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MALE MATE-LOCATING BEHAVIOR IN THE COMMON EGGFLY, *HYPOLIMNAS BOLINA* (NYMPHALIDAE)

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ABSTRACT. The mate-locating behavior of males of the common eggfly, *Hypolimnas bolina,* was studied in north Queensland, Australia. Males defended perching sites used in mate location from about 0900 to 1600 h on clear sunny days. Some popular sites contained the larval foodplant, *Sida rhombifolia,* and individual males defended such sites in many cases for several days or more. The form and outcome of interactions between site occupants and intruding males suggested that residents typically win. Observations on site defense by resident males whose color has been altered suggest that color is not important in the maintenance of residence status. These observations and others suggest that male color pattern may be more important in intersexual than intrasexual interactions.

Additional key words: intrasexual competition, coloration, sexual selection, territoriality.

As part of his presentation of sexual selection theory, Darwin (1874) proposed that the brilliant male coloration found in many species of butterflies evolved because of females preferences for brightly colored males. This hypothesis has been discussed frequently in the literature since Darwin (e.g. Turner 1978, Smith 1984). Although empirical evidence for female choice in butterflies is growing (Rutowski 1985, Krebs & West 1988, Wiernasz 1989) and generally supports Darwin's hypothesis, the female-choice hypothesis has had its detractors (e.g. Wallace 1889, Silberglied 1984).

In his review of butterfly reproductive behavior, Silberglied (1984) reiterated and promoted an alternative hypothesis, namely, that brilliant male coloration evolved in another context of sexual selection, male-male competition. Although he did not specify how coloration would act in this context, he clearly thought that male coloration would mediate male-male interactions. If true, this hypothesis should be especially applicable to those butterfly species in which males defend prime positions at encounter sites, and it makes the prediction that alteration of male color will affect the outcome of their interactions with other males.

The common eggfly, *Hypolimnas bolina* Fabricius (Nymphalidae), is a nymphalid butterfly that is widespread in the Indo-Australian region and sexually dimorphic in color. Males of this species are aggressive and site tenacious (Valentine 1989). Here I describe the reproductive behavior of this species, especially patterns of site occupation and defense in males. This was done to evaluate the function of the males' behavior and in conjunction with experiments and observations that bear on the potential role of male color in interactions with conspecifics.

Males of *H. bolina* have a distinctive dorsal coloration throughout

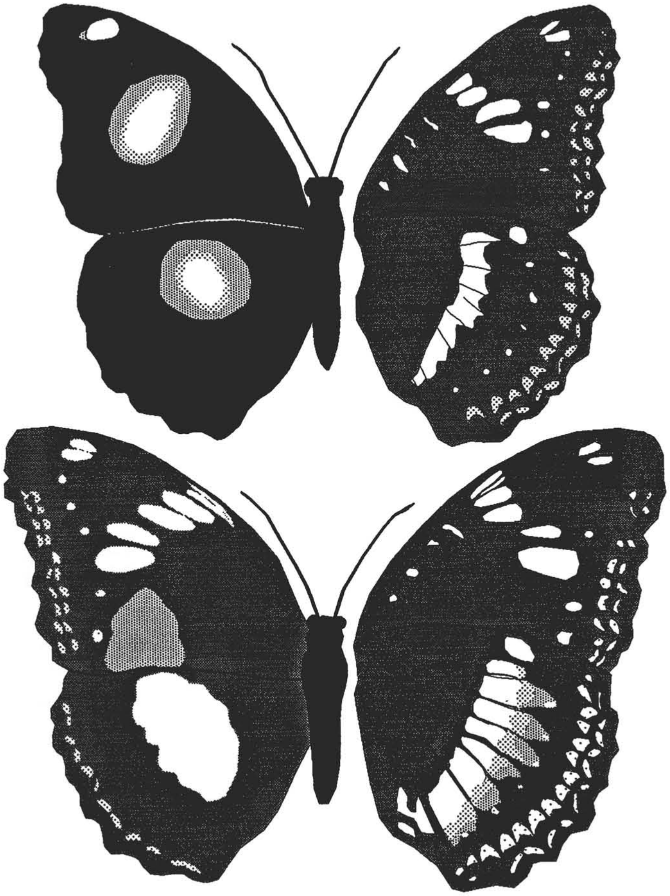

FIG. 1. Dorsal (left) and ventral (right) views of a typical *H. bolina* male (top) and female (bottom).

their range. There is a large white spot near the center of the black background on each wing and a smaller white spot near the tip of each forewing (Fig. 1 top). Each white spot is ringed with violet and the violet extends part way into the white area. The violet coloration associated with the spots is directional and has an ultraviolet component (pers. obs.), as it does in a similarly-colored congener, *H. misippus* Linnaeus (Nymphalidae) (Silberglied 1984). Females are similar in a general way to males, but they vary in color geographically and their dorsal markings are much less brilliant and clearly defined than male markings (Fig. 1; Clark & Sheppard 1975). In addition, they may have large orange spots on the dorsal wing surface. The ventral markings of males and females are similar.

