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Diversity in structural ultraviolet coloration among female sulphur butterflies (Coliadinae, Pieridae)

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Abstract

In some species of sulphur butterflies (Pieridae: Coliadinae) females as well as males display bright structural reflectance on their dorsal wing surfaces, although comparatively little attention has been paid to this coloration in females. We examined the spectral properties of female dorsal coloration and scale structure in three species of sulphurs for which published images show bright UV reflectance in females: the Neotropical *Anteos clorinde* and two species of Indo-Australian *Eurema*, *E. hecabe* and *E. candida*. In *A. clorinde* and *E. hecabe*, female UV reflectance is iridescent and produced by thin film interference in a system of ridges and lamellae, as it is in conspecific males. Female *A. clorinde* exhibit the same spatial distribution and chromaticity of UV reflectance as seen in males, but the UV reflectance in female *E. hecabe* is much smaller in area compared to that of conspecific males and is both less bright and less chromatic than observed in males. In contrast, UV reflectance in *E. candida* females is diffuse, and arises from a lack of pterin pigments in the wings, which permits a broad-band scattered reflection to be seen. This is the mechanism that is known to produce bright UV reflectance in females of the confamilial whites. Our results highlight the diversity of UV reflectances and underlying mechanisms in sulphurs and suggest multiple evolutionary pathways leading to this diversity in female sulphur butterflies.
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1. Introduction

In many animals, especially birds, fish and butterflies, males display bright colors that are known or suspected to enhance male mating success (Andersson, 1994). Given the costs sometimes associated with producing and bearing conspicuous ornaments, such signals typically do not evolve in females (Andersson, 1994). Yet, there are species in which females bear these color ornaments, and the extent of signal expression can vary inter- and intraspecifically (e.g. Hill, 1993). There are two broad hypotheses for the evolution of bright female coloration. First, the expression of this trait in females could be an incidental and non-functional result of genetic correlations between the sexes. Strong selection for this trait in males and low costs of bearing the trait for females could lead to penetrating genes that express the trait in females (Lande, 1987). Second, the expression of the color in females could be adaptive and enhance fitness either in the context of choice by males (Muma and Weatherhead, 1989; Hill, 1993), avoidance of male harassment by unreceptive females, competitive interactions with other females, or perhaps interactions with predators. The most frequently tested idea has been that female ornamental coloration has adaptive consequences in mating interactions, but supporting results have been mixed (e.g. LeBas and Marshall, 2000; Parn et al., 2005; Hanssen et al., 2006).

When ornamental coloration is present in females, even at a reduced degree compared to the male, one can ask if the color production mechanisms are the same in both sexes. Possessing the same color production mechanisms provides

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support for the proposition of a common underlying genetic architecture—a prerequisite for the genetic correlation hypothesis. The functional hypotheses make no predictions about the similarities of male and female color production mechanisms. Hence, examining the structures that produce colors in females that are exaggerated in males will at least begin to inform our understanding of potential evolutionary paths leading to female expression of these exaggerated colors.

Sulphur butterflies (Pieridae: Coliadinae) present a worthy model group for the study of interspecific variation in female expression of exaggerated male ornamental traits. In a number of coliadine species, males display brilliant ultraviolet (UV) reflectance on the dorsal wing surface that results from dedicated surface nanostructures. This coloration is bright, highly chromatic and typically iridescent. Some female sulphurs also exhibit UV reflectance of a putatively structural provenance, and interspecific variation in female UV reflectance occurs as one of three basic patterns:

(1) Female dorsal wing surfaces reflect little or no UV wavelengths: *Eurema lisa* (Ghiradella et al., 1972; Rutowski, 1977) and many other sulphurs (Silberglied, 1969)
(2) Female dorsal wing surfaces reflect UV wavelengths, but from a smaller area than the male: *Eurema hecabe*, *E. sana*, *E. laeta* (Common and Waterhouse, 1982)
(3) Female dorsal wing surfaces reflect UV wavelengths from a color patch that is similar in size and shape to that of the male: *Eurema candida*, *E. herla* (Common and Waterhouse, 1982), *Anteos clorinde* (Silberglied, 1969)

Our goal in this study was to characterize the structural UV reflectance in both sexes of three coliadines that display different forms and degrees of UV sexual dichromatism. We examined *A. clorinde*, *E. hecabe*, and *E. candida* using three investigative methods. First, we imaged the butterflies in both human visible and UV wavelengths to assess sexual differences in coloration on all wing surfaces. Second, we used scanning electron microscopy (SEM) to examine the architecture of scales from the UV-reflecting wing regions. Specifically we looked for the system of ridges and lamellae on the scales that are known to produce iridescent UV reflectance in other species (e.g., Ghiradella et al., 1972; Ghiradella, 1984; Vukusic et al., 2001). In addition to conducting measurements of lamellar properties for heuristic comparisons among the study species, SEM also permitted us to detect pigment granules that absorb diffuse broad-band scattered light that extends well into the UV (Rutowski et al., 2005).

Finally, we investigated whether the wavelength of maximum reflectance from the UV-reflecting areas varied with incident light angle and angle of view. Hue shift is a definitive property of iridescence produced by thin film interference, where the peak wavelength of reflectance decreases as the angle of incident illumination and viewing increases (Ghiradella et al., 1972). The presence/absence of angle-dependent UV reflectance thus permitted an additional means to evaluate UV color production mechanisms in our study species.

2. Methods

2.1. Specimens

We obtained papered specimens of *Anteos clorinde* (New World tropics) from a commercial supplier. These specimens were relaxed by injecting hot water into the thorax and pinned with wings spread in standard entomological style. Spread museum specimens of *Eurema candida* and *Eurema hecabe* (Indo-Australia region) were obtained on loan from the Natural History Museum of Los Angeles County. Additional *E. hecabe* specimens were collected in the field by one of us (DJK) in the vicinity of Cairns, Queensland, Australia.

