(d) of the worm is 200 μm (see Supplementary Information). All assumptions are conservative and result in an overestimation of sulphide flux from the sediment (see Supplementary Information). Internal sulphide production from the symbionts is based on SRRs measured in worms incubated in sand (Table 1), assuming that all sulphide produced is consumed by the sulphide-oxidizing symbionts. SRRs in the worms are assumed to be underestimated, given that no external electron donor was used and experimental conditions are suboptimal in comparison to the natural environment.

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Reproductive isolation caused by colour pattern mimicry

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Speciation is facilitated if ecological adaptation directly causes assortative mating[1], but few natural examples are known. Here we show that a shift in colour pattern mimicry was crucial in the origin of two butterfly species. The sister species *Heliconius melpomene* and *Heliconius cydno* recently diverged to mimic different model taxa, and our experiments show that their mimetic coloration is also important in choosing mates. Assortative mating between the sister species means that hybridization is rare in nature, and the few hybrids that are produced are non-mimetic, poorly adapted intermediates. Thus, the mimetic shift has caused both pre-mating and post-mating isolation. In addition, individuals from a population of *H. melpomene* allopatric to *H. cydno* court and mate with *H. cydno* more readily than those from a sympatric population. This suggests that assortative mating has been enhanced in sympatry.

Mimicry is viewed mainly as a clear, visual demonstration of natural selection within species. But this was not always so: mimicry among Amazonian butterflies was originally presented as a striking example of speciation due to natural selection[2]. More recently, it has been argued that divergence in mimetic pattern can result in intermediates having low fitness because they are non-mimetic and, if colour pattern is also used in mate recognition, assortative mating. Therefore, both pre-mating and post-mating reproductive isolation might result from the evolution of mimicry[3–5]. Here we study mate choice in *Heliconius* butterflies, a group well known for Müllerian mimicry (mimicry between distasteful species)[2,4,5]. Closely related *Heliconius* species generally differ in mimetic colour pattern, as though adaptive radiation has occurred[6,7]. The sister species *H. melpomene* and *H. cydno* are sympatric throughout Central America and the Andean foothills, where they differ in mimicry (Fig. 1) and habitat use[8]. They occasionally hybridize and backcross in nature: hybrid females are sterile, but males are fertile and can be used in the laboratory to introgress genes between the species[8–10]. In most areas, *H. melpomene* mimics the black, red and yellow pattern of *H. erato*, whilst *H. cydno* mimics the black and white pattern of *H. sapho*. *Heliconius cydno* and *H. melpomene* separated in the last 10^6 years, much more recently than the non-sister species *H. sapho* and *H. erato* (Fig. 1)[11]. This and other evidence implies that *H. cydno* and *H. melpomene* have diverged to mimic *H. sapho* and *H. erato*, rather than vice versa[12].

Sympatric Panamanian *H. melpomene* and *H. cydno* did not mate with one another in choice experiments (Tables 1 and 2), although they will do so in no-choice tests[8–10]. Males from sympatric populations spent over 25 times longer courting virgin females of their own race than heterospecifics (Fig. 2). *Heliconius* females mate soon after eclosion, when they are unable to reject males, so that courtship and assortative mating is largely due to male choice[7]. To test whether males use mimetic colour pattern as a cue in choosing mates, we investigated the response of males to moving models made with either natural wings or coloured paper. Panama *H. melpomene* males approached *H. cydno* colour patterns about half as frequently as those of their own type, and were much less likely (2–4%) to court them (Fig. 3). Similarly, *H. cydno* males were a third as likely to court a *H. melpomene* pattern as their own type, although

