

Wing Colors of Chrysozephyrus Butterflies (Lepidoptera; Lycaenidae): Ultraviolet Reflection by Males

Authors: Imafuku, Michio, Hirose, Yukihiro, and Takeuchi, Tsuyoshi

Source: Zoological Science, 19(2) : 175-183

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.19.175>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Wing Colors of *Chrysozephyrus* Butterflies (Lepidoptera; Lycaenidae): Ultraviolet Reflection by Males

Michio Imafuku*, Yukihiro Hirose and Tsuyoshi Takeuchi

Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto, 606-8502, Japan

ABSTRACT—Wing colors of the four species of *Chrysozephyrus* butterflies were analyzed by a spectrophotometer. As the dorsal wing surface of males showed a strong reflectance when the specimen was tilted, measurements were made by the tilting method. The dorsal wing surface of males which appears green to the human eye reflected UV (315–350 nm) as well as green light (530–550 nm). The reflectance rate of UV to visible green light varied among species with a higher rate for *C. hisamatsusanus* and *C. ataxus*, and a lower rate for *C. smaragdinus* and *C. brilliantinus*. The peak wavelength and the peak height did not shift when the specimen was exposed to direct sunlight at least for 16 hr. Artificial removal of scales by scratching the wing surface decreased reflectance. Blue marks on the forewings of *C. brilliantinus*, *C. hisamatsusanus* and *C. ataxus* females reflected UV to visible light of short wavelength, and orange marks on the dorsal surface of the forewing and the ventral surface of the hindwing of *C. smaragdinus* females showed a higher reflectance at longer wavelengths.

Key words: butterfly, wing color, UV-light reflection, *Chrysozephyrus*, Lycaenidae

INTRODUCTION

The colorful wing patterns of butterflies are thought to have some biological significance. In 1909, Darwin proposed that the color pattern of the dorsal wing surface has an intraspecific signaling role, including attraction of females by males in sexually dimorphic species, and that of the ventral wing surface displayed in a perched posture has interspecific effects as protection from predators. Since then, some experiments have been carried out to address the functions of wing color patterns; a clue to mate recognition for *Arginnis paphia* (Magnus, 1958), *Pieris rapae* (Obara and Hidaka, 1968; Obara, 1970) and *P. protodice* (Rutowski, 1981), *Colias eurytheme* (Silberglied and Taylor, 1978) and *Papilio xuthus* (Hidaka and Yamashita, 1975), and anti-predatory effect as aposematic coloration for *Heliconius erato* (Benson, 1972) and as mimicry for some North American species (Brower, 1958a, b, c). However, the number of species examined is limited, and male-specific brilliant coloration has rarely been subjected to experimental studies (for exception, Lederhouse and Scriber 1996).

For understanding of the biological significance of butterfly wing colors, it is prerequisite to learn the range of colors or wavelengths reflected from the wing surface, along with the perceptible range of wavelengths in potential

receivers such as conspecific individuals or predators. Concerning the latter problem, the perceived range is known to somewhat differ between humans and insects or other animals (Silberglied, 1979), and thus, analyses based on physical measurements of wavelengths reflected from butterfly wings are needed (Crane, 1954). In this study, we analyzed the wing colors of four species of *Chrysozephyrus* butterflies which show conspicuous sexually dimorphic coloration on their wings, with males showing brilliant green wings in contrast to females with mostly dark brown wings. Further, the effects of direct sunlight and dislodging of scales on potential change of color, and the effect on reflectance of angles in which light is reflected were examined.

MATERIALS AND METHODS

Measurement of wavelength

Four species of genus *Chrysozephyrus* distributed in Japan were examined; *C. smaragdinus*, *C. brilliantinus*, *C. hisamatsusanus* and *C. ataxus*. The dorsal wing surface of males of these species appears metallic green to the human eye, and that of females basically dark brown with an orange and/or a blue mark only on the forewing. Ventral wing surfaces are similar between sexes with gray to brown, except for *C. ataxus* which shows a complex pattern in females, as shown in Fig. 1.

For measurement of wavelength of the light reflected from the wing surface, the central part of the wing was cut out in a 10×15 mm piece and settled on the stage of a spectrophotometer (Shimadzu, UV-240). The measured range was from 200 to 700 nm. For measurement of specific colored parts of the wing, those parts were used (CB21, CH21 and CA21 in Fig. 7B; CA21b and CA21w

* Corresponding author: Tel. +81-75-753-4073;
FAX. +81-75-753-4113.
E-mail: ima@ci.zool.kyoto-u.ac.jp



Fig. 1. Four species of *Chrysozephyrus* butterflies. Upper left and right sections are males and females, respectively, in dorsal view. Lower sections are the same as upper, but ventral view. For each section, top left, top right, bottom left and bottom right are, respectively, *C. smaragdinus* (male: CS2, female: CS21), *C. brillantinus* (CB1, CB21), *C. hisamatsusanus* (CH1, CH21) and *C. ataxus* (CA1, CA21). For reflection spectra of these specimens, see Figs. 3 and 7.

in Fig. 7E), by putting the corresponding areas on the left and right wings together (CS21o and CS21c in Fig. 7B).

In a preliminary observation, the dorsal wing surface of males was found to look more brilliant when viewed from the front or inside at a lower angle (nearly parallel to the wing surface), and thus, the specimen was set on the spectrophotometer at a tilt angle of 45° for the dorsal wing surface of males as mentioned next.

