

Evaluating a putative mimetic relationship between two butterflies, *Adelpha bredowii* and *Limenitis lorquini*

KATHLEEN L. PRUDIC,¹ ARTHUR M. SHAPIRO¹ and

NICOLA S. CLAYTON^{2,*} ¹Section of Evolution and Ecology and ²Section of Neurobiology, Physiology and Behavior, University of California, Davis, U.S.A.

Abstract. 1. A laboratory bioassay experiment was performed in order to investigate a long-standing putative mimetic relationship between two butterflies, the Lorquin's admiral *Limenitis lorquini* and the California sister *Adelpha bredowii* (Lepidoptera, Nymphalidae). These butterfly species are commonly sympatric in their broad distribution on the west coast of the United States. The wing colour pattern of *L. lorquini* differs from the patterns exhibited by its North American congeners, resembling *A. bredowii* instead.

2. The feeding responses of California scrub jays *Aphelocoma californica* (Passeriformes, Corvidae) to these prey types and a known palatable control, the buckeye butterfly *Junonia coenia* (Lepidoptera, Nymphalidae), were examined quantitatively. The birds usually demonstrated long handling times of *A. bredowii* before consumption, while *L. lorquini* was manipulated and consumed at the same rate as the control butterfly. The birds also exhibited feather ruffling and bill wiping after consuming *A. bredowii* while they did not exhibit such behaviours after consuming *L. lorquini* and *J. coenia*.

3. The birds did not discriminate between the dorsal colour patterns of the two species in a choice experiment.

4. Because *A. bredowii* was moderately unpalatable to the captive scrub jays and the birds were not discriminating in their choice, this suggests a Batesian mimetic relationship between *L. lorquini* and *A. bredowii*.

Key words. *Adelpha bredowii*, bioassay, *Limenitis lorquini*, mimicry, palatability.

Introduction

In defensive mimicry, one species gains protection from predation through the evolution of phenotypic similarities to an unpalatable or defended species. This can be categorised as Batesian mimicry, with a palatable mimic and an unpalatable model, or Müllerian mimicry, with two or more unpalatable types converging to a similar aposematic colour pattern (Wickler, 1968). Thus, mimetic systems are evaluated by two parameters: palatability and phenotypic similarity. Predators learn to associate diagnostic

phenotypes with unpleasant experiences (i.e. bad taste) and avoid consuming any individual that exhibits those colouration patterns (Coppinger, 1970). Establishing the existence of a mimetic relationship requires the examination of both the prey's palatability and the predator's behaviour towards the prey.

In North America, the best-studied butterfly mimetic relationship is between the viceroy *Limenitis archippus archippus* (Nymphalidae) and the monarch *Danaus plexippus* (Nymphalidae). Traditionally, this association has been regarded as Batesian mimicry, with the viceroy as the palatable mimic and the monarch as the unpalatable model (e.g. Brower, 1958a; Platt, 1983). Recent experiments have suggested that this relationship is Müllerian rather than Batesian mimicry, i.e. both the viceroy and the monarch are unpalatable (Ritland & Brower, 1991). The distinction between Batesian and Müllerian mimicry in this system becomes obscure when temporal and geographic differences

Correspondence: Kathleen L. Prudic, Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Campus Box 334, Boulder, CO 80309-0334, U.S.A. E-mail: kathleen.prudic@colorado.edu

*Present address: Department of Experimental Psychology, University of Cambridge, UK.

in unpalatability are considered (Turner, 1984; Ritland, 1991), however the differences between the concepts of Batesian and Müllerian mimicry remain valuable, particularly when the temporal and geographic information is more limited.

Interestingly, the genus *Limenitis* (Nymphalidae, Nymphalinae) contains at least four species involved in some type of mimicry with models that belong to three different butterfly sub-families. In several bioassay studies, *Danaus plexippus*, *Danaus gilippus* (both Danainae), and *Battus philenor* (Papilioninae) have been shown to be effective models for *Limenitis archippus archippus*, *Limenitis archippus floridensis*, and *Limenitis arthemis astyanax* respectively (Brower, 1958a,c; Platt *et al.*, 1971). The fourth species of *Limenitis*, *L. lorquini*, has been postulated to mimic *Adelpha bredowii* (Nymphalinae) (e.g. Poulton, 1909; Platt, 1983; Porter, 1987) but this relationship had never been examined experimentally (Platt, 1983).

