

GREGARIOUS OVIPOSITION IN BUTTERFLIES

Additional key words: *Heliconius*, *Aglais*, clutch size.

Here I compile and discuss records of gregarious oviposition in butterflies. There have been field observations of this behavior in seven species of butterflies, all from the nymphalid genera *Heliconius*, *Aglais*, and *Euphydryas*. This concentration of observations in only a few unrelated genera suggests that the behavior has evolved multiple times in butterflies. It appears that in most cases described, multiple females aggregated together to oviposit over a short period of time, even when host plants may not have been a limited resource. Some possible adaptive functions of this behavior are discussed.

Most butterfly examples of gregarious oviposition are from the genus *Heliconius*, with four different species in the genus having been observed to aggregate while laying eggs. Mallet and Jackson (1980) observed two individuals of *Heliconius xanthocles* contributing to a collective egg clutch of 41 eggs over a 25 min period. During this time the authors also captured a third female who appeared to be ready to contribute to the clutch. A published photograph illustrates the two females ovipositing simultaneously on the tip of *Passiflora praeacuta* shoot. On a separate occasion, Mallet and Jackson (1980) also observed two individuals of *Heliconius (Laparus) doris* contributing to a collective clutch of more than 200 eggs over a period of 50 min on the upper surface of a young, folded leaf of *P. praeacuta*. Further circumstantial evidence for gregarious oviposition by *H. doris* include Benson et al.'s (1975) discovery of a clutch of over 800 eggs and J. Mallet's remarkable observation of a cluster of over 1200 pupae (pers. comm.). Turner (1971) reported observing two wild females of *Heliconius sara* "taking turns at laying their eggs in a shared batch". Jocelyn Crane also observed two *H. sara* ovipositing together in an insectary (Mallet & Jackson 1980), although captive observations may not be representative of behavior in nature.

Of all butterflies, the most data for gregarious oviposition are from *Heliconius hewitsoni*. Regarding this species, Longino (1984) reported "more than one female may contribute eggs simultaneously to the same egg cluster" and Duckett (1989) that "more than one female often will lay her eggs on the same shoot." L. Gilbert (pers. comm.) has consistently observed gregarious oviposition by *H. hewitsoni* in the field for

over 15 years, indicating that the behavior is not a seasonal aberration or a rare chance event. In Costa Rica during the summer of 2001 I personally observed 12 cases of gregarious oviposition by *H. hewitsoni* (Fig. 1A-D) and found that an average of 4.5 females would contribute to a single collective clutch over an average of 1.1 h, even when local host plant was abundant (Reed 2003). In one particularly extreme example of the behavior, I observed 10 females contributing to a single clutch of 156 eggs. Longino (1984) noted "Interaction of *H. hewitsoni* females at oviposition appears to be aggressive. Females on the shoot hold their wings down over the shoot, as if fending off approaching females", a behavior I have also observed and photographed (Fig. 1B). Interestingly, male *H. hewitsoni* guarding potential pupal mates display an identical wing stance (Deinert et al. 1994).

Sourakov (1997, 1998) photographed two females of *Aglais cashmirensis* simultaneously contributing to a single, discrete egg cluster. Within 20 min the females produced a "multilayered heap" of approximately 100 eggs before being interrupted by the observer. This occurred when there were large patches of *Urtica* host plant in the vicinity that were not hosting eggs or larvae, suggesting that aggregation during oviposition was due to choice, as in *H. hewitsoni*. Thomas and Lewington (1991) described reports of multiple females of *Aglais urticae* contributing to collective clutches of up to a thousand eggs. Regarding *A. urticae*, they further stated "it is not unusual to find two females laying simultaneously on the same leaf." Unfortunately, however, their report did not include any quantitative data or specific observations.

R. Rutowski (pers. comm.) photographed two females of *Euphydryas chalcedona* ovipositing on a single host plant (Fig. 1E), although specific data were not taken regarding the collective clutch size or duration of the oviposition event. In this case, the females produced separate, discrete egg clutches that were located near each other. This should be contrasted with the *Heliconius* and *Aglais* examples where multiple females contributed eggs to a single collective clutch. On several occasions Rutowski (pers. comm.) has observed collections of several hundred *E. chalcedona* eggs on a single host plant, a number that far exceeds the expected clutch size of a single female. A

