Locomotor Mimicry in Butterflies? A Critical Review of the Evidence

Andrew V.Z. Brower

Phil. Trans. R. Soc. Lond. B 1995 **347**, 413-425
doi: 10.1098/rstb.1995.0033

Locomotor mimicry in butterflies? A critical review of the evidence

ANDREW V. Z. BROWER

Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, U.S.A.

SUMMARY

The hypothesis of locomotor mimicry in butterflies presented by Srygley (*Phil. Trans. R. Soc. Lond.* B **343**, 145–155 (1994)) is criticized as unparsimonious, from two perspectives. First, the existence of mimicry between palatable but unprofitable prey is disputed on theoretical and empirical grounds. The lack of a strong predator aversion stimulus seriously undermines the unprofitable prey scenario, and supposed cases of mimicry of unprofitable models are explicable by traditional mimetic modes. Second, correlations of phenotypic characters used to support alternative adaptive peaks for palatable and unpalatable butterflies are criticized for failing to account for phylogenetic relationships. Virtually all of the relevant variation in flight-related morphology is shown to be due to differences between clades, rather than mimicry groups. An alternative hypothesis emphasizing phylogenetic constraint in the evolution of morphological characters associated with predator avoidance is proposed.

> The ground rule – or perhaps *doctrine* would be a better term – is that adaptation is a special and onerous concept that should be used only where it is really necessary. When it must be recognized, it should be attributed to no higher a level of organization than is demanded by the evidence. In explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternate alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice.
>
> G. C. Williams (1966, pp. 4–5).

1. INTRODUCTION

G. C. Williams (1966) stressed the importance of parsimony in the recognition of adaptations, and the primacy of the hierarchical structure within which natural selection acts. Although Williams emphasized the significance of selection at less inclusive levels (his essay was primarily a criticism of group selection), his doctrine is no less applicable to the invocation of current selection to explain traits that exist due to historical effects at a more inclusive level of organization. Interpretation of adaptive scenarios from a phylogenetic perspective may provide simpler, or at least equally plausible, alternative hypotheses to explain the distribution of characters among taxa (Gould & Lewontin 1979; Wanntorp 1983; Coddington 1988; Miller & Wenzel 1995). To mirror Williams' (1966) dictum, selection should also be attributed to a level of organization no *lower* than that which is demanded by the evidence.

A recent paper by Srygley (1994) hypothesized the evolution of locomotor mimicry among groups of mimetic neotropical nymphalid butterflies. This phenomenon is distinct from traditional mimicry, Srygley argued, because it entails adaptive convergence of physiological and morphological features that result in similar flight biomechanics and behaviour, rather than the convergence of characters producing superficial visual resemblance. Srygley and colleagues have provided detailed data on flight-related characters from numerous neotropical butterflies, and have demonstrated significant correlations between these features and the palatability of the species tested (Chai 1990; Dudley 1990; Srygley & Chai 1990; Srygley & Dudley 1993; Srygley 1994). Srygley (1994) concluded that not only the slow, regular flight, long wings and abdomens, and small thoraces of unpalatable butterflies, but also the rapid, erratic flight, short wings and abdomens, and large thoraces of palatable butterflies, represent alternative adaptive strategies to avoid predation. Although these arguments seem intuitively sound (indeed, behavioural similarity has been noted as a component of mimicry from the start (Bates 1862; Wallace 1867*a*; Meldola 1878)), Srygley (1994) addressed his hypothesis from a fairly strict functional-adaptationist perspective. His discussion does not consider several theoretical and methodological issues that bear fundamentally on the interpretation of the data.

The study of mimicry stands at the intersection between population genetics, animal behaviour, functional ecology, ecological chemistry and phylogenetics, and represents 'the greatest post-Darwinian application of natural selection' (Fisher 1958, p. 163). Thus, the scope of relevant literature approaches overwhelming proportions. A century ago, E. B. Poulton could write a 100 page paper reviewing the state of knowledge on mimicry with only 12 citations in it. Today, it is impossible to write a 12 page paper with 100 citations that begins to synthesize relevant data from these

Phil. Trans. R. Soc. Lond. B (1995) **347**, 413–425
Printed in Great Britain

diverse fields. In this paper, I employ evidence from the literature to address two problems (discussed in §§2 and 3 respectively) raised by Srygley's (1994) hypothesis of locomotor mimicry:

1. Is the evolution of mimicry between palatable butterfly species that are effective escapers, and thus represent 'unprofitable prey' (Lindroth 1971; Hespenheide 1973; Baker & Parker 1979), a plausible phenomenon? Has it been shown to occur in nature?
2. Do aspects of flight behaviour shared between phenotypically similar species represent adaptations (adaptive convergence due to selection for similarity) that provide a means to fool predators?

2. MIMICRY WITHOUT UNPALATABILITY?

(*a*) *Background*

Although classical mimicry theory is well established, and empirical observation and experiments have largely borne out its predictions, a brief review is relevant to the points in question (see also Rettenmeyer 1970; Vane-Wright 1976; Turner 1977; Huheey 1984; Mallet & Singer 1987). According to standard theories, the evolution of mimicry in butterflies depends upon the prior existence of aposematism in the model (Bates 1862; Poulton 1898; Sheppard 1958). The selective force that drives the evolution of mimetic convergence is the ability of predators to discriminate between potential prey, based on generalized association of their appearance with memory of prior encounters. Although experimental evidence distinguishing among specific models is scarce (Guilford 1990), it is generally held that foul-tasting prey with bright colouration or contrasting patterns are more memorable (or easier to recognize) to predators than nondescript prey, thus providing a selective impetus for the evolution of warning colouration in unpalatable species (Wallace 1867*b*; Darwin 1871; Gittleman & Harvey 1980; Guilford 1986).

Müllerian mimicry (Müller 1879) evolves when multiple aposematic species converge independently upon the same signalling system. Batesian mimicry (Bates 1862) evolves when palatable species co-opt the aposematic signalling system of unpalatable species, to take advantage of the conditioned avoidance behaviour of potential predators that have had a previous negative experience with the model. At opposite extremes, Müllerian mimicry is positively density-dependent (the greater the number of unpalatable participant species (or individuals), the more effective the deterrant), while Batesian mimicry is negatively density-dependent (the greater the number of palatable participant species (or individuals), the less effective the deterrent colour pattern) (Fisher 1958; Turner *et al.* 1984; Speed 1993). Of course, there is no disjunction between Batesian and Müllerian mimicry (Brower *et al.* 1968; Turner 1984), and many individual cases may lie on a continuum between the two extremes (e.g. Brower 1958; Ritland 1991).

The effectiveness of mimicry relies on the individual predator's memory of encounters with aposematic prey, and thus it cannot evolve without the previous existence of a signalling system between model and predator (Sheppard 1958). As recognized from the onset by Bates (1862), the noxiousness of the aposematic model is not restricted to chemical unpalatability, but may also include such defensive mechanisms as stings and repellent secretions, which do not depend upon oral stimuli to deter the predator. However, under traditional models of warning-colour evolution, the predator's sudden and unpleasant sensory–physiological response produced by the prey's defensive stimulus is fundamental to the predator's learning and retention of the prey's semiotic system (Alcock 1970). Further, the maintenance of successful Batesian mimicry requires periodic reinforcement of the predator's association of the colour pattern with the model's defence mechanism (Cott 1940). The relative frequency of the predator's encounters with the model versus the mimic presents a strong constraint to the efficacy of Batesian mimicry (Brower 1960; Turner *et al.* 1984). This, it is argued, is why Batesian mimicry is frequently sex-limited and not expressed in males, and why some Batesian mimics exhibit polymorphic convergence to multiple model species with different colour patterns (Darwin 1871; Ford 1953; but see Turner 1978).

Despite this theoretical framework, van Someren & Jackson (1959) and Guillaumin (1979) argued that 'primitive mimicry' exists among groups of similar-looking African butterflies, regardless of their palatability, simply due to the numerical advantage of sharing a common pattern. Using a generalization of Müller's original formulation for mimicry between unpalatable prey, they maintained that if more species share a particular colour pattern, fewer individuals of each species will be attacked, even if they are completely palatable. For example, a pattern shared by 20 equally abundant species is mutually beneficial to all of them because only 1/20 as many butterflies of each species will be consumed by the predator. This model, which predicts that the predation pressure on individuals bearing a shared colour pattern is inversely proportional to the relative abundance of the colour pattern in a particular ecosystem, is ecologically untenable. Under natural circumstances (such as non-extreme prey density), predators do not selectively attack rare, palatable prey (Allen 1988). If a particular colour pattern is abundant, it will be attacked more frequently, and all species bearing it will suffer proportionally equivalent losses to species which do not. Holling's (1965) model showed that a short-term advantage to primitive mimicry could accrue if predators become satiated due to very high prey density, but he argued that this was unlikely. Such an abundant prey resource would probably be rapidly diminished by predator immigration or enhanced fecundity. Thus, there is no plausible selective advantage for palatable prey to converge on a colour pattern, as predators have nothing to lose by failing to recognize the signal. In fact, there is great potential for predators to develop a search image for the common pattern (more generally, positive density-dependent preference, or apostatic selection), which would tend to actively disfavour shared patterns among palatable

