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INTERPRETATION OF WING PATTERN ELEMENTS IN RELATION TO BIRD PREDATION ON ADULT *HYALOPHORA* (SATURNIIDAE)

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ABSTRACT. A large sample of trapped adult males of *Hyalophora euryalus*, *H. columbia gloveri*, and intergrades from a hybrid zone between these taxa were scored for seven categories of wing damage. A total of 6.1% of 471 adults showed wing damage consistent with bird strikes. Among categories of wing damage, a significantly higher frequency of strikes involved the HW discal spot and the apical eye spot. Patterns of wing damage and behavior of adults when threatened were evaluated in the context of formal models of wing markings as anti-predator mechanisms. Discal spots may act to intimidate predators, while apical eye spots may deflect attacks away from the body. Certain markings are highly conserved and concordant with DNA-based saturniid phylogeny.

Additional key words: anti-predator mechanism, defensive behavior, defense mechanism, discal spot, eye spot, silk moth.

Biologists historically have been fascinated with interpreting the adaptive significance of wing patterns in Lepidoptera, and have categorized them as playing a role in mating behavior, crypsis and camouflage, mimicry, or as anti-predator mechanisms (Bates 1863, Blest 1957, Brakefield & Monteiro 2003, Carpenter 1941, Cott 1940, Darwin 1859, Poulton 1890).

Birds are considered important predators of butterflies and of moths at rest during daytime. Observations of bird predation on Lepidoptera in the wild, outside of staged situations, are understandably rare. Experimental evidence is provided in Bowers et al. (1985), the classic work by Kettlewell (1958), Majerus (2009), and Sargent (1973; 1976; 1990). Shapiro (1974; pers. corres.) states, based on extensive field experience, that birds are more likely to attack resting butterflies, especially just after daybreak, than they are likely to take them on the wing.

The adults of many saturniids display conspicuous patterns and markings, including discal spots and apical markings, some of which closely resemble vertebrate eyes. Recently, Howse & Wolfe (2012) illustrated many types of saturniid wing patterns and, as a stimulus for research on the role of wing patterns in defense, offer their interpretation of what natural objects a given marking may resemble in the eyes of a predator. Experimentally demonstrating how a predator perceives a specific wing marking and establishing the true adaptive role of such markings in saturniids and other Lepidoptera is difficult. A scientifically rigorous study requires understanding the physiology of vision in a predator (in contrast to human perception), as well as conducting experiments that reveal the behavior of both predator and prey in the wild (Stevens 2005). This is not a controlled study of this type. Rather, I used an extant series of trapped males to analyze types of wing damage in order to estimate the relative frequency of predator attacks directed toward specific wing pattern elements. I discuss pattern features, such as discal spots and the apical eye spot, in terms of current models of the adaptive role wing pattern elements may play as anti-predator mechanisms.

Methods and Materials

Long series of adult *Hyalophora euryalus* and *H. columbia gloveri* (hereafter *gloveri*) from various geographic populations, including a hybrid zone between them, were amassed over many years in connection with phylogeographic studies (e.g. Collins 1984; 1997). Those males collected in funnel traps, baited with virgin females as a pheromone source, were segregated and examined for wing damage characteristic of bird attacks. The studies of Sargent (1973; 1976; 1990) depict patterns of wing damage, primarily in underwing moths (*Catocala*: Noctuidae), based on observations of bird attacks in the field and with captive birds. Wing damage due to avian predation on butterflies has been characterized by Bowers et al. (1985) and Bowers & Wiernasz (1979). Bird strikes tend to produce characteristic damage, often with straight edges and in some cases V-shaped marks or tears on the wings, typically cutting through one or more wing veins. Underwing moths rest with their wings flattened, the fore wing drawn back over the hind wing, while *Hyalophora* rest butterfly-like, with the wings held vertically. Thus, in comparing the damage seen in *Catocala* to the putative bird strikes on *Hyalophora*, the shape of a bird strike could be expected to be similar in the two moth families but the position of the strike is likely to be different. Birds are hypothesized to be the most likely predator responsible for the characteristic damage I observed in my sample set. I attempted to use

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a method of scoring and analysis that is not biased by this prediction, but rather seeks to evaluate if there is a non-random association of damage with respect to wing pattern elements. Damage due to encounters with inanimate objects is unlikely to be disproportionately associated with specific wing markings.

