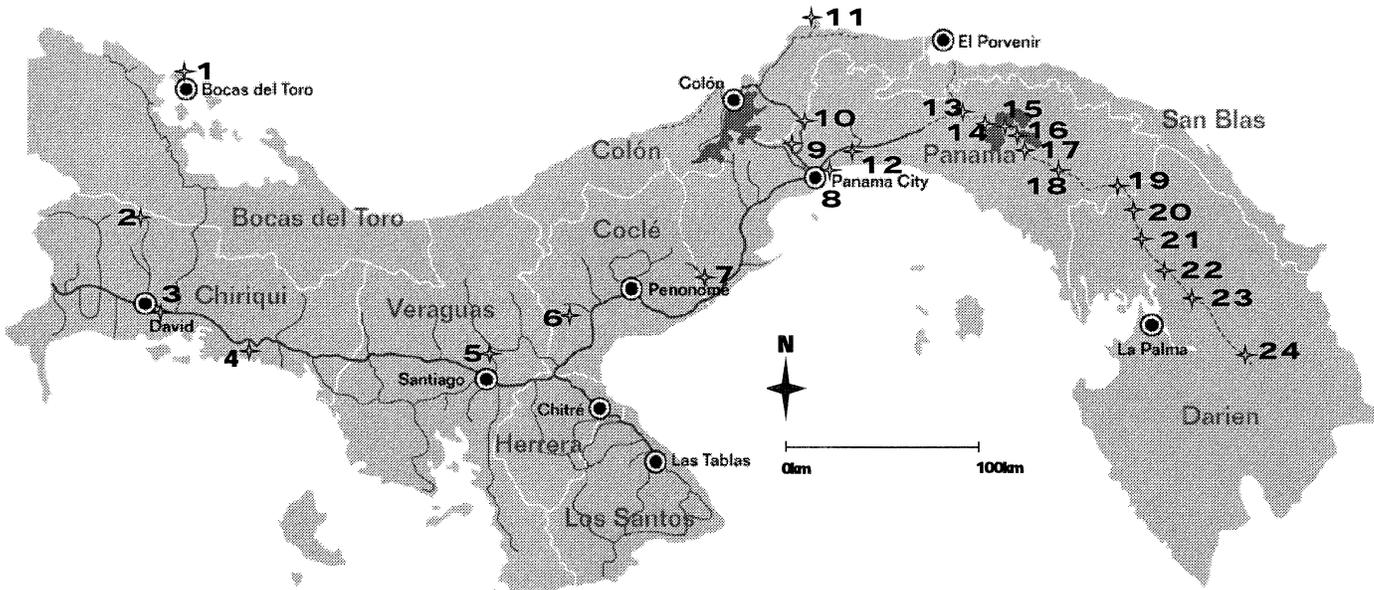


FIG. 2. Sample sites in Panama referenced to major roads, cities, and inland water bodies. Sample sites are noted with diamonds. The 1999–2000 transect runs parallel to the Pan-American Highway between David and Yaviza. Site numbers correspond to names in Table 1.

cations along with sample sizes of *H. erato* categorized by genotype.

H. erato individuals were genotyped for expression of the yellow hindwing bar, and frequencies of the yellow bar allele were directly estimated as

$$p = \frac{\text{no. cr}_{ca}\text{cr}_{ca} + \frac{\text{no. Cr cr}_{ca}}{2}}{\text{total}} \quad (1)$$

from the samples from each site. Using a maximum-likelihood (ML) approach, I then fitted sigmoidal tanh clines to the 1982 and 1999–2000 population frequency data across sites through the ‘Fit 1-D Cline’ routine in Analyse 1.30 PPC (Barton and Baird 1996). After setting F_{ST} to approximate zero (Dasmahapatra et al. 2002), I then set the p_{max} and p_{min} (the maximum and minimum gene frequency values at the tail ends of the clines) as one and zero, respectively, while allowing both the cline centers and cline widths to vary. Following the approach of B. L. Phillips, S. J. Baird, and C. Moritz, (unpubl. ms.), I built likelihood profiles for both cline positions and widths to compare the 1982 and 1999–2000 cline shapes (Hilborn et al. 1997). For each sampling period, likelihood surfaces were constructed stepwise along axes for either center position or width, with all other parameters varying freely. The ML estimate for the 1999–2000 cline center was then compared to the \log_e likelihood value obtained for the 1982 center position. This comparison and the reciprocal 1982 to 1999–2000 comparison were done using likelihood-ratio tests, under the assumption that twice the difference in \log_e likelihood ($G = -2\Delta LL$) between two models asymptotically follows a χ^2 distribution with the degrees of freedom corresponding to the difference in the number of parameters. Thus, if the ML estimate of one cline center fell beyond two units of the ML estimate for the other, the clines from the two sampling periods were considered non-