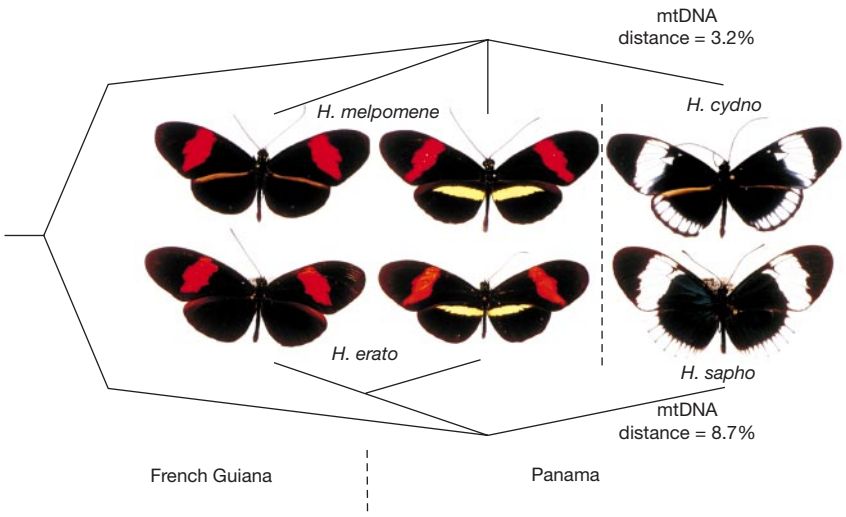

Figure 1 *Heliconius melpomene melpomene* (left, French Guiana), *H. melpomene rosina* (centre, Panama), *H. cydno chioneus* (right, Panama) are shown together with co-mimics (below) *H. erato hydara*, *H. erato cf. petiveranus* and *H. sapho sapho* respectively. Molecular phylogenies (enclosing butterflies) show that the two races of *H. melpomene* and *H. cydno* form an unresolved trichotomy. Mitochondrial sequences suggest *H. melpomene* is paraphyletic with respect to *H. cydno*[11], whereas unpublished sequences from nuclear loci show reticulate or mutually monophyletic relationships between the two species (V. Bull and M. Beltrán, personal communication). Divergence between mitochondrial sequences of *H. erato* and *H. sapho* is almost three times that between *H. melpomene* and *H. cydno* (percentage distance across 940 base pairs of the COI, leu-tRNA and COII genes)[11], suggesting that *H. melpomene* and *H. cydno* diverged to mimic *H. erato* and *H. sapho* rather than vice versa. mtDNA, mitochondrial DNA. COI, Cytochrome oxidase I; COII, cytochrome oxidase II.

the probability of initial approach did not differ from that towards conspecifics (Fig. 3). The initial attraction of male *H. cydno* to the red *H. melpomene* pattern may be due to a generalized attraction of *Heliconius* to red flowers. The butterflies clearly responded to visual cues in these experiments, as neither attraction nor courtship differed significantly in comparisons between paper models and real butterfly wings (Fig. 3).

Heliconius melpomene males from French Guiana, where *H. cydno* does not occur, courted live *H. cydno* females twenty times more vigorously than *H. melpomene* males from sympatry with *H. cydno* in Panama (Fig. 2), and the mating experiments showed a similar trend ($G_1 = 3.78$, $P \simeq 0.06$; Table 2). This was again a response to colour pattern, as *H. melpomene* males from French Guiana were also more likely than Panamanian *H. melpomene* males to court a *H. cydno* model (combined results from the coloured model and real wing experiments; $G_1 = 8.02$, $P < 0.01$; Fig. 3). In addition, *H. melpomene* males from Panama only reluctantly courted live French Guianan *H. melpomene* females, whereas French Guianan *H. melpomene* males showed no discrimination (Fig. 2); indeed all French Guiana × Panama *H. melpomene* matings in these tests involved French Guiana males (Table 1). Among *H. melpomene* races, males showed greater discrimination between live females (Fig. 2 and Table 1) than between models (Fig. 3), indicating that cues other than colour pattern, such as pheromones, may be involved. Hence, *H. melpomene* males sympatric with *H. cydno* discriminated more strongly than *H. melpomene* allopatric to *H. cydno*. This pattern is expected if mate preference has been 'reinforced' to prevent the production of unfit hybrid offspring in sympatry[13,14], although the evidence would be strengthened if replicated with other allopatric and sympatric populations[14,15]. Of course, character displacement between non-hybridizing species cannot be ruled out. For example, the presence of *H. sapho* might

Table 1 Number of matings in tetrad mate choice experiments

Female	Male	Male
Sympatric populations		
	H. melpomene (Panama)	*H. cydno* (Panama)
H. melpomene (Panama)	14	0
H. cydno (Panama)	0	11
Allopatric populations		
	H. melpomene (Panama)	*H. melpomene* (Guiana)
H. melpomene (Panama)	9.5	4
H. melpomene (Guiana)	0	13.5
	H. melpomene (Guiana)	*H. cydno* (Panama)
H. melpomene (Guiana)	14.5	0
H. cydno (Panama)	3	12.5

Mating results of 0.5 are due to two cases of virtually simultaneous mating by both pairs in a tetrad (see Methods).