I surveyed all damaged specimens and scored them for seven categories of wing damage: **a** - a missing portion of the fore wing (FW) apex; **b** - a more-or-less rectangular piece torn from the inner margin of the FW and the adjacent costa of the hind wing (HW); **c** - a U- or V-shaped segment torn from the HW outer margin, directed toward, and in some cases touching, the HW discal spot; **d** - a U- or V-shaped segment of the FW outer margin similarly directed toward the FW discal spot; **e** - a hole in, or encompassing, the FW discal spot; **f** - a corresponding hole in the HW discal spot; **g** - a more-or-less rectangular section missing from the HW inner margin including the anal angle (Fig. 1).

Wing damage, often in the form of nearly uniform frayed edges on all four wings, occurs due to wear and tear as a consequence of males seeking "calling" females. This damage is cumulative, so that one can distinguish newly eclosed adult males from those several days old. In captivity males live from 5 to 8 days but judging the exact age of wild-caught males is difficult. Predator strikes may be superimposed on this kind of damage, but in most cases the two can be distinguished, in part from the characteristic shape of bird strikes and also, although deep tears may occur between wing veins in worn specimens, wing veins are usually nearly intact in worn specimens or broken only near their terminus (as typically seen in captive, ovipositing females). Wing damage scores were totaled by category and by taxon and compared for significant difference in frequency by means of χ^2 tests. A null hypothesis of equal probability of a predator strike was assigned to each wing damage category.

RESULTS

The results of the wing damage survey are presented in Table 1. Representative specimens illustrating wing damage by category are shown in Fig. 2. An average of 6.1% of the total of 471 adult males for all species and populations showed wing damage judged to be likely due to bird strikes. Twenty one specimens displayed multiple strikes, with an average of 1.9 strikes per damaged moth (56 total strikes / 29 damaged individuals). Eight moths showed single strikes and of these six were damaged at the FW apex. Predation rates were higher in *euryalus* (8.46%) compared to *gloveri* (4.52%), a suggestive but not significant difference (χ^2 = 2.56, P > 0.10). By its very nature, the hybrid zone population (Monitor Pass, Alpine and Mono Cos., CA) displays a great deal of variation in many wing pattern characters, but the relatively small sample (3/71) could not be statistically analyzed for individual wing damage categories in comparison to the parental taxa.

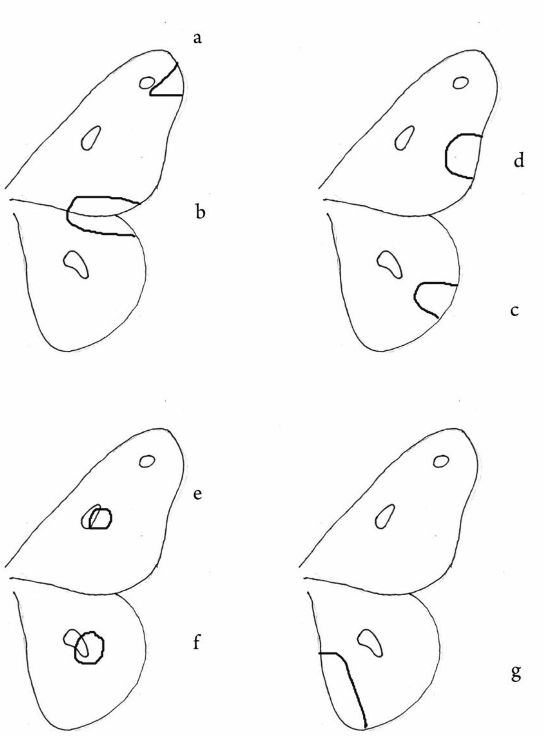

FIG. 1. Wing Damage Categories. Letter designations for categories follows Methods section.

