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Overlapping Distribution of Two Groups of the Butterfly *Eurema hecabe* Differing in the Expression of Seasonal Morphs on Okinawa-jima Island

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ABSTRACT—In Japan, *Eurema hecabe* (L.) has two geographically separated groups (subtropical and temperate) differing not only in the color pattern expression of the wings associated with ovarian arrest, but also in the fringe color of the wings and host-plant utilization. In a field survey (Kato, 1999), it was found that individuals with different fringe color of the forewing (brown or yellow type) inhabit Okinawa-jima Island located in north of the subtropical region, and that fringe-color is linked with seasonal morph expression. In the present study, rearing experiments were done to investigate whether these sympatric individuals are different forms within one species or belong to different species. The results show that each population of brown- and yellow-types maintained its own seasonal morph response to photoperiod and temperature through three generations. Host-plant utilization by the larvae and the fringe-color also differed between them and was maintained. These findings strongly suggest that *E. hecabe* of Okinawa-jima Island is divided into two distinct populations, and that one belongs to the temperate and the other to the subtropical group.

INTRODUCTION

Geographical variations in diapause and other seasonal adaptations of insects have been studied within the same species or among closely related species (Danilevsky, 1961; Danks, 1987; Tauber *et al*., 1986). Such variations come from geographical differences in climatic conditions, but are primarily based on genetic differences. Furthermore, for phytophagous insects living in the temperate or northern regions, larval food-plant supply during winter is limited, and climatic adaptation is often linked with host selection (Masaki and Yata,1988; Scriber, 1982). Therefore, comparisons between tropical or southern and temperate or northern populations may be important in understanding the evolution of climatic adaptations, including host selection.

The pierid butterfly *Eurema hecabe* (L.) occurs widely from the Oriental tropics through subtropical to temperate zones. It is multivoltine and shows seasonal polyphenism in wing color-pattern (summer or wet-season morph and autumn or dry-season morph) (Yata, 1989). In Japan, this species consists of (at least) two geographically separated groups differing in seasonal expression of wing color pattern; one occurs in the temperate main islands (e.g., Honshu) where the adults (autumn morphs) overwinter with reproductive diapause while the other occurs in the subtropical Ryukyu Islands (e.g., Ishigaki-jima Is.) where the diapause is less clear (Fukuda *et al*., 1982). We experimentally demonstrated that these populations from Honshu and Ishigaki-jima Is. differ in the seasonal morph response to photoperiod and temperature and in the degree of ovarian arrest (Kato and Sano, 1987; Kato and Handa, 1992). The degree of autumn morph response is higher in the temperate population than in the subtropical one. These populations also differ in their use of host plants, which has climatic dependence (Kato *et al*., 1992). Thus, it would be interesting to know the precise geographical distribution and ecological characteristics of other populations.

In a recent field survey (Kato, 1999), it was found that individuals with different characters inhabit Okinawa-jima Island (Fig. 1), which is located between Ishigaki-jima Is. and the main islands of Japan. These individuals have two kinds of fringe color (brown and yellow types). Fringe-color type is linked with seasonal morph expression. Furthermore, butterflies of the brown type have seasonal wing pattern similar to the individuals from Ishigaki-jima while those of the yellow type resemble those from Honshu.

In the present study, rearing experiments were done using individuals from Okinawa-jima Is. Specifically, fringe color and seasonal morph response, including host use, were compared among the individuals of the Island.

MATERIALS AND METHODS

Adult females of brown or yellow type were caught at several localities (Kato, 1999) on Okinawa-jima Is. (26.1°N at Naha), Okinawa Prefecture, in May 1993 and 1994.

To compare the influence of photoperiod and temperature on seasonal morph response, wild-caught females (summer morph) of brown or yellow type were used. Eggs obtained from one female were