coincident. The same procedure was followed to assess cline concordance by comparing the ML estimates for static width values to values reflecting width change. Support limits for the ML estimates for the cline center positions and widths were obtained from the likelihood profiles, delimited by the first values with \log_e likelihood estimates more than two units below the maximum (Dasmahapatra et al. 2002).

RESULTS AND DISCUSSION

Current Width, Position and Velocity of the Hybrid Zone

A total of 421 individuals were caught along the transect between Boquete and Yaviza. An additional 41 individuals were caught at sites off the transect (Table 1). The sample size per site along the transect ranged between four and 51 individuals, with a mean of 20 per site. Much of the difference (total numbers, number of individuals/site) between the current collection and Mallet’s (1986a) 1982 collection reflect reductions in forest distribution adjacent to the Pan-American Highway. *H. erato* races are associated with forest habitat, because both adult and larval food plants commonly grow in secondary forest, or gap and edge conditions near primary forest.

The 1999–2000 ML cline of the recessive yellow bar allele is compared to the 1982 ML cline in Figure 3. Because the yellow bar allele distinguishes the two races, this allelic cline can be used to demarcate the position and shape of the hybrid zone. Comparison of the 1982 and 1999–2000 collection data indicates that the current center of the zone now lies approximately 47 km to the west of its 1982 position ($G_{1999-1982} = 40.47$, $P < 0.001$; $G_{1982-1999} = 38.72$, $P < 0.001$). In 1982 the center of the cline was just west of Cañazas, roughly 167 km (146–175 km) east of Panama City. The center is now located along the east shore of Lago Bayano, 120 km (107–133 km) east of Panama City.

TABLE 1. *Heliconius erato* butterflies sampled per location in 1999–2000. Numbers before location names correspond to numbers in Figure 1. Numbers in parentheses following location names correspond to sites visited by Mallet in 1982 (1) and/or Blum in 1999–2000 (2). Coordinates correspond to sample locations. An asterisk denotes a site off the primary transect.

Location	Latitude (N)	Longitude (W)	<i>H. e. petiverana</i>	Heterozygotes	<i>H. e. hydara</i>	Total
1. Bocas del Toro, B. del Toro (2)*	09'23.415	082'14.330	26	0	0	26
2. Boquete, Chiriquí (2)	08'46.448	082'26.318	19	1	0	20
3. David, Chiriquí (2)	08'22.896	082'19.965	10	0	0	10
4. Remedios, Chiriquí (2)	08'12.707	081'49.071	12	0	0	12
5. Calobre, Veraguas (2)	08'15.296	080'46.693	11	0	0	11
6. El Copé, Coclé (1, 2)	08'31.792	080'31.025	10	0	0	10
7. El Valle, Coclé (2)	08'29.464	080'01.380	11	2	0	13
8. Panama City, Panamá (1, 2)	08'54.891	079'31.833	42	4	0	46
9. Pipeline Road, Panamá (2)*	09'09.840	079'44.173	11	1	0	12
10. Madden Dam, Panamá (1, 2)*	09'12.964	079'37.291	3	0	0	3
11. Isla Grande, Colón (2)*	09'37.843	079'34.460	2	0	0	2
12. Tocumen, Panamá (1, 2)	09'12.025	079'23.715	1	0	0	1
13. El Llano, Panamá (1, 2)	09'14.007	078'57.483	19	6	0	25
14. Loma de Naranjo, Panamá (2)	09'10.811	078'53.084	26	14	0	40
15. Corp. Bayano, Panamá (1, 2)	09'10.486	078'44.549	13	30	8	51
16. 10 km east of Bayano, Panamá (2)	09'10.126	078'43.000	5	13	4	22
17. 20 km east of Bayano, Panamá (2)	09'06.435	078'40.808	5	12	4	21
18. Rio Ipetí, Panamá (2)	08'58.459	078'29.035	1	6	19	26
19. Cañazas, Panamá (1, 2)	08'53.927	078'13.322	0	2	6	8
20. Agua Fria #1, Darién (2)	08'50.403	078'11.625	0	5	17	22
21. Quebrada Mono, Darién (1, 2)	08'37.775	078'06.216	0	1	4	5
22. Metetí, Darién (1, 2)	08'38.017	078'06.374	0	2	2	4
23. Canglón, Darién (1, 2)	08'16.805	077'48.574	0	1	24	25
24. Near Yaviza, Darién (1, 2)	08'12.277	077'43.095	2	1	44	47
Total numbers collected						462

