The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2015, ••, ••–••. With 3 figures.

A test of fundamental questions in mimicry theory using long-term datasets

ELIZABETH C. LONG[1,2]*, KYLE F. EDWARDS[3] and ARTHUR M. SHAPIRO[4]

[1]*La Kretz Center for California Conservation Science, University of California Los Angeles, Los Angeles, CA, 90095-1496, USA*
[2]*Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA, 90007, USA*
[3]*Department of Oceanography, University of Hawaii at Manoa, Honolulu, HI, 96822, USA*
[4]*Department of Evolution and Ecology, University of California Davis, Davis, CA, 95616, USA*

Received 11 March 2015; revised 13 May 2015; accepted for publication 14 May 2015

Since the phenomenon of mimicry was first described by Bates in 1862 it has become one of the foundational examples of adaptive evolution. Numerous subcategories of mimicry and dozens of hypotheses pertaining to its evolution and maintenance have been proposed. Many of these hypotheses, however, are difficult to test in experimental settings, and data from natural observations are often inadequate. Here we use data from a long-term survey of butterfly presence and abundance to test several hypotheses pertaining to Batesian and female-limited polymorphic mimicry (FPM; a special case of Batesian mimicry). We found strong evidence that models outnumber mimics in both mimicry systems, but no evidence for an increase in relative abundance of FPM mimics to their Batesian counterparts. Tests of the early-emergence/model first hypothesis showed strong evidence that the Batesian mimic routinely emerges after the model, while emergence timing in the FPM system was site specific, suggesting that other ecological factors are at play. These results demonstrate the importance of long-term field observations for testing evolutionary and ecological hypotheses. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **00**, 000–000.

ADDITIONAL KEYWORDS: *Adelpha* – Batesian mimicry – *Chlosyne* – *Euphydryas* – female-limited polymorphic mimicry – *Limenitis* – long-term ecological surveys.

BACKGROUND

Mimicry is one of the best-studied examples of adaptive evolution (Wickler, 1968). The phenomenon was first described in, and is often associated with, Lepidoptera, although cases of mimicry have been described across numerous taxa. Since Bates first published an account of mimicry in 1862, numerous categories of mimicry have been described (Bates, 1862; Wickler, 1968). Among the most common and well recognized of these is Batesian mimicry, consisting of an unpalatable model and a palatable mimic. This category has led to numerous empirical studies and theoretical predictions pertaining to the selective pressures (e.g. predator community, strength of penalty involved, predator learning ability) that shape the natural history of Batesian mimicry systems (Bates, 1862; Van Zandt, 1958, 1960; Mappes, Marples & Endler, 2005).

Female-limited polymorphic mimicry (FPM) is a type of Batesian mimicry in which the mimetic phenotype only manifests in females (Wickler, 1968). Hypotheses for the evolution and maintenance of FPM invoke the role of selective forces such as frequency dependence, phenology, predator guild composition, and interspecific competition. Sexual selection has been hypothesized to play a role in shaping FPM systems through inter- and intraspecific competition, mate choice, relative abundance and/or sex ratio perturbation (Wickler, 1968; Turner, 1978; Stamps & Gon, 1983; Estrada & Jiggins, 2008; Kunte, 2009; Allen, Zwaan & Brakefield, 2011).

Although the amount of literature pertaining to mimicry is quite large, it is often difficult to experimentally test many of these different hypotheses that the field has spawned. Mesocosms cannot

*Corresponding author. E-mail: elong@nhm.org

accurately reproduce the breadth of the predator guild, nor can they sustain a large, climate-controlled habitat to support experimental populations of models and mimics for an extended period of time. Most observational and experimental field trials are only able to capture a short snapshot of time and thus cannot account for demographic stochasticity and the effects of short-term environmental fluctuation (Carpenter, 1920; Ford, 1936; Brower & Van Zandt, 1962; Pfennig, Harcombe & Pfennig, 2001; Howarth, Edmunds & Gilbert, 2004; Kikuchi & Pfennig, 2010). By incorporating biotic and abiotic interactions in a natural setting over an extended time period long-term ecological surveys represent an ideal opportunity to address some of these foundational questions regarding the adaptive pressures that shape and maintain mimicry systems.