Limenitis lorquini and *Adelpha bredowii* exhibit several morphological and behavioural similarities. The dorsal surfaces of both species have a brown–black ground colour with an orange area on the apex of the forewing. There is also a white band that extends from the upper forewing to the hindwing in both species (Plate 1). In contrast, there is little phenotypic resemblance between the ventral surfaces of the two species. When at rest, *L. lorquini* and *A. bredowii* often hold their wings open, displaying the dorsal wing pattern. Behaviourally, the species have similar flight patterns, gliding for long intervals on open wings with only infrequent beats. These shared behaviours tend to maximise their similar colour patterns and resemblance to a human observer (A. Shapiro and K. Prudic, pers. obs.). Consequently, unlike many butterfly species in which ventral mimicry is considered important (Codella & Lederhouse, 1989), the resemblance

of dorsal wing patterns may be more significant for the *L. lorquini* and *A. bredowii* mimetic system.

The suspected mimetic relationship between *A. bredowii* and *L. lorquini* was investigated by quantifying the palatability of both butterfly species to a model predator and by determining whether these predators did or did not discriminate between the two species. These experiments were performed using California scrub jays *Aphelocoma californica*. These jays are closely related to the Florida scrub jay, the gray jay, and the eastern blue jay used by Brower (1958b), Bowers and Farley (1990), and Platt *et al.* (1971) respectively in other palatability bioassays.

Methods

Prey

Adelpha bredowii feeds on oak species, commonly interior live oak *Quercus wislizenii* (Fagaceae) in interior lowland California; *Limenitis lorquini* feeds on willow species *Salix* spp. (Salicaceae) (Opler & Wright, 1999). The role of sequestered plant compounds in the palatability of these two insects has not been established. *Junonia coenia*, the palatable control, feeds on plants containing bitter iridoid glycosides, including members of the Plantaginaceae (Bowers, 1984), on which it was reared; however, these glycosides are not retained through metamorphosis, and the adult is highly palatable (Bowers & Farley, 1990). *Junonia coenia* were used as a control species in order to ensure that the birds were not rejecting butterflies due to a novel stimulus, in this case unfamiliar taste or appearance (Coppinger, 1970). *Junonia coenia* is common in the same habitats as *A. bredowii* and *L. lorquini* and, like them, it has

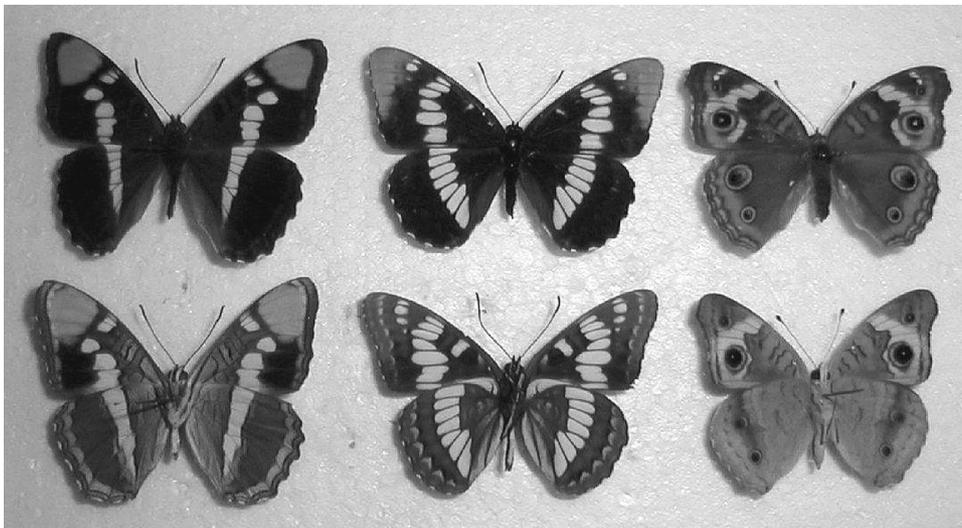


Plate 1. Dorsal and ventral views of the three butterfly species. From upper left *Adelpha bredowii* (model), *Limenitis lorquini* (mimic), and *Junonia coenia* (palatable control).

a white band on the dorsal wing. Overall, *J. coenia* has a dissimilar colour pattern (Plate 1).

Individuals of the three butterfly species, *A. bredowii*, *L. lorquini*, and *J. coenia*, were collected in the field and/or raised from eggs obtained from field-collected females. Raising the insects in the laboratory standardises the host plant. Ideally, enough laboratory-reared individuals would have been available, however for both *A. bredowii* and *L. lorquini*, wild-collected material was also used because, unlike *J. coenia*, these animals proved difficult to rear in large numbers. Several local populations were sampled due to difficulties with private property.

Of the 96 *A. bredowii* used in the experiments, 64 were collected from two field sites located 157 km apart in northern California: Mix Canyon (38°24'42"N, 122°02'57"W) and Dutch Flat (39°12'22"N, 120°50'12"W). The laboratory-reared *A. bredowii* were raised on *Q. wislizenii* (Fagaceae). All *L. lorquini* were field-collected in Mix Canyon and in West Sacramento (38°34'50"N, 121°31'45"W), California. All *J. coenia* were reared in the laboratory on *Plantago major* and *Plantago lanceolata*.

