TROPICAL LEPIDOPTERA, 12(1-2): 1-15 (2004)

# IS APOSEMATISM A VALID CONCEPT IN PREDATOR-PREY RELATIONSHIPS BETWEEN BIRDS AND BUTTERFLIES? A DIFFERENT POINT OF VIEW

**LUKA KASSAROV**[1]

Florida State Collection of Arthropods, DPI, FDACS, P.O.Box 147100, Gainesville, Florida, 32614-7100, USA

ABSTRACT.– The concept of aposematism, especially in regard to butterflies, is discussed in terms of the close interrelationship between butterflies, as prey, and birds, as their predators, in their common environment. Vision, in a broad sense, and especially in terms of the visual capabilities of the avian eye, is discussed as a basis for understanding the difference between the aerial hawker insectivorous bird predators of butterflies, and all other birds, regardless of whether considered primarily insectivorous or not. The marked differences in foraging behavior determine how a bird perceives the bright color patterns of butterflies. For aposematic color patterns to be effective, they have to be seen by the bird as an optical device advertising distasteful or toxic qualities of the potential prey so that the predator avoids them by sight. It is argued here that birds that prey on butterflies do not perceive them as an aposematic insect, as postulated by the concept of aposematism. The bird does not reject a butterfly on the basis of color pattern, but on the basis of characteristic morphological and behavioral patterns which provide the bird with a signal as to whether the butterfly is energetically profitable or unprofitable for the bird as a food source.

KEY WORDS: *Agraulis*, *Agrias*, *Anaea*, aposematic butterflies, aposematic coloration, aposematism, Arctiidae, Aves, avian visual system, *Battus*, behavior, cardenolides, Cerambycidae, Coccinellidae, Coleoptera, color patterns, cryptic coloration, Danainae, *Delias*, *Dismorphia*, flight patterns, foraging behavior, Heliconiinae, *Heliconius*, Hemiptera, hostplants, Hymenoptera, insectivorous birds, Ithomiinae, *Mechanitis*, *Neruda*, Nymphalidae, Papilionidae, *Papilio*, *Parides*, Pieridae, *Pieris*, Rhopalocera, toxicity, *Tyria*, vision.

Darwin (1839, 1859), in his theory of evolution and origin of species, argued that butterflies use their colorful patterns for mate selection. He was, however, puzzled that some of their "sexless embryos" also exhibited a colorful pattern which seemed "maladaptive, for they habitually display themselves openly, catching the eye of every passing bird." He found the answer in Wallace's (1867) hypothesis, that conspicuously colored caterpillars were protected by having a nauseous taste, but, "distastefulness alone would be insufficient to protect a caterpillar, unless there were some outward signals to indicate to its would be destroyer that his contemplated prey would prove a disgusting morsel, and so deter him from attack" and that, it "would be highly advantageous to a caterpillar to be consistently recognized as unpalatable by all birds and other animals."

Thus, the concept of aposematism was "born" nearly 135 years ago and is still followed almost unchanged. In the present paper, I dispute the validity of this concept in regard to butterflies and birds as their principal predators. I realize that this paper will be considered heresey by many readers. I also realize that the engine that drives the progress of science runs on rails made of disputed hypotheses, disputed concepts and of tolerance to consideration of different points of view.

## THE CONCEPT OF APOSEMATISM

Wallace's hypothesis still remains the basis of the concept of aposematism. So, for example, "Distastefulness loses a great part of its protective value unless accompanied by coloration or habits which make for conspicuousness and thus advertises the unpleasant qualities of the insect" (Marshall, 1909). By definition, aposematic coloration functions as a "potential avoidance inducing signal to predators" (Matthews, 1977). Aposematic insects signal to potential consumers an objectionable condition arising from the possession of noxious or disagreeable substances (Cott, 1940; Eisner, 1970; Pasteels *et al.*, 1983). "Warning colors (aposematism) are colors and patterns of prey that are adaptive because they signal to predators a potential cost of making an attack." (Mallet and Singer, 1987). Obviously, by definition, aposematic coloration is equivalent to advertising coloration.

The concept of aposematism deals primarily with the interrelationship between insects and their visually hunting vertebrate predators, mainly birds. If advertisement — which is one of the cornerstones of the theory of aposematism — is to be effective, the warning color patterns must be exhibited where they can be seen and will be seen by the bird predator as an advertising optical device. Evidently, aposematic color patterns to be effective have to be perceived by the predator as advertising distasteful or toxic quality of a potential prey, i.e., there must be a strong relation between visual advertisement and visual perception. In fact, the concept of aposematism is based on the proposition that the bird predator perceives the color patterns of an "aposematic butterfly" as advertising its distastefulness. Without this proposition the whole concept falls apart. Evidently, a main question to be answered is: does the bird predator perceive the bright color patterns of a butterfly as advertising in the sense of the theory of aposematism? To find the answer to this question, the problem should be viewed in terms of 1) birds as predators of butterflies, 2) the common natural environment shared by both the bearer of the color patterns and the bird perceiving these patterns, and 3) the visual capability of the avian eye.

For better understanding of avian vision, this author considers a basic knowledge of vision in general as absolutely necessary. This paper focuses, as seen by the title, predominantly on butterflies as examples of aposematic insects.

## BIRDS AS PREDATORS OF BUTTERFLIES: DO ALL INSECTIVOROUS BIRDS PREY ON BUTTERFLIES?

It should be made clear that, despite the fact that birds are considered the main predators of butterflies, the term insectivorous birds does not necessarily mean birds that prey on butterflies. The

---

[1] Research Associate, FSCA. Corresponding address: 130 Spruce Street 28 B, Philadelphia PA 19106, USA.

TABLE 1. Classification of birds as predators of insects according to their foraging behavior.

| **Insectivorous Birds** | | **Granivorous Birds**<br>**Frugivorous Birds** | **Omnivorous Birds** |
|---|---|---|---|
| **Aerial Hawkers*** | **Foliage Gleaners**<br>**Ground Gleaners** | | |
| Prey: insects (incl. butterflies) | Prey: insects and other arthropods; occasionally butterflies | Prey: some insects, but not the primary food; rarely attack flying butterflies | Prey: anything of nutritional value, incl. insects (not butterflies); no particular food preference |

* the main predators of butterflies; do not recognize stationary or dead insects as prey.

problem should be approached from the point of view of their foraging behavior. In this aspect they can be placed in three main categories: 1) primarily insectivorous birds, 2) granivorous and frugivorous birds, and 3) omnivorous birds.

The primarily insectivorous birds have two main ways of foraging: staying in a good spot (perch) and waiting for the prey, an insect, to approach (sit-and-wait strategy), or by actively searching for food. They can be divided into (a) aerial hawkers, which pursue and capture their prey (flying insects) in mid-air (butterflies comprise a significant fraction of their diet, at least part of the year); and (b) birds actively searching their prey, which tends to be relatively immobile and hides within vegetation (foliage- and ground gleaners). Their foraging behavior consists of examining the predominantly underside of branches and leaves for insects which they pick directly from the leaves or making flutterihg sallies after an insect they disturb. Their prey consists mainly of Arachnida, Lepidoptera larvae, Orthoptera, cercopoid and folgoroid Homoptera, Coleoptera, and other arthropods. In fact they are rarely exclusively insectivorous, so that in this group can be placed also many of the granivorous birds (with different degree of granivory) and many frugivorous birds (with different degree of frugivory) as, for example, the large group of tanagers, systematically placed with Thraupinae, whose diet consists of fruits and insects in different proportions, depending on the species (for details see Snow and Snow, 1971). They hunt also insects, especially during the breeding season, for feeding their altritial young a supplement high in protein and fat. The ground (terrestrial) gleaners search for food in decaying foliage, fallen fruits, animals feces, etc. All these birds occasionally attack butterflies, especially flying butterflies (see Chai, 1986). This classification of birds is summarized in Table 1.

The large group of omnivorous birds includes wild birds such as, for example Blue Jay (*Cyanocitta cristata*) and the Florida Scrub Jay (*Aphelocoma coerulescens*) which have been used widely in experiments with butterflies as prey items. It also includes domestic birds such as chickens, pigeon, and many suburban and garden birds, which feed on a large variety of foods, such as seeds, fruits, worms, insect larvae on the ground, different arthropods etc., practically everything that has nutritional value, without special preference to one kind of food type. All these opportunistic "insectivorous" birds very seldom attack butterflies in the field. They are not adapted to catch insects on the wing like the aerial hawkers, which at times, acrobatically pursue evasive prey in flight. Their role in butterfly predation should be considered negligible in comparison to that of the aerial hawker insectivorous birds, which are the real predators of butterflies, in fact, their main predators (see Chai, 1986, 1988; Beccaloni, 1997).

## INTERRELATION BETWEEN PREDATOR AND PREY IN THEIR NATURAL ENVIRONMENT

The only way to understand the interrelation between predators and prey is in terms of their common natural environment. In nature, the mature larva of the swallowtail, *Papilio machaon* Linnaeus (Papilionidae), is cryptic at a distance but aposematic close up (Beddart, 1985; Jarvi, Sillén-Tullberg and Wiklund (1981). The larvae of the cinnabar moth, *Tyria jacobaea* (Linnaeus) (Arctiidae), are cryptic when among the flowers of their host plant *Senecio jacobaea* (Compositae), whereas their yellow and black stripes render the larvae wasp-like and aposematic at close quarters (Windecker, 1939, Rothschild, 1973). For that matter, wasps and other noxious insects can be cryptic when seen at a distance. On the basis of these findings, Jarvi, Sillén-Tullberg and Wiklund (1981) reached the conclusion that "it is not necessary to assume that aposematic coloration is equivalent to advertising coloration which serves to make the presence of its bearer apparent to all nearby potential predators, because it may render an insect simultaneously cryptic and aposematic."

## THE ROLE OF BACKGROUND IN AVIAN PREDATION ON BUTTERFLIES

We should not lose sight of the fact that visual stimuli rarely exist in the absence of a background or surrounding conditions which is why contrast is such an important aspect of detection in the visual world. The interaction between the surrounding and the target can have dramatic effects on the apparent brightness, color or size of the target (see Hodos, 1993). Obviously, the effect of a given type of coloration may depend critically on the background against which it is seen (Baker, 1970). All birds preying on stationary or relatively slow moving insects (group b) see the object from a relatively very close distance against a constant, unchanging and uniformly bright or dark background. The aerial hawker-insectivorous bird, however, sees a flying butterfly against a changing background which may vary widely from moment to moment during flight, i. e., against a background with changing luminance and contrast. What is very important is that the butterfly not only changes its position in space, but also its shape during the process of flaying, flapping the wings with different speed, depending on the species (Fig. 1). As a result, as it will be further discussed, also the luminance and the contrast of the object which the birds has to follow, the flying butterfly, is changing with the changing background. It is obvious that the background against which a bird sees a butterfly, especially a flying butterfly, in nature, differs from that in a cage experiment in every possible aspect.

## THE ROLE OF PREY-TO-BACKGROUND DISTANCE

If the distance from prey to background is less than that from predator to prey, as is the case with foliage gleaners and the ground gleaner, the scale of color pattern should be the same as the background in order to be cryptic. If, however, the predator sees the prey from a distance which is more or less of the same order of magnitude as that of the prey to the background (the case with an

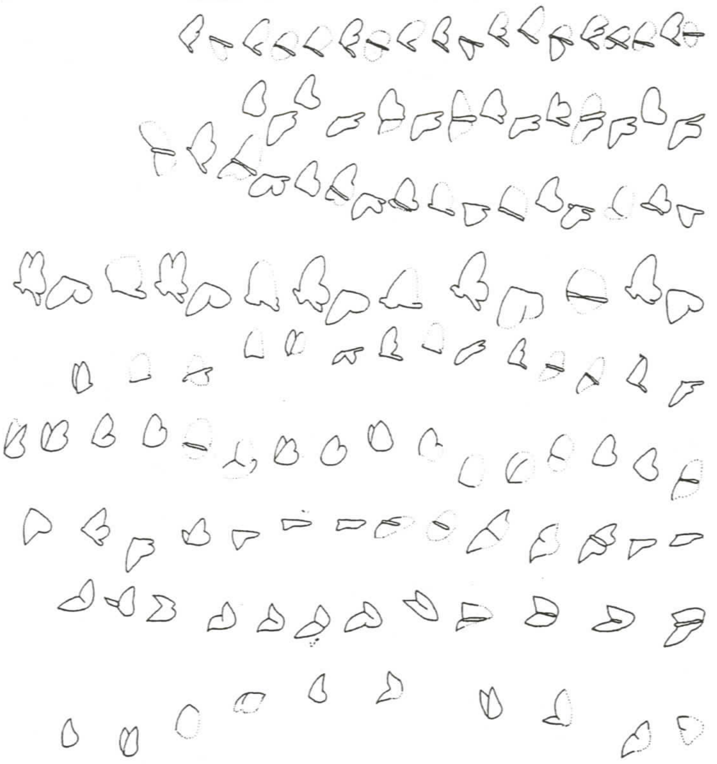

Fig. 1. Examples of flight patterns of 9 species of butterflies arranged according to their relative flight speed. From top: *Mechanitis lysimnia* (32 wing lengths per second (wls)), *Tithorea pinthias* (34 wls), *Heliconius pachinus* (35 wls), *Parides childrenae* (39 wls), *Dismorphia amphiona* (47 wls), *Ascia monuste* (51 wls), *Dryas julia* (53 wls), *Pyrrhogyra neaerea* (71 wls), and *Memphis eurypyla confusa* (89 wls). (from Chai and Srygley, 1990). Note: that "since the tracing simplifies the three-dimensional path into two dimensions and measures positions only every 1/30 second, the actual distance should be longer than the estimate." For details see p. 752 of their paper.

aerial hawker), then the absolute scales (millimeters, etc.) may be different so that they match from the predator's point of view, and the predator sees the prey as more or less cryptic. Thus, the prey may not match the background when seen close to it, but matches the background when seen from a distance (see Endler, 1978, in which the prey-to-background distance is discussed in detail).