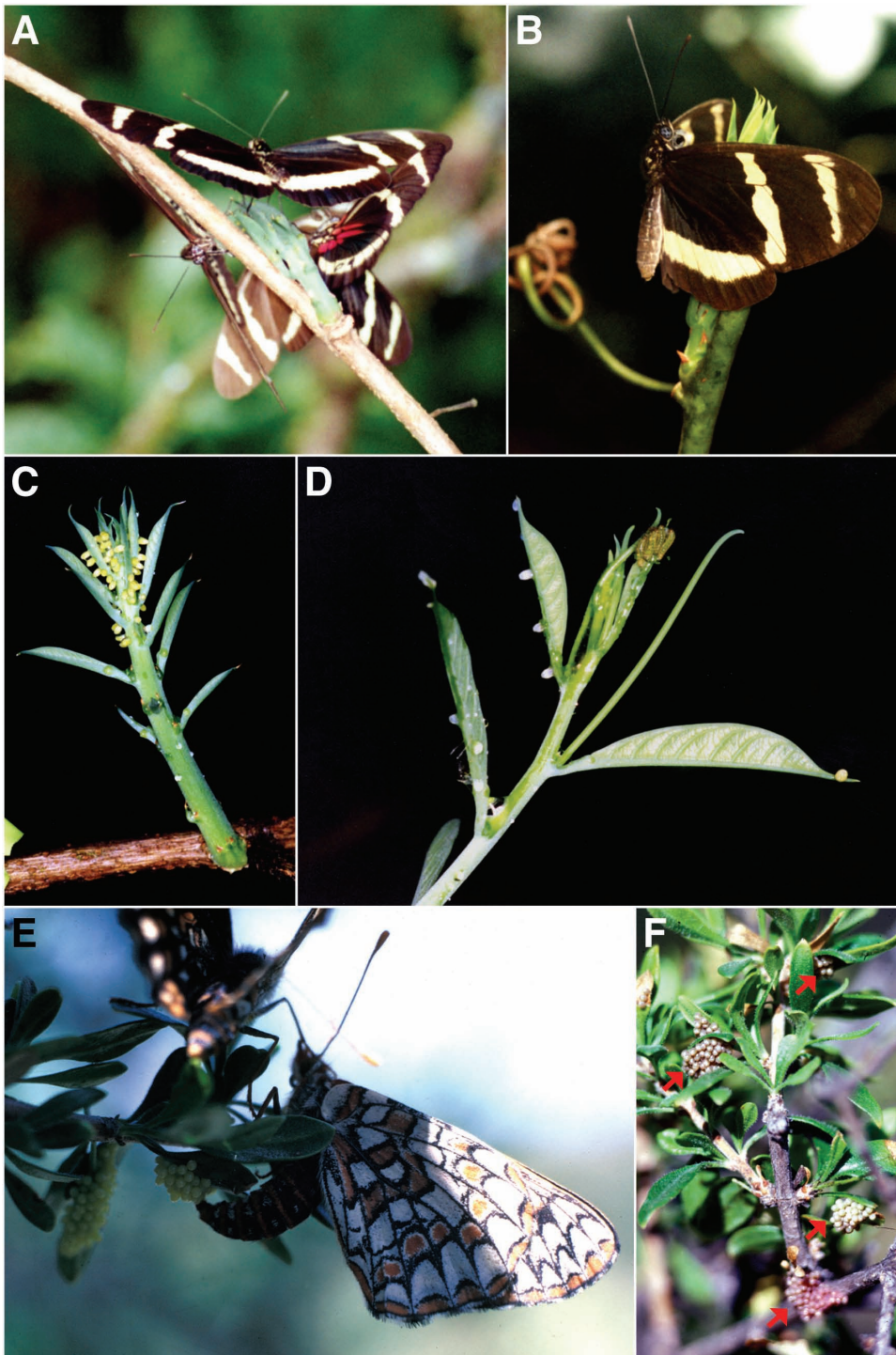


FIG. 1. Gregarious oviposition in *Heliconius hewitsoni* and *Euphydryas chalcedona*. A, four *H. hewitsoni* showing oviposition behavior on a young *Passiflora pittieri* (Passifloraceae) shoot near Sirena Biological Station, Costa Rica, July 2001; B, *H. hewitsoni* female perched on a young *P. pittieri* shoot; C, a cluster of 63 *H. hewitsoni* eggs that has been slightly spaced due to shoot growth. The number of eggs in this clutch suggests that three or four females contributed to it (Reed 2003); D, aggregation of newly hatched *H. hewitsoni* larvae on a host plant shoot tip, note the wide spacing of the egg shells; E, two *E. chalcedona* showing oviposition behavior on *Keckiella antirrhinoides* (Scrophulariaceae) near Sunflower, Arizona, Spring 1985; F, multiple discrete *E. chalcedona* egg clutches (red arrows) in close proximity on *K. antirrhinoides*. The color differences between egg masses suggest they were laid at different times. (E and F photos courtesy of R. L. Rutowski).

photograph of multiple *E. chalcidona* clutches on a single host plant shows that the clutches are of slightly different colors (Fig. 1F). These color differences may indicate that the clutches were laid at different times, which again contrasts with the *Heliconius* and *Aglais* examples where females tended to aggregate temporally.

There is circumstantial evidence for gregarious oviposition from several other butterflies. Stamp (1980) reported observing multiple *Euphydryas phaeton* clutches on single host plant leaves, but it was unknown if these clutches were from multiple females. Likewise, in *Eueides vibilia unifasciatus* multiple clutches have been observed on single leaves, although oviposition was not directly observed (K.S. Brown Jr., pers. comm.). Also, in *Pieris brassicae* egg clusters appear to attract conspecific females (Mitchell 1977). While this suggests a possible mechanism for gregarious oviposition, I am unaware of published records of multiple *P. brassicae* females contributing to egg clusters.