Tilt angle examination

A small rubber stage (10×10 mm at the base) whose top was cut at a certain angle (0°=no cut, 15°, 30°, 45 and 60°) was inserted between the fitting plate and the specimen. Thus, on the spectrophotometer, the incident light was applied to the wing piece from the direction shown with line L in Fig. 2, and the reflected light that returned in the same course was measured. The direction of tilt was at right angle to the frontal edge for the forewing and toward the base for the hindwing, which was determined by a naked-eye observation as to perceive the strongest reflection. For the exami-

nation of tilt angle (α in Fig. 2), the left fore- and hindwings of three individuals of *C. smaragdinus* (CS1, CS2 and CS3) were used.

Scale loss

Since butterflies are thought to lose their scales during active flight in the field which may cause wing color change, the effect of scale loss on reflectance was examined.

A piece of the wing specimen was softly swept off with a writing brush, and the number of cover scales on the surface was counted on photos taken under a microscope with illumination from oblique above; as the brilliant male coloration is derived from the green cover scales, only these scales (except for dark brown basal scales) were counted. For counting, five sampling sites were selected around the center of the wing; four corners and the center of a 3×3 mm square. An average value of these five counts was used as the number of scales for the wing. The specimen was then subjected to a spectrophotometric measurement.

This examination was made by using the right hindwings of

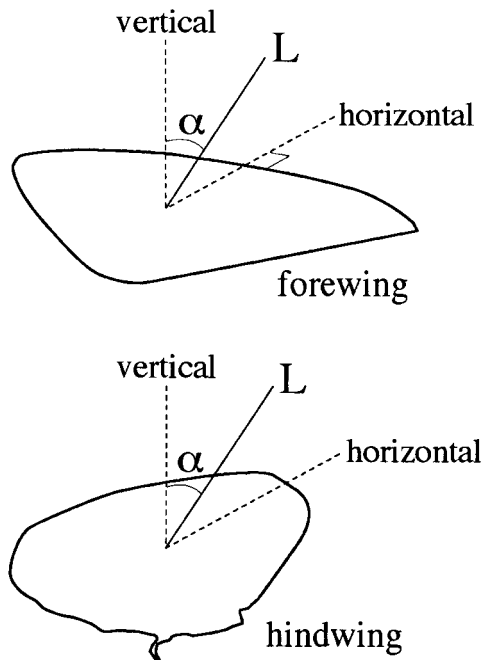


Fig. 2. Measuring method for tilt angle. The incident light and the reflected light to be measured were adjusted on line L which was tilted from the vertical axis toward the horizontal axis by an angle of α .

three individuals of *C. smaragdinus* (CS1, CS2 and CS3).

Effect of direct sunlight

Since old specimens of butterflies show a faded wing color, probably due to a result of exposure to light, wing specimens were exposed to direct sunlight and their reflectance was measured at various intervals. For exposure, specimens were put on a cylindrical drum which was rotated once a day and whose axis was adjusted for the specimens to continuously receive the sunlight vertically. The light intensity was measured at the same time; the sensor of the photometer was also attached to the drum. Exposure was made between 9 a.m. and 3 p.m. on fine days from November 2000 to January 2001. The light intensity was $8.14 \pm 1.68 \times 10^4$ lux (mean \pm SD). The left fore- and hindwings of three individuals of *C. smaragdinus* (CS1, CS2 and CS3) were used.

Specimens

Ten male and one female specimen were used for *C. smaragdinus* and *C. brilliantinus* and five male and one female specimen for *C. hisamatsusanus* and *C. ataxus*. All of them were derived from field collections, except for the *C. hisamatsusanus* female which was difficult to capture in nature and thus, reared from eggs. The specimens used in the present experiments are summarized in Appendix.

Statistical analyses

For comparison of wavelengths and reflectance rates between two species (Table 1), a Mann-Whitney U-test was carried out with the use of Statview J-4.5 software (Abacus Concepts). For the cluster analysis for Fig. 8, Ward's method on JMP ver. 3 software (SAS Institute) was adopted.

RESULTS

1. The dorsal wing surface of the *C. smaragdinus* male

Reflectance on the dorsal surface of the four wings of a *C. smaragdinus* male (CS2) is shown in Fig. 3. The reflectance was measured tilted at an angle of 45° , except for LF0 which was measured without tilting. The four wings showed a similar pattern of reflectance with two large peaks at about 315 nm (UV region) and 525 nm (green region), with a minor difference between the fore- and hindwings; the forewings tended to reflect slightly shorter wavelengths than the hindwings both in the UV and green regions, and the tendency was confirmed for the other two individuals (CS1 and CS3). The heights of the two peaks in the UV and green regions were not largely different; thus, a *C. smaragdinus* male reflected ultraviolet light nearly as strongly as visible green light.

Effect of tilt angle

When the tilt angle of the specimen was increased, the reflectance also increased (Fig. 4; also compare LF and LF0 in Fig. 3). At an angle of 45° , it was about three times as strong as that without tilting. On the other hand, the peak wavelength did not largely shift with the change in tilt angle. A high reflectance by tilting of the wing in such a way as shown in Fig. 2 suggests that green and UV lights are reflected strongly forward and inward.

Effect of scale loss

Reflectance clearly declined with decreased scales both for UV and green regions (Fig. 5, also compare RH and RHs in Fig. 3).

Effect of direct sunlight

The peak wavelength and the peak height did not change when the specimens were subjected to exposure to direct sunlight at least for 16 hr (Fig. 6).

Table 1. The peak wavelength in UV and green regions (nm) and the ratio of the peak height of UV to that of green region. The left hindwings were used. Mean \pm SD.