Table 1. *Hypothetical cases of arithmetic mimicry discussed in the text*

(Alternate hypotheses as described in text: 1, palatability is unknown (one or more members of complex may be unpalatable); 2, convergence for crypsis in similar microhabitats; 3, similarity due to common ancestry.)

taxa	distribution	references	alternate hypotheses
Nymphalidae: Charaxinae			
Charaxes (11 cases)	afrotropical	Van Someren & Jackson (1959)	3
Limenitinae			
Euphaedra/Euryphene (5 cases)	afrotropical	Van Someren & Jackson (1959)	1,3
Euryphene/Diestogyna	afrotropical	Van Someren & Jackson (1959)	1,3
Euphaedra/Bebearia	afrotropical	Guillaumin (1979)	1,3
Adelpha/(Doxocopa/Nymula)[a]	neotropical	Mallet & Singer (1987)	1,3
Heliconiinae			
Euptoieta/Agraulis/Dione	neotropical	Srygley (1994)	1,3
Philaethria/Siproeta[b]	neotropical	Srygley (1994)	1,2
Satyrinae			
Lasiophila/Pedaliodes	neotropical	Adams (1986)	1,2
Physcopedaliodes/Panyapedaliodes	neotropical	Adams (1986)	1,2
Chloreuptychia/Cepheuptychia	neotropical	Mallet & Singer (1987)	2,3
Chloreuptychia/Eusalesia[c]	neotropical	Mallet & Singer (1987)	1,2
'*Euptychia*'	neotropical	Mallet & Singer (1987)	1,2,3
Brassolinae			
Catoblepia	neotropical	Bristow (1981)	1,3
Pieridae: Pierinae			
Colotis	afrotropical	Van Someren & Jackson (1959)	1,3
Lycaenidae: Lipteninae			
Liptena/Eresina	afrotropical	Van Someren & Jackson (1959)	1,2
Teriomima/Eresinopsis	afrotropical	Van Someren & Jackson (1959)	1,2
Epitola	afrotropical	Van Someren & Jackson (1959)	1,3
Ornipholidotos	afrotropical	Van Someren & Jackson (1959)	1,3
Lycaeninae			
Argiolaus/Dapidodigma/Epamera	afrotropical	Van Someren & Jackson (1959)	1,3
Anthene (2 cases)	afrotropical	Van Someren & Jackson (1959)	1,3
Virachola/Anthene (2 cases)	afrotropical	Van Someren & Jackson (1959)	1,3
Chloroselas/Desmolycaena	afrotropical	Van Someren & Jackson (1959)	1,3

[a] *Doxocopa* in Apaturinae, *Nymula* in Riodininae (Lycaenidae): alternate hypothesis 3 applies only to similarity within *Adelpha*.
[b] *Siproeta* in Nymphalinae.
[c] *Eusalesia* in Riodininae (Lycaenidae).

species (e.g. Tinbergen 1960; Murton 1971; Allen 1988; Endler 1988).

(*b*) *Reconciliation of evidence with traditional theory*

The fundamental observation of van Someren & Jackson (1959) that there are numerous groups of similar-looking, sympatric and apparently palatable butterflies can be explained in four ways without overthrowing traditional mimicry theory. These explanations are not mutually exclusive, and they undoubtedly apply in various degrees and combinations to the different examples illustrated by van Someren & Jackson (1959), as well as to additional examples listed by Bristow (1981), Adams (1986) and Mallet & Singer (1987) (see table 1). First, as the palatability of the majority of the species is unknown, some members of the 'mimicry groups' might in fact be traditional, unpalatable models (as suggested by Adams and Bristow for pronophiline satyrines and brassolines, respectively). This trivial explanation does not explain why some 'mimicry groups' which are known to be palatable look the same (e.g. mimicry among *Charaxes* species; Swynnerton 1926; Poulton 1926). Second, Papageorgis (1975) and Brown (1988) argued that many species may converge on similar patterns because they are optimally cryptic in particular microhabitats. This may explain Mallet & Singer's (1987) case of lycaenids, satyrines and riodinids that dwell near the forest floor and share flashing, blue patterns that seem to disappear when they alight. In these instances, 'mimicry' may simply be an epiphenomenon of the parallel response to a common environmental attribute. A third important explanation is discussed at length in the second section of this paper: similar colour patterns are shared due to common descent, and not to mimetic convergence.

A fourth explanation is that large, fast-flying butterflies that are especially proficient at escaping from predators act as models for less vigorous mimics. It has long been recognized that unpalatable butterfly taxa tend to be tough and hard to kill (Trimen 1870), although not because they have 'more wing venation... near the wing tips to assure durability when grasped,' as Srygley (1994) hypothesized (wing venation patterns are highly conserved within lepidopteran groups (Comstock 1918)). The idea that edible prey species are avoided by predators because they are too difficult to catch or consume has been applied specifically to palatable butterflies on several occasions (Swynnerton 1926; Poulton 1926; Jones 1932; van Someren & Jackson 1959), foreshadowing Baker & Parker's (1979) unprofitability hypothesis. Srygley (1994) invokes unprofitability to explain the similarity of colour patterns between apparently palatable, yet 'mimetic' species, such as *Philaethria dido* and *Siproeta stelenes*. Observational data from nature (Chai 1986) suggest, to the contrary, that large palatable butterflies are at a disproportionate risk to specialist predators: the generally large and powerful Brassolinae and Charaxinae (genera and species not identified) were the two most frequent prey groups taken by jacamars, together comprising 46% of all observed kills, although the groups represent only 12% of the Costa Rican butterfly fauna (excluding Lycaenidae and Hesperiidae; De Vries, 1987).

For mimicry to evolve among palatable species, an unprofitable model must exist, and there must be an underlying selective advantage of being mistaken for that model by a predator. Gibson (1974) showed that, in experiments with captive star finches (*Bathilda ruficauda*) preying on painted millet seeds, and with captive European robins (*Erithacus rubecula*) preying on differentially painted mealworms (*Tenebrio molitor*) (1980), predators could be conditioned to avoid prey that were effective escapers. However, in either case, once the 'training period' was concluded, the birds retained their conditioned aversion to models and mimics for only a few days. Hancox & Allen (1991) performed similar studies with wild tits and robins, and again found relatively short aversion retention periods once unprofitable prey became profitable.

These results showing quick loss of aversion to prey unprofitable by reason of effective escape are in marked contrast to reports of long-term aversion to aposematic prey. With no subsequent conditioning after the initial negative experience, crows (*Corvus corone*) and tits (*Parus major*, *Machlolophus xanthogenys*) rejected unpalatable insects after 9 and 12 months, respectively (Rothschild 1964). Alcock (1970) showed experimentally that aversive conditioning in white-throated sparrows (*Zonotrichia albicollis*) was directly proportional to the strength of the negative stimulus. Pilecki & O'Donald (1971) likewise reported that sparrows remember distasteful prey for long periods. Waldbauer and colleagues (Waldbauer & Sheldon 1971; Evans & Waldbauer 1982; Waldbauer 1988) have shown that the flight season of bumblebee-mimicking syrphid flies occurs prior to fledging of young insectivorous birds, and confers a significant selective advantage by avoiding naive predators. This advantage is derived because the adult birds remember the mimetic association from previous years. All these data strongly suggest that the effect of learning by exposure to unpleasant stimuli is far more lasting than the effect of learning by frustration, which offers no aversive stimulus at all. Because, as discussed above, sufficient length of the decay time of the conditioned aversion (i.e. predator memory span) is a fundamental requirement of the evolution of mimicry (Brower *et al.* 1970; Turner *et al.* 1984), evolving to mimic a model unprofitable by reason of effective escape seems difficult, unless the model is vastly more abundant than the mimic, and always successful at avoiding predation, thereby continually reinforcing the negative stimulus.

Lindroth's (1971) report of phenotypic convergence between species of *Lebia* (Carabidae) and flea beetles (Chrysomelidae, Alticinae), particularly the association between *Lebia vittata* and *Disonycha scapularis*, has been the keystone natural example of mimicry due to effective escape (on the part of the flea beetles) between otherwise apparently palatable prey. However, the study was flawed in several ways. Lindroth's evidence that the model species are palatable was anecdotal and fairly inconclusive: he fed a few to some birds at the Copenhagen Zoological Garden, and observed them to be 'caught and swallowed... in rapid succession.' He also reported that they had been found in the contents of a number of bird stomachs, occasionally in great numbers (700 in a sage grouse, *Centrocercus urophasianus*). Although these data suggest that *Disonycha* may well be palatable under certain conditions, they do not say much for the efficacy of its escape mechanism. The instantaneous leap of *Disonycha* could well be more useful in escaping invertebrate predators like *Lebia* than in escaping large, visually oriented vertebrate predators. Subsequent evidence suggests that neither carabids nor alticines are particularly palatable: *Lebia* was shown to produce formic acid, and other bad-smelling defensive secretions (Moore 1979), indicating that the various species are Müllerian and not Batesian mimics. Chrysomelids (including *Salix* feeders like *Disonycha*) likewise are noted for sequestering or endogenously producing defensive chemicals (Rothschild 1972; Pasteels *et al.* 1984; Dettner 1987; Whitman *et al.* 1990). Hespenheide's (1973) beetle-and-fly mimicry example suffers from the same difficulties: he assumed the beetles were palatable (at least some may not be (Dettner 1987)), and then rationalized why agile flies might act as their models.