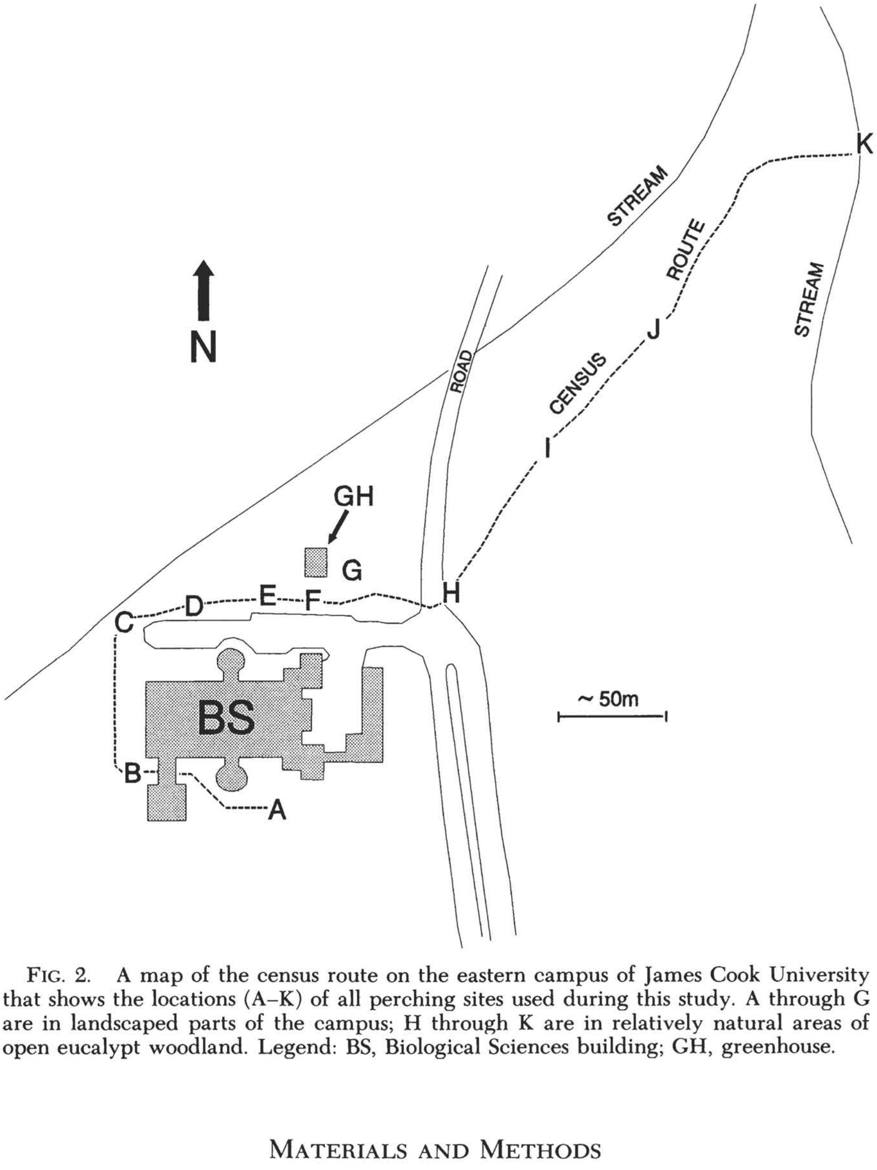

FIG. 2. A map of the census route on the eastern campus of James Cook University that shows the locations (A–K) of all perching sites used during this study. A through G are in landscaped parts of the campus; H through K are in relatively natural areas of open eucalypt woodland. Legend: BS, Biological Sciences building; GH, greenhouse.

MATERIALS AND METHODS

Study Site and Dates

Field observations were made from January to June 1989, on or within 10 km of the campus of James Cook University of North Queensland, Townsville, Australia. The habitat was an open eucalypt woodland with an understory of grasses. The vegetation was denser along water courses where the common eggfly was found most often. Observations also were made on males and females in landscaped and watered areas on campus.