It has long been hypothesized that the relative population size of Batesian model vs. mimic species is crucial to the evolution and maintenance of this type of mimicry system. Most models predict that, in order for Batesian mimicry to evolve and be maintained, the predator must encounter the mimic less often than it encounters the model, and this situation should typically result in a low mimic:model ratio (Ford, 1936, 1965; Fisher, 1958; Van Zandt, 1960; Huheey, 1964, 1980a; Wickler, 1968; Turner, 1977, 1978; Holen & Johnstone, 2004). Many selective forces, e.g. strength of penalty, learning and retention ability of predators, etc., are likely to have an effect on this ratio, so it is difficult to predict that ratio *a priori* (although it should always be < 1; Prudic, Oliver & Sperling, 2007; Estrada & Jiggins, 2008; Nokelainen *et al.*, 2012).

The constraint on mimic population size means that the mimic is more susceptible than the model to selective pressures associated with small population size, e.g. demographic, environmental, and genetic effects. Thus, there may be conflicting selective forces acting to regulate individual survival of mimics vs. the total size of the population. One evolutionary solution to this conflict is to restrict the mimetic phenotype to a subset of the population, e.g. to only one of the sexes, to one age class, etc. This solution is in fact suggested as one possible reason for the evolution and/or maintenance of FPM in butterflies (Wickler, 1968; Turner, 1978; Kunte, 2009; Allen *et al.*, 2011). When only the female sex is mimetic, the number of true mimics in the population is reduced by one-half, assuming an equal sex ratio, and thus the alleles that confer mimicry are more easily established (Sheppard, 1962; Barrett, 1976; Turner, 1978). Thus, according to this abundance hypothesis of FPM evolution, a FPM species should be able to maintain a higher relative population size than a Batesian mimic.

Predators impose a large selective force on the maintenance of mimicry systems. Predators do not always retain prolonged memory of negative experience(s) with models and may require periodic 'retraining' (Van Zandt, 1958, 1960; Mallet & Joron, 1999; Lynn, 2005; Nelson, Crossland & Shine, 2011). This situation has led to varying predictions pertaining to the optimal timing of model and mimic emergence relative to that of their predators, although most models predict that both model and mimic benefit from early model emergence (the model first hypothesis; Bobisud, 1978; Huheey, 1980b). In species that are not able to overcome constraints (climate, host plant phenology, etc.) and delay emergence until after model abundance peaks, the same effect could be achieved by restricting mimetic phenotype to the female sex. Protandry, the phenomenon where the emergence of adult males precedes that of adult females, is widespread in Lepidoptera (Fagerstrom & Wiklund, 1982; Zonneveld, 1992). Thus, in an FPM system where model and mimic emergence times are synchronized, individuals showing the mimetic phenotype (females) would still emerge after the model.

Using data collected from an ecological survey of butterflies at multiple sites across several decades, we tested for evidence that supported these hypotheses. Specifically, we looked for evidence that models outnumber mimics in both Batesian and FPM systems; for an increased relative abundance of FPM mimics to models compared with Batesian systems; and for evidence of selection on phenology towards model first emergence.

METHODS

Surveys

Data were collected by a single observer (A.M.S.) using a modified Pollard Walk method designed to reflect presence/absence, and at Gates Canyon, seasonal cumulative species abundance, described at http://butterfly.ucdavis.edu/ (Pollard, 1977; Casner *et al.*, 2014). Briefly, sites were surveyed approximately every 14 days and species presence was recorded. Data were used to determine yearly first flight date for each species at three sites as described below, and total abundance of each species at Gates Canyon. Full site descriptions can be found in Supporting Information (Data S1) and are available at http://butterfly.ucdavis.edu/.

Gates Canyon (Gates)

Located in the Vaca Hills in Solano County, CA, the transect is approximately 9.6 km long and runs from an elevation of 190–600 m. Gates contains limited

agricultural areas and chaparral but is dominated by riparian and foothill woodland oak canyon. It is surveyed year round.

Washington (Wash)
This transect includes the town of Washington in Nevada County, CA as well as a serpentine barren, a riparian zone along Washington Creek, and a portion of the South Yuba River. The ~13.5 km transect ranges from 850 to 1200 m in height and is mostly in mixed-mesic habitat in the Sierra Nevada foothills (west slope). It is typically surveyed March–October.