Most direct knowledge of insect palatability is based on experiments with individual captive predators (e.g. Swynnerton 1926; Cott 1940; Brower *et al.* 1963), and the relevance of captive palatability trials to preferences of predators under natural conditions should also briefly be considered. Srygley and Chai's data (Chai 1986, 1990; Srygley & Chai 1990) on butterfly palatability were obtained primarily from feeding trials on five jacamars (*Galbula ruficauda*) housed in small ($< 1\ \text{m}^3$) cages. Each bird was exposed to numerous butterflies over a considerable time period, and it is not clear from results presented how previous exposure, hunger, and cage effects might have affected their behaviours towards different butterfly species. For instance, Chai (1986) reported that one jacamar ate 10 of 17 *Heliconius erato* presented, but these data are not reflected in Srygley & Chai (1990) or Srygley (1994), in which *H. erato* is reported to be completely unpalatable (0/32) to the same predator species, and (apparently) to one of the same individual birds. Chai

(1986) reports that in each trial he presented the butterflies in presumed increasing order of palatability, which may have promoted enhanced predation on marginally palatable butterflies (birds were 'very hungry' at the onset of the trials). The relation between prey acceptable to a hungry, caged bird and prey preferred by a wild bird is largely unexplored (Coppinger 1970; Brower 1984), and it is likely that palatability is more relative than absolute. Acceptability of particular prey species to a particular predator in nature depends on the availability of preferred alternate prey and the predator's physiological state and previous experience (Swynnerton 1915; Dixey 1920; Sheppard 1958; Cook *et al.* 1969).

Some butterfly species reported by Srygley & Chai (Chai 1986, 1990; Srygley & Chai 1990) to be largely palatable to captive jacamars were shown to be far less so to silverbeak tanagers (*Ramphocelus carbo*) in a test of butterly predation with 62 caged individual birds in Trinidad (Brower *et al.* 1963). The heliconiines *Dryas iulia* and *Agraulis vanillae* were 92% and 75% eaten, respectively in Chai's (1990) study, and only 25% each in Brower *et al.*'s (1963). Likewise, Aiello (1984) inferred at least some *Adelpha* species to be unpalatable, but Chai's (1986, 1990) jacamars ate all the *Adelpha* individuals that were presented to them. These conflicting reports suggest that substantial differences may occur in sensitivity to unpalatability of particular prey species between different predators, as hypothesized by Frazer & Rothschild (1960). An additional or alternative factor could be regional variation in butterflies' unpalatability due to changes in larval host plant chemistry, or geographical shifts to alternate host plant species with different chemistries. Both differential predator susceptibility and intraspecific variation in prey palatability have been well-documented in the monarch, *Danaus plexippus* (Brower 1984 and references cited therein, 1988).

In this section, I have attempted to show that mimicry of a palatable but unprofitable model is far less likely than traditional Batesian mimicry of an unpalatable model on theoretical grounds, and that the purported examples of it are poorly supported. Recently, the existence of completely palatable mimics has been questioned (Vane-Wright 1991), let alone the models. Understanding the dynamics of complex predator–prey communities continues to be hampered by a lack of data from the laboratory and the field. To help resolve the questions addressed here, experiments should be conducted to test the relative retention times of predators' negative associations with unpalatability and unprofitability due to effective escape. Additional reports of predation in the wild would also be enlightening.

3. PHYLOGENY, PALATABILITY AND FUNCTIONAL MORPHOLOGY

(*a*) *History of approaches to the problem*

Many morphological and behavioural traits of organisms are phylogenetically conservative, as is intuitively manifest in our ability to develop relatively stable hypotheses of phylogenetic relationships for the diversity of living things. Thus, the presence of a particular feature in a particular species does not constitute evidence that that feature is an evolutionary novelty that arose to perform its current function in that species (Gould & Lewontin 1979). The concepts of adaptation as a process, and of adaptations as features of organisms, must be considered in appropriate phylogenetic context if their significance to current ecological utility is to be meaningfully interpreted. These ideas are not new: Darwin (1859, p. 199) stated, 'the chief part of the organization of every being is simply due to inheritance.' Lewontin and Gould's attacks on sociobiology and the adaptationist paradigm (Lewontin 1978, 1979; Gould & Lewontin 1979) advocated phylogenetic constraint as an alternative to adaptation. These authors' emphasis on appropriate levels of analysis and the use of the parsimony criterion harks back to Williams' (1966) doctrine, quoted at the beginning of this article. (Interestingly, Williams (1992, p. 104) stated a preference for design over phylogenetic constraint as a criterion for discovering particular adaptive character states.)

A growing number of systematists and ecologists are attempting to incorporate phylogenetic relationships in their study of adaptive characters (Lauder 1982; Wanntorp 1983; Dobson 1985; Brooks & McLennan 1991; Vane-Wright & Smith 1991; Garland 1992; Gittleman & Luh 1992; Miller & Wenzel 1995), often under a set of methodologies referred to as 'the comparative method' (Harvey & Pagel 1991). A major current endeavor of proponents of the comparative method is to remove the 'confounding variable' of phylogeny from analyses of the distributions of putatively adaptive characters (Harvey & Pagel 1991, p. 36), allowing for independent contrasts between clades. Others (e.g. Miller & Wenzel 1995, Brower 1995) feel that phylogeny provides the foundation for understanding adaptation, and cannot and should not be mitigated by statistical gymnastics. Recently, there has been a philosophical recidivism to the counterposition that phylogeny and evolutionary history are irrelevant to questions of 'phenotype existence' (Reeve & Sherman 1993), and further that phylogenetic reconstruction is too weak a tool to aid in the study of adaptation (Frumhoff & Reeve 1994). Srygley's (1994) study of locomotor mimicry exemplifies (perhaps not consciously) this style of phylogeny-free examination of adaptation. In the remainder of this essay I will re-examine his results, and other examples of mimicry from the butterfly literature, to show how ignorance of phylogeny can lead to erroneous conclusions about adaptation.

Implicit to the most fundamental concept of mimicry is the idea of analogous similarity, or independent convergence upon a common phenotype. Similarity among close relatives is most parsimoniously explained as an epiphenomenon of recent common ancestry (Roessler 1986). If such similarities are plesiomorphies, then they are still most easily explained by absence of evolutionary change, even if the taxa bearing them diverged a long time ago. Only when there is clear evidence that similar patterns have evolved in phylogenetically independent lineages, is adaptive convergence a parsimonious explanation of the character distribution. Even before Bates' formulation of his theory, the distinction between phylogenetic affinity and mimetic analogy was clear to researchers (see references in Poulton 1898), although without the unifying principle of evolution via natural selection, there was no plausible theoretical context to explain either phylogeny or adaptation. Bates' theory itself (1862) sprang from his revision of the tangled systematics of the 'Heliconii', a heterogeneous Linnaean group of long-winged neotropical butterflies including members of the pierid Dismorphiinae and the nymphalid Heliconiinae, Ithomiinae and Danainae. He recognized by careful morphological study that the superficial similarities between these diverse groups were due not to common ancestry, but to independent, adaptive evolution. It became rapidly apparent (Wallace 1866, 1867*a*; Trimen 1870) that mimicry was a geographically widespread and common phenomenon among butterflies, and their gross wing shapes and colours were not especially useful in determining affinity.

While butterfly wing patterns are evolutionarily labile, they appear to develop as modifications of a relatively conserved basic plan (Schwanwitch 1924; Süffert 1927, Goldschmidt 1938; Nijhout 1991). Many pattern elements are shared generally among members of higher-level taxa, for instance the red spots at the apex of the hind wing anal margin in swallowtails (Papilionidae) and the forewing transverse discal bars of limentitines (Nymphalidae). However, quite complex patterns can be remarkably similar between taxa with no obvious phylogenetic or mimetic affinities, such as the afrotropical-neotropical look-alikes *Charaxes smaragdalis* (Charaxinae) and *Baeotus baeotus* (Limenitinae), and *Graphium leonidas* (Papilionidae) and *Siproeta stelenes* (Nymphalinae). Another excellent example of this phenomenon is illustrated in Ackery & Vane-Wright (1984, plate XI, figures 140 and 141). Evidence of this type suggests that butterfly wing patterns evolve as subtle yet precise variations on a few simple themes, and that particular patterns can recur solely due to coincidence (Nijhout 1991). Wing shapes likewise appear to be relatively conservative, and differences between them are largely due to allometric variation (Strauss 1990) and programmed cell death at wing margins during imaginal development (Süffert 1929; Nijhout 1991), again implying a relatively simple underlying genetic architecture.