2.2. Wing color imaging

We collected two types of images in order to document color pattern on the wings. First, we produced images in the human visible wavelengths (400–700 nm) using a Nikon D70 35-mm digital camera and a ring flash. Second, we made images comprised only of UV wavelengths by illuminating the wings with a fluorescent 'black light'. The output of this light source exhibited a broad energy peak between 300 and 400 nm centered on 350 nm, with virtually no energy at wavelengths longer than 450 nm. For these UV images the camera lens was fitted with a Wratten 18A filter that absorbed wavelengths between 400 and 700 nm. UV iridescence was also explored in a preliminary manner by replacing the 35-mm camera with a Motic CCD video camera fitted with the Wratten 18A filter. The image displayed in a video monitor was observed for substantial changes in UV reflectance intensity while altering the angle of the wing relative to the black light beam.

2.3. Examination of scale morphology

Scales from UV reflecting and non-UV reflecting areas of the dorsal wing surface were collected on the tip of a small paintbrush and placed onto a carbon adhesive disc atop a SEM stub. A new paintbrush was used for each target area of each specimen. Scales were sputter-coated with gold and examined with a Leica-Cambridge Stereoscan 360FE scanning electron microscope with acceleration voltage at 15 kV and probe size between 75 and 90 pA. SEM micrographs were captured with IXRF software at 1028 lines of resolution and saved as TIFF files. Three properties of UV scale morphology were examined from SEM micrographs using Scion Image (Scion Corp.) and ImageTool (University of Texas Health Science Center, San Antonio): (1) the number of lamellae per ridge, (2) lamellar ridge density across the dorsal scale surface, and (3) angle that the lamellae intersected with the plane of the basal lamina. Obtaining lamellar measurements from SEM micrographs typically was limited to scales that were broken, which allowed viewing at an angle that was approximately perpendicular to the plane of the ridges. Unfortunately, scale breakage often results in some scale deformation. Although such deformation has no effect on counts of lamellae

comprising a ridge, it can affect measurements of lamellae insertion angles. Thus, for angle-of-insertion measurements we chose ridges that appeared to be minimally affected by scale breakage distortion.

2.4. Spectrophotometric analysis

Spectrophotometric data were gathered from the left forewing of three males and three females of each species as follows. For *A. clorinde* and *E. hecabe*, each forewing was laid, dorsal surface up, on matte black card stock. This card was placed on a universal stage and illuminated with a xenon light source (Ocean Optics PX-2) in an otherwise darkened room, via an optical fiber fitted with a collimating lens (Ocean Optics 74-UV). The illuminating fiber was positioned normal to the plane of the wing surface. The collecting fiber, also fitted with a collimating lens, was located perpendicular to the attachment point of the wing and angled downward at 45° (elevation 45°), and transmitted collected light to an Ocean Optics USB2000 spectrometer connected to a desktop computer running OOIBASE32 software. A glass microscope slide coated with magnesium oxide was used as the reflectance standard, which was rescanned for each specimen and at each angle of measurement (see below). For the *E. candida* museum specimens, whole butterflies were placed on the universal stage in a manner that resembled as closely as possible the placement of forewings for the other two species.

Spectra were gathered near the center of the UV-reflecting area on the wings sampled. For reflectance readings, two spectra were recorded from each target area: one in which UV intensity was maximized (UV+ orientation) and one in which it was minimized (UV− orientation). To obtain the UV+ reading, all axes of the universal stage were set to 0°, and subtle adjustments were made in the position of the wing on the stage until the location that yielded the strongest UV reflectance was found. Small changes in wing 'roll' usually increased UV reflectance, so the roll axis of the stage was varied until maximal UV intensity again was observed. This spectrum then was recorded. Finally, the contribution of iridescent wavelengths to wing reflectance was minimized (UV− orientation) by rotating the stage 180° in the horizontal plane from the UV+ orientation and recording that spectrum.

Changes in UV wavelength reflected at maximum intensity with changes in wing angle were determined as follows. With the left forewing in the UV+ orientation and all stage axes set to 0°, the collecting fiber was moved incrementally in 5° steps, from 10–40°, relative to the illumination fiber. All study specimens were measured at one collection fiber angle before the angle was changed.

3. Results

3.1. Anteos clorinde

3.1.1. Results from images

The dorsal wing surfaces of both sexes are predominantly white to the human eye, although in females the white coloration is less bright than that of the male (Fig. 1A,C). Both sexes have a prominent yellow patch on each dorsal forewing that extends posteriorly from the wing edge about midway along the anterior wing margin to just beyond the discal cell. Compared to the female, this patch is more chromatic in the male and contrasts strongly with the surrounding bright white scales. A black discal dot, surrounded by a thin ring of orange, also is present on each wing. The UV photographs reveal that, while the white areas of the dorsal wing surface appear UV absorbing, an area of strong UV reflectance on the dorsal forewing coincides with the yellow patch in both sexes (Fig. 1B,D). Preliminary assessment suggested that this UV reflectance is iridescent but that the iridescence vanishes only at extreme angles of view relative to the wing surface. The ventral wing surface (not shown) is light green in both sexes.

3.1.2. Scale nanostructures

In the yellow patch on male and female forewings, but not in other wing areas, cover scales possess longitudinal rows of tall ridges comprised of stacks of lamellae (Fig. 2A,B: "RL"). These scales exhibited an inter-ridge mean spacing of 0.70 ± 0.01 ridges/μm ($N = 3$ males, 2 females; differences between the sexes fell within the standard error of the mean). In *A. clorinde* each lamella appeared to run the entire length of the ridge. In contrast to ridge density, the number of lamellae per ridge differed between the sexes, with males possessing more lamellae (10.63 ± 0.56, $N = 3$) than females (7.92 ± 0.38, $N = 3$). As is common in the Pieridae, arrays of pigment granules (e.g., Ghiradella et al., 1972) project downward beneath the basal lamina in the space between the scale architecture and the smooth scale 'floor' (Fig. 2B: "PG"). In *A. clorinde* these pigment granules are elongated in comparison to those of our *Eurema* study species and to those of other pierids (e.g., Ghiradella, 1984; Stavenga et al., 2004).