Census Techniques

To document where and when males were most often found, a census route (Fig. 2) was established on campus that was approximately 500 m in length and about evenly divided between landscaped and natural habitats. This route was walked hourly for several days to establish the daily pattern of male activity. Each census took about 20 minutes. The location, identity, and behavior (perched or flying) was recorded for each male seen. However, once the basic patterns were established censuses were taken only at 1000, 1200, and 1400 h.

Two techniques were used to identify individual males. Some were marked with numbers on the hindwings using white correction fluid (Swan brand). This was used infrequently as males subjected to the marking procedure usually abandoned the area and were not seen again. The second technique involved the use of distinctive wing wear patterns. I closely approached and inspected perched males and made detailed notes on tears, beak marks, and imperfections that were distinctive and could be used to recognize individuals.

Observations on Interactions

During the censuses written records were made of any interactions that were observed among males. The form, outcome, and, if measured, the duration of each interaction were recorded. In addition, interactions between conspecific males and heterospecifics were observed and recorded during the experiments described below.

Observations on interactions between males and females were made by releasing hand-reared virgin and mated females near perched males in a large (20 m × 20 m × 3 m) flight cage and on a few occasions in the field. Females were reared on cuttings of *Sida rhombifolia* Linnaeus (Malvaceae) from eggs obtained from field-caught females in oviposition cages in the lab.

Male Color Alteration Protocol

Three groups of males were established. Untreated males were those that were observed without any handling. Treated males, experimental and control, were removed from their territory at about 1530 h, marked with a black marking pen (Pentel N50 permanent marker), given a white letter with correction fluid on the ventral left hindwing, and placed in a glassine envelope. The envelope was then placed on ice for 90 to 120 seconds. After chilling, the treated male was released onto a leaf or branch about 2 m off the ground. Observations on treated males

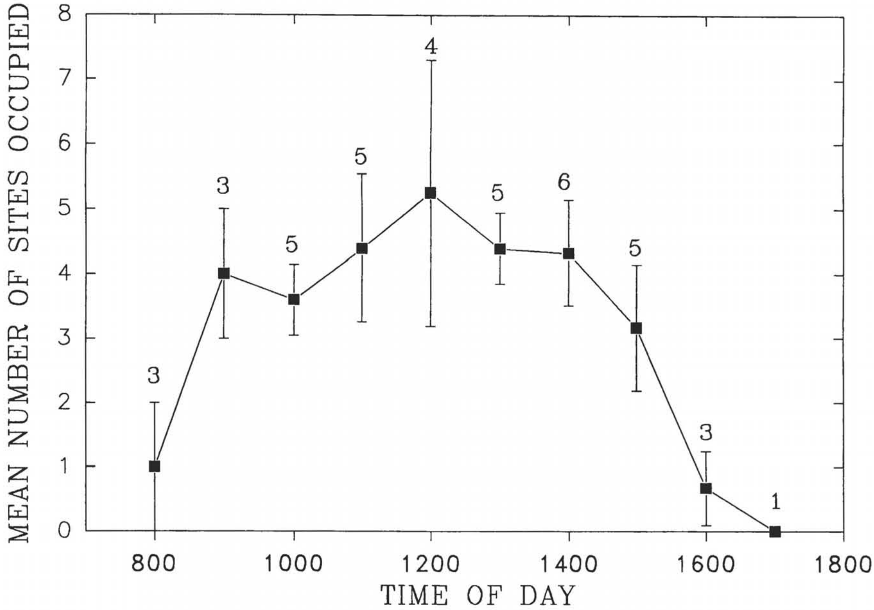

FIG. 3. The relationship between male activity (measured as number of sites occupied) and time of day calculated from data collected 8–10 and 13–15 February 1989. The number over each time period is the number of days of data on which the mean ± 1 SD are based.

were made the following morning if they appeared at the site of capture. There were two groups of treated males: experimentals which had the black pen applied to the white and violet spots on the dorsal wing surface, and controls which had the black pen applied to black areas on the dorsal wing surfaces.

Observations were made on treated and untreated males by arriving at the site in the morning before the subject male arrived. If another male arrived before the subject male, the intruder was removed. This guaranteed that the subject male could reclaim his site without contest and thereby be the clear resident in all cases. I then remained at the site for several hours observing all interactions that occurred.