	<i>C. smaragdinus</i>	<i>C. brilliantinus</i>	<i>C. hisamatsusanus</i>	<i>C. ataxus</i>
N	10	10	5	5
UV region	318 \pm 5 ^a	321 \pm 6 ^a	348 \pm 4 ^b	341 \pm 5 ^b
Green region	530 \pm 9 ^c	535 \pm 10 ^c	539 \pm 17 ^{c,d}	547 \pm 4 ^d
Reflectance ratio	0.89 \pm 0.08	0.81 \pm 0.06	1.17 \pm 0.12 ^e	1.21 \pm 0.08 ^e

The same letters at the shoulders indicate no significant difference at a level of $p=0.05$.

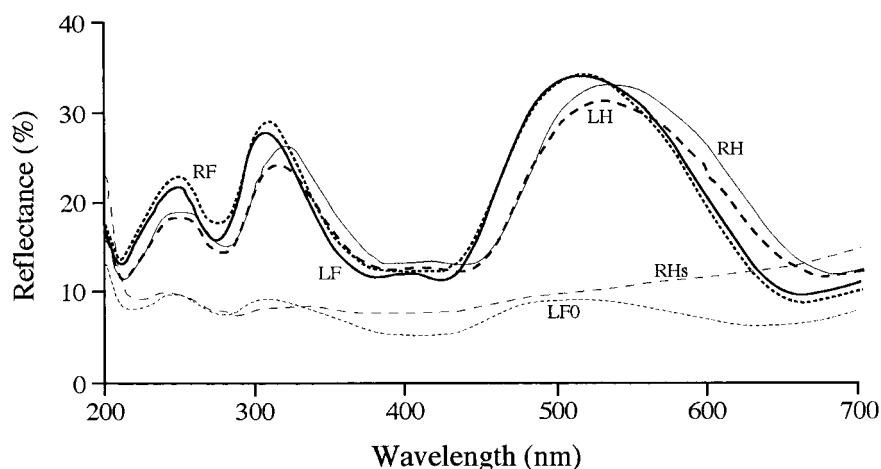


Fig. 3. Reflectance of the dorsal wing surface of a *C. samaragdinus* male (CS2). Four wings (left forewing=LF, left hindwing=LH, right forewing=RF and right hindwing=RH) were measured at a tilt angle of 45°. For the left forewing, measurement was also done without tilting (LF0). The graph RHs indicates reflectance of the right hindwing with scales removed (tilt angle=45°). For the natural color of this specimen, see Fig. 1.

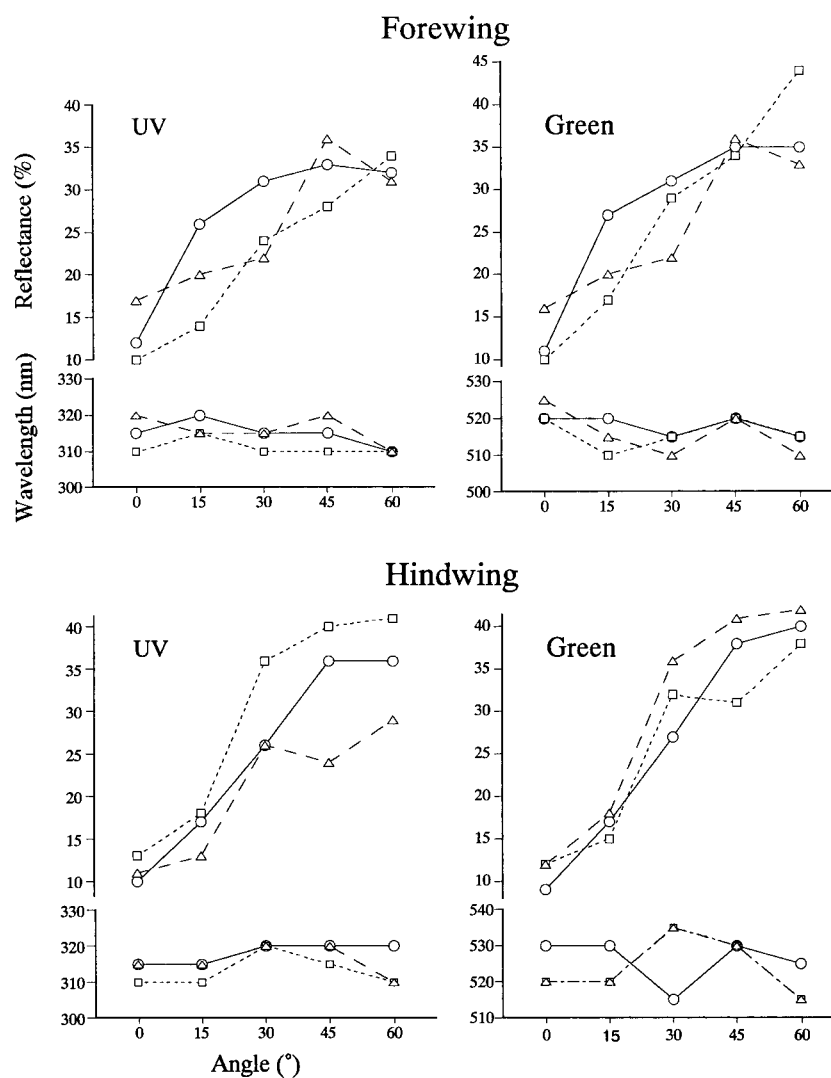


Fig. 4. Effect of tilt angle on the peak reflectance and the peak wavelength in UV and green regions. The left fore- and hindwings of CS1 (circle), CS2 (square) and CS3 (triangle) were used.