3.1.3. Spectrophotometric results

In the UV+ orientation, the yellow/UV spot of both sexes exhibited similar reflectance spectra (Fig. 3A,B). Compared to females, reflectance spectra of males showed a steeper upslope at ≈500 nm and lower minimum reflectance at ≈450 nm in the UV+ orientation, which is consistent with their brighter and more chromatic appearance. The narrow, Gaussian-shaped UV reflectance peak is characteristic of coherent scattering. Capturing UV+ spectra proved difficult in this species, as small changes in the position of the wing on the stage resulted in large shifts in the shape (spectral distribution) of the UV reflectance. Thus, the minor sex differences in UV peak intensity and shape illustrated (Fig. 3A,B) are a consequence of the particular spectral samples and probably do not represent consistent sex differences. Spectra obtained in the UV− orientation were much less affected by minor changes in the position of the wing on the stage. In this wing orientation, females consistently exhibited weaker UV reflectance than males (Fig. 3A,B).

The wavelength of UV peak intensity (λ_{max}) decreased steadily in both sexes as the angle between the illuminating beam and collection fiber increased (Fig. 4A,B). We were

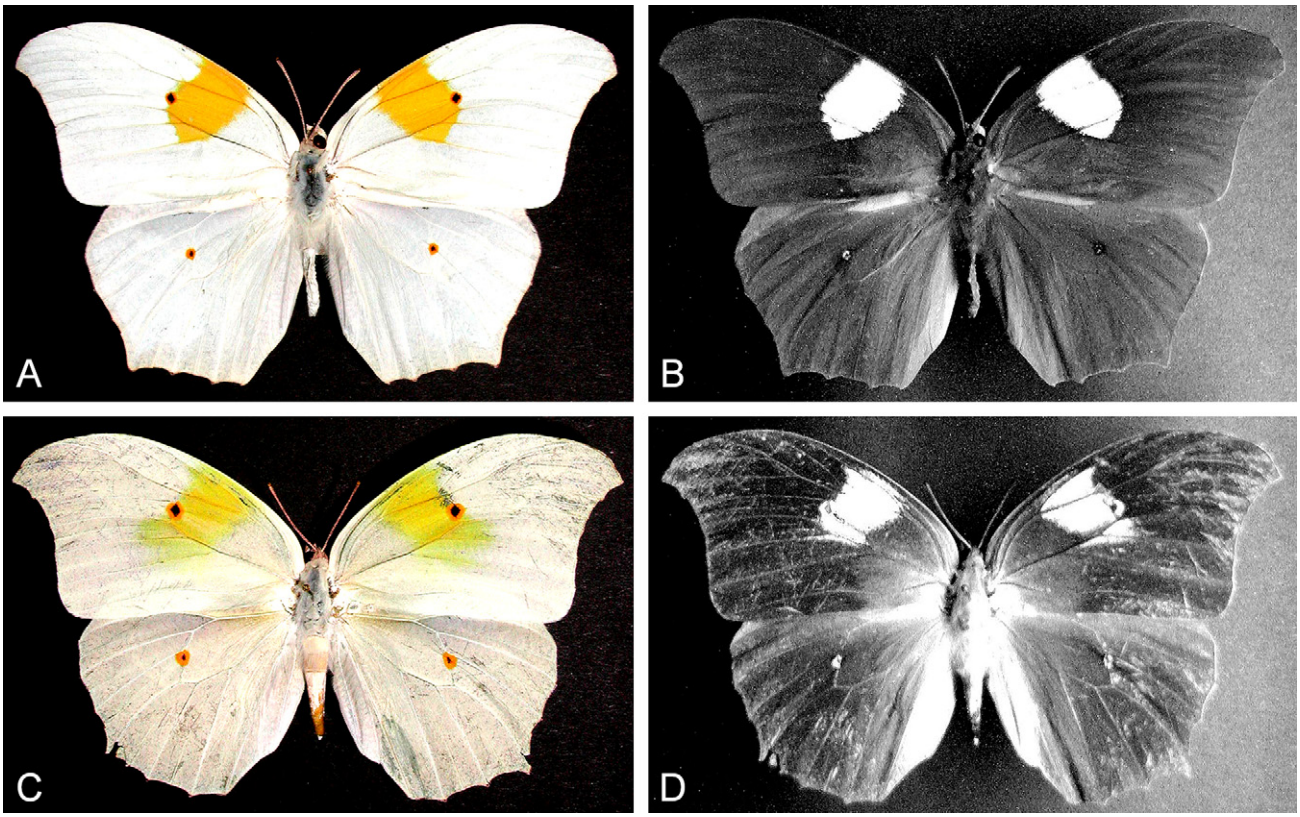

Fig. 1. Dorsal wing surfaces of male (A,B) and female (C,D) *Anteos clorinde* in visible (left panels) and ultraviolet (right panels) light.

unable to obtain a reliable reading for male *A. clorinde* at 40°, and have excluded that data point. Likewise, only one female *A. clorinde* specimen provided a reliable reading at 20° and 25°, which accounts for the absence of SE bars at those angles in Fig. 4B.