RESULTS

Daily Pattern of Activity

The greatest number of males was seen along the census route between 0900 and 1400 h on clear sunny days (Fig. 3). On exceptionally windy or rainy days males were not seen along the census route or elsewhere. Males also disappeared if the weather became poor during the middle of the day.

TABLE 1. Descriptions of perching sites A–K shown in Fig. 3 and their relative frequency of occupation as determined from 52 censuses run between 8 and 20 February 1989. Asterisks indicate sites where *Sida rhombifolia* was found growing.

Site	% Censuses occupied	Description
A*	15.4	Single tree about 3 m high and 10 m from other vegetation
B*	23.1	Two trees about 2–3 m high and 2 m apart
C*	5.8	North side of line of tall (>8 m) trees along carpark; faces out onto lawn
D*	50.0	Same as C
E*	34.6	Same as C
F*	7.7	Same as C
G*	67.3	Tree adjacent to greenhouse
H	1.9	Two small (<3 m) trees at beginning of path
I	5.8	Tree on edge of 2-m-wide path cut through tall grass
J	84.6	Same as I
K	61.5	Tall trees along edge of stream channel

Males were seen more often at some points along the census route than others. The locations of these areas are shown in Fig. 2 and their descriptions and relative frequencies of occupation are given in Table 1. All perching areas included trees with low branches and leaves that were used as perches. There were no other obviously distinctive characteristics of perching sites although some of the most frequently occupied sites included moist, shaded understory areas with dense patches of the larval foodplant (*Sida rhombifolia*), which rarely grew to a height of more than 1 m. Little or no *S. rhombofolia* was found along the path between these sites.

Females were seen on the censuses (Fig. 4) between 0900 and 1500 h in the vicinity of the carpark or the greenhouse. The likelihood of seeing a female on a census did not change with time of day during this period. Most were either resting or ovipositing while perched on the larval foodplant, which was abundant in these areas. Ovipositing females laid a single egg on the underside of a *S. rhombifolia* leaf before flying off.

Male Behavior

Each site was occupied by a single male that when not interacting with a conspecific or other animal perched either on the ground in an open area or, most often, 1 to 2 m or more above the ground on the outer leaves of vegetation adjacent to an open area. From their perches, males flew out and chased flying conspecifics as well as other species of butterflies, including *Cressida cressida* Fabricius (Papilionidae), *Danaus hamatus* Macleay (Nymphalidae), *Euploea core* Macleay (Nymphalidae), *Catopsilia pomona* Fabricius (Pieridae), and *Eurema*

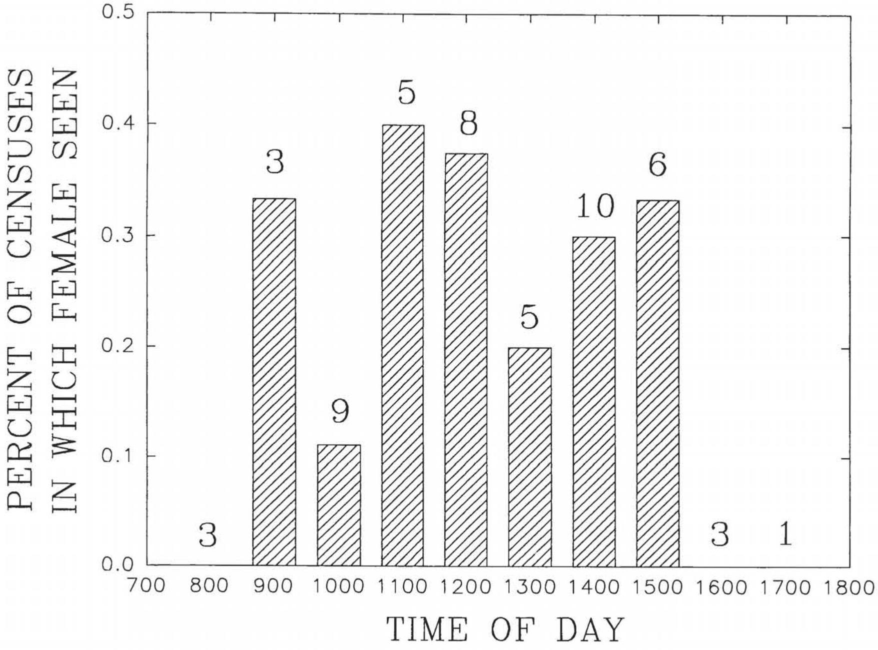

FIG. 4. The likelihood of observing one or more females on a census as a function of the time of day. The number over each bar is the number of days on which censuses were made.

hecabe Butler (Pieridae), other insects (e.g. black dragonflies (Odonata)), and even passing birds. After a chase, a male returned to the original perch or a perch within a few meters of the original.