As discussed above, van Someren & Jackson (1959) argued that mimicry could occur among palatable species, with large, common species acting as the model. They identified numerous 'arithmetic mimicry groups' among species within single genera or groups of closely-related genera, including *Charaxes*, *Euphaedra* + *Euryphene* + *Diestogyna*, *Colotis*, and *Argiolaus* (see table 1). Likewise, Mallet & Singer (1987) tentatively cited several examples of mimicry among closely related palatable species (e.g. *Euptychia*), which may mimic one another, or riodinids of unknown palatability (sexual dimorphism in both groups suggests that sexual selection may also play a role in pattern evolution). Mallet & Singer suggested that arithmetic mimicry might work if the model species were so abundant that it swamped the predator population's ability to attack all the available prey (as predicted by Holling's (1965) model). However, even relatively unpalatable butterflies in large aggregations can be literally decimated by bird predation although they are only available as a seasonal resource (Brower & Calvert 1985). Although the critical tests evaluating arithmetic mimetic wing pattern evolution are not currently possible due to the lack of phylogenetic hypotheses for these groups, the dominant pattern among the 'mimics' is clearly one of similarity due to phylogenetic relatedness, rather than due to convergence (at least 25 of 28 examples in van Someren & Jackson (1959), and three of five in Mallet & Singer (1987)). If arithmetic mimicry were an important evolutionary mechanism, we would expect it to occur as commonly between unrelated butterfly taxa as between close relatives, given the evidence for the relatively simple basis of wing pattern diversity discussed above, but this is evidently not the case.

(*b*) *Independence and adaptation in Srygley* (*1994*)

Srygley (1994) identified 11 mimicry groups based on colour patterns in his study of locomotor mimicry. Although he attempted to factor out phylogenetic correlations by adjusting for mimicry, his assignment of species to these putative groups and subsequent treatment of the groups as statistically independent entities, disregarding relationships of species within and among them, leads to conclusions that may be misleading. Two 'groups' (*Heliconius ismenius*, *H. charithonia*) contain only a single species, and thus cannot be considered to be mimetic, although they are probably aposematic. *H. ismenius* is included in this discussion with the four members of Srygley's "tiger 1" group (*Eueides isabella*, *Lycorea cleobaea*, *Mechanitis polymnia*, *Eresia mechanitis*, *Consul fabius* and *Perrhybris pyrrha*), because it is very similar to members of that group in other parts of its range. The 'tiger 1' group represents a mimicry complex endemic to Central America, which undergoes a transition into the mimicry complex characteristic of the northwestern South-American biogeographic realm in the area where the *ismenius* specimens were apparently sampled. Ecological contact among participant species is a fundamental aspect of the evolution of mimicry (Wallace 1867*a*; Dixey 1920) that Srygley seems to have neglected in this case. *H. charithonia* has no obvious mimics in Central America, but De Vries (1987) suggested that it serves as a generalized model for *Siproeta stelenes* (and presumably *Philaethria dido* as well). If this is so, then perhaps these three species should be included in a single group, as is done below ('green/zebra'). (Interestingly, Brown (1988) suggested that *Siproeta* and *Philaethria* may mimic the unpalatable ithomiines *Roswellia*, *Patricia* and *Athesis*.)

Four of Srygley's groups comprise mimetic pairs of *Heliconius*. Although these pairs obviously represent different mimicry groups at the level of wing coloration, the uniformity of these taxa in morphological characters other than wing pattern is most easily explained by common ancestry. If the *Heliconius*

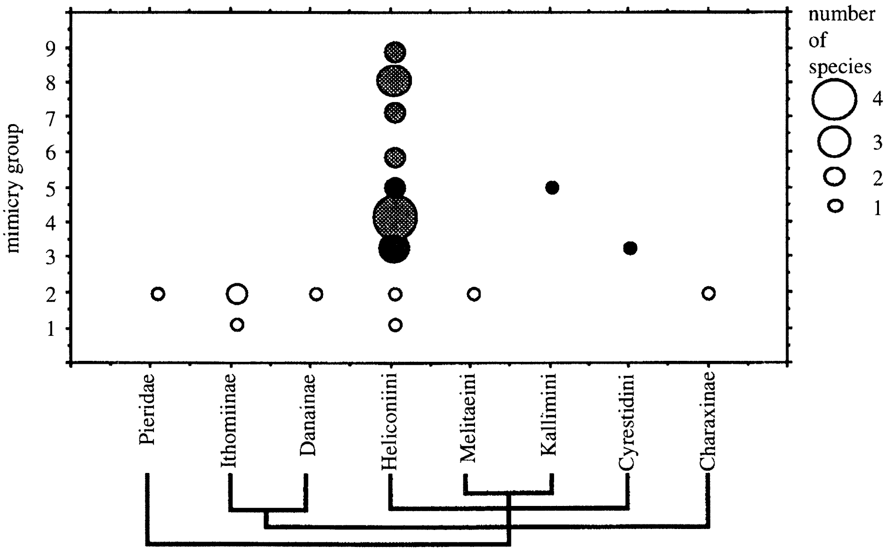

Figure 1. Plot of taxa listed in Appendix 1 of Srygley (1994), grouped systematically by unambiguous monophyletic group (*x* axis) and mimicry complex (*y* axis). Mimicry groups are: 1 = tiger 2; 2 = tiger 1; 3 = basal plan; 4 = orange; 5 = green/zebra; 6 = blue/yellow; 7 = black/red/yellow; 8 = black/white; 9 = black/yellow. Shaded circles represent mimicry groups composed solely of heliconiines; filled circles represent the doubtful green/zebra and basal plan groups; open circles represent the two undisputed examples of mimicry that exhibit morphological convergence in addition to convergence of wing colour patterns. Hypothesized phylogenetic relationships are shown (based on the classification of Harvey 1991).

common ancestor possessed the same morphology, which is the most parsimonious explanation of the data, then only one evolutionary event need be invoked to explain the distribution of the characters. Thus, these groups, together with the other *Heliconius* represented in the sample, constitute a single observation, and not four multiple independent observations, for statistical analysis of flight morphology characteristics.

The inclusion of *Marpesia petreus* in the otherwise heliconiine 'orange group' over the 'basal plan' group seems completely arbitrary: it looks more like *Dione juno* (basal plan group) than *Dryas iulia* to me, and I have seen it associate with *D. juno* at mud puddles in Darien, Panama, Rondonia, Brazil and western Ecuador. Given the discussions of unprofitability, mimicry and wing pattern evolution above, the very existence of a 'ground plan' mimicry group composed of largely palatable butterflies with relatively ancestral wing patterns seems doubtful. The *Agraulis–Euptoieta* pattern, shared by hundreds of other species in the Heliconiinae that occur all over the world, is almost certainly a symplesiomorphy and not an adaptation for mimetic resemblance. In summary, of Srygley's 11 groups, only three that contain representatives of more than a single higher-level clade whose morphological similarities are more likely to be due to adaptive mimetic convergence than common descent or chance: 'tiger 1', 'tiger 2' (*H. hecale* and *Melinaea scylax*), and 'green/zebra' (see figure 1).

Srygley (1994) used principal component analysis to identify five main characteristics that explained the variance in his morphological data (20 morphological measurements). He described the three largest components, in descending order, as centre of mass of the body, wing shape, and centre of mass of the wing, which explained 42.8%, 22.9% and 16.6% of the variance, respectively. He used discriminant function analysis and stepwise regression of the principal components (PCs) on mean palatability of the 11 mimicry groups to find associations of morphological characters with palatability, and then based his discussion of locomotor mimicry on these results. He admitted that his variable group sizes violate the assumptions of the statistical analyses, but nevertheless drew strong conclusions based on these results. Although I do not attempt to reconstruct his analyses or reanalyze his raw data here, I suggest that these violations, combined with the lack of statistical independence of the mimicry groups, represent far more confounding difficulties than Srygley stated in his article.

Despite Srygley's (1994) claim to have factored out phylogeny from his analyses, figure 2 (drawn from data in his Appendix 1 table) shows that phylogeny represents a major component of the associations among his data. This figure is essentially the same as Srygley's figure 3, except that instead of highlighting hypothetical adaptive zones, I have highlighted the only two monophyletic groups represented by more than a single species in Srygley's data set. As can be seen, both the genus *Heliconius* (sensu Brower 1994) and the Ithomiinae+Danainae (sensu Ackery 1984; now collapsed to a single subfamily, Danainae; R. I. Vane-Wright, personal communication) form convex clouds of points, suggesting strong phylogenetic correlations in the two plotted variables. In fact, Srygley's PC1 appears mainly to segregate the Ithomiinae+Danainae from the other sampled butterflies, whereas PC3 explains much of the difference between *Heliconius* and the others. However, figure 3 shows that relatively little of the correlation in the data is associated with mimicry group, as we might expect if mimicry among taxa is manifest primarily in superficial characters. The box here, again identifying *Heliconius*, contains repre-