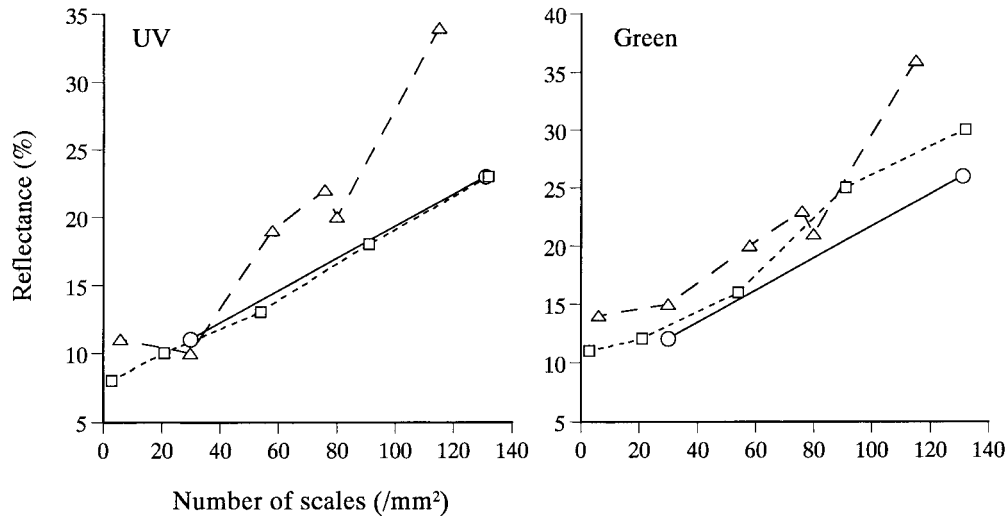


Fig. 5. Effect of scale loss. The right hindwings of CS1 (circle), CS2 (square) and CS3 (triangle) were measured at different degrees of scale loss.

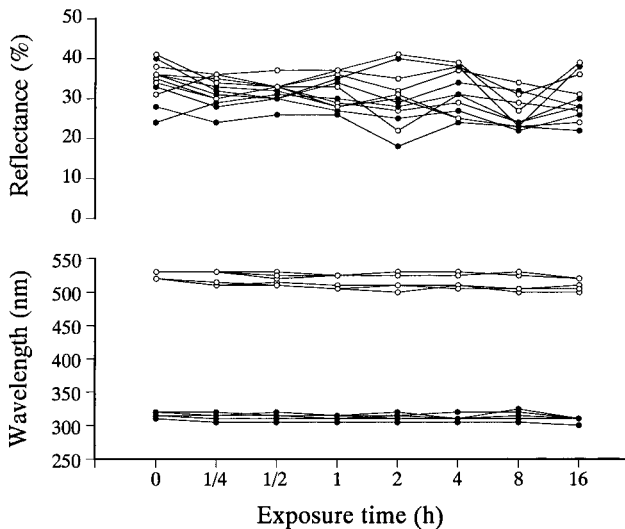


Fig. 6. Effect of direct sunlight. The wing pieces were subjected to exposure to the direct sunlight of about 80,000 lux. Data from the six wings of the left fore- and hindwings of three individuals (CS1, CS2 and CS3) were compiled. Reflectance (top) and the peak wavelength (bottom) of UV (solid circle) and visible (open circle) light region are shown.

2. Dorsal wing surface of males for the four species of *Chrysozephyrus*

The dorsal wing surface of males appeared similarly brilliant green in all four species (Fig. 1). Analyses by spectrophotometry revealed that these species also reflected UV light at different intensities among the species (Fig. 7A).

The height of the peak should be affected by the number of scales lost during flight activity in nature, as expected from the scale-loss experiment (ref. Fig. 5). Thus, the ratio of the peak height of UV region to that of the green region was compared among species. It was higher in *C. ataxus* and *C. hisamatsusanus*, and lower in *C. smaragdinus* and

C. brilliantinus (Table 1). A cluster analysis of color characteristics with use of average values of the peak wavelengths and the reflectance ratios revealed that *C. smaragdinus* and *C. brilliantinus* are nearest (distance=0.6), followed by *C. ataxus* and *C. hisamatsusanus* (0.9), and the two groups differed by a distance of 2.8 (Fig. 8).

3. Dorsal wing surface of females for the four species

Four types are known for *Chrysozephyrus* females (Kawazoé and Wakabayashi, 1976); type A possesses an orange mark, type B a blue mark, type AB an orange and a blue mark, and type O has no mark on the dorsal surface of the forewing.

A large orange mark of *C. smaragdinus* showed a higher reflectance at a longer wavelength (CS21o in Fig. 7B). Blue marks of *C. brilliantinus*, *C. hisamatsusanus* and *C. ataxus* reflected shorter visible lights and longer UV lights with a peak around 400 nm; 415, 420 and 395 nm, respectively (Fig. 7B). The dark hindwing showed no peak from 300 to 700 nm wavelengths for all the species examined (Fig. 7C).

4. Ventral wing surface of males and females

The ventral wing surface of these butterflies, except for *C. ataxus*, is basically gray to brown with white stripe and an orange mark at the posterior corner of the hindwing (Figs. 1, 7D and 7E). In *C. ataxus*, the male is white, showing a higher reflectance from 300 to 700 nm (CA 1 in Fig. 7D). The female shows a complex pattern composed of white (CA 21w in Fig. 7E) and brown (CA 21b), the former being similar to the ventral wing surface of the male.

The orange mark at the posterior corner of the hindwing of *C. smaragdinus* (CS21c in Fig. 7B) showed almost the same reflection pattern as the orange mark of the forewing (CS21o).