3.2. Eurema hecabe

3.2.1. Results from images

The dorsal wing surfaces of males and females are yellow with a broad peripheral melanic margins on the forewings that varies in width antero-posteriorly (Fig. 5). The ventral wing surfaces also are yellow (in both sexes) and contain variable amounts of melanic spotting. Both sexes display bright UV reflectance but differ in the size and shape of the wing area that reflects UV. The forewings and hind wings of males reflect UV strongly throughout most of the area of yellow coloration, but females reflect UV only in a small area near the forewing attachment point. UV video observations suggested that UV reflectance is iridescent in females as well as in males.

3.2.2. Scale nanostructures

Cover scales in the UV-reflecting wing areas of both sexes contain ridge lamellae (Fig. 2C,D). On these scales, males exhibited slightly more lamellae per ridge (7.07 ± 0.18) than females (6.00 ± 0.33), but sex differences in inter-ridge mean spacing fell within the standard error of the mean (1.12 ± 0.02 ridges/μm; $N = 2$ specimens of each sex). In contrast to *A. clorinde*, lamellae in angled stacks (Fig. 2C,D). Female lamellae exhibited steeper insertion angles ($9.89 \pm 0.36°$, $N = 3$ specimens) than did those of males ($7.92 \pm 0.40°$, $N = 4$ specimens). Pending confirmation with larger sample sizes, however, these apparent sex differences in lamellar insertion angle should be considered tentative (see Section 2).

3.2.3. Spectrophotometric results

Compared to females, the male's more chromatic long wavelength-reflecting coloration is a result of reflectance intensity that increases rapidly around 500 nm from a minimum near 450 nm. Similarly, UV coloration in males is brighter and more chromatic than that of females (Fig. 3C,D).

In *E. hecabe* males, the wavelength of maximum UV reflectance decreased in a relatively linear manner with increasing angle between the illumination beam and collector (Fig. 4C). The same pattern of hue shift was observed in females (Fig. 4D), although individual variance was greater in females (potentially due to greater wing wear in our samples).

3.3. Eurema candida

3.3.1. Results from images

E. candida are sexually dichromatic both in the human-visible and UV wavelengths (Fig. 6). Dorsal wing surfaces in males are bright yellow with broad and dark peripheral melanic margins, but in females the same wing surfaces are white