## THE ROLE OF DISTANCE AT WHICH THE BIRD VIEWS THE PREY

Contrast sensitivity is usually studied by means of gratings of various spatial frequencies. A grating of bars consists of two elements: the bars and the distance between the bars. As a visual object, the bar can be broken up into its component spatial frequencies. The low spatial frequencies are the ones that allow us to see the overall size and shape of an object, but not its fine details (for the bar the sharpness of the sides and the corners, for the color pattern, the details of the patches as a whole and, the sharpness and shape of the individual elements of the color pattern). Fine details are represented by the high spatial frequencies. Thus low spatial frequencies would let the bird discriminate a butterfly from a leaf of roughly the same size. But they would be inadequate to see the fine details of the wing color pattern or the leaf pattern.

The bars of the grating can be with the same width or the individual bars can be with a different width. The grating can consist of bars with the same frequency or the frequency of the bars can be different, i.e., the distance between the bars can be the same or different. Obviously, because the spatial frequencies depend on the distance, for a grating of bars with equal width and equal distance between them, as the distance from the eye increases, the spaces between the bars in the retinal image of the grating will decrease until finally they fuse. If, however, the width of the bars and the distance between them is different, as the distance from the eye increases, the distance between some of the bars will decrease to a point when they get enough close, or even fuse; they will no more be seen as two separate bars with different width but as only one wider bar. Other bars will still be seen as separate, however, with a more or less reduced distance between them. All this causes a marked steady change of the retinal image of the grating. The same changes, however in reverse, will be observed with decreasing the distance at which the bars are viewed. All these considerations for changes of the retinal image of the grating are valid for an observer changing the distance at which he/she sees a nonmoving (fixed) object. A similar consideration applies to a color pattern of a butterfly consisting of color patches with different colors, different size, shape and different distance between them. The situation becomes more complicated because at a distance the colors will blend in additive mixture. As a result, the aerial hawker insectivorous bird sees a fast changing pattern; it cannot see the color markings bellow a certain size as separate, as for example, the small white or yellow markings of the forewing of many *Heliconius* (Nymphalidae) subspecies or the yellow, orange-brown or brown with different shape, size and length, broken markings of ithomiids. They may blend to match the background (see Schultz and Bernard, 1989). The blending distance decreases as the luminance decreases, which is especially true, as it will be shown, for birds, in contrast to other vertebrates, including mammals. Evidently, "an insect can be cryptic at long distance to the bird, yet be conspicuous for mates" (Endler, 1978, 1991). The example of the cinnabar moth (*Tyria jacobeae*) larvae illustrates this very well.

Depending on the distance at which the color pattern is viewed by the bird, despite the distal stimulus (in our case, the color pattern on the wings of the butterfly) remaining unchanged, the proximal stimulus (the image of the object on the retina) will change. Let us say that the patches of the pattern viewed at 10 m from the eye have a spatial frequency of 10 cycles/degree on the retina; however, seen from a distance of 1m, the spatial frequency of these patches drops to 1 cycle/degree, even though the shape and size of the separate patches of the pattern and the distance between them have not changed. Spatial frequencies (on the retina) too high to be seen at 20m could become quite visible at 5m. Likewise, a spatial frequency of 0.1 cycles/degree which would be too low to be seen at 5m would become visible at 20m. To be more precise, as an example, let us suppose that an aerial hawker insectivorous bird approaches a butterfly from a distance of, let us say, 8m and the butterfly has thick wing bars and also fine bars and tiny flecks. From a distance of 8m, only the thick bars could be seen by the bird. At this distance, the retinal image of the thick bars is so small that they would produce retinal images (the only things that count in vision) that fall in the high spatial frequency range of the bird. At 4 m, the thin bars now can be seen. These thin bars make retinal images that fall in the bird's high spatial frequency range, while the retinal images of the coarse bars now fall in the bird's intermediate frequency range. Finally, at 0.5 m, now even the tiny flecks can be seen because their retinal images have gotten large enough that they fall in the bird's high spatial frequency range. At the same, time, the thin bars are making larger retinal images (lower spatial frequencies) and are now in the intermediate frequency range of the bird while the retinal images of the coarse bars are now so big that they are in the bird's low spatial frequency range and the bird sees only their global properties, such as overall shape and size but no fine details. (Hodos, pers. comm.; see also the subtitle "The visual capability of the avian eye").

The situation becomes most complicated for aerial hawker insectivorous birds catching their prey on the wing. Now we are dealing with a very dynamic form of vision in which, not only is distance changing in a fraction of a second, but also the surround, against which the butterfly is seen is changing rapidly. Finally, the shape of the butterfly changes as it changes its orientation with respect to the observing bird. This causes the luminance, contrast, and retinal image size of the butterfly, as well as its color pattern as a whole to change. This, evidently, has a profound effect on what the bird sees. Because during flight, the position of the wing is changing constantly, the visual angle (the angle separating two points or objects in the visual field which are just distinguishable as separate) also changes constantly (see Fig. 1). This markedly contributes to the inability of the bird to see details in the color pattern of the wing. To complicate the situation further, Mullen (1990) reports that at low spatial frequencies, the color of the object is more important than its luminance. Because of the changing picture, the bird is unable to recognize the pattern; if it cannot recognize the pattern it cannot remember it. That a bird must recognize and remember a color pattern is a prerequisite for the evolution of mimicry, and for birds to be considered the most important selective factor for the evolution of color patterns of butterflies.

The time interval between the initiations of the attack and the forceful impact with the butterfly is very short, lasting only a few seconds. The whole complex of variables changes quickly as the predator closes in. In seconds, a color pattern consisting, for example, of three patches with different size, shape, and color and different distance between them, seen at some distance as a unicolored object (additive mixture) will change very fast to a pattern of two and then to a pattern with three different colored elements. Even if the bird's eye is able to adjust to this fast changing color pattern, in that short period of time, the bird could hardly react and "change" its decision. So, the flight pattern of the butterfly is the first stimulus what the bird sees, not the color pattern. Obviously it is the specific flight pattern which is the decisive factor that determines the decision of the bird to attack or not to attack the butterfly, not the color pattern. For a bird that preys on a stationary prey from a relatively very close distance (foliage gleaners, terrestrial gleaners and most omnivorous birds) this complex of variables does not exist. Evidently, the difference between birds preying on insects on the wing and that of birds preying on stationary prey or slow moving insects, in regard to the way they see the prey, is profound. It is a static versus a very dynamic form of vision in which distance, illumination and size, shape and color pattern of the butterfly change in fractoins of a second.

## ADDITIVE (OPTICAL) MIXTURE

In contrast to a subtractive mixture, in which the color pigments are physically mixed in the object, in additive mixture the colors are separate in the object and are mixed in the eye of the beholder: the color pattern of the butterfly's wing, consisting of small patches of different size, shape and colors, become visually fused (additive mixture) when seen at a distance. An optical mixture gives rise to a much greater lightness of the overall color than the subtractive mixture made of the same components. The result is an overall attenuation of the color; even quite pure and saturated colors when mixed in an optical mixture can result in rather faint colors (see Lanthony, 1997). In general, the additive mixture looks rather light, i.e., at a distance, because of additive mixture; the colored butterfly will be seen as a whole with a lighter color than it actually is (if the brightness of the surround remains unchanged, Hodos, pers. comm).

The role of optical mixture and spatial frequency in vision is well demonstrated in the paintings of Seurat (1859-1891), the formost painter of the school known as "Neoimpressionism." The main technique used by Seurat and other neoimpressionists was pointillism, a term referring to the little dots that were the basis of his pictorial method. When one is close to the canvas, the spatial frequency of the dots is low and one perceives a texture surface made of spots, a grain with various hues, saturation, and lightness. These spots appear in vivid colors and the whole painting gives the impression of a multicolored area; the colored dots are perceived as discrete objects. But Seurat's paintings were not intended for such a close examination. When the viewer walks back and views the picture at a distance from the canvas, the spatial frequency on the dots is high and one no longer sees colored spots but only larger surfaces of rather uniform color with some shaded granulation: both colors and dots blend imperceptibly. This is the range of spatial frequency in which optical mixture is complete. Thus, because the spatial frequency vary with distance, when the colors are near in hue and lightness (as in Ithomiinae, Nymphalidae), they blend easily, even at a short distance. A big difference in hues (some Heliconiinae, Nymphalidae) makes optical mixture more difficult; a greater distance is necessary for a complete optical mixture. Depending on the observed painting, one's eye can be in the range of contrast, dissociation, assimilation, or optical mixture (for details, excellent figures and examples, see Lanthony, 1997). A further complexity of color perception is the fact that the ability to see colors depends in part on size of the colored objects being viewed. Contrast sensitivity is the capacity of the eye to discriminate two juxtaposed (placed side by side) stimuli according to differences (i.e., contrast) in hue, saturation, or lightness. Optical mixture can be considered the reverse of contrast sensitivity, as it diminishes the viewer's capacity to discriminate between juxtaposed stimuli of different size, shape and color (Lanthony, 1997).

## BRIGHTNESS CONTRAST

Brightness contrast is an important example of visual interaction. "The brightness of a visual area is lowered by increasing the brightness of nearby areas, and conversely. Thus a small area of moderate light intensity may appear white when it is present on a dark background. With sufficiently brilliant surround, the original white object may even be transformed to a black" (Purdy, 1935). This is because the eye judges the ratio of light coming from the object and the light coming from the background to decide what is bright and what is dark. The retina analyzes whether an object is lighter or darker that another. A lighter background makes a gray object appear dark by contrast, while a dark background makes it appear light. Because visual acuity is the capacity to discriminate the fine details of the object in the field of view (Riggs, 1965), the visual acuity of an observer, including an avian observer, will be affected by a number of stimulus parameters, such as the luminance, contrast, or color (Hodos *et al.*, 1976; Hodos and Liebowitz, 1977; Hodos, 1993) For example, the acuity of the observer (in our case the bird), declines as a function of target luminance (Hodos *et al.*, 1976). The finer the details, the greater the contrast to render it visible (Weale, 1997). This is especially important, as will be shown, for the vision of birds.

Brightness perception depends on the assumption that the object and the background are in the same illumination (Goldstein, 1984). This is the situation of the foliage gleaners or terrestrial feeders when they see a non-moving or slowly crawling insect which still remains in the same illumination as that of the practically unchanged background, for example, a nonmoving insect seen by the bird on a leaf. The bird perceives a nonchanging color pattern of the insect. The aerial hawker insectivorous bird, however, sees the moving object (a flying butterfly) against a background with changing illumination; i.e., the object and the background are not only in different illumination, but the illumination of the background is changing more or less rapidly, depending on the speed with which the object is moving. As a result, the bird perceives the color pattern of the butterfly in a different illumination: the brightness of the different colors of the pattern changes from one moment to other. That is, as mentioned above, a bright element of the color pattern seen against a very well illuminated background (sun patch) can become a dark even black and dark colored element of the color pattern seen against a darker background can become a bright one. As a result, the color pattern of an aposematic butterfly appears different at different points in space, which practically renders the butterfly cryptic. The detailed pattern of the complex stimuli can no longer be discerned by the eye, i.e., the aerial hawker bird cannot recognize specific details of the color pattern of the flying butterfly and therefore is, which is most important, not able to remember specific color pattern. In the following paragraphs, it will be shown that for the aerial hawker insectivorous bird, the problem is far more complicated.

