SPECIALIZED AVIAN PREDATORS REPEATEDLY ATTACK NOVEL COLOR MORPHS OF *HELICONIUS* BUTTERFLIES

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Abstract.—The persistence of Müllerian mimicry and geographically distinct wing patterns, as observed in many *Heliconius* species (Lepidoptera: Nymphalidae), is difficult to explain from a predator's perspective: predator selection against locally rare patterns must persist despite avoidance learning. Maintaining spatial color-pattern polymorphism requires local pattern avoidance, fine-scale discrimination among similar wing patterns, and repeated attacks on novel color patterns. I tested for these behaviors by presenting 80 adult rufous-tailed jacamars (*Galbula ruficauda*) with three morphs of *Heliconius* butterflies, and then presenting the same suite of butterflies to 46 of these jacamars between four and 429 days later. These trials offer the first direct evidence of the selective predator behavior required to maintain aposematic polymorphism: jacamars avoid local aposematic morphs while repeatedly attacking similar but novel morphs over time.

Key words.—Aposematic, avian predators, frequency-dependent selection, *Heliconius* butterflies, jacamars, Müllerian mimicry.

When two or more aposematic species (i.e., those harboring noxious chemicals and having bright coloration) share a common warning-color pattern, they are said to be Müllerian mimics (Allen 1988; Joron and Mallet 1998; Joron et al. 1999; Mallet and Joron 1997). Müllerian mimicry is thought to be locally stable since selection is highest against morphological deviations from the most common model (Allen 1988; Endler 1988; Joron and Mallet 1998; Speed 2000). However, spatially polymorphic mimicry (i.e., geographic variation in warning-color patterns among the same species) is potentially less stable due to increased gene flow, and its persistence remains difficult to explain despite over a century of research (Poulton 1890; Fisher 1930; Carpenter and Ford 1933).

For spatially polymorphic mimicry systems to be maintained, higher selection against rare morphs (i.e., positive frequency-dependent selection) is needed to counter variation introduced by dispersal and hybridization (Greenwood 1986; Mallet and Barton 1989). Positive frequency-dependent selection can arise only with unpalatable prey because aposematism, associated with unpalatability, discourages predation on familiar, common morphs (Thompson 1984; Greenwood 1986; Church et al. 1997). Thus, when encountering aposematic prey a predator avoids locally common color patterns but may attack novel color patterns. Müllerian mimicry is thought to exist as a means to reduce predator attacks through aversion learning of the color morph (Brower et al. 1968; Thompson 1984) and, as the major diurnal insectivores, avian predators are the most likely agents of selection in aposematic mimicry systems.

Heliconius butterflies are among the most remarkable and best-studied polymorphic mimicry systems (Mallet and Joron 1999). *Heliconius erato* and *H. melpomene* are spatially polymorphic, converging on 28 geographically distinct races such that adjacent intraspecific races of each species often have strikingly different wing patterns (Brower et al. 1963; Benson

1972; Brown and Benson 1974; Mallet and Barton 1989). Spatial polymorphism in the *Heliconius* butterfly mimicry system exists despite convergent selection driving mimicry; therefore, the existence of polymorphism in this mimicry system remains difficult to explain (Brown and Benson 1974; Joron et al. 1999). Furthermore, the maintenance of narrow contact zones found in the *H. erato–melpomene* complex are thought to result from predator selection countering butterfly dispersal of one morph type into the other (Mallet et al. 1990). Thus, locally convergent mimicry and intraspecific contact zones separating these spatial patterns in the *H. erato–melpomene* mimicry system are best explained by predators that select against novel wing patterns. Strong selection by predators on *Heliconius* is suggested by reduced butterfly recapture rates of translocated individuals (Mallet and Barton 1989; Kapan 2001) and reduced recapture rates and wing damage to local *Heliconius* with wing patterns modified by ink (Benson 1972).

Maintaining consistent selection against novel wing patterns in the *Heliconius* mimicry complex, despite the expectation that initial predator attack rates on locally rare wing patterns should decrease over time as predators become familiar with less abundant morphs (Kapan 2001), is a paradox. The paradox of increased familiarity with wing patterns being associated with decreased selection pressure against rare wing patterns could be resolved through a variety of mechanisms. At the population level, naïve juveniles in the predator population may attack novel prey to learn local butterflies (Chai 1986, 1988). Additionally, high turnover rates in the predator population due to short life span or high dispersal rates may be such that even if pattern memory is good, turnover resets the average predator experience levels. At the individual level, a predator may require multiple attacks on the same morph to learn wing or color patterns, or a predator may have high forgetting rates (Turner and Speed 1996; Speed 2000). Additionally, a predator with fine-scale discrimination may learn to avoid specific patterns yet continue to attack similar novel morphs.

Two difficulties, however, exist with any explanation in-

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voking avian predators: (1) direct evidence that *Heliconius* predators possess the necessary cognitive abilities to generate positive frequency-dependent selection, and (2) evidence that a predator capable of learning to avoid toxic color morphs will repeatedly sample toxic prey. A straightforward solution would be experimental evidence that a small population of avian predators would repeatedly attack aposematic butterflies having novel wing patterns despite strong pattern learning.

Jacamars (Galbulidae) are frequently suggested as important agents of selection in butterfly mimicry systems, including *Heliconius* butterflies (Mallet and Joron 1999; Kapan 2001). Jacamars specialize in preying on fast-flying insects, such as dragonflies and butterflies. In pioneering trials, Chai (1986, 1988) presented caged jacamars with a varied butterfly fauna. His results suggested that jacamars are capable of discriminating among numerous butterfly species. When foraging, jacamars observe flying prey, leave the perch to capture it, and then often return to the same perch. Once back at the perch, jacamars appear to taste-sample prey and either release or consume it (Chai 1986, 1988; G. M. Langham, pers. obs.). Although other avian insectivore species (e.g., *Tyrannus* and *Myiarchus* flycatchers) are certain to contribute to the evolution of butterfly mimicry systems generally (Pinheiro 1996, 2003), no direct evidence exists that they exert positive frequency-dependent selection, and no other group of birds is known to feed on butterflies to the same extent as do jacamars. Jacamars, therefore, represent the most likely predators capable of generating the selection required to maintain the spatial polymorphism in *Heliconius*.

I investigated the predator behaviors required of jacamars to exert positive frequency-dependent selection on *Heliconius* butterflies: (1) local pattern avoidance, (2) fine-scale discrimination, and (3) repeated attacks on novel wing patterns. I tested for these behaviors by presenting 80 adult rufous-tailed jacamars (*Galbula ruficauda*) with three morphs of *Heliconius* butterflies, and then presenting the same suite of butterflies to 46 of these jacamars between four and 429 days later.

MATERIALS AND METHODS

Trials

I conducted two cage trials on 80 adult jacamars (40 males and 40 females) with the help of seven field assistants (one to three per season). In the first trial, I presented three *Heliconius* to each jacamar for 2.5 h. One butterfly was the local morph predicted to be avoided. The other two butterflies were novel morphs, one red and one black (Fig. 1A), predicted to be attacked, as these were unfamiliar *Heliconius* morphs. The red and local morphs differed only in wing-patch brightness (Fig. 1B), which provided a test of fine-scale discrimination. A follow-up trial was designed to test for pattern forgetting over time and to determine whether individual jacamars behaved consistently between trials.

Site

I conducted trials at Los Cerrajones ranch in the llanos (savannas) of western Venezuela (225 m elevation; 9°12′N,
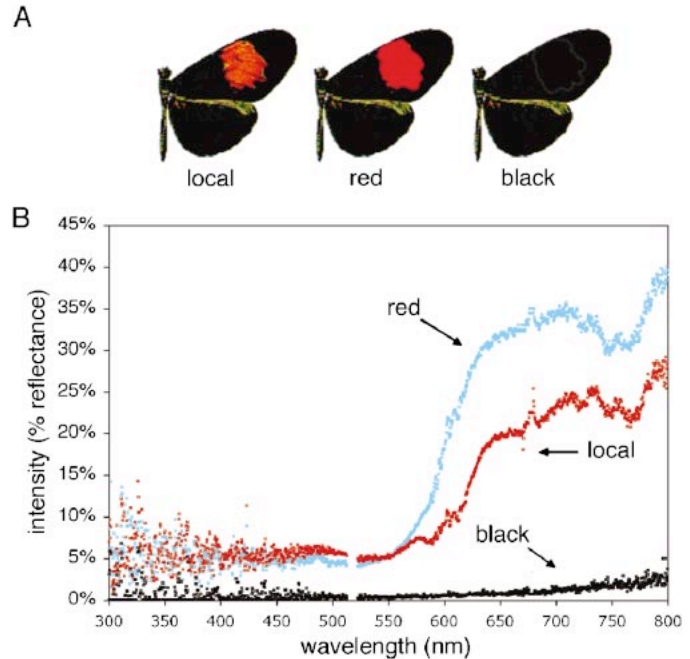

FIG. 1. Appearance and reflectance spectra of experimental butterfly morphs. (A) Illustration of each *Heliconius erato* morph. Red and black morphs, altered with permanent ink, retained wing shape and behavior of the unaltered local morph. (B) Reflectance spectra for morph wing-patches. Scattering in the ultraviolet range (300–400 nm) was similar in all three wing patches, indicating that variation in ultraviolet signals was not an important factor (a potential concern because some birds are sensitive to UV signals). The red morph showed more reflectance in the 570–790 nm range, indicative of the noticeably brighter patch of this artificially brightened morph. The black morph showed similar reflectance to the black body parts of all morphs.

69°43′W) over three dry seasons (February–March 1998, December 1999–February 2000, and December 2000–April 2001). Only one color pattern exists in the region for each local race of the *H. erato–melpomene* mimicry complex (*H. e. hydara* and *H. m. melpomene*). The nearest distinct color pattern in this complex was more than 500 km distant.

Butterflies and Birds

Butterflies were wild caught and novel morphs were carefully marked, ventrally and dorsally, on the red forewing patch with either a red or black Sharpie pen (Sanford Corp., Bellwood, IL; after Benson 1972). Handling time to mark novel butterflies lasted approximately 2 min, and after the ink dried, butterflies appeared to behave and fly normally. Marked and unmarked butterflies lived up to three months in captivity. Only *H. erato* was used in trials because this species is much more common, though both species are thought to be chemically protected (Nahrstedt and Davis 1983) and, therefore, should be functionally interchangeable. Butterflies and birds were kept in outdoor cages (2 × 2 × 4 m) of Lumite mesh (Bio Quip Products, Rancho Dominguez, CA) supported by wooden frames with a tree branch across the center of the cage as a perch.

Jacamars were captured using nylon mist nets and conspecific playbacks to attract birds into the nets. Of the 80

jacamars tested in the first trial, 46 birds were recaptured up to two years after the first trial in order to conduct a second, follow-up trial. Birds showing signs of stress were released without testing (four birds over three seasons). Jacamars were captured before 1300 h and placed individually in a cage with 15 live dragonflies (total 8–11 g) as food. The first morning after birds were captured, three *H. erato* (an unaltered local morph, an altered red morph, and an altered black morph) were placed into glassine envelopes, released into the cage, and allowed to fly freely for 2.5 hrs. Observers sat 25 m away and watched with 10×42 binoculars. A sampling event was recorded when: (1) a bird captured a butterfly with its bill and brought it to the perch, or (2) aerial sampling was suspected and the butterfly showed clear wing damage or bill marks after the trial. Misses were not recorded as sampling events. Since some butterflies observed to be captured by jacamars often showed no wing damage or marks, estimates of sampling rates are conservative. Butterflies were captured after each trial and examined closely for wing damage and bill marks. Only butterflies without wing damage were presented to birds. After each trial, birds were released at the capture site. Jacamars were kept under Cornell University IACUC protocol number 98–96.

Color Measurement

Forewing patch reflectance was measured for each experimental group (Fig. 1) with an Ocean Optics S2000 spectrometer (Dunedin, FL) combined with a deuterium tungsten halogen light source (Analytical Instrument Systems, Inc., Flemington, NJ). The combined-spectrum light source provided illumination in both the ultraviolet and human visual spectrum (300–800 nm). Measurements were taken with a metal fiber-optic probe that provides illumination from the light source and transfers reflected light to the spectrometer. I held the probe perpendicular to the measurement surface at a distance of 2 mm using a cover that excluded all external light from the measurement area. All measurements were expressed as the percent reflectance relative to the reflectance of a Spectralon white standard (Pro-Lite Technology, Crantfield, U.K.), which reflects 97–99% of incident light. All wings were measured in a single session, and only one butterfly was measured for each experimental morph. A measurement session consisted of a reference reading followed by a Spectralon reading. I measured each color region three times, placing the probe at an arbitrary location within the color region before taking each reading. I then calculated average frequency-reflectance curves for each color region for each wing sample.

RESULTS

Cage trials were performed over three breeding seasons with 2, 38, and 40 tested birds, respectively, for the first trial (Table 1). I detected no difference in sampling behavior among breeding seasons (homogeneity of odds-ratios test among breeding seasons, $P = 0.48$), and results were combined in all subsequent analyses. A standardized date value for each trial (Julian date) was calculated for all three seasons to the earliest experimental date (December 6) to look for trends within the breeding season. In the 1999–2000 season,

TABLE 1. First trial attack behavior of rufous-tailed jacamars across breeding seasons in northwestern Venezuela.

Season[1] (n)	Males[2] (n = 40)		Females (n = 40)	
	Attack	Avoid	Attack	Avoid
1998 (2)	2	0	0	0
1999–2000 (38)	9	9	5	15
2000–2001 (40)	10	10	3	17
Total	21	19	8	32

[1] Homogeneity of odds-ratio test among breeding seasons showed no difference ($P = 0.48$).

[2] Common odds-ratio test between sexes was significant (Mantel-Haenszel variance; $P < 0.01$).

nine of the first 10 males sampled a novel morph whereas only two of the second 10 sampled, suggesting Julian date might influence sampling behavior. Despite the appearance of a trend, however, Julian date was not a significant predictor of sampling behavior (logistic regression: $R^2 = 0.003$, $P > 0.5$). Number of days between trials was also not a significant predictor of attack behavior (logistic regression: $R^2 = 0.0035$, $P > 0.75$).

Overall, a novel (red or black) *Heliconius* was attacked by 29 of 80 jacamars (36%) in the first trial and 17 of 46 (37%) in the second trial, whereas the local morph was completely avoided in all 126 trials (Fig. 2). Forty males and 40 females were tested in the first trial, and 28 males and 18 females were recaptured for the second trial. The proportion of jacamars that attacked butterflies did not differ between trials (Fig. 2: Fisher's exact tests; overall: $P = 0.642$; males: $P = 0.185$; females: $P = 0.264$). Males but not females sampled more black than red morphs in the first trial (Fig. 2: $\chi^2_{0.05,1} = 13.8$, $n = 40$, $P < 0.001$), but such a bias was not evident in the second trial ($\chi^2_{0.05,1} = 0.08$, $n = 28$, $P > 0.75$). Seven birds made multiple attacks during a single trial. Two males and two females sampled both red and black morphs. Two males sampled the black morph twice and another male sampled it four times.

Individuals showed a tendency to repeat sampling behavior from the first trial. Of the 46 birds tested in a second trial, 39 maintained the same attack behavior: 14 of 18 first trial attackers sampled a red or black morph again, while 25 of 28 nonsamplers remained nonsamplers (Fisher's exact test, $P < 0.001$). Of the 14 resamplers, eight switched to the other novel morph. Individual jacamars, therefore, maintained similar attack predilections toward novel wing patterns and specific pattern avoidance. These results indicate that forgetting was not a significant factor despite the importance usually placed on learning and forgetting wing patterns (MacDougall and Dawkins 1998; Mallet and Joron 1999; Speed 2000). Moreover, the number of days between first and second trials was not a significant predictor of attack behavior (logistic regression: $R^2 = 0.0035$, $n = 18$, $P > 0.75$), which provides no evidence that forgetting increases in a simple manner with time.

DISCUSSION

This study provides direct evidence that jacamars avoid a familiar *Heliconius* butterfly while selecting against similar but novel morphs over time. Benson (1972) conducted a re-
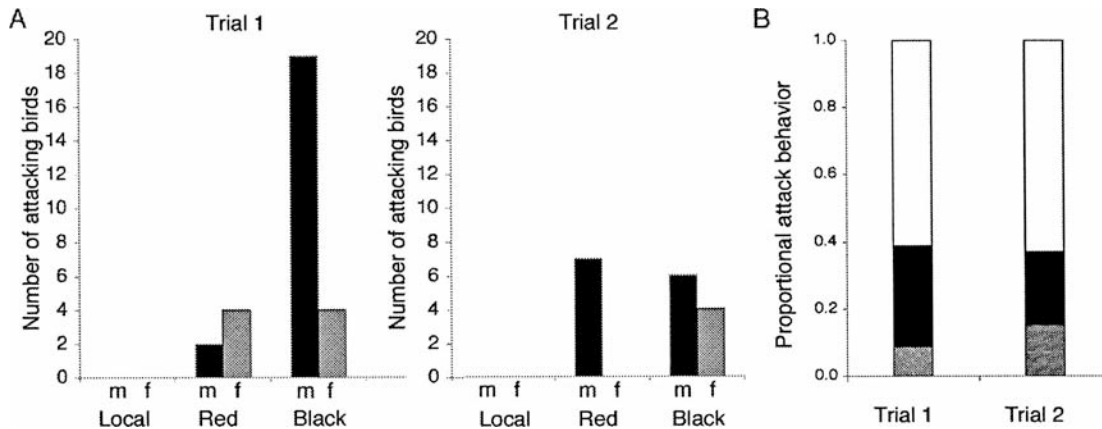
FIG. 2. (A) Number of male (m) and female (f) rufous-tailed jacamars attacking experimental morphs during the first cage trial (trial 1, n = 80) and after subsequent recapture (trial 2, n = 46). Only the first morph attacked in each trial is graphed. (B) Proportional attack behavior for each trial. Black (black morph) and gray (red morph) indicate the proportion of birds attacking respective morphs; white indicates proportion of birds attacking no morphs.

lated field trial by marking *H. erato* in Costa Rica at roost sites and following altered and unaltered individuals over time. Benson found that altered (i.e., inked forewings) individuals were less likely to return to the roost and were more likely to suffer wing damage than unaltered butterflies. Although causes of wing damage are difficult to assign to definite sources, several of Benson's altered butterflies reportedly showed beak marks from rufous-tailed jacamars. The present study results, combined with Benson's field results, suggest that jacamars can exert selection against novel warning color morphs of *H. erato* butterflies.

Past experiments directly testing birds demonstrated a range of responses to aposematic prey items. At one end of the spectrum, jays were willing to attack novel, aposematic butterflies, but after experiencing the emetic qualities of protective chemicals, individuals ceased to sample even imperfect Batesian mimics (Brower et al. 1963, 1964, 1968). Cliff flycatchers (*Hirundinea ferruginea*) near cities in Brazil showed a tendency to attack and consume aposematic butterflies, whereas flycatchers away from cities avoided aposematic species (Pinheiro 1996, 2003). This result suggested that birds had prior experience with aposematic butterflies. Kingbirds learned to avoid only butterfly species protected by the most noxious chemicals (Pinheiro 1996). These intriguing results should be extended to other flycatchers in the same subfamily, Tyranninae. The question remaining, in terms of the *Heliconius* system, is whether flycatchers have generalized avoidance learning like jays, or the pattern-specific avoidance learning, like jacamars, required to maintain a spatially polymorphic *Heliconius* system.

Past studies examining the predator's perspective in mimicry systems have also employed simulations based on general psychology models of learning and forgetting rates (Speed 2000). My results do not support the idea that predators are more likely to forget a pattern over time and then resample it, but further investigations are needed to control for age, sex, and breeding condition.

The local morph and the red morph differed only by 15% forewing brightness, yet the local morph was never attacked, whereas the red morph was attacked a total of 16 times. These results suggest that jacamars are capable of fine-scale discrimination among *Heliconius* morphs that leads to differential attack rates. Fine-scale discrimination among similar morphs and specific, rather than generalized, pattern avoidance suggests a resolution to the fundamental paradox of why birds that learn so well would continue to attack novel toxic prey. In the diverse butterfly faunas of the New World tropics, which are rich in Batesian mimics of variable mimicry precision, jacamars appear to be sampling novel prey, presumably in search of palatable mimics, and refining their search images and avoidance templates of available butterflies in the process. Acute sensitivity to differences in color patterns, required for the maintenance of spatial polymorphism, contrasts with the generalized pattern avoidance demonstrated in previous trials with toxic prey and avian predators (Brower et al. 1963, 1964; Greenwood et al. 1989). For example, Brower's classic study of jays demonstrated that naïve birds attack monarch butterflies but subsequently avoid all orange and black wing patterns, including harmless mimics (Brower et al. 1964). However, additional studies should investigate the importance of other visual cues such as polarized light, hue, and saturation.

Positive frequency-dependent selection is rare because it places cognitive demands on predators, and in most contexts this attack behavior seems to lack any foraging benefit. Jacamars' ability to sample prey items prior to consuming them (i.e., taste) may reduce the costs of sampling considerably. The long bills of jacamars and other insectivorous groups in other parts of the world, such as bee eaters, may have evolved in part to assist in determining the palatability of captured prey.

Among polymorphic *Heliconius* species, intraspecific hybridization is common along contact zones, producing up to 24 highly variable hybrid morphs, many of which look similar (Mallet and Barton 1989; Mallet and Joron 1999). In the present study, fine-scale discrimination and novel-pattern sampling provide evidence that birds can maintain narrow contact zones by a combination of pattern discrimination among numerous intermediate morphs and specific pattern avoidance of the dominant local morph. By contrast, most

behavioral models of warning coloration and mimicry assume that rates of avian predation are strongly dependent on learning and forgetting rates and that predators have general patterns of attack behavior (Turner and Speed 1996; Speed 2000). Finally, chickadees showed the ability to associate symbols, such as squares and circles, with almonds treated and untreated with chemicals (Lindstrom et al. 2001). These differences in pattern learning and memory indicate that a general model of avian attack behavior is likely not attainable.

Early mimicry theory assumed that predators take a fixed number of unpalatable prey each season (Müller 1879), and the persistent sampling of rare prey by some jacamars supports this idea. Most individuals, however, did not sample any of the *Heliconius* morphs, suggesting that sampling is not a general rule among jacamars. Thus the majority of selection may be generated by only a subset of the predator population: those birds that are persistent samplers. The present study provides the first experimental evidence that those predators that actually co-exist with mimetic *Heliconius* butterflies display behavior necessary to drive mimicry between species and maintain spatially divergent polymorphic forms.

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