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Evolution of larval gregariousness in relation to repellent defences and warning coloration in tree-feeding Macrolepidoptera: a phylogenetic analysis based on independent contrasts

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Gregariousness in insects is often associated with aposematism, which has two distinct properties, repellent defence and warning coloration. Theoretically, both repellent defence and warning coloration are expected to facilitate the evolution of gregariousness. This paper investigates whether the likelihood for gregariousness to evolve is higher (1) in the presence of chemical/physical defence and (2) in the presence of warning coloration, in a sample of over 800 tree-living macrolepidopteran species. A new phylogenetic technique for investigating the correlation between two discrete characters, based on independent contrasts, is used. For each of nine contrasts, based on presence/absence of repellent defence that included transitions to gregariousness, the frequency of such transitions was highest in the lineage with repellent defence present. Similarly, out of 12 contrasts based on presence/absence of warning coloration 10 had the highest frequency of transitions to gregariousness in the lineage with warning coloration. Thus, gregariousness is more likely to evolve in lineages with repellent defence and in lineages with warning coloration, but it is concluded that, since these traits are strongly intercorrelated, it is very difficult to distinguish between their separate effects on the evolution of gregariousness. Our findings indicate, however, that potentially, the presence of repellent defence may be sufficient for the evolution of gregariousness.

ADDITIONAL KEY WORDS:—contrast analysis – discrete characters – phylogenies – gregariousness – aposematism – repellent defence – warning coloration.

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INTRODUCTION

Many insects that live gregariously are also aposematic (Fisher, 1930; Cott, 1940; Edmunds, 1974), and several different explanations have been proposed concerning the evolutionary background to this correlation. Aposematism includes two components, repellent defences operating during an encounter with a predator (a type of secondary defence, *sensu* Edmunds, 1974), and warning coloration that signals such repellent defences (a type of primary defence, *sensu* Edmunds, 1974). While repellent defences and warning colours are usually associated, some insects have repellent defences without being warningly coloured, and others are warningly coloured without repellent defence, i.e. Batesian mimics.

Several different evolutionary scenarios have been proposed to account for the correlation between repellent defences and warning coloration on one hand and gregariousness on the other, and these scenarios differ with respect to the relative order in which the characters evolve. Thus, Cott (1940) proposed that gregariousness evolves to enhance the effect of warning coloration, which presumes that gregariousness evolves after warning coloration. Most insect aggregations consist of closely related individuals (typically sibs), and Fisher (1930) proposed that noxiousness evolves in kin groups, which presupposes that gregariousness precedes the evolution of repellent defences. Theoretically, kin selection may operate in the evolution of warning coloration (e.g. Harvey *et al*., 1982; Leimar, Enquist & Sillén-Tullberg, 1986), in which case gregariousness is expected to precede warning coloration. However, recent theoretical work suggests that repellent defences should be an important precondition, and a sufficient one, for the evolution of gregariousness in many insects (Sillén-Tullberg & Bryant, 1983; Sillén-Tullberg & Leimar, 1988) and also that warning coloration may facilitate the evolution of gregariousness (Sillén-Tullberg & Leimar, 1988). This predicts gregariousness to evolve after repellent defences and most likely after warning coloration as well. It is therefore important to establish temporal sequences for the evolution of these traits, especially to try to separate between repellent defences and warning colours, and to investigate whether the presence of each of these traits can increase the likelihood for gregariousness to evolve.

In insects such as lepidopteran larvae, warning coloration is a much more widespread trait than is gregariousness (e.g. Nothnagle & Schultz, 1987; Fitzgerald, 1993). Therefore one could suspect, without access to phylogenetic information, that gregariousness generally has evolved in lineages where warning coloration is already present (Järvi, Sillén-Tullberg & Wiklund, 1981). This suspicion was confirmed in phylogenetic analyses of larval gregariousness in butterflies (Sillén-Tullberg, 1988). This study was subsequently questioned on the ground that it had not been shown that the *probability* of a transition to gregariousness is higher for branches with warning colours (Maddison, 1990; Harvey & Pagel, 1991). However, this problem was addressed in an additional study, where clades with cryptic and warningly coloured taxa were resolved to the same degree, and where it indeed could be shown that gregariousness originated more frequently in warning branches (Sillén-Tullberg, 1993). On the other hand, origins of gregariousness were definitely concentrated in certain clades in the butterfly phylogeny, and it could therefore be argued that the significant relationship between larval gregariousness and warning colours found in butterflies is due to some other, unknown, factor(s) operating in a few clades. In conclusion the problem of phylogenetic dependence was only partly resolved in that study. The purpose of the present study is to make a more extensive analysis that accounts for separate origins of warning colours and repellent defences, as well as gregariousness. That is, an analysis that considers separate origins of all characters under study.

PHYLOGENETIC INDEPENDENCE IN DISCRETE CHARACTERS

There has recently been a lot of work devoted to statistical techniques for investigating the correlation between characters in phylogenetic trees (e.g. Grafen, 1989; Harvey & Pagel, 1991; Martins & Garland, 1991). Most of the methods developed so far are derived from Felsenstein (1985), use phylogenetically independent contrasts as observations, and are applicable to continuous, not discrete characters (e.g. Purvis 1991; Garland *et al.*, 1993).