Lang Crossing (Lang)
Lang is located at mid-elevation (1500–1700 m) on the Sierra Nevada west slope. The South Yuba and Bear River drainages converge here in Nevada and Placer counties, CA. The 13.5 km transect consists of a variety of ecological habitat including xeric rock balds, mesic mixed forest, and various successional habitats. This site is typically surveyed March–October.

Species

Both of the mimicry systems described here represent the only known butterfly mimicry systems present at the study sites.

Batesian system
The Batesian mimic *Limenitis lorquinii* Boisduval (Nymphalidae) and its model *Adelpha californica* Butler (Nymphalidae) are resident at all three study sites used in the analysis. Prudic, Shapiro & Clayton (2002) demonstrated that, in laboratory experiments, a generalized avian predator will reject *L. lorquinii* after a negative experience with *A. californica*.

FPM system
The butterfly *Euphydryas chalcedona* [Doubleday] (Nymphalidae) sequesters iridoid glycosides from its host plant, making it unpalatable to birds (Bowers, 1981). In the portion of the range covered by the study area, most females of the mimic species, *Chlosyne palla* Boisduval (Nymphalidae) closely resemble *E. chalcedona* wing colour and pattern (black form), while all males and some females are non-mimetic (red form; Shapiro & Manolis, 2007). Palatability experiments indicate that the black form of *C. palla* is a FPM of the black form of *E. chalcedona* (Long, Hahn & Shapiro, 2014).

Test for difference in abundance between model and mimic

Using abundance data recorded during each visit at Gates between the years 1999–2010, we tested whether models consistently outnumber mimics. Abundance counts from each site visit were summed for each year in order to estimate the cumulative level of predators' exposure to the butterfly prey. We performed a separate comparison of model and mimic for each system, i.e. the Batesian model was compared with Batesian mimic while the FPM model was compared with the FPM mimic. (In the case of the FPM mimic *Chlosyne palla*, numbers given refer to total number of individuals present. Data on males verus females or on colour morphs were not recorded.) The yearly abundance of all butterfly fauna is expected to be strongly influenced by abiotic factors and thus interannual comparisons may not accurately characterize the questions under study (Weiss, Murphy & White, 1988; Boggs & Inouye, 2012).

We used a linear mixed model in which log abundance was the response variable. We included a fixed effect for species, and a random effect for year to capture interannual variability shared between the two species. There was no evidence that residual variation within a species was autocorrelated over time. We tested for a significant difference between species by comparing the log likelihood of this model to the log likelihood of a model with no fixed effect for species; a parametric bootstrap using the simpler model was used to generate a null distribution for the difference in log likelihoods. All statistical analyses were performed using R version 2.14.2 software (R Development Core Team, 2012) and packages lme4 (Bates, Maechler & Bolker, 2014) and pbkrtest (Halekoh, 2014).

Test for difference in relative abundance between systems

We addressed the question of whether FPM is associated with increased population size of mimics. We did this by comparing relative abundance of Batesian models and mimics to that of FPM models and mimics. For both systems we divided the number of mimics by the number of models in each year to calculate relative abundance per year. Because there was no evidence for temporal autocorrelation in the time series of relative abundances, we tested whether FPM mimics were at a higher relative abundance by resampling each time series with replacement 1000 times, each time saving the mean relative abundance of FPM and Batesian mimics, and finally calculating the proportion of resamples in which FPM mimics were relatively more abundant than Batesian mimics.

Test for difference in emergence phenology between model and mimic

The first flight date (FFD) for each species is defined as the earliest date during each calendar year that

the observer recorded an adult of a given species. This date was then converted to day number of the year (i.e. 1–365, or ordinal date). FFD was recorded at Gates from 1976 thru 2011, at Lang from 1977 thru 2011, and at Washington from 1989 thru 2011. During some years, site visits were insufficient in number and/or frequency to accurately gauge FFD, and these years were excluded from the analyses. Excluded years are as follows: Lang 1979–1981 and 1987; Washington 1988 and 1991; Gates none.

