

Population differences in predation on Batesian mimics in allopatry with their model: selection against mimics is strongest when they are common

David W. Pfennig · George R. Harper Jr ·
Abel F. Brumo · William R. Harcombe ·
Karin S. Pfennig

Received: 23 March 2006 / Revised: 22 July 2006 / Accepted: 20 August 2006 / Published online: 5 October 2006
© Springer-Verlag 2006

Abstract Batesian mimicry evolves when a palatable species, the “mimic,” resembles a dangerous species, the “model,” because both receive protection from predation. Yet, this protection should break down where the model is absent, because predators in such areas would not be under selection to avoid the model. Here, we test this prediction in a coral snake mimicry complex. We exposed plasticine replicas of milk snakes that closely mimic coral snakes to natural predators to determine if good mimetic milk snakes are preferentially attacked in allopatry with their model. Moreover, we evaluated whether attack rates on these replicas varied among three different allopatric regions that differed in the type of mimic found locally (i.e., good mimic, poor mimic, or no mimic). When all three regions were considered together, mimics were not preferentially attacked. When regions were analyzed separately, however, attacks on mimics were significantly greater than randomness only where good mimics were found. These variable levels of predation on good mimics might reflect frequency-dependent (i.e., apostatic) predation. In allopatric regions where good mimics are present, predators might have learned or evolved preferences for conspicuous, palatable prey that they

encounter frequently. By contrast, in allopatric regions where good mimics are absent, predators might not have learned or evolved preferences for novel phenotypes. Thus, when predation is frequency-dependent, as long as good mimics are rare, they might not experience elevated levels of predation in allopatry with their model as predicted by the Batesian mimicry hypothesis.

Keywords Apostatic predation · Batesian mimicry · Frequency-dependent selection · Predation

Introduction

Most organisms are at risk of being eaten, and one way to mitigate this hazard is to resemble a species that predators avoid (Bates 1862; Wickler 1968). For instance, predators normally shun toxic or venomous species (reviewed in Endler 1991; Ruxton et al. 2004). Any palatable species that resembles a dangerous species may therefore receive protection from predation (Bates 1862). In this way, adaptive resemblances between a dangerous species (the “model”) and an unrelated palatable species (the “mimic”) may evolve by natural selection through a process known as “Batesian mimicry” (the evidence for and the principles of mimicry are reviewed in Wickler 1968; Edmunds 1974; Endler 1991; Mallet and Joron 1999; Brodie and Brodie 2004; Ruxton et al. 2004).

The protection afforded a Batesian mimic should break down in areas where their model is absent (i.e., in allopatry). Predators that do not co-occur with the model will not be under selection to recognize it, or any other species that resemble it, as dangerous (Wallace 1870; Waldbauer and Sternburg 1987; Pfennig et al. 2001).

Communicated by P. Weatherhead

D. W. Pfennig (✉) · G. R. Harper Jr · K. S. Pfennig
Department of Biology, University of North Carolina,
Chapel Hill, NC, USA
e-mail: dpfennig@email.unc.edu

A. F. Brumo
Department of Fisheries and Wildlife, Oregon State University,
Corvallis, OR, USA

W. R. Harcombe
Section of Integrative Biology, University of Texas,
Austin, TX, USA

Moreover, because mimics often resemble models that are conspicuous or aposematic (reviewed in Endler 1991; Ruxton et al. 2004), predation in allopatry on these more apparent, but unprotected, mimics might be especially intense. Yet, despite this prediction, mimics often occur in allopatry, where their model is absent (Clarke and Sheppard 1975; Greene and McDiarmid 1981; Gordon and Smith 1998; Koch et al. 2000; Pfennig et al. 2001; Prudic et al. 2002), suggesting that mimics in allopatry may suffer less intense predation than expected.

We examined whether predation selects against allopatric mimics by asking if mimetic milk snakes that occur outside the range of their deadly coral snake model suffer greater predation than expected by chance. We also asked if attack rates on good mimetic milk snakes vary among different allopatric regions that differ in the type of mimic that is found locally (i.e., good mimic, poor mimic, or no mimic). Such variable levels of predation might be expected if predators engage in frequency-dependent (i.e., apostatic) predation (Holling 1965, 1966; Murdoch 1969; Curio 1976; Allen 1988; Endler 1986, 1988, 1991; Merilaita 2006). Following Endler (1988), we use the phrase “frequency-dependent predation” to include density- or number-dependent predation, since the absolute number of prey encountered can be as important to predation as frequency (Greenwood 1969; Mallet and Joron 1999; Mallet 2001). In allopatric regions where good mimics are present, predators might develop through learning (or evolve) preferences for conspicuous, palatable prey that they encounter frequently. By contrast, in neighboring allopatric regions where good mimics are absent, predators may not be able to develop or evolve preferences for phenotypes they do not encounter.

