EVOLUTION OF GREGARIOUSNESS IN APOSEMATIC BUTTERFLY LARVAE: A PHYLOGENETIC ANALYSIS

BIRGITTA SILLEN-TULLBERG

Department of Zoology, University of Stockholm, S-106 91 Stockholm, SWEDEN

Abstract.—Gregariousness ought to be disadvantageous for palatable organisms that live exposed and are relatively immobile and small in comparison to potential predators. Therefore, the idea that unpalatability generally evolves before egg clustering/larval gregariousness in butterflies was tested. Aposematic coloration in the larva was used as the criterion of unpalatability (it is argued that Batesian mimicry is rare in butterfly larvae), and the relative order of evolution of aposematism and gregariousness was inferred through phylogenetic analysis. Here, existing phylogenies were used, and the analysis was based on an assumption of a minimum number of evolutionary changes (parsimony). A total of 23 cases of independent evolution of gregariousness and 12 cases of independent evolution of aposematic coloration were found. In five cases, gregariousness evolved in cryptic species, the palatability of which is unknown. For lineages in which both unpalatability, as evidenced by aposematic coloration, and gregariousness were found and the two evolutionary events could be separated, unpalatability always preceded gregariousness: five cases of independent evolution of warning coloration were followed by a total of 15 cases of independent evolution of gregariousness. In no lineage did gregariousness evolve before warning coloration. It is thus concluded that unpalatability is an important predisposing factor for the evolution of egg clustering and larval gregariousness in butterflies. Insofar as kin selection is related to larval gregariousness, this study indicates that kin selection is of minor importance for the evolution of both unpalatability and warning coloration.

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In the life cycles of butterflies and other insects, aggregation is not uncommon, and individuals may aggregate in the adult or in the larval stage. Adult aggregations are usually formed in connection with inactive phases in life, such as sleeping and hibernation (e.g., Turner, 1975; Monteith, 1982), and they are formed through migration of the participating individuals. Larval aggregations, on the other hand, usually come about through the female clustering her eggs. More specifically, in butterflies there seems to be a one-to-one relationship between egg-clustering and larval aggregation, so that all aggregations are a consequence of egg-clustering and all cases of egg-clustering give rise to aggregation in at least the first larval instar(s) (Stamp, 1980; Young, 1983; Chew and Robbins, 1984).

Among butterfly species, egg-clustering with concomitant larval gregariousness is rare in comparison to solitary oviposition. Stamp (1980) estimates that around 5% (never more than 10% in a given geographical area) of the world’s butterfly species deposit their eggs in clusters. It is apparent from her study that the occurrence of this behavior is not independent of taxonomy.

In some groups, (e.g., Acraeinae) almost all species lay eggs in clusters; others (e.g., Danainae) consist almost entirely of species that lay their eggs singly.

The adaptive significance of egg-clustering and larval gregariousness in butterflies is at present not well understood. Different authors emphasize different selective agents for the evolution of these behaviors (cf. Stamp, 1980; Young, 1983; Chew and Robbins, 1984; Courtney, 1984). For a long time it has been recognized that there is a correlation between gregariousness and aposematic coloration in insects (e.g., Fisher, 1930; Cott, 1940; Rettenmeyer, 1970; Edmunds, 1974), and Stamp (1980) concludes that “the advantage of egg-clustering appears to be related to aposematic coloration in butterflies (eggs, larvae, and adults).” Courtney (1984), on the other hand, states that “distastefulness and especially aposematism are unlikely to influence the evolution of the trait of clustering,” and he believes that increased fecundity as a result of decreased search time for oviposition sites is the most important factor to account for egg-clustering. Again, Young (1983) mentions a combination of ecological factors as
determinants of butterfly-oviposition pattern, most of them thought to influence female fecundity and larval nutrition.

Due to the frequent co-occurrence of larval aggregation and warning coloration, Fisher (1930) suggested that the trait of being distasteful may be selected in an indirect way, through kin living in close propinquity. Later, kin selection was thought to be responsible also for the evolution of aposematic coloration (e.g., Turner, 1971; Harvey et al., 1982). Thus, distastefulness and warning coloration have been regarded as altruistic traits, being of no direct advantage to the individual, and in the case of aposematic coloration, giving a disadvantage (increased discovery) to the individual that interacts with the predator. However, these ideas have been called into question by experiments showing that distasteful prey can survive predator sampling during avoidance learning (Boyden, 1976; Järvi et al., 1981a; Wiklund and Järvi, 1982) and that aposematism may confer higher survival on distasteful prey due to a higher degree of predator avoidance (Sillén-Tullberg, 1985a, 1985b). Many aposematic species are solitary (Järvi et al., 1981b), and theoretical models also show that both unpalatability and aposematic coloration can evolve through individual selection (Sillén-Tullberg and Bryant, 1983; Engen et al., 1986; Leimar et al., 1986).