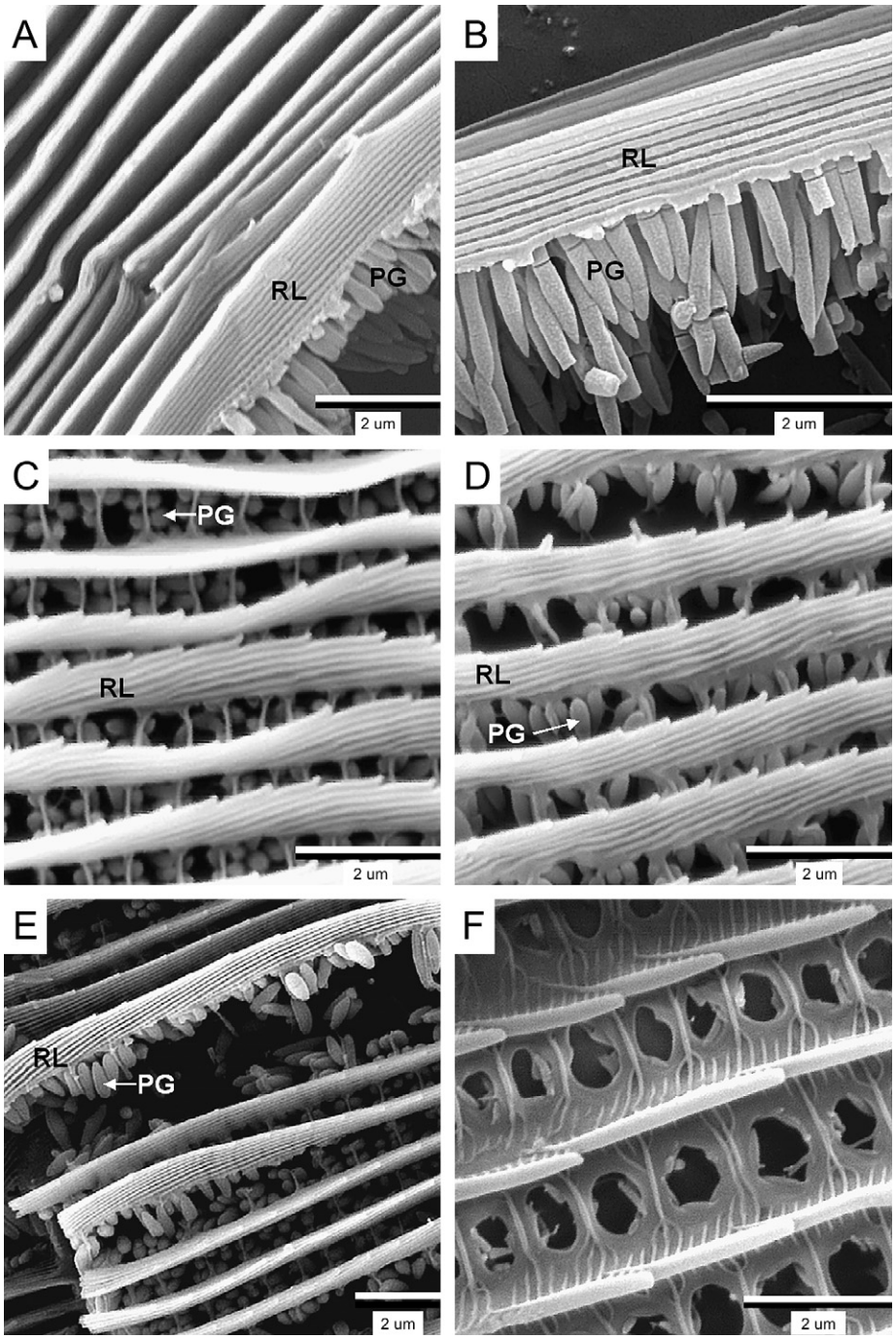

Fig. 2. SEMs of the study species. (A,B) UV-reflecting scales from the yellow patch of *Anteos clorinde* male and female dorsal forewings, respectively. Densely packed ridge lamellae (“RL”) are arranged as parallel stacks of ‘bars’, which appear to run unbroken for the entire length of the ridge. Ellipsoid objects projecting downward from the lamellae are pigment granules (“PG”). (C,D) UV-reflecting scales from the dorsal forewings of a *Eurema hecabe* male and female, respectively. Ridge lamellae overlap considerably, but are stacked in a shingle-like arrangement. (E) UV-reflecting scale from the dorsal forewing of a *Eurema candida* male. Lamellae are stacked in a shingle-like arrangement. (F) Typical dorsal forewing scale of a female *E. candida*. No UV scales are present on the wing, and scales present possess few or no pigment granules. The scale bar at the bottom right of each image indicates a distance of 2 μm.

with paler brown margins. The non-melanic areas of the dorsal wing surfaces were bright in the UV images of both sexes, but only male UV reflectance appeared to be iridescent (Fig. 6B,F).

Ventral wing coloration in this species is unique among sulphur butterflies in several ways. First, the melanic wing margins of the dorsal wing surface are mirrored on the ventral wing surface in both sexes (Fig. 6). This is the only example, of which we are aware, of such a color pattern in the coliadines. Second, although the female dorsal wing surfaces are white except for the margins, both sexes have pattern-less yellow ventral wing coloration (Fig. 6).

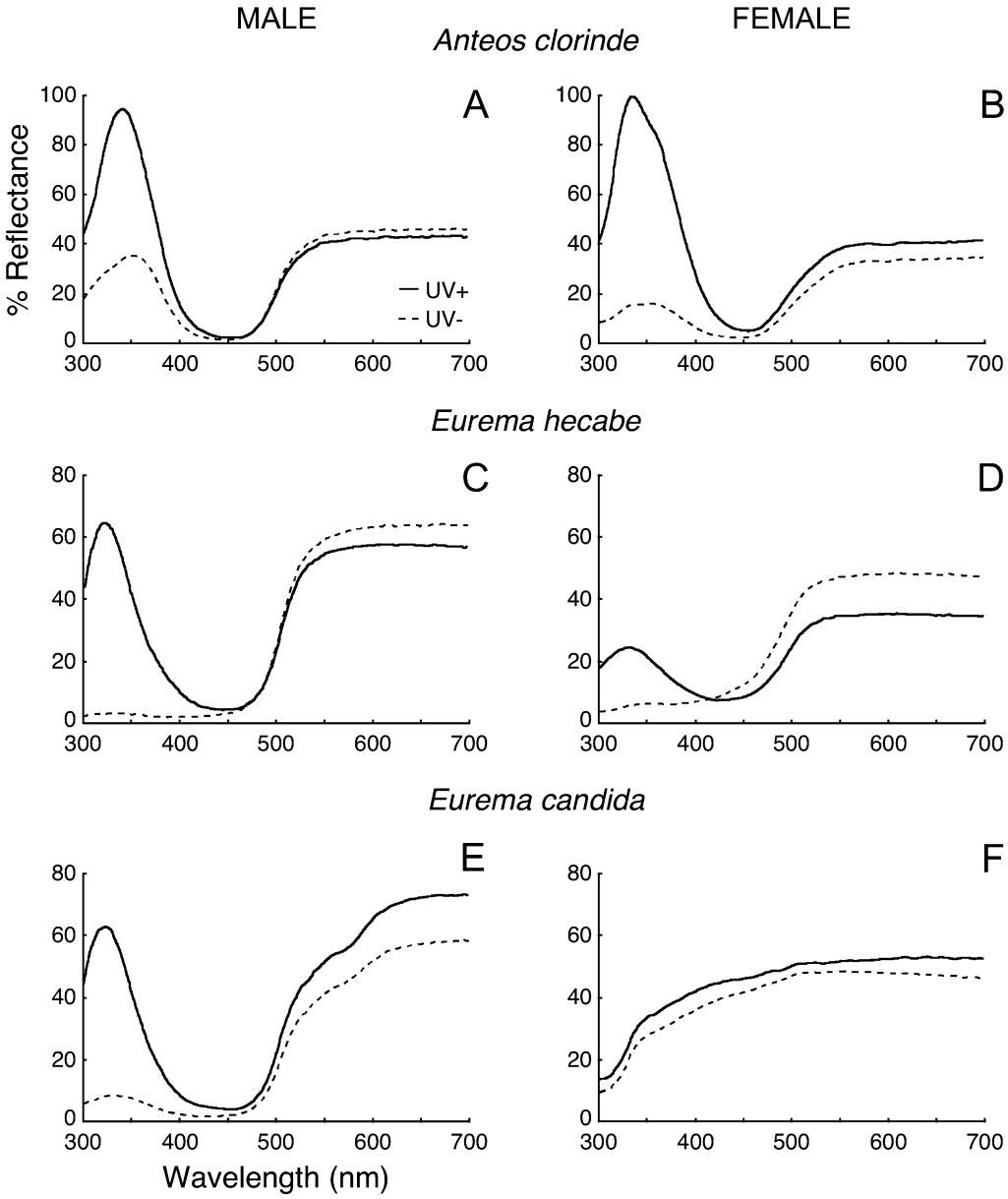

Fig. 3. Mean forewing reflectance spectra in UV maximum (UV+) and UV minimum (UV−) wing orientations for males ($N = 3$) and females ($N = 3$) of the three study species. Spectra gathered with collector at elevation 45° and azimuth 90° relative to the attachment point of the left forewing (prior to removal) with the body (UV+, solid lines) and the distal edge of the left forewing (UV−, dashed lines).