Materials and methods

Background

Elapid coral snakes of the Neotropics and Nearctic are highly venomous and frequently brightly colored, with rings of red, yellow (or white), and black encircling the body (Roze 1996). Predators typically avoid tricolor ringed patterns (Brodie 1993; Brodie and Janzen 1995; Hinman et al. 1997; Pfennig et al. 2001), often without prior experience (Smith 1975, 1977). Numerous nonvenomous colubrid snakes of the Neotropics and Nearctic (e.g., kingsnakes and milk snakes) converge on similar tricolor ringed patterns, which has led many to suggest that these snake are Batesian mimics of coral snakes (reviewed in Greene and McDiarmid 1981; Brodie and Brodie 2004).

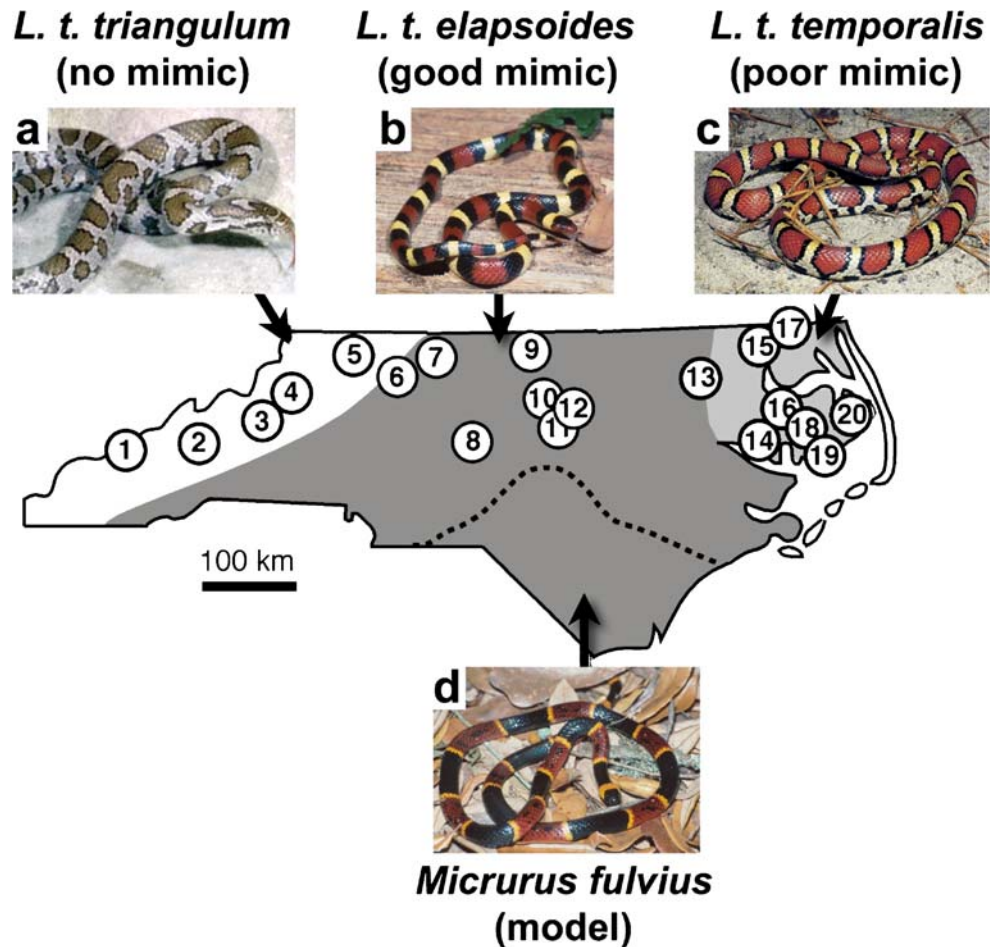
If tricolor ringed colubrids are indeed Batesian mimics of coral snakes, then such patterns should confer protection from predation where they actually co-occur with coral