In this paper, I question the idea proposed by Fisher (1930) that aggregation among butterfly larvae arises before the evolution of unpalatability for the following reason (see also Sillén-Tullberg and Bryant [1983] and Turner [1984 p. 349]). For an exposed edible prey organism that is relatively immobile and small in comparison to potential predators, to live gregariously ought to be dangerous, since a predator that finds an aggregation could consume all of the individuals. For an unpalatable organism, on the other hand, gregariousness is more likely to be favored, since a predator avoids prey after some encounters (Sillén-Tullberg and Leimar, unpubl.). Thus, one would expect unpalatability to evolve before gregariousness.

The objective of this study is to establish the relative sequence of the evolution of larval unpalatability and gregariousness among butterfly species. I also investigate the relationship between the evolution of gregariousness and aposematic coloration, since aposematism has been used as a criterion for unpalatability.

**Materials and Methods**

*The Criterion for Unpalatability and Gregariousness*

In a comparative study involving many species, a practical problem is how to know whether an organism is distasteful, since it is not feasible to let predators experimentally taste all species. Therefore, I have used warning coloration as a criterion for unpalatability. It is a useful criterion, since Batesian mimicry appears to be rare in butterfly larvae and since data on larval coloration are readily available. However, this criterion gives a conservative estimate, since it will exclude distasteful species that are cryptic. I have classified conspicuous colors like black and combinations of black and red, orange, yellow, or white as aposematic (Cott, 1940).

For a species to be classified as gregarious, a minimum of 10 eggs must be included in the range of cluster sizes (Stamp [1980] uses an average of 10 eggs as criterion for egg-clustering). This criterion separates distinctly solitary and gregarious species. Species that generally lay solitary eggs may occasionally clump a few eggs together; however, when the range includes 10 eggs it almost never includes solitary eggs.

*A Phylogenetic Approach*

A main problem in all comparative studies of adaptation is how to distinguish between historical and adaptive reasons for organismal design (e.g., Clutton-Brock and Harvey, 1979; Harvey and Mace, 1982). One solution to this problem, at least for studies involving discrete variables, is that advocated by Ridley (1983). The basic idea is to count the number of times that a certain trait has evolved and to see whether the number of cases of independent evolution of the trait in question is correlated with certain environmental conditions. The method uses existing phylogenies to infer changes in character states and is parsimonious in the same way as the cladistic
method (Hennig, 1966; Wiley, 1981). Thus, the least possible number of character changes is assumed to have taken place during evolution (see Ridley [1983] for a detailed account of the method).

A crucial question in a comparative study is that of causation. More specifically, if two traits often occur together, then which trait influences the other? This question should be answerable from phylogenies or cladograms simply by observing which trait generally precedes the other (see Fig. 1 and also Chew and Robbins [1984 p. 76]), although if two characters are highly correlated, it is impossible to make inferences about causation.

**Working Procedure**

The general working procedure has been to use existing phylogenies and, through outgroup analysis (Ridley, 1983), to decide where in these phylogenies evolutionary changes have occurred. The important principle throughout the analysis has been to infer a minimum number of changes necessary to give the observed distribution of character states (parsimony). Unresolved groups present a problem, and it has been necessary to exclude such groups as Morphinae and most Pierinae from the analysis, due to the lack of phylogenies. Ridley (1983) proposes that, when cladograms are missing, one should use existing taxonomies as if they were phylogenies (for the reason that one thus gets a better estimate of phylogeny than if one assumes that all species are equally related [Ridley, 1983 p. 24]). I have followed this proposition insofar as assuming that species within genera and species groups (e.g., *Battus*) form monophyletic groups. In addition, I have made tentative phylogenies based on taxonomic literature for the Acraeinae and Nymphalini. I have also included Apaturinae in the analysis, in spite of the fact that the group is completely unresolved. The procedure for each of these groups is described in detail below. Again, I stress that the important principle throughout the analysis has been to keep the number of evolutionary changes at a minimum. For cases in which there have been several equally parsimonious alternatives (Pierinae, Nymphalini, and Heliconiini), I have chosen the one that biases the results the least.