## THE ROLE OF MOVEMENT OF THE WINGS IN FLIGHT

The moving of the wings during flight by itself changes constantly the shape and size of the wing and what is more important, also the luminance, the contrast. The bird sees the color pattern of the flying butterfly from different angles because the shape of the moving wing changes constantly, even at times, the color pattern on one side of the wing fully disappears and only the color pattern of the other side remains exposed, passing through an intermediate position (the wings are open, then they start to close, they close and start opening again). The unique figure in Chai and Srygley (1990), which I present in this paper (Fig. 1), demonstrates this perfectly. The brightness of the wings changes with the change of the luminance. All of that causes the spatial frequencies of the wings as a whole, and that of their color markings, to change continuously during the flight, so that the high spatial frequencies loose their detectability for the bird. Thus with increasing distance, the observer will no longer be able to resolve accurately the fine details of the object. It sees not only an additive mixture of the color pattern but also a composite image of the wings (the bird sees the butterfly passing through different size and shape). Unchanged, however remains the flight pattern of the butterfly (slow vs. fast, straight vs. erratic, evasive vs. nonevasive, fluttering vs. nonfluttering). It is not so for a bird preying on relatively stationary insects. It is not so also in cage experiments with dead butterflies placed, practically, under the beak of the bird.

## THE ROLE OF FLICKER FUSION FREQUENCY

If a colored object is moving sufficiently rapidly so that the travel of the color patch elements across the visual field of the observer is more rapid than the flicker fusion frequency, then the patches will not be perceived as separate and will blend together. For example, the very conspicuous black, red and yellow colors of coral snakes during their escape movement blend to an additive dark brown color, so that the snake becomes unicolored, mimicking the leaf litter (see Cott, 1940; Pough, 1976; Jackson *et al.*, 1976). The role of flicker fusion in bird's perception of a flying butterfly is questionable. The flicker fusion threshold in human is about 30 Hz. Birds, however, have a fusion threshold of 100-120 Hz., so that what fuses for our eye may still be quite discrete for the bird's eye (Hodos, pers. comm.). Flicker fusion may, probably, play a role in the bird's perception of very fast flying insects as some Hymenotera, Diptera and Coleoptera.

## VISUAL PERCEPTION OF THE PREY BY INSECTIVOROUS BIRDS

Thus the hunting method and foraging behavior (search and capture) of the birds belonging to the different groups (see Table 1) is very different, based mainly on the fact that they visually perceive their prey differently. A *Coccinella* beetle (*Coccinellidae*), an example of a whole family of aposematic insects (Cott, 1940; Pasteels *et al.*, 1983) is seen by a foliage gleaner insectivorous bird at a close distance on a fairly constant background, for example, on a leaf, as an insect with its bright color patterns, red or yellow, contrasting on a green or brown background. The same *Coccinella*, however, when flying with raised elytrae exposing also the black body and seen against a background of varied masses of light, shade and shadow, becomes a uniformly dark object (cryptic) for an aerial insectivorous bird hunting insects on the wing. Evidently, an aerial hawker insectivorous bird cannot perceive a flying *Coccinella* as an aposematic insect. This is valid for other Coleoptera, regardless of color patterns, when on the wing.

Every entomologist collecting flying Coleoptera with an insect net knows, by experience, that the flying insect is, most probably, a beetle, but is not able to determine its color pattern. From the flight pattern he can recognize, for example, that most probably it belongs to the family Cerambycidae, but still cannot recognize the color pattern. He is able to see the pattern only when the insect lies motionless in the net. This is valid also for Hymenoptera, Hemiptera and other flying insects. For an omnivorous bird, or a foliage gleaner, stinging Hymenoptera which are not flying are highly "aposematic" and rejected by an experienced bird by sight. Bumblebees, honeybees and wasps are known to be eaten by fly-catchers, bee-catchers and other aerial hawker insectivorous birds when flying (see Cott, 1940; Davis, 1977). Their colors of bright yellow and black stripes are not perceived as aposematic by these birds. The encounter between the bird and the fast flying insect is quick, and if the insect is small, it is swallowed before the bird reaches the perch, i. e., before the bird is able to recognize whether the prey is aposematic or not. What is a bright color pattern for a ground feeding bird becomes a cryptic color pattern for an aerial insectivorous bird in the environment and habitat in which it hunts. What is, for us, an "advertising" color pattern of a butterfly seen in the drawer in a butterfly collection, can become cryptic for the aerial hawker insectivorous bird in its natural environment and habitat. If a coloration is not perceived as aposematic by aerial hawkers insectivorous birds, which are the main predators of butterflies in their adult stage of life, the term "aposematic butterfly" becomes a misconception. If the aerial hawker insectivorous bird avoids the butterfly, it is not because it is warned by the color pattern of the prey that it is facing a distasteful or toxic prey. Evidently, it is not the bright, so called "aposematic", color pattern that enables the bird to differentiate, for example, between a *Heliconius melpomene melpomene* (Linnaeus) and a non-aposematic *Agrias sardanapalus* Bates ssp. which have the same coloration of the wings but it is their different flight behavior.

Smith (1974), Endler (1978, 1988), and Guilford and Dawkins (1987) argue that a conspicuous color pattern may be detected from a longer distance sooner than a cryptic color pattern. A longer distance between detection of the prey gives the predator more time to decide whether to attack or not to attack, leads to fewer mistakes, and reduces the energy expenditure which increases the predator's foraging efficiency. No doubt, they are right, but for an aerial hawker insectivorous bird, this will be true only if the conspicuous coloration is perceived as aposematic at a long distance. If not, the supposed aposematic color pattern looses its alleged protective properties. Also lost is the supposed advantage which the bearer of the aposematic coloration theoretically gains. A *Heliconius* or ithomiine are easily recognizable from a distance by the bird predator not because of their color patterns, but, as it will be argued, because the bird recognizes their common flight pattern, their characteristic slow, deliberate, fluttery flight.

## THE VISUAL CAPABILITY OF THE AVIAN EYE

Of all the vertebrate classes, birds are the most vision dependent. Many aspects of their adaptation to the environment and their survival depends on precise, and sometimes quite subtle, visual discrimination. (Hodos, 1993). The avian visual system is highly complex, with tetrachromacy complicated by a number of intra-retinal color filters. It is now clear that a number of bird species process 4 to 5 visual pigments maximally sensitive to different regions of the spectrum, in contrast to humans, which process only three pigments. In addition, up to five differently colored oil droplets may be present in the cone photoreceptors, each associated with different visual pigments to give perhaps as many as nine different types of photoreceptors which suggest that the avian color vision has a richness beyond our appreciation (Bowmaker, 1986). Also, the presence of UV vision in birds was found by Huth and Burkhardt, 1972; Wright, 1972; reviewed in Bennet and Cuthill, 1994). This is based on a visual pigment with a maximum sensitivity at about 350 nm. The spectral sensitivity of the passerine bird, the red-billed *Leiotrix* (Peking robin), *Leiotrix lutea* (Muscicapidae) was found to be highest in the UV (Burkhardt and Maier, 1989). The high sensitivity in the UV indicates that UV plays an important role in visually guided behavior of birds (see the elegant paper of Bennett, Cuthill and Norris, 1994). This assumption is supported by the finding that, in addition to the reflectance in the "visible" range of the spectrum, many fruits and feathers exhibit a considerable UV reflectance (Burkhardt and Maier, 1989; Burkhardt, 1989). We should realize that different feathers that look fairly similar to man almost certainly look different to a bird. Furthermore, some birds might be sexually dimorphic in UV patterns, similar to some butterflies (Burkhardt, 1989; Bennet, Cuthill and Norris, 1994).

In addition to their ability to detect small differences in the size of stimuli, birds are excellent at the detection of the fine details of stimuli. Such ability is known as visual acuity (the ability to detect fine details against a high contrast background, such as the small block letters on this white page). The visual acuity of a pigeon is approximately 12.7 cycles/deg, which would correspond to human acuity on the Snellen eye chart of approximately 20/50. This corresponds well with the values reported by Fite *et al.* (1975) for blue jays, and by Blough (1971) for the acuity of pigeons, when they were viewing distant targets. In practical terms, this means that in good illumination the pigeon could just barely detect a seed with a width of 0.3mm at a distance of 50cm. Excellent as the pigeon's visual acuity is, however, it does not rival that of predatory birds such as hawks and eagles, which is better than that of pigeons by at least an order of magnitude (Fox *et al.*, 1976; Hodos, 1993).

Visual acuity tells us about a bird's or a person's ability to resolve small differences between objects that have high contrast. There is, however, more to vision than visual acuity. For example, an image, such as a square, a separate bar or the individual markings of the wing pattern of a butterfly, consists of low spatial-frequency components that give us information about global properties of the stimulus such as overall shape and size. They also contain high spatial frequency components that tell us about the small details, such as, for example, the sharpness of the corners and edges of the square. High-frequency filtering of the optical image of the square would thus round the corners of the square and make its edges blurry. Visual acuity only tells us how the visual or optical system handles the fine details; high contrast is required to see these fine details. It tells us nothing about the ability to detect the low-frequency or intermediate frequencies properties of stimuli.

Contrast is the difference between the darkest and lightest parts of an image, expressed as percentage of the total luminance. A major difference between the contrast sensitivity of birds and mammals is that birds require considerably more contrast at their optimal frequencies than do mammals. The optimal spatial frequency for any species is that spatial frequency at which they require the least contrast to detect the object. The peak pigeon contrast sensitivity was found to be approximately 14, which corresponds to about 7 % contrast. The falcon's peak sensitivity was 28 (3.6% contrast). The humans, however peaked at about 150, which equals 0.7% contrast. Peak sensitivities of humans, and mammals in general, are in the contrast sensitivity range of 100-200 (see Fig. 4.1 in Hodos, 1993, 1997). It should be noted that all the above data are for achromatic stimuli. To-date, all studies of contrast sensitivity of birds have used achromatic stimuli, so that we know nothing about avian chromatic sensitivity. Most diurnal falconiformes (Falconidae), including falcons, hawks and eagles, have eyes adapted to high resolution spatial vision. Such adaptation allows for high acuity. The attainment of maximum acuity is, as mentioned, highly luminance dependent. The reason it is difficult to see at dusk is that everything is gray with little contrast to help the retina make distinctions (see Marmor, 1997). With decreasing luminance of the object, the visual acuity of birds declines much more rapidly and sharply than in man (Reymond, 1985, 1987; see also Snyder *et al.*, 1977, and Hodos, 1993). Even in moderate illumination, the eagle's visual acuity falls sharply. This is consistent with field observation of their behavior; they actively hunt in bright light and roost soon after sunset (Price-Jones, 1983). Why birds, which have a visual system so highly adapted for virtually every aspect of the visual world, should be so relatively poor at detecting low contrast targets is not clear. Without doubt, birds are well adapted to the high-contrast properties of the visual world. Their weaker ability to detect low-contrast properties of the visual environment may reflect a tradeoff in the optical design of the eye to permit high acuity with relatively small eyes and relatively small pupils. Most of the presentation of the visual capabilities of birds in this paragraph is taken from Hodos (1993), and personal communications with him, which I present in support of my thesis.

## PAPAGEORGIS'S HYPOTHESIS

Papageorgis (1975), in her work on the convergence of color patterns among several coexisting mimicry complexes of neotropical butterflies, approaches the problem in terms of the natural environment which the birds as predators and butterflies as prey share. She pointed out that each mimicry complex has a characteristic color pattern and a different range of height of flight and, accordingly, is seen by a bird predator against a different background of color patterns in the forest. The interplay of light and vegetation in a forest from the floor through the middle layers to the canopy, creates the background against which a butterfly is seen. Because the background changes through vertical levels of the forest, the color patterns give the best blending into the distribution of patches of light and shade at the level in the vegetation at which the butterfly flies, so that each pattern is most effectively cryptic at each appropriate level. She also suggested that the high contrast in the background makes prey capture more difficult because the predator's eyes cannot accommodate rapidly to the differences between the sun flecks and shady patches: a bird predator will have difficulty following an individual insect in and out of sun and shade. In the sun, only the bright parts of the butterfly's pattern would stand out against the background, while, as soon as it passed into shade, the pattern would appear entirely different (see also Thayer, 1909). Obviously, in light of Papageorgis (1975) hypothesis, the color patterns of the supposedly aposematic butterflies in a rainforest are not meant for advertisement but for concealment. They do not attract the attention of predators, but just the opposite: they render the butterflies essentially cryptic in their natural surrounding, i. e. the bright color patterns are not advertising the distastefulness of the insect but are making the butterflies cryptic at the level of vegetation at which they fly.