snakes. This protection should break down, however, in areas where coral snakes are absent (i.e., in allopatry) because predators would not be under selection to avoid coral snakes or anything resembling them. Prior work by Pfennig et al. (2001) found support for this prediction. In this previous study, plasticine replicas of nonvenomous scarlet kingsnakes (*Lampropeltis triangulum elapsoides*), a presumed mimic of the deadly eastern coral snake (*Micrurus fulvius*), were placed in numerous sites along a latitudinal transect, encompassing areas where coral snakes were present and where they were absent (in the eastern US, *M. fulvius* is not found north of latitude 35.1°N; Palmer and Braswell 1995). Attacks on mimetic patterns were significantly lower in sympatry than in allopatry. Moreover, attack frequencies were positively correlated with latitude, hence, with declining *M. fulvius* abundance, suggesting that predators engaged in frequency-dependent predation (Pfennig et al. 2001; the fact that the relationship between model abundance and attack rates on mimetic patterns increased linearly is more consistent with frequency-dependent selection than with number-dependent selection, where the relationship is predicted to be sigmoidal; e.g., see Fig. 1 in Mallet and Joron 1999).

Although this earlier study demonstrated that *L. t. elapsoides* are Batesian mimics of *M. fulvius*, it did not establish whether mimics suffer more intense predation in allopatry than expected by chance. Thus, it is unclear if mimics incur a cost in allopatry. Moreover, the fact that mimics appear to be subject to frequency-dependent predation (Pfennig et al. 2001) raises the possibility that predators might prey on good mimics more often in allopatric areas where such mimics are locally abundant.

Milk snakes found in North Carolina, USA are excellent subjects for addressing the above issues. Three different phenotypes occur in nonoverlapping regions of the state. Morphological analyses suggest that these three phenotypes vary in their resemblance to *M. fulvius* such that one can be considered a good mimic, one a poor mimic, and one not mimetic (i.e., “no mimic”) of *M. fulvius* (Harper and D. Pfennig, unpublished data). In particular, eastern milk snakes (*L. t. triangulum*), which inhabit western North Carolina, have a gray to reddish dorsum with large brown, grayish, or reddish body blotches with black margins (Fig. 1a). They bear no resemblance to *M. fulvius* in coloration or pattern and can be considered as not a mimic of the coral snake (Fig. 1d). Scarlet kingsnakes (*L. t. elapsoides*), which inhabit central North Carolina, are good Batesian mimics of *M. fulvius* (compare Fig. 1b to d; see above also). Finally, “coastal plain milk snakes” (formerly *L. t. temporalis*; Cope 1893; Conant 1943), which inhabit northeastern North Carolina, were once thought to represent intergrades between the above two subspecies and are intermediate between them in phenotype (Williams 1978). They are, at best, poor Batesian mimics of *M. fulvius* (Fig. 1c).

Fig. 1 Map of North Carolina showing nonoverlapping ranges of three subspecies of harmless milk snakes (*Lampropeltis triangulum*), which vary in their resemblance to deadly coral snakes: **a** eastern milk snakes, *L. t. triangulum* (geographical range, *white region*), **b** scarlet kingsnakes, *L. t. elapsoides* (geographical range, *dark gray region*), and **c** “coastal plain milk snakes,” formerly *L. t. temporalis* (geographical range, *light gray region*). Dashed line northern limit of **d** eastern coral snakes (*Micrurus fulvius*), **Circled numbers** locations of study sites. Photos **a**, **b**, **d** courtesy of Wayne Van Devender, and **c** courtesy of Richard D. Bartlett. (To see this image in color, go to Behav Ecol Sociobiol online)



The aim of this study was to answer the following two questions. First, do mimetic milk snakes that exist in allopatry with coral snakes suffer more intense predation than expected by chance? Second, do attack rates on good mimics (i.e., *L. t. elapsoides*) vary among different allopatric regions depending on whether the local milk snake is a good mimic (i.e., *L. t. elapsoides*), a poor mimic (i.e., *L. t. temporalis*), or no mimic (i.e., *L. t. triangulum*)?