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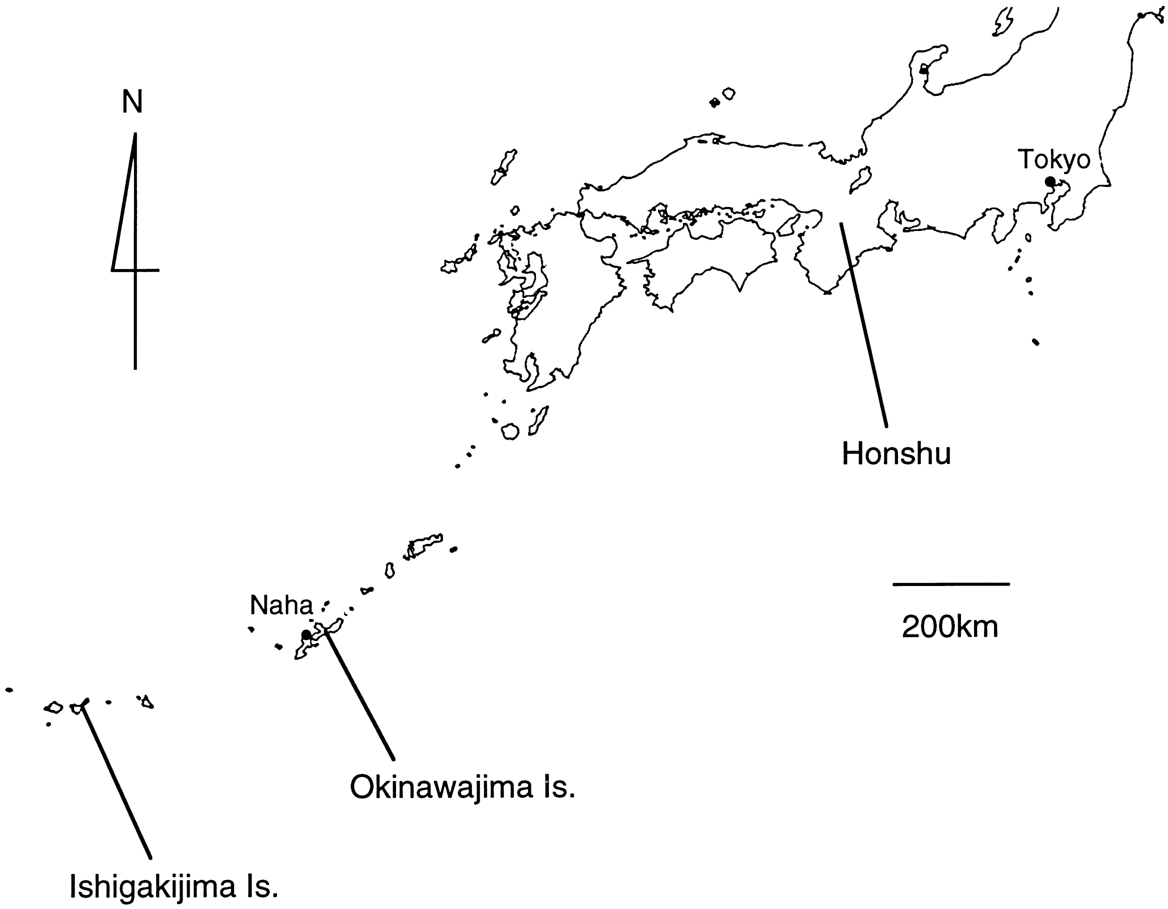

Fig. 1. A map of the Ryukyu Islands and neighboring mainlands of Japan.

divided into four groups, and kept in plastic cups (9cm×5cm) under different environmental conditions (20 or 25°C and 12L–12D or 16L–8D). Fresh cuttings of *Albizia julibrissin* (Fabacaeae), an adequate foodplant for subtropical or temperate populations (Kato *et al.*, 1992) were provided. Further, cluster analysis of the females based on data of wing response at 20°C and 12L–12D was done using STATISTICA (StatSoft Inc.).

To examine whether wing morph response and fringe color are inherited, second and third generations were obtained from the offspring of each type of female, and reared under both autumn-morph (12L–12D at 20°C and summer-morph (16L–8D at 25°C) inducing conditions. In this experiment, other legume plants (*Ormocarpum cochinchinense* for the offspring of the brown type and *Lespedeza cuneata* for those of the yellow type) were provided as food.

To know whether expressions of the wing morph and fringe color are linked with host use, eggs or young larvae (1st–3rd instar) were collected from various host-plant species in the field in May 1993 and 1994, and then reared on the same host species under 20°C and 12L–12D, or 25°C and 16L–8D. Wing morph and fringe-color of the adults obtained were recorded. For the fringe-color, individuals with a yellow fringe were referred to as yellow type while those with a brown or brown/yellow one were designated as brown type (Kato,1999) (Fig. 2).

The classification of wing color patterns followed Kato and Handa (1992). For the forewing upperside, the area and shape of the black border was classified into seven grades (score B0 is the typical summer morph while score B6 is the typical autumn morph), while for the forewing underside, the strength of the subapical marking was classified into four grades (score M0 to score M3) (Fig. 3).

To compare ovarian development between the offspring of each fringe-color type, newly eclosed females of summer (B0–B1) and autumn morphs (B3–B4 and B5-B6 for each type) were kept individually under 12L–12D at 25°C in plastic cups (11 cm×6 cm) provided with a cotton ball soaked with 10% sucrose solution. Females of various ages after eclosion were dissected and the ratio of females having mature eggs with a hard chorion was recorded.

RESULTS

Wing morph response and fringe-color of individuals from wild-caught females of each type

(a) Wing morph: Table 1 shows the range of B-score and its median in individuals from brown- or yellow-type females under various environmental conditions. At 20°C and 12L–12D, both males and females showed significant differeces in B-score between the brown type and yellow one, and the median values of the offspring were higher for the yellow type than for the brown one. At 20°C and 16L–8D, only the median of male offspring was siginificantly different between them, and it was higher for the brown type than for the yellow one. At 25°C and 12L–12D, the median B-score was higher for the brown type than for the yellow one in the males but not in the females. At 25°C and 16L–8D, the median B-score was low and its range did not differ between the types.