The butterflies were frozen at -10°C until used. At the end of the second experiment, there was a shortage of *A. bredowii* butterflies, so nine old *A. bredowii* raised in the laboratory on *Q. wislizenii* and frozen at -10°C since 1989 were used. These specimens were rehydrated with distilled water.

Predators

Because avian predators exhibit keen visual discrimination and a tendency to associate distasteful prey with similar colour patterns, they are generally used in preference to other potential predators to assess mimicry (D. Ritland, pers. comm.). The jays had been in captivity for 4 years and did not encounter any butterfly prey during that time. As such, they were regarded as naive, which is a desired characteristic for predators in a butterfly palatability study (Brower, 1958a; Coppinger, 1970). Also, jays appear to be average in terms of taste sensitivity and diet breadth, which potentially allows this species to serve as a model for a range of potential predators (Brower, 1958a; Platt *et al.*, 1971; Codella & Lederhouse, 1989; Bowers & Farley, 1990).

Three of the scrub jays were collected in the wild as young adults on the University of California, Davis campus. They were caught in January 1996 in potter's traps. The other jay (no. 1) was captured as a nestling and hand reared. All jays were collected under California State and Federal Scientific Collecting Permit 801079. These jays were used in a spatial memory experiment during their first year in captivity and were subsequently housed in an outdoor aviary at the campus. All jays were fed on a maintenance diet of dry dog food supplemented by walnuts, peanuts and apples. All four jays were adults, however their sex was not determined.

Predator housing and cage design

The experiment was conducted indoors with a LD 10:14 h photoperiod (08.00–18.00 hours). The temperature was held constant at 27.8°C throughout the experiment. Each individual cage was 87 × 61 × 62 cm with four doors, two on the front and two on the back. The cages were 2 × 4 cm metal mesh. There were two sliding trays on the bottom of the cages to limit contact between experimenter and jays. The cages were placed on a rack, two cages to a shelf. They were separated during the trials by a metal plate so that the jays could not view one another. The food bowls were inside and had to be replenished by opening the cage. This method of feeding had been standard protocol for the previous 4 years for these jays.

Conditioning

The scrub jays were first conditioned to consume butterflies with the wings closed. Each jay was forced to fast overnight starting at 16.00 hours, and was presented with one control butterfly in a compartmentalised plastic dish at 09.00 hours. The dish was slid underneath the right side of the cage via the sliding tray. It was covered until it was situated in the correct location then uncovered when the experiment began. The dish was placed in the same place each time for each bird. This method was used in order to decrease direct contact between the jays and the experimenter and to maintain continuity in prey presentation. Each jay was fed separately, always in the same order. The experimenter left the room for 5 min after the butterfly was presented to the jay. The reactions of the jays from presentation to consumption were recorded using a video camera, and the duration of each phase of the process was ascertained. The tripod stayed in the room continually while the video camera was only present during the trials. The conditioning period was four trials. The scrub jays were conditioned quickly to the new food item, as other predators had been in several previous studies (e.g. Brower, 1958a; Ritland & Brower, 1993).

Experiment 1: palatability

This experiment was designed to determine whether the scrub jays found one or both butterfly species distasteful. Over the course of the palatability experiment, each jay received 12 controls (*J. coenia*), six *A. bredowii* (putative model), and six *L. lorquini* (putative mimic), all with the ventral wing surface exposed. The underside of all three species is very distinct (Fig. 1) so it was considered to be difficult for a scrub jay to mistake one species for another. Because the potential source of unpalatability was unknown, the wings of the butterflies were not removed.

Each bird was first fed a control butterfly to ensure that if rejection of *L. limenitis* or *A. bredowii* occurred it was due to unpalatability, not satiation. The scrub jays were then fed

randomly either a wild-caught *A. bredowii* or a wild-caught *L. lorquini* with the wings closed. Laboratory-reared *A. bredowii* were not used because there were not enough individuals for 24 trials. Each jay had 5 min in which to consume each butterfly under the same procedure as the conditioning trials. The behaviour of the scrub jay towards each butterfly species was scored as eaten or not eaten and with or without bill wiping. Bill wiping is a behaviour in birds often associated with unpalatability (Brower, 1958a; Coppinger, 1970). Attack time (time from presentation to first prey contact) and handling time (time from first prey contact to prey consumption) were also recorded for each trial. The order in which each bird received either *L. lorquini* or *A. bredowii* was randomised. The sampling was without replacement, so that each jay would only experience six *A. bredowii* and six *L. lorquini*. In order to ensure the health of the scrub jays, each bird completed one trial per day for 4 consecutive days followed by 2 days with neither trials nor fasting. Each week, the scrub jays were weighed to ascertain whether the fasting schedule was too rigorous.

