

COURTSHIP BEHAVIOR OF THE GULF FRITILLARY, *AGRAULIS VANILLAE* (NYMPHALIDAE)

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ABSTRACT. The courtship behavior of the Gulf Fritillary, *Agraulis vanillae* L., is described from motion picture records of successful and unsuccessful courtships between free-flying males and tethered virgin females. During most but not all courtships the male performs a previously undescribed wing clap display in which he alights next to the female and repeatedly claps his wings together, often catching the female's antenna between his wings during each clap. In the discussion it is suggested that this display presents chemical signals to the female and has evolved in response to female choice for males that clearly announce their species identity to the female.

In recent years substantial literature has developed concerning the behavior and ecology of the heliconiine butterflies (for review: Brown, 1981). Surprisingly, only two papers (Crane, 1955; Gilbert, 1976) have dealt specifically with the mating behavior of heliconiines in spite of a growing amount of information on the nutritious materials passed by males to females during copulation and the female's use of these materials in oogenesis (Boggs and Gilbert, 1979; Boggs, 1981). The only courtship description *per se* for a heliconiine is to be found in Crane's paper on *Heliconius erato* Hewitson. Information on courtship behavior is essential in any attempt to evaluate the selective consequences of inter- and intra-specific variation in male's abilities to produce accessory gland secretions during copulation (Rutowski et al., 1983).

The following study expands our knowledge of the behavior of heliconiines by describing the courtship of a member of this subfamily that is common in the southern United States, the Gulf Fritillary (*Agraulis vanillae* Linnaeus). Particular attention during this study was directed at describing a previously unreported display performed by *A. vanillae* males and its role in successful courtship. The discussion will focus on the potential functions of this unique display.

METHODS

Observations were made on a population of *A. vanillae* in suburban Tempe, Arizona. Preliminary studies in the spring of 1980 led to intensive study from March to June in 1981. From about 0800 h to 1600 h, adults of *A. vanillae* frequently visit *Lantana* spp. (adult nectar source) and *Passiflora* spp. (larval foodplant). Virgin females were obtained from larvae and eggs collected on *Passiflora* spp. either in the field or in cages in the laboratory. Larvae were reared to adulthood in translucent plastic shoeboxes (9 × 16 × 30 cm) on cuttings of *Passiflora*. The shoeboxes were kept near a window which exposed the

larvae to a normal light-dark regime. Temperature and humidity were not controlled.

To observe courtship, newly emerged, virgin females no more than four to five days old (most were one day old) were tethered (for technique: Rutowski, 1978) and placed on a conspicuous perch on a *Pas-siflora* plant. Usually within a few minutes, passing males approached and courted the female. Courtships, both successful and unsuccessful, were filmed at 24 and 70 frames per sec with a Beaulieu 4008 ZM 2 super-8 movie camera.

RESULTS

Successful Courtship

By separating males and females immediately after coupling, twenty-five successful courtships (leading to copulation) were filmed using ten females. No single female was used to film more than three courtships. Of these 25 courtships, one involved two males and so, was disregarded, leaving 24 for the detailed analysis that gave rise to the description that follows.

Courtship began when either the male alit next to the female or the female began a flutter response as the male approached. Both were often preceded by a brief period during which the male hovered about 15 cm over the female before descending and initiating physical contact. Once the male alit he positioned himself with his wings open, his head close to that of the female, and the long axis of his body forming about a 45 degree angle with that of the female (Fig. 1). Once in this position the male began what will hereafter be referred to as the **wing clap display**. During this display the male's body remained in position but he repeatedly clapped his wings shut and then quickly reopened them. Between claps the wings were opened to about 90 degrees relative to one another. It was typical that in the position assumed by the male, the female's antenna on the side next to the male was laid back between the male's wings and was caught between them during each clap. During wing clapping and in some instances even before the male alit, the male's claspers were visibly spread. Just as, or before, the male ceased clapping his wings he began probing by curling his abdomen toward the female's hindwings and attempting to insert its tip up between her closed wings. Coupling occurred between the female's hindwings where its occurrence could not be closely monitored. However, it is assumed that either when it occurred or shortly thereafter the male became still briefly before he began slowly waving his wings and moving to a position facing away from the female while still



FIG. 1. **Above:** an *A. vanillae* male (**left**) as he appears when courting a female (**right**) with a wing clap display. **Below:** the same pair except that the male has now begun probing. In both figures, note that the female's antenna on the side next to the male is laid back between his wings.

TABLE 1. Temporal structure of successful courtship in *Agraulis vanillae*.

Event	Time event occurs before end of courtship					
	Courtships with wing clap display			Courtships without wing clap display		
	$\bar{x} \pm \text{SD (s)}$	range (sec)	n	$\bar{x} \pm \text{SD (s)}$	range (sec)	n
First contact by δ	10.9 \pm 5.1	2.7–23.6	17	8.04 \pm 3.67	5.43–15.3	6
Last contact by δ	8.1 \pm 3.92	2.29–15.8	17	5.18 \pm 2.17	1.8–7.46	6
δ begins wing clap display	7.53 \pm 4.1	1.92–15.8	17	—	—	—
δ begins probing	3.53 \pm 3.13	0.5–13.0	14	2.97 \pm 1.46	1.46–5.53	5
δ ends wing clap display	2.8 \pm 2.86	0.37–12.8	17	—	—	—
δ stops moving	0			0		

coupled. Wing waving often evolved directly into strong wing flapping by the male in an effort to initiate a post-nuptial flight.