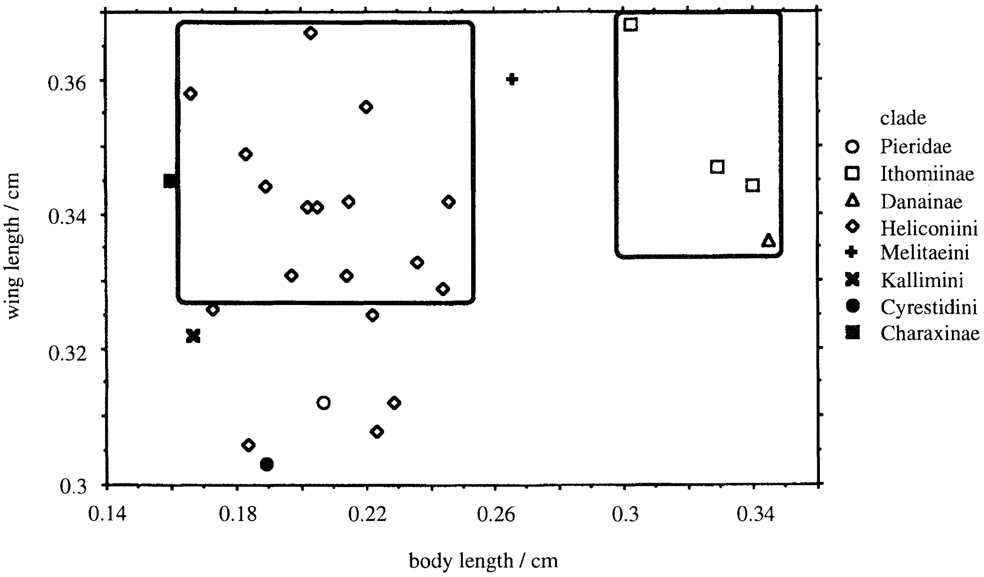

Figure 2. Plot showing phylogenetic component of flight-related morphological characters. Data from appendix of Srygley (1994), yielding point distribution similar to Srygley's figure 3. Large box contains members of the genus *Heliconius*, small box members of Danainae + Ithomiinae. *H. hewitsoni* (group 9) and *Euptoieta hegesia* (group 3) are not shown, as their values are missing from Srygley (1994). The pierid data point is positioned at the coordinates dictated by Srygley's (1994) Appendix 1.

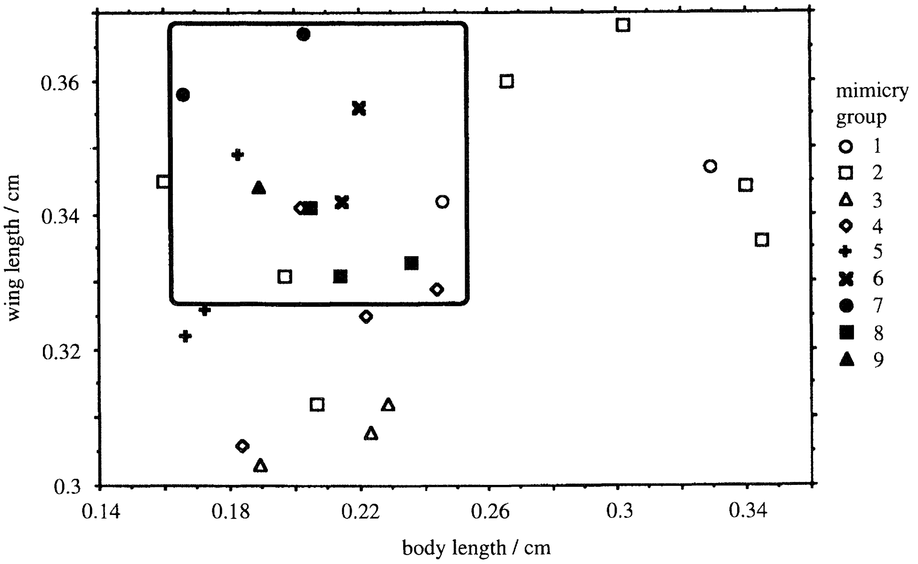

Figure 3. Same plot as figure 2, but with points labelled by mimicry group (see figure 1 and text). Members of all mimicry groups except the doubtful basal group (3) fall inside the *Heliconius* box, suggesting the inflated statistical contribution of this genus to Srygley's (1994) results.

sentatives of eight of the nine mimicry groups I have retained from Srygley's 11. The only one not represented is the 'ground plan' group 3, whose existence is dubious. Given that the axes (major contributing variables to PCs 1 and 3) were selected to maximize the variance for mimicry (Srygley found PC2 not to predict palatability or mimetic associations), it is notable now little structure is evident beyond phylogenetic associations. Note that within *Heliconius*, mimetic pairs do not markedly associate with one another.

The observation that phylogenetic patterns play an important role in the conservative distribution of morphometric characters is neither new nor surprising (Strauss 1990), but begs the questions, when during phylogenetic history did the changes between groups occur, and what causes were responsible? Srygley (1994; Srygley & Chai 1990; Srygley & Dudley 1993) has developed elaborate scenarios to explain the alternate adaptive character suites he has advocated (palatability, brittleness, fast flight, short wings and abdomens and sunny microhabitat versus aposematism, toughness, slow flight, long wings and abdomens and shadier microhabitat). Based on the available data, the character syndromes associated with these apparent alternate solutions to the problem of avian predation seem to be in large part due to phylogenetic correlations. Of course, better sampling of putative Batesian mimetic taxa (e.g. *Dismorphia* and *Eurytides*) and additional mimicry complexes might provide more compelling evidence for Srygley's hypothesis, or at least add more examples of mimicry between phylogenetically distinct groups. However the hypothesized adaptive character suites may also be complicated substantially by the study of additional taxa. A few examples are discussed here.

Members of the Dismorphiinae (Pieridae) exhibit long wings and abdomens like ithomiines and heliconiines, and are traditionally considered to be palatable (e.g. Bates, 1862), although their palatability has never been tested. Inference from shared hostplant associations, however, suggest that they are palatable: De Vries (1987) reports various *Inga* species (Mimosaceae) as hostplants for Costa Rican dismorphiine species, as well as for *Morpho* (Morphinae) and *Prepona* (Charaxinae), nymphalid subfamilies whose neotropical representatives, at least, appear to be uniformly palatable (Chai 1990). Because palatability of butterflies is often strongly correlated with the chemistry of their hostplants, it seems reasonable to hypothesize that dismorphiines are palatable. This group contains some members that are evidently non-mimetic, and others that closely resemble ithomiine models. Furthermore, there is considerable sexual dimorphism, the females achieving a much greater resemblance to unpalatable models than the males, as is the norm in sexually dimorphic mimetic species (Ford 1953). The Dismorphiinae therefore represent a good system to test for 'locomotor mimicry', by comparison of flight characteristics between mimetic and non-mimetic species.

Study of additional taxa might complicate the hypothesized correlations between unpalatability and particular morphological and life history traits, as well. Acraeine nymphalids (*Actinote*, in the neotropics) are unpalatable and warningly coloured, fly slowly, but have relatively short wings and abdomens (De Vries 1987). Most satyrines (e.g. *Euptychia*) are relatively slow fliers, in spite of being palatable (Brower 1984, but see Singer *et al.* 1971), and live almost exclusively in the shady understory (De Vries 1987). Many of the smaller ithomiines have rounded wings and are quite cryptic (Brown 1988). Swallowtails (Papilionidae) exhibit the complete range of palatability, from completely edible to toxic, yet display a fairly low diversity of wing shapes and flight behaviours, compared to taxa of comparable age (De Vries 1987). All fly rapidly and are capable of dizzyingly evasive manoeuvres. These observations only hint at the complexity of patterns that underlie mimetic relation in the neotropics. As pointed out by R. I. Vane-Wright (personal communication), the long-wing-and-abdomen Müllerian mimicry complexes are absent in the Old World, where unpalatable butterflies exhibit substantially different thermal characteristics (Dudley 1991*a*). These examples suggest that a broader taxonomic and geographical comparison of butterflies would not support Srygley's morphological/physiological dichotomy between palatable and unpalatable butterflies.

(*c*) *A phylogenetically constrained adaptive scenario*

Srygley (1994) viewed the morphological and behavioural differences he found between palatable and unpalatable butterflies as alternative adaptive responses to the current ecological problem of predation. Another explanation for the observed correlations (Srygley & Chai 1990; Srygley & Dudley 1993; Srygley 1994) is that the investment in equipment for rapid flight is an adaptive constraint that unpalatable butterflies, and to some extent the butterflies that mimic them, have been able to escape. Under this scenario, palatable butterflies, being large and conspicuous potential prey items for diurnal, visually oriented predators, must maintain their flight capabilities, because their main defense is to flee. There is nothing surprising about the anterior position of the centre of mass of the body in palatable, fast-flying butterflies: their large thoracic flight muscle mass should account for this all by itself. However, aposematic butterflies do not need to fly fast, especially not if they have conspicuous patterns that advertise their noxiousness. Those groups that have evolved unpalatability are freed from the constraint of pursuit by predators, and can invest their energies in other aspects of their life histories. Thus, the posterior shift of body mass in heliconiines and ithomiines may simply be a side-effect of their having a relatively small thorax. In addition, because these taxa have reduced their energetic expenditure on flight muscle (Dudley 1991*b*; Marden & Chai 1991), they can devote relatively more of their resources to reproduction. The enlargement of reproductive organs, located in the terminal segments of the abdomen, may be another reason why body mass has undergone the observed shift to the posterior in unpalatable lineages (Srygley & Chai 1990; Marden & Chai 1991).

