

# The aerodynamic costs of warning signals in palatable mimetic butterflies and their distasteful models

Robert B. Srygley<sup>1,2\*</sup>

<sup>1</sup>Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama

<sup>2</sup>Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

Bates hypothesized that some butterfly species that are palatable gain protection from predation by appearing similar to distasteful butterflies. When undisturbed, distasteful butterflies fly slowly and in a straight line, and palatable Batesian mimics also adopt this nonchalant behaviour. When seized by predators, distasteful butterflies are defended by toxic or nauseous chemicals. Lacking chemical defences, Batesian mimics depend on flight to escape attacks. Here, I demonstrate that flight in warning-coloured mimetic butterflies and their distasteful models is more costly than in closely related non-mimetic butterflies. The increased cost is the result of differences in both wing shape and kinematics. Batesian mimics and their models slow the angular velocity of their wings to enhance the colour signal but at an aerodynamic cost. Moreover, the design for flight in Batesian mimics has an additional energetic cost over that of its models. The added cost may cause Batesian mimics to be rare, explaining a general pattern that Bates first observed.

**Keywords:** locomotor mimicry; insect flight; aerodynamics; mutualism; communication; Müllerian mimicry

## 1. INTRODUCTION

One signal common in nature is bright coloration that warns the predator that the signal bearer is well defended (Yachi & Higashi 1998). Many distasteful animals are brightly coloured, and thus possess aposematic signals, which warn predators that the prey is toxic (Brower 1964) or otherwise not worth pursuing. Aposematic signals increase the risk of detection such that the signaller is often at greater risk of being predated than are cryptic counterparts (Lindström *et al.* 1999, 2001). Recent models by Sherratt (2002) suggest that selection operates on the signals of unpalatable prey so that predators do not mistake them for more profitable prey (see also Srygley & Chai 1990*a,b*; Srygley 1999*a*).

Associated with warning coloration are sluggish or predictable behaviours that honestly signal the prey's defensive qualities (Srygley 1999*a*; Hatle *et al.* 2002; Sherratt & Beatty 2003). In butterflies, distasteful species differ from more palatable ones in their flight pattern. Butterflies that are protected by defensive chemicals fly slowly relative to those that are palatable. Indeed, many palatable butterflies fly erratically and therefore exhibit protean defence behaviours (Chai & Srygley 1990). Moreover, palatable butterflies must quickly manoeuvre to escape from birds when attacked. This difference in escape tactics between palatable and distasteful species is associated with a suite of morphological, physiological and behavioural traits (summarized in table 1 in Srygley (1994)).

What remains unclear is whether the slow flight of distasteful butterflies is an energetically costly signal to the predator that the butterfly is distasteful. If it is, then the

evidence would support the hypothesis that slow flight is a signal of distastefulness. In addition, it may serve as a handicap (Zahavi 1993), and thus make the signal reliable to the predators. Alternatively, slow flight may be beneficial solely as a result of a reduction in the energetic cost of flight relative to that of palatable species. In this instance, if slow flight is a signal at all, then it is a conventional signal (Guilford & Dawkins 1993).

Mimicry in butterflies provides a unique opportunity to examine these two hypotheses. One of the classic examples of evolution by natural selection, Batesian mimics bear warning coloration although they are undefended and nutritious (Bates 1862). Here, I analyse the aerodynamic costs of flight behaviours in butterflies that mimic one another in coloration. The energetic cost of flying so as to reveal warning colours in distasteful models is greater than the cost of flying in non-mimetic palatable butterflies and deters cheating of the locomotory signal. I report here that cheaters pay an even higher cost per second of flight than distasteful aposematic species of the same mass.

Predation as the selective force on colour mimicry is well supported empirically (Gilbert 1983; Brower 1984) and theoretically (Huheey 1988; Mallet & Joron 2000). Müllerian mimicry is the convergence of distasteful or otherwise harmful prey on a common colour pattern to educate the predators more efficiently than the coloration is associated with distastefulness. Batesian mimicry is the similarity of a palatable profitable prey to an unpalatable or unprofitable species (called a 'model'). In this paper, I focus on the flight energetics of these two types of mimetic butterflies from a single low-elevation rainforest community in the Panama Canal region of the Republic of Panama. The costs of flight are compared with those for closely related palatable butterfly species (figure 1).