Experiment 2: visual discrimination and mimicry

If the jays were able to discriminate visually between *A. bredowii* and *L. lorquini*, it would be expected that they would attack *L. lorquini* (which was treated as palatable in expt 1 – see Results) first in the choice trials. A second experiment was conducted using the same four birds to determine this. The trials began 2 weeks after expt 1 was completed. In expt 2, the scrub jays were presented simultaneously with two open-winged, dorsally presented butterflies, and they had to make a decision about which butterfly to eat first and which second. First, the jays were conditioned for 1 week (four trials) with two open-winged *J. coenia* after the same overnight fasting period as in expt 1. The serving device was two of the plastic dishes taped together with clear tape. The presentation and fasting procedures described above were followed.

After the conditioning trials were completed, *A. bredowii* and *L. lorquini* were presented simultaneously with open wings to the jays in order to assay the effectiveness of the putative mimetic resemblance. Each butterfly pair was matched on the basis of size, colouration, condition, and, whenever possible, sex. Because there were not enough wild-caught individuals, laboratory-reared butterflies were also used. The position of the butterflies was randomised.

The same fasting and trial schedule as in expt 1 was followed. The jays had 5 min in which to consume both insects after the experimenter left the room, and each bird was presented a total of 12 pairs of butterflies.

Results

Experiment 1: palatability

The attack times were the same for all butterfly species and also the same among individual jays (Table 1). The jays ate all of the butterflies presented within 5 min, with the exception that jay no. 2 ignored the last *A. bredowii* completely. The jays removed the wings of the butterflies before consuming the body.

A planned contrast repeated measures ANOVA was used to evaluate palatability assessed by handling time, because the data were distributed normally. The results indicate that *A. bredowii* were handled for significantly longer than *L. lorquini* and *J. coenia* (Table 2).

The incidences of bill wiping also indicated differences in palatability. The scrub jays almost always exhibited bill wiping after eating *A. bredowii* but not after eating *L. lorquini* or *J. coenia* (repeated measures ANOVA, $F = 54.02$, $P < 0.001$; Fig. 1). These data provide support for the suggestion that *A. bredowii* was less palatable to the scrub jays than *L. lorquini* or *J. coenia*.

Experiment 2: visual discrimination and mimicry

The scrub jays exhibited no discrimination between *A. bredowii* and *L. lorquini* when the insects were presented side by side with open wings; the butterfly species chosen first by the avian predators did not differ from random ($\chi^2 = 0.004$, $P = \text{NS}$). Jay no. 2 was not included in the statistical analysis because it contributed only three data points. The three other jays did not favour either side of the dish ($\chi^2 = 0.003$, $P = \text{NS}$). The jays were unable or unwilling to discern consistently between the dorsal colour patterns of the two species, unlike their responses to the ventral patterns in the previous experiment. The jays did not learn over time to eat just the more palatable *L. lorquini*.

The first attack time was consistent with the results of expt 1. On average, each jay took 11.03 s to attack the first individual butterfly. The handling times for each butterfly

Table 1. Means, standard deviations, and planned contrast repeated measures ANOVA results of attack time in expt 1, the palatability experiment. There was no significant difference ($\alpha = 0.05$) in time from presentation to first contact for each scrub jay regardless of the butterfly species presented.

Contrast comparison	Means	SDs	F	P
<i>Adelpha bredowii</i> vs.	14.83,	10.07,	2.220	NS
<i>Limnitis lorquini</i> and <i>Junonia coenia</i>	13.33, 12.33	15.39, 5.34		
<i>Limnitis lorquini</i> vs.	13.33,		0.672	NS
<i>Junonia coenia</i>	12.33			

Table 2. Means, standard deviations, and planned contrast repeated measures ANOVA results of handling time in expt 1, the palatability experiment. Time from first contact to consumption was significantly longer ($\alpha=0.05$) for *Adelpha bredowii* than for *Limenitis lorquini*, indicating that *A. bredowii* (putative model) is more unpalatable than *L. lorquini* (putative mimic) to the model avian predator, *Aphelocoma californica*.

Contrast comparison	Means	SDs	F	P
<i>Adelpha bredowii</i> vs. <i>Limenitis lorquini</i> and <i>Junonia coenia</i>	80.72,	48.59,	28.52	0.011
<i>Limenitis lorquini</i> vs. <i>Junonia coenia</i>	13.17,	10.10,	1.02	0.860
	10.44	5.44		

species were also consistent with expt 1: *A. bredowii* was handled for an average of 48.35 s (SD = 20.32) and *L. lorquini* was handled for an average of 7.95 s (SD = 4.71). Excluding jay no. 2, which did not complete the experiment, there was no bird effect on attack times in this experiment (repeated measures ANOVA, $F=1.74$, $P=NS$).