3.3.2. Scale nanostructures

Male UV-reflecting scales possess a ridge lamellar structure that appears to be identical to that of *E. hecabe*, and quite unlike that of *A. clorinde* (Fig. 2E). Male *E. candida* exhibited slightly fewer lamellae per ridge (6.75 ± 0.25) and a slightly greater inter-ridge spacing (1.44 ± 0.02 ridges/μm, $N = 2$ specimens) than was observed in male *E. hecabe*. Lamellar insertion angles ($9.02 \pm 0.52°$, $N = 3$ specimens) were similar to those of *E. hecabe*. In contrast to males, female *E. candida* lack scales with ridge lamellar stacks (Fig. 2F). Also unlike males, pigment granules are rare on the dorsal scales of females.

3.3.3. Spectrophotometric analyses

The reflectance spectrum of male *E. candida* differs from that of male *E. hecabe* in several ways. Most conspicuous is that, in *E. candida* males, reflectance intensity continues to increase throughout the visible wavelengths, whereas in *E. hecabe* the male's reflectance intensity plateaus between 575 and 600 nm (Fig. 3E). UV reflectance in males of the two species is virtually identical, except that *E. candida* exhibits some degree of iridescent UV reflectance in the UV− wing orientation (Fig. 3E). Females of *E. candida* are unique in our study species, and perhaps among all coliadines, in exhibiting diffuse (non-iridescent) UV reflectance (Fig. 3F).

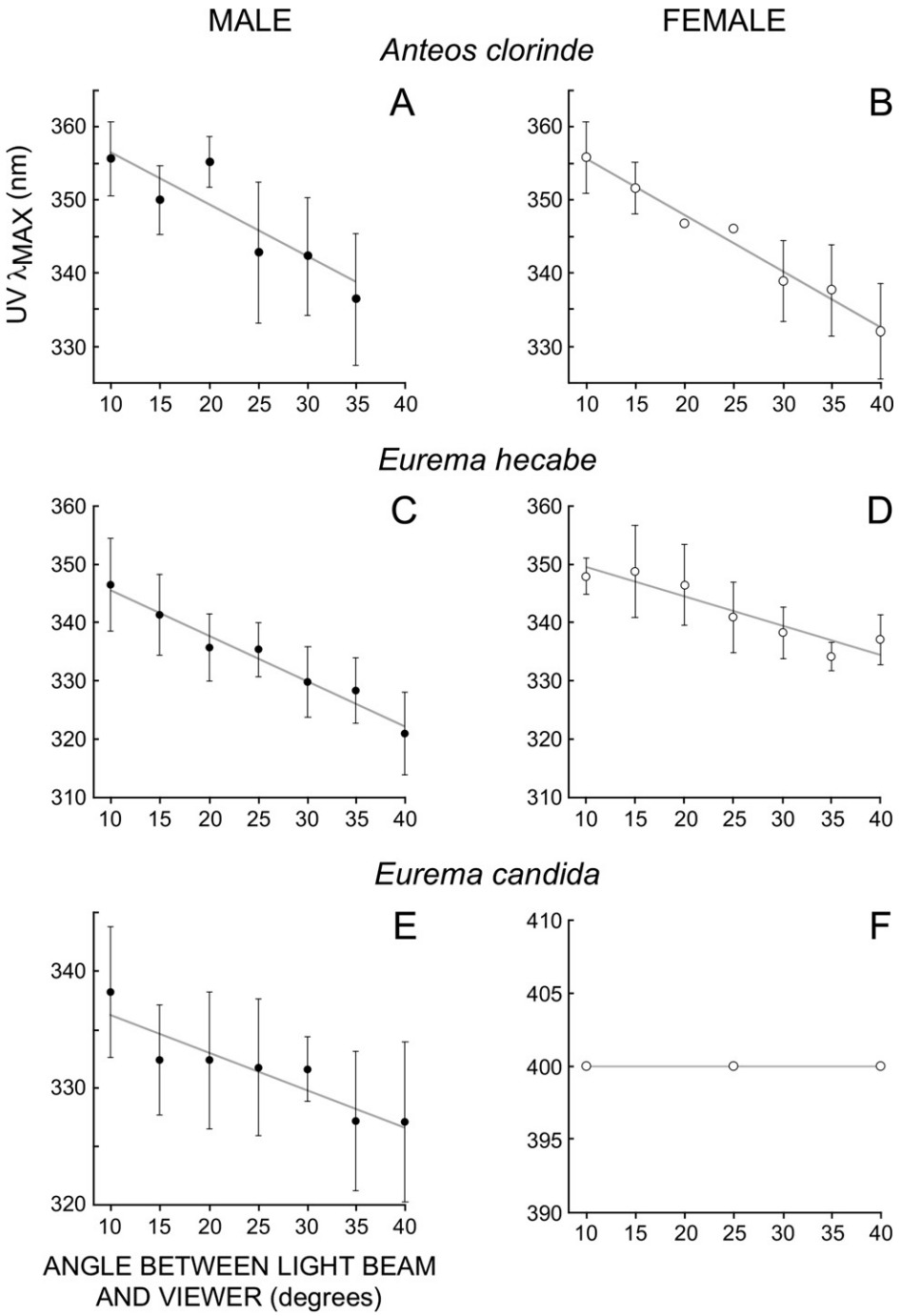

Fig. 4. Changes in peak UV reflectance (λ_{max}, mean ± SE) of the forewing with changes in collector position relative to the light source. Gray lines denote best-fit linear regressions. In contrast to *E. hecabe* (C,D) and *E. candida* males (E), obtaining Gaussian-shaped UV iridescence reflectance curves in *A. clorinde* (A,B) proved difficult, as the shape of the curve changed dramatically with the slightest alteration in the position of the wing on the stage. Thus, data for this species are less complete than for *Eurema.*

The absence of a difference in spectral shape between UV+ and UV− orientations of the female dorsal wing surface constitutes evidence for a lack of iridescence.