The ML estimate for the 1982 width of 66 km (41–98 km), is not measurably different from the 58 km (44–101 km) ML estimate of the 1999–2000 cline width ($G_{1999-1982} = 0.28$, $P > 0.50$; $G_{1982-1999} = 0.24$, $P > 0.50$). A width of 58–66 km for a dominant cline suggests that *H. erato* migrate (σ) roughly 9.4–18.7 km, assuming a range of plausible selection coefficients of $s = 0.21$ – 0.64 (Benson 1972; Mallet 1986a; Mallet and Barton 1989b; Mallet et al. 1990; Kapan 2001), where

$$w = \sqrt{\frac{8\sigma^2}{s}} \quad (2)$$

(Mallet and Barton 1989b). Values of σ have been suggested to be as low as 0.293 km and as high as 10 km (Mallet 1986a,b; Mallet et al. 1990). The observed velocity, v , of the *H. erato* hybrid zone is approximately 2.6 km per year. With four generations a year, and if $s = 0.21$ – 0.64 , σ would be 5.7–10 km, where

$$v = 0.1\sqrt{2\sigma^2s} \quad (3)$$

and $s_{petiverana} = s_{hydara} = s$. This equation assumes that the cline moves under a selective asymmetry generated by dominance alone (Mallet and Barton 1989b). These results agree with the result obtained by jointly solving for selection and migration using equations (2) and (3) as a pair of simultaneous equations (Dasmahapatra et al. 2002): $\sigma = 10.4$ – 9.71 km, and $s = 0.20$ – 0.22 for cline width estimates based on 1982 and 1999–2000 values, respectively.

Is an Allelic Asymmetry Forcing the Shift?

Mallet's (1986a) simulations showed that dominance drive could force the color pattern cline to move even if there is

equal selection on phenotypes, and his prediction of westward motion by 2 km per year via dominance drive is remarkably close to the observed velocity. Dominance drive may therefore be a considerably important third force, alongside migration asymmetry and selective advantage of phenotypes, influencing the position and fate of hybrid zones (Mallet 1986a; Phillips 1993). Although the observed velocity suggests that dominance drive is a likely force moving the hybrid zone, the motion may be due to a combination of forces because dominance drive may augment or counteract migration or selection asymmetries. It is therefore worth considering whether there have been any significant landscape changes that may have forced the cline to move by causing asymmetrical migration to the hybrid zone. It is also worth assessing whether selection on the parental phenotypes is equal, and if not, how the imbalance would affect the velocity of the cline motion.

Landscape change is relevant because the Río Bayano watershed was flooded only 5–6 years before Mallet (1986a) collected along the Pan-American Highway. Lago Bayano filled a large proportion of the lower watershed and created an inland peninsula in what was once a contiguous valley running between the Serranía de Maje and the Serranía de San Blas. Because the lake could act as a partial barrier to gene flow and falls within one cline width of the zone center, it could plausibly have forced the zone to move westward (Endler 1977; Barton 1979; Barton and Hewitt 1985). Yet evidence indicates that the lake has not disrupted migration to and from the *H. erato* zone. If the creation of Lago Bayano led to a broad disruption of migration patterns, it is likely that the *H. melpomene rosina*–*H. melpomene melpomene* zone would have exhibited a shift concordant with the *H. erato*