Experiment 2 also demonstrated a palatability difference between the two butterfly species. Attack time on the second individual appeared to be dependent on the first species chosen. For example, if *L. lorquini* was eaten first, *A. bredowii* was attacked immediately (average 7 s) after the consumption of *L. lorquini*. If *A. bredowii* was eaten first, *L. lorquini* was not touched for an average of 50 s (Fig. 2). Because these data were not distributed normally, a non-parametric Mann–Whitney U test was used ($P < 0.001$). Furthermore, the jays exhibited a high incidence of bill wiping after consuming *A. bredowii* but not after consuming *L. lorquini* or *J. coenia* (Fig. 1). These results support the finding in the palatability experiment that *A. bredowii* was less palatable than *L. lorquini* to the model predators.

There was no significant difference in handling time between the laboratory-reared and the wild-caught *A. bredowii* ($\chi^2=0.084$, $P=NS$). The test was performed for all butterflies used, pooled, because subsets based on sex were too small for statistical testing. Nine *A. bredowii* raised for a previous experiment in 1989 appeared to produce the

same effects on handling time as did the other butterflies ($\chi^2=0.02$, $P=NS$).

Discussion

This experiment is the first to examine the palatability of *A. bredowii* and *L. lorquini* experimentally. It supports the postulated Batesian mimetic relationship, at least within the geographic area surveyed and with the predator employed. *Adelpha bredowii* from two different locations in California were moderately unpalatable to a model avian predator, the scrub jay. There was a significant difference in handling times between *A. bredowii* and the other two species, again indicating a substantial difference in palatability between *A. bredowii* and *L. lorquini*. Preliminary contact with some external surface of the butterfly (e.g. wings) or exposure to internal chemicals was presumably unpleasant in some way and caused the jays to hesitate and delay before they consumed the insect completely. This delay would presumably provide a live *A. bredowii* ample opportunity for escape.

The behaviour of the birds towards the three butterfly species also supported Batesian mimicry between *Adelpha bredowii* and *Limenitis lorquini*. Bill wiping is a classic behaviour after handling unpalatable food items for scrub jays and other bird species (Bowers, 1980; Ritland &

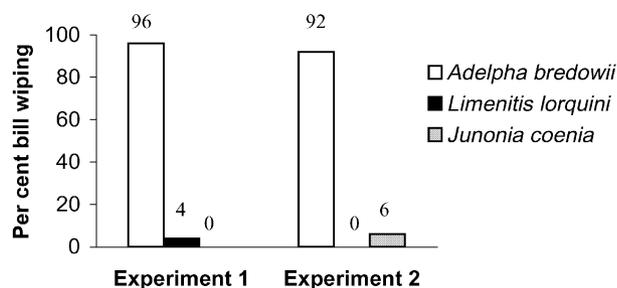


Fig. 1. Percentages of bill wiping after consuming each butterfly species in expts 1 and 2. Repeated measures ANOVA results indicate that the incidence of bill wiping differs significantly between *Adelpha bredowii* and the other two species, *Limenitis lorquini* and *Junonia coenia* ($P < 0.001$). These results give further support to the prediction that *A. bredowii* is unpalatable to avian predators.

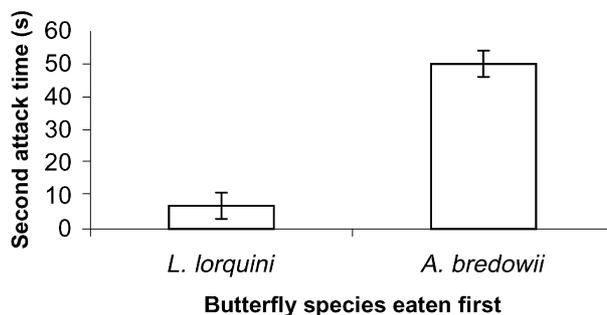


Fig. 2. Average time to second attack in expt 2. These values depended on the butterfly species chosen first by the jay. If *Limenitis lorquini* (mimic) was chosen first, the average time to touch *Adelpha bredowii* (model) was 7 s. If *A. bredowii* was chosen first, *L. lorquini* was attacked 50 s after consumption of *A. bredowii*. Mann–Whitney U results of time to second attack with the grouping variable as attack time indicated $P < 0.001$.

Brower, 1993). Over 90% of the time, the jays responded with bill wiping after consuming *A. bredowii*, however such behaviour was exhibited <5% of the time after consumption of *J. coenia* or *L. lorquini*.

In some instances, female butterflies are routinely more unpalatable than male butterflies (e.g. *Ascia monuste*, Pieridae; Pough & Brower, 1977), however there was no indication that female *A. bredowii* were more unpalatable than their male counterparts. This is not totally unexpected because there is no sexual dimorphism in this species.