The observation that unpalatable butterflies survive handling by predators more often than palatable butterflies (Chai 1990) is undoubtedly in part due to their toughness (Trimen 1870), but also due to the fact that predators release them because they taste bad (Bowers & Wiernasz 1979; Brower 1984). Although a butterfly's escape from, or release by a bird may appear the same to the observer, they represent entirely different events. It is possible that the brittleness of palatable butterflies' wings, rather than the toughness of unpalatable butterflies' wings, represents the evolutionary novelty, enabling palatable species to tear free from the predator's grasp. Swynnerton (1926) noted that palatable *Charaxes* struggled vigorously to escape from birds, often resulting in many tears to their wing margins. Such escape tactics may be accompanied by deceptive patterns. The 'false heads' on the hindwings of lycaenids may direct the attention of predators away from vital body parts and towards a part of the wing that tears away easily, facilitating escape (Robbins 1981). By contrast, unpalatable butterflies (Ithomiinae, Danainae, Acraeinae, *Heliconius* and Troidinae) often 'play dead' when being handled, a behaviour which may reduce wing damage (A. V. Z. Brower, unpublished data). The proportional over-representation of beakmarks on unpalatable species in collections (Carpenter 1941) is further evidence that birds frequently release them effectively unharmed.

Implicit to the adaptive constraint scenario is the idea that unpalatability and its accompanying morphological characters are a derived condition relative to palatability. The data on neither butterfly phylogeny nor palatability and host associations are yet complete enough to allow the conclusive phylogenetic tests, but the information we have suggests that this is true. Many unpalatable butterflies sequester poisons or precursors from their larval or adult food plants (Brower 1984; Spencer 1988; Brown *et al.* 1991), and associations between toxic plants and unpalatable herbivores tend to be conservative (Ehrlich & Raven 1964; Feeny 1991; Farrell *et al.* 1992), which means that colonization events are rare, and the insects tend to stay on the hosts once they arrive. Host plant shifts that do occur appear to be mediated by chemical similarity, if not phylogeny (Feeny 1991; Farrell *et al.* 1992). Although unpalatability via plant chemistry has evolved numerous times in butterflies (Sillén-Tullberg 1988), it appears to have occurred independently in each lineage: different groups have found separate solutions to the predation problem (Brower & Brower 1964; Ackery 1988; Bowers 1992).

If unpalatability and its associated morphological characters (small thorax, long wings, large abdomen, slow flight, etc.) are derived conditions in the Papilionoidea, then the ancestral butterfly must have been palatable, and possessed the associated morphological traits (large thorax, small abdomen, rapid flight, etc.). The sister taxon of the Papilionoidea is generally considered to be the Hesperioidea (skippers) (Kristensen 1976; Minet 1991), which share the large body and palatability of this hypothetical ur-butterfly. However, Scoble (1986, 1992) has suggested that the Hedylidae, a small neotropical group of thin-bodied, long winged moths, may be the sister taxon of the Papilionoidea, to the exclusion of the Hesperioidea. Most hedylids are cryptic and nocturnal, but some hedylids are day-flying (Scoble 1992) and appear to be mimics of clear winged ithomiines (A. V. Z. Brower, unpublished data). The palatability of the hedylids has not been reported, but colour patterns, behavioural evidence and host plant association (Sterculiaceae) suggest they may be palatable (Scoble 1992). The molecular data of Weller & Pashley (1995) support the placement of the hedylids as sister taxon to the Papilionoidea + Hesperioidea. Obviously, mimetic hedylids must have evolved after their aposematic models, implying that the transition to diurnality in this group may have been relatively recent. Thus, the hypothesis that the ancestral butterfly possessed characters associated with palatability is not seriously challenged by close relationship to the feeble hedylids. However plausible (or implausible) these speculations may be, much better data on host plant associations, palatability and phylogeny must be gathered before a clear understanding of the evolution of butterfly diversity is possible.

4. CONCLUSION

In this paper I have endeavoured to highlight the fundamental contributions of evolutionary history to patterns of current adaptation in butterflies. Most of the ideas I present support the traditional views of students of mimicry over the last 130 years. Srygley and colleagues (Chai & Srygley 1990; Srygley & Chai 1990; Srygley & Dudley 1993; Srygley 1994) have done an admirable job of quantifying complex morphological traits and correlating them with palatability and flight behaviour for a range of neotropical butterflies. However, Srygley has erred in his assumption that phylogenetic correlations can be factored out of the equation by statistical transformations (at least, by the ones he has performed). His assumption that 'adjustment for mimicry' is equivalent to factoring out phylogenetic relatedness is not only false, but actually enhances the effect of phylogenetic correlation in his analyses. This error has yielded misleading support for his results. More importantly, his deemphasis of the role of phylogenetic relationships has led to conclusions about adaptation that are unwarranted with respect to his own results, and contradicted by previous evidence available in the literature.

I thank J. S. Miller, P. Z. Goldstein, K. R. Sime, A. P. Vogler, R. DeSalle, L. P. Brower and J. V. Z. Dingman, for valuable discussions; R. I. Wright and an anonymous reviewer for comments and criticisms; and the libraries of Cornell University and the American Museum of Natural History for providing the 'data.' I am supported at the AMNH by NSF postdoctoral fellowship DEB-9303251.

REFERENCES

Ackery, P.R. 1984 Systematic and faunistic studies on butterflies. In *The biology of butterflies* (ed. R.I. Vane-Wright & P.R. Ackery) pp. 9–24. Princeton, New Jersey: Princeton University Press.

Ackery, P.R. 1988 Hostplants and classification: a review of nymphalid butterflies. *Biol. J. Linn. Soc.* **33**, 95–203.

Ackery, P.R. & Vane-Wright, R.I. 1984 *Milkweed butterflies.* London: British Museum of Natural History.

Adams, M.J. 1986 Pronophiline butterflies (Satyridae) of the three Andean cordilleras of Colombia. *Zool. J. Linn. Soc.* **87**, 235–320.

Aiello, A. 1984 *Adelpha* (Nymphalidae): deception on the wing. *Psyche* **91**, 1–45.

Alcock, J. 1970 Punishment levels and the response of white-throated sparrows (*Zonotrichia albicollis*) to three kinds of artificial models and mimics. *Anim. Behav.* **18**, 733–739.

Allen, J.A. 1988 Frequency-dependent selection by predators. *Phil. Trans. R. Soc. Lond.* B **319**, 485–503.

Baker, R.R. & Parker, G.A. 1979 The evolution of bird coloration. *Phil. Trans. R. Soc. Lond.* B **287**, 63–130.

Bates, H.W. 1862 Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Trans. Linn. Soc. Lond.* **23**, 495–566.

Bowers, M.D. 1992 The evolution of unpalatability and the cost of chemical defense in insects. In *Insect chemical ecology* (ed. B.D. Roitberg & M.B. Isman), pp. 216–244. New York: Chapman & Hall.

Bowers, M.D. & Wiernasz, D.C. 1979 Avian predation in a palatable butterfly, *Cercyonis pegala* (Satyridae). *Ecol. Ent.* **4**, 205–209.

Bristow, C.R. 1981 A revision of the brassoline genus *Catoblepia* (Lepidoptera: Rhopalocera). *Zool. J. Linn. Soc. Lond.* **72**, 117–163.

Brooks, D.R. & McLennan, D.A. 1991 *Phylogeny, ecology and behavior*. University of Chicago Press.

Brower, A.V.Z. 1994 Phylogeny of *Heliconius* butterflies inferred from mitochondrial DNA sequences (Lepidoptera: Nymphalidae). *Molec. Phylogenet. Evol.* **3**, 159–174.

Brower, A.V.Z. 1995 Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution*. (In the press.)

Brower, J.V.Z. 1958 Experimental studies of mimicry in some North American butterflies. Part I. The monarch, *Danaus plexippus* and the viceroy, *Limenitis archippus archippus*. *Evolution* **12**, 32–47.

Brower, J.V.Z. 1960 Experimental studies of mimicry. 4. The reactions of starlings to different proportions of models and mimics. *Am. Nat.* **94**, 271–282.

Brower, L.P. 1984 Chemical defence in butterflies. In *The biology of butterflies* (ed. P.R. Ackery & R.I. Vane-Wright), pp. 109–134. Princeton University Press.

Brower, L.P. 1988 Avian predation on the monarch butterfly and its implications for mimicry theory. In *Mimicry and the evolutionary process* (ed. L.P. Brower), pp. 4–6. University of Chicago Press.

Brower, L.P. & Brower, J.V.Z. 1964 Birds, butterflies, and plant poisons: a study in ecological chemistry. *Zoologica N.Y.* **49**, 137–159.

Brower, L.P., Brower, J.V.Z. & Collins, C.T. 1963 Experimental studies of mimicry 7: relative palatability and Müllerian mimicry among neotropical butterflies of the subfamily Heliconiinae. *Zoologica* **48**, 65–84.

Brower, L.P. & Calvert, W.H. 1985 Foraging dynamics of bird predators on overwintering monarch butterflies in Mexico. *Evolution* **39**, 852–868.

Brower, L.P., Ryerson, W.N., Coppinger, L.L. & Glazier, S.C. 1968 Ecological chemistry and the palatability spectrum. *Science, Wash.* **161**, 1349–1351.