Is gregarious oviposition a common behavior among butterflies? Unfortunately there are too few data to address this. The serendipitous nature of observing oviposition in the field hinders any kind of quantitative conclusion in this respect. Repeated observations of gregarious oviposition in *H. hewitsoni* (L.E. Gilbert pers. comm., Reed 2003) and *A. urticae* (Thomas & Lewington 1991) indicate that the behavior may be common in these species. While most observations of gregarious oviposition are anecdotal, the phylogenetic clustering of observations in the genera *Heliconius* and *Aglais* suggests that the behavior may be an important life history trait within these groups. In fact, there seems to have been at least two independent origins of gregarious oviposition in *Heliconius*; one origin in the *xanthocles / doris* clade, and one or two origins in the clade that includes *sara*, *hewitsoni*, *sapho*, and *eleuchia* (see phylogeny by Brower & Egan 1997). Both *Aglais* and *Heliconius* contain multiple clutch-laying species, and it is reasonable to speculate that the evolution of clutch laying behavior is a prerequisite for developing a gregarious oviposition strategy. I am unaware of reports of gregarious oviposition in species that are single-egg layers.

When considering adaptive explanations for gregarious oviposition in butterflies it is important to separate hypotheses into two categories: (1) the basic advantages of clutch-laying, and (2) the advantages of clutches of mixed relatedness. There is a literature on the evolution of clutch-laying in butterflies, much of which cites Stamp's (1980) comparative review. Some hypotheses that have been proposed to account for the evolution of clutch-laying in general include prevention

of egg desiccation (Stamp 1980), enhancement of egg aposematism (Stamp 1980), decrease of exposure to predators and parasitoids (Stamp 1980), minimization of female search time (Stamp 1980), evolutionary response to increased fecundity (Courtney 1984), and the facilitation of larval aggregation (Stamp 1980). Gregarious oviposition could quantitatively enhance most of these effects.

The desiccation, aposematism, and anti-predation hypotheses rely on eggs being in close proximity to each other, with eggs on the outside of clusters acting as "insulation" for more internal eggs (Stamp 1980, Clark & Faeth 1998). While it is possible that gregarious oviposition could enhance these specific effects in gregarious *Aglais*, it would probably have little influence in *Heliconius* or *E. chalcidona*. The fast growth rate of young *Passiflora* shoots often results in clustered *Heliconius* eggs being well spaced within a day or two of being laid (Fig. 1C, D), while *E. chalcidona* apparently do not combine clutches (Fig. 1E, F).

Stamp (1980) proposed that females might lay eggs in clusters in order to minimize personal exposure to predators and other hazards. This may be plausible for *E. chalcidona* or gregarious *Aglais*, however it may not be as applicable to *Heliconius*. *Heliconius* butterflies, being relatively unpalatable Müllerian mimics, possess a modicum of protection from predators such as birds (eg. Kapan 2001). Furthermore, prolonged daily shoot inspections (Reed 2003) suggest that females may not be overly concerned with minimizing their oviposition-related flight time.

All Lepidoptera known to have gregarious larvae are also clutch-layers (Sillén-Tullberg 1988), supporting the idea that a primary function of clutch-laying is to facilitate larval aggregation. Several adaptive hypotheses have been proposed to explain larval aggregation in insects, including enhancement of larval aposematism (Stamp 1980), group defensive strategies (Hamilton 1971), enhancement of larval feeding efficiency by increased thermoregulatory ability (Casey 1993), increased social stimulation to feed (Long 1953), and increased ability to overcome leaf toughness (Ghent 1960). These hypotheses are plausible as selective forces playing a role in the evolution of gregarious oviposition in various cases.

Beyond the general benefits of aggregation described above, the formation of aggregations of mixed relatedness through gregarious oviposition adds a new dimension to adaptive interpretations of clutch-laying. Evidently there is a selective advantage to large larval aggregations that outweighs the cost of intraspecific competition. Sourakov (1997) suggested that gregarious oviposition could be a way to minimize the number of

clutches in a locality in order to decrease egg apparency to parasitoids. Another possibility is that large aggregations of conspecifics result in a prey dilution effect (Turner & Pitcher 1986, Vulinec 1990), decreasing the probability of a female's offspring being lost per predation event. There is evidence from *H. hewitsoni* that variation in the number of females contributing to a clutch may be a mechanism for host quality-dependent clutch size adjustment (Reed 2003), an effect that has also been observed in parasitic mantispids that communally adjust clutch size in respect to the concentration of their spider hosts (Rice 1986). Whatever their benefits may be, mixed-relatedness aggregations are possibly a widespread phenomenon in Lepidoptera, as examples have also been described from some moth species (Porter et al. 1997, Costa & Ross 1993). Future work that explicitly tests some of the adaptive hypotheses outlined above would be helpful for understanding why gregarious oviposition has arisen repeatedly during butterfly evolution.

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