Furthermore, the discrimination experiment revealed that the birds were unable to discern consistently between the two butterfly species when they were presented side by side. Even jay no. 2, which stopped participating in expt 2 after the third trial, exhibited an apparent unwillingness to discriminate between the two species after its previous experience with *A. bredowii*. Jay no. 2 would continue to consume *L. lorquini* with its wings closed and *J. coenia* with its wings both open and closed. This individual did not even touch closed-winged *A. bredowii* in three separate time trials after an overnight fast.

The data from both the palatability and discrimination experiments indicate that the putative mimetic relationship between *A. bredowii* and *L. lorquini* is indeed an example of Batesian mimicry in the geographic region studied. The unpalatable model is *A. bredowii* and the palatable mimic is *L. lorquini*. According to mimicry theory (Brower & Brower, 1972), this relationship developed through evolutionary time by way of advergence, not convergence. The mimic tracks the diverging colour pattern of the model, and the selection pressure is on the predators to discriminate between the two forms, one palatable and one unpalatable (Mallet & Joron, 2000). The similarity between *A. bredowii* and other members of the genus *Adelpha* (Aiello, 1984) provides support for the claim that it is *L. lorquini* that has changed phenotypically through time to mimic *A. bredowii*.

Because *A. bredowii* is only moderately distasteful, it would be expected that mimicry would only be beneficial if *A. bredowii* occurred at a high density. Although *A. bredowii* is a relatively rare species, it is locally abundant; and current distributions and abundance are not necessarily representative of the past. Selective pressures required to drive the mimetic phenotype to an adaptive peak in the past might be different from the selective pressures maintaining that peak today. Superficially, *A. bredowii* appears to be more common in areas of sympatry with *L. lorquini*. Also, *L. lorquini* usually emerges shortly after *A. bredowii* when they co-occur (K. Prudic, pers. obs.).

The chemical basis of unpalatability in *A. bredowii* has yet to be investigated. All jays were relatively consistent about accepting and consuming *A. bredowii* in the palatability experiment after a lengthy fasting period. The insects were not emetic or toxic but seemingly mildly distasteful. As such, their putative chemical defences could be described as class II chemical defence chemicals, not class I, which are considered noxious (Brower, 1984). *Adelpha bredowii* larvae feed on oaks, commonly *Q. wislizenii*, which contain tannins.

Those seem unlikely candidates for a sequestered chemical defence because no other insect is known to sequester them due to the heavy molecular weight and protein binding capabilities of tannins (Deveau & Schultz, 1992). Other phenolic compounds are possibilities because these chemicals are incorporated into defence strategies of willow-feeding Coleoptera (*Phratora*, Chrysomelidae) (Pasteels *et al.*, 1983). Alternatively, *A. bredowii* might synthesise a defensive chemical *de novo*. This is the case in heliconiid butterflies, which synthesise cyanogenic glycosides (Nahrstedt & Davis, 1983; Ackery, 1987). It is also possible that *A. bredowii* obtain the defensive chemicals from adult feeding sources as documented in Ithomiinae butterfly species (Brown, 1987) but there is no evidence that this is likely.

It has been speculated that in the neotropics, Rubiaceae feeding *Adelpha* are models for non-Rubiaceae feeding congeners (Aiello, 1984). This certainly does not seem to be the case in the *A. bredowii* and *L. lorquini* relationship because *A. bredowii* is the model. Pinheiro (1996) examined the palatability of several aposematic neotropical butterfly species including some members of the genus *Adelpha*, using wild kingbirds *Tyrannus melancholicus* (Tyrannidae) as a model predator. The kingbirds consumed most individuals and never learned to reject any *Adelpha* on sight. Two *Adelpha* species were Rubiaceae feeders while two species were not, however kingbirds appear to be more tolerant of butterfly chemical defences than other tropical avian predators such as jacamars *Galbula ruficauda* (Galbulidae) (Chai, 1986). *Adelpha* might still be involved in neotropical mimicry rings with other Nymphalidae such as *Doxocopa* and even possibly Riodinidae such as *Nymula phlasis* and *Synargis velabrum* as it superficially appears to be (Aiello, 1984; see illustrations in D'Abrera, 1984, 1994).