The frequency with which different categories of wing damage were observed was highly significant, based on an assumption of equal probability of a strike for all categories (χ^2 = 19.76, P < 0.005). To address the potential problem of small sample size, especially for the important discal spot categories, the χ^2 was recalculated combining categories **e** and **f**: χ^2 = 11.53, P < 0.05, still a significant difference among categories of wing damage.

Categories **a** (the FW apex where the small "vertebrate eye" spot occurs) and **c** (near the HW discal spot) each comprised 25% of strikes, category **b** (at the junction of the margins of the FW and HW) made up 21.4%. The size and shape of the elongated, comma-shaped, HW discal spot of *euryalus* is significantly different compared to the smaller, kidney-shaped spot in *gloveri* (Collins 1984). However, the rate of attack on the HW discal spot does not differ significantly between the two species, using the combined scores for all categories associated with the HW discal spot (**c** + **f** + **g**) (χ^2 = 3.67, P > 0.90). In considering the role the HW

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FIG. 2. Sample specimens scored for wing damage by category (**a–g**; l = left side, r = right side). (**2-1**) *euryalus* **a, b** –l. CA Alpine Co., Crystal Sp. Cmpgd. 4 June 1978. (**2-2**) *gloveri* **b**-l,r; **d**-r. MT Madison/Gallatin Co. line. hwy 287, 15 June 1983. (**2-3**) *euryalus* **e**-l, **f**-l,r. CA Alpine Co., Carson Cn. 3 June 1979. (**2-4**) *intergrade* **d**-l, **c**-l,r. CA Mono Co., **e** Sonora Pass, 10 June 1979. (**2-5**) *gloveri* **e**-l, **c**-l,r , **b**-r. CA Inyo Co. Death Valley NM, Thorndike Cmpgd. 30 May 1981. (**2-6**) *gloveri* **g**-l. CA Mono Co., Bridgeport. 28 May 1966.

discal spot may play in affecting predator behavior, one damaged *euryalus* specimen is particularly noteworthy; this male (Fig. 2–3; scored for both **e** and **f** categories) displayed neat holes in three of the four discal spots, precisely centered in the spot, presumably from bird pecks and likely the result of a single attack. Such multiple occurrences of damage, of a shape unlikely to be caused by wear and tear and in such close association with specific wing pattern features, strongly supports the interpretation of avian predation directed toward such features.

DISCUSSION

An inherent complication in a forensic study of this kind is that predation on the two test subjects—*euryalus* and *gloveri*—is occurring not in a single controlled environment but in separate biological realms (essentially Sierra/Cascade vs. Great Basin and Rocky Mt.), which differ in many key elements, such as plant community types, species of predator, their abundance, and their predatory behavior. In considering the higher predation rate for *euryalus* compared to *gloveri*, and especially should future work find that

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TABLE 1. Wing damage scores of trapped *Hyalophora* males by damage category.

Taxon	Locality	Wing Damage Category							# ♂♂ Damaged	Total ♂♂ Scored	% Damaged
		A	B	C	D	E	F	G			
H. c. gloveri	Rocky Mts.	2	4	1	1	1	1	0	5	130	3.85
H. c. gloveri	CA e slope Sierra Nevada	3	0	1	1	0	0	1	4	69	5.8
	Subtotal	5	4	2	2	1	1	1	9	199	4.52
Intergrades	CA Monitor Pass Alpine/Mono Co.	2	2	2	1	0	0	1	3	71	4.23
H. euryalus	CA Sierra Nevada	2	1	3	1	0	0	0	5	82	6.10
	CA Alpine Co. Ebbett's Pass-Markleeville	5	5	7	2	2	3	1	12	119	10.10
	Subtotal	7	6	10	3	2	3	1	17	201	8.46
Total		14	12	14	6	3	4	3	29	471	6.1
Expected		8	8	8	8	8	8	8			
% of 56 total, all categories		25.0	21.4	25.0	10.7	5.4	7.1	5.4			

difference to be statistically significant, it is important to remember that the frequency of recovery of wing-damaged moths cannot be extrapolated directly to survival rates. Either *gloveri* or *euryalus* might suffer significantly more attacks, but better survive such encounters compared to the other species.