\* Address for correspondence: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948 USA (bob.srygley@zoo.ox.ac.uk).

Table 1. Morphology, kinematics and aerodynamic power requirements (mean  $\pm$  s.e.) with taxonomic groupings (in bold), colour or mimetic group and sample size for each butterfly species.

sample size, $n$		body mass, $m$ (mg)	wing length, $R$ (mm)	aspect ratio, AR	forward velocity, $V$ (m s <sup>-1</sup> )	Reynold's number, $Re$	mean wing chord, $c$ (mm)	wing beat frequency, $f$ (Hz)	mean wing tip flapping velocity, $U$ (m s <sup>-1</sup> )	aerodynamic power, $P_{aero}$ (W kg <sup>-1</sup> )
<b>Nymphalinae group I</b>										
green	4	255 $\pm$ 19	48 $\pm$ 1	3.8 $\pm$ 0.0	1.0 $\pm$ 0.1	2813 $\pm$ 123	26 $\pm$ 0	11.7 $\pm$ 0.4	0.8 $\pm$ 0.0	6.2 $\pm$ 0.2
Batesian <sup>a</sup>	1	175	38	3.7	1.0	1864	21	9.6	0.7	7.6
<b>Nymphalinae group II</b>										
green	7	288 $\pm$ 17	43 $\pm$ 0	2.8 $\pm$ 0.0	1.1 $\pm$ 0.1	3013 $\pm$ 240	31 $\pm$ 1	9.7 $\pm$ 0.8	1.0 $\pm$ 0.1	6.4 $\pm$ 0.1
Batesian	1	46	26	3.7	0.3	880	14	13.2	0.5	7.8
<b>Danainae</b>										
Müllerian <sup>b</sup>	2	415 $\pm$ 75	47 $\pm$ 0	3.5 $\pm$ 0.1	0.8 $\pm$ 0.0	2859 $\pm$ 277	27 $\pm$ 1	9.3	0.9 $\pm$ 0.1	6.9 $\pm$ 0.2
<b>Ithomiinae</b>										
Müllerian	4	92 $\pm$ 10	34 $\pm$ 0	4.4 $\pm$ 0.2	0.9 $\pm$ 0.3	1302 $\pm$ 66	16 $\pm$ 1	12.5 $\pm$ 0.6	0.6 $\pm$ 0.0	6.0 $\pm$ 0.1
<b>Charaxinae</b>										
Batesian	1	268	—	3.1	0.7	2027	28	8.3	0.7	7.4
<b>Pierinae</b>										
Müllerian	1	76	34	3.2	1.2	1886	21	10.4	0.8	6.4

<sup>a</sup> Batesian mimics are palatable; <sup>b</sup> Müllerian mimics are unpalatable and also the models for the Batesian mimics.

## 2. MATERIAL AND METHODS

Systematic groupings of the species were derived from the most recent phylogenetic hypothesis (Harvey 1991). The tiger mimics span a broad phylogenetic range (figure 2) and include the extremely distasteful Müllerian mimics *Mechanitis polymnia*, *Lycorea cleobaea* and *Perrhybris pyrha*. These species serve as models for the palatable Batesian mimics *Consul fabius*, *Eucides isabella* and *Eresia mechanitis*. *Eucides isabella* and *Er. mechanitis* are each sister taxon to a palatable green butterfly, *Philaethria dido* and *Siproeta stelenes*, respectively. Here, I refer to *Ph. dido* and *S. stelenes* as the green palatable group. Palatability for all species except *Er. mechanitis* was measured as the proportion of butterflies eaten in presentation experiments by rufous-tailed jacamars, *Galbula ruficauda* (Srygley & Chai 1990a). Recent evidence indicates that *Er. mechanitis* is palatable and a Batesian mimic. Although related genera in the Melitaeini tribe of the Nymphalidae sequester iridoid compounds, *Eresia* species feed on host plants that do not contain iridoids (Wahlberg 2001).