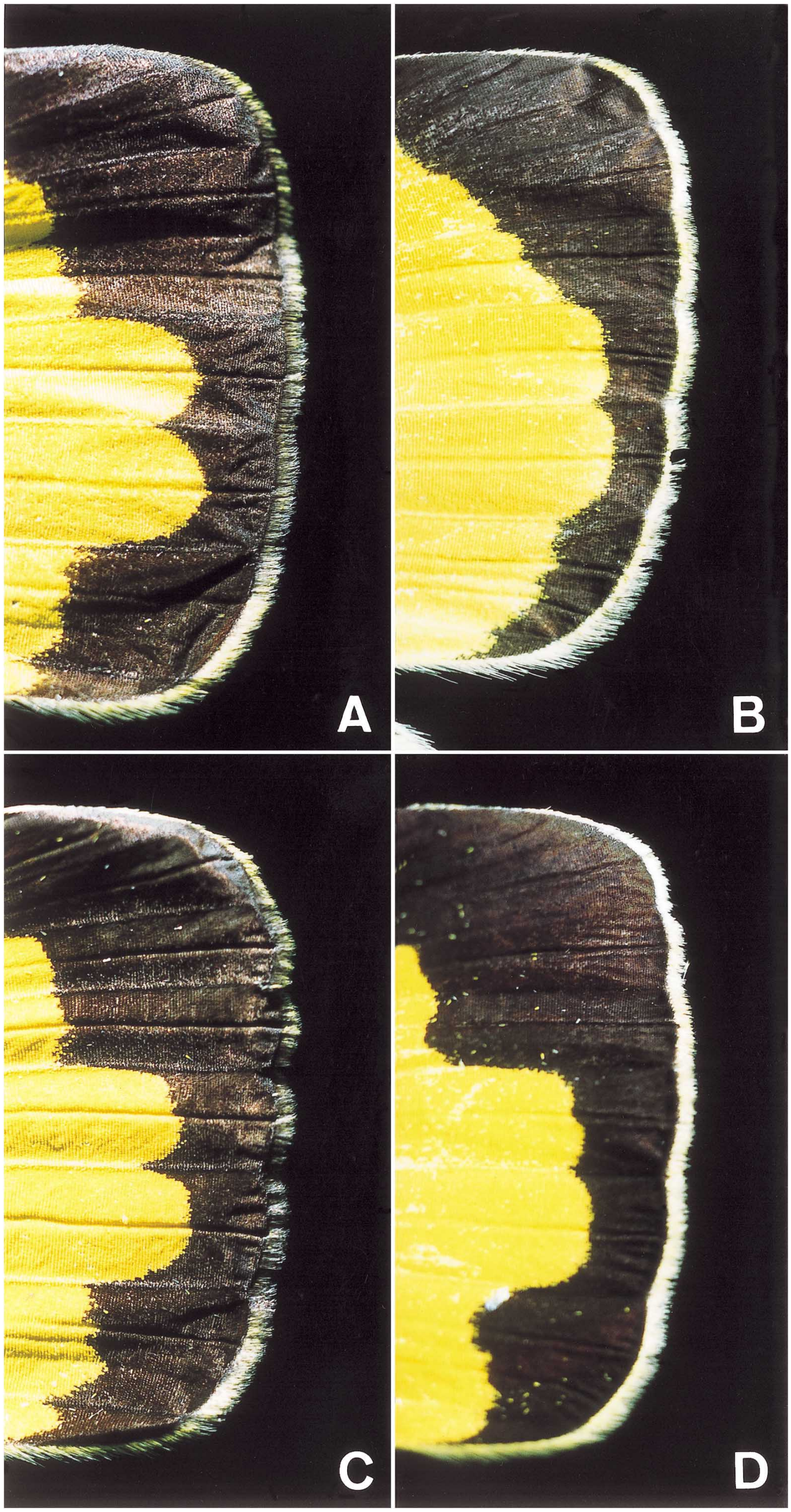

Fig. 2. Fringe coloration of forewing upperside in *E. hecabe* (L) from Okimawa-jima Is. and neighboring regions.Brown (A) and yellow (B) type individuals from Okinawa-jima Is. Brown type from Ishigaki-jima Is.(C) and yellow type individuals from Honshu (D).