Interactions between conspecific males in which the resident won varied in duration from 8 to 306 sec (Fig. 5). In interactions of less than 20 to 30 sec, the intruder, chased by the resident, quickly left the area flying with a distinctive flap-glide flight that was not seen at other times. In longer interactions, the intruder turned to face the approaching resident and the two males began flying rapidly around one another. Their wings sometimes clashed audibly during these confrontations. These interactions ended when one male turned and flew off with the flap-glide flight described earlier.

Three lengthy interactions (306, 433, and 675 sec) were observed during the experiments in which the identities and recent histories of the males were known. All three involved treated control males and were between the resident and an intruder that arrived and perched while the resident was on an investigatory sortie or in a fight. For example, a treated control male (T) that was under observation left his perch at site D to chase a crow butterfly (*Euploea core*) for an unusually

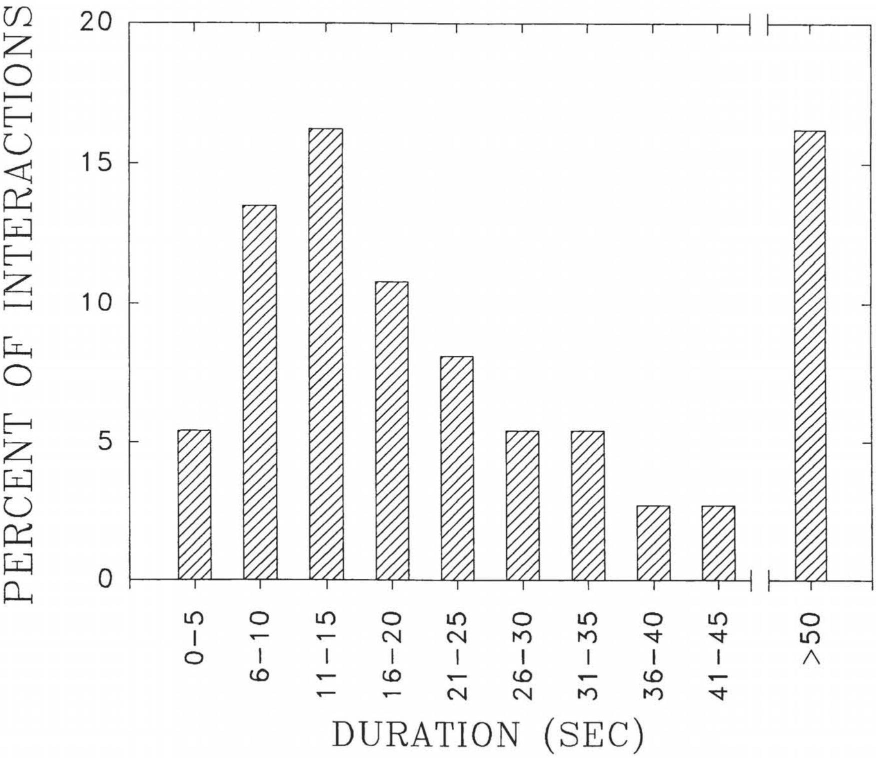

FIG. 5. The relative frequency of interactions of various durations between territorial *H. bolina* males and intruding conspecific males.

long time that exceeded 60 sec. While male T was gone an unmarked male entered and perched in male T's perching area. When male T returned he was approached and chased by the unmarked male. During the next 7 min the males flew rapidly around one another, face to face. After 433 sec, male T flew away using the flap-glide flight.

Interactions with heterospecific butterflies were characteristically brief, lasting only a second or two (Fig. 6). Interestingly, males spent significantly less time chasing butterflies of other species that were white or yellow than they did butterflies that were mostly black (Wilcoxon rank sum test, $P < 0.05$).