The methodology for videotaping butterflies in flight, digitizing video recordings of the butterfly flight sequences and the kinematic and aerodynamic analyses has been detailed recently (Srygley 1994, 1999b; Srygley & Ellington 1999a,b). Based on the morphology and wing motion of each individual butterfly, I used a blade-element analysis based on quasi-steady aerodynamics to calculate the power required for the insect to fly forward (Srygley & Ellington 1999b). In brief, aerodynamic power requirements for flight ( $P_{aero}$ ; Ellington 1984a,b) may be divided into the power required to overcome drag on the wings (profile power,  $P_{pro}$ ), the power required to overcome drag on the body (parasite power,  $P_{par}$ ) and the power required to balance the body weight (induced power,  $P_{ind}$ ).  $P_{pro}$  was estimated as the product of profile drag and relative velocity for each element of the wings.  $P_{ind}$  was estimated using momentum jet theory after Willmott & Ellington (1997), and  $P_{par}$  was estimated as the product of the parasite drag and forward flight speed. Because of the high profile drag of the wings,  $P_{aero}$  is greater than the power required to accelerate the wings ( $P_{acc}$ ). Thus  $P_{aero}$  during the decelerating halves of the downstroke and upstroke can not be supplied by the excess kinetic energy of the decelerating wing ( $P_{acc}$ ), and the total power requirement for flight is simply equal to  $P_{aero}$ . Formulae and further details are available in Srygley & Ellington (1999b).

Using analysis of covariance, aerodynamic power requirements were covaried with body mass to determine whether there was a difference in mass-specific flight energetics among mimicry groups.

## 3. RESULTS

The total aerodynamic power ( $P_{aero}$ ) required for forward flight was linearly related to body mass ( $p < 0.0001$ ). Power increased at 7.2 W kg<sup>-1</sup> body mass. Because the interaction of body mass with the mimicry group was not significant (ANCOVA:  $p = 0.92$ ), the slopes were parallel for the three groups. I then tested for a difference in mass-adjusted aerodynamic power among the mimicry groups.

Adjusting for body mass, flight associated with warning coloration was energetically more demanding than that of the green palatable species. There was an added cost of masquerading as unpalatable butterflies: the mass-specific aerodynamic cost of flight was greater for the Batesian