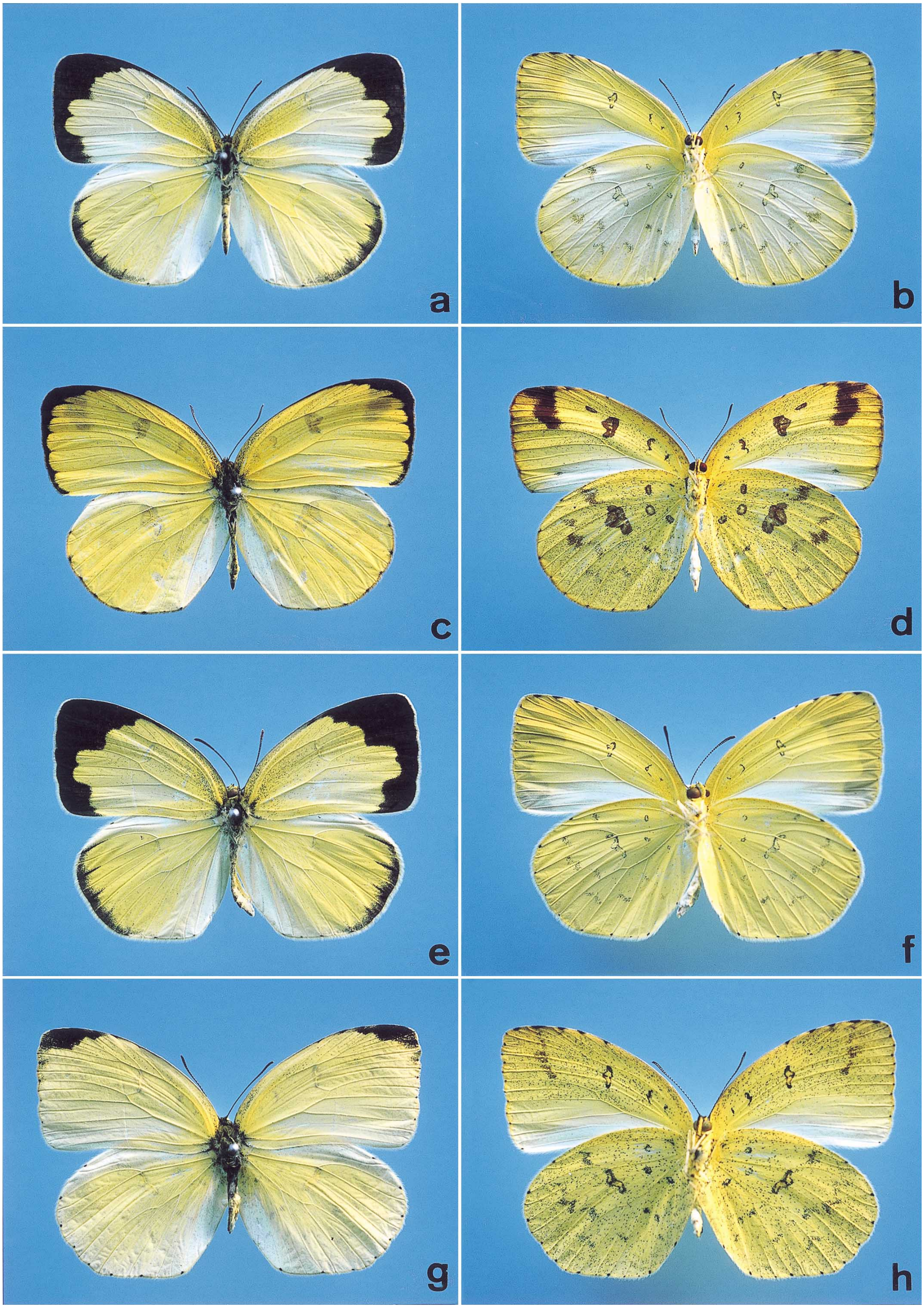

Fig. 3. Summer and autumn morphs of the adults in *Eurema hecabe* (L.) from Okinawa-jima Is..(a–d) Brown type. (e–g) Yellow type. (a) Upperside (B0 for B-score) and (b) underside (M0 for M-score) of typical summer morphs. (c) Upperside (B4) and (d) underside (M3) of typical autumn morphs. (e) Upperside (B0 for B-score) and (f) Underside (M0 for M-score) of typical summer morphs. (g) Upperside (B6) and (d) Underside (M1) of typical autumn morphs. Here the female specimens are shown.

Table 1. Median values of B-core and its range in siblings from the wild-caught females of the brown and yellow type under various rearing conditions

Sex of offspring	Parents		20°C		25°C	
	Fringe color	No	12L–12D	16L–8D	12L–12D	16L–8D
Male	Brown	18	4 (3–4)	2 (1–2.5)	2.5 (1–4)	1.2 (0–3)
			**	**	*	*
	Yellow	13	5 (4–5.5)	0.5 (0–2)	0 (0–3)	0 (0–1)
Female	Brown	18	3.7 (2–4)	0 (0–1.5)	0 (0–3)	0 (0–0.5)
			**			
	Yellow	13	5.5 (5–6)	0 (0–2)	0 (0–2.5)	0 (0–0.5)

*p < 0.05, **p < 0.01, Significant, Mann-Whitney U-test.

Table 2. Median values of M-core and its range in siblings from the wild-caught females of the brown and yellow type under various rearing conditions

Sex of offspring	Parents		20°C		25°C	
	Fringe color	No	12L–12D	16L–8D	12L–12D	16L–8D
Male	Brown	18	2 (1–2.5)	0 (0–1.5)	0.5 (0–1)	0 (0)
					*	
	Yellow	13	1.5 (1–2.5)	0 (0–0.5)	0 (0–0.5)	0 (0)
Female	Brown	18	3 (2–3)	1 (0–2)	0 (0–2.5)	0 (0)
			**	**	**	
	Yellow	13	2 (1–2)	0 (0)	0 (0)	0 (0)

*p < 0.05, **p < 0.01, Significant, Mann–Whitney U–test.