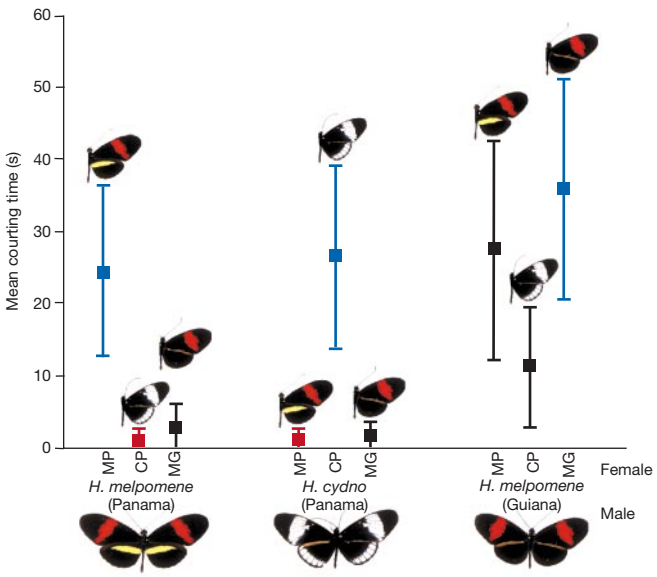

Figure 2 Time spent courting live females in 10-min trials with 95% confidence intervals. Red, comparisons between sympatric populations; black, comparisons between allopatric populations; blue, comparisons between males and females of the same genotype. MP, *H. melpomene* (Panama); CP, *H. cydno* (Panama); MG, *H. melpomene* (Guiana).

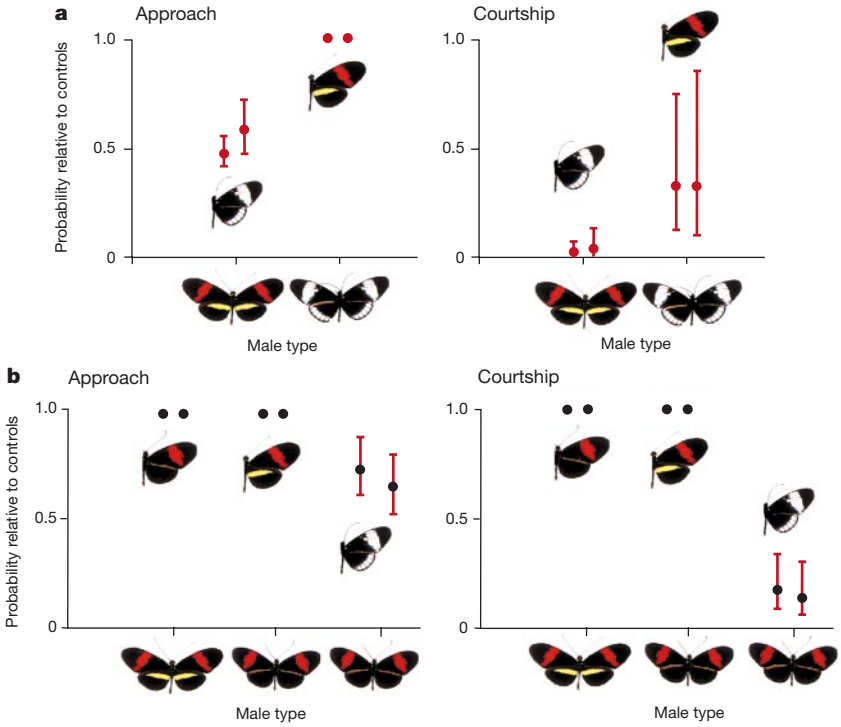

Figure 3 Relative probabilities of male approach and courtship of colour pattern models. Comparisons between Panama populations (sympatry) (**a**) and with the Guiana population (allopatry) (**b**). Values are estimated relative to within-race controls (equal to 1 in each case). Paired data points for experiments using real wings (left) and coloured paper models (right) are shown for each comparison. Values of Q_A (approach) and Q_H (hovering courtship) were estimated with support limits under the ten-parameter model. Setting real wing and paper model parameters equal gives no significant reduction of fit ($G_5 = 3.70$).

also lead to enhanced rejection of the shared *Heliconius sapho*/*H. cydno* pattern by *H. melpomene*.

