



Female iridescent colour ornamentation in a butterfly that displays mutual ornamentation: is it a sexual signal?



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In species wherein males display elaborate sexually selected traits or ornaments, conspecific females may also express these traits in full or partial form. This is called mutual ornamentation, and the co-occurrence of such traits in males and females remains poorly understood. In many sulphur butterflies (subfamily Coliadinae), males have a brilliant ultraviolet (UV) iridescence on their dorsal wing surfaces that functions as a sexual signal in courtship. In some of these sulphurs, such as the large grass yellow, *Eurema hecabe*, females also display dorsal iridescent patches, albeit smaller, restricted to the forewings and less bright than the male's, but the reasons for its occurrence in females are unknown. Here we present a study testing two functional hypotheses for the female UV-reflecting patch: an antiharassment hypothesis and a male mate choice hypothesis. The daily activity pattern of this species suggests that males are most likely to harass or choose among females from midday on. Observations made at this time of day on the characteristics of females related to male courtship duration suggest that males may preferentially court females with a large UV patch. Experiments with colour-manipulated models also suggest that males court with equal intensity females with and without a basal UV patch. Taken together the results provide no support for the antiharassment hypothesis. Because support for the male mate choice hypothesis was relatively weak and because of the limited potential for selection on female coloration due to male choice in these butterflies, the nonfunctional sexual correlation hypothesis remains a viable explanation for the female ornament.

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Elaborate male ornaments occur in many species of animals and are well documented to have evolved in the explicit sexually selected contexts of male–male competition, female mate choice, or both (Andersson, 1994; Clutton-Brock, 2007). In some of these species, females may display some level of development or expression of the male ornament. For example, in stalk-eyed flies in which the stalks that bear eyes in males and are important in male–male interactions and female choice, females also bear their eyes on stalks (Chapman, Pomiankowski, & Fowler, 2005; Wilkinson & Dodson, 1997). This case and others like it are referred to as mutual ornamentation (Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007). While in many cases of mutual ornamentation the evolutionary processes driving the expression and elaboration of the ornament in males is clear, what is not clear is why the

ornament appears in females even in a relatively less developed state.

There are two major classes of hypotheses to explain female possession of an ornament found in conspecific males (Houde, 2001; Kraaijeveld et al., 2007). First, females may display the trait as an incidental result of genetic correlations between the sexes and produce no direct benefit for the female. That is, strong selection for the ornament in males may have led to highly penetrating genes that incidentally get expressed during development in the female. Second, females that display the ornament may accrue some fitness benefit through its effect on male behaviour. This could happen in one or more ways. For one, males may choose mates from among available females based on the development of the ornament. In this case, ornament expression in a female may be indicative of her potential quality as a mate and so increase her attractiveness to males and thereby her mating success (e.g. Amundsen & Forsgren, 2001; Cotton, Cotton, Small, & Pomiankowski, 2014; Nordeide, Kekäläinen, Janhunen, & Kortet, 2013). For another, females may express the trait to appear male-like and, thus, unattractive to males, thereby reducing male

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courtship attempts and persistence and the time and energy costs that they may impose on females. Finally, females and males may display the ornament because it functions as a social signal in nonmating interactions. To date, there have been relatively few systems that permit a multipronged approach to addressing these hypotheses for the expression of an ornament in females. In particular, systems have been few and far between that permit evaluation of genetic as well as behavioural hypotheses (Kraaijeveld et al., 2007).

In the sulphur butterflies (family Pieridae, subfamily Coliadinae), males often display a brilliant iridescent ultraviolet (UV) reflection from virtually all yellow or orange areas on their dorsal wing surface. Several studies suggest that the male's iridescent coloration is used by females in mate choice (Kemp, 2008a; Papke, Kemp, & Rutowski, 2007; Silberglied & Taylor, 1977) and by males to distinguish females from other males (Rutowski, 1977). Interestingly, in some of the species in which males have iridescent patches, females also display iridescent patches but they are typically smaller, less bright and restricted to the base of their dorsal forewings (Common & Waterhouse, 1982; Kemp, 2008b; Rutowski, Macedonia, Kemp, & Taylor-Taft, 2007; White, Macedonia, Birch, Dawes, & Kemp, 2012). In these species, the iridescence of both males and females is produced by the same multilayer interference mechanism on the wing scales (Rutowski et al., 2007; White et al., 2012).