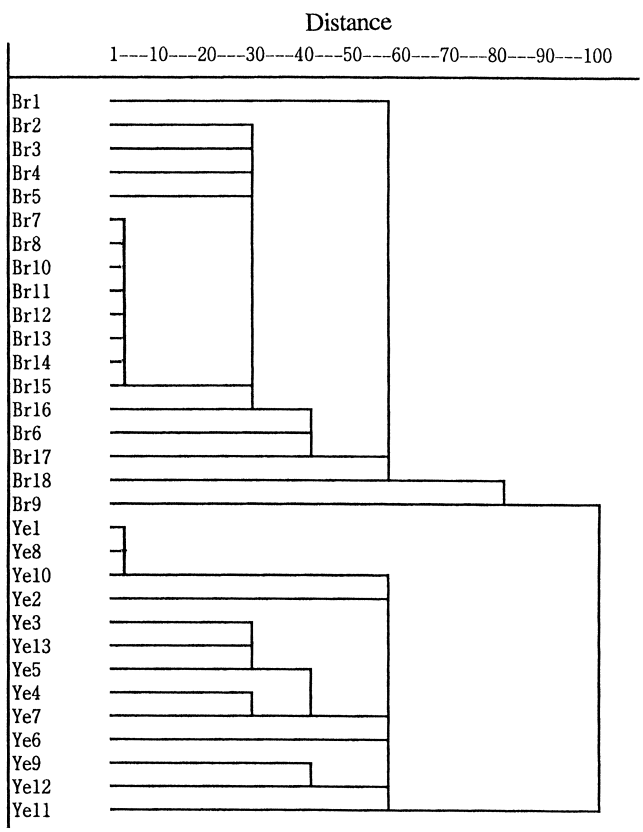

Fig. 4. Clustering of wild-caught females (brown and yellow types) based on median values of B- and M-scores of the first generation at 20°C and 12L–12D.

At 20°C and 12L–12D, although M-score level was higher for the brown type than for the yellow one in both sexes, the median score of the males did not differ between the brown and yellow types while that of the females differed significantly between them (Table 2). At 20°C and 16L–8D, the median of the males did not differ between the brown and yellows, but that of the females differed significantly. At 25°C and 12L–12D, the median M-score was higher for the brown type than for the yellow one for both sexes. At 25°C and 16L–8D, the means of M-scores did not differ between the brown and yellow types. All scored M0 for both types.

Furthermore, cluster analysis of 31 females based on median B- and M-score values of their offspring was done. Fig. 4 shows that wild-caught females were clearly divided into two separate clusters depending on their fringe-color.

(b) Fringe-color: Table 3 shows the relationship of fringe color between wild-caught females and their offspring. All eighteen females of the brown type produced individuals of the same type in the first generation. However, 10 out of 13 females of the yellow type produced individuals of yellow type in all cases, and the remaining three females produced individuals of both brown and yellow types, although in these cases, the percentage of brown type individuals was very low (8.6% and 7.0%).

Wing morph response and fringe-color in the second and third generations

The production of B5 and B6 wing morphs or of M3 morphs in the 2nd and 3rd generations was examined. The results are shown in Tables 4, 5 and 6.

Table 3. Relationship between fringe color of wild-caught females of the brown and yellow type and that of offspring

Fringe color of parents	No	Individuals producing the offspring of		
		Brown type	Brown and yellow type	Yellow type
Brown type	18	18 (778)	0 (–)	0 (–)
Yellow type	13	0 (–)	3 (86)	+ 10 (413)

Numerals in parentheses show total number of offspring. + τ=0.941, p<0.01

Table 4. Median values of B–score and its range in siblings of the 2nd and 3rd generations of the brown and yellow type under two rearing conditions

Sex of Offspring	Fringe color of parents	2nd			3rd		
		No	20°C 12L–12D	25°C 16L–8D	No	20°C 12L–12D	25°C 16L–8D
Male	Brown	4	4 (3.5–4)	0.75 (0–1.5)	5	4 (3–4)	0 (0–0.5)
	Yellow	5	* 5 (4–5.5)	0 (0–1)	7	** 5 (4.5–5.5)	0 (0)
Female	Brown	4	4 (3.5–4)	0 (0–0.5)	5	4 (4)	0 (0)
	Yellow	5	** 5.5 (5–6)	0 (0)	7	** 6 (5.5–6)	0 (0–0.5)

*p<0.05, **p<0.01, Significant, Mann–Whitney U–test.

Table 5. Median values of M-score and its range in siblings of the 2nd and 3rd generations of the brown and yellow type under two rearing conditions

Sex of Offspring	Fringe color of parents	2nd			3rd		
		No	20°C 12L–12D	25°C 16L–8D	No	20°C 12L–12D	25°C 16L–8D
Male	Brown	4	2 (1.5–3)	0.75 (0–1)	5	4 (3–4)	0 (0–0.5)
	Yellow	5	** 1.75 (1–2)	0 (0–1)	7	5 (4.5–5.5)	0 (0)
Female	Brown	4	3 (2.5–3)	0 (0)	5	4 (4)	0 (0)
	Yellow	5	** 1 (1–1.5)	0 (0)	7	** 6 (5.5–6)	0 (0–0.5)

*p<0.05, **p<0.01, Significant, Mann–Whitney U–test.