Male Site Tenacity

Males typically did not change their defended site within a day's activity period or between days. In 33 cases in which an individual was seen at 1000, 1200, and 1400 h on one day, each was seen at the same perching site at all three times. Males displayed a similar day-to-day

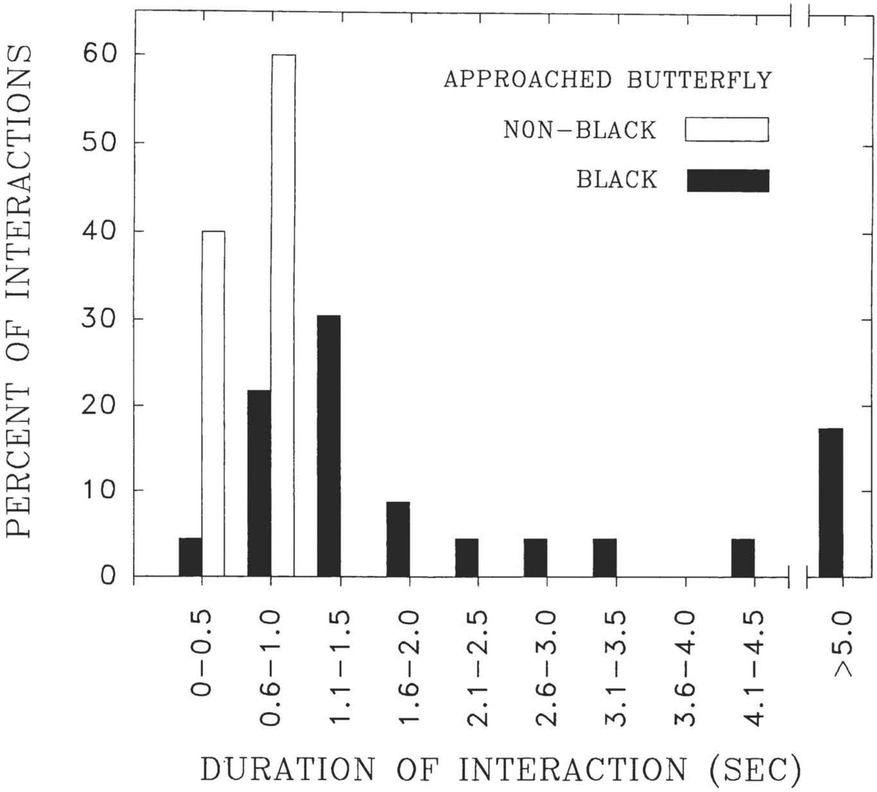

FIG. 6. The relative frequency of various durations of interactions between territorial *H. bolina* males and heterospecific butterflies in two color classes.

site tenacity. In 61 of 67 cases (extracted from records on 17 males) in which an individual was seen on two successive days, he was seen at the same perch site on both days. Five of the six shifts in location between days were made by the male seen over 23 days, but he was always at a site in the same part of the census route (sites D, E, F, and G).

Figure 7 summarizes the observations on all identified males during the 24 days when at least one census was run each day. One male was seen on the census route over a period of 23 days. This graph no doubt underestimates the typical stay of a male in that some data are from males that were treated as part of the experiments and some are from males that were still on the study site when the regular censuses stopped. Also, the natural marks used to identify males may have changed so they were no longer recognizable.

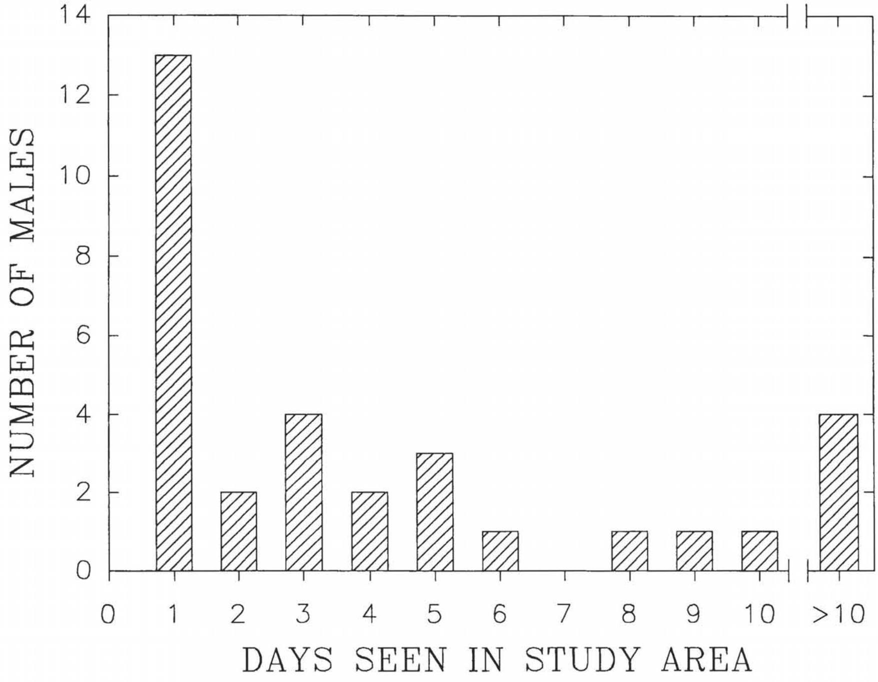

FIG. 7. The tenure of males on the study site for all males during a 24-day period. See text for details.