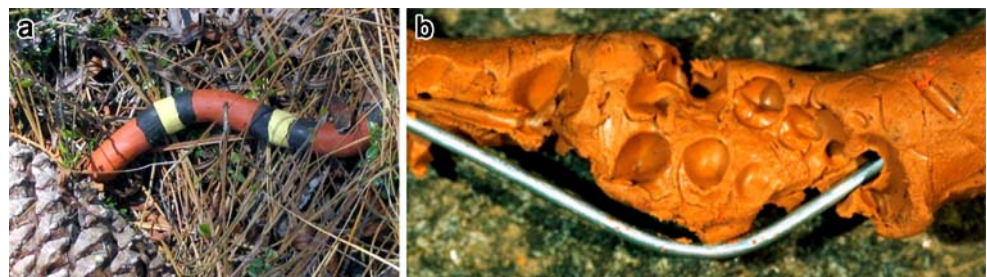
Experimental procedures

To address the above two questions, we used artificial models of snakes constructed of cylinders of precolored, nontoxic plasticine threaded onto an S-shaped wire

(Fig. 2a). By placing these replicas in natural habitat, we were able to record predation attempts by observing the teeth imprints left in the plasticine by natural predators (Fig. 2b; Madsen 1987; Brodie 1993; Brodie and Janzen 1995; Hinman et al. 1997; Pfennig et al. 2001).

We constructed snake replicas (1.5×18 cm) with a tricolor ringed pattern, a striped pattern with identical colors and proportions as ringed replicas, and a plain brown pattern. Ringed replicas were modeled after a typical scarlet kingsnake, *L. t. elapsoides*, from south-central North Carolina and resembled them in size, color hue, color order, and ring width (Palmer and Braswell 1995). Striped and brown replicas served as controls. Brown replicas resembled several abundant, nonvenomous snakes found

Fig. 2 **a** Replica of a scarlet kingsnake (*L. t. elapsoides*) in situ. **b** Control replica, showing teeth marks left from a black bear attack. Photos by David W. Pfennig. (To see this image in color, go to Behav Ecol Sociobiol online)



throughout allopatry (Palmer and Braswell 1995), including eastern earth snakes (*Virginia valeriae*), northern redbelly snakes (*Storeria occipitomaculata*), brown snakes (*Storeria dekayi*), queen snakes (*Regina septemvittata*), and eastern worm snakes (*Carphophis amoenus*).

We conducted experiments during May and June of 2000 and 2001 at 20 different sites in North Carolina (Fig. 1). In 2000, we arranged at each site three different replicas (ringed, striped, and brown: hereafter referred to as “triplets”) 2 m apart in natural habitat (e.g., see Fig. 2a). In 2001, we arranged two different replicas (ringed and brown: hereafter referred to as “doublets”) 2 m apart. We then walked in a straight line for approximately 75 m and positioned another triplet/doublet, repeating the procedure until we had formed a 750-m long transect containing ten triplets/doublets. Each replica was used only once. There were eight transects in the central piedmont region, where only *L. t. elapsoides* were present (“good” mimic), seven transects in the northeastern coastal plain, where only *L. t. temporalis* were present (“poor” mimic), and five transects in the mountains, where only *L. t. triangulum* were present (no mimic).

We collected replicas 4 weeks after their placement. After the collection, a person without knowledge of the replica’s location scored attacks by noting any impressions corresponding to a predator. We considered a replica to have been “attacked” only if it contained teeth marks of a carnivore (e.g. black bear, bobcat, coyote, fox, raccoon). The fact that most carnivores possess dichromatic vision (having cones for blue and green light) and appear to lack trichromatic (“true”) color vision does not seem to preclude their being able to distinguish good mimics from poor mimics (Pfennig et al. 2001). Presumably, different pattern resemblances to coral snakes can be detected even without color vision, since patterns and degrees of shading differ among snakes that represent good, poor, and no mimics (e.g., see Fig. 1). Moreover, scent likely did not play in role in these experiments, because all replicas were made of the same plasticine material and thus would have had similar scent. Impressions made by rodents or insects were excluded from the analysis, because these animals would not have represented a threat to a live snake. There were no bird attacks. Typically, only one replica in any given triplet/doublet was attacked, suggesting that predators “chose” among the different types of replicas.

For the analyses, we also excluded attacks on striped replicas, because these replicas were used only in 2000 (the striped pattern was used in 2000 to control for the possibility that predators might simply avoid all brightly colored objects, regardless of pattern; however, because we found no evidence of any such generalized avoidance of brightly colored objects, we did not use these patterns in 2001; Pfennig et al. 2001). Our response measure for both years was the proportion of ringed replicas attacked along

each transect (= number of ringed replicas attacked divided by the total number of ringed and brown replicas attacked). Because there were no significant year effects on the total number of attacks or on the mean proportion of ringed replicas attacked, we pooled data across years. Data from 8 allopatric sites collected in 2000 are also presented in Pfennig et al. (2001).