Evidently, in light of Papageorgis's thesis, the so-called aposematic coloration does not have any abstract warning property (Landing, 1984a). Crypticity does not necessarily imply "dull" coloration (Endler, 1978, 1984; Endler and Lyles, 1989). Papageorgis's thesis is based on accurate field observation without taking into account the visual capabilities of the avian eye. Regardless of this, her conclusions are, in many aspects, correct. For a critical view of her hypothesis, see Mallet and Gilbert (1995). A considerable volume of important very detailed information about the variation in light environments in the forest and the perceived color pattern in animals are included in Endler (1993).

According to Endler (1978): "a brightly colored animal has a double advantage when the sun is shining: crypsis against a bright, colorful background and a rapidly changing contrast when moving in and out of sun flecks. Thus, a brightly colored animal could be cryptic when the sun is shining but visible at other times, unless it hides. If a species is most subject to predation when the forest is sunny, then bright colors should evolve for crypsis, but if visual predation is most intense when it is cloudy, or at dawn and dusk, then the cryptic color patterns should be less colorful and show less contrast. Species of the upper level of the tropical forest (tanagers, orioles, heliconiids, ithomiids) tend to be brightly colored and most active when the sun is shining, but as soon as a cloud passes over, their activity greatly diminishes, or, in the case of many heliconiid and ithomiid butterflies, stops entirely." Endler is correct but I do not agree with his examples and interpretation in support of his view. The activity of Heliconiinae and Ithomiinae does not stop because the factor causing their color patterns to become cryptic is lost when there is no sunshine, and consequently, they become more conspicuous. It is very hard to assume that this is a defensive reaction, that these butterflies "sense" that it is becoming risky to fly. The activity of all diurnal butterflies, with the exception of some very dark-colored satyrids which fly also at dusk, stops regardless of whether they are brightly colored or cryptic. Butterflies need the sun mainly for thermoregulation. The activity of the diurnal birds, however, stops because the attainment of maximum acuity which is necessary for hunting is highly illumination-dependent, and with decreasing illumination, their acuity rapidly and sharply declines. With the decrease of illumination, their hunting ability drops to a level which cannot support their nutritional and energetic needs. They have to reduce their energy expenditure to a minimum. They go to roost and start hunting in the morning when the illumination (and hance the contrast of the object against its shadow) increases and they can rely on their excellent visual acuity. For diurnal birds, the luminosity of the prey is a critical, most important factor. This is especially true for aerial hawker insectivorous birds. A butterfly with a low contrast color pattern, as for example, most satyrids and most ithomiines, especially the clearwings, flying near the ground or in the understory of the forest with dense vegetation, is seen by mammals including man, as a cryptic butterfly against a background with the lowest luminescence in the forest. A bird, especially an aerial hawker insectivorous bird, however, despite its excellent vision, because it has much less contrast sensitivity than mammals, will hardly be able to see the butterfly (Hodos, pers. comm.).

## SHOULD ITHOMIINAE BE CONSIDERED APOSEMATIC BUTTERFLIES?

A prey's color pattern is cryptic if it resembles a random sample of the visual background as perceived by the predator at the time and place at which it is most vulnerable to predation. Color patterns can be regarded as mosaics of patches which vary in size, shape, brightness (relative reflectance) and color (reflectance, spectrum, shape). Therefore an animal is cryptic if the distribution of these four attributes could have been drawn at random from the visual background against which the animal is seen by its most dangerous predators (Endler, 1991). Following this definition, it is disputable whether Ithomiinae, which are considered a classical example of aposematic butterflies, have a bright conspicuous coloration.

The subfamily Ithomiinae comprises about 52 genera with approximately 310 species (Brown and Freitas, 1994; see also Beccaloni, 1997). They can be divided into two groups: 1) with transparent or partially, but still mostly transparent, wings, and 2) with wings totally covered with scales or with only small transparent areas left. The transparent representative of the first group (more than half of the genera of this large subfamily), with the exception of representatives of the Large Yellow Transparent Complex (see Beccaloni, 1997), seen against the background, the surrounding vegetation or dry decaying leaves and dark soil, are almost invisible. Seen against the low vegetation, where they fly, they blend with the dark green foliage, and the white apical band on some of the species appear merely as a flickering sun speck changing its position, resembling a moving gleam of light, but not as a butterfly. Thus, the transparency of their wings renders a great part of these widely considered aposematic butterflies not less cryptic than the dark colored satyrids considered as a classical example of cryptic butterflies. Both fly characteristically low, one, rarely above one, meters above the ground and in the lower vegetation. This part of the forest has the lowest light intensity which increases their crypticity, especially to birds. This habitat is not the preferred hunting ground of aerial insectivorous birds. It is an environment which naturally hinders pursuit and favors escape by providing the butterfly with a shelter in the nearby vegetation. Obviously, the clearwing ithomiines cannot be considered aposematic, but a good example of cryptic butterflies. They are considered cryptic butterflies by many entomologists, e.g., Thyer (1918), Brown (1973) and Mallet and Gilbert, Jr, (1995). Mallet and Singer (1987) consider these ithomiines, however, "not cryptic as there are white and yellow streaks and spots on the wings and bodies". But, does a aerial hawker insectivorous bird see these details in a flying butterfly at a distance?

A significant part of the non-transparent species of Ithomiinae have wings with very subdued, mottled 'tiger' patterns. The markings generally consist of a complicated, broken or irregular undulated outline colored not with bright but more or less dull, pastel yellow or orange, brownish-yellow or brownish-orange, different shades of brown, i.e. with slight degree of contrast in color and tone of the adjacent elements on the black background of the wings. The contrast between the yellow components and that of the brown-orange or brown colors is very reduced, especially because the reduced light intensity of the dark environment near the floor of the forest. This makes them barely visible to an aerial hawker insectivorous bird because its poor ability to detect low contrast targets; especially in flight at a distance, the color patterns are seen more or less as an additive color mixture.

All this gives these ithomiids a camouflaged uniform, resembling that of the special forces of the army, which definitely does not advertise their fighting ability and excellent armament. In fact, only a small part, less than one forth of all genera of Ithomiinae, have brightly colored wing patterns. Evidently, a bird catching its prey on the wing cannot perceive ithomiines as aposematic butterflies. If a flying butterfly is not perceived by its main predator (practically its only predator) as aposematic, how, in this case, ithomiines are generally considered aposematic and given as a classical example for aposematic butterflies? The classification of these typically cryptic butterflies as aposematic remains unexplainable for this author who considers the general classification of ithomiines as aposematic butterflies a misconception, based on the assumption that unpalatable butterflies are warningly colored, i.e., a "distasteful insect should be aposematic". Regardless of whether ithomiines are with or without bright color patterns, they are avoided by bird predators, evidently not on the basis of color pattern but, as it will be argued in the following paragraphs, on the basis of their typical flight pattern.

## THE VISUAL CAPABILITY OF BUTTERFLIES

Crane (1955), experimenting with *Heliconius erato hydara* Hewitson in Trinidad, established conclusively that the visible spectrum for these butterflies and for a number of other genera of butterflies extends from at least the near ultraviolet to at least up to 610 nm. The presence of both red-sensitive and green-sensitive photoreceptors in butterflies provides a functional basis for excellent discrimination between similar orange and yellow colors. The red-absorbing rhodopsin, with a peak at about 610 nm, is by far the visual pigment of greatest lambda-max. for any retinal based visual pigment, vertebrate or invertebrate (Bernard, 1979). Considering that some butterfly eyes also contain receptors sensitive to ultraviolet (Post and Goldsmith, 1969, Bernard 1977; Stavenga *et al.*, 1977), their visible spectrum is the broadest known of any animal, including man (Crane, 1954). Striking ultraviolet patterns occur in butterflies, notably in the family of Pieridae, where sexual dimorphism in some species is barely apparent to us, but pronounced in the ultraviolet. (Post and Goldsmith, 1969). Both sexes of *Pieris rapae* (Linnaeus) (Pieridae) appear white to us, but this species is strongly sexually dimorphic when viewed with the butterfly's vision (Obara, 1970). The sensitivity of these butterflies to ultraviolet light provides the basis for recognition in courtship and social behavior (Eisner et al., 1969). Swihart and Swihart (1970) confirmed Crane's (1954, 1955) findings. Their experiments demonstrated that *Heliconius charithonia* (Linnaeus) clearly sensed the difference between two shades of yellow and that the butterfly appreciated the differences. "Obviously, *H. charithonia* is capable of great precision in wavelength discrimination, particularly in the yellow portion of the spectrum. This *Heliconius* species can be conditioned to select virtually any color in its feeding behavior" (Swihart and Swihart, 1970; Swihart, 1971).

Swihart (1964) found the existence of several neural pathways in *H. erato*, showing that the visual process in this butterfly is apparently highly developed to provide accurate information concerning color, intensity and movement, specifically relevant to the requirements of the organism's behavior pattern. Some experiments (Swihart and Gordon, 1970) suggest that *Heliconius erato* can be also conditioned to select any color in its feeding behavior, and that such adaptability must, indeed, be of considerable importance in this polymorphic *Heliconius* species which in various localities may have a forewing patch that is red, yellow, white or even entirely absent (see Emsley, 1964). The behavioral sensitivity of *H. erato* seems to be related to the development of pathways which select the output from those receptors which transduce information with special biological significance (see Swihart, 1963, 1964). On the basis of observations using the spectral efficiency curves and wing spectral reflectance characteristics of six different butterflies, including three *Heliconius* species (*H. erato*, *H. ricini* (Linnaeus) and *H. sarae* Fabricius) and the more primitive *Agraulis vanillae* (Linnaeus), Swihart (1967) suggested that butterflies possess a neural mechanism which "selects" the output from various receptors in such a manner so as to make the visual system respond maximally to stimulation with colors approximating the wing pigmentation.

## COLOR PATTERNS AS FUNDAMENTAL STIMULI IN MATING AND SOCIAL BEHAVIOR

Crane (1955) presented experimental evidence that female odor(s) alone is not sufficient to inaugurate courtship in *Heliconius erato*. In all butterflies whose mating habits have been examined, optical stimuli are, in all probability, a fundamental component of their mating and social behavior (see Magnus, 1963). Color patterns which are used in species recognition and courtship (species-specific sexual marks) must be as distinct as possible, so that no mistakes are made and courtship proceeds as quickly as possible (Otte, 1974; Brown, 1975). There is no doubt that color patterns are a most important factor to the male in the initial approach toward the female. In the approach-flight, the male is optically stimulated by the color-patterns and movements of the female. The olfactory stimuli play a decisive role in the endstage of the whole process, i.e., in carrying the courtship to completion. The female sexual odor(s) appear to be perceptual to the male not more than a few centimeters from her, and for this reason the male often seeks to make antennal contact with the female while still in flight (Magnus, 1963). If the contact is positive, the courtship will end with copulation. It seems that in butterflies which are supposed to be involved in Mullerian mimicry, the more the overall patterns are cryptic (danaids and most of the ithomiines), the greater the role of olfactory cues for efficient intraspecific communication. It is hardly incidental that Ithomiinae and Danaidae are endowed with far more elaborate scent-disseminating organs than Heliconiinae and the pharmacophagous group of Papilionidae which have distinct, bright, very contrasting and relatively simple color markings.

The great variety of complicated color pattern in closely related species of Ithomiinae and Danaidae make it very difficult for a male to distinguish that a female belongs to the same species. Once a female is located and approached by the male, using visual markers, the male depends more on olfactory cues for species recognition to bring the courtship to successful mating. At short distance the male and the female act in the same way as the moths, that is to say, they react to the intra-specific sexual olfactory stimuli (see Endler, 1978).

In addition to the fundamental role which colors plays in the mating and social behavior in butterflies, they also play an important role, in their feeding behavior. The fact that the visual spectrum of butterflies is one of the broadest known in any animal, including birds, indicates, unequivocally, that color vision plays a most important role in the physiology of butterflies. The fact that butterflies, and birds also, are among the most colorful members in the kingdom of animals indicates, unequivocally, that their color pattern play a most important role in their physiology, but, as I argue, not to protect them from predation.