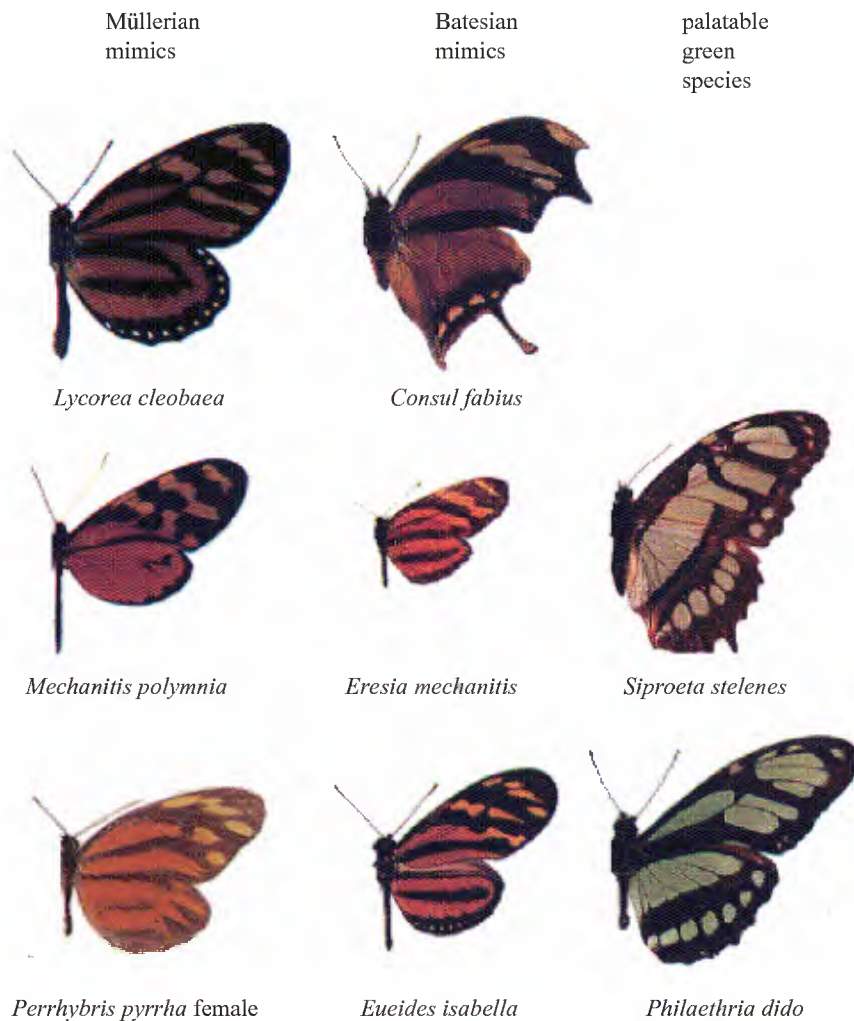


Figure 1. Butterfly species (dorsal view) analysed for their aerodynamic power requirements for flight. The species are grouped into three categories based on their palatability and wing coloration. Male *Perrhybris pyrrrha* are not mimetic, and only the female was analysed. Palatable green species are shown to the right of their Batesian sister taxa.

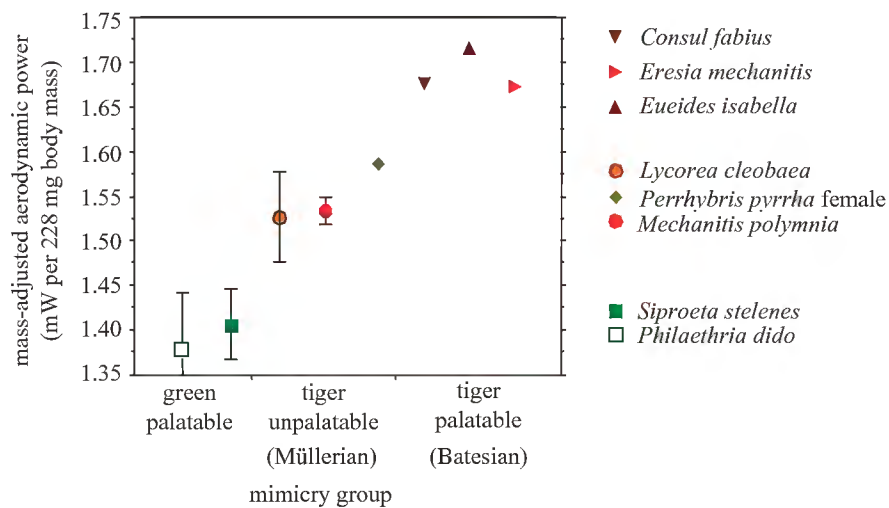


Figure 2. Aerodynamic costs (mean  $\pm$  s.e.) of warning signals in Müllerian unpalatable models, palatable Batesian mimics and palatable green butterflies, adjusted to a mean body mass of 228 mg. Honest aposematic signals were costly for the distasteful species relative to the cost of flight for palatable green butterflies. The cost of cheating as a Batesian mimic was even greater than the cost of an honest signal. For palatable mimetic species (Batesian mimics), energy was expended at a mass-specific rate that was *ca.* 20% greater than that of the palatable green butterflies.

mimics than for their Müllerian models. Aerodynamic power requirements adjusted to the mean body mass for all sampled individuals are shown in figure 2.

Hence, the three groups differed in their aerodynamic cost of flight. At any given body mass, green palatable butterflies had the lowest aerodynamic cost, distasteful tiger mimics were intermediate and the Batesian tiger mimics were expending the most energy for flight. Sample sizes varied depending on the availability of butterflies in the lowland rainforests of Panama. Using species means so that species were not weighted by their abundance in the analyses did not qualitatively alter the results. For *Er. mechanitis* and *E. isabella* the increases in the aerodynamic cost of flight represent two independent evolutionary divergences from the costs of flight of their sister genera *S. stelenes* and *Ph. dido*, respectively.