As seen in *A. clorinde* and in *E. hecabe*, UV peak intensity (λ_{max}) in male *E. candida* decreased in a relatively linear manner with incremental increases in the angle between the light source and collector (Fig. 4E). In contrast, there was no change in UV peak intensity with change in collector angle for female *E. candida* (Fig. 4F). As this result for females was anticipated, we chose three representative angles at which to record reflectance spectra, rather than at all seven angles. UV peak intensity is constant at 400 nm (Fig. 4F) simply

Fig. 5. Dorsal and ventral wing surfaces of male and female *Eurema hecabe* in visible (left panels) and ultraviolet (right panels) light. (A,B) male dorsal surface, (C,D) male ventral surface, (E,F) female dorsal surface, (G,H) female ventral surface.

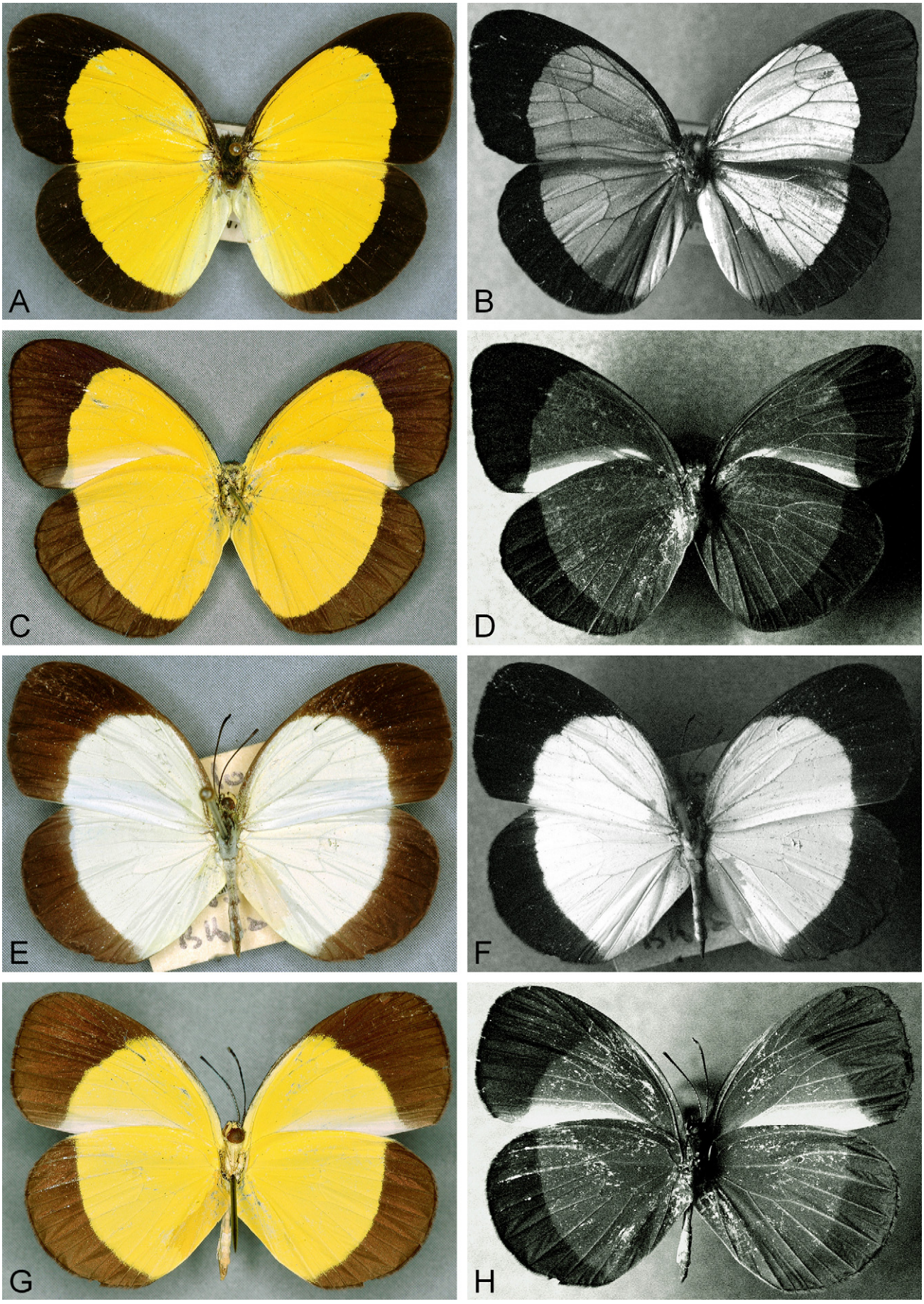

Fig. 6. Dorsal and ventral wing surfaces of male and female *Eurema candida* in visible (left panels) and ultraviolet (right panels) light. (A,B) male dorsal surface, (C,D) male ventral surface, (E,F) female dorsal surface, (G,H) female ventral surface.

because the range of wavelengths examined for UV only spanned from 300 to 400 nm, and reflectance is greatest at 400 nm.

4. Discussion

Our results show that, in some species of sulphurs, the mechanisms that produce bright UV iridescence in females are the same as in males; that is, a thin-film multilayer system of ridges with lamellae on the scales. This result implies that during evolution the genes that produce the scale architecture requisite for producing iridescence in males have come to be expressed in females. However, the area of the wing in which this scale trait is expressed in females varies dramatically from species to species. Nevertheless, there is at least one species in which the mechanism producing bright UV reflectance in females is very different from that of males, which suggests that bright female UV reflectance evolved through changes in scale pigmentation rather than scale architecture. Although the functional significance of these UV reflections remains unclear, our results suggest two pathways by which scales can be modified to produce such reflections. The specific findings for each species examined will be discussed below.

