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Does Brightness Mean Warning Colouration in Butterfly Wings?

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Butterflies (Lepidoptera: Rhopalocera) are a monophyletic group that has departed from the usual habit of its order in two outstanding ways. While most moths are nocturnal, with drab, cryptic colouration, butterflies are mainly diurnal and conspicuously colourful as adults. Barcant (1970) recorded 617 species of butterflies from the island of Trinidad, West Indies.

It is well documented that unpalatable and poisonous animals tend to have bright, contrasting colouration (Edmunds 1974; Owen 1982; Wickler 1968), a phenomenon known from some butterflies (e.g. Berenbaum 1993; Scoble 1995). But is warning colouration a general factor in the variable brightness of butterfly wings? We present here a test of this association.

This test was suggested by Larsen's (1983) notes on relative palatability (to himself) of eight butterfly species from Ethiopia and Madagascar. He reported that more strikingly coloured species tended to be more unpalatable, "in accord with *a priori* expectations."

We collected a sample of butterflies in fields in central Trinidad. The few that appeared excessively worn were discarded. Butterflies were immobilized by thorax pinching and preserved by freezing. The 51 individual butterflies represented 18 species from four families (Table 1).

On the day of the test, we thawed the butterflies and laid them on a medium-brown board intended to represent a neutral background. Each species was ranked on a scale of 0-4 for contrast of the wings above and below against the background, in which 4 was maximum contrast. As seen in Table 1, in most species the upper side was ranked as more contrasting than the lower side.

We then formed ourselves into two groups. Group 1, out of sight of Group 2, removed the wings from each numbered butterfly and macerated the body. The two groups then reassembled, and members of Group 2 tasted all of the butterflies — between one and six individuals per species — in a single-blind test. Each butterfly was raised on a fresh toothpick and tasted for 30 seconds (except as noted below), at the end of which it was ranked on a scale of 0-5, as follows:

0 slightly pleasant or tasteless.
1 innocuous or only weakly distasteful.
2 noticeably distasteful.
3 very definitely distasteful, usually bitter.
4 extremely distasteful, so that it required fortitude to retain it in the mouth for 30 sec.
5 so strongly distasteful that the experimenter could not bear to retain it for 30 sec.

Table 1. Contrast and palatability scores of Trinidad butterflies. The classification follows Scoble (1995). Palatability scores are for individual butterflies. Brower and Brower (1964) treated congeners of the asterisked species in their experimental study.

	Contrast		Palatability					
	Above	Below						
Hesperiidae								
Astraptes anaphus	0	1	1					
Pyrgus oileus	1	1	0	1				
Nymphalidae: Acraeinae								
Actinote pellenea	2	1	0	2	4			
Nymphalidae: Brassolinae								
Caligo teucer	2	3	0	1	2	4		
Nymphalidae: Danainae								
**Danaus plexippus*	3	3	1	2	3	3	4	
**Danaus eresimus*	3	1	3	4				
Nymphalidae: Heliconiinae								
Dione juno	3	2	0					
Dryas julia	3	2	3	4	5			
Euides aliphera	3	1	2	2				
**Heliconius doris*	4	3	3					
**Heliconius erato*	4	3	4	4	4			
Nymphalidae: Nymphalinae								
**Anartia jatrophae*	2	1	0	1	1	1	2	4
**Biblis hyperia*	4	2	1	2	2	2		
Junonia genoveva	2	1	0	3				
Janatella leucodesma	1	1	0	2	2			
Nymphalidae: Satyrinae								
**Euptychia* prob. *renata*	0	0	2	5				
Papilionidae								
Papilio anchisiades	4	3	4					
**Parides anchises*	4	3	4	4				
Pieridae								
Eurema venusta	3	3	0	0	1	1		

This scale was intended to match that used by Larsen (1983). In order to ensure some degree of calibration among experimenters, we first each tasted the most abundant species, *Anartia amathea*, and assigned it a palatability rank of 1. This species was not included in the main test. Our results are given in Table 1.

The data plainly do not support a simple association, in which more contrastingly coloured butterflies are consistently more distasteful. However, there is a significant positive correlation of unpalatability with both upper-side contrast (Spearman's rank correlation, $r = 0.32$, $p < 0.05$) and lower-side contrast ($r = 0.49$, $p < 0.01$).

A key assumption of this test is that humans rank butterflies for distastefulness much as do their natural predators, presumably mostly birds and lizards. This assumption gains support from Brower & Brower's (1964) experimental study, in which individuals of 10 Trinidad butterfly species were offered to North American blue jays, *Cyanocitta cristata*. This robust generalist predator can be regarded as an analogue of the kiskadee, *Pitangus sulphuratus*. Among the genera treated in the present study, the blue jays ate more than half of the *Anartia*, *Biblis* and *Euptychia* offered, but very few of the *Danaus*, *Heliconius* or *Parides*. As seen in Table 1, human tasters found members of the first group of genera on average far more palatable than those of the second group.

The palatability scores show considerable within-species variation. Of the 10 species which three or more individuals tasted, only two received identical scores from all individuals. Some of this is likely due to real variation in the composition of conspecific butterflies. In the one species from which he tasted a number of individuals, *Danaus chrysippus*, Larsen (1983) recorded variability much like our results for *D. plexippus*. Within-species variation of this sort is believed to be common in unpalatable butterflies (e.g. Douglas 1986). However, we do not discount the possibility of significant differences in the perception of individual experimenters.

Our results are consistent with the hypothesis of anti-predator warning as a general factor in the variably contrasting colouration of butterfly wings. Although this limited data-set from a single locality cannot serve as a general test, we note that the sample has fair taxonomic breadth. It bears mention that we explicitly disregarded batesian mimicry as a confounding factor. A broader, more finely-focused treatment of this general question would have to take mimicry into account.

It is notable that wing colouration below showed a stronger positive correlation with unpalatability than did colouration above. If such a difference is borne out by broader, more rigorous studies, then the wings would seem to be more completely involved in warning colouration when the butterfly is at rest — at which times the wings are usually closed and only the lower sides are exposed — than when it is in flight. This would make sense if warning colouration is confounded by additional functions, e.g. sexual signaling, when a butterfly flies or sits with its wings opening and closing. Our result can be interpreted in various ways with respect to Owen's (1971) suggestion that the generally duller lower side of the wings provides cryptic colouration.

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