

## COURTSHIP BEHAVIOR OF THE CHECKERED WHITE, *PIERIS PROTODICE* (PIERIDAE)

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**ABSTRACT.** Courtship behavior leading to copulation is described for the checkered white, *Pieris protodice*, from film records of courtships with perched virgin females and written records of courtships elicited by releasing virgin females near free-flying males. Temporal and sequential patterns of successful courtships follow those seen in other pierid butterflies in that the interactions are simple and rapid, averaging about 3 seconds in duration. Unsuccessful courtships are also described and conform to patterns documented for other pierids. The checkered white differs from con-familials only in that there is no abdominal extension by females during successful courtship and after copulation a post-nuptial flight may occur. The possible functions of post-nuptial flights are discussed.

Although ethologists have been interested in butterfly courtship for many years (Scott, 1974; Silberglied, 1975) few quantitative studies of the temporal and sequential structure of butterfly courtship can be found in the literature. Detailed information is essential for comparative studies of butterfly courtship which in the past have proven useful in deducing the ecological factors influencing the structure of both successful and unsuccessful courtships (Brower *et al.*, 1965; Pliske, 1975; Rutowski, 1978a).

In this paper the courtship of the checkered white, *Pieris protodice* Boisduval and Le Conte, is described in detail. Attention will be focused on the structure of successful courtships so that this account can be compared to previous studies of a similar nature, with special reference to the function of post-nuptial flights in butterflies. It should be noted that a brief description of *P. protodice* courtship was given in Abbott (1959). However, Shapiro (1970) has pointed out the interpretational problems surrounding that description, so it will not be dealt with here.

### METHODS

All observations were made and all animals obtained from March through June in 1976 and 1977 at the Arizona State University Field Laboratory, Tempe, Arizona. To obtain virgin females, eggs were collected by placing field-caught females in tubular cheesecloth cages (1 m high, 0.28 m diameter) with cuttings of the local larval foodplant, *Sisymbrium irio* L. The larvae from these eggs were reared to adulthood in the laboratory on *S. irio*. The humidity and light regimen in the rearing area were not regulated and variable.

All behavioral observations were made on clear days between 0900 and 1500 when the butterflies were most active. Naturally-occurring interactions between males and between males and females were observed and the form, outcome, and duration (as timed with a stopwatch) of each recorded. Similar records were made of interactions initiated by releasing virgins near free-flying males.

During late May 1977, films of successful courtships were made at 24 and 70 frames per second using a Beaulieu 4008 ZM II super-8 movie camera. In all cases a virgin female was placed near the top of an exposed perch in a large patch of *S. irio* where there was a dense population of flying males. By activating the camera as a male approached a complete record of the courtship could be obtained. Temporal and sequential data were gathered via frame-by-frame analysis of the film records.

Where pertinent, summary statistics are given as mean  $\pm$  standard error of the mean.

## RESULTS

### I. Successful Courtship

Using 38 virgin females, 27 successful courtships (= ending in copulation) were recorded on film and 58 were observed after releasing virgin females near free-flying males. Temporal data from the films will be summarized first to give a general impression of the structure of *P. protodice* courtship.

#### A. Film records

Successful courtship with a perched female began when the male's wings or legs made physical contact with the female. In 67 percent of the filmed courtships this contact was made with the legs as the male alit on the female and immediately walked toward her thorax. In all other film records the male broke and then renewed contact with the female at least once, and as many as four times, before positioning himself on the female's thorax. Once on the female's thorax in a head-to-head orientation the male curled his abdomen out from between his hindwings and inserted the tip between the female's hindwings, often after several unsuccessful attempts. It was not possible to determine when genital contact was made. The courtship ended when the male stopped moving his wings and assumed a quiescent posture. Males showed no preference for the side of the female from which they effected copulation (13 right vs. 14 left;  $\chi^2 = 0.037$ ,  $p = 0.85$ ).