Table 6. Comparison of fringe color of adult wings in the 2nd and 3rd generations

Generation	Parents		Individuals producing the offspring of		
	Fringe color	No	Brown type	Brown and yellow type	Yellow type
2nd	Brown	4	4 (148)	0 (–)	0 (–)
	Yellow	5	0 (–)	1 (20)	+ 10 (413)
3rd	Brown	5	5 (165)	0 (–)	0 (–)
	Yellow	7	0 (–)	1 (23)	++ 6 (127)

Numerals in parentheses show total number of offspring. + τ=0.941, p<0.01. ++ τ=0.9923, p<0.01

(a) Wing morph: In both sexes of the 2nd and 3rd generations, the median B-score significantly differed between the brown and yellow types at 20°C and 12L–12D (Table 4). However, at 25°C and 16L–8D, the scores of both sexes were low and did not differ between them in either the 2nd or the 3rd generation.

In both sexes of the 2nd generation, the median M-score significantly differed between the brown and yellow types, while in the 3rd generation only the median of the females differed significantly (Table 5). However, its range was higher for the brown type than for the yellow type in the males of the 3rd generation.

(b) Fringe color: In the 2nd and 3rd genarations, all progeny from brown type females were of the brown type (Table 6). However, offspring of the 2nd and 3rd generations from yellow type females were of the yellow type with the exception of offspring from two females, which produced individuals of the yellow and brown type, although in these cases, the percentage of the brown type individuals was low (8.3% and 2.9%).

Wing morph response and fringe color of individuals from different host-plant species

(a) Wing morph: When the larvae from the plant species *Ormocarpum cochinchinense*, the main host species in the population of Ishigaki-jima Is. (Kato *et al*., 1992), were reared at 20°C and 12L–12D on this plant, the median B-score of the upperside was B3 or B4 and no individuals gave values of B5 or higher (Fig. 5). Conversely, when larvae from three other plant species, *i.e. Lespedeza cuneata* (Fabaceae), *Berchemia lineata* (Rhamnaceae) and *Rhamnus liukiuensis* (Rhamnaceae) were reared on their respective hosts at 20°C and 12L–12D, medians ranged from B3 to B6, and individuals with scores of B5 and B6 were produced. In particular, a significant difference in the median B-score was found between individuals from *O. cochinchinense* and the other three plant species.

For the underside (Fig. 5), median M-scores was M2 or M3 for *O. cochinchinense.* From the other three host plants, the highest score was M2, with medians ranging from M0.5 to M2. However, only the females showed a significant difference in the median M-score. When the larvae were reared at 25°C and 16L–8D, the median B-and M-scores were generally low for all host-plants, although in individuals from *O. cochinchinense* the range of B score was relatively wide. No difference in the median B-score was found in any cases.

(b) Fringe color: The fringe color of individuals from each host species is shown in Table 7. All individuals from *O. cochinchinense* were of the brown type while those from the other three hosts were mainly of the yellow type.

Ovarian maturation of adult females

In Fig. 6, the changes in the percentage of females with mature eggs are compared between females of the brown and yellow types, and between summer and autumn morphs. For the yellow type females, ovarian maturation was lower in the autumn morphs than in the summer ones at 5 or 7 days, while for the brown type females the maturation did not differ significantly between them. However it was found that level of the maturation in autumn morphs tended to be slightly low during those days.