4.1. Anteos clorinde

Unlike most coliadines, all aspects of UV reflectance in *A. clorinde* females are fundamentally the same as in males. Both sexes possess ridge-lamellar architecture within the yellow patch area of the forewing, although males appear to have more lamellae than females. Why a greater number of lamellae in males did not result in stronger UV reflectance than observed in females is unclear. This may be related to the difficulty of obtaining UV reflectance spectra with consistent intensity and wavelength peaks at a particular location within the yellow area of the forewing. Cursory examination of the yellow patch using a light microscope, failed to reveal any conspicuous variation in scale morphology or arrangement that might produce highly variable iridescent UV spectral intensity/shape over small distances. Interestingly, another sulphur that is white with a yellow forewing patch, *Kricogonia lyside*, exhibits the same phenomenon of local variation in iridescent UV reflectance intensity/shape and possesses the same planar system of ridge lamellae (personal observation). This shared nanostructural morphology does not appear to explain the phenomenon in question, however, because the same architecture is present in other pierids (e.g., the euchloine genus, *Colotis*) but is not accompanied by large shifts in UV spectral intensity and hue with small changes in wing orientation (personal observation). More work is needed to understand why iridescent UV reflectance behaves in an unusually variable manner in *Anteos* and *Kricogonia*.

The yellowish-orange coloration of the *A. clorinde* forewing patches results from the absorbing properties of pterin pigments. In another sulphur, *Colias eurytheme*, these short-wavelength-absorbing pterins have been argued to enhance the purity and contrast of the iridescent UV signal in males (Rutowski et al., 2005). Whether an absolute relationship exists in the Coliadinae between iridescent UV reflectance and the presence of yellow/orange pterins is an issue that has yet to be investigated, but this particular structure–pigment relationship appears to be a specialization of the sulphurs.

4.2. Eurema hecabe

Compared to males, iridescent UV reflectance in female *E. hecabe* is reduced both in intensity and in the size of the area over which UV reflecting scales are distributed. Sex differences in lamellar ridge nanostructure were subtle, with males having on the average one more lamella per ridge and having more shallow lamellae insertion angles. It seems unlikely that these seemingly minor differences can explain the approximately 40% difference in UV reflectance intensity between the sexes, however. Wing wear may account for at least a portion of this sex difference, as our female specimens were more worn than were the males.

4.3. Eurema candida

Whereas male *E. candida* are rather 'typical' sulphur males in having iridescent UV reflectance produced by ridge-lamellae, the diffuse white (including UV) reflectance of female *E. candida* appears to be unique within the Coliadinae. This is the first case to our knowledge where UV reflectance in a sulphur butterfly involves incoherent, broad-band scattering and echoes the mechanism underlying bright UV reflectance in white butterflies such as *Pieris rapae* (Giraldo and Stavenga, 2006; Morehouse et al., 2007). For example, white coloration in the female 'alba' morph of many *Colias* species reflects little UV (approx. 10% at 350 nm; personal observation), given that the UV wavelengths are absorbed by pterins. Rutowski et al. (2005) showed that chemical removal of the pterin pigment granules in male *Colias eurytheme* produced a broad-band reflectance that, in the UV– orientation, is strikingly similar in spectral shape to the white dorsal wing surface of *E. candida* females. This diffuse white/UV reflectance in pterin-extracted *C. eurytheme* was attributed to light scattering by the microscopic architectural features of the scales, and the same interpretation appears to apply to the natural white/UV wing coloration of *E. candida* females.

4.4. UV reflectance in female sulphurs

In most sulphurs only the male displays iridescent UV reflectance. It has been shown in *C. eurytheme* that this sex difference in coloration is used by males in sexual discrimination (Silberglied and Taylor, 1978) and by females in mate assessment (Papke et al., 2007). Sex differentiation based on UV coloration should be straightforward for *E. candida*, given the dramatic difference in the appearance of specular (male) and diffuse (female) UV reflectance. Sex discrimination via UV reflectance also should be possible in *E. hecabe*, both because the amount of wing area devoted to UV-reflecting scales differs considerably between the sexes and because reflectance

within the UV scale areas appears to be much brighter in males. In contrast, the possibility that *A. clorinde* can use UV reflectance in sexual recognition seems highly unlikely, as the UV signal does not appear to be sexually dimorphic. The difference in spectral purity of colors in the (human) visible wavelengths may be sufficient for this purpose in *A. clorinde*, however, because whereas the male yellowish-orange patch is sharply delineated from the bright white scales that surround it, this patch is yellowish and surrounded by a greenish 'wash' in females.

One intriguing question is why any female sulphur exhibits UV iridescence, given that this trait appears to be a primary male sex recognition mechanism in the coliadines. We propose two potential explanations. The first concerns the avoidance of interspecific mating, through character displacement, in the context of sympatric speciation (e.g., Brown and Wilson, 1956). In many coliadine sister taxa, males in only one member of the species pair exhibit iridescent UV reflectance. As male courtship harassment poses costs for females (e.g., Graham et al., 1980; Gilchrist and Rutowski, 1986), a coloration trait that distinguishes females of related sympatric species could reduce interspecific male harassment and thereby increase time available for egg laying and feeding. The second potential explanation is that female UV reflectance is used by males as an indicator of mate quality. Because males give females a costly nutrient investment during mating in the form of a spermatophore (Boggs and Gilbert, 1979; Rutowski et al., 1987), they may be selected to discriminate among potential mates on the basis of potential fecundity indicators (such as age and/or body size), which could be mediated by female UV. Whether or not males are sensitive to female coloration in this manner stands to be explored behaviorally.

Acknowledgments

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