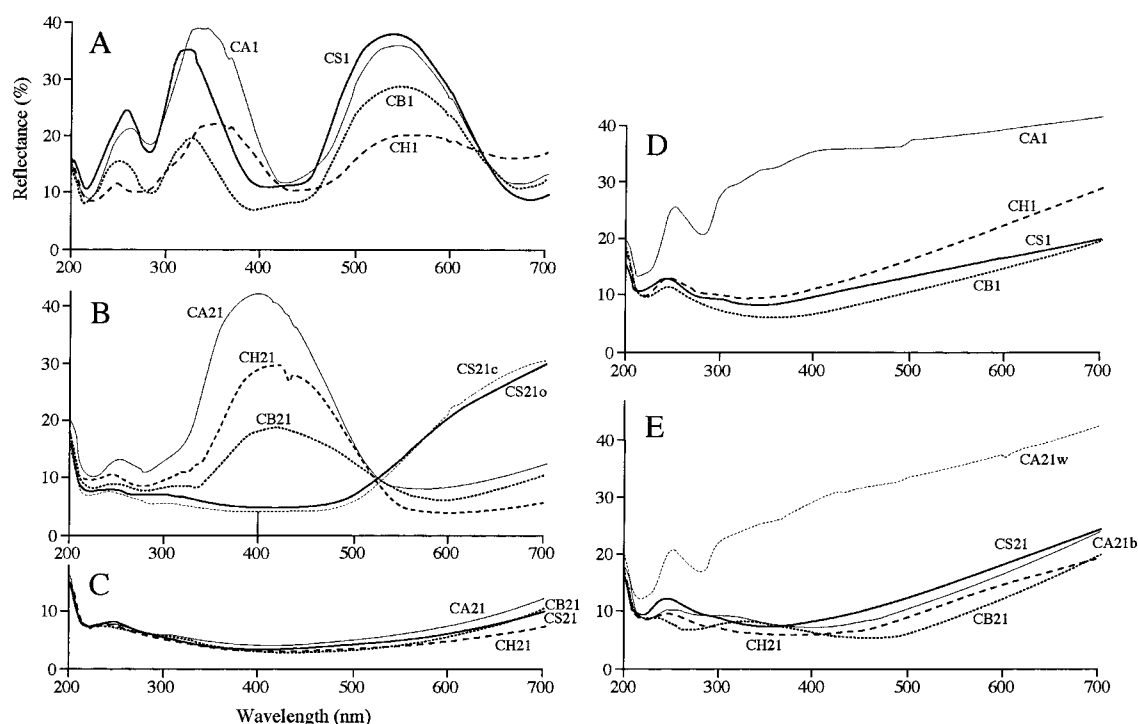


Fig. 7. Reflectance of the wing surface for the four species of *Chrysozephyrus* butterflies. CS1, CB1, CH1 and CA1 are males of *C. smaragdinus*, *C. brilliantinus*, *C. hisamatsusanus* and *C. ataxus*, respectively. CS 21, CB 21, CH 21 and CA 21 are females of *C. smaragdinus*, *C. brilliantinus*, *C. hisamatsusanus* and *C. ataxus*, respectively. For natural color of these specimens, except for CS1, see Fig. 1.

A: Dorsal surface of the left hindwings of males.

B: Orange and blue marks on the female forewings. Graphs CB21, CH21 and CA21 are blue marks of *C. brilliantinus*, *C. hisamatsusanus* and *C. ataxus*, respectively. Graphs CS21o and CS21c are orange marks, respectively, on the dorsal surface of the forewing and at the posterior corner of the ventral surface of the hindwing of *C. smaragdinus*.

C: Dorsal surface of the left hindwings of females.

D: Ventral surface of the left hindwings of males.

E: Ventral surface of the left wings of females. The hindwings were measured, except for *C. ataxus* in which the brown part was measured with the hindwing (CA21b) and white part with the forewing (CA21w).

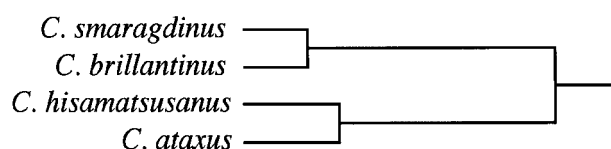


Fig. 8. Color similarity among 4 species of *Chrysozephyrus*. Abscissa indicates distance, calculated by a cluster analysis, with use of average values of wavelengths and of ratios of peak heights shown in Table 1.

DISCUSSION

In the present study, the wing colors of *Chrysozephyrus* butterflies were analysed. The dorsal and ventral wing surfaces of females and the ventral wing surface of males were shown to exhibit color patterns expected from our optical perception, whereas the dorsal wing surface of males was found to strongly reflect ultraviolet light imperceptible to humans. So, we concentrate the discussion here on the reflection characteristic of male wings of *C. smaragdinus* and the UV-light reflection of *Chrysozephyrus* butterflies.

1. Reflection characteristic of male wings of *C. smaragdinus*

In some of the present experiments (Figs. 4, 5 and 6), some variation was seen in reflectance measurements, even when the same sample was measured repeatedly. Such variation seems to be attributable to a slight difference in the area sampled on the uneven surface of the wing with vanes, from one test to another, by the spectrophotometer that sampled a small area of 5×8 mm.

In spite of such variation, the dorsal wing surface of males reflected stronger light when it was measured at a larger angle (Fig. 4) from the perpendicular axis (see Fig. 2). Thus, the reflection by *Chrysozephyrus* butterflies is directional. This is the case for the UV and visible light peaks. Directional reflection is known for males of *Gonepteryx rhamni* (Nekurtenko, 1965), *Phoebis rurina* (Eisner *et al.*, 1969), *Eurema lisa* (Ghiradella *et al.*, 1972) and *Colias eurytheme* (Silberglied and Taylor, 1973). In *Eurema lisa*, Ghiradella *et al.* (1972) obtained the strongest reflection when the horizontally held wing was measured, under top illumination, at 40° inward (toward the body axis) from the

perpendicular. Rutowski (1977) confirmed UV light reflection when he opened a pair of wings of a butterfly illuminated and observed from the top by more than 120° from each other. The latter method is similar to ours in that the incident and observed lights passed almost the same course. Thus, the angle that yields a strong reflection differs between *Eurema* and *Chrysozephyrus*; the former species reflected a strong UV-light at smaller angles from the perpendicular and the latter species at larger angles. The difference may be related to arrangement of scales on the wing (Shinkawa, pers. com.).