For the statistical analyses, we compared the proportion of ringed replicas attacked along each transect with the proportion expected if attacks were random with respect to pattern (0.5). We also used a one-way ANOVA to determine if the proportion of ringed replicas attacked along each transect varied among different allopatric regions that differed in the type of mimic found locally (i.e., a good mimic, a poor mimic, or no mimic; Fig. 1). Proportion data were arcsine-square root transformed before the analysis to meet parametric assumptions.

We also determined if the proportion of ringed replicas attacked depended on the similarity of the ringed replica to the local milk snake. To do so, we assigned rank order scores to each transect based on the similarity of the local milk snake’s phenotype to that of the ringed replica. We assigned a score of “0” to the five transects in the *L. t. triangulum* region, because this subspecies bore the least resemblance to the ringed replicas (e.g., compare Fig. 1a–c to Fig. 2a). We assigned a score of “1” to the eight transects in the *L. t. elapsoides* region, because the ringed replicas were modeled on this subspecies and were therefore most similar to them (see above). Finally, we assigned a score of “0.5” to the seven transects in the *L. t. temporalis* region, because this subspecies is intermediate in phenotype between *L. t. triangulum* and *L. t. elapsoides* (Williams 1978) and, therefore, bore an intermediate resemblance to the ringed replicas. We then used a Spearman’s (nonparametric) correlation analysis to determine if the proportion of ringed replicas attacked along transects was associated with these ranked measures of similarity between the ringed replica and the local milk snake.

Finally, at the site of each triplet/doublet, we also characterized the surrounding woodland as deciduous, coniferous, or a mixture. This information was used to determine if regions differed in vegetation, and if any such variation in vegetation might account for differences in the proportion of ringed replicas attacked (against certain backgrounds, transverse rings or bands may break up the form of an elongate body, generating a disruptive effect; Brattstrom 1955; Pough 1976).

Results

Overall, 66 out of 400 (16.5%) replicas were attacked by carnivores. The number of replicas attacked did not differ

significantly across regions (mean±SEM number of total attacks on both types of replicas in the *L. t. triangulum* region =2.20±1.16, $N=5$ sites; *L. t. elapsoides* region =2.38±0.45, $N=8$ sites; *L. t. temporalis* region =5.14±0.98, $N=7$ sites; ANOVA: $F_{2,17}=2.7$, $P=0.0926$). Moreover, a similar suite of carnivores (black bear, bobcat, coyote, fox, and raccoon) appeared to be responsible for attacks in all three regions.

There were significant differences among regions in the mean proportion of ringed replicas attacked (ANOVA: $F_{2,17}=10.03$, $P=0.0013$; Fig. 3). Indeed, the mean proportion attacked in the *L. t. elapsoides* region (0.809±0.078, $N=8$ sites) was significantly greater than that in either the *L. t. triangulum* region (0.266±0.098, $N=5$ sites) or the *L. t. temporalis* region (0.483±0.083, $N=7$ sites; Tukey–Kramer HSD test: $P<0.05$ for both contrasts).

When all three regions were considered together, the mean proportion of ringed replicas attacked (0.559±0.069, $N=20$ sites) did not differ significantly from the proportion expected if attacks were random with respect to color pattern (0.5; two-tailed Wilcoxon signed rank test, $P=0.438$). When regions were considered separately, this proportion did not differ significantly from randomness in the *L. t. triangulum* region (two-tailed Wilcoxon signed rank test, $P=0.250$) nor in the *L. t. temporalis* region (two-tailed Wilcoxon signed rank test, $P=1.0$). In contrast, the mean proportion of ringed replicas attacked was significantly greater than randomness in the *L. t. elapsoides* region (two-tailed Wilcoxon signed rank test, $P=0.039$). Thus, attacks on mimics were significantly greater than randomness only where good mimics (i.e., *L. t. elapsoides*) occur.