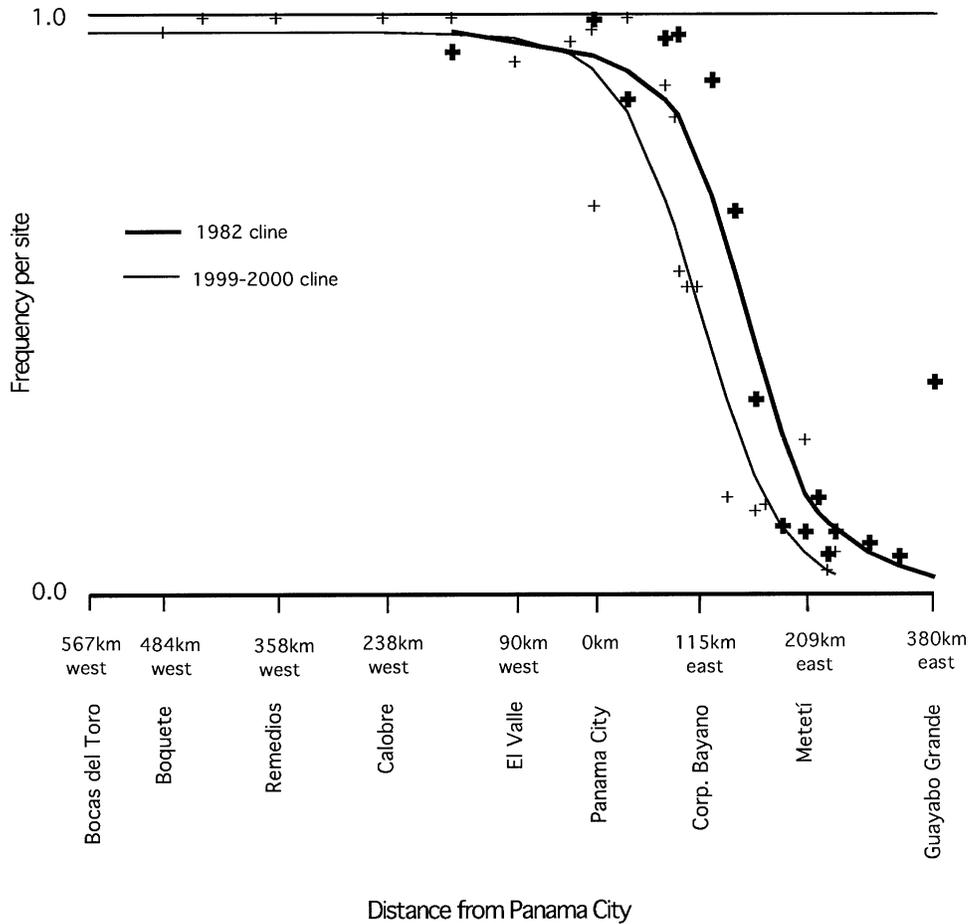


FIG. 3. Comparison of clines representing the frequency of the yellow hindwing bar allele at sites along the Panama transect in 1982 (Mallet 1986a) and in 1999–2000. The center of the 1999–2000 cline has shifted approximately 47 km to the west of its 1982 position.

zone. In 1982, this hybrid zone was also located near Cañazas, with the *H. erato* zone. Preliminary data suggests that the center of the *H. melpomene* zone remains close to its 1982 position (M. J. Blum, unpubl. data). Contrary evidence also comes from a third butterfly hybrid zone located in eastern Panama. Although the slope of the corresponding character clines are steeper, and therefore the creation of the lake may have less influence on position of the zone, the *Anartia fatima*–*A. amathea* zone has shifted eastward at roughly the same rate as the *H. erato* zone's westward movement (Dasmahapatra et al. 2002).

As Mallet (1986a) pointed out, there is no available evidence indicating asymmetric selection in favor of one *H. erato* color pattern race over the other. Nevertheless, an argument for asymmetric selection can be made in light of recent land-use changes and observed habitat preferences of the different races. A corridor of deforestation has been cut through eastern Panamá and western Darién Provinces over the past 17 years, with the affected area running adjacent to the Pan-American Highway until the road's end at Yaviza. The subsequent conversion of the land to agricultural production has produced savannah-like conditions in recently deforested areas. Although nearly all *H. erato* races require forest edge and high light conditions, *H. erato hydara* is notable for inhabiting forest-savannah habitat mosaics

throughout its range from Panama to French Guiana (J. Mallet, pers. comm., M. J. Blum, pers. obs.). J. Mallet (pers. comm.) has suggested that *H. erato hydara* may have a slight advantage in savannah-like conditions to the exclusion of other races. This selective advantage may have led to asymmetric selection or migration in favor of *H. erato hydara*, thus moving the *H. erato* zone westward. If the cline is maintained by frequency-dependent selection equivalent to underdominance (Mallet and Barton 1989b), the observed velocity can be used to estimate this selective advantage of *H. erato hydara* over *H. erato petiverana* (Barton 1979; Dasmahapatra et al. 2002). Where s is the selection coefficient of heterozygote disadvantage or frequency dependent selection against hybrids, we can solve