This sequence of events was observed in 14 of the 24 courtships filmed. In another three records the male broke contact with the perch and alit again at least once but no more than twice. In one case the male performed a bout of probing while perched the first time. After alighting a final time, all of these males performed wing claps before probing.

A more striking variant of the courtships described above was observed in seven courtships in which the wing clap display was completely omitted. In these cases the male simply began probing immediately after alighting for the last time as they did in some of the courtships with wing claps but in these cases the males were successful. Hence, the wing clap display is not a requisite part of successful courtship.

Females opened and closed or fluttered their wings in only eight of the 24 courtships. In six of these the female performed a single flutter before or at the time of first contact by the male. If the male made repeated contact each contact often elicited a single flutter. Twice flutters were observed during the wing clap display and twice after the male had become still. Fluttering in immediate response to male contact was observed in three of the seven courtships in which males did not wing clap.

The temporal structure of courtships in which the male performed a wing clap display is shown in Table 1. In these summaries, there are some courtships in which the first contact was also the last; hence, some data points were used in the summaries for both events. Also, for convenience and summary purposes, we regarded the last time the male initiated probing as the time when the male began probing. This was not true of three courtships. The sample size of the summary of

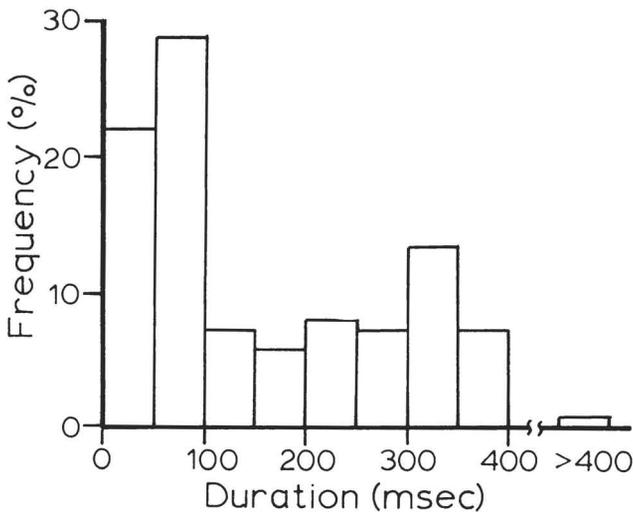


FIG. 2. The frequency distribution of duration for 132 wing claps. See text for details.

this event is less than that for the other events because in three cases the angle of filming did not permit viewing of the beginning of probing.

Courtships with the wing clap display have an average duration of about 11 sec and wing clapping begins within a second after the male alights for the last time. Probing usually began in the second before the display ended and slow wing waving followed coupling within 2 sec.

Table 1 also summarizes the temporal structure of courtships in which the male did not perform a wing clap display. The sample size for some events is less than seven, either because the film record began after the event occurred or because the filming angle prohibited viewing the event. Statistical comparisons of the time of occurrence of events held in common between the courtships with and without the wing clap display revealed that none of the differences were significant. In particular, neither the time of first contact nor the time of last contact differed from one type of courtship to the next. Factors contributing to this lack of differences were the high variances associated with the times of occurrence and the small sample sizes for courtships without the wing clap display.

The average duration of the wing clap display was 4.73 ± 3.34 sec ($n = 17$). Fig. 2 shows the average duration of each clap from the time the wings start to close from their spread position until they start to close for the next clap. The data are taken from 132 wing claps per-

formed in five displays of 6, 12, 16, 41, and 57 claps, respectively, and filmed at 70 frames per sec. The histogram shows a mild but distinct bimodality. This reflects the fact that during the display the temporal patterning of the claps may take one of three forms: (1) a series of long claps, (2) a series of short claps, and (3) a series of alternating long and short claps. From the films we also measured that, regardless of overall clap duration, the wings were closed an average of 26.4 ± 9.37 msec ($n = 127$). Hence, the difference in duration between long and short claps is due primarily to a difference between them in the time the wings are open.

Most courtships were filmed at 24 frames per sec which made counting of individual wing claps difficult; thus, we were unable to obtain a good average for the number of wing claps per courtship. However, using a mean wing clap display duration of 4.73 sec and an average of 165 msec per clap, it may be estimated that in the typical courtship the male performs about 30 wing claps.