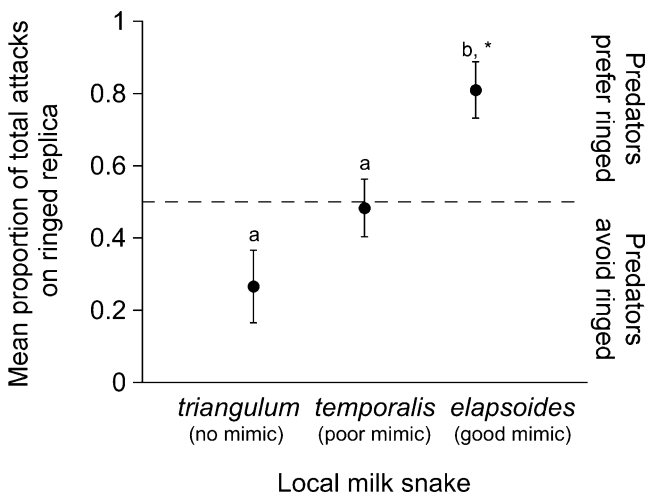


Fig. 3 The mean (±SEM) proportion of carnivore attacks on ringed replicas of *L. t. elapsoides* (the “good mimic” of *M. fulvius*) was significantly greater than randomness (dashed line) only in allopatric regions where *L. t. elapsoides* are found. By contrast, attacks were not significantly different from randomness in regions where only *L. t. triangulum* or *L. t. temporalis* are present. Data points not connected by the same letter are significantly different. An asterisk denotes a value significantly different from randomness (0.5)

The proportion of ringed replicas attacked along transects was significantly positively correlated with the rank order degree of match of the local milk snake to the ringed replica (recall that the ringed replica resembled the good mimic, *L. t. elapsoides*, most closely; Spearman rank order correlation coefficient =0.66, $P=0.002$, $N=20$ transects). In particular, attacks on ringed replicas were lowest in the *L. t. triangulum* region (where resemblance of the local milk snake *L. t. triangulum* to the ringed replica was lowest), intermediate in the *L. t. temporalis* region (where resemblance of the local milk snake *L. t. temporalis* to the ringed replica was intermediate), and highest in the *L. t. elapsoides* region (where resemblance of the local milk snake *L. t. elapsoides* to the ringed replica was highest).

Finally, differences among regions in attacks on ringed replicas could not be ascribed to any differences among regions in vegetation type for two reasons. First, regions did not differ in our vegetation measures: an ordinal vegetation score (1 = deciduous, 0 = conifer, 0.5 = mix) did not differ significantly across regions (mean score in *L. t. triangulum* region =0.88±0.13, $N=5$ sites; *L. t. elapsoides* region =0.80±0.10, $N=8$ sites; *L. t. temporalis* region =0.65±0.11, $N=7$ sites; ANOVA: $F_{2,17}=0.903$, $P=0.424$). Second, there was no significant relationship between a site’s mean vegetation score and the proportion of ringed replicas attacked in that site (Spearman rank order correlation coefficient =0.253, $P=0.282$, $N=20$ transects).

Discussion

We predicted that mimics should suffer intense predation pressure where their model is absent (i.e., in allopatry), because mimic and model share phenotypes that are conspicuous to predators, but predators in such regions would not be under selection to recognize the model or any other species resembling it as dangerous. We tested this prediction in a coral snake mimicry complex by exposing plasticine snake replicas to natural predators (Fig. 2). We then asked two questions. First, are good mimetic milk snakes (i.e., *L. t. elapsoides*) preferentially attacked where they do not occur with their coral snake model? Second, do attack rates on these good mimetic milk snakes vary among different allopatric regions that differ in the type of mimic found locally (i.e., a good mimic, a poor mimic, or no mimic; Fig. 1)?

We found that when all three types of regions were considered together, good mimics were not preferentially attacked. When regions were analyzed separately, however, attacks on good mimics were significantly greater than randomness only in the region where good mimics (i.e., *L. t. elapsoides*) are actually found (Fig. 3). Thus, as predicted, good mimics do suffer intense predation pressure where their model is absent, but only in allopatric

regions where such mimetic phenotypes would have historically been encountered frequently by predators.

These variable levels of predation on good mimics might reflect frequency-dependent (i.e., apostatic) predation (Holling 1965, 1966; Murdoch 1969; Curio 1976; Allen 1988, Endler 1986, 1988, 1991; Merilaita 2006). In allopatric regions where good mimics are present, predators might have learned or evolved preferences for conspicuous, palatable prey that they encounter frequently. By contrast, in allopatric regions where good mimics are absent, predators might not have learned or evolved preferences for novel phenotypes that they do not encounter even though these phenotypes may be conspicuous.