The difference in mass-specific power requirements among the three groups of butterflies was the result of differences in wing shape and the relative motion of the aerodynamic centre (mean chord) in palatable green butterflies, the Batesian mimics and their distasteful models (table 1). First, green palatable butterflies had a larger mean wing chord,  $c$ . Mass-adjusted  $c$  was significantly greater for the green palatable butterflies relative to that of the palatable mimics and their models ( $p = 0.0056$ ). Mass-adjusted  $c$  was not significantly different between models and mimics. Second, wing shape, measured as aspect ratio (AR), was significantly less for the green palatable butterflies than for the distasteful models ( $p = 0.0085$ ). Mean AR for Batesian mimics was intermediate and not significantly different from either the green palatable butterflies or the distasteful models (Student's  $t$ -tests:  $p > 0.05$ ). Third, the relative motion of the wing tip,  $U$ , was faster in green palatable butterflies. Mass-adjusted  $U$  was significantly greater for the green palatable butterflies than for the Batesian mimicry group and their models ( $p = 0.039$ ). However, mass-adjusted  $U$  was not significantly different between models and mimics. As a result of these differences in wing shape and kinematics, the Reynold's numbers ( $Re$ ), indicative of the drag forces on the wings, were significantly greater in the green palatable species than in the Batesian mimics and their models ( $p < 0.001$ ).  $Re$  was not different between the models and mimics (Student's  $t$ -test:  $p > 0.05$ ). Although the tiger models and mimics tended to fly more slowly than the palatable butterflies, the difference was not significant ( $F$ -test: d.f. = 2,18,  $p = 0.09$ ).

#### 4. DISCUSSION

These results affirm that locomotor mimicry exists within distasteful Müllerian mimics. Moreover, locomotor mimicry between Batesian mimics and their models is demonstrated here for the first time. Although mimetic locomotion in distasteful butterflies that mimic one another in coloration has supporting morphological, kinematic and aerodynamic evidence (Srygley 1994, 1999*a,b*; Srygley & Ellington 1999*a,b*), there remained scepticism about whether it exists (Brower 1995, but see Sherratt *et al.* 2004). As predicted from morphological analyses (Srygley 1994), convergence in aerodynamic power and kinematic features that determine aerodynamic power requirements was evident among the Müllerian tiger

mimics. In addition, the more deliberate behaviours of the Müllerian mimics incurred an aerodynamic cost relative to those of more palatable butterflies. Hence, biomechanical analyses provide a new perspective on the evolution of mimetic signals in flying organisms.

Furthermore, current aerodynamic theory for forward flight of insects may be used to predict the local optima for behavioural adaptations in the evolution of functional traits. For example, I hypothesize that the behaviours of the distasteful models in the tiger mimicry group are local optima for the Batesian mimics in the present study. Although the energetic cost of flight for the Batesian mimics was greater than for the models, none of the traits that enter into the quasi-steady aerodynamic analysis was significantly different between the two groups. I suggest that the lack of a clearly discernible difference results from my need to group the Batesian mimics together for comparison with the models. In the present study, a single Batesian mimic was sampled for each species owing to their extreme rarity. However, if each Batesian mimic was analysed separately, we would probably find that each species is on a different evolutionary pathway towards the traits of its model or models. This is sensible because each Batesian mimic originates from a different taxonomic group of the Nymphalidae (table 1). Evidently they are all aerodynamically suboptimal relative to their models, which suggests genetic or functional constraints on design. Further work will elucidate the features that lead to the added cost of flight.

One common feature of the Batesian mimics is that they retain the wide thorax and powerful flight muscles from their palatable ancestry to power rapid escape flights when detected by predators (Srygley & Chai 1990*b*; Srygley 1994). This difference between the Batesian mimics and their models may influence body drag. The slopes of body diameter on body mass were significantly different between the Batesian mimics and their models ( $p = 0.002$ ), such that Batesian mimics had disproportionately wider bodies than their distasteful models with increasing body size. However, parasite power (power required to overcome body drag) was not different between the two groups ( $p = 0.31$ ) following adjustment for body mass (ANCOVA:  $p < 0.05$ ). Moreover, parasite power is such a small component of the aerodynamic cost that it is negligible relative to the difference observed between Batesian mimics and their models in their aerodynamic power requirements.

The slow motion of the mean wing chord of the Batesian mimics and their models relative to that of the palatable green butterflies probably makes colour details on the flapping wings more apparent. Thus, the slow angular motion wards off avian predators but with an aerodynamic cost. Hence, the difference in the cost of flight among the palatable butterflies, the palatable Batesian mimics and their distasteful models is an estimate of the energetic cost of conveying an aposematic signal that the butterfly is distasteful.

The locomotory behaviours associated with warning coloration permit the predators to capture and taste the prey more readily, although subsequently the prey are typically released unharmed. Hence, the locomotory behaviours reliably signal the edibility of the butterflies to the predators.