Quantifying wing damage due to predation is inevitably somewhat subjective and subject to several sources of error, including: (1) missed scores due to extensively frayed wings, (2) frayed wings mistakenly scored as damaged by predator attack, (3) damage attributed to birds but actually due to other predators, such as bats, rodents, or lizards, and (4) missing certain strikes that were obscured by subsequent damage suffered during multiple strikes. Nevertheless, the results demonstrate that predators (probably birds) appear to direct their attacks primarily toward the discal spots and the apical eyespot, even though we cannot know for sure how a given bird species perceives and discriminates a given element as part of the entire wing pattern in *Hyalophora*.

Behavior of Hyalophora with respect to predation. Adults of *Hyalophora* rest with their wings folded dorsally, with the HW largely obscuring the FW. While brightly colored on the upper surface, the undersurface wing color is drab–dull reddish brown to dark brown in *euryalus* and dull grey to nearly black in *gloveri*, with white scales giving a salt-and-pepper effect, especially in *gloveri* (Collins 2007, pl. 12; Tuskes et al. 1996). The "ecological image" of resting *Hyalophora* is much more similar among all taxa than that seen in the upper wing surfaces. The upper surface color in *euryalus* ranges from a bright red to reddish brown; that in *gloveri* is a bright wine-red to dark red or burgundy. The small subspecies *H. columbia columbia* from the Great Lakes region is significantly darker, in some specimens the upper surfaces are nearly black.

My observations of western *Hyalophora* closely parallel that of Evans (1978) for *H. cecropia*. If disturbed during the day adults quickly open their wings and slowly fan them rhythmically open and closed. This response may be triggered even in response to nearby motion. Resting adults cannot fly immediately but must first vibrate their wings at high frequency but small amplitude in a "shivering" behavior. Such behavior raises wing muscle temperature to a minimum required for flight, the duration of shivering dependent on ambient temperature (Hannegan & Heath 1970, Heinrich 1981, Tuskes et al. 1996). Males may disperse at dusk, but their mating flight occurs from about 0300 until dawn. Females remain inactive until mated and then begin their oviposition flight the following night.

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As is typical of most saturniids, *Hyalophora* populations occur at low density, widely dispersed, and usually over a range of plant communities (Ferguson 1971, Tuskes et al. 1996). This population structure, in conjunction with their relatively short life spans, would appear to minimize the likelihood that birds or other predators could form a search image or otherwise concentrate their search for prey on saturniids such as *Hyalophora*. The behavior of *Hyalophora* adults in relation to predation can thus be summarized as follows. Adults resting during the day are more-or-less cryptic or at least inconspicuous. If disturbed during the day they first display their upper wing surfaces; both the large discal spots and the apical eyespot are presented, the former set off against a reddish background and the latter set maximally apart at the wing tips. Display behavior and wing markings are thus closely integrated aspects of an anti-predator defense mechanism. If attacked by a bird it seems likely that an adult would be able to fly only if the attack was somehow delayed or prolonged and ineffective. Presumably the majority of trapped adults bearing what appear to be bird strikes were discovered during the day while at rest and survived by either deflecting the attack away from their bodies or by intimidating their attacker.

Little information is available to judge the ability of adults taking flight during the day to survive bird attacks. I have several times released adult *Hyalophora euryalus* and *Antheraea polyphemus* (which possess very large, eye-like HW discal spots) and provoked them into flight during the day. Invariably, they flew some distance until out of sight, and the *polyphemus* adults especially flew well up into the crowns of large oaks (in an oak-mixed conifer forest of the western Sierra Nevada). Although I did not keep exact records, about half of perhaps ten releases for both species resulted in vigorous attacks by Steller's jays (*Cyanocitta stelleri*), which in all cases quickly killed and consumed the moths after perching on a nearby branch.