As I am not a systematist, I am in no position to evaluate thoroughly various phylogenies. Therefore, I have used all available phylogenies that I could find, and in the few cases for which there have been several alternative phylogenies for a group (e.g., Papilionidae) I have simply used the latest one. I have started out with Scott's (1984) phylogeny for the larger groups (families and subfamilies) and then used special literature for each of these groups whenever necessary.

Data on egg-laying habits/larval sociality and larval coloration have been collected from the literature. I have used the following symbols for the character states: G (gregarious) and S (solitary); W (warning coloration) and C (crypsis).

**RESULTS**

The family-level phylogeny accepted by Scott (1984; Fig. 2) is similar to that of Ehrlich (1958) and deviates from that of Kristensen (1976) in that the Papilionidae and Pieridae form a monophyletic group, which branches off the ancestral line leading to Lycaenidae, Libytheidae, and Nymphalidae.

Two of the six butterfly families (Hesperiidae and Lycaenidae; Fig. 2) have been
excluded from this study due to their specialized lifestyles: the larvae of Hesperiidae live hidden in straw-nests, and Lycaenidae is characterized by a high degree of association with ants. These specializations change the preconditions with respect to predation, relative to those of the other four families.

Among the four families considered in this study, I have found egg-clustering/larval gregariousness in the Papilionidae, Pieridae, and Hesperiidae. Gregariousness has probably arisen independently within each of these three families as indicated by 1) outgroup comparisons for each family (see below), and 2) an outgroup comparison for the Papilionoidea as a whole, where Hesperioidea, the outgroup, seems to consist mainly of species that lay eggs singly. Thus, I conclude that solitary egg-laying is ancestral (plesiomorphic) for the Papilionoidea as a group. It will be shown that gregariousness has evolved independently several times in each of these families. It seems that cryptic coloration of the larva is the ancestral condition within the Papilionoidea (see outgroup comparisons below) and that warning coloration has evolved independently in the three families with larval gregariousness.

**Papilionidae**

In the Papilionidae, I have found egg-clustering species in three tribes (Fig. 3). The subfamily Baroniinae may function as an outgroup for the rest of the family, and the one species in this group has cryptic, solitary larvae (Tyler, 1975; Hancock, 1983). Accordingly, I regard these traits as ancestral for the family as a whole.

Larval warning coloration (red tubercles) is a general trait of the Parnassiinae and the Troidini. The question is whether this trait evolved in the ancestral line leading to Parnassiinae and Papilioninae, which would mean that reversals to cryptis have taken place separately in Leptocircini and Papilionini. This view seems to be advocated by Scott (1984). The alternative is that red-tuberculate larvae evolved separately in the lines leading to Parnassiinae and Troidini (Hancock, 1983). I choose the latter alternative, since it is the most parsimonious (Fig. 3). However, with regard to the relative appearance of warning coloration and aggregation, this choice has no significance.
then two alternatives concerning the evolution of gregariousness in the genus *Battus*. One, is that it arose in the common ancestor to the two sister groups and that solitary living was secondarily derived at least once in each group. This requires a minimum of three evolutionary changes. The alternative possibility is that gregariousness evolved once in each of the two groups, and this is the most parsimonious alternative, since it only requires two evolutionary changes. Thus, in the Troidini there are two cases of evolution of larval gregariousness following the evolution of warning coloration.

In the tribe Papilionini, I have found gregariousness in three species/species-groups (Fig. 4). These are *Heraclides* (*Papilio*) *anchisiades* (Miles Moss, 1920; Young et al., 1986) in the *anchisiades* group (Hancock, 1983), *Princeps* (*Papilio*) *liomedon* (Wynter-Blyth, 1957) belonging to the *demolion* group (Munroe, 1961) and the *Chilasa* (*Papilio*) *laglaizei* group (Hancock, 1983). These species/species groups are so widely separated phylogenetically (Fig. 4), that three cases of independent evolution are likely. Most larvae of the Papilionini are not aposematic, and *P. liomedon* (Wynter-Blyth, 1957) and *H. anchisiades* (Young et al., 1986) have evolved gregariousness while cryptic. Young et al. (1986) even go so far as to suggest that gregariousness in *anchisiades* has the effect of making the larvae more cryptic in that they together mimic pieces of bark on a tree trunk. The younger larvae, however, might be more conspicuous: Miles Moss (1920) writes about their yellow, oily, maggot-like appearance.