Examination of the dorsal wing surface of *C. smaragdinus* males revealed that the wavelength of light reflected from the forewing was slightly shorter than that from the hindwing both in UV and green light ranges (Fig. 3). This difference may be caused by the method of measurements; the tilt angle direction of the incident (and also the measured) light was adjusted to different courses relative to the base of the wing between the fore- and hindwings (Fig. 2). A shift in wavelength according to observation angles was shown in a sulfur butterfly (Ghiradella *et al.*, 1972). For *Chrysozephyrus* butterflies, close examination by employment of incident light from various tilt angle directions is needed for each of fore- and hindwings.

Wing colors of *C. smaragdinus* males were unaffected by exposure to direct sunlight at least for 16 hr (Fig. 6). This duration corresponds approximately to 3 days of natural activity of this species, as they are known to be active 5 to 6 hr a day (Imafuku, unpublished). Butterflies being less likely always to receive direct sunlight perpendicularly on their wings in nature, as expected at time other than around noon, the exposure time applied in the present experiment seems to correspond to more days in nature. Even though such a long term exposure, the color of the wing never changed. On the other hand, colors of some other butterflies are said to fade in time, even during their life time (Crane, 1954). The stable nature of the wing color of *C. smaragdinus* males may be related to a color producing mechanism in the cover scales; by "interference" as expected from directional reflectance of this species. It is interesting to compare color stability to sunlight between butterflies with interference coloration and those with pigmentary coloration.

2. Ultraviolet Reflection in *Chrysozephyrus* butterflies

In the present experiments, the dorsal wing surface of males was found to reflect UV light as well as green light for all of the *Chrysozephyrus* species examined. The UV light reflection is known for many other butterflies belonging to Nympharidae, Acraeidae, Pieridae, Morphidae, Blassolidae, Papilionidae and Lycaenidae (Lutz, 1933, Makino *et al.*, 1952, Crane, 1954, Mazokhin-Porshniakov, 1957, Obara and Hidaka 1968, Eisner *et al.*, 1969, Silberglied and Taylor, 1973, Yonekubo and Saito, 1973, Rutowski, 1981). Reflection patterns of UV differs considerably among species. UV is reflected from the whole wing surface or a part of it. In the latter case, wings that look evenly monochrome to the

human eye seems to appear in an utterly different pattern to their bearers' eyes, as expected in *Gonepteryx rhamni* (Mazokhin-Porshniakov, 1957), *Anteos clorinde* and *Phoebis rurina* (Eisner *et al.*, 1969). In many species, the reflection pattern of UV differs between sexes; females reflect UV whereas males do not for *Pieris rapae* (Makino *et al.*, 1952, Obara and Hidaka, 1968), *P. protodice* (Rutowski, 1981) and *Belenois zochalia* (Silberglied, 1979), and the situation is utterly opposite for *Phoebis sennae* (Crane, 1954), *Gonepteryx rhamni* (Mazokhin-Porshniakov, 1957), *Eurema lisa* (Ghiradella *et al.*, 1972), *Colias eurytheme* and *C. chrysotheme* (Silberglied and Taylor, 1973). In either case, butterflies could discriminate sex by UV-light reflection, not possible by the human eye. In the case of *Chrysozephyrus* butterflies, sexual discrimination seems to be easier, because reflection patterns differ between sexes in the UV as well as the visible light range. A further interesting point in *Chrysozephyrus* butterflies is that male wings in this group look green, to us, the same color as that of leaves on which they habitually alight, but will appear, for butterflies, in a different color because of UV-light reflection, thus outstanding out from the background. Term "private channel" (Silberglied, 1984) for UV light, therefore, seems to be quite adequate for this situation, though recent investigations have been revealing UV perception in some birds (Bennet and Cuthill, 1994).

UV reflection by butterflies is known to be produced in two ways; absence of UV absorbing pigments, and "interference" based on thin-layers. In *Pieris rapae*, a pigment, leucopterine, is shown to be one of absorbents of UV, especially rich in male wings that reflect least UV light (Makino *et al.*, 1952). Contrary to this, UV reflection in *Chrysozephyrus* and some other butterflies is based on interference. In *Chrysozephyrus* butterflies, both of UV and visible lights are thought to be produced by interference, because both are directional. Interestingly, the wavelength of the visible light (530–550 nm) is approximately twice of that of the shorter UV peak (260–270 nm) (Figs. 3 and 7A), and thus, it is probable that the visible light is a secondary reflection by a structure that produces the shorter UV light. Contrary to *Chrysozephyrus* butterflies, some Coliadinae butterflies are known to produce visible yellow light by pigments whereas UV light by interference as seen in *Eurema* (Ghiradella *et al.*, 1972) and *Colias* (Silberglied and Taylor, 1973).