This study used individuals from only two geographic locations where the two species are commonly sympatric. It is possible that both species exhibit a spectrum of palatability and thus a continuum of mimicry when the entire geographic range of each species is examined (Turner, 1984). That has certainly been the case with the monarch-viceroy mimetic relationship (Brower, 1984; Ritland, 1994). Both *A. bredowii* and *L. lorquini* rely on an array of larval and adult food plants that could vary in chemical composition within a population (e.g. Matsuki & Maclean, 1994; Reed & McCarthy, 1996). Plant chemical production might also vary according to phenology. For example, Florida queens *Danaus gilippus* (Nymphalidae) exhibit geographic and temporal chemical variation due to differing cardiac glycoside compositions in larval host plant species (Moranz & Brower, 1998). Genetic variation between *A. bredowii* and *L. lorquini* populations might affect the ability of each species to sequester or synthesise defensive compounds. Nevertheless, because the *L. lorquini* studied were not any less palatable than the control, their mimetic relationship with *A. bredowii* can be regarded as Batesian mimicry within the geographic range studied.

Further investigation is required to elucidate fully the mimetic relationship between *A. bredowii* and *L. lorquini*. Such relationships are often quite complicated (e.g. Brower,

1984; Bowers, 1988; Ritland, 1995). A possible approach would be to bioassay additional geographic locations of both species. The use of other avian predators such as flycatchers, which have been observed chasing both butterfly species in the field (K. Prudic, pers. obs.), or invertebrate predators might help to assess the validity of the conclusions drawn from the behaviour of the scrub jays. For the time being, the data support the long-standing hypothesis that *Adelpha bredowii* is the unpalatable model in a Batesian mimetic relationship with the palatable *Limnitis lorquini*.

Acknowledgements

The experiments involving vertebrate animals were conducted in accordance with the *Guiding principles in care and use of animals* as approved by the Council of American Physiological Society. This experiment was performed in compliance with the current laws of the U.S.A. and the State of California. This work was supported by a President's Undergraduate Fellowship at University of California, Davis to K. L. Prudic. National Institute of Health and Whitehall Foundation grants to N. S. Clayton funded bird food and supplies. Many thanks to D. Lee and J. Fordyce for statistical support, D. Ritland for experimental insights, J. Greig for bird care, D. Bowers for editorial comments, J. Oliver for collecting assistance, and two anonymous reviewers for helpful insights.