The larvae of *C. laglaizei* are warningly colored (Hancock, 1983), and the most parsimonious alternative, namely that warning coloration arose in the ancestor to the genera *Eleppone* and *Chilasa* (Fig. 4), suggests that gregariousness evolved after aposematism. Thus, for the Papilionini, there are three cases of independent evolution of gregariousness: two in cryptic species and one after the evolution of warning coloration. To sum up the results for Papilionidae, there are six cases of independent evolution of larval gregariousness, of which two took place in cryptic species and four occurred in aposematic species (i.e., after the evolution of aposematic coloration).
**Pieridae**

The family Pieridae consists of four subfamilies, whose relationships are shown in Figure 5. The only subfamily in which I have found cases of larval gregariousness is the Pierinae. However, the trait might occur in the Coliadinae as well. In Emmel (1976), there is a photograph of gregarious yellow/black larvae of the species *Eurema hecabe*. However, other literature does not mention larval gregariousness, either for this widely distributed species (Van Son, 1949; Wynter Blyth, 1957; Common and Waterhouse, 1972) or for other species in the genus (Scott, 1986). Thus, I decided not to include this uncertain case in the analysis.

In the Pierinae, egg clustering/larval gregariousness has been reported for species in several genera: *Pinaconteryx, Colotis, Bellenois, Dixeia*, and *Mylothris* (Van Son, 1949); *Ascia, Neophasia*, and *Eucheria* (Scott, 1986); *Delias* and *Anaphaedes* (Common and Waterhouse, 1972); and *Aporia* and *Pieris* (Shirôzu and Hara, 1960; Henricksen and Kreutzer, 1982). Many of these species/genera are aposematic, but some are cryptic. The problem is that the relationship among all these genera is practically unknown (see for instance Klots [1931], where all of the above-mentioned genera except *Pinaconteryx* are included in the tribe Pierini, with altogether 36 genera of unknown mutual relationship). The only phylogeny I have been able to find is that of Geiger (1980), which is based on electrophoretic data and concerns European taxa only (Fig. 6). The gregarious species included in this phylogeny are *Pieris brassicae, P. cheiranthe* (which is sometimes regarded as a subspecies of *P. brassicae* [e.g., Higgins and Hargreaves, 1983]), and *Aporia crafetapi*. The relationship between the evolution of warning coloration and gregariousness is difficult to establish, since there are several equally parsimonious alternatives concerning evolutionary changes in coloration. If it is assumed that the ancestral condition for Pierinae is crypsis (which is likely, since crypsis is the general condition in the outgroup Coliadinae), then one can infer that warning coloration evolved once in the common ancestor to all of the species in Figure 6 and that reversals to crypsis took place in the two *Artogeia* lines and the *Anthocharis* line. This makes four evolutionary changes. Alternatively, we may infer that warning coloration evolved separately four times (Fig. 6). I have chosen this latter alternative, because, since it does not separate between the evolutionary events of warning coloration and gregariousness, it does not bias the analysis in any direction. Thus, the results for this large butterfly family involve
two cases of "inseparable" evolution of aposematism and gregariousness.

**Nymphalidae**

In the Nymphalidae, I have found cases of larval gregariousness in seven out of the nine subfamilies (Fig. 7). Three of these, namely the Acraeinae, Nymphalinae, and Danainae, consist almost entirely of species with waringly colored larvae, with the exception of some Nymphalini (see below). Thus, I suggest that warning coloration has evolved once in the ancestral line leading to Acraeinae/Nymphalinae and once in the Danainae ancestral line (Fig. 7). For the other subfamilies, which consist both of species with aposomatic and cryptic larvae, I infer that there has been independent evolution of aposematism within each family. The Satyrinae is the only subfamily in which gregariousness has been found and in which all species have cryptic larvae.