## SIMILARITY BETWEEN THE VISUAL CAPABILITY OF BIRDS AND BUTTERFLIES

Evidently, there is a very close similarity between birds and butterflies in relation to their visual capability. Both are among the most colorful masterpieces of nature; their visible spectrum is the broadest known in any animal, including man. No doubt, vision and coloration have the same purpose and play the same role in their visually guided behavior, their intra- and interspecific behavior, especially in mating (sexual recognition in courtship), social behavior and feeding. Viewed from a distance the bright coloration of birds blends with the vegetation, especially of high trees (Cott, 1940), and when flying, a bird is seen mostly as a dark object against a bright background or as a monocolored object. Even the markedly contrasting bright red, blue and yellow colors of a flying *Ara ara* (Psittacidae, parrots) cannot be seen from a distance. As prey, their predators are also hawkers (Falconiformes). Their predators see them, in the same way as the aerial hawker insectivorous bird sees a flying butterfly from a distance, as a flying object without to see the details in their color patterns.

## MORPHOLOGIC AND BEHAVIORAL CHARACTERISTICS OF UNPALATABLE AND PALATABLE BUTTERFLIES

The arguments presented in this paper against the concept of aposematism still do not answer the question as to why the supposed aposematic butterflies are avoided by bird predators. To answer this question, the morphology of the butterfly prey and the foraging behavior of birds as predators of butterflies will be discussed.

In general, unpalatable butterflies are characterized by a long body, narrow thorax, elongated wings, fluttering wing beats, and a slow flight in a straight and regular path. Despite that their characteristic flight pattern facilitates a predator bird to pursue and capture them, they are rarely attacked. In contrast, the palatable butterflies have a shorter and stout body, wide thorax, relatively shorter wings, and a fast, evasive, irregular flight. They are, however, the preferred prey for birds, despite the fact that they more easily escape when attacked (Marshall, 1909; Chai, 1986, 1988; Chai and Srygley, 1990; Srygley and Chai, 1990; Srygley, 1994; Pinheiro, 1996). In experiments with jacamars, Chai (1986) found that missed attacks with jacamars accounted for about 40% of all of the observed attacks. The foraging behavior of aerial hawkers of butterflies is contrary to the view of Brower *et al.*, (1960); Edmunds (1974); Davis (1977) and Wourms and Wasserman (1985), that predators attack and consume prey that are relatively easy to capture. This is evidently not valid for aerial hawker insectivorous birds hunting their prey on the wing. The negative correlation found between unpalatability and escape ability is seen as supporting the assumption that these traits evolved in butterflies as alternative strategies to avoid predation by birds, as predicted by many authors (Poulton, 1890; Fisher, 1930; Chai, 1990; Chai and Srygley, 1990; Endler, 1991; Malkolm, 1992; Srygley, 1994). The assumption that a prerequisite for the evolution of aposematic coloration is a negative correlation between the probability of seizure and the degree of aposematic coloration (see Sillen-Tullberg and Bryant, 1983) is logically correct. This assumption, however, should be valid for butterflies only if based on a valid theory: if the theory of aposematism is valid for butterflies as prey and birds as predators. If this assumption is correct, how can we explain why the fast flying butterflies, which are difficult to catch, and, which the bird has less than 60% chance to catch, are those which the bird attacks and eats, and avoids the butterflies with a slow, elaborate regular flight which are easier to catch? The answer will be found in the following paragraphs.

## THE ENERGETIC BALANCE AND HUNGER AS MAIN FACTORS DETERMINING THE SELECTION OF PREY

As mentioned above, palatable butterflies tend to have wider thoraxes. This trait is highly correlated with thoracic mass and especially with thoracic muscle mass (Chai and Srygley, 1990; Srygley, 1994). Palatable butterflies possess massive flight muscles; in fact, most of the thoracic cage is filled with flight muscles for quick take off, acceleration and increased flight speed (see Hockings, 1985; Ellington, 1991). In contrast, unpalatable butterflies and their mimics have a markedly elongated slender thorax, associated with their slow, more regular, not evasive flight, and accordingly, weak flight muscles. The longer and more slender the abdomen of the butterfly, the more the indigestible chitinous cuticle in respect to the digestible (non chitinous) tissue, i.e., the less the nutritional value per body mass, the less the profitability as food. In contrast, the amount of digestible tissue in the shorter and stouter fat abdomen of the palatable butterflies is significantly higher in relation to the chitinous cuticle; accordingly, the higher the nutritional value of the butterfly as food. Obviously, the palatable butterflies with their stout fatty abdomen and wide thorax, practically filled with flight muscles (protein) have a nutritional value many times that of the "unpalatable" butterflies with their elongated, slender abdomen and thin thorax with relatively poor nutrient content. A butterfly with low nutritional value will be avoided by birds, regardless of color pattern and whether it is easy or not easy to catch. It is obviously a question of energetic balance. To pursue such a butterfly will be a waste of energy which a bird cannot afford and therefore, avoids. In nature a bird will spend energy to pursue a prey only if the energetic balance is positive or, if hunger becomes a factor affecting the foraging behavior of the bird. This is a fundamental rule of nature. Of great interest is the observation of Swynnerton (1915a, 1915b, 1919) that a variety of African birds, when hungry, consume unacceptable insects, including danaids and acraeine butterflies, despite being markedly aposematic, *without showing any ill effects*.

In support of my thesis are the experiments performed by Chai (1986) with jacamars (Galbulidae) and by Pinheiro (1996) with Tyrant-flycatchers. Jacamars are one of the most specialized insectivorous birds. In the field, aposematic butterflies, such as *Parides*, Heliconiinae, and Ithomiinae were entirely ignored by the birds. However, in experiments with caged birds deprived of food for 3-4 h before feeding, in order to "keep the birds hungry and responsive" one of the two experimental birds sampled these butterflies "in direct proportion to the time it had been without food". The bird, in two cases, after a long period without food, ate four *Heliconius* within one hour "without any sign of sickness." Evidently, the aposematic advertising coloration and the alleged chemical defense of these butterflies were fully ignored by the bird.

These experiments prove, 1) that, at least for jacamars, there are no chemical compounds in *Heliconius* to provide them with a chemical defense (see Kassarov, 2001) — if there were, the bird would not eat a total of nine *Heliconius* without any signs of sickness or signs of distaste —; 2) in the field jacamars avoid *Heliconius*, not because they are protected by a chemical defense, but for other reasons; and 3) the aposematic coloration does not play the role of warning the bird predator that it faces a distasteful prey as postulated in the concept of aposematism. It was fully ignored by the bird. In experiments in which a mixture of unacceptable and acceptable butterflies was offered to the two birds, the second bird did not attack unacceptable butterflies, as long as acceptable ones were available; the attacks on unacceptable butterflies occur after it had consumed all acceptable ones. This bird sampled proportionately fewer unacceptable butterflies (32% vs. 71%).

## WHY DOES THE FORAGING BEHAVIOR OF CAGED BIRDS DIFFER SO MARKEDLY FROM THAT OF BIRDS UNDER NATURAL CONDITIONS?

Foraging involves energy expenditure in searching for, pursuing, and handling the prey. In the small cage, with prey placed literally under the beak of the bird, there is no waste of energy for hunting; hunting effort is practically eliminated. No time is lost in search of prey, which is supplied at regular intervals by the experimenter, so that the searching time, and then the travel time are reduced to a minimum (in fact, there is no travel time), and the chance for successful hunting (capture) of the prey is dramatically increased. There is no way for the butterfly to escape and no risk for the bird to be predated during the predation sequence. The gain of energy per unit of time invested is increased, practically, to the possible maximum. All this makes the energetic balance for the caged bird positive. In the tropical environment, where food is in abundance and the birds encounter a high insect species diversity, hunger very rarely becomes a decisive factor determining the foraging behavior of the bird. Not so in cage experiments with birds deprived of food to "keep them hungry and responsive", to check their preference of food by giving them only one butterfly as food without any choice of other insects during the experimental trial. Animals will be more selective in their choice when satiated or when food is common, more indiscriminate when starved or when food is scarce (Emlen, 1966). This may well explain why in the wild jacamars frequently ignore passing butterflies that a caged bird readily attacks and consumes, as observed by Chai (1986).

Tyrant-flycatchers (Tyrannidae), comprise one of the largest passerine (perching birds) families in the world, representing approximately 10% of the bird species throughout the Neotropics (Sherry, 1984). They are primarily ( 90%) insectivorous (see Schoener, 1968) and, for many species, attacks on adult Lepidoptera are well documented (e.g. Cook, Brower and Alkock, 1969; Collins and Wattson, 1983; Sherry, 1984; Pinheiro and Martins, 1992; Poulin, Lefebre and McNeil, 1994). Tyrannidae form one of the most diverse bird families in the New World (Schauensee, 1970; Sick, 1993) and vary markedly with respect to prey capture method. Except for *Battus* and three *Parides* (Papilionidae), all other aposematic butterflies, including *Heliconius* and Ithomiinae, were generally eaten by the birds (Pinheiro, 1996). The aposematic concept seems invalid also for the bird species used in his experiments. Characteristic for Tyrannidae is that they swallow the whole butterfly without discarding the wings, whereas jacamars and other more specialized insectivorous birds usually do not eat the wings (Davies, 1977, Pinheiro, 1996) or discard most of the wings (see Chai, 1998). By swallowing the butterfly whole, the handling (processing) time, which can be the longest in the whole process of hunting, and can be very energy consuming, is reduced to a minimum. As a result, the bird also gains time for hunting, thus increasing the total daily available food. By decreasing the cost and increasing the benefit, the energy balance is shifted in a positive direction. The rule of nature remains in force; for the bird to survive, the energy gain during foraging has to be higher than the energy lost. Prey selection depends first and foremost on energy profitability (see Royma's, 1970 profitable hypothesis, also Zach and Falls, 1978, and the review of the Optimal foraging theory by Pike *et al*., 1997).

It is well known that many nectar-feeding insects select a single type of flower thereby directing their effort toward those blossoms which yield the greatest amount of nectar at that particular time. Such behavioral adaptation clearly increases the efficiency of their feeding activity (Grant, 1963). It is safe to assume that, in the same way, many insectivorous birds direct their effort towards those insects that yield the greatest amount of protein and fat at that particular time, which increases their efficiency of feeding activity. During the breeding season, there is a strong natural selection for high fecundity. The breeding success of many birds seems to be limited by the ability of the parents to bring food to their always hungry chicks (Davis and Krebs, 1978). Natural selection has preferred those individuals which produce more offspring than others. Many small passerine birds make as many as 500 feeding visits to the nest per day, feeding flight thus being a major occupation (Norberg, 1981). A parent bird to maximize the amount of food delivered to its young, should fly faster, at the penalty of increased energy expenditure on travel, than the maximal range speed (which involves minimal energy cost per unit distance flown). Regardless of the distance flown, the bird should increase speed as long as the concomitant increment in travel cost can be more than compensated by foraging in the time saved. The bird should, obviously, fly with at least its maximum range speed. If it were to fly slowly, it would not only expend more energy (and have to divert more of the collected food to itself and less food to its chicks), but would also require more time for travel, leaving less time for foraging. The higher the food availability and hence, the rate of energy gain during foraging, the higher the optimal speed during foraging flight (see Norberg, 1981). For details about bird flight energetics, see Pennicuick, 1969, 1975). In nature, energy is not wasted; the energetic balance has to be always positive for life to be sustained. Again, a bird will avoid a butterfly with low nutritional value regardless of color patterns. An insectivorous bird avoids the easy-to-catch *H. erato hydara* or *H. melpomene melpomene* but attacks and eats the difficult-to-catch *Agrias amidon* Hewitson or *A. sardanapalus* ssp. which have very similar color pattern, even more conspicuous than that of the *Heliconius*, but they have a short, stout, fatty abdomen and a wide thorax filled with flight muscles.

## GENERAL DISCUSSION CRITICAL TO THE CONCEPT OF APOSEMATISM AS APPLIED TO BUTTERFLIES

One of the characteristics of butterflies is that they are brightly colored, and some of the most brightly colored are palatable to birds (Chai, 1986). By definition, a bright coloration can be considered aposematic only if it is associated with another property of a butterfly, for example, distastefulness, which it advertises. Following this logic, if a butterfly is not distasteful but has only the bright color component of the definition, i.e., this component not being associated with distastefulness, but with palatability, what is the bright coloration advertising? Evidently, not palatability in the sense of "Here I am. I am tasty. Eat me". The question arises: How does a bird predator recognize that in one case the bright color patterns advertises unpalatability and in another does not, that in one case they are "aposematic", in other they are not "aposematic"? It is logical to assume that, if the bright color pattern are the decisive factor, an experienced bird should avoid all butterflies with similar color pattern or with the same color (monocolored butterflies): this also applies to butterflies which the bird sees as similarly colored due to an additive mixture of colors. It is, obviously, not so! Evidently, the bright conspicuous coloration does not have the assumed by definition advertising properties. It is another characteristic feature of of the butterfly which signals to the predator whether to accept it as palatable or as not palatable. It should be something very characteristic of the butterfly which is easily recognizable from a distance. Otherwise, the bird's foraging ability will be markedly compromised and the bird to satisfy its energy needs has no other choice but to attack every potential prey losing precious energy which it cannot afford, and, no doubt, nature will not allow such an inefficient foraging behavior.