References

- Ackery, P.R. (1987) Hostplant and classification: a review of nymphalid butterflies. *Biological Journal of the Linnean Society*, **33**, 95–203.
- Aiello, A. (1984) *Adelpha* (Nymphalidae): deception on the wing. *Psyche*, **91**, 1–45.
- Bowers, M.D. (1980) Unpalatability as a defense strategy of *Euphydryas phaeton*. *Evolution*, **34**, 586–600.
- Bowers, M.D. (1984) Iridoid glycosides and host-plant specificity in larvae of the buckeye butterfly, *Junonia coenia* (Nymphalidae). *Journal of Chemical Ecology*, **10**, 1567–1577.
- Bowers, M.D. (1988) Plant allelochemistry and mimicry. *Novel Aspects of Insect-plant Interactions* (ed. by P. Barbosa and D. K. Letourneau), pp. 273–311. John Wiley and Sons, New York.
- Bowers, M.D. & Farley, S. (1990) The behavior of gray jays, *Perisoreus canadensis*, towards palatable and unpalatable Lepidoptera. *Animal Behavior*, **39**, 699–705.
- Brower, J.V.Z. (1958a) Experimental studies of mimicry in some North American butterflies. I. The monarch, *Danaus plexippus*, and the viceroy, *Limnitis archippus*. *Evolution*, **12**, 32–47.
- Brower, J.V.Z. (1958b) Experimental studies of mimicry in some North American butterflies. II. *Battus philenor* and *Papilio trolius*, *P. polyxenes* and *P. glaucus*. *Evolution*, **12**, 123–136.
- Brower, J.V.Z. (1958c) Experimental studies of mimicry in some North American butterflies. III. *Danaus gilippus bernice* and *Limnitis archippus floridensis*. *Evolution*, **12**, 273–285.
- Brower, L.P. (1984) Chemical defense in butterflies. *The Biology of Butterflies* (ed. by R. I. Vane-Wright and P. R. Ackery), pp. 109–134. Academic Press, London.
- Brower, L.P. & Brower, J.V.Z. (1972) Parallelism, convergence, divergence and the new concept of advergence in the evolution of mimicry. *Transactions of the Connecticut Academy of Arts and Sciences*, New Haven, Connecticut, pp. 59–67.
- Brown, K.S., Jr (1987) Chemistry at the Solanaceae/Itomiinae interface. *Annals of Missouri Botanical Garden*, **74**, 359–397.
- Chai, P. (1986) Field observation and feeding experiments on the responses of rufous-tailed jacamars (*Galbula ruficauda*) to free-flying butterflies in a tropical rainforest. *Biological Journal of the Linnean Society*, **29**, 161–189.
- Codella, S.G. & Lederhouse, R.C. (1989) Intersexual comparison of mimetic protection in black swallowtail butterfly, *Papilio polyxenes*, experiments with captive blue jay predators. *Evolution*, **43**, 410–420.
- 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 naïve birds to novel insects. *American Naturalist*, **104**, 323–335.
- D'Abrera, B. (1984) *Butterflies of the Neotropical Region. Part IV: Nymphalidae*. Hill House, Victoria, Australia.
- D'Abrera, B. (1994) *Butterflies of the Neotropical Region. Part VI: Riodinidae*. Hill House, Victoria, Australia.
- Deveau, E.J.I. & Schultz, J.C. (1992) Reassessment of interaction between gut detergents and tannins in Lepidoptera and significance for gypsy-moth larvae. *Journal of Chemical Ecology*, **18**, 1437–1453.
- Mallet, J. & Joron, M. (2000) Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics*, **30**, 201–233.
- Matsuki, M. & Maclean, S.F. (1994) Effects of different leaf traits on growth-rates of insect herbivores on willows. *Oecologia*, **100**, 141–152.
- Moranz, R. & Brower, L.P. (1998) Geographic and temporal variation of cardenolide-based chemical defenses of queen butterfly (*Danaus gilippus*) in northern Florida. *Journal of Chemical Ecology*, **24**, 905–932.
- Nahrstedt, A. & Davis, R.H. (1983) Occurrence, variation and biosynthesis for the cyanogenic glucosides linamarin and lotaustralin in species of the Heliconiini (Insecta: Lepidoptera). *Comparative Biochemistry and Physiology*, **75B**, 65–73.
- Opler, P.A. & Wright, A.B. (1999) *A Field Guide to Western Butterflies*, 2nd edn. Houghton Mifflin Company, New York.
- Pasteels, J.M., Rowell-Rahier, M., Brakeman, J.C. & Dupont, A. (1983) Salicin from host plant as precursor of salicylaldehyde in defensive secretion of chrysomeline larvae. *Physiological Entomology*, **8**, 307–314.
- Pinheiro, C.E.G. (1996) Palatability and escaping ability in neotropical butterflies: tests with wild kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biological Journal of the Linnean Society*, **59**, 351–365.
- Platt, A.P. (1983) Evolution of North American admiral butterflies. *Bulletin of the Entomological Society of America*, **29**, 10–22.
- Platt, A.P., Coppinger, R.P. & Brower, L.P. (1971) Demonstration of the selective advantage of mimetic *Limnitis* butterflies presented to caged avian predators. *Evolution*, **25**, 692–701.
- Porter, A.H. (1987) Courtship of a model (*Adelpha*; Nymphalidae) by its probable Batesian mimic (*Limnitis*; Nymphalidae). *Journal of Research on the Lepidoptera*, **26**, 255–256.
- Pough, F.H. & Brower, L.P. (1977) Predation by birds on great southern white butterfly as a function of palatability, sex and habitat. *American Midland Naturalist*, **98**, 50–58.

- Poulton, E.B. (1909) Mimicry in butterflies of North America. *Annals of the Entomological Society of America*, **2**, 203–242.
- Reed, J.L. & McCarthy, B.C. (1996) Patterns of leaf tannin variation in chestnut oak (*Quercus prinus*) and black oak (*Quercus fluting*) with respect to topography in a southeastern Ohio oak–hickory forest. *Bulletin of the Torrey Botanical Club*, **123**, 243–248.
- Ritland, D.B. (1991) Unpalatability of viceroy butterfly (*Limenitis archippus*) and its proposed mimicry model, the Florida queen (*Danaus gilippus*). *Oecologia*, **88**, 102–108.
- Ritland, D.B. (1994) Variation in palatability of queen butterflies (*Danaus gilippus*) and implications regarding mimicry. *Ecology*, **75**, 732–746.
- Ritland, D.B. (1995) Comparative unpalatability of mimetic viceroy butterflies (*Limenitis archippus*) from four south-eastern United States populations. *Oecologia*, **103**, 327–336.
- Ritland, D.B. & Brower, L.P. (1991) The viceroy butterfly is not a Batesian mimic. *Nature*, **350**, 497–498.
- Ritland, D.B. & Brower, L.P. (1993) A reassessment of the mimicry relationship among viceroy, queens, and monarchs in Florida. *Biology and Conservation of the Monarch Butterfly (Contributions in Science)* (ed. by S. B. Malcolm and M. P. Zalucki), pp. 129–139. Natural History Museum of Los Angeles County, California.
- Turner, J.R.G. (1984) Mimicry: the palatability spectrum and its consequences. *The Biology of Butterflies* (ed. by R. I. Vane-Wright and P. R. Ackery), pp. 141–161. Academic Press, London.
- Wickler, W. (1968) *Mimicry in Plants and Animals*. McGraw-Hill Co., New York.

Accepted 25 April 2001