In the subfamily Acraeinae, there are two tribes, Pardopsideini with the genus *Pardopsis* and Acraeini with the genera *Acraea* and *Bematinestes* (Van Son, 1963; Owen, 1971). I have assumed that these taxa are related to each other as shown in Figure 8. *Pardopsis*, with its solitary species, functions as an outgroup, and I suggest that there is one case of independent evolution of gregariousness in the common ancestor to the Acraeini and one reversal to solitary living in the genus *Acraea*. An alternative that also requires two evolutionary changes is that gregariousness evolved independently in *Bematinestes* and *Acraea*. That could be only if *A. nohara*, the only solitary species (Van Son, 1963), were the outgroup to the rest of the *Acraea* species. Since I do not know the phylogenetic relationships within the genus, this seems to be a far-fetched solution. Thus, for the Acraeinae I infer one case of evolution of gregariousness after warning coloration.

The relationship between the four tribes in the subfamily Nymphalinae is, according to Scott (1984), not clear, except that Argynnini and Heliconiini form one monophyletic group (Fig. 9). Melitaeni consists entirely of gregarious species, whereas the other three groups have both types of species. Since gregariousness appears to be derived separately in the Argynnini, Nymphalini, and Heliconiini (see below), the most parsimonious solution for Nymphalinae would be that gregariousness evolved once in the Melitaenii ancestral line (Fig. 9).

For the most part, the species in Argynnini are solitary, but egg-clustering has been reported for two out of 14 American *Boloria* species (*B. eumomia* and *B. polaris*; Scott, 1986). I thus infer that gregariousness has evolved once within this genus.

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**Fig. 7.** Phylogeny of the subfamilies in the Nymphalidae (after Scott [1984]). Larval gregariousness (G) has been found in seven of the subfamilies. At the level of this phylogeny, warning coloration (W) is inferred to have evolved once in the common ancestor to Acraeinae and Nymphalinae (with a reversal to crypsis in the tribe Nymphalini) and once in the ancestor to Danainae.

**Fig. 8.** Presumed phylogeny of the genera and tribes in Acraeinae (all waringly colored; based on the taxonomy in Van Son [1963] and Owen [1971]), with the number of species in each genus. It is argued that gregariousness (G) has evolved once in the Acraeini line (see text).
There are many reports of egg-clustering in the Nymphalini (Shirôzu and Hara, 1960; Common and Waterhouse, 1972; Henriksen and Kreutzer, 1982; Scott, 1986). Among European genera the following are gregarious: *Inachis*, *Aglais*, *Nymphalis*, and *Araschnia*. Solitary genera are *Limenitis*, *Neptis*, *Polygona*, and *Vanessa*. The phylogenetic relationships among these genera are, unfortunately, poorly resolved, although three subgroups may be recognized: 1) *Limenitis/Neptis*, 2) *Araschnia*, and 3) the rest (Niculescu, 1985). Higgins and Hargreaves (1983) suggest a relatively close relationship between subgroups 2 and 3, and the tentative phylogeny in Figure 10 follows this reasoning. I have inferred the minimum of one case of evolution of gregariousness in this group of genera and then a reversal to solitary living in *Vanessa/Polygona*. (An equally parsimonious solution would be that solitary living was retained as the ancestral condition in *Vanessa/Polygona* and that gregariousness evolved twice, i.e., once in the *Araschnia* line and once in a line leading to *Inachis/Aglais/Nymphalis*. The unique habit of laying string-formed batches in *Araschnia* could be seen as lending support to the possibility of separate evolution of gregariousness in this line.)

Additional genera of Nymphalini for which gregariousness has been reported are *Hypolimnas* (Common and Waterhouse, 1972; Scott, 1986), *Symbrenthia* (Johnston and Johnston, 1980), *Mynes* and *Doleschallia* (Common and Waterhouse, 1972), and *Hamadryas* (Scott, 1986), but since the relationship among these genera is unknown, they cannot be used in the analysis. For the Nymphalini, I thus count two cases of independent evolution of gregariousness after warning coloration.

For the tribe Heliconiini there is detailed knowledge both about egg-laying patterns and phylogenetic relationships among species, summarized in Brown (1981). For the Austral-Asian genera *Cethosia* and *Vin- dula*, which together form a sister group to the rest of the genera (all Neotropical; Fig. 10), I have found two reports on gregariousness, namely, in *C. cydippe* (Common and Waterhouse, 1972) and *C. biblis* (Johnston and Johnston, 1980). I thus infer that gregariousness has evolved at least once in the genus *Cethosia*. For the Neotropical species, I have, as usual, inferred a minimum number of evolutionary changes and, in addition, a minimum number of independent evolution of gregariousness (see the genus *Dione*, for which an alternative to the assumed one case of gregariousness and then reversal to solitary living would be two cases of gregariousness). This makes a total of five cases of independent evolution of gregariousness (Fig. 11). Then, for Heliconiini we have a total of six cases of gregariousness evolving after warning coloration. Thus, for
the minimum number of cases of evolution of gregariousness is one, without any previous evolution of warning coloration. However, warning coloration has evolved separately once.