I propose that, when locomotory costs are included, the warning signals in this group of aerial prey communicating to avian predators are handicap signals. A general feature of the handicap hypothesis is that the cost of a signal ensures that the signal reliably conveys the genotypic or phenotypic quality of the signaller to the receiver (Zahavi 1993). This hypothesis assumes that the signal is costly to produce or maintain and its inherent cost is higher for low-quality than for high-quality signallers. Warning colours and Batesian mimicry have previously been used to refute the handicap hypothesis in signal design because warning colours are not a costly signal that only defended prey can afford (Guilford & Dawkins 1993). However, the cost of behaviours associated with warning signals was not assessed. Here, I have shown that palatable Batesian mimics expend more energy when flying, and thereby advertising their warning coloration, than do their distasteful models.

Are Batesian mimics less capable than their models of affording the higher cost of flight? To test this I covaried abdominal mass, as a measure of lipid reserves (Srygley & Chai 1990b), with body mass and tested for a difference among the Batesian mimics, Müllerian models and palatable green butterflies. The three groups were significantly different in body-mass-adjusted abdominal mass ( $p < 0.005$ ). Müllerian mimics had the greatest energy reserves, Batesian mimics had less, and the palatable green butterflies had the least mass allocated to the abdomen. As predicted by the handicap principle, the models were best capable of meeting the aerodynamic power requirements for flight, and the Batesian mimics or 'signal cheaters' both incurred a higher energetic cost and had less reserves available to meet that cost. More direct evidence for locomotor mimicry as a handicap would arise from intraspecific analyses of the reliability of the behavioural signal and its association with the energy reserves of the individual. However, the requisite data are not yet available.

Sherratt & Beatty (2003) found that defended prey evolve towards traits that increase their differences from palatable prey so that predators were less likely to pursue them, even if such traits were less conspicuous than those of the palatable species. Furthermore, Sherratt *et al.* (2004) found that slower more deliberate motion is a result of active selection on distasteful prey to advertise warningly. These experiments confirmed that Batesian colour mimics do not mimic their models in locomotion when they possess other means to escape. However, flexibility in behaviour such as that exhibited in natural species was not incorporated into the simulated prey. In nature, undisturbed Batesian mimics fly slowly and deliberately like their models (R. B. Srygley, personal observation), but when pursued, they typically adopt the more rapid and erratic flight behaviours that are observed in other palatable species. Perhaps it is this strategy to be a jack-of-all-trades in escape design that results in less-than-optimal design and greater aerodynamic costs for flight.

Ultimately, an energetic cost to aposematic signals in both distasteful Müllerian mimics and palatable Batesian mimics invokes a selection force against the evolution of the signal. The added cost for cheating may be one reason why Batesian mimicry is uncommon in nature.

and C. P. Ellington FRS for invaluable consultations and the use of his aerodynamic model for forward flight. L. Gilbert provided inspiration in his pursuit of mimicry from passion-vine leaf shapes to butterflies. E. Leigh and A. Herre commented on an early version of the manuscript. The Autoridad Nacional del Ambiente (ANAM) granted permission to conduct the research in Panama. The Brain Pool Program of the Korean Federation of Science and Technology Societies supported the author during preparation of the manuscript.