Fig. 1 shows the temporal pattern of the following major events in a successful courtship with a perched female: male contacts female, male

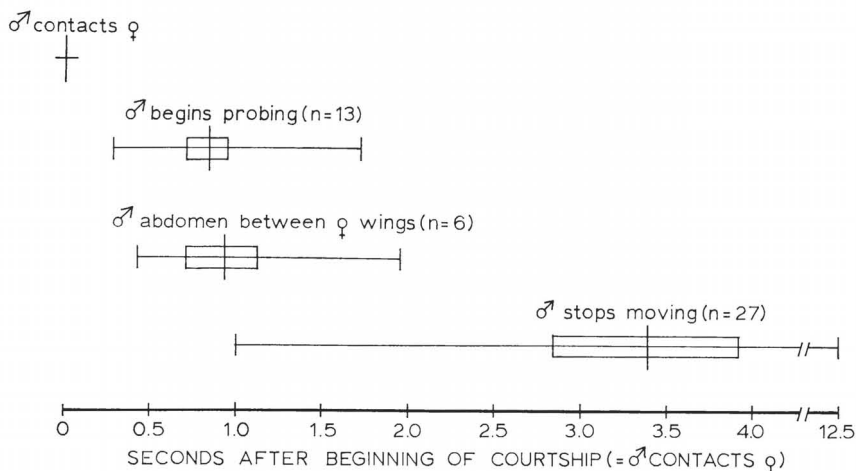


FIG. 1. Temporal relationships between the major behavioral events in the successful courtship of *P. protodice*. The mean time of occurrence, standard error (open bar), range line, and sample size ( $n$ ) are shown for each behavior. See text for details.

begins probing (abdomen appears from between hindwings), male abdomen between female hindwings, male stops moving. There were no observed variations in the sequence of these events. In 45 percent of the courtships the female performed a low amplitude flutter response. Of these, 25 percent began before the male first contact and 75 percent after, and they ended most often before the male began probing but sometimes not until he had inserted his abdomen between the female's hindwings. Detailed quantitative information on these points was difficult to gather because of 1) the viewing angle of many of the film records and 2) the low amplitude of the flutter response. In any event, flutter responses had no significant effect on the duration of courtship (courtships with flutter response:  $2.8 \pm 0.37$  sec,  $n = 12$ ; courtships without flutter response:  $3.86 \pm 0.93$  sec,  $n = 15$ ;  $t = 0.968$ ,  $p = 0.66$ ).

Shortly after coupling some males attempted to fly away from the perch carrying the female. In the 11 courtships where these attempts were filmed the males broke contact with the perch on the average  $3.71 \pm 0.586$  sec (range = 1.71–7.34 sec) after they had stopped moving their wings. In 8 of these attempted "post-nuptial flights" (Brower *et al.*, 1965) the female did not release her grip on the perch and the male dangled from the female's abdomen at the end of the attempt. In the other 3 cases the male flew off carrying the female to a distant and usually less exposed perch. Systematic data on these points or on the duration of successful post-nuptial flights was not collected.

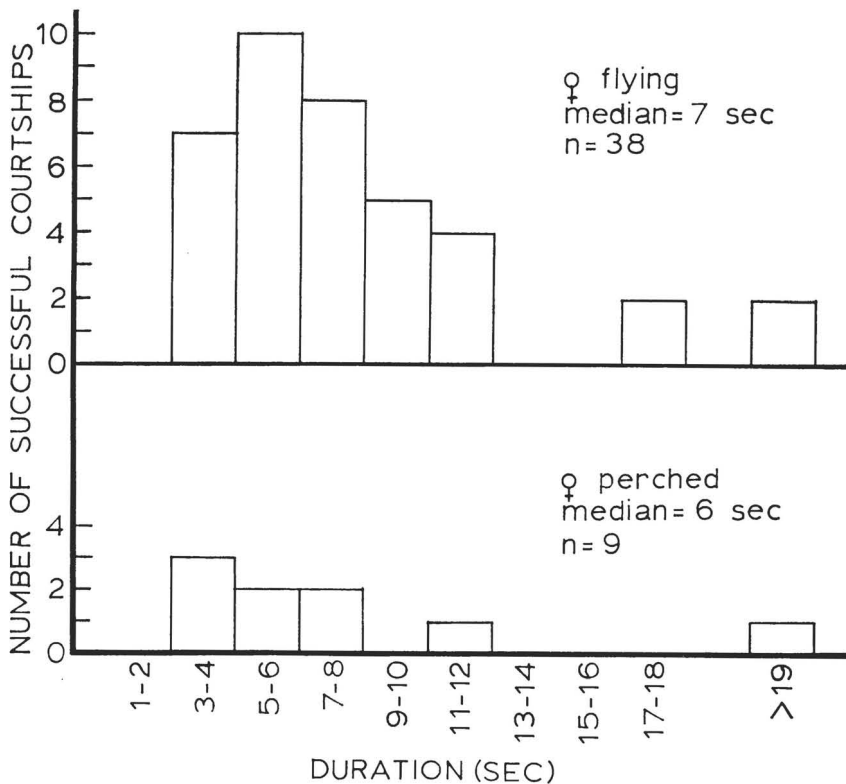


FIG. 2. A frequency histogram of the duration of successful courtships with perched and flying females. Courtships were elicited by releasing females near free-flying males and were timed with a stopwatch.  $n$  = number of courtships.