In the Satyrinae I have found one species with gregarious larvae, *Neope goschkevit-schii* (Shirôzu and Hara, 1962). As with all species in this group of butterflies, the larvae are cryptic. Accordingly, there is one case of evolution of gregariousness without warning coloration.

According to Scott (1984), there is a general propensity for communal larval feeding in the subfamily Morphinae. Unfortunately, this subfamily is, to a great extent, unresolved phylogenetically. For instance, the genera included in Morphinae by Ehrlich (1958) are subdivided into three subfamilies by Ackery (1984), namely “Brassoliniae” and “Morphinae” (both Neotropical) and “Amathusiinae” (the species of which belong to the Indo-Australian tropics). Scott (1984) includes “Brassolini” in the Morphinae, but does not mention the “Amathusiinae.”

Larval gregariousness has been reported for species in the genera *Discophora* and *Faunis* (Wynter Blyth, 1957; Johnston and Johnston, 1980) in “Amathusiinae” (sensu Ackery, 1984), and the larvae in this group are warningly colored. In the brassolids, gregariousness has been reported for *Opsiphanes cassini* (Young, 1983) and *Caligo eurilochus* (Malo and Willis, 1961). The larvae of *C. eurilochus* seem to be aposomatic in at least some instars (Malo and Willis, 1961), whereas those of *Opsiphanes* are cryptic (Young, 1983). Finally, in the large genus *Morpho* (“Morphinae” [sensu Ackery, 1984]), the larvae of which are aposomatic according to Young (1983), there are several reports of larval gregariousness (e.g., Young, 1973, 1983).

In spite of the many well documented cases of gregariousness in the Morphinae, I feel that too little is known about the relationships within this family to warrant an analysis based on phylogeny. Thus, I have chosen to leave it out of this study.

In the two remaining subfamilies, Danainae and Ithomiinae, the species of which are known to be distasteful, the overwhelming majority place their eggs singly (e.g.,
Young, 1983; Ackery and Vane-Wright, 1984). In the Danainae, there is only one species that lays eggs in clusters, namely *Amauris albimaculata* (Van Son, 1955). Another 14 species are included in this genus, all of which are solitary (Fig. 12), and accordingly, I suggest that gregariousness has evolved once in this genus. All Danainae species have aposomatic larvae, and I have previously suggested that warning coloration is the ancestral condition for the subfamily (Fig. 7). Accordingly, there is one case of evolution of gregariousness after warning coloration in the Danainae.

In the Ithomiinae, larval gregariousness has been reported in *Mechanitis isthmia* (Fox, 1967; Rathcke and Poole, 1975) and *M. polymnia* (Fox, 1967), and the larvae of *Mechanitis* are “subtly colored,” according to Young (1983). *Mechanitis* is one of five genera in the tribe Mechanitini (Fig. 13), and there are seven other species of *Mechanitis*, which presumably have solitary larvae. Thus, the most parsimonious conclusion is that gregariousness evolved once within this genus.

There is another report on gregariousness in the Ithomiinae, namely in the species *Hypothyris euclea*, which has aposomatic larvae (Young, 1977, 1983). This species belongs to the tribe Napeogenini (Fox, 1956; Young, 1977), but since I know neither the coloration of other species in the tribe nor their phylogenetic positions, I cannot determine the sequence for the evolution of gregariousness and warning coloration. Thus, for the Ithomiinae there are two cases of independent evolution of gregariousness: one without warning coloration and one that is inseparable from it.

In conclusion, for the family Nymphalidae, there are 15 cases of independent evolution of gregariousness; eleven of these took place after warning coloration had evolved, and three took place in cryptic species. In one case, I cannot separate between the two evolutionary events.