The great majority of diurnal butterflies, with the exception of most satyrids and hesperids, have a typically cryptic underside and a more or less bright colored upperside of their wings. For example, almost all species of the genus *Agrias* surpass *Heliconius* in their bright red, orange and yellow coloration contrasting on the black or bluish background of their wings. Most species of the large genus *Anaea* (divided in many subgenera), with their black on white, orange or yellow on black, orange-red, markedly contrasting scarlet red colors on the upperside, have an underside which matches the background against which they are seen when they rest or feed. Their underside, especially that of *Anaea*, is one of the best known example of crypticity. Evidently, the tendency is crypticity when resting and displaying the bright colored upperside when flying. Why should a butterfly be cryptic when not in danger of being predated by their main predator, the aerial hawker insectivorous birds, and announces its presence just when it is most vulnerable to predation? Since advertising their location is not of advantage but of disadvantage to these palatable (unprotected) butterflies, it is safe to assume that the color patterns they display when flying should also be cryptic. Evolutionary and selective pressures should not act in opposite directions and the tendency should be the development of crypticity not only on the under side but also on the upper side of the wings. This is evidently not the case. Obviously, palatable butterflies displaying conspicuous bright colors when most vulnerable to bird predators is not an incidental phenomenon. Definitely, exposing the bright color patterns during flight serve a special very important function. The color markings are important for the male for initial recognition of a female of the same species as suitable for courting.

If advertising their distastefulness is advantageous for aposematic butterflies, why do some markedly aposematic butterflies have an underside with dull cryptic coloration? For example, *Heliconius erato hydara* Hewitson, *H. erato phyllis* Fabricius *H. melpomene euryades* Boisduval, *H. melpomene melpomene* (Linnaeus), *H. melpomene amandus* Grose-Smith & Kirby and other *Heliconius* subspecies have a scarlet red band on their upper wings contrasting markedly on the black background, but a corresponding, more or less, pale pinkish white band on the underside of the wings which hardly can be considered conspicuous (aposematic). For a male *Heliconius*, however, this pale, pinkish white band strongly reflects all wavelengths including the ultraviolet (see Crane, 1954). Their underside coloration should also show advertising bright colors so that their advertising patterns are not hidden at rest. This is also valid, for *H. astrea* Staudinger, *H. atthis* Doubleday, *H. burneyi* Hübner, *H. ethilla* Godart, *H. himera* Hewitson, etc. which have a markedly different and more or less cryptic underside. The basic concept behind Müllerian mimicry suggests that a protected species and its mimics should benefit by having the same protective warning color patterns on both the upper and underside of the wings. Obviously, the aposematic coloration should best serve the butterfly if both sides of the wings are aposematic. *Heliconius*, which are the most often given example of aposematic butterflies, contradict the generally accepted view that the so called "aposematic" butterflies have brightly colored conspicuous upper- and under-side (Kaye, 1914; Chai, 1986; see Mallet and Singer, 1987) presumably "because predators find a single pattern i.e., one repeated on both wing surfaces, easier to learn than two patterns i.e., a different upperside and underside pattern (see Beccaloni, 1997).

The genus *Delias* (Pieridae) of the Australasian and South-East Asian regions includes over 110 species which have as their host-plant mistletoes (Lorantaceae) growing in the upper level of trees or the canopy (see Landing, 1984b). The Lorantaceae plants contain alkaloids and cardenolides, and larval mistletoe feeding is supposed to confer distasteful and toxic properties to *Delias* butterflies (Rothschild, 1973), many of which are involved in mimicry complexes. Female butterflies typically fly lower than the males, most of the time during the day, looking for the host plant and oviposition. Therefore, in order to locate the female, the visual cue to the male should be on the upperside of the wings. Characteristic for *Delias* is that most of the species have an almost identical upper side of their wings but markedly different and, most often, striking "warning" colored underside. In many habitats in Irian Jaya, mostly along rivers, in an area of less than a few kilometers, one can encounter more than ten different species of this genus with the same size and the same white upperside and markedly "aposematic" colored underside (personal observation). The females of *Delias*, looking for the host plant of this genus, which grows at the upper level of high trees, fly higher than the males. This is the main reason why the female of many *Delias* species are still unknown and females are rare in collections. Obviously, the visual cue to the male for recognition that the female is of the same species, and to avoid spending energy chasing females not belonging to the same species, should be on the underside of the wing. This is exactly the case with most representatives of the genus *Delias*.

An aerial hawker insectivorous bird attempting to catch a flying butterfly must first recognize it as a potential prey. The optimal conditions for a successful attack exist when the butterfly is attacked from above, the predator diving against the prey. The angle of attack should be more than zero degree, the bird viewing the prey from above not against the sunlight or the bright sky (see Landing, 1984b). Evidently, the bright color patterns of *Delias* to be warning should be on the upperside, not on the underside of the wings. This is, however, not the case with most of *Delias* species. If aposematic coloration evolved for advertising the distasteful or toxic properties of butterflies, and advertising these properties is advantageous for the butterflies, the *Delias* butterflies are a good example opposing this view, which, in fact, is the basis on which the aposematic concept rests. Are the bright yellow, orange and red color markings of *Delias* aposematic? Do they warn the bird predators that the bearer of these color markings are distasteful or toxic, according to the classical theory of aposematism? Obviously, no. Definitely the color markings serve a more important physiological or behavioral purpose for these butterflies than to advertise their unpalatability.

Most unpalatable butterflies are, evidently, very different in morphology and flying patterns from that of the palatable, and this very characteristic difference can be easily noticed from a distance. The close association between color pattern, flight behavior, and body shape found by Chai (1986) and Chai and Srygley (1990), enables the birds, even naïve juveniles, to learn rapidly and to assess visually the palatability of many butterflies. "In most cases when the birds saw a given butterfly, they somehow 'guessed' its palatability. They were only uncertain about a small proportion of the total butterfly morph tested and those they tended to sample." The flight pattern of butterflies, do not signal palatability or unpalatability, distastefulness or edibility as assumed by Chai, (1986); Guilford (1986); Chai and Srygley (1990) Srygley, (1994); it is a morphological feature serving as a reliable signal of whether the potential prey is *energetically* profitable or unprofitable. The bird sees the characteristic flight pattern, before it can observe the color pattern. It is the flight pattern which indicates whether it will be *energetically* profitable for the bird to pursue the approaching butterfly. Thus, discrimination between *energetically profitable* and *energetically nonprofitable* prey increases hunting efficiency. The bird sees *Heliconius* and ithomiines, and their mimics, it will be argued, as one type of prey with similar characteristic morphological and flight pattern.

The marked differences in color markings, especially in genus *Heliconius*, and complicated patterns in Ithomiinae play, I argue, no role in the foraging behavior of an aerial hawker insectivorous bird. This is very well manifested in Bolivia where the zone of intergradation of several *Heliconius* subspecies is several hundreds of kilometers in depth and width, and with an enormous variety of color forms (paper in preparation). As do their parental forms, all *Heliconius* intergrades have bright color patterns. The colors are the same: red, orange, yellow, white on a black background. They differ, more or less, in size or absence of one or more of the colored elements shaping the color pattern as a whole. It is this marked difference in the single color elements which creates the marked polymorphism in the zone and makes the intergrades "aberrant" individuals. Such individuals are, however, supposed to be the least protected in an aposematic complex. Novel warning colored "variants" gain no protection from their colors since predators had no previous encounter and did not learn their color patterns. The rarer morph will suffer proportionally more attacks, due to its lower number. The fitness of a morph is therefore frequency-dependent. This leads to a frequency-dependent disadvantage (Mallet and Singer, 1987). Rare variant forms should be penalized by antiapostatic (negative) frequency-dependent selection (Greenwood, 1984; Endler, 1988), because they have a reduced chance of being recognized as belonging to a class of prey that is already ranked as distasteful (see Guilford, 1992). The intergrades should be at a selective disadvantage, which should lead to their elimination if the birds are not able to recognize the flight pattern, which is common for all of them, their parental subspecies and all the other *Heliconius* species flying together in the zone. Not only is there no selective elimination of the intergrades, but they survive in the zone, and in many areas of the zone more intergrade forms are observed flying than parental forms. (pers.

observ.) and share with them the same protection against bird predators. This is valid also for the intergradation zone in French Guiana (pers. observ.) where, at some localities, parental forms are very rare to find.

It is hard to suppose that the birds in the intergrade zone could ever learn to distinguish and remember all these different color patterns, let alone, single elements in the color patterns. The facts, however, that the birds avoid them, and that they have the same fitness as the parental forms and other *Heliconius* species and subspecies in the zone, suggest that they all wear a common badge which the birds learn to recognize and avoid. Despite the marked variety of color forms; the birds perceive them as one type of prey. The birds exercise "*Gestalt* perception"; they perceive the behavioral patterns of the intergrades as a whole, rather than responding to single elements of the color patterns. All these fascinating, elegant butterflies have markedly elongated wings, a long slender body, and most important, a peculiar slow fluttery flight! By recognition of the flight pattern and not the color pattern by the birds, the zone remains markedly polymorphic and the polymorphism increases, because there is not only interbreeding between intergrade forms and their parental forms, but also interbreeding between the intergrades themselves. Similarly, the birds cannot recognize the complicated color markings of the different species and subspecies of Ithomiinae and their mimics but they all have something in common, their characteristic flight pattern.

Is it an incidental biological phenomenon that the great majority of the considered "aposematic" butterflies belong to two of the largest subfamilies, which members differ from the great majority of Lepidoptera as a whole, mainly by their very characteristic physical and behavioral pattern? Their color patterns differ widely from typically cryptic (the majority of Ithomiinae) to typically "aposematic" (the *Heliconius*). Is it an incidental biological phenomenon that the mimics of *Heliconius* and Ithomiinae have a flight pattern which is similar to that of their models? Members of the subfamily Dismorphiinae, which mimic unpalatable Ithomiinae, have a slow regular flight similar to their models. So, for example, *Dismorphia amphione* (Cramer) most closely resembles the ithomiine *Mechanitis lysimnia* Fabricius (DeVries, 1985) not so much in color pattern but in the slow regular flight. Characteristic for *Parides* is their markedly reduced flight speed which can make them, at times, difficult to differentiate from the *Heliconius* species flying in the same habitat. In contrast, the palatable Papilionidae have a fast, eratic, evasive flight.

The fact that the aerial hawker insectivorous birds hunting on butterflies on the wing are not able to recognize details of the color patterns of their prey, but see only an additive color mixture of these pattern, disputes Beccaloni's (1997) hypothesis that the selection for mimicry between these species must largely taken place when they are in flight. This hypothesis is based on his observation, 1) that although ithomiine and mimic species have similar flight behavior, seemingly large differences were observed to occur between the resting behavior of ithomiines and many species of mimic, and 2) predators of butterflies are species which specialize in on the wing capture of insects.

For the same reason, I do not accept the division of Ithomiinae into 8 discrete complexes (see Beccaloni, 1997). The reason for Beccaloni to argue that these complexes are discrete is the existence of polymorphism between most of them, which he considers as an indirect evidence that their natural predators, like humans, perceive the aposematic patterns of these complexes, to be discrete. "Thus, if we accept that mimetic morphs of a species are adaptive, then their existence can only be explained if the color pattern of each morph is perceived as a discrete signal by predators." If, however, an aerial hawker of butterflies cannot recognize details within the color patterns of flying butterflies, they are not able to remember the pattern, which is a prerequisite for adaptive learning necessary to avoid mimics of distasteful models. For example, the bird is hardly able to differentiate between the color pattern of the Yellow Bar Tiger complex and the Orange and Black Tiger complex. It does not see these complexes as the taxonomist sees them in a collection drawer, at the optimal distance, pinned, nicely spread (non moving) against a nonchanging background, with the best illumination and contrast. Beccaloni's approach is an example of considering perception from the point of view of humans rather than the bird (see also Dittrich et al., 1993). In the best case, they see, the clearwings of Ithomiineae not as separate species or subspecies with distinct color pattern, but as members of a "grand genus" of the subfamily Ithomiinae, and the tiger-patterned members of the subfamily as another "grand genus" (including many genera). They generalize. The aerial hawker insectivorous bird cannot differentiate between a *H. hecale* (Fabricius), a *H. ethilla* or a *H. ismenius* Latreille (the 'tiger' ring) or even between an ithomiid with a size close to that of the mentioned *Heliconius*. For them, all *Heliconius* with dennis and rays belong to one type of prey. They cannot differentiate between a *Heliconius elevatus taraquanus* Bryk and a *H. reductimacula* Bryk, or a "*H. aoede aoede* f. *postalbimaculata* Bryk (now in the genus *Neruda*), a *H. egeria homogena* Bryk, and also a *H. melpomene* from a *H. xantocles* Bates, or a *Neruda*. If they cannot, another most important question arises: can birds, as predators of butterflies, be one of the main factors contributing to the evolution of the wing color patterns of butterflies, a view which is generally assumed and supported (Shepard, 1960; Brower, 1963; Holling, 1963, Kettlewell, 1973; Sargent, 1776; Boyden, 1976 Robbins, 1983; to mention a few)? Brower (1984) considers birds as the principal biotic agent driving evolution of defensive adaptations in adult butterflies. If birds hunting on the wings are unable to recognize the separate elements of a color pattern, how could they contribute to the development of the different color pattern of different species, their subspecies and forms? How could birds be a selective factor? All these considerations, and the many arguments presented in this paper, raise the question of whether the so-called "aposematic" color pattern are, in fact, really mimetic.