Perception of UV light is known for insects belonging to Hymenoptera (Kühn, 1927) and Coleoptera (Weiss, 1943). According to observations by Weiss, the strongest response was induced by light of 365 nm and the second peak by blue-blue green light of 492 nm. For butterflies, UV light perception is also proved by behavioral examinations (Obara, 1970, Rutowski, 1977, 1981, Silberglied and Taylor, 1978) and by physiological analyses (Bernard and Remington, 1991, Arikawa *et al.* 1987). In these studies, near UV, or ultraviolet A covering 315–400 nm (Silberglied, 1979), is shown to be effective. In the case of *Chrysozephyrus* butterflies, two peaks were detected in the UV range; one around

250 nm and the other around 320 nm. Only the 320 nm peak or its longer side shoulder could be perceived by these butterflies.

In the present study, the reflection pattern was found to be slightly different among species. Difference in UV reflection is known among relative species or subspecies; *Colias* (Silberglied and Taylor, 1973), *Phoebis* (Silberglied, 1979) and *Pieris* (Roland, 1978, Obara and Majerus, 2000). In the case of *Chrysozephyrus* butterflies, the difference is small. *C. hisamatsusanus* and *C. ataxus* reflected UV light more strongly than green light, whereas the pattern was reversed in *C. smaragdinus* and *C. brillantinus* (Table 1). Based on cluster analysis, the former two species and the latter two species are respectively categorized in different groups (Fig. 8). Though this does not always suggest a systematic relationship, it is interesting to know that the two groups differ from each other to some extent in ecological aspects. Species in the former group live in laural forests in the southern parts of Japan with the northern limit at Niigata and Kanagawa Prefecture, whereas those in the latter group live in deciduous broad-leaved forests over most of Japan including Hokkaido and Kyushu (Fukuda *et al.*, 1984). Color patterns in butterflies should be considered from ecological viewpoints such as conspecific signaling and/or predator avoidance (Darwin, 1909), on the basis of systematic constraint inferred from morphological (Shirôzu and Yamamoto, 1956) and DNA analyses. The latter study is in progress (Saigusa and Odagiri, 2000).

ACKNOWLEDGMENTS

We thank Hiroyuki Okazaki in Tokyo and Shin Goto of the Nature Center, Tanabe City, for providing specimens difficult to obtain, and Manabu Kajita of our laboratory for information of the UV-perception in birds.

REFERENCE

- Arikawa K, Inokuma K, Eguchi E (1987) Pentachromatic visual system in a butterfly. *Naturwissenschaften* 74: 297–298
- Bennett ATD, Cuthill IC (1994) Ultraviolet vision in birds; what is its function? *Vision Res* 34: 1471–1478
- Benson WW (1972) Natural selection for Müllerian mimicry in *Hericonius erato* in Costa Rica. *Science* 176: 936–939
- Bernard GD, Remington CL (1991) Color vision in *Lycaena* butterflies: spectral tuning of receptor arrays in relation to behavioral ecology. *Proc Natl Acad Sci USA* 88: 2783–2787
- Brower JVZ (1958a) Experimental studies of mimicry in some North American butterflies. Part I. The monarch, *Danaus plexippus* and viceroy *Limnitis archippus archippus*. *Evolution* 12: 32–47
- Brower JVZ (1958b) Experimental studies of mimicry in some North American butterflies. Part II. *Battus philenor* and *Papilio troilus*, *P. polyxenes* and *P. glaucus*. *Evolution* 12: 123–136
- Brower JVZ (1958c) Experimental studies of mimicry in some North American butterflies. Part III. *Danaus gilippus berenice* and *Limnitis archippus floridensis*. *Evolution* 12: 273–285
- Crane J (1954) Spectral reflectance characteristics of butterflies (Lepidoptera) from Trinidad, B. W. I. *Zoologica* 39: 85–115
- Darwin C (1909) *The Descent of Man and Selection in Relation to Sex*. J. Murray, London
- Eisner T, Silberglied RE, Aneshansley D, Carrel JE, Howland HC (1969) Ultraviolet videoviewing: the television camera as an insect eye. *Science* 166: 1172–1174
- Fukuda H, Hama E, Kuzuya T, Takahashi A, Takahashi M, Tanaka B, Tanaka H, Wakabayashi M, Watanabe Y (1984) *The Life History of Butterflies in Japan 3*. Hoikusha, Osaka (in Japanese)
- Ghiradella H, Aneshansley D, Eisner T, Silberglied RE, Hinton HE (1972) Ultraviolet reflection of a male butterfly: interference color caused by thin-layer elaboration of wing scales. *Science* 178: 1214–1216
- Hidaka T, Yamashita K (1975) Wing color pattern as the release of mating behavior in the swallowtail butterfly, *Papilio xuthus* L. (Lepidoptera: Papilionidae). *Appl Ent Zool* 10: 263–267
- Kawazoé A, Wakabayashi M (1976) *Coloured Illustrations of the Butterflies of Japan*. Hoikusha, Osaka (in Japanese)
- Kühn A (1927) Über den Farbensinn der Bienen. *Z vergl Physiol* 5: 762–800
- Lederhouse RC, Scriber JM (1996) Intrasexual selection constrains the evolution of the dorsal color pattern of male black swallowtail butterflies, *Papilio polyxenes*. *Evolution* 50: 717–722
- Lutz FE (1933) “Invisible” colors of flowers and butterflies. *Nat Hist* 33: 565–567
- Magnus D (1958) Experimentelle Untersuchungen zur Bionomie und Ethologie des Kaisermantels *Arginnis paphia* L. (Lep. Nymph.). *Z Tierpsychol* 15: 397–426
- Makino K, Satoh K, Koike M, Ueno N (1952) Sex in *Pieris rapae* L. and the pteridin content of their wings. *Nature* 170: 933–934
- Mazokhin-Porshniakov GA (1957) Reflecting properties of butterfly-wings and role of ultra-violet rays in the vision of insects. *Biophysics* 2: 352–362
- Nekrutenko YP (1965) ‘Gynandromorphic effect’ and the optical nature of hidden wing-pattern in *Gonepteryx rhamni* L. *Nature* 205: 417–418
- Obara Y (1970) Studies on the mating behavior of the white cabbage butterfly, *Pieris rapae crucivora* Boisduval. III. Near-ultraviolet reflection as the signal of intraspecific communication. *Z vergl Physiol* 69: 99–116
- Obara Y, Hidaka T (1968) Recognition of the female by the male, on the basis of ultra-violet reflection, in the white cabbage butterfly, *Pieris rapae crucivora* Boisduval. *Proc Japan Acad* 44: 829–832
- Obara Y, Majerus MEN (2000) Initial mate recognition in the British cabbage butterfly, *Pieris rapae rapae*. *Zool Sci* 17: 725–730
- Roland J (1978) Variation in spectral reflectance of alpine and arctic *Colias* (Lepidoptera: Pieridae). *Can J Zool* 56: 1447–1453
- Rutowski RL (1977) The use of visual cues in sexual and species discrimination by males of the small sulphur butterfly *Eurema lisa* (Lepidoptera, Pieridae). *J Comp Physiol* 115: 61–74
- Rutowski RL (1981) Sexual discrimination using visual cues in the checkered white butterfly (*Pieris protodice*). *Z Tierpsychol* 55: 325–334
- Saigusa T, Odagiri K (2000) Recent advances in studies of the “Zephyrus” hairstreaks (Lepidoptera, Lycaenidae). *Gekkan-Mushi* 348: 2–9 (in Japanese)
- Shirôzu T, Yamamoto H (1956) A generic revision and the phylogeny of the tribe Theclini (Lepidoptera; Lycaenidae). *Sieboldia* 1: 329–421
- Silberglied RE (1979) Communication in the ultraviolet. *Ann Rev Ecol Syst* 10: 373–398
- Silberglied RE (1984) Visual communication and sexual selection among butterflies. In “*The Biology of Butterflies*” Ed by R Vane-Wright, P Ackery, P DeVries, Academic Press, New York, pp 207–223
- Silberglied RE, Taylor OR (1973) Ultraviolet differences between the sulphur butterflies, *Colias eurytheme* and *C. philodice*, and a possible isolating mechanism. *Nature* 241: 405–408