Consistent with this frequency-dependent predation hypothesis, we found that attacks on replicas of *L. t. elapsoides* (the good mimic) were greatest in sites where *L. t. elapsoides* are actually present in the wild (Fig. 1). By contrast, attacks on replicas of *L. t. elapsoides* were intermediate in sites inhabited by *L. t. temporalis* (Fig. 1c), which bear a slight resemblance to *L. t. elapsoides*. Finally, attacks on replicas of *L. t. elapsoides* were lowest in sites inhabited by *L. t. triangulum* (Fig. 1a), which bear no resemblance to *L. t. elapsoides*. These differences among regions may indicate that predators have the strongest preferences (or search image template) for phenotypes of local milk snakes. Such templates might be genetically encoded (as with avoidance of coral snake patterns; Smith 1975, 1977) or they might involve learned detection of prey phenotypes frequently encountered (e.g., see Kamil 1989). The possibility that predators possess a search image for local prey explains not only why predation was highest on replicas of *L. t. elapsoides* where they actually occur, but also why predation rates were positively correlated with the similarity of the replicas to the local milk snake species (see “Results”).

If mimics potentially suffer high predation in allopatry, why do mimetic snakes occur where coral snakes are absent? This phenomenon is not unusual—in many mimicry complexes, mimics occur where their model is absent (Clarke and Sheppard 1975; Gordon and Smith 1998; Koch et al. 2000; Pfennig et al. 2001; Prudic et al. 2002). In our system, mimetic snakes appear to occur outside the range of their coral snake model because they have expanded into such regions relatively recently (i.e., in the past 10,000 years; Harper and D. Pfennig, unpublished data). Nevertheless, if mimics suffer significantly high predation in allopatric regions where they are common (e.g., see Fig. 3), then selection should ultimately break down the seemingly maladaptive phenotype. As predicted, in North Carolina, allopatric *L. t. elapsoides* bear less resemblance to coral snakes than do sympatric *L. t. elapsoides* (Harper and D. Pfennig, unpublished data).

However, our data also suggest that selection will not be equally strong against mimetic patterns in every allopatric

population. Specifically, good mimics may not suffer from intense predation in allopatric regions where they are rare. Indeed, although the good mimic (*L. t. elapsoides*) occurs hundreds of kilometers outside the range of its model in the east-central US (e.g., west of the Appalachian Mountains, where *L. t. elapsoides* are sympatric with *L. t. triangulum*; Williams 1978; Greene and McDiarmid 1981; Conant and Collins 1998), they tend to be rare in such areas (Williams 1978). Thus, good mimics may persist in allopatry with their model as long as they are not common. If this hypothesis is correct, then the mimetic pattern should not break down as much in allopatric regions where *L. t. elapsoides* are rare (e.g., west of the Appalachian Mountains) as in allopatric regions where *L. t. elapsoides* are common (e.g., east of the Appalachian Mountains in central North Carolina). Thus, frequency-dependent (apostatic) predation may cause the strength of selection against mimetic phenotypes to differ among allopatric populations. Consequently, apostatic predation, coupled with variation in mimic abundance, may generate a geographical mosaic (sensu, Thompson 2005) among allopatric mimics in their degree of phenotypic resemblance to the model.

Acknowledgements We thank two anonymous referees for helpful comments on our paper. This research was supported by grants from the National Science Foundation to D. Pfennig and K. Pfennig.

References

- Allen JA (1988) Frequency-dependent selection by predators. *Philos Trans R Soc Lond Ser B* 319:485–503
- Bates HW (1862) Contributions to an insect fauna of the Amazon valley. *Lepidoptera: Heliconidae*. *Trans Linn Soc Lond* 23:495–566
- Brattstrom BH (1955) The coral snake “mimic” problem and protective coloration. *Evolution* 9:217–219
- Brodie ED III (1993) Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* 47:227–235
- Brodie ED III, Janzen FJ (1995) Experimental studies of coral snake mimicry: generalized avoidance of ringed snake patterns by free-ranging avian predators. *Funct Ecol* 9:186–190
- Brodie ED III, Brodie ED Jr (2004) Venomous snake mimicry. In: Campbell JA, Lamar WW (eds) *The venomous reptiles of the western hemisphere*, vol II. Comstock, Ithaca, NY, pp 617–633
- Clarke C, Sheppard PM (1975) The genetics of the mimetic butterfly *Hypolimnas bolina* (L.). *Philos Trans R Soc Lond Ser B* 272:229–265
- Conant R (1943) The milk snakes of the Atlantic coastal plain. *Proc New Engl Zool Club* 22:3–24
- Conant R, Collins JT (1998) *A field guide to reptiles and amphibians of eastern and central North America*, 3rd edn. Houghton Mifflin, Boston, MA
- Cope ED (1893) The color variation of the milk snake. *Am Nat* 27:1066–1071
- Curio E (1976) *The ethology of predation*. Springer, Berlin Heidelberg New York
- Edmunds M (1974) *Defense in animals. A survey of anti-predator defenses*. Longmans, London