Nocturnal flight in *Hyalophora* must minimize exposure of both sexes to bird predation, and the early morning flight of males may avoid the period of peak activity of bats (Collins 2007). Predation by rodents or other mammalian predators on resting saturniids at night, outside periods of mate-seeking or oviposition, is largely unstudied. The defensive value of wing patterns at night must be ineffective or at least greatly reduced.

Interpretation of the defensive role of wing pattern elements. The defensive value of wing markings in *Hyalophora* can be discussed in the context of two general and formal models of anti-predator mechanism in Lepidoptera: intimidation of the potential predator and deflection of attack away from the body (Stevens 2005). Intimidation by wing markings in Lepidoptera is most often discussed in connection with markings that resemble vertebrate eyes. In this study, the apical marking near the FW apex resembling a vertebrate eye (category **a**) shared first place with the HW discal spot (category **c**) as the wing pattern element most often attacked. In the intimidation model a predator perceives specific markings, usually displayed in pairs, as belonging to an enemy, which causes the predator to either flee or delay attack. Markings other than eye-like features may also intimidate a predator because they are conspicuous, either in their novel appearance (inducing neophobia) or because they are suddenly displayed, eliciting a startle response. These two qualities are only subtly different, but the former may be represented by the oval discal spots in *Hyalophora*, displayed against a brightly-colored, contrasting background, and the latter has been exemplified by the flash of HW color in underwing moths, normally camouflaged at rest (Sargent 1973).

The apical markings in saturniids, including those in *Hyalophora*, closely resemble vertebrate eyes and appear to fit the criteria of a signal that produces deflection in attack. They occur at a maximum distance from body, and a strike directed at the apical spot would deflect the attack away from the vulnerable body region. These markings could also be seen as a threat to the predator, especially in conjunction with waving motion of the wings. Discal spots in *Hyalophora* are conspicuous, novel features highlighted by the brightly colored upper wing surface. Endler (1992) and Blest (1957) discuss the effect of background in highlighting eyespots and other such markings; either reflective light-colored areas or dark, brightly-colored patches surrounding the spot amplify its intimidation or startling effect. In this regard, it is interesting to note that the small but detailed discal eye spots on *Saturnia mendocino* and *S. walterorum* fit this model. Those on the dark brown FW (cryptic against the bark of their host plant manzanita (*Arctostaphylos* spp.) are often surrounded by white patches, while those on the HW are set in a yellow background. The HWs are covered at rest, and revealed when the moths are disturbed. Discal spots in *Hyalophora* may function either to deflect an attack (they somewhat resemble vertebrate eyes), or as novel, conspicuous images, set against a bright background, they may intimidate a predator. Again, the motion of the wings may amplify the defensive effect of discal spots.

Category **b** attacks, directed toward the inner margin of the FW and the adjacent costa of the HW, are not consistent with an attack on a moth at rest. An attack on a resting moth, with wings held together vertically

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would tend to produce characteristic paired symmetrical wing damage. Interpretation of this category of damage is uncertain; it could represent an attack generally directed toward the discal spots, or as a somewhat random strike, or as a strike missing an intended target due to the motion of the wings during displaying behavior or while the moth was in flight.

The damage seen in *Hyalophora*—often with somewhat ragged edges—differs from the neatly defined cuts, and V-shaped bill imprints typically seen in other Lepidoptera (e.g. Sargent 1973, Shapiro 1974, Stevens 2005). Could this be due partly to the large size and therefore perhaps tougher wings of this and similar saturniids? Large size in itself might intimidate predators, and it would be worthwhile to assay the family to determine if a correlation exists between types of wing markings (e.g. discal spots, eyespots, bright coloration) and size of adult. Evans (1978) reported that captive catbirds refused to eat live *H. cecropia*, although these and other bird species readily ate the smaller *Callosamia promethea*. Since Waldbauer and Sternburg, in their extensive ecological studies of *H. cecropia* at the University of Illinois, often observed bird predation on cecropia (in litt., pers. com.), it seems likely that large size in itself may have intimidated the catbirds. I have often witnessed jays, robins and other bird species feeding at dawn on *Hyalophora* spp. attracted to lights. Such attacks cannot be directly extrapolated into speculation on predation in nature (the moths are in an unnatural setting, and birds quickly learn to exploit such situations), but there is no evidence, either from formal studies (Evans 1978) or from anecdotal observation, that adult *Hyalophora* are in any way distasteful or toxic.