Here we show that mimetic colour patterns are also important in mate recognition. Assortative mating contributes to speciation because post-mating isolation between *H. melpomene* and *H. cydno* is incomplete[8,9]. As in inter-racial hybrid zones, intermediate colour patterns are unlikely to be recognized as distasteful by predators, generating strong disruptive selection[16]. Selection on mimicry may be strong, $S \approx 0.2$–0.3 per locus in inter-racial hybrid zones giving $S \approx 0.6$ overall[8,16], comparable to that caused by F_1 female sterility ($S \approx 0.5$). Mimicry therefore provides an example of a trait under strong ecological selection that is also used as a mating cue. Such pleiotropy between mate choice and disruptive selection is an important feature of speciation theory, because it can trigger rapid speciation with a high probability[1,17,18], but only a few other examples are known[19–21].

The great diversity of colour pattern races within many *Heliconius* species shows that mimetic shifts rarely lead to speciation. Only where a shift dramatically changes colour or appearance, such as that between *H. melpomene* and *H. cydno*, will mate choice co-evolve sufficiently with mimicry to generate pre-mating isolation.

Table 2 Relative probabilities of mating between genotypes

Female	Male	Male	Male
	H. melpomene (Panama)	*H. cydno* (Panama)	*H. melpomene* (Guiana)
H. melpomene (Panama)	1	0 (0, 0.167)	0.348 (0.099, 0.921)
H. cydno (Panama)	0 (0, 0.167)	1	0.222 (0.051, 0.641)
H. melpomene (Guiana)	0 (0, 0.182)	0 (0, 0.154)	[1]

Probabilities were estimated relative to *H. melpomene* (Guiana) × *H. melpomene* (Guiana), which was set to 1 (square brackets). Support limits are shown in parentheses (values of 1 without support limits are not significantly different from 1).

In addition, *H. melpomene* and its co-mimic *H. erato* occur in light gaps and secondary forest, whereas *H. cydno* and *H. sapho* are found in more primary forest, albeit with considerable overlap[8,22]. This habitat shift, associated with mimicry, will itself contribute further to pre-mating isolation. In conclusion, pre- and post-mating isolation between *H. melpomene* and *H. cydno* has resulted from an adaptive shift in ecology and mimicry, in association with partial hybrid sterility. Subsequently, assortative mating between sympatric populations has become enhanced, possibly owing to reinforcement. This and other recent examples suggest that ecological adaptation can result in assortative mating as a byproduct and may be an important and largely overlooked cause of speciation[19–21]. □

Methods

Heliconius melpomene melpomene were collected near Cayenne, French Guiana in May 1998 (around 35 individuals) and February 1999 (58 individuals). *Heliconius cydno chioneus* and *H. melpomene rosina* were obtained continually from near Gamboa, Panama. Experiments were performed with descendents (three or fewer generations after collection), in insectaries[7] in Gamboa in 1998–1999.

Mate choice experiments

'Tetrad' experiments, consisting of a recently emerged virgin female (1 day old or less) and a mature male (more than 5 days old) of each of two genotypes, were performed in 1 × 1 × 2 m insectaries. The first mating was recorded for each experiment; individuals were not reused. On two occasions, both pairs mated simultaneously and so were scored as each having 0.5 matings. At least 25 experiments were performed per comparison.

Likelihood was used to estimate the probability $P_{i\times j}$ of a mating[7] between female type i and male type j, relative to $P_{mg\times mg}$ of a mating within Guiana *H. melpomene* (MG), which was set to 1. The overall multinomial probability of the results for each experiment were then estimated, e.g. for the Panama *H. melpomene* (MP) × Panama *H. cydno* (CP) comparison, $\Phi_{mp\times mp} = P_{mp\times mp}/(P_{mp\times mp} + P_{mp\times cp} + P_{cp\times mp} + P_{cp\times cp})$, $\Phi_{mp\times cp} = P_{mp\times cp}/(P_{mp\times mp} + P_{mp\times cp} + P_{cp\times mp} + P_{cp\times cp})$ and so on. ($\Sigma\Phi = 1$ for each tetrad). The $\log_e$ likelihood was therefore $\Sigma(X_{mp\times mp} \log_e \Phi_{mp\times mp} + X_{mp\times cp} \log_e \Phi_{mp\times cp}$ and so on) where $X_{mp\times mp}$ is the number of MP × MP matings and $X_{mp\times cp}$ the number of MP × CP matings in that tetrad. Likelihoods were summed over all experiments and maximized by

varying $P_{i\times j}$ values. Setting $P_{i\times i} = 1$ (within all genotypes) did not significantly reduce the fit ($G_2 = 0.81$, not significant), suggesting similar mating propensity among genotypes. Asymmetries ($P_{i\times j} \neq P_{j\times i}$) can therefore be presumed to be due to mate choice rather than mating propensity. Parameters and support limits (asymptotically equivalent to 95% confidence intervals[23]) were estimated under the simpler six-parameter model.