We tested the early-emergence hypothesis by looking for differences between FFD in model and mimic for each system. For each comparison we used a linear mixed model with a fixed effect for species and a random effect for year. There was no evidence for temporal autocorrelation of within-species residuals. To test the significance of the species effect in each model, we used the same parametric bootstrapping approach described above.

RESULTS

Abundance

The mixed model test for differences in mimic and model abundance showed that for both systems the model is present in significantly greater numbers than its mimic: Batesian model mean = 98.3 (SD = 41.7) while mimic = 38.1 (SD = 13.6, $P << 0.01$); FPM model mean = 81.3 (SD = 48.9) while mimic mean= 18.3 (SD = 3.5, $P << 0.01$; Fig. 1).

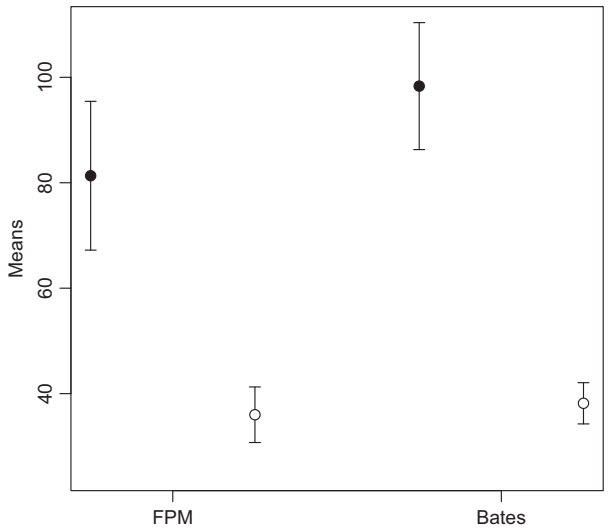

Figure 1. Mean annual abundance and standard error for FPM (left) and Batesian (right) systems. Abundance was significantly higher for models (closed circles) than for mimics (open circles) in both the FPM system (left) and the Batesian system (right).

Relative abundance

The test for differences in mimic:model relative abundance between Batesian (mean = 0.43, SD = 0.18) and FPM (mean = 0.54, SD = 0.28) systems showed no evidence that the mimic species were relatively less abundant in the FPM system compared to the Batesian system, or vice versa (bootstrap $P = 0.89$; Fig. 2).

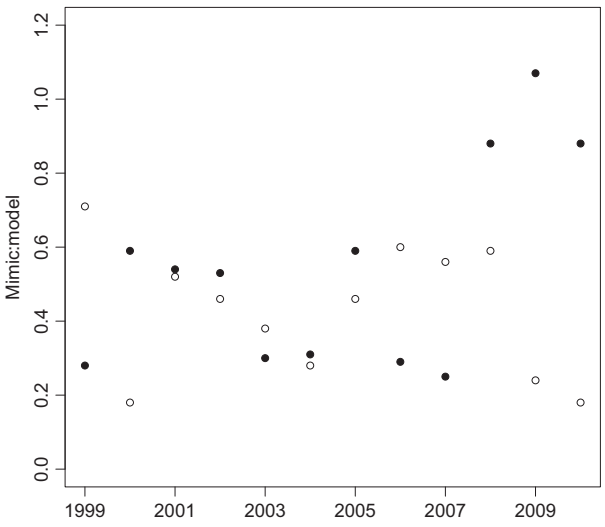

Figure 2. Comparison of relative abundance of mimic: model from 1999 to 2010 between FPM (closed circles) and Batesian (open circles) systems. No statistically significant trend was evident.

First flight date

The test for differences in flight dates between the mimic and model of each system indicated that trends varied by system and by site. (Table 1, Fig. 3).

Table 1. Difference (in days) between mean first flight date of model and mimic at each site

System and site	Model FFD	Mimic FFD	Difference in days (*P*-value)
Batesian			
Gates	105.94 (15.15)	109.53 (11.63)	−3.59 (0.31)
Washington	138.27 (18.58)	142.85 (20.54)	−4.58 (<< 0.01)
Lang	154.61 (17.56)	170.08 (20.79)	−15.47 (<< 0.01)
FPM			
Gates	118.36 (16.02)	111.19 (15.37)	+7.17 (<< 0.01)
Washington	137.86 (16.22)	117.5 (17.14)	+20.36 (<< 0.01)
Lang	138.32 (19.72)	144.32 (16.75)	−6.0 (< 0.04)

Negative values indicate that the model emerged first, while positive values indicate that the mimic emerged first.