The results for the entire study are summarized in Table 1. In lineages where unpalatability (as evidenced by aposomatic coloration) has evolved together with gregariousness and where the two evolutionary events can be separated, unpalatability always precedes gregariousness. Gregariousness has also evolved in cryptic species, which may or may not be unpalatable (see Discussion). For a total of 12 cases of independent evolution of aposomatic coloration in butterfly larvae, all took place without evidence of previous gregariousness.

**DISCUSSION**

This study shows that egg-clustering/larval gregariousness in butterflies is more likely to evolve in species with unpalatable larvae than in species with edible larvae. A recent model (Sillén-Tullberg and Leimar, unpubl.) also shows that, since unpalatability may give rise to a dilution effect (Bertram, 1978; Turner and Pitcher, 1986), it can favor the evolution of gregariousness in insects. Gregariousness could also evolve if distasteful individuals have the ability to pool obnoxious substances and thereby lower attack risk (e.g., Aldrich and Blum, 1978; Sillén-Tullberg, unpubl.).

I have used warning coloration as a criterion for unpalatability and one may question the suitability of this criterion. In particular, it is important to determine whether there is any likelihood that aposomatic species are edible or that unpalatable species are cryptic. The only likely reason for an edible species to evolve aposomatic color-
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Table 1. Cases of independent evolution of larval warning coloration and gregariousness in butterflies. Warning coloration has been used as evidence for unpalatability. In lineages that have evolved both unpalatability (warning coloration) and gregariousness and in which the two evolutionary events can be separated, unpalatability (warning coloration) invariably precedes gregariousness. A total of 12 cases of warning coloration and 23 cases of gregariousness were found in this study.

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Protocols would be to mimic another species that is unpalatable (i.e., Batesian mimicry). Although this phenomenon is very common in adult butterflies (e.g., Bates, 1862; Brower, 1958), it seems to be rare or non-existent in larvae. This difference between larvae and adults is in itself an interesting problem, which warrants further study. On the other hand, there is a high probability that some species in this study are unpalatable without being aposematic. The reason is that warning coloration is not a necessary consequence of unpalatability (e.g., Leimar et al., 1986). In sawflies, for instance, there are several species that have cryptic (green, green/black) distasteful larvae (Prop, 1960). Aposematism is thus a conservative criterion for distastefulness.

Among the groups that include the five cryptic gregarious species (Table 1), it is very likely that the ithomiines are unpalatable (due to their solanaceous hosts; Rathcke and Poole, 1975). The papilionines may also be unpalatable: there is experimental evidence for distastefulness in Papilio machaon (Järvi et al., 1981a), and all papilionids have an osmeterium, an eversible gland with defensive functions (e.g., Eisner and Meinwald, 1963); however, Young et al. (1986) observed a bird predator, which, upon discovering a group of P. anchisiades, devoured all of the larvae. I do not know the palatability of the Apaturinae. Finally, I find it unlikely that the satyriines are distasteful, but an investigation of the gregarious species in question is necessary.

Since most cases of independent evolution of gregariousness in butterfly larvae are preceded by the evolution of aposematism, it is relevant to ask whether this type of coloration could promote selection for gregariousness, i.e., whether predator avoidance is enhanced in an aggregation (e.g., Cott, 1940; Rettenmeyer, 1970; Edmunds, 1974). Unfortunately, this question cannot be answered until it can be experimentally verified that aggregations do have a more deterrent effect than solitary aposematic individuals (Sillén-Tullberg, unpubl.).

As previously mentioned, there might be other factors, unrelated to predation, that influence oviposition pattern/larval gregariousness in butterflies. One of these is female fecundity. Hebert (1983) has convincingly shown that, in moths, the frequency of egg-clustering species is higher for taxa in which the adult has reduced mouth parts, and he ascribes this to selection for increased fecundity at the expense of flight in these taxa (see also Wiklund et al. [1987] concerning egg clustering in the Pierinae). It would also be interesting to see whether egg-clustering in moths is correlated with distastefulness. My prediction is that, due to the similar life-styles of larvae of moths and butterflies, an analysis based on phy-
logy would yield much the same result as this study.

This study shows the great significance of unpalatability for the evolution of gregariousness. Since there was no case in which aposematism evolved after gregariousness, the study also indicates that kin selection is of little significance for the evolution of aposematic coloration, assuming that the degree to which kin selection takes place is proportional to the degree of larval gregariousness. Thus, individual selection is probably of much greater importance than kin selection for the evolution of warning coloration in butterfly larvae.

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