Live female courtship experiments

We placed two or three males (more than 5 days old) of different genotypes in an insectary and introduced a single virgin female (1–5 days old). Courtship (sustained hovering by the male over the female) was recorded over a period of 10 min. The female genotype was then substituted, with genotype order randomized. On mating, pairs were quickly and gently separated, which did not disrupt subsequent behaviour. Males were never reused, but females were drawn randomly from a pool of three to four individuals per genotype. In all, 840 min of observations were made in 19 replicates with all three male genotypes and a further nine with MP and MG males alone.

Colour pattern models

Between five and fifteen males in a 2×2×2 m insectary were presented with dissected natural wings or a colour pattern model, fixed to a length of flexible wire on a lightweight handle. Models were manipulated to simulate *Heliconius* flight in the centre of a spherical area (60 cm diameter) demarcated by a bamboo cross. Randomly ordered pairs of 5-min experiments were carried out: (1) a control flight with a model of the male's own colour pattern and (2) an experimental flight with a different colour pattern. Entry to the sphere was recorded as 'approach' and sustained fluttering directed at the model as 'courtship'. At least ten replicates were carried out per comparison. Each procedure was repeated with real female wings and paper models colour-matched using commercially available permanent marker pens. Reflectance spectra of real and paper models were similar (Supplementary Information), and male behaviour towards wings and models did not differ significantly (see below).

Numbers of approaches (X_A) and hovering courtship interactions (X_H) are given in the Supplementary Information. We estimated the probabilities $Q_{i\times j}$ that males of type j approached or courted models of type i relative to that of their own type j, using likelihood. Thus, for MP males with MP versus CP models, the actual probabilities are $Q_{A\,cp\times mp}/(Q_{A\,cp\times mp}+1)$ that males approach CP and $1/(Q_{A\,cp\times mp}+1)$ that they approach MP. The $\log_e$ likelihood for this experiment is therefore $\Sigma[X_{A\,cp\times mp}\log_e\{Q_{A\,cp\times mp}/(Q_{A\,cp\times mp}+1)\} + X_{A\,mp\times mp}\log_e\{1/(Q_{A\,cp\times mp}+1)\}]$, where $X_{A\,cp\times mp}$ is the number of MP males approaching CP and $X_{A\,mp\times mp}$ is the number approaching MP. Similarly $Q_{H\,i\times j}$ parameters were estimated for probability of hovering courtship of the model. Estimates were obtained for paper models as well as real wings, giving a total of 20 parameters. The summed $\log_e$ likelihood was maximized over all experiments by varying the $Q_{i\times j}$ parameters. Subsequently, all comparisons within *H. melpomene* and $Q_{A\,mp\times cp}$ parameters were set to 1 without loss of fit ($G_{10} = 11.02$, not significant). Parameter values for the resultant ten-parameter model are shown in Fig. 3. Real and paper model parameters do not differ significantly ($G_5 = 3.70$), giving a combined five-parameter model.

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Lesions of the human amygdala impair enhanced perception of emotionally salient events

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Commensurate with the importance of rapidly and efficiently evaluating motivationally significant stimuli, humans are probably endowed with distinct faculties[1,2] and maintain specialized neural structures to enhance their detection. Here we consider that a critical function of the human amygdala[3,4] is to enhance the perception of stimuli that have emotional significance. Under conditions of limited attention for normal perceptual awareness—that is, the attentional blink[5,6]—we show that healthy observers demonstrate robust benefits for the perception of verbal stimuli of aversive content compared with stimuli of neutral content. In contrast, a patient with bilateral amygdala damage has no enhanced perception for such aversive stimulus events. Examination of patients with either left or right amygdala resections shows that the enhanced perception of aversive words depends specifically on the left amygdala. All patients comprehend normally the affective meaning of the stimulus events, despite the lack of evidence for enhanced perceptual encoding of these events in patients with left amygdala lesions. Our results reveal a neural substrate for affective influences on perception, indicating that similar neural mechanisms may underlie the affective modulation of both recollective[7–9] and perceptual experience.

The amygdala supports substantial projections to primary and higher-order sensory areas and the hippocampal formation[10]. Thus, the amygdala is strategically placed to allow emotional value[4,11] both to modulate perceptual sensitivity to incoming information and to bolster its post-encoding consolidation into memory. Much evidence has shown that the amygdala is involved in the latter of these

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