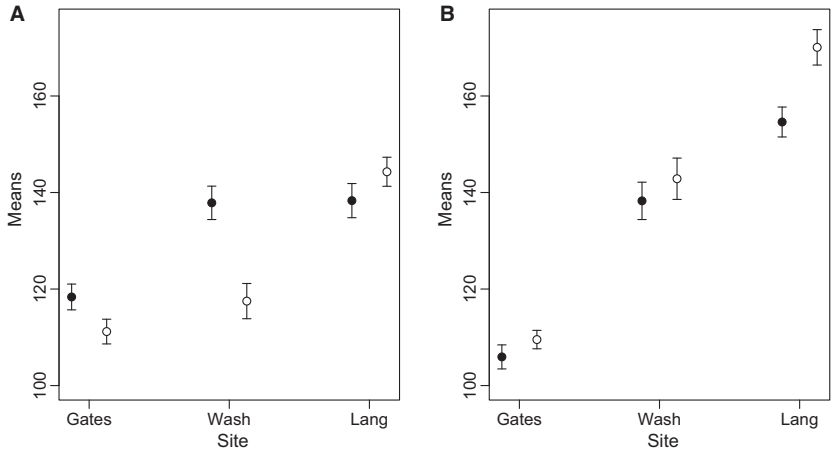

Figure 3. A, Mean first flight date with standard error bars for FPM model *Euphydryas chalcedona* (closed circles) and mimic *Chlosyne palla* (open circles). B, Mean first flight date with standard error bars for Batesian model *Adelpha californica* (closed circles) and mimic *Limenitis lorquinii* (open circles). *Y*-axis indicates ordinal dates.

In the case of the Batesian system, the model emerged first at each of the sites, and the differences in FFD were significant at Washington and Lang but not at Gates. In the FPM system, the model emerged significantly earlier than the mimic only at Lang; at Gates and Washington, the mimic emerged significantly before the model (Table 1).

DISCUSSION

Previous studies of mimicry have noted anecdotally that models often outnumber their mimics and/or have speculated on the FFD of models and mimics (Prudic *et al.*, 2002). Some previous studies have documented actual counts of model and mimic abundance (Ford, 1936; Brower & Van Zandt, 1962; Howarth *et al.*, 2004; Penney *et al.*, 2012); however, this is the first study of which we are aware that has addressed this question using long-term monitoring. The value of this approach became apparent when looking at yearly fluctuations in abundance and FFD. For example, if taken singularly, observations on relative abundance in 1999 (FPM = 0.28, Batesian = 0.71) would be interpreted quite differently than observations in 2000 (FPM = 0.59 and Batesian = 0.18; Fig. 2).

Although we did see fluctuation in the magnitude of difference from year to year, there was a constant trend of higher model abundance compared with the mimic in both Batesian and FPM systems. While mimetic relations are certainly not the only factors influencing population size, we found clear evidence to support the idea that models significantly and consistently outnumber their Batesian and FPM mimics (Ford, 1936; Van Zandt, 1960; Huheey, 1964, 1980a).

The abundance hypothesis of FPM evolution speculates that the population size of the FPM species can be higher relative to its model than can their Batesian counterparts. By restricting the mimetic phenotype to half of the population (or less in polymorphic species, e.g. *Papilio dardanus*, *C. palla*), the number of true mimics in the population is lowered and the entire population can be maintained at twice the overall abundance than it could otherwise (assuming equal sex ratios). The ability to maintain a larger population size is beneficial as small populations are more susceptible than large populations to negative effects of demographic and environmental stochasticity (Harmon & Braude, 2010). However, when we compared relative abundance for the two systems we found no evidence that either the Batesian or the FPM mimic was present in higher relative abundance than the other, and therefore no support for the abundance hypothesis of FPM evolution. However, we caution against taking these results as evidence refuting this hypothesis. It is possible, for example, that other selective forces acting on this FPM system would necessitate an even lower population size were it not polymorphic. These observations and questions warrant further study, both at additional sites and with additional species.