Unsuccessful Courtships

Courtships that did not lead to copulation were studied in less detail than those that lead to copulation. This was because unsuccessful courtships were more variable and difficult to characterize. In addition many of the film records of unsuccessful courtship were incomplete. However, 20 complete records were obtained and are summarized here. In five of these courtships the male contacted the female and hovered over her briefly before departing. In the other 15 the male alit next to the female at least once during the courtship. Of the males that alit, four departed without performing a wing clap display while the other 11 performed the display at some point in the courtship. Two males actually probed before wing clapping while three did not begin probing until they had wing clapped for some time. The other six males left the female after wing clapping without probing. During these courtships the females either did nothing (10 cases), fluttered the wings (8 cases), or assumed a posture like the pierid mate refusal posture (Obara, 1964) with the wings spread and the abdomen held perpendicular to the plane of the wings (2 cases). When females fluttered or spread their wings it could be seen that the pair of glands associated with the tergites at the end of the abdomen were periodically everted. Whether or not this occurs when the wings are closed was not determined.

In summary, courtship terminated before coupling either because the male left before an attempt (males did not probe in 16 cases) or because the female did not behave in a way that permitted coupling (4 cases).

DISCUSSION

The wing clap display performed by males of *Agraulis vanillae* is clearly an important part of successful courtship. Its form is reminiscent of displays performed by males of some other nymphalids. The male of the grayling (*Hipparchia* (= *Eumenis*) *semele* Linnaeus) after alighting next to a perched female moves so that he is face to face with the female and, by rocking forward with the wings open, catches the female's antennae between his forewings. The male then closes his wings and rocks gently back, drawing the female's antennae across patches of scent scales on the male's forewings (Tinbergen et al., 1942). During the courtship of the great spangled fritillary (*Speyeria cybele* Fabricius), the male assumes a position perched next to the female like that seen in *A. vanillae*, and "at intervals he would suddenly open and close his wings" (Clark, 1932:110). The interval between these openings and closings becomes less as the courtship progresses. Magnus (1950) reports that males of the fritillary (*Argynnis paphia* Linnaeus) when perched alongside and facing a female, clap their wings in such a way that the female's head and antennae are caught between them. In *Heliconius erato*, the closest relative of *A. vanillae* that has been carefully studied, the male persists in flapping his wings after alighting and while moving into position for coupling (Crane, 1955). Perhaps this behavior was the one from which the wing clapping display of *A. vanillae* was evolutionarily derived.

Indications are that the wing clapping display is involved in presenting chemical signals to the female. Obviously, the male's position behind and to the side of the female is poor for presentation of visual stimuli, and the fact that the female's antenna is between the male's forewings during the display suggests that the display is designed to deliver a chemical signal. This conclusion is reinforced by the observation that androconia that are likely to be scent-producing are found on the dorsal surface of the male's forewings along several of the veins (M_1 , M_2 , M_3 , Cu_1 , Cu_2 , $2A$; Muller, 1877). In addition there are large apparently glandular structures associated with the internal faces of the claspers that might produce a chemical signal. The claspers are often spread or opened during most of the courtship. Experiments are planned to determine the roles of these structures in the courtship behavior of *A. vanillae*.

Rutowski (1983) has recently discussed the selection pressures that have led to the evolution of species-specific male courtship displays in butterflies. A similar analysis of the courtship of *A. vanillae* suggests that selection for signals that announce the species identity of the male to the female has been of particular importance. The nutrient investment of *A. vanillae* males and the general ecology and behavior of

this species is not so different from that of the other species of butterflies as to suggest that they led to the evolution of the wing clapping display (Rutowski et al., 1983). In addition, although *A. vanillae* females may occasionally approach and chase males as observed in other species (Crane, 1955; Rutowski, 1980; Rutowski et al., 1981; Wiklund, 1982), it does not seem that problems of sexual discrimination for females are any more severe than they are in *Heliconius erato*, which like *A. vanillae*, is essentially sexually monomorphic with respect to visual characters but whose courtship lacks the wing clap display (Crane, 1955).

Species discrimination would seem, however, to pose a potential problem for *A. vanillae* females. A field guide to the butterflies of North America (Pyle, 1981) reveals that there are at least eight butterflies sympatric with *A. vanillae* that are very similar in color and markings. These species include *Danaus gilippus* Cramer, *D. plexippus* Linnaeus, *Dryas julia* Fabricius, *Marpesia petreus* Cramer, *Limenitis archippus* Cramer, *Dione moneta* Hübner, *Anaea floralis* Johnson and Comstock, and *A. andria* Scudder. Given that an *A. vanillae* female is likely to be approached and courted by males of any of these species, selection might favor those females that prefer conspecific males that perform a display or offer a signal clearly indicative of their species identity. While it is known that the danaids have their own unique male courtship behavior (hairpencilling: Brower et al., 1965; Pliske, 1975) the other species are not behaviorally well-known enough to assess the extent to which their courtships are different from that of *A. vanillae*.

A final question about the wing clap display concerns the fact that it is not performed in all successful courtships like the wing spread display sometimes performed by males of the pierid, *Nathalis iole* Boisduval (Rutowski, 1981(83)). Why do some females accept a male without the performance of the display? Obviously, females vary in receptivity, and some will accept males without the display. These may be males with such potent chemical signals that they are able to satisfactorily stimulate the female without the display. In any event it seems from both successful and unsuccessful courtships that males will attempt copulation without wing clapping, which in turn suggests that the display has certain costs for males. Just what these costs are or might be is currently not clear (although, see: Burk, 1982).

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