Discrete characters have in most cases been treated in a different way from continuous characters (see Nylin & Wedell, 1994). First, discrete characters are usually reconstructed over a phylogenetic tree using cladistic techniques (e.g. Ridley, 1983). Second, methods proposed for the investigation of correlation between discrete characters and that also account for the temporal order of character transitions inferred from parsimony analysis, use branches as separate observations, not contrasts (Maddison, 1990; Sillén-Tullberg, 1993).

Consider two characters, each with two states. One character is regarded as independent, for example coloration with the states cryptic and warning, and the other character is regarded as dependent, for instance lifestyle with the states solitary and gregarious. After reconstructing each character over a phylogenetic tree, the methods investigate whether a certain type of transition in the dependent character is more likely to occur in the presence of a certain state of the independent character. For instance, are transitions to gregariousness more likely to occur on branches with warning than with cryptic coloration?

Both the methods pool all the branches with warning coloration and all the branches with crypsis, respectively, over the whole tree. Thus, for a given number of branches in the tree, neither method distinguishes between a situation where a certain number of transitions to gregariousness takes place within different clades, each of which has independently derived warning coloration, and the case where the transitions take place in a clade where warning coloration has originated once. Especially in the latter situation there is an elevated risk that a significant correlation may be due to an unknown variable operating in this specific clade.

In this paper we use a method where we form independent contrasts in the independent character, where both states, say cryptic and warning coloration, are represented in each contrast. The two types of branches in each contrast are then compared with regard to the proportion of branches carrying a transition to gregariousness, and a sign-test is subsequently applied to see whether there are significantly more contrasts with the highest proportion of such transitions in branches with warning coloration. This type of test requires a fairly large phylogeny, since several transitions are needed, not only in the dependent character, but in the independent character as well. We apply the test to a sample of forest Lepidoptera consisting of over 800 species and ask whether larval gregariousness is more likely to evolve (1) in the presence of warning coloration, and (2) in the presence of physical or chemical defence against predators.

MATERIAL AND METHODS

The characters

Data on larval characteristics were gathered from published literature on North American, British, and North European tree and shrub-feeding Macrolepidoptera as part of a larger comparative study of their population dynamics (Hunter, 1991, 1995). Major sources were the Canadian Forest Insect Survey (McGugan, 1958; Prentice, 1962, 1963), books on forest insects, identification guides and taxonomic works. In addition to the references cited in Hunter (1991), we used Furniss & Carolin (1977), Rose & Lindquist (1984, 1985, 1992), and Bolte (1990) for North American coniferophagous species and Buckler (1896), Carter (1984), Emmet & Heath (1991), Skou (1986) and Stokoe & Stovin (1948) for European species. Nomenclature follows Hodges *et al*. (1983), and Scott (1986) for North America and Emmet & Heath (1991), and Higgins & Riley (1970) for Europe.

The characters were defined as follows:

Lifestyle. Species were considered gregarious if the larvae feed in groups during the whole or a part of their development. Thus, species which feed in groups initially, generally up to the 3rd instar, but individually in later instars, are considered gregarious. Species which cluster their eggs but disperse before initiating feeding are considered solitary. States: (1) solitary, (2) gregarious.

Coloration. Larvae strikingly marked with combinations of black and yellow, red and/or white were scored as warningly coloured, others as cryptic. This information was obtained from photographs, coloured drawings or verbal descriptions of larvae. States: (1) cryptic, (2) warning.

Defence. Larvae with splines, sharp tubercules or many long setae were considered to have physical defences. Chemical defences encompass urticating hairs, distastefulness to predators, and scent glands with deterrent properties. Information on the use of leaf rolls or ties which may deter predators was also incorporated. Leaf rolls/ties may be regarded as a primary defence with a similar function as crypsis, namely to escape detection by a predator. However, Damman (1987) has shown that this type of defence provides a powerful physical barrier, and that the shelter effect of a leaf roll is more important than concealment for a pyralid moth larva. Moreover, leaf tiers were found to be the most palatable larvae in a comparison among different defence categories (Bernays & Cornelius, 1989), indicating that they may rely on their shelter also for secondary defence. Repellent defences are probably under-reported in the literature, especially for species of little economic importance (90% of species here). Warningly coloured species for which we found no information concerning repellent defences were considered as missing values for the defence character. This is because, although such species are likely to have chemical defence since Batesian mimicry seems to be rare in lepidopteran (and other) larvae (Sillén-Tullberg, 1988), it is more conservative to consider them as missing values than to assume that they have repellent defences. Cryptic species without any documented defence were considered to lack defence. States: (1) cryptic, (2) leaf roll or tie, (3) chemical, (4) physical.

The taxa

Five superfamilies are represented in the data: Bombycoidea, Geometroidea, Papilionoidea, Hesperioidea, and Noctuoidea (Appendix).

The relationships among the superfamilies within the monophyletic Macrolepidoptera are mostly unresolved (Nielsen, 1989). However, Hesperioidea and Papilionoidea are closely related to each other (Nielsen, 1989). For within-family phylogenetic relationships we used published phylogenies where available, and otherwise taxonomic arrangement. Taxonomies are frequently used in comparative studies (see Harvey & Pagel, 1991); we consider them suboptimal compared with phylogenetic information, but better than assuming that all taxa in a group are equally related to each other. We will discuