RELATIONSHIPS BETWEEN BUTTERFLY FLIGHT AND WING COLORATION AND PATTERNING

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Abstract: Butterflies use several different defense systems against predators including camouflage and bright coloration that warns of chemical defenses. Butterflies lacking either of these defense systems may have to rely on evasive flight behavior. We quantified several aspects of flight pattern of 21 Costa Rican butterfly species to determine how individuals with different wing patterns and coloration respond to a simulated predation event. Solid colored butterflies with neither camouflage nor bright coloration exhibited faster, more evasive flight traits. These results suggest that butterflies with neither crypsis nor aposematism depend on evasive flight to avoid predation.

Key words: aposematism, butterflies, camouflage, chemical defenses, crypsis, flight patterns

INTRODUCTION

Butterflies are subject to attacks from numerous predators, which has led to the evolution of defense mechanisms such as camouflage, chemical defenses, and evasive behavior. Camouflage functions to blend the organism into the background, making it difficult to detect (DeVries 1987). This can take the form of matching natural objects such as a leaf litter and ground cover or disruptive patterning that breaks up the butterfly's outline making it difficult to detect (Sbordoni 1998). Chemical defenses involve the butterflies' incorporation of toxins that make them distasteful. Chemically defended butterflies tend to advertise their toxin with bright red and orange coloration, such as the Monarch butterfly (*Danaus plexippus)* with its bright orange color (DeVries 1987). Certain butterflies lack camouflage and chemical defense, and may avoid predators through evasive behavior (Chai et al. 1990).

In this study, we examined the evasive behavior of butterflies in relation to their predator avoidance strategies. We hypothesize that butterfly species vary in flight pattern according to their need for predator protection. Based on pattern, indicating lack or presence of camouflage, and coloration, indicating lack or presence of chemical defense, we predict differences in turning frequency, flight duration, relative speed, and average height of flight. Specifically, butterflies lacking camouflage and chemical defense should exhibit more evasive flight traits than those with camouflage or warning coloration.

METHODS

We visually assessed the behavior and appearance of butterflies encountered haphazardly on the morning of 12 January 2004 near the OTS field station at Palo Verde National Park, Guanacaste, Costa Rica. We observed butterflies in three different habitats: an open field near a marsh, a forested area near the water hole approximately 3 km east of the field station, and the lower slope of the tropical dry forest behind the field station. We measured flight traits of each individual butterfly after being disturbed (prodding with a meter stick) from a perched position. These measurements included number of mid-air turns (> ~ 90° change in direction), relative speed (0 = slow, 1 = medium, 2 = fast), average height of flight (0 - 1 m, 1 - 2 m, and > 2 m above ground), and total flight time, as responses to disturbance.

We used descriptive keys to identify

morphospecies and to categorize by pattern and coloration (DeVries 1987, Rainforest Publications 2001). Patterns were grouped into three categories: mottled, disruptive, and solid. "Mottled" characterized butterflies that resembled ground cover such as leaf litter, and tended to have different shades of brown and white that occurred in variegated spots and stripes. *Anartia jatrophae* is an example of a mottled butterfly (DeVries 1987: plate 28). "Disruptive" characterized butterflies with intermittent blotches of two or more colors, creating many distinct lines that functioned to break up the butterfly's entire outline. Disruptive also included those species with one bright stripe, often white, running across the wing that also functioned to break up the outline. *Siproeta stelenes biplagiata* is an example of a disruptive butterfly (DeVries 1987: plate 28). "Solid" characterized butterflies that had no patterning, and those we observed were all white or all yellow. The butterflies of the *Eurema* genus exemplify solid butterflies (DeVries 1987: plate 10). Coloration categories were determined by the amount of red and orange color of the butterfly's wings. Butterflies with > 50% red/orange coloration were considered to be a potentially toxic butterfly, and all others with < 50% red/orange were categorized separately. *Euides isabella* is an example of a predominately red/orange colored butterfly (DeVries 1987: plate 31).

Across all three habitats, we observed a total of 21 species (N = 5, 9, and 7 each for disruptive, mottled and solid butterflies respectively; N= 4 and 17 each for red/orange and non red/orange butterflies). We observed one to twelve individuals per species (mean = 5).

Analyses were conducted with JMP 5.0 (SAS 2003) with method EMS (traditional). We used a nested analysis of variance (ANOVA), with species as a random effect nested within pattern and coloration. Tests for pattern and coloration were based upon the number of species in each category that were observed. Statistical inferences from nested ANOVA regarding pattern and coloration were the same as with one-way ANOVAs of species means, but the nested model also provided tests of the extent to which individuals within a species showed repeatable flight pattern. Flight duration and number of turns were log-transformed to correct for heteroscedasticity.

RESULTS

All measured flight patterns were reasonably repeatable within a species; significant effects of species indicated that there was less variance among individuals of the same species than among individuals of different species (Tables 1, 2)

Table 1. Results from nested ANOVAs comparing flight traits among butterfly species with mottled, disruptive, or solid wing pattern.

		Log(time)		Log(turns/s)		Speed		Height	
Source	DF	MS	F	MS	F	MS	F	MS	F
Pattern	2	0.290	2.28	0.754	3.38*	3.494	5.80**	0.625	0.56
Species (pattern)	18	0.165	2.49**	0.318	4.42**	0.734	1.87*	1.589	4.62**
Error	83	0.066		0.072		0.392		0.344	

* P < 0.05, ** P < 0.01

Table 2. Results from nested ANOVAs comparing flight traits among butterfly species with red/orange coloration vs. others.

		Log(time)		Log(turns/s)		Speed		Height	
Source	DF	MS	F	MS	F	MS	F	MS	F
Color	1	0.733	7.03*	0.574	3.59†	1.100	1.67	5.569	8.24**
Species (color)	19	0.190	2.86**	0.360	5.00**	1.269	3.24**	1.435	4.17**
Error	83	0.066		0.072		0.392		0.344	

* P < 0.05, ** P < 0.01, † P = 0.0655 (marginally significant)

Flight duration

Flight duration did not vary across pattern, but did vary with red/orange coloration (Table 1, 2); red/orange butterflies had longer-flight duration that non red/orange butterflies (Fig. 1).

Turning frequency

Disruptive butterflies had significantly fewer turns per second than mottled and solid butterflies (Fig. 4, Table 1). Red/orange butterflies showed fewer (marginally significant: P = 0.065) turns per second than non red/orange butterflies (Fig. 2, Table 2).

Speed

Disruptive butterflies flew significantly slower that mottled and solid butterflies (Fig. 5, Table 1). Speed did not vary with coloration (Table 2).

Height

Height of flight did not vary with pattern, but did vary with red/orange coloration (Table 1, 2); red/orange butterflies flew significantly higher than non red/orange butterflies (Fig. 3).

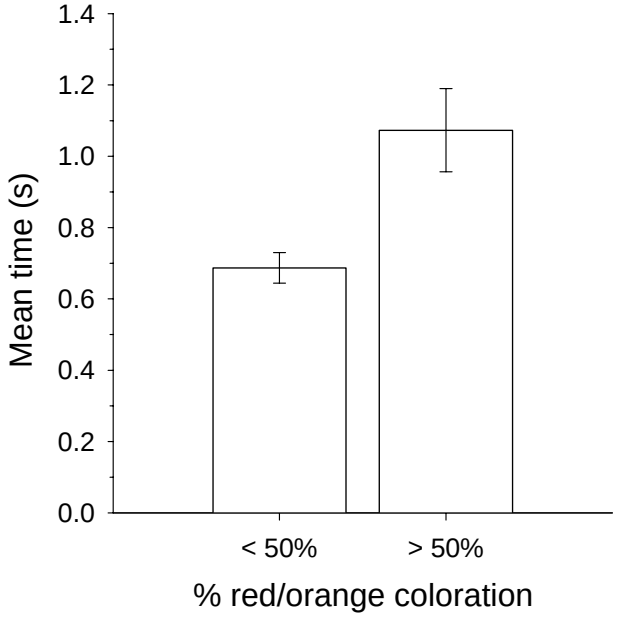

Figure 1. Flight duration of butterfly morphospecies with different coloration. Bars show means ± S.E, calculated from species means.

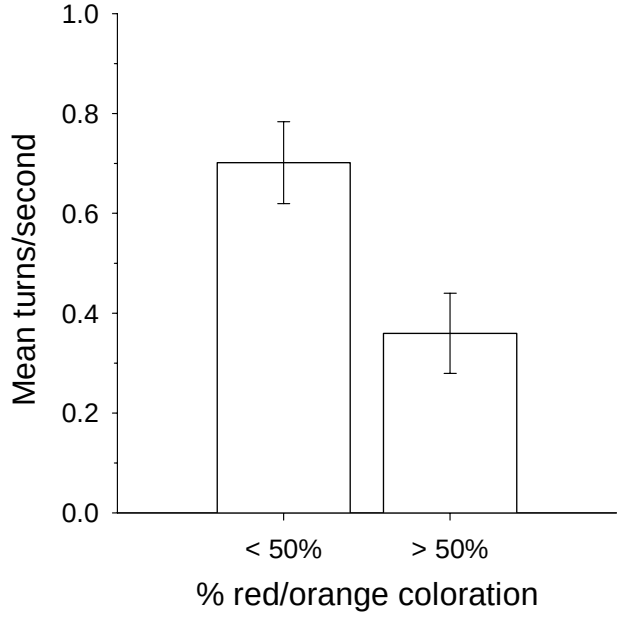

Figure 2. Turning frequency of butterfly morphospecies with different coloration. Bars show means ± S.E, calculated from species means.

DISCUSSION

Our analysis of butterfly flight pattern showed differences in measured flight traits among butterflies of different patterns and coloration. This suggests that butterflies lacking both camouflage and bright coloration rely more on evasive flight as a defense strategy, although not every flight trait measured showed significant differences.

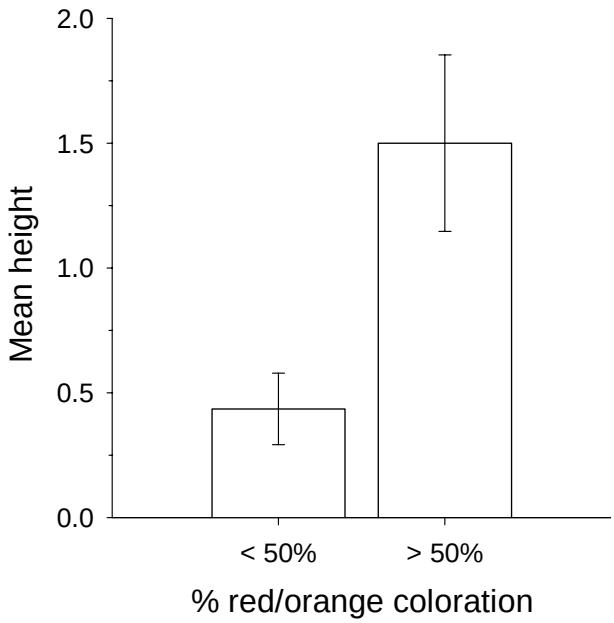

Figure 3. Mean height of flight of butterfly morphospecies with different coloration. Bars show means ± S.E, calculated from species means.

Disruptive butterflies tend to fly straighter and slower that mottled and solid butterflies. The camouflage of disruptive butterflies may be most effective in flight. As a disruptive butterfly flaps its wings, its outline can flash in and out of visibility, causing a predator to easily lose sight of its potential prey. Thus, fast, evasive flight has probably not evolved in this butterfly. In contrast, mottled butterflies may benefit more from landing and blending into the background. When in flight, the mottled butterfly may be just as visible as the solid butterfly lacking patterning, thus explaining their fast, evasive flight. Like mottled butterflies, solid butterflies have fast, evasive flight. These butterflies may rely on flight as an escape method because they lack any form of camouflage.

Butterflies with > 50% red/orange coloration had higher flight durations, lower turning

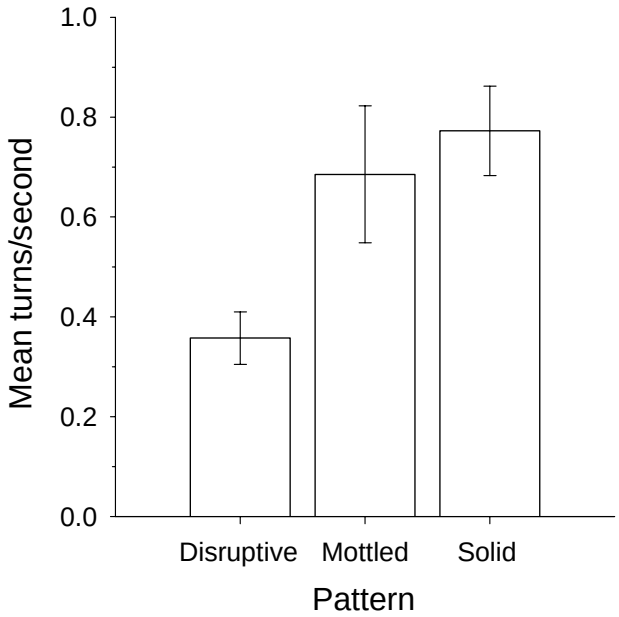

Figure 4. Turns per unit time of butterfly morphospecies with different wing pattern types. Bars show means ± S.E, calculated from species means.

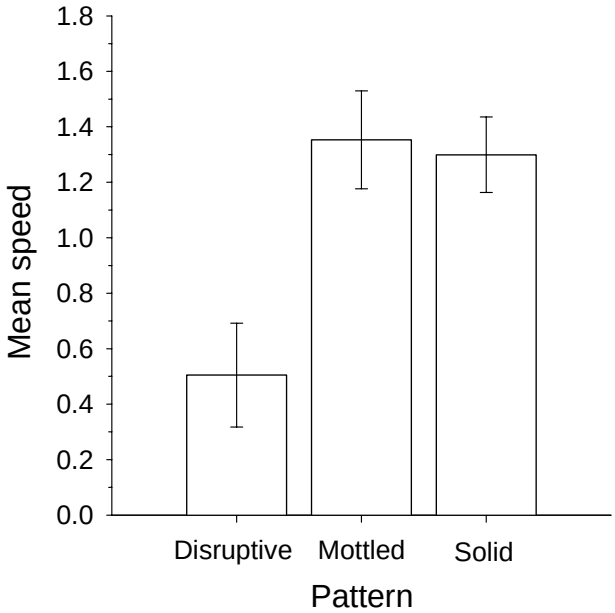

Figure 5. Relative speed of butterfly morphospecies with different wing pattern types. Bars show means ± S.E, calculated from species means.

frequency, and a relatively high level of flight. If these butterflies contain chemical defenses, they might not need to use flight as a mechanism of predator evasion. In fact, a direct, long, high flight should function to more effectively display warning coloration to a predator.

The camouflage of mottled and disruptive butterflies may be indicative of crypsis, a defense strategy that causes predators to lose sight or become confused about the location of the potential prey (DeVries 1987, Sbordoni 1998, Janzen 1983). The coloration of red/orange butterflies may be indicative of aposematism, a defense strategy where chemical defense is advertised with a brightly colored warning (DeVries 1987). Numerous studies show that crypsis and aposematism are effective forms of defense in many types of organisms, with butterflies being commonly cited examples (Begon et al. 1990). Thus butterflies lacking both crypsis and aposematism would logically have evolved other forms of defense. Our study suggests this alternate form of defense may be evasive flight.

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