In addition to questions pertaining to abundance we also investigated differences in adult emergence times between species and systems. The model first hypothesis predicts that the model should emerge prior to the mimic so that predators' initial encounter with the aposematic phenotype is an honest encounter for which they are penalized (Bobisud, 1978). In this way, predators are more likely to quickly learn to avoid the aposematic phenotype, and by the time that the mimic emerges many individuals in the communities'

predator guild may have learned to avoid the phenotype, thus conferring protection on both species. The mimic directly benefits from this delayed emergence, and the model may benefit as well, since the mimic will not be present to dilute the learning ability of the predator.

When we investigated the model first hypothesis, the patterns that we found varied by system and by site. In agreement with predictions, the Batesian system showed consistent trends across all three sites with the mimic emerging later than the model. This trend was significant at Washington and Lang but not at Gates, with the largest interval between species occurring at Lang. We interpret this as support for the model first hypothesis in Batesian systems but acknowledge that data from additional sites and additional species would be beneficial.

Our tests for variation in FFD in the FPM showed different trends by site. At Lang Crossing we found that the model emerges before the mimic, consistent with the Batesian model first hypothesis. However, despite a difference in magnitude, the two lowest-elevation sites, Gates Canyon and Washington, both showed a clear trend of mimics first.

Lepidoptera development is often highly canalized and tightly regulated by environmental factors, so mimicry-imposed selection may conflict with costs associated with change in emergence times (exposure to extreme temperatures, tolerance in daylight length, host plant development, etc.; Dobkin, Olivieri & Ehrlich, 1987; Nylin, Wickman & Wiklund, 1989; Kingsolver & Nagle, 2007). However, this problem could be avoided if FPM could evolve under a scenario whereby mimics emerge later than non-mimetic phenotypes. Because many butterflies, including the subjects of this study, experience protandry as a mechanism to reduce male–male competition for mates, FPM mimics may have evolved a novel solution to conflicting pressures between developmental constraints and predation pressure. In the case of *C. palla*, females emerge ~10 days after the males on average (A.M.S. personal observation). As the mimetic phenotype is limited to the female sex, synchronized emergence between model and mimic species means that the mimetic phenotype emerges after the model and would thus still be consistent with the model first hypothesis. Unfortunately data on male verus female abundance/emergence was not recorded for this study. However, if we estimate female emergence to be ~10 days after the males, then on average the mimetic form of *C. palla* would emerge ~3 days after the model at Gates but ~10 days before the model at Washington. Under this assumption, the model first hypothesis is supported at Gates (admittedly by a small interval) but not at Washington.

The trend of FPM mimic-first was reversed at the highest-elevation site studied, Lang Crossing. This site at ~1600 m in the Sierras experiences very different weather conditions than Gates or Washington. The winters are colder, and snowpack lasting weeks at a time is a regular occurrence late fall through early spring. Differences in emergence time between the Lang population and those at the other two sites may simply be due to genetic drift, or may be due to conflicting selection pressures. Despite the presence of significant results for these FPM sites, the overall pattern is inconclusive. Further study on factors governing emergence controls in both of the species in the FPM system, as well as data from additional systems, would help to shed more light on this question.

CONCLUSIONS

This study shows the value of long-term ecological monitoring in addressing fundamental questions pertaining to ecology and evolution. Data on abundance in both systems lend support to the Batesian mimicry hypothesis that models typically outnumber mimics. However, data do not show support for an abundance-related role of FPM evolution. We also found that the FFD data support the model first hypothesis in Batesian mimicry systems but is inconclusive in FPM systems. This analysis lays the groundwork for additional studies involving other species and localities, as well as for experimental studies to investigate the role of environmental cues in regulating life stage development.

ACKNOWLEDGEMENTS

We wish to thank S. Heard, B. May, M. Delany, and several anonymous reviewers for helpful comments that greatly improved this manuscript.

FUNDING

Database funding was provided to A.M.S. and J.F. Quinn via NSF grant (DBI-0317483).