### B. Written records

The successful courtships elicited by releasing virgin females near free-flying males were timed beginning when the two animals arrived within 1 to 2 cm of each other. The distance at which these observations were made did not allow the use of contact as a criterion for when courtship began. This coupled with the lack of precision in determining when courtship ended resulted in the apparent greater length of these courtships relative to those timed from film records. These courtships were divided into two groups depending on whether the female was flying or perched when the male arrived within 1 to 2 cm of her (Fig. 2). The differences between these two types of courtships in the distribution of durations and median durations were slight suggesting that aerial components were of short duration. In fact, flying females typically landed immediately when approached by a male. The form and sequence of all

ground components of these courtships were exactly like those described from the film records.

Post-nuptial flights were attempted in 27 of the 58 successful courtships with released females. This should not be taken as an absolute indicator of the frequency of attempted post-nuptial flights because no firm protocol was established for how long a copulating pair should be watched after the courtship to wait for the onset of a post-nuptial flight attempt. Of the observed attempts 9 were unsuccessful, i.e., the female did not release her grip on the perch where copulation occurred.

The duration of copulation was timed for 15 pairs. Thirteen of these pairs copulated for less than 35 min ( $27.2 \pm 1.17$  min). The other two pairs copulated for 179 and 236 minutes, respectively.

## II. Unsuccessful Courtships

Interactions between males and virgin females that did not result in copulation are here referred to as unsuccessful courtships. Film records of unsuccessful courtships were not made because of the great variation in their form and duration. Data on the following five general types were derived from written records of 34 unsuccessful courtships between males and released virgins. The number of observations ( $n$ ) and the percent of all documented unsuccessful courtships is given for each type. All types terminated when the male departed.

Type A. The female continued flying on a level course ( $n = 17, 50\%$ ). These interactions were of short duration (2 to 15 sec). The males were probably of low courtship persistence like those seen by Rutowski (1978b) in *Colias* butterflies.

Type B. The female continued flying and initiated an ascending flight ( $n = 1, 3\%$ ). As well as the one interaction with a virgin female, seven naturally-occurring interactions were seen in which the females (presumably mated, see Shapiro, 1970) initiated ascending flights when courted by males. The interactions ranged in duration from 5 to more than 35 sec. Since all observed ascending flights were between males and females and since none ended in copulation it is assumed that they were attempts by mated females to curtail the courtship of persistent males as has been documented for the ascending flights of *Colias* butterflies (Rutowski, 1978b).

Type C. The female alit on vegetation or on the ground; the male may or may not have attempted copulation ( $n = 7, 20\%$ ). Since these unsuccessful courtships ranged in duration from 3 to 10 sec, the males were probably of low persistence as in type A.

Type D. The female alit on vegetation or on the ground and performed a flutter response, a pierid mate refusal posture, or both ( $n = 9, 26\%$ ). These interactions were from 10 to 68 sec in duration. When perched females spread their wings and elevated the abdomen they were said to have performed the mate refusal posture first described by Obara (1964) for *P. rapae* and reported for several other pierids (Scott, 1973). Abbott (1959) previously and incorrectly described the mate-refusal posture as an immediate invitation to copulation in *P. protodice*. This posture mechanically impedes the male's copulatory attempts. Females achieved the same effect in other situations by performing the flutter response, a rapid opening and closing of the wings (Obara, 1964; Rutowski, 1978a).

Type E. The male was displaced by another male ( $n = 1, 3\%$ ). This was only seen once with a virgin although I have also seen it occur with wild females. A

courting male terminated his courtship attempt when another male approached the female and began courtship. The second male was also unsuccessful. The female in this case was perched during the displacement. In naturally occurring unsuccessful courtships two males courting the same perched or flying female may leave together while circling each other in rapid flight.