All "proofs" that birds can recognize certain points within the color pattern of butterflies were obtained in experiments using numerous species of caged birds (e.g., chickens, pigeons, rollers, blackbirds, hornbills, wood-hoopoes, jays, tits, starlings, grackles, tanagers, sparrows and tyrant flycatchers) (see Chai, 1986, 1998). "Although a taxonomically diverse set of bird species has been tested with inactive butterflies, except for European rollers (*Coracies garullus*) and fork tailed flycatchers (*Muscivora tyrannus*) aerial hawkers of flying insects, all are omnivorous, foliage or ground gleaners, which seldom attack butterflies in the field. The responses of birds to dead or immobilized specimens, were recorded with the implicit assumption that similar responses would be elicited in these and other birds by live prey in nature" (Chai, 1986). Aerial hawkers insectivorous birds consume only winged insects and do not recognize an insects as prey, unless it is moving (see Davies, 1977, Chai, 1986 1988; Chai and Srygley, 1990; Pinheiro, 1996), It is of interest to note that "color and motion are handled separately (at least by the human visual system) and that color provides only a weak 'cue', at best, to movement perception" (Ramachandran and Gregory, 1978). Motion and color are analyzed by separate channels in the visual system (for references see Ramachandran, 1987).

With some exception (e.g., the experiments reported by Chai, 1986, 1988, and Pinheiro, 1996), the prey, consisting of dead insects or artificial "prey", usually pastries made of flour and lard, is placed practically below the beak of the bird, on a simple background, for example, a Petri dish, mono-colored or bi-colored cards without a pattern, or differing in one feature only, mostly a very simple one (black bar, dot(s), double bar, etc.). The conclusions made on the basis of such experimental designs are very speculative and, more or less, misleading (see Chai, 1988). Therefore they cannot, and should not, be extrapolated to the different reality which aerial hawkers face under natural conditions in their environment, and especially, to their foraging behavior. They cannot be extrapolated to butterflies also, especially flying butterflies. An experimental design must be sufficiently realistic to be meaningful.

It is generally accepted that there are two important factors, in addition to predation by birds, which have played a role in the development of the amazingly different butterfly coloration: 1) the divergent advantage of protective (warning or mimetic) coloration over ancestral coloration, and 2) the conservative force of sexual selection (maintaining species recognition by the other sex). The role of the protective coloration as a factor contributing to the evolution of butterfly coloration is disputed in this paper. Indisputable, however, remains the role of sexual selection (again back to Darwin). The fact that the visual spectrum of butterflies is one of the broadest known in any animal, including birds, proves unequivocally that sexual selection is the major force driving the evolution of color patterns in butterflies. The same is true for birds which, as the butterflies have the most sophisticated color vision of any vertebrates, perhaps any animal (Goldsmith, 1990; see Bennett, Cuthill and Norris, 1994). If the aerial hawker insectivorous birds, which are the main predators of adult butterflies, do not perceive their bright conspicuous coloration as a warning signal, the bright coloration of butterflies cannot have a warning function, as required by the concept of aposematism. Back to the title of the paper: Is aposematism a valid concept in predator-prey relationship between birds and butterflies?

## ACKNOWLEDGMENTS

I had the opportunity to consult Dr. William Hodos (Prof. University of Maryland) concerning many aspects of avian vision and vision in general. His help and contributions in presenting this part of the paper dealing with vision are deeply appreciated. I thank Dr. Thomas C. Emmel for careful reading of the manuscript, for suggesting a number of useful improvements, and for his strong encouragement to publish the manuscript. Special thanks also to Dr. Albert G. Moat (Emeritus Prof., Marshall Univ. Sch. Med.) for critical reading and many very helpful suggestions and comments during the preparation of the manuscript.

## LITERATURE CITED

**Amadon, D.**
1944. A preliminary life history study of the Florida Jay, *Cyanocitta c. coerulescens. Amer. Mus. Novit.* (New York), 1252:1-22.

**Baker, R. R.**
1970. Bird predation as a selective pressure on the immature stages of the cabbage butterflies, *Pieris rapae* and *P. brassicae. J. Zool.* (London), 162:43-59.

**Bates H. W.**
1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconiinae. *Trans. Linn. Soc. London*, 23:49 5-655.

**Beddard, F. E.**
1895. *Animal Coloration*. London: Wan Sonnenschein. 288pp.

**Bent, A. C.**
1946. Life history of North American Jays, Crows, and Titmice. *Bull. U. S. Nat. Mus.* (Washington), 191:77-88.

**Bennet, A. T. D., and I. C. Cuthill**
1994. Ultraviolet vision in birds: what is its function? *Vision Res.* (Oxford), 34:1471-1478.

**Bennett A. T. D., I. C. Cuthill, and K. J. Norris**
1994. Sexual selection and the mismeasure of color. *Amer. Nat.* (Lancaster), 144:848-860.

**Bernard, G. D.**
1977. Noninvasive microspectrophotometry of butterfly photoreceptors. *J. Opt. Soc. Amer.* (Washington), 67:1362.
1979. Red-absorbing visual pigment of butterflies. *Science* (Washington), 203:1125-1127.

**Blough, P. M.**
1971. The visual acuity of the pigeon for distant targets. *J. Exp. Anal. Behav.* (Bloomington), 15:57-68.

**Boshouwers, F. M. E. Nicaise**
1992. Responses of broiler chickens to high- frequency and low- frequency fluorescent light. *Brit. Poult. Sci.* (Abingdon), 33:711-717.

**Bowmaker, J. K.**
1986. Avian color vision and the environment. *Acta XIX Intern. Congr. Ornitol. Ottawa*, 1:1284-1294. Canada: Univ. Ottawa Pr.

**Brower, J. V. Z.**
1958. Experimental studies of mimicry in some North American butterflies. Part I. The Monarch, *Danaus plexippus* and Viceroy, *Limenitis archippus. Evol.* (Lancaster), 12:32-47.
1963. Experimental studies and new evidence on the evolution of mimicry in butterflies. *Proc. Int. Cong. Zool. (London)*, 4: 156-161.

**Brower, L. P.**
1984. Chemical defence in butterflies. *Symp. Roy. Ent. Soc. London*, 11: 109-134.

**Brower, L. P., J. V. Z. Brower, and P. W. Westcott**
1960. The reaction of toads (*Bufo terrestris*) to bumblebees (*Bombus americanum*) and their robberfly mimics (*Mallophora bomboides*) with a discussion of aggressive mimicry. *Amer. Nat.* (Lancaster), 94:343-355.

**Brown, K. S., Jr.**
1973. *A Portfolio of Neotropical Lepidopterology*. Rio de Janeiro: Ortag. 28pp.

**Brown, J. L.**
1975. *The Evolution of Behavior*. New York: W. W. Norton. 761pp.

**Burkhardt, D.**
1989. UV vision: a bird's eye view of feathers. *J. Comp. Physiol.* (A) (Berlin), 164:787-796.

**Burkhardt, D., and E. Maier**
1989. The spectral sensitivity of a Passerine bird is highest in the UV. *Naturwissenschaften* (Berlin), 76:82-83.

**Chai, P.**
1986. Field observations and feeding experiments on the responses of rufous-tailed jacamars (*Galbula ruficunda*) to free-flying butterflies in the tropical rainforest. *Biol. J. Linn. Soc. London*, 29:161-189.

**Chai, P,, and R. B. Srygley**
1990. Predation and the flight, morphology, and temperature of Neotropical rainforest butterflies. *Amer. Nat.* (Lancaster), 135:748-765.

**Collins, C. T,, and A. Watson**
1983. Field observations of birds predation on Neotropical moths. *Biotropica* (Washington), 15:53-60.

**Cott, H. B.**
1940. *Adaptive Coloration in Animals*. London: Methuen. 508pp.

**Crane, J.**
1955. Imaginal behavior of a Trinidat butterfly, *Heliconius erato hydara* Hewitson, with special reference to the social use of color. *Zoologica* (New York), 40:167-195.

**Cook L. M,, L. P. Brower, and J. Alcock**
1969. An attempt to verify mimetic advantage in neotropical environment. *Evol.* (Lancaster), 23:339-345.

**Darwin, C. R.**
1839. *Narrative of the Surveying Voyages of His Majesty's Ships Adventure and Beagle, between the Years 1826 and 1836, describing their Examination of the Southern Shores of South America, and the Beagle's Circumnavigation of the Globe. Vol. 3. Journal of Remarks. 1832-1836.* London: H. Colburn. 615pp.
1859. *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London. 458pp.

**Davis, N. B.**
1977. Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): a field study on optimal foraging. *Anim. Behav.* (London), 25:1016-1033.

**Davis, N. B., and J. R. Krebs**
1977. Introduction: Ecology, natural selection and social behavior. *In* J. R.

Krebs and N. B. Davis (eds.), *Behavioral Ecology*, 1-18. Oxford: Blackwell Sci. Pub.

**Edmunds, M.**
1974. *Defence in Animals: a Survey of Anti-Predator Defences*. Longman: Burnt Mill. 357pp.

**Ellington, C. P.**
1991. Limitations on animal flight performance. *J. Exp. Biol.* (Cambridge), 160:71-91.

**Emlen, J. M.**
1966. The role of the time and energy in food preference. *Amer. Nat.* (Lancaster), 100:611-617.

**Emsley, M. G.**
1964. The geographical distribution of the color-pattern components of *Heliconius erato* and *Heliconius melpomene* with genetical evidence for the systematic relationship between the two species. *Zoologica* (New York), 43:245-386.

**Endler, J. A.**
1978. A predator's view of animal color patterns. *In* M. K. Hecht, W. C. Steere and B. Wallace (eds.), *Evolutionary Biology*, 11:319- 364. New York: Plenum Pr.
1984. Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc. London*, 22:187-231.
1991. Interactions between predators and prey. *In* J. R. Krebs and N. B. Davis (eds.), *Behavioral Ecology*, 169-196. Oxford: Blackwell Sci. Publ.
1993. The color of light in forest and its implication. *Ecol. Monog.* (Tempe), 63:1-27.

**Eisner, T., R. E. Sillberglied, D. Aneshansley, J. E. Carrel, and H. C. Howland**
1969. Ultraviolet video-viewing: the television camera as an insect eye. *Science* (Washington), 166:1172-1174.

**Fisher, R. A.**
1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Pr. 272pp.

**Fite, K. V., R. J. Stone, and M. Conley**
1975. Visual acuity in the northern blue jay: behavioral and anatomical correlates. *Neurosci. Abstr.* (Oxford), 1:82.

**Fox, R., S. W. Lehmkuhle, and D. H. Westendorf**
1976. Falcon visual acuity. *Science* (Washington), 192:263-265.

**Goldstein, B.**
1984. *Sensation and Perception*. Belmont, CA: Wadsworth. 481pp.

**Grant, V.**
1963. *The Origins of Adaptations*. New York: Columbia Univ. Pr. 606 pp.

**Guilford, T.**
1986. How do 'warning colours' work? Conspicuousness may reduce recognition errors in experienced predators. *Anim. Behav.* (London), 32:459-467.
1992. Predator psychology and the evolution of prey coloration. *In* M. J. Crawley, *Natural Enemies: the Population Biology of Predators, Parasites and Diseases*, 377-394. Oxford: Blackwell Sci. Publ.

**Hocking, B.**
1958. Insect flight. *Sci. Amer.* (New York), 199:92-98.

**Hodos, W.**
1976. Vision and the visual system: A bird's eye view. *In* J. M. Sprague and A. M. Epstein (eds.), *Progress in Psychology and Psysiological Psychology*, 29-62. New York: Academic Pr.
1993. The visual capabilities of birds. *In* H. P. Zeigler and H.-J. Bishof (eds), *Vision, Brain, and Behavior in Birds*, 63-75. London: MIT Pr.