$$v = \frac{S}{2\sqrt{\frac{2\sigma^2}{s}}} \quad (4)$$

for S to determine the relative fitness of one race over the other (where the fitness of *hydara* homozygotes = $1 + 2S$, heterozygotes = $1 - s + S$, and *petiverana* homozygotes = 1). Thus, if dominance drive is not influencing the *H. erato* zone, *H. erato hydara* would have a selective advantage of 0.039–0.045 (where $\sqrt{\sigma^2/s} = 20.5$ – 23.3 km) over *H. erato petiverana* to explain the observed velocity. The advantage of *H. erato hydara* would be some fraction of this if domi-

nance drive and asymmetric selection were acting together to move the zone. Additional work on other *H. erato* hybrid zones may clarify whether habitat-dependent selection asymmetries exist among the races.

Warning Color Pattern Evolution and the Shifting Balance

Coyne et al.'s (1997) commentary on whether evolution proceeds via Fisherian mass selection or by Wright's shifting balance model lists *H. erato*–*H. melpomene* butterfly mimicry as one of six natural systems that are the likeliest candidates of shifting balance evolution. The authors conclude that, although some work suggests these butterflies evolve via the shifting balance process, no study clearly shows that divergence (i.e., color pattern radiation) involves all three phases (Coyne et al. 1997). Insufficient evidence for the spread of one color pattern at the expense of another is an important criticism of the shifting balance model of *Heliconius* evolution. Yet this study clearly shows that zone motion may lead to the replacement of one color pattern by another.

Although the *H. erato petiverana*–*H. erato hydara* hybrid zone shift may have many of the hallmarks of phase III acting in a natural system, it does not fully correspond to all the conditions of Wright's original shifting balance model. This is in part due to the possible action of dominance drive, but it is also due to the apparently simple genetic architecture of the wing color pattern differences between the two races. Both Mallet (1986a) and Phillips (1993) showed that a trait that is not favored by individual selection can nevertheless spread via cline movement if the trait involves a genetic asymmetry such as dominance. Therefore if the color pattern cline movement is due entirely to dominance drive, it would not necessarily enhance overall fitness and therefore would not be a good example of fitness maximization by the shifting balance. Yet dominance greatly increases the invasiveness of an adaptive trait during phase III (Barton 1992; Phillips 1993). Given that the observed velocity exceeds the expected velocity for dominance drive acting alone, it may be that the observed shift is driven by dominance augmenting a slight competitive advantage of one race over the other, leading to differential migration. Dominance drive may therefore be facilitating fitness maximization that under other conditions may act over extended time periods or may not occur at all. In the case of *Heliconius* mimicry, this could take the form of reduced predator recognition error for an invading, novel pattern as it becomes more frequent in a given area.

Because the Panama *H. erato* cline appears to only involve a single locus, it would represent a simplified version of Wright's (1932) original shifting balance model. Subsequent work by Lande (1984) and Barton (1992) describes the process for a single underdominant locus, and Phillips (1993) has shown that phase III is greatly facilitated if it only involves a few loci. Nonetheless, Wright (1932) notes that the shifting balance process involves the spread of a fitness enhancing, complex trait that arises from epistatic interactions between multiple genetic elements. Although the cline motion observed in this study clearly involves the invasion and spread of a dominant locus, it is unclear whether the color pattern difference between the two races has the simple architecture of a single gene. Mallet (1989) has suggested that

Heliconius wing color patterns are generated by supergene complexes with epistatic interactions. These complexes may be strongly linked, and will therefore be influenced by selection on a specific region controlling color pattern expression. Even if the *H. erato petiverana*–*hydara* color pattern difference is produced by a single gene, the spread of the *H. erato hydara* pattern may still provide a demonstration of a more general process involving more loci or epistasis.

ACKNOWLEDGMENTS

I thank K. Zigler, T. Duda, and D. Pope, among others, for helping collect specimens. I also thank E. Bermingham for sponsoring this project and providing valuable advice through the course of the study. This study would not have been possible without the support and permits obtained from the Panamanian government offices of ANAM and INREN-ARE. This study was funded by: the Smithsonian Tropical Research Institute, the National Securities Education Program, the Explorer's Club, and the Duke University Latin America Studies Program. MJB was also supported by a National Science Foundation predoctoral fellowship.

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