Systematic observations of unsuccessful courtships with mated females were not made but casual observation suggests that they may only be of type A, B, D, or E. Shapiro (1970) noted that such courtships may be very lengthy in duration, up to 30 min or more.

#### DISCUSSION

Successful courtship in *Pieris protodice* is rapid and highly stereotyped. There are no prolonged aerial components and once the female alights on vegetation or on the ground the male does little more than land on her thorax and couple with her. This description closely fits that given for the temporal and sequential characteristics of the courtships of other pierids including *Eurema lisa* Boisduval (Rutowski, 1978a), *Colias eurytheme* Boisduval, *C. philodice* Latreille (Silberglied and Taylor, 1978), and four species of *Pieris* in Japan (Suzuki *et al.*, 1977). *Pieris protodice* also shares components of its courtship with *Leptidea synapsis* Linnaeus although the latter's courtship is apparently longer and includes some striking male displays (Wiklund, 1977). However, the most obvious difference between the courtship of species in the genus *Pieris* and that of other pierids is the lack of an abdominal extension response on the part of the female. In *E. lisa*, *L. synapsis*, and *Colias* species the male cannot couple with the female unless she extends her abdomen ventrally out from between the hindwings. Chemical and tactile cues delivered as the male courts the female elicit this response in *E. lisa* females (Rutowski, 1977). A male of *P. protodice* must insert his abdomen between the female's hindwings to reach her abdomen and couple. At present the proximate and ultimate causes of this variation are unknown.

The unsuccessful courtships of *P. protodice* also follow patterns observed in other pierids. Males vary in persistence and females utilize mate refusal postures, flutter responses, and ascending flights to curtail or impede the copulatory attempts of persistent males. Interestingly, all three behavior patterns were displayed by virgins as well as mated females suggesting that males vary in their attractiveness to virgin females which may be selective in their choice of a mating partner. Similar responses to males by virgin *E. lisa* females have been hypothesized to serve the same function (Rutowski, 1978a). The rejection responses of virgin *Colias* females definitely play a role in avoiding courtships with males of the wrong species (Taylor, 1973).

Post-nuptial flights have been previously reported only for danaids by

Brower *et al.* (1965) and Pliske (1975). It should be noted that these post-nuptial flights are spontaneous and as such are distinguished from the induced flights of copulating pairs summarized in Shields and Emmel (1973). To date the only function attributed to post-nuptial flights is that of removing the copulating pair from the place where courtship activity has made them conspicuous to one where they are less visible (Brower *et al.*, 1965). In *P. protodice* courtships, females often land on exposed perches. Presumably this facilitates copulation since males frequently appear to have trouble locating and mating with females that land in dense vegetation. Thus, post-nuptial flights in this species may also serve an anti-predator function. As an extension of this hypothesis, post-nuptial flights may also remove animals from exposed perches where thermal stress might become a problem, especially on warm days.

The selective pressures of predation and thermal stress should act equally on copulating males and females. However, the data clearly indicate that males and females are not equally willing to participate in post-nuptial flights. I suggest that there may be conflict between males and females as a result of male-male competition. Most courtships occur in or near stands of larval foodplant where males look for receptive ovipositing females or newly-eclosed virgin females. During copulation, pairs are often buffeted by single males in a way that makes them conspicuous to potential predators or may result in the separation of the pair. From the male's perspective both would be detrimental to his fitness and select for copulating males who initiate post-nuptial flights and move to areas of low male density. However, from the female's perspective it may be advantageous to remain in the vicinity of a stand of larval foodplant for the following reason. Because males do not defend resources of interest to females, females may select males only on the basis of behavioral cues that are correlated with high genetic quality. One of these cues may be the male's ability to defend the pair against interruptions by other males during copulation. If so, then it may be to the female's advantage to stay in an area of high male density thereby forcing the male to fend off the onslaughts of other males. If he cannot, then the female might benefit by copulating with another male.

In summary, I propose that selection does not act equally on males and females with respect to their participation in post-nuptial flights. In particular, there appear to be ecological circumstances in which males benefit from post-nuptial flights but at least some females do not because the potential benefits of preventing post-nuptial flights and inciting male-male competition outweigh the potential costs of increased predation and

thermal stress. The ecological conditions that give rise to this situation remain to be defined.

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