**Hodos, W., R. S. Leibowitz, and J. C. Bonbright, Jr.**
1976. Near-field visual acuity of pigeons: Effects of head location and stimulus luminance. *J. Exp. Anal. Behav.* (Bloomington), 25:129-141.

**Hodos, W., and R. W. Leibowitz**
1978. Simultaneous brightness contrast induction in pigeons. *Vision Res.* (Oxford), 18:179-181.

**Holling, C. S.**
1963. Mimicry and predator behavior. *Proc. Int. Cong. Zool.* (London), 4:166-173.

**Huth, H. H., and D. Burkhardt**
1972. Der spectrale Sehenbereich eines Violettohr-Kolibris. *Naturwissenschaften* (Berlin), 59:650.

**Ikin, M., and J. R. G. Turner**
1972. Experiments on mimicry: Gestalt perception and the evolution of genetic linkage. *Nature* (London), 239:525-527.

**Jackson, J. F., III, W. Ingram and H. W. Campbel**
1976. The dorsal pigmentation of snakes as an anti-predator strategy: a multivariate approach. *Amer. Nat.* (Lancaster), 110:1029-1053.

**Jarvi, T., B. Sillen-Tullberg, and C. Wiklund**
1981. The cost of being aposematic. An experimental study of predation on larvae of *Papilio machaon* by the great tit *Parus mayor*. *Oikos* (Copenhagen), 36:267-272.

**Kassarov, L.**
2001. Do cyanogenic glycosides and pyrrolizidine alkaloids provide some butterflies with a chemical defense against their bird predators? A different point of view. *Behav.* (London), 138:45-67.

**Kettlewell, H. B. D.**
1973 *The Evolution of Melanism: a Study of a Recurring Necessity*. Oxford: Oxford Univ. 423pp.

**Landing, B. H.**
1984a. Visceral memory-the values to predators of employing this method of "learning" to avoid toxic food items, and the values to prey (butterflies) of exploiting this system. *In* B. H. Landing (ed.), *Factors in the Distribution of Butterfly Color and Behavior Patterns – Selected Aspects*, 107-121. Los Angeles.
1984b. Color pattern and geographic distribution of butterflies whose larvae feed on Mistletoes. *In* B. H. Landing (ed.), *Factors in the Distribution of Butterfly Color and Behavior Patterns – Selected aspects*, 146-168. Los Angeles.

**Lathony, P.**
1997. Optical mixture. Seurat's pointillism. Optical mixture and color texture. *In.* M. F. Marmor and J. G. Ravin, *The Eye of the Artist*, 118-129. New York: M. Mosby.

**Malcolm, S. B.**
1992. Prey defense and predator foraging. *In* M. J. Crawley (ed.), *Natural Enemies: the 14opulation Biology of 14redators, Parasites and Diseases*, 458-475. Oxford: Blackwell Sci. Publ.

**Mallet, J.**
1989. The genetics of warning colour in Peruvian hybrid zones of *Heliconius melpomene*. *Proc. Roy. Soc. London* (B), 236:163-185.

**Mallet, J. L. B., and M C. Singer.**
1987. Individual selection, kin selection, and the shifting balance in the evolution of warning colors; the evidence from butterflies. *Biol. J. Linn. Soc.* (London), 32:337-350.

**Mallet, J., and L. E. Gilbert, Jr.**
1995. Why are there so many mimicry rings? Correlation between habitat, behaviour and mimicry in *Heliconius* butterflies. *Biol. J. Linn. Soc.* (London), 55:159-180.

**Marmor, M. F.**
1997. The eye and art. *In.* M. F. Marmor and J. G. Ravin, *The Eye of the Artist*, 2-25. New York: M. Mosby.

**Marshall, G. A. K.**
1909. Birds as a factor in the production of mimetic resemblances among butterflies. *Trans. Roy. Ent. Soc. London*, 1909(3):329-383.

**Matthews, E. G.**
1977. Signal-based frequency-dependent defense strategies and the evolution of mimicry. *Amer. Natur.* (Lancaster), 111:213-222.

**Norberg, R. A.**
1981. Optimal flight speed in birds when feeding young. *J. Anim. Ecol.* (London), 50:473-477.

**Obara, Y.**
1970. Studies on the mating behaviour of the white cabbage butterfly, *Pieris rapae crucivora* Boisduval. III. Near ultra-violet reflection as the signal of intraspecific communication. *Zeit. Vgl. Physiol.* (Berlin), 69:99-116.

**Otte, D.**
1974. Effects and functions in the evolution of signaling systems. *Ann. Rev. Ecol.* (Palo Alto), 5:385-417.

**Papageorgis, C.**
1975. Mimicry in Neotropical butterflies. *Amer. Sci.* (New Haven), 63: 522-532.

**Pennycuick, C. J.**
1969. The mechanism of bird migration. *Ibis* (London), 111:525-556.
1975. Mechanism of flight. *In* D. S. Farner, J. R. King and K. S. Parkes (eds), *Avian Biology*, 5: 1-75. New York: Acad. Pr.

**Pinheiro, C. E. G.**
1996. Palatability and escaping ability in Neotropical butterflies: tests with wild kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biol. J. Linn.*

*Soc.* (London), 59:351-365.

**Pinheiro, C. E. G., and M. Martins**
1992. Palatability of seven butterfly species (Nymphalidae) to two tyrant-flycatchers in Brazil. *J. Lepid. Soc.* (Los Angeles), 46:77- 79.

**Post, C. T., and T. H. Goldsmith**
1969. Psychological evidence for color receptors in the eye of a butterfly. *Ann. Ent. Soc. Amer.* (Lanham), 62:1497-1498.

**Pough, F. H.**
1976. Multiple cryptic effects of cross-banded and ringed patterns of snakes. *Copeia* (Washington), 4:834-836.

**Poulin, B., G. Lefebre, and R. McNeil**
1994. Diets of land-birds from northeastern Venezuela. *Condor* (Santa Barbara), 96:354-367.

**Poulton, E. B.**
1890. *The Colour of Animals, their Meaning and Use, Especially Considered in the Case of Insects*. London: Kegan, Trench & Trubner. 360pp.

**Price-Jones, D.**
1983. *Australian Birds of Prey*. Doubleday, Australia. 127pp.

**Purdy, D. M.**
1935. Vision. *In* E. G. Boring, H. S. Langfeld and H. P. Weld (eds), *Psychology*, 57-101 New York: J.Wiley.

**Pyke, G. H, H. R Pulliam, and E. R. Charnow**
1977. Optimal foraging: a selective review of theory and tests. *Qtr. Rev. Biol.* (Stony Brook), 52:137-154.

**Ramachandran, V. S.**
1987. Interaction between colour and motion in human vision. *Nature* (London), 328:645-647.

**Ramachandran, V. S., and R. L. Gregory**
1978. Does colour provide an input to human motion perception. *Nature* (London), 275:55-56.

**Reymond, L.**
1985. Spatial visual acuity of the eagle, *Aquila audax*: a behavioural, optical and anatomical investigation. *Vision Res.* (Oxford), 21: 263-271.
1987. Spatial visual acuity of the falcon, *Falco berigora*: a behavioural, optical and anatomical investigation. *Vision Res.* (Oxford), 27: 1859-1874.

**Riggs, L. A.**
1965. Visual acuity. *In* C. H. Graham (ed.), *Visual Perception*, 321-349. New York: J. Wiley.

**Robbins, R. K.**
1981. The lycaenid "false head" hypothesis: Predation and wing pattern variation of lycaenid butterflies. *Amer. Natur.* (Lancaster) 118: 770-775.

**Rothschild, M.**
1973. Insect/plant relationships. *In* H. F. von Emden (ed.), *Symposia Roy. Ent. Soc.*, 6:59-83. London: Halsted Pr.

**Sargent, T. D.**
1973. Studies on the *Catocala* (*Noctuidae*) of Southern New England. IV. *J. Lepid. Soc.* (Los Angeles), 27:175-192.

**Schauensee, R. M. D.**
1970. *A Guide to the Birds of South America*. (Reprinted 1982, by the Academy of Natural Science of Philadelphia). 470pp.

**Schoener, T. W.**
1968. Size of feeding territories among birds. *Ecol.* (New York), 49:123-141.

**Sheppard, P. M.**
1960. *Natural Slection and Heredity*. New York: Harper & Row. 209pp.

**Sherry, T. W.**
1984. Comparative dietary ecology of sympartic, insectivorous neotropical flycatchers (Tyrannidae). *Ecol. Monogr.* (Durham), 54:313-338.

**Sick, H.**
1993. *Birds in Brazil: a Natural History*. Princeton: Princeton Univ. Pr. 703pp.

**Sillén-Tullberg B., and E. H. Bryant**
1983. The evolution of aposematic coloration in distasteful prey: an individual selection model. *Evol.* (London), 37:993-1000.

**Shneider A. W., S. Laughlin, and B. Stavenag**
1977. Information capacity of eyes. *Vision Res.* (Oxford), 17:1163-1175.

**Sprunt, A., Jr.**
1954. *Florida Bird Life*. New York: Coward-McCann Inc., and Nat. Audubon Soc. 527pp.

**Srygley, R. B.**
1994. Locomotor mimicry in butterflies? The association of positions of centers of mass among groups of mimetic, unprofitable prey. *Phil. Trans. Roy. Soc. London* (B), 343:145-155.

**Stavenga, D. G., J. A. J. Numan, J. Tinbergen, and J. W Kuiper**
1977. Insect pupil mechanisms II. Pigment migration in retinal cells of butterflies. *J. Comp. Physiol.* (Berlin), 113:73-93.

**Stephens, D. W., and J. R. Krebs**
1986. *Foraging Theory*. Princeton: Princeton Univ. Pr. 247pp.

**Swihart, C. A.**
1971. Colour discrimination by the butterfly, *Heliconius charitonius* Linn. *Anim. Behav.* (London), 19:156-164.

**Swihart, C. A., and W. C. Gordon**
1971. Red photo receptor on the eyes of butterflies. *Nature* (London), 231:126-127.

**Swihart, C. A., and S. L. Swihart**
1970. Colour selection and learning feeding preferences in the butterfly, *Heliconius charitonius* Linn. *Anim. Behav.* (London), 18:60-64.

**Swihart, S. L.**
1963. The electroretinogram of *Heliconius erato* (Lepidoptera) and its possible relationship to established behavior patterns. *Zoologica* (New York), 48:155-165.
1964. The nature of the electroretinogram of a tropical butterfly. *J. Insect Physiol.* (Oxford), 10:47-562.
1967. Neural adaptations in the visual pathway of certain heliconiine butterflies, and related forms, to variations in wing coloration. *Zoologica* (New York), 52:1-20.

**Swynnerton, C. F. M.**
1915a. Experiments on some carnivorous insects, especially the driver ant *Dorylus*, and with butterflies' eggs as prey. *Trans. Ent. Soc. London*, 1915:317-350.
1915b. Further notes on the eggs of butterflies. *Trans. Ent. Soc. London*, 1915:428-430.
1919. Experiments and observations bearing on the explanation of form and colouring, 1908-1913. Africa. *Zool. J. Linn. Soc. London*, 33: 203-385.

**Thayer, G. H.**
1909. *Concealing-Coloration in the Animal Kingdom: an Exposition of the Laws of Disguise through Color and Patterm: being a Summary of Abott H. Thayer's Discoveries*. New York: MacMillan Co. 260pp.

**Wallace, A. R.**
1867. [Note]. *Proc. Ent. Soc. London*, (3) 5(6):xxxviii-xxxix.

**Weale, R. A.**
1997. Age and art. *In*. M. F. Marmor and J. G. Ravin, *The Eye of the Artist*, 26-35. New York: M. Mosby.

**Windecker, W.**
1939. *Euchelia* (*Hypocrita*) *jacobaea* L. und das Schutztrachtenproblem. *Zeit. Morph. Oecol. Tiere* (Berlin), 35:84-138.

**Wourms, M. K., and F. E. Wasserman**
1985. Prey choice by blue jays based on movement patterns of artificial prey. *Can. J. Zool.* (Ottawa), 63:781-784.

**Wright, A. A.**
1972. Psychometric and psychophysical hue discrimination functions for the pigeon. *Vision Res.* (Oxford), 12:1447-1464.

**Zach, R., and B. Falls**
1978. Prey selection by captive ovenbirds (Aves: Parulidae). *J. Anim. Ecol.* (London), 47:929-943.