- Endler JA (1986) Natural selection in the wild. Princeton University Press, Princeton, NJ
- Endler JA (1988) Frequency-dependent predation, crypsis and aposematic coloration. *Philos Trans R Soc Lond Ser B* 319:505–523
- Endler JA (1991) Interactions between predators and prey. In: Krebs JR, Davies NB (eds) *Behavioural ecology. An evolutionary approach*, 3rd edn. Blackwell, London, pp 169–196
- Gordon IJ, Smith DAS (1998) Body size and colour-pattern genetics in the polymorphic butterfly *Hypolimnna misippus* (L). *Heredity* 80:62–69
- Greene HW, McDiarmid RY (1981) Coral snake mimicry: does it occur? *Science* 213:1207–1212
- Greenwood JJD (1969) Apostatic selection and population density. *Heredity* 24:157–161
- Hinman KE, Throop HL, Adams KL, Dake AJ, McLauchlan KK, McKone MJ (1997) Predation by free-ranging birds on partial coral snake mimics: the importance of ring width and color. *Evolution* 51:1011–1014
- Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Mem Entomol Soc Can* 45:1–60
- Holling CS (1966) The functional response of invertebrate predators to prey density. *Mem Entomol Soc Can* 47:3–86
- Kamil AC (1989) Studies of learning and memory in natural contexts: integrating functional and mechanistic approaches to behaviour. In: Blanchard RJ, Brain P, Blanchard DC, Parmigiani S (eds) *Ethoexperimental approaches to the study of behavior*. Kluwer Academic, Dordrecht, pp 30–50
- Koch PB, Behnecke B, French-Constant RH (2000) The molecular basis of melanism and mimicry in a swallowtail butterfly. *Curr Biol* 10:591–594
- Madsen T (1987) Are juvenile grass snakes, *Natrix natrix*, aposematically colored? *Oikos* 48:265–267
- Mallet J (2001) Mimicry: an interface between psychology and Evolution. *Proc Natl Acad Sci USA* 98:8928–8930
- Mallet J, Joron M (1999) Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Ann Rev Ecol Syst* 30:201–233
- Merilaita S (2006) Frequency-dependent predation and maintenance of prey polymorphism. *J Evol Biol* (in press). DOI 10.1111/j.1420-9101.2006.01137.x
- Murdoch WW (1969) Switching in general predators: experiments of predator specificity and stability of prey populations. *Ecol Monogr* 39:335–354
- Palmer WM, Braswell AL (1995) *Reptiles of North Carolina*. University of North Carolina Press, Chapel Hill, NC
- Pfennig DW, Harcombe WR, Pfennig KS (2001) Frequency-dependent Batesian mimicry. *Nature* 410:323
- Pough FH (1976) Multiple cryptic effects of crossbanded and ringed patterns of snakes. *Copeia* 1976:335–365
- Prudic KL, Shapiro AM, Clayton NS (2002) Evaluating a putative mimetic relationship between two butterflies, *Adelpha bredowii* and *Limenitis lorquini*. *Ecol Entomol* 27:68–75
- Roze JA (1996) Coral snakes of the Americas: biology, identification, and venoms. Krieger, Malabar, FL
- Ruxton GD, Sherratt TN, Speed MP (2004) *Avoiding attack: the Evolutionary ecology of crypsis, warning signals and mimicry*. Oxford University Press, Oxford
- Smith SM (1975) Innate recognition of coral snake pattern by a possible avian predator. *Science* 187:759–760
- Smith SM (1977) Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature* 265:535–536
- Thompson JN (2005) *The geographic mosaic of coEvolution*. University of Chicago Press, Chicago, IL
- Waldbauer GP, Sternburg JG (1987) Experimental field demonstration that two aposematic butterfly color patterns do not confer protection against birds in Northern Michigan. *Am Midl Nat* 118:145–152
- Wallace AR (1870) *Contributions to the theory of natural selection*. Macmillan, London
- Wickler W (1968) *Mimicry in plants and animals*. McGraw-Hill, New York
- Williams KL (1978) Systematics and natural history of the American milk snake, *Lampropeltis triangulum*. Milwaukee Public Museum Publications in Biology and Geology 2:1–258