One of the pierid butterflies that displays mutual iridescent ornamentation is the large grass yellow, *Eurema hecabe*, and this species shows special promise as a system for testing hypotheses for the female iridescence. This species is widespread and occurs from Africa through Asia to Australia (Braby, 2000). In tropical Australia, this species is common during the late wet season and early dry season, which permits behavioural tests of potential signal function, and it is easily reared in the laboratory (Kemp, 2008b), which permits the genetic dissection of features of the iridescence wing colour in both males and females. Studies of both sorts have already been done with males and their iridescent ornaments. Behavioural experiments have shown that females preferentially mate with males with bright iridescence (Kemp, 2008a). In addition, rearing experiments have shown that the brightness of the male's iridescence is condition dependent, as would be expected of a sexually selected indicator trait (Kemp, 2008b). Finally, in those same rearing experiments, female iridescence was also condition dependent (Kemp, 2008b). Interestingly, these data allowed a preliminary and unpublished genetic analyses that failed to reveal a significant genetic correlation between males and females in the brightness of the iridescent patch reflectance. While this demonstrates the potential to pursue such questions in this species, more certain conclusions await a dedicated study.

This potential lack of genetic ties in ornament brightness between males and females compelled an investigation into the potential for the female iridescent patch to function as an adaptive signal. Because there is no known social system (e.g. night-time aggregations, social foraging, communal breeding, etc.) reported in these butterflies beyond the mating system, there is no context for the iridescence to evolve as a social signal. This leaves two potential behavioural hypotheses for the signal's function. First, males may discriminate among females based on the iridescence, which leads to the prediction that male courtship persistence will positively correlate with characteristics of the female's iridescence. There is evidence for male mate preferences among conspecific females in *E. hecabe* (Takanashi, Hiroki, Satoh, & Obara, 1997) and other species of pierids (Rutowski, 1982, 1985). These studies agree that males court most intensely younger (less worn) and, for *E. hecabe* and *Pieris protodice* at least, larger females. However, whether such preferences in butterflies will lead to significant

variation in female mating success and thereby selection on female coloration is a point of disagreement in the literature (Finkbeiner, Briscoe, & Reed, 2014; Kemp & Macedonia, 2006; Kunte, 2009).

Second, females may benefit from displaying UV iridescent patches and thereby reducing the potential costs of harassment by males. In pierids, females typically mate within hours or even minutes after eclosion and then enter a period of being unreceptive to male mating attempts (e.g. Rutowski, 1978; Rutowski, Long, Marshall, & Vetter, 1981a). During this time, they feed and oviposit, which means that male harassment could impose significant time and energy costs on females, especially at high male population densities (Kemp & Rutowski, 2011). Male harassment might be curtailed by displaying a patch of UV iridescence and looking somewhat like males, which are avoided by other males (Rutowski, 1977; Silberglied & Taylor, 1978). This hypothesis leads to the prediction that female iridescence should reduce the duration of male courtship attempts.

Our general aim in this study was to test these functional hypotheses for iridescent wing patches in *E. hecabe* females. We had four specific aims that we addressed in sequence.

- (1) Male courtship persistence patterns vary with time of day in sulphurs (Marshall, 1982). Therefore, we first evaluated the daily pattern of changes in male courtship persistence in *E. hecabe* in the field to indicate when during a day mate choice and harassment of females by males were likely to occur.
- (2) As an additional part of our assessment of the daily pattern of male behaviour we also evaluated the mating histories of females found in copula at different times of the day to evaluate whether the mating status of females that males are likely to encounter changes with time of day.
- (3) During the period of the day when males are most persistent in courtship there is still a good deal of variation in how persistent males are. We thus examined whether this variation is related to the characteristics of focal females during this period of high male persistence. Again, females that are the target of an intense courtship effort should, according to the mate choice hypothesis, be those with bright or large iridescent patches and, according to the antiharassment hypothesis, be those with dull or small iridescent patches.
- (4) We tested whether aspects of female coloration influence how intensely females are courted by males by presenting males with models created from the wings of males and females, and then experimentally manipulating their coloration.

METHODS

Study Populations and Locales

The field work was done from February to May in 2008 with two populations of *E. hecabe* near the Cairns campus of James Cook University, in North Queensland, Australia. One population inhabited a pair of vacant lots in a subdivision near Trinity Beach (16°47'7"S, 145°41'49"E), which was adjacent to a large mowed area and dense stands of *Aeschynomene indica*, a larval food plant for *E. hecabe*. The other population was in a clearing between a forest and the northern edge of the university campus in Smithfield (16°48'60"S, 145°41'18"E). All individuals in these populations were of the wet (or summer) season form (Kobayashi, Hiroki, & Kato, 2001). At this site an alternative larval food plant, *Sesbania cannabina*, was abundant. In both locations, the most commonly used nectar source was snake weed (*Stachytarpheta* spp.).

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