Observations on Control and Color Altered Males

Although sample sizes are small, the results suggest that resident males are treated as such by intruders regardless of the treatment group to which they belong (Table 2). Even when color-altered, residents readily displaced intruders. Two fights were lost by treated control males but only in circumstances that suggest that they may have lost sole resident advantage by being absent from the site. Male R flew up from his perch to chase a conspecific in an interaction that lasted more than 12 sec and whose conclusion was not seen. While male R was away, two other males were seen fighting near male R's original perch. While these males were fighting, male R returned and perched. The winner of the second fight then flew into male R's perching site and was immediately challenged by male R. The ensuing fight lasted 675 sec and ended with male R leaving the area and the other male returning to male R's original perch. Within a few minutes male R was seen successfully defending another less frequently occupied perching site about 15 m away.

The escalated interaction over site D involving male T was described

TABLE 2. Summary of observations on interactions involving males in various treatment groups that were residents.

Group	Males	No. of fights	Duration of fight		Lost?
			Median	Range	
Control					
Untreated	2	11	18 sec	8–90 sec	0
Treated	3	14	15 sec	3–675 sec	2
Experimental	2	9	10 sec	8–12 sec	0

earlier. Male T lost this fight but returned within 20 min to site D and challenged the unmarked resident. An escalated fight ensued that lasted over 5 min. At the end of this the unmarked male returned to nearby site E and male T flew off but reappeared perched at site D about 12 min later. This interaction was not included in Table 2 because male T's relationship to the site was no longer clear.

Male-Female Interactions: Courtship and Mating

I carefully observed and described, but did not time, fifteen interactions between males and hand-reared females of which four led to copulation. Casual observations were made on several other courtships. Interactions leading to copulation can be summarized as follows. All occurred in cages with hand-reared virgin females and began with the female flying. If the male was perched he flew up from his perch to the female or if flying he approached her from behind. Next, he positioned himself below the female and flew with shallow wingbeats and with the wings spread. The female then alighted and the male, after landing behind but facing the female, moved up alongside her so that his head was about half way along the length of her body. He then curled his abdomen toward the female from between his wings and inserted it between the inner margins of the female's hindwings. In one case, coupling occurred at this time. In the other three, probing by the male caused the female to turn her abdomen away from the male and then fly off. The male pursued and repeated the sequence of events described above. In these cases, coupling occurred only after this sequence was repeated three or more times over what seemed to be a minute or more. Once coupled the male moved to face away from the female.

Unsuccessful courtships ranged from those in which the male flew up and investigated a virgin for only a few seconds before departing to those in which the male followed the pattern for successful courtship described above for up to what seemed to be a minute or more but never succeeded in coupling.

Observations on five mating pairs (courtships not seen for all) produced times from when first seen coupled to when first seen separated of 50, 77, 90, 120, and 129 minutes, which suggests that copulation lasts one to two hours. Three of the females from these pairs were dissected. None contained more than one spermatophore. Using techniques described in Rutowski et al. (1983), I estimated that the males passed no more than 2.6, 3.5, and 3.8 percent, respectively, of their body mass as spermatophore and accessory secretions during copulation.

Three field caught females were dissected, one that was fresh and two that were very worn in appearance. All were mated and none carried more than one spermatophore.

DISCUSSION

Male Mate-Locating Behavior in the Common Eggfly

The behavior of males of the common eggfly is similar in a number of ways to that described for other species in which males have been observed to defend perching sites (Rutowski 1991) including its congener, *Hypolimnas misippus* (Stride 1956). (1) Males select exposed perches on the edge of large open areas. (2) Perched males chase flying males and females. Males are chased for a distance of some meters after which the approaching male returns to his original perch or one nearby. Females are approached and courted. If the female is found to be unreceptive the male returns to his original perch or to one within a few meters. (3) Conspecific males are not tolerated in the vicinity of a perched male. A conspecific male may enter a site and perch undetected, but is chased away as soon as he flies and is detected by the resident. (4) A male typically occupies the same perching site for several days. (5) Perching site preferences are apparently consistent across males; in spite of changes in the identity of the resident the same areas are occupied. (6) Sites contain little or nothing in the way of adult food resources. Males observed during this study were never seen feeding at their perching site. (7) Males pass relatively small spermatophores like those seen in other species that engage in site defense (Rutowski & Gilchrist 1988).