Tough wings, resistant to tearing during bird strikes, might allow escape following attack. On the other hand, a weaker wing in the region of the apical spot might minimize damage to the apex during defected attacks. Hill and Vaca (2004) found that the wings of *Pierella astyoche* (Erichson, 1849), which possesses wing margin marks thought to produce deflection in bird attacks, had thinner, more easily torn wings in comparison to congeners lacking such markings. Wing strength in saturniids should be measured in a comparison of species with or without conspicuous eye spots, and for different regions of the wings.

Ability of wing-damaged males to respond to calling females. No quantitative mark-release-recapture studies were conducted, but examination of the males bearing evidence of bird strikes reveals several that were severely damaged but still able to locate and fly into traps baited with calling females. In order to be trapped a male must follow a pheromone trail upwind, locate the general location of the trap, and then precisely locate the caged, calling female, and upon touching the metal funnel fall into the trap. Of the total of 29 males scored as attacked, 6 (including *euryalus*, *gloveri* and hybrids) either had at least 50% of one wing removed, or about 50% of total wing area (FW and HW) removed from one side. Of these, two were missing nearly the entire HW on one side (as in Fig. 2–5).

Brief remarks regarding wing pattern elements and the phylogeny of attacine Saturniidae. The resting posture of *Hyalophora*, with the wings held vertically, also occurs in the closely related genus *Callosamia*, whose species—although more cryptically colored, especially in females—share with *Hyalophora* the small vertebrate-like eye spot at the wing apex and also fan their wings to display wing markings. The other New World attacine genera, *Rothschildia* and *Eupackardia*, rest with their wings opened horizontally, and their apical spots do not as closely resemble a vertebrate eye. In the Old World, the adults of *Samia* and *Epiphora* possess an apical eyespot nearly identical to that in *Hyalophora*. In a phylogenetic study of the Saturniidae, Regier et al. (2002) place *Epiphora* as ancestral to the clade containing *Samia*, *Callosamia*, and *Hyalophora*, indicating that the expression of a vertebrate eye-like apical spot may be concordant with a DNA-based phylogeny, and that the apical spot appears evolutionarily conservative (although its role in defense may be more labile).

CONCLUSION

In conclusion, wing damage consistent with that hypothesized to be caused by bird strikes occurred more often in *H. euryalus* (8.46%) than in *H. columbia gloveri* (4.52%), averaging 6.1% in a total of 471 specimens (collected with funnel traps). Damage differed significantly in frequency among seven standardized categories of wing damage. Damage to the FW apex, HW discal spot area, and the area of overlap of the FW inner margin and HW costa occurred in approximately equal frequencies, comprising together about 71% of total attacks. The location and appearance of the apical spot and wing-waving display behavior of threatened moths, all support the hypothesis that the vertebrate eye-like apical spot functions to deflect attacks away from the body. The HW discal spot, set in a brightly-colored background, may function as an intimidation or startle image. The relatively large size of *Hyalophora* adults, in keeping with a trend for large size among Saturniidae, may bolster the effectiveness of specific wing markings in defense. This hypothesis should be investigated, as well as the tear strength of saturniid wings as a measure of their ability to withstand

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attack and retain flight capability. The apical eye spot and certain other saturniid wing pattern elements appear to be evolutionarily conservative and concordant with DNA-based phylogenies, suggesting that they are of significant adaptive value, probably as anti-predator mechanisms.

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