## REFERENCES

- Bates, H. W. 1862 Contributions to an insect fauna of the Amazon valley (Lepidoptera: Heliconidae). *Trans. Linn. Soc. Lond.* **23**, 495–566.
- Brower, A. V. Z. 1995 Locomotor mimicry in butterflies? A critical review of the evidence. *Phil. Trans. R. Soc. Lond. B* **347**, 413–425.
- Brower, L. P. 1964 Chemical defenses in butterflies. *Symp. R. Entomol. Soc. Lond.* **11**, 109–134.
- Brower, L. P. 1984 Chemical defence in butterflies. In *The biology of butterflies* (ed. R. I. Vane-Wright & P. R. Ackery), pp. 109–134. New York: Academic.
- Chai, P. & Srygley, R. B. 1990 Predation and the flight, morphology, and temperature of neotropical rainforest butterflies. *Am. Nat.* **135**, 748–765.
- Ellington, C. P. 1984a The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Phil. Trans. R. Soc. Lond. B* **305**, 79–113.
- Ellington, C. P. 1984b The aerodynamics of hovering insect flight. V. A vortex theory. *Phil. Trans. R. Soc. Lond. B* **305**, 115–144.
- Gilbert, L. E. 1983 Coevolution and mimicry. In *Coevolution* (ed. D. J. Futuyma & M. Slatkin), pp. 263–281. Sunderland, MA: Sinauer.
- Guilford, T. & Dawkins, M. S. 1993 Are warning colors handicaps? *Evolution* **47**, 400–416.
- Harvey, D. J. 1991 Appendix B: higher classification of the Nymphalidae. In *The development and evolution of butterfly wing patterns* (ed. F. H. Nijhout), pp. 255–273. Washington, DC: Smithsonian Institution Press.
- Hatle, J. D., Salazar, B. A. & Whitman, D. W. 2002 Survival advantage of sluggish individuals in aggregations of aposematic prey, during encounters with ambush predators. *Evol. Ecol.* **16**, 415–431.
- Huhecy, J. E. 1988 Mathematical models of mimicry. In *Mimicry and the evolutionary process* (ed. L. P. Brower), pp. 22–41. University of Chicago Press.
- Lindström, L., Alatalo, R. V., Mappes, J., Riipi, M. & Ver-tainen, L. 1999 Can aposematism evolve by gradual change? *Nature* **397**, 249–251.
- Lindström, L., Alatalo, R. V., Lyytinen, A. & Mappes, J. 2001 Strong antiapostatic selection against novel rare aposematic prey. *Proc. Natl Acad. Sci. USA* **98**, 9181–9184.
- Mallet, J. & Joron, M. 2000 Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *A. Rev. Ecol. Syst.* **30**, 201–234.
- Sherratt, T. N. 2002 The coevolution of warning signals. *Proc. R. Soc. Lond. B* **269**, 741–746. (DOI 10.1098/rspb.2001.1944.)
- Sherratt, T. N. & Beatty, C. D. 2003 The evolution of warning signals as reliable indicators of prey defense. *Am. Nat.* **162**, 377–389.
- Sherratt, T. N., Rashed, A. & Beatty, C. D. 2004 The evolution of locomotory behaviour in profitable and unprofitable simulated prey. *Oecologia* **138**, 143–150.
- 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.

I thank the Smithsonian Institution for financial support, the Smithsonian Tropical Research Institute for logistical support,

- Srygley, R. B. 1999a Incorporating motion into mimicry. *Evol. Ecol.* **13**, 691–708.
- Srygley, R. B. 1999b Locomotor mimicry in *Heliconius* butterflies: contrast analyses of flight morphology and kinematics. *Phil. Trans. R. Soc. Lond. B* **354**, 203–214. (DOI 10.1098/rstb.1999.0372.)
- Srygley, R. B. & Chai, P. 1990a Predation and the elevation of thoracic temperature in brightly colored neotropical butterflies. *Am. Nat.* **135**, 766–787.
- Srygley, R. B. & Chai, P. 1990b Flight morphology of neotropical butterflies: palatability and distribution of mass to the thorax and abdomen. *Oecologia* **84**, 491–499.
- Srygley, R. B. & Ellington, C. P. 1999a Discrimination of flying mimetic, passion-vine butterflies *Heliconius*. *Proc. R. Soc. Lond. B* **266**, 2137–2140. (DOI 10.1098/rspb.1999.0899.)
- Srygley, R. B. & Ellington, C. P. 1999b Estimating the relative fitness of local adaptive peaks: the aerodynamic costs of flight in mimetic passion-vine butterflies *Heliconius*. *Proc. R. Soc. Lond. B* **266**, 2239–2245. (DOI 10.1098/rspb.1999.0914.)
- Wahlberg, N. 2001 The phylogenetics and biochemistry of host-plant specialization in melitacine butterflies (Lepidoptera: Nymphalidae). *Evolution* **55**, 522–537.
- Willmott, A. P. & Ellington, C. P. 1997 The mechanics of flight in the hawkmoth *Manduca sexta*. II. Aerodynamic consequences of kinematic and morphological variation. *J. Exp. Biol.* **200**, 2723–2745.
- Yachi, S. & Higashi, M. 1998 The evolution of warning signals. *Nature* **394**, 882–884.
- Zahavi, A. 1993 The fallacy of conventional signaling. *Phil. Trans. R. Soc. Lond. B* **340**, 227–230.