From these observations I conclude that males of *H. bolina* defend perching areas as a mate-locating tactic, that is, to maximize their chances of being the first to detect receptive females. Some features of the sites might make them good places to contact females. First, many sites were along paths or stream beds through the bush. These open paths may be used as flyways by females. Second, many popular perching areas were over shaded areas where the larval foodplant grew and females oviposited. The spermatophore counts from field-caught *H. bolina* females described here and in Ehrlich and Ehrlich (1978; 2

females each with one spermatophore) suggest that females probably do not often mate more than once. Mated females oviposited near male perching sites but during this study no mated female was ever seen to be receptive. Hence, males probably are defending these sites as places where virgin females are likely to be eclosing and taking their first flight, or where virgin females actively go to encounter potential mates.

Defense of encounter sites at or near female emergence areas is known for other butterflies (Rutowski 1991) and does not fall readily into traditional categories such as female defense polygyny or resource defense polygyny (Emlen & Oring 1977). However, because the occupation and defense of sites appears to be important to male reproductive success, males are subject to sexual selection in the context of intrasexual competition. Their coloration may have evolved in this context.

Indications are that in *H. bolina* residents have the advantage in male-male competition as has been observed in other species (Davies 1978, Rutowski 1984, 1991, Thornhill & Alcock 1983). So long as one male is a clear occupant and the other a clear intruder, male-male interactions are brief. Escalated interactions are most likely when both males sense that they are the perching site occupant or resident. This was demonstrated by the several interactions in which one male that had occupied the site for some time returned to the site after an interaction to find another male that had occupied the site in the original male's absence. Escalated interactions have been seen under similar circumstances, sometimes experimentally induced, in a butterfly (Davies 1978, Wickman & Wiklund 1983), a damselfly (Marden & Waage 1990) and a wasp (Alcock & O'Neill 1987).

Male Coloration and the Mating Behavior of *H. bolina*

Data presented here on *H. bolina* and by Stride (1956, 1957, 1958) on *H. misippus* are relevant to the discussion of the role of male coloration in the mating behavior of butterflies. Selection could favor the brilliant coloration of *Hypolimnas* males in intraspecific contexts in three ways. First, intruding males may be more readily stimulated to leave the territory by brilliant coloration in the resident either by making the resident more quickly apparent, making his identity as a conspecific more quickly detectable, or by indicating something about the resident's fighting ability. The results presented here suggest that this is not the case in that intruders left quickly when chased by residents whose color had been altered by obliteration of the most striking pattern components, the white and violet dorsal spots.

Second, intruders may have evolved a coloration that affects the behavior of the residents in some way advantageous to the intruder. Several studies show that intruder color affects resident response. As seen in this study, intruding butterflies that have an overall black appearance elicit the strongest resident responses. Stride (1956) working with *H. misippus* made the observation that "large pale butterflies . . . appeared to be of little interest to the *Hypolimnas* males" and, using models of various colors, he showed that white models elicited little more than a brief investigatory approach. Stride (1956, 1957) also showed in *H. misippus* that, after the initial approach, males used visual cues to discriminate females from males, i.e. only female coloration elicited courtship. Edmund (1969) showed that one of the female color morphs was especially attractive to males. These results, if anything suggest, the potential for selection against, rather than for, dark colored intruders. On the other hand, brilliant coloration may clearly announce intruder sexual identity and thereby curtail the sexual advances of residents. In any event, the behavior of intruders in territorial interactions does not suggest that intruders attempt to transmit clearly a visual signal.

Third, brilliant male color may be favored in the context of mate choice by females. Male behavior during the aerial phase of courtship is consistent with the notion that a visual signal is being delivered to the female. The position of the male relative to the female and the male's shallow wingbeats clearly display both the white and the directional violet wing markings to the female. Stride (1958) observed the same behavior in *H. misippus* and called it the "quivering flight." He also made a few observations on the response of females to males whose coloration had been altered and to control males. Males rendered colorless by the removal of wings scales were unsuccessful at obtaining matings whereas both control males and males with the white, but not the violet, dorsal wing spots removed were successful in courting females.

Taken together, the various observations on male color and the mating behavior of this genus suggests that female choice may have been important in the evolution of male dorsal coloration. A fruitful line of inquiry would be to design additional experiments to determine if the detection of these markings does affect female receptivity.

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