Brower, L.P. Pough, F.H. & Meck, H.R. 1970 Theoretical investigations of automimicry, I. Single-trial learning. *Proc. natn. Acad. Sci. U.S.A.* **66**, 1059–1066.

Brown, K.S., Jr 1988 Mimicry, aposematism and crypsis in neotropical Lepidoptera: the importance of dual signals. *Bull. Soc. Zool. Fr.* **113**, 83–101, plates 1–16.

Brown, K.S., Jr, Trigo, J.R., Francini, R.B., Barros de Morais, A.B. & Motta, P.C. 1991 Aposematic insects on toxic host plants: coevolution, colonization and chemical emancipation. In *Plant–animal interactions: evolutionary ecology in tropical and temperate regions* (ed. P.W. Price, T.M. Lewinsohn, G.W. Fernandes, & W.W. Benson), pp. 375–402. New York: John Wiley and Sons.

Carpenter, G.D.H. 1941 The relative frequency of beak-marks on butterflies of different edibility to birds. *Proc. zool. Soc. Lond.* **111** (A), 223–231.

Chai, P. 1986 Field observations and feeding experiments on the responses of rufous-tailed jacamars (*Galbula ruficauda*) to free-flying butterflies in a tropical rainforest. *Biol. J. Linn. Soc.* **29**, 161–189.

Chai, P. 1990 Relationships between visual characteristics of rainforest butterflies and responses of a specialized insectivorous bird. In *Adaptive coloration in invertebrates* (ed. M. Wicksten), pp. 31–60. Galveston, Texas: Seagrant College Program, Texas A & M University.

Chai, P. & Srygley, R.B. 1990 Predation and the flight, morphology, and temperature of neotropical rain-forest butterflies. *Amer. Nat.* **135**, 748–765.

Coddington, J.A. 1988 Cladistic tests of adaptational hypotheses. *Cladistics* **4**, 3–22.

Comstock, J.H. 1918 *The wings of insects*. Ithaca, New York: Comstock Publishing Co.

Cook, L.M., Brower, L.P. & Alcock, J. 1969 An attempt to verify mimetic advantage in a neotropical environment. *Evolution* **23**, 339–345.

Coppinger, R.P. 1970 The effect of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies. II. Reactions of naive birds to novel insects. *Am. Nat.* **104**, 323–334.

Cott, H.B. 1940 *Adaptive coloration in animals*. London: Methuen.

Darwin, C. 1859 *On the origin of species* (1964 facsimile edition). Harvard University Press.

Darwin, C. 1871 *The descent of man, and selection in relation to sex* (1981 facsimile edition): Princeton University Press.

Dettner, K. 1987 Chemosystematics and evolution of beetle chemical defenses. *A. Rev. Ent.* **32**, 17–48.

De Vries, P.J. 1987 *The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae*. Princeton University Press.

Dixey, F.A. 1920 The geographical factor in mimicry (presidential address, §D). *Rep. Brit. Assoc. Adv. Sci.* **87**, 199–207.

Dobson, F.S. 1985 The use of phylogeny in behavior and ecology. *Evolution* **39**, 1384–1388.

Dudley, R. 1990 Mechanisms of flight in neotropical butterflies: morphometrics and kinematics. *J. exp. Biol.* **150**, 37–53.

Dudley, R. 1991*a* Thermoregulation in unpalatable danaine butterflies. *Funct. Ecol.* **5**, 503–506.

Dudley, R. 1991*b* Biomechanics of flight in neotropical butterflies: aerodynamics and mechanical power requirements. *J. exp. Biol.* **159**, 335–357.

Ehrlich, P.R. & Raven, P.H. 1964 Butterflies and plants: a study in coevolution. *Evolution* **18**, 586–608.

Endler, J.A. 1988 Frequency-dependent predation, crypsis and aposematic coloration. *Phil. Trans. R. Soc. Lond.* B **319**, 459–472.

Evans, D.L. & Waldbauer, G.P. 1982 Behavior of adult and naive birds when presented with a bumblebee and its mimic. *Z. Tierpsychol.* **59**, 247–259.

Farrell, B.D., Mitter, C. & Futuyma, D.J. 1992 Diversification at the insect-plant interface. *BioScience* **42**, 34–42.

Feeny, P. 1991 Chemical constraints on the evolution of swallowtail butterflies. In *Plant–animal interactions: evolutionary ecology in tropical and temperate regions* (ed. P.W. Price, T.M. Lewinsohn, G.W. Fernandes & W.W. Benson), pp. 315–340. New York: John Wiley and Sons.

Fisher, R.A. 1958 *The genetical theory of natural selection*, 2nd edn. New York: Dover Publications.

Ford, E.B. 1953 The genetics of polymorphism in the Lepidoptera. *Adv. Genet.* **5**, 43–87.

Frazer, J.F.D. & Rothschild, M. 1960 Defence mechanisms in warningly-coloured moths and other insects. *Proc. XI Ent. Congr. Entomol. (Wien)* **3**, 249–256.

Frumhoff, P.C. & Reeve, H.K. 1994 Using phylogenies to test adaptationist hypotheses: a critique of some current proposals. *Evolution* **48**, 172–180.

Garland, T., Jr 1992 Rate tests for phenotypic evolution using phylogenetically independent contrasts. *Am. Nat.* **140**, 509–519.

Gibson, D.O. 1974 Batesian mimicry without distastefulness? *Nature, Lond.* **250**, 77–79.

Gibson, D.O. 1980 The role of escape in mimicry and polymorphism: I. The response of captive birds to artificial prey. *Biol. J. Linn. Soc.* **14**, 201–214.

Gittleman, J.L. & Harvey, P.H. 1980 Why are distasteful prey not cryptic? *Nature, Lond.* **286**, 149–150.

Gittleman, J.L. & Luh, H.-K. 1992 On comparing comparative methods. *A. Rev. Ecol. Syst.* **23**, 383–404.

Goldschmidt, R. 1938 *Physiological genetics*. New York and London: McGraw-Hill.

Gould, S.J. & Lewontin, R.C. 1979 The spandrels of San Marco and the Panglossean paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond.* B **205**, 581–598.

Guilford, T. 1986 How do 'warning colours' work? – Conspicuousness may reduce recognition errors in experienced predators. *Anim. Behav.* **34**, 286–288.

Guilford, T. 1990 The secrets of aposematism: unlearned responses to specific colours and patterns. *TREE* **5**, 323.

Guillaumin, M. 1979 Participation des *Euphaedra* et *Bebearia* (Lep. Nymphalidae) aux associations mimétique de la forêt equatoriale africaine. II. Associations mimétiques sans modèles toxiques. *Bull. Soc. Zool. Fr.* **104**, 435–445.

Hancox, A.P. & Allen, J.A. 1991 A simulation of evasive mimicry in the wild. *J. Zool., Lond.* **223**, 9–13.

Harvey, D.J. 1991 Higher classification of the Nymphalidae. In *The development and evolution of butterfly wing patterns* (ed. H.F. Nijhout), pp. 255–273. Washington D.C.: Smithsonian Institution Press.

Harvey, P.H. & Pagel, M.D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.

Hespenheide, H.A. 1973 A novel mimicry complex: beetles and flies. *J. Ent.* A **48**, 49–56.

Holling, C.S. 1965 The functional responses of predators to prey density and its role in mimicry and population regulation. *Mem. ent. Soc. Can.* **45**, 1–60.

Huheey, J.E. 1984 Warning coloration and mimicry. In *Chemical ecology of insects* (ed. W.J. Bell & R.T. Cardé), pp. 257–297. Sunderland, Massachusetts: Sinauer.

Jones, F.M. 1932 Insect coloration and the relative acceptability of insects to birds. *Trans. Ent. Soc. Lond.* **80**, 345–385, with plates XVIII to XXVIII.

Kristensen, N.P. 1976 Remarks on the family-level phylogeny of butterflies (Insecta, Lepidoptera, Rhopalocera). *Zeit. Zool. Syst. Evol.* **14**, 25–33.

Lauder, G.V. 1982 Historical biology and the problem of design. *J. theor. Biol.* **97**, 57–67.

Lewontin, R.C. 1978 Adaptation. *Scient. Am.* **239**, 213–230.

Lewontin, R.C. 1979 Sociobiology as an adaptationist program. *Behav. Sci.* **24**, 5–14.

Lindroth, C.H. 1971 Disappearance as a protective factor. *Ent. Scand.* **2**, 41–48.

Mallet, J. & Singer, M.C. 1987 Individual selection, kin selection, and the shifting balance in the evolution of warning colours: the evidence from butterflies. *Biol. J. Linn. Soc.* **32**, 337–350.

Marden, J.H. & Chai, P. 1991 Aerial predation and butterfly design: how palatability, mimicry, and the need for evasive flight constrain mass allocation. *Am. Nat.* **138**, 15–36.

Meldola, R. 1878 Entomological notes bearing on evolution. *Ann. Mag. Nat. Hist.* **1**, (series 5) 155–161.

Miller, J.S. & Wenzel, J.W. 1995 Ecological characters and phylogeny. *A. Rev. Ent.* **40**, 389–415.

Minet, J. 1991 Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). *Ent. Scand.* **22**, 69–95.