REFERENCES

Allen CE, Zwaan BJ, Brakefield PM. 2011. Evolution of sexual dimorphism in the Lepidoptera. *Annual Review of Entomology* **56:** 445–464.

Barrett JA. 1976. The maintenance of non-mimetic forms in a dimorphic Batesian mimic species. *Evolution* **30:** 82–85.

Bates HW. 1862. Contributions to an insect fauna of the Amazon valley (Lepidoptera: Heliconidae). *Transactions of the Linnean Society of London* **23:** 495–566.

Bates D, Maechler M, Bolker B. 2014. *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7. Available at: http://CRAN.R-project.org/package=lme4.

Bobisud LE. 1978. Optimal time of appearance of mimics. *The American Naturalist* **112:** 962–965.

Boggs CL, Inouye DW. 2012. A single climate driver has direct and indirect effects on insect population dynamics. *Ecology Letters* **15:** 502–508.

Bowers MD. 1981. Unpalatability as a defense strategy of western checkerspot butterflies (Euphydryas scudder, Nymphalidae). *Evolution* **35:** 367–375.

Brower LP, Van Zandt BJ. 1962. The relative abundance of model and mimic butterflies in natural populations of the battus philenor mimicry complex. *Ecology* **43:** 154–158.

Carpenter GDH. 1920. Natural selection. *Transactions of the Royal Entomological Society of London* **68:** 84–98.

Casner KL, Forister ML, Ram K, Shapiro AM. 2014. The utility of repeated presence data as a surrogate for counts: a case study using butterflies. *Journal of Insect Conservation* **18:** 13–27.

Dobkin DS, Olivieri I, Ehrlich PR. 1987. Rainfall and the interaction of microclimate with larval resources in the population dynamics of checkerspot butterflies (*Euphydryas editha*) inhabiting serpentine grassland. *Oecologia* **71:** 161–166.

Estrada C, Jiggins CD. 2008. Interspecific sexual attraction because of convergence in warning colouration: is there a conflict between natural and sexual selection in mimetic species? *Journal of Evolutionary Biology* **21:** 749–760.

Fagerstrom T, Wiklund C. 1982. Why do males emerge before females? Protandry as a mating strategy in male and female butterflies. *Oecologia* **52:** 164–166.

Fisher RA. 1958. *The genetical theory of natural selection*. New York: Dover.

Ford EB. 1936. The genetics of *Papilio dardanus* Brown (Lep.). *Transactions of the Royal Entomological Society of London* **85:** 435–466.

Ford EB. 1965. *Genetic polymorphism*. London: Faber and Faber.

Harmon LJ, Braude S. 2010. Conservation of small populations: effective population sizes, inbreeding, and the 50/500 rule. *An Introduction to Methods and Models in Ecology and Conservation Biology* 125–138.

Halekoh U, Højsgaard S. 2014. A Kenward-Roger Approximation and Parametric Bootstrap Methods for Tests in Linear Mixed Models - The R Package pbkrtest. *Journal of Statistical Software* **59:** 1–30.

Holen ØH, Johnstone RA. 2004. The evolution of mimicry under constraints. *The American Naturalist* **164:** 598–613.

Howarth B, Edmunds M, Gilbert F. 2004. Does the abundance of hoverfly (Syrphidae) mimics depend on the number of their hymenopteran models? *Evolution* **58:** 367–375.

Huheey JE. 1964. Studies of warning coloration and mimicry. IV. A. Mathematical model of model-mimic frequencies. *Ecology* **45:** 185–188.

Huheey JE. 1980a. Studies in waring coloration and mimicry VIII. Further evidence for a frequency-dependent model of predation. *Journal of Herpetology* **14:** 223–230.

Huheey JE. 1980b. The question of synchrony or 'temporal sympatry' in mimicry. *Evolution* **34:** 614–616.

Kikuchi DW, Pfennig DW. 2010. High-model abundance may permit the gradual evolution of Batesian mimicry: an experimental test. *Proceedings of the Royal Society B: Biological Sciences* **277:** 1041–1048.

Kingsolver JG, Nagle A. 2007. Evolutionary divergence in thermal sensitivity and diapause of field and laboratory populations of manduca sexta. *Physiological and Biochemical Zoology* **80:** 473–479.