- Silberglied RE Taylor OR Jr (1978) Ultraviolet reflection and its behavioral role in the courtship of the sulfur butterflies *Colias eurytheme* and *C. philodice* (Lepidoptera, Pieridae). Behav Ecol Sociobiol 3: 203–243
- Weiss HB (1943) The group behavior of 14,000 insects to colors. Ent News 54: 152–156
- Yonekubo T, Saito T (1973) Studies on *Chrysozephyrus ataxus kirishimaensis* Okajima with reference to construction of Suzuka Toll Road. VI. Electrophysiological study on the vision of *Chrysozephyrus ataxus kirishimaensis* Okajima. Nat Sci Stud Concerning Suzuka Toll Road, Sci Res Group of Mie Pref 147–156

(Received August 2, 2001 / Accepted October 30, 2001)

Appendix. A list of specimens used in the present experiments.

Chrysozephyrus smaragdinus

CS1	12-VII-2000	Kinasa, Nagano
CS2	9-VII-1995	Mt. Hira, Shiga
CS3	11-VII-2000	Kinasa, Nagano
CS4	10-VII-1984	Takizawa, Iwate
CS5	10-VII-1984	Takizawa, Iwate
CS6	19-VII-1998	Mt. Iwaki, Aomori
CS7	11-VII-1993	Sakyo, Kyoto
CS8	11-VII-2000	Kinasa, Nagano
CS9	22-VI-2000	Oto village, Wakayama
CS10	11-VII-2000	Kinasa, Nagano
CS21	18-VII-1998	Mt. Iwaki, Aomori

Chrysozephyrus brilliantinus

CB1	31-VII-1982	Kitasaku-gun, Nagano
CB2	9-VII-1983	Sakyo, Kyoto
CB3	22-VII-2000	Mt. Iwaki, Aomori
CB4	20-VII-1998	Mt. Iwaki, Aomori
CB5	20-VII-1998	Mt. Iwaki, Aomori
CB6	20-VII-1998	Mt. Iwaki, Aomori
CB7	10-VII-1995	Mt. Hira, Shiga
CB8	20-VII-1999	Mt. Iwaki, Aomori
CB9	20-VII-1998	Mt. Iwaki, Aomori
CB10	20-VII-1998	Mt. Iwaki, Aomori
CB21	9-VII-1983	Sakyo, Kyoto

Chrysozephyrus hisamatsusanus

CH1	4-VII-1983	Sakyo, Kyoto
CH2	1-VII-1984	Sakyo, Kyoto
CH3	18-VI-1998	Mikata-gun, Hyogo
CH4	5-VII-2000	Mikata-gun, Hyogo
CH5	5-VII-2000	Mikata-gun, Hyogo
CH21*	7-V-1999	Otsu, Shiga

Chrysozephyrus ataxus

CA1	3-VIII-1997	Komono-gun, Mie	
CA2	25-VII-1984	the Hatenashi range, Wakayama	
CA3	10-VII-1994	the Hatenashi range, Wakayama	Goto
CA4	29-VII-2000	Numazu, Shizuoka	Okazaki
CA5	29-VII-2000	Numazu, Shizuoka	Okazaki
CA21	12-VIII-1993	the Hatenashi range, Wakayama	

* reared. Collection site of the egg and date of emergence are shown.

The right column indicates the collector who provided the specimen.