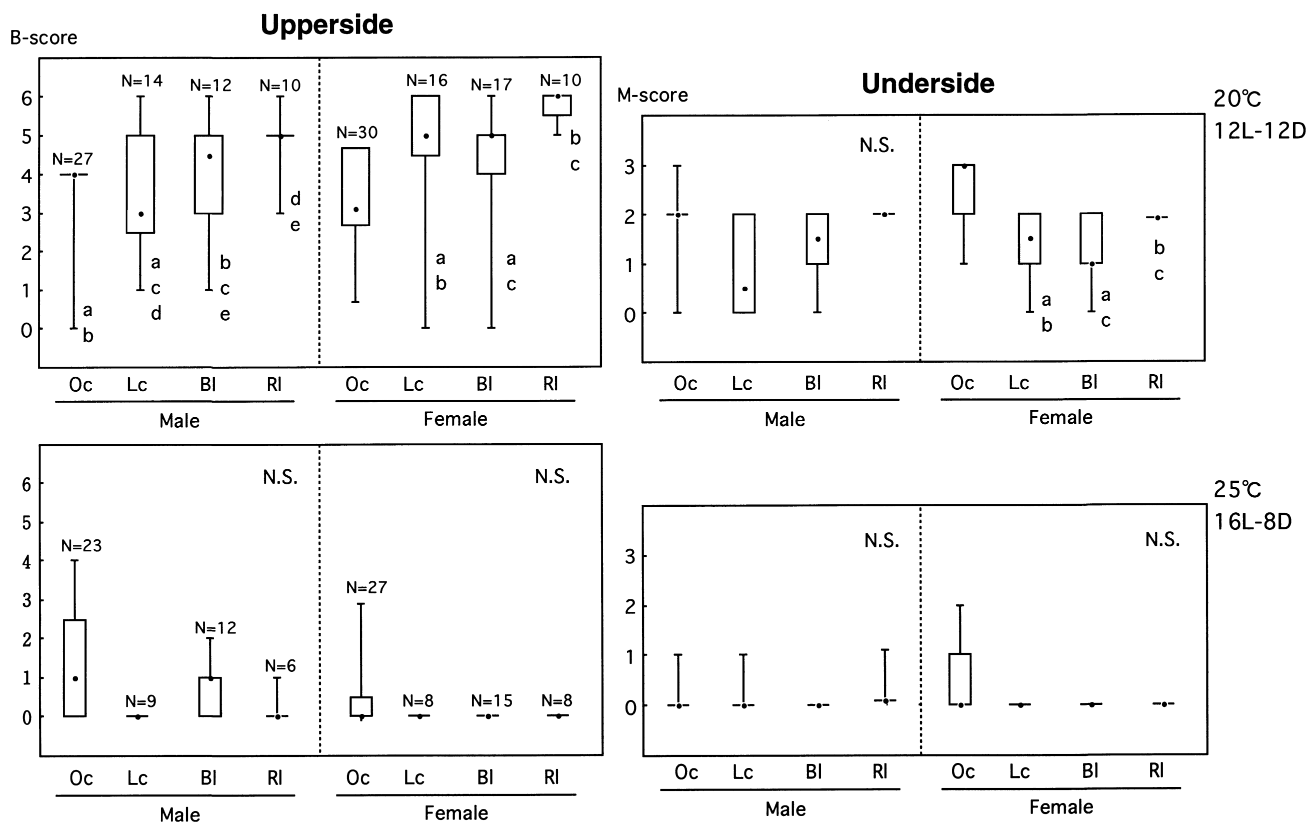

Fig. 5. Median values of B-score (A) and M-score (B), and their ranges for individuals on different host plants in the field. Oc: *Ormocarupum cochinchinense*, Lc: *Lespedeza cuneata*, Bl: *Berchemia lineata*, Rl: *Rhamnus liukiuensis*. Black dot and bars show median value and range, respectively. Box shows interquartiles. P>0.05 (Mann-Whitney U test), non-significant between the common letters within the same frames. N.S. shows non-significance among categories within the same frames. The p-values were adjusted by a sequential Bonferroni procedure (Rice, 1989).

Table 7. Comparison of fringe color among adults from individuals on different host plants in the field

Fringe color	Plant species			
	Oc	ab Lc	ac Bl	bc Rl
Brown	107	6	3	3
Yellow	0	42	52	34
Total	107	58	55	37

Numerals are sample size.
Oc: *Ormocarpum cochinchinense*, Lc: *Lespedeza cuneata*, Bl: *Berchemia lineata*, Rl: *Rhamnus liukiuensis*.
p>0.05 (chi-square test), non-significant between the common letters.
The p values were adjusted by a Bonfferoni procedure (Rice, 1989).

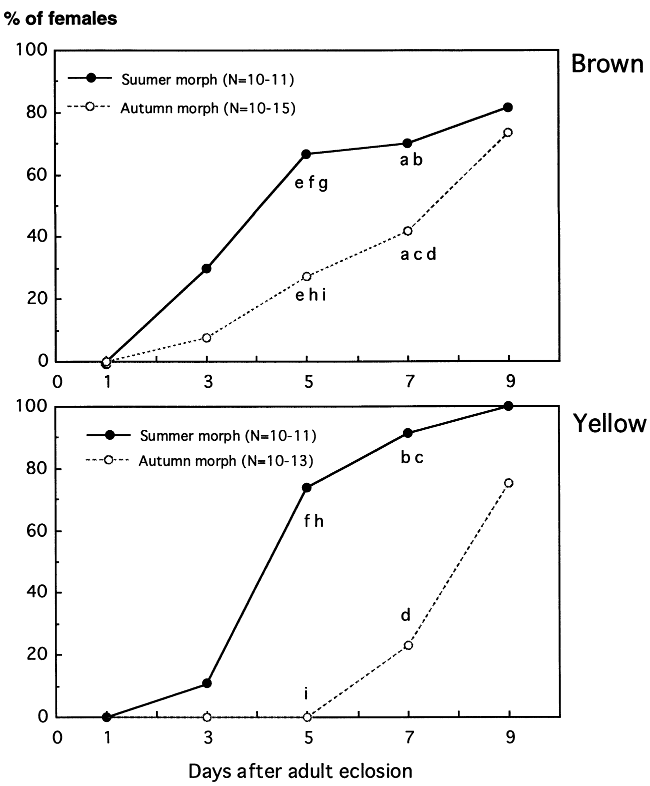

Fig. 6. Comparison of ovarian maturation between brown- and yellow-type females. P>0.05 (Fisher's exact probability test), non-significant between the common letters on the same days. The p-values were adjusted by a sequential Bonferroni procedure (Rice, 1989).