Kunte K. 2009. Female-limited mimetic polymorphism: a review of theories and a critique of sexual selection as balancing selection. *Animal Behaviour* **78:** 1029–1036.

Long EC, Hahn TP, Shapiro AM. 2014. Variation in wing pattern and palatability in a female-limited polymorphic mimicry system. *Ecology and Evolution* **4:** 4543–4552.

Lynn S. 2005. Learning to avoid aposematic prey. *Animal Behaviour* **70:** 1221–1226.

Mallet J, Joron M. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics* **30:** 201–233.

Mappes J, Marples N, Endler JA. 2005. The complex business of survival by aposematism. *Trends in Ecology and Evolution* **20:** 598–603.

Nelson DWM, Crossland MR, Shine R. 2011. Foraging responses of predators to novel toxic prey: effects of predator learning and relative prey abundance. *Oikos* **120:** 152–158.

Nokelainen O, Hegna RH, Reudler JH, Lindstedt C, Mappes J. 2012. Trade-off between warning signal efficacy and mating success in the wood tiger moth. *Proceedings of the Royal Society B: Biological Sciences* **279:** 257–265.

Nylin S, Wickman PO, Wiklund C. 1989. Seasonal plasticity in growth and development of the speckled wood butterfly, Pararge aegeria (Satyrinae). *Biological Journal of the Linnean Society* **38:** 155–171.

Penney HD, Hassall C, Skevington JH, Abbott KR, Sherratt TN. 2012. A comparative analysis of the evolution of imperfect mimicry. *Nature* **483:** 461–464.

Pfennig DW, Harcombe WR, Pfennig KS. 2001. Frequency-dependent Batesian mimicry. *Nature* **410:** 323.

Pollard E. 1977. A Method for assessing changes in the abundance of butterflies. *Biological Conservation* **12:** 115–134.

Prudic KL, Shapiro AM, Clayton NS. 2002. Evaluating a putative mimetic relationship between two butterflies, *Adelpha bredowii* and *Limenitis lorquinii*. *Ecological Entomology* **27:** 68–75.

Prudic KL, Oliver JC, Sperling FAH. 2007. The signal environment is more important than diet or chemical specialization in the evolution of warning coloration. *Proceedings of the National Academy of Sciences of the United States of America* **104:** 19381–19386.

R Development Core Team. 2012. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: http://www.R-project.org. ISBN 3-900051-07-0.

Shapiro AM, Manolis TD. 2007. *Field guide to butterflies of the San Francisco Bay and Sacramento regions*. Berkeley and Los Angeles, CA: University of California Press.

Sheppard PM. 1962. Some aspects of the geography, genetics, and taxonomy of a butterfly. In: Nichols D, ed. *Taxonomy and geography*. Oxford: Systematics Association, 135–152.

Stamps JA, Gon SM III. 1983. Sex-biased pattern variation in the prey of birds. *Annual Review of Ecology and Systematics* **14:** 231–253.

Turner JRG. 1977. Butterfly mimicry: the genetical evolution of an adaptation. In: Hecht MK, Steer MC, Wallace B, eds. *Evolutionary biology, Vol. 10*. New York: Plenum, 163–206.

Turner JRG. 1978. Why male butterflies are non-mimetic: natural selection, sexual selection, group selection, modification and sieving*. *Biological Journal of the Linnean Society* **10:** 385–432.

Van Zandt BJ. 1958. Experimental studies of mimicry in some North American butterflies: part I. The Monarch, *Danaus plexippus*, and Viceroy, *Limenitis archippus archippus*. *Evolution* **12:** 32–47.

Van Zandt BJ. 1960. Experimental studies of mimicry. IV. The reactions of starlings to different proportions of models and mimics. *The American Naturalist* **94:** 271–282.

Weiss SB, Murphy DD, White RR. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* **69:** 1486–1496.

Wickler W. 1968. *Mimicry in plants and animals*. New York: World University Library McGraw Hill.

Zonneveld C. 1992. Polyandry and protandry in butterflies. *Bulletin of Mathematical Biology* **54:** 957–976.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Data S1. Site descriptions as shown on http://butterfly.ucdavis.edu/sites/map.