Moore, B.P. 1979 Chemical defense in carabids and its bearing on phylogeny. In *Carabid beetles: their evolution, natural history and classification* (ed. T.L. Erwin). The Hague: Dr. W. Junk.

Müller, F. 1879 *Ituna* and *Thyridia*; a remarkable case of mimicry in butterflies. *Proc. R. Ent. Soc. Lond.* **1879**, xx–xxix.

Murton, R.K. 1971 The significance of a specific search image in the feeding behaviour of the wood-pigeon. *Behaviour* **40**, 10–42.

Nijhout, H.F. 1991 *The development and evolution of butterfly wing patterns*. Washington D.C. and London: Smithsonian Institution Press.

Papageorgis, C. 1975 Mimicry in Neotropical butterflies. *Am. Scient.* **63**, 522–532.

Pasteels, J.M., Rowell-Rahier, M., Braekman, J.-C. & Daloze, D. 1984 Chemical defences in leaf beetles and their larvae: the ecological, evolutionary and taxonomic significance. *Biochem. Syst. Ecol.* **12**, 395–406.

Pilecki, C. & O'Donald, P. 1971 The effects of predation on artificial mimetic polymorphisms with perfect and imperfect mimics at varying frequencies. *Evolution* **25**, 365–370.

Poulton, E.B. 1898 Natural selection and the cause of mimetic resemblance and common warning colours. *J. Linn. Soc. Lond., Zool.* **26**, 558–612, plates 40–44.

Poulton, E.B. 1926 Mimicry in African butterflies of the genus *Charaxes*, with a classification of the species. *Verh. III int. ent. Kongr.* **2**, 518–575.

Reeve, H.K. & Sherman, P.W. 1993 Adaptation and the goals of evolutionary research. *Quart. Rev. Biol.* **68**, 1–32.

Rettenmeyer, C.W. 1970 Insect mimicry. *A. Rev. Ent.* **15**, 43–74.

Ritland, D.B. 1991 Revising a classic butterfly mimicry scenario: demonstration of Müllerian mimicry between Florida viceroys (*Limenitis archippus floridensis*) and queens (*Danaus gilippus berenice*). *Evolution* **45**, 918–934.

Robbins, R.K. 1981 The 'false head' hypothesis: predation and wing pattern variation of lycaenid butterflies. *Am. Nat.* **118**, 770–775.

Roesler, R.-U. 1986 Mimikry und Phylogenie. *Bull. Soc. Zool. Fr.* **111**, 253–260.

Rothschild, M. 1964 An extension of Dr. Lincoln Brower's theory on bird predation and food specificity, together with some observations on bird memory in relation to aposematic colour patterns. *Entomologist* **97**, 73–78.

Rothschild, M. 1972 Colour and poisons in insect protection. *New Scient.* **54**, 318–320.

Schwanwitch, B.N. 1924 On the ground-plan of wing-pattern in nymphalids and certain other families of rhopalocerous Lepidoptera. *Proc. zool. Soc. Lond.* B **34**, 509–528.

Scoble, M.J. 1986 The structure and affinities of the Hedyloidea: a new concept of the butterflies. *Bull. Br. Mus. nat. Hist.* **53**, 251–286.

Scoble, M.J. 1992 *The Lepidoptera*. Oxford University Press.

Sheppard, P.M. 1958 *Natural selection and heredity*. New York: Harper & Brothers.

Sillén-Tullberg, B. 1988 Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. *Evolution* **42**, 293–305.

Singer, M.C., Ehrlich, P.R. & Gilbert, L.E. 1971 Butterfly feeding on lycopsid. *Science, Wash.* **172**, 1341–1342.

Speed, M.P. 1993 Muellerian mimicry and the psychology of predation. *Anim. Behav.* **45**, 571–580.

Spencer, K.C. 1988 Chemical mediation of coevolution in the *Passiflora-Heliconius* interaction. In *chemical mediation of coevolution* (ed. K.C. Spencer), pp. 167–240. San Diego, California: Academic Press, Inc.

Srygley, R.B. 1994 Locomotor mimicry in butterflies? The associations of positions of centres of mass among groups of mimetic, unprofitable prey. *Phil. Trans. R. Soc. Lond.* B **343**, 145–155.

Srygley, R.B. & Chai, P. 1990 Flight morphology of Neotropical butterflies: palatability and the distribution of mass to the thorax and abdomen. *Oecologia* **84**, 491–499.

Srygley, R.B. & Dudley, R. 1993 Correlations of the position of center of body mass with butterfly escape tactics. *J. exp. Biol.* **174**, 155–166.

Strauss, R.E. 1990 Patterns of quantitative variation in lepidopteran wing morphology: the convergent groups

Heliconiinae and Ithomiinae (Papilionoidea: Nymphalidae). *Evolution* **44**, 86–103.

Süffert, F. 1927 Zur vergleichende Analyse der Schmetterlingszeichnung. *Biol. Zbl.* **47**, 385–413.

Süffert, F. 1929 Due Ausbildung des imaginalen Fluegelschnittes in der Schmetterlingspuppe. *Z. Morph. Ökol. Tiere* **14**, 338–359.

Swynnerton, C.F.M. 1915 A brief preliminary statement of a few of the results of five years' special testing of the theories of mimicry. *Proc. ent. Soc. Lond.* **1915**, xxxii–xliii.

Swynnerton, C.F.M. 1926 An investigation into the defences of butterflies of the genus *Charaxes*. *Verh. III int. ent. Kongr.* **2**, 478–506; 2 plates.

Tinbergen, L. 1960 The natural control of insects in pinewoods. I: Factors influencing the intensity of predation by songbirds. *Arch. Néerl. Zool.* **13**, 266–336.

Trimen, R. 1870 On some remarkable mimetic analogies among African butterflies. *Trans. Linn. Soc. Lond.* **26**, 497–522; 2 plates.

Turner, J.R.G. 1977 Butterfly mimicry: the genetical evolution of an adaptation. In *Evolutionary biology* (ed. M.K. Hecht, W.C. Steere & B. Wallace), pp. 163–206. New York: Plenum Press.

Turner, J.R.G. 1978 Why male butterflies are non-mimetic: natural selection, sexual selection, group selection, modification, and sieving. *Biol. J. Linn. Soc. Lond.* **10**, 385–432.

Turner, J.R.G. 1984 Mimicry: the palatability spectrum and its consequences. In *The biology of butterflies* (ed. R.I. Vane-Wright & P.R. Ackery), pp. 141–161. Princeton, New Jersey: Princeton University Press.

Turner, J.R.G., Kearney, E.P. & Exton, L.S. 1984 Mimicry and the Monte Carlo predator: the palatability spectrum and the origins of mimicry. *Biol. J. Linn. Soc.* **23**, 247–268.

Vane-Wright, R.I. 1976 A unified classification of mimetic resemblances. *Biol. J. Linn. Soc.* **8**, 25–56.

Vane-Wright, R.I. 1991 A case of self-deception. *Nature, Lond.* **350**, 460–461.

Vane-Wright, R.I. & Smith, C.R. 1991 Phylogenetic relationships of three African swallowtail butterflies, *Papilio dardanus*, *P. phorcas* and *P. constantinus*: a cladistic analysis (Lepidoptera: Papilionidae). *Syst. Ent.* **16**, 275–291.

van Someren, V.G.L. & Jackson, T.H.E. 1959 Some comments on protective resemblance amongst African Lepidoptera (Rhopalocera). *J. Lepid. Soc.* **13**, 121–150.

Waldbauer, G.P. 1988 Asynchrony between mimics and their models. *Am. Nat.* **131** (suppl.), 103–121.

Waldbauer, G.P. & Sheldon, J.K. 1971 Phenological relationships of some aculeate Hymenoptera, their dipteran mimics, and insectivorous birds. *Evolution* **25**, 371–382.

Wallace, A.R. 1866 On the phenomenon of variation and geographical distribution as illustrated by the Papilionidae of the Malayan region. *Trans. Linn. Soc. Lond.* **25**, 1–71; 8 plates.

Wallace, A.R. 1867*a* Mimicry, and other protective resemblances among animals. *Westminster Review* (new series) **32**, 1–43 (reprinted in Wallace, 1870. *Contributions to the theory of natural selection*. London: Macmillan & Co., pp. 45–129).

Wallace, A.R. 1867*b* (on caterpillar colouration) *Proc. Ent. Soc. Lond., ser. 3* **1867**, lxxx–lxxxi.

Wanntorp, H.E. 1983 Historical constraints in adaptation theory: traits and non-traits. *Oikos* **41**, 157–160.

Weller, S.J. & Pashley, D.P. 1995 In search of butterfly origins. *Molec. Phylogenet. Evol.* (In the Press.)

Whitman, D.W., Blum, M.S. & Alsop, D.W. 1990 Allomones: chemicals for defense. In *Insect defenses* (ed. D.L. Evans & J.O. Schmidt), pp. 291–351. Albany, New York: State University of New York Press.

Williams, G.C. 1966 *Adaptation and natural selection*. Princeton University Press.

Williams, G.C. 1992 *Natural selection: domains, levels, and challenges*. Oxford University Press.

Received 2 September 1994; accepted 1 November 1994