DISCUSSION

A field observation (Kato, 1999) showed that wild-caught individuals of *E. hecabe* on Okinawa-jima Is. were classified into two types (brown and yellow) based on fringe color of the forewing upperside, this division being linked with seasonal morph expression. The aim of the present study was to clarifiy whether these variations on Okinawa-jima Is. are forms within a single species or come from two distinct populations.

The present results clearly show that fringe color (brown or yellow type) of the forewing upperside and wing morph response are inherited over three generations. That is, all progeny from brown type females had fringes of the brown type while nearly all of those from yellow type females had yellow fringes. Wing morph response to photoperiod and temperature also differed between offspring from brown and yellow type females. Reared at 20°C and 12L–12D, particularly, the B-scores of the former were up to B4 while those of the latter were B5 or B6 for the upperside forewing. Photoperiodic differences were also found in the M-scores of the underside forewing between offspring of these types of female. Such a difference in M-score was clear in the females compared to the males. Ovarian maturation in the adult females also differed between the brown type and yellow type populations. These strongly suggest that the Okinawa-jima 'population' consists of two distinct populations.

The present experiments where individuals from different host plant species were reared in the laboratory, showed that all individuals from *O. chochinchinense* have the fringe-color of the brown type while nearly most individuals from the other three plant species (*Lespedeza cuneata*, *Berchemia lineata* and *Rhamnus rhiukiuensis*) have that of the yellow type. For the latter, a few individuals were of the brown type. The cause of these few exceptions is unknown. Wing morph response to 20°C and 12L–12D, but not to 25°C and 16L–8D, was also different between individuals from *O. chochinchinense* and those from the other three plants. It was observed in the field that females with different fringe colors oviposit on different host species described here (Kato, 1999). Therefore, each population of this species on Okinawa-jima Is. seems to utilize different species as host.

The range of wing morph response by individuals from the brown type females on Okinawa-jima Is. was similar to that from a more southern subtropical population (Ishigaki-jima Is.: 24.3°N) (Kato and Handa, 1992), with wing morph response of individuals from the yellow type being similar to those from temperate populations (Tokyo: 35.7°N) (Kato and Sano, 1987). Differences in fringe-color and host-species also exist between two populations on this Island and between the populations of Ishigaki-jima and Tokyo. Thus, it is considered that one population from Okinawa-jima belongs to the subtropical group and the other to the temperate group.

However, it may be noted that geographical differences were found within the subtropical and temperate groups. For the brown type population of Okinawa-jima Is., scores of wing upperside at a short photoperiod were higher (scores B3 and B4) than those from a more southern subtropical region (Ishigaki-jima Is.) in which the score of most individuals were up to B3 (Kato and Handa, 1992). For the yellow type population of Okinawa-jima Is., most morphs scoring B4 were produced at 20°C while morphs of scores B5 and B6 were produced at 25°C but not at 20°C. This contrasts with the population from the mainland (Tokyo) in which autumn morphs with such scores were produced both at 20°C and 25°C (Kato and Sano, 1987). Thus, it is clear that, even within the same climatic group, the expression of the seasonal mophs varies with latitude.

It is known that in the temperate region, host plant species of *E. hecabe* commonly belong to the Fabaceae while in the subtropics, Fabaceae, Rhamnaceae and Euphorbiaceae species are utilized (Yata, 1989). In the present observations, however, use of Rhamnaceae was clearly limited to the yellow type population. Unpublished data show that the larvae from temperate Honshu, which naturally feed on temperate species of Fabaceae, can also grow on Rhamnaceae. Thus, Rhamnaceae is a host-plant for the temperate group, but not for the subtropical one.

The fringe color of the forewing upperside in *E. hecabe* is normally yellow in the temperate region of Japan (Kawazoe and Wakabayashi, 1976; Shirozu 1960). However, Kawazoe and Wakabayashi (1976) noticed that some individuals of *E. hecabe* have the brown fringe in the southern parts of the Ryukyu Islands. I confirmed this for the population from Ishigaki- jima Is. where all individuals caught are of the brown type (Kato, 1999). *Eurema hecabe* from tropical regions also have brown fringes (Kato and Kimura, 1994). Furthermore, in Taiwan (Shirozu, 1986) and some other parts of the Ryukyu Is. (unpublished observations), the situation is similar to that in Okinawa-jima Is. where butterflies of both fringe-color types are seen. Considering the present results, the possibility remains that such butterflies from outside Okinawa-jima Is., which differ in fringe color, may also be differenciated into two separate populations.

In conclusion, Japanese *Eurema hecabe* should be divided into two distinct groups, on the basis of differences in seasonal morph response, ovarian maturation, larval host-use and fringe color of the adults. In addition, it was recently reported that area of UV reflection on the male wing differed between temperate and subtropical groups of this species (Matsuno, 1999). It would be interesting to know how and where these two groups differentiated and evolved, and the exact extent of their differentiation. To do so, analyses of genetic and reproductive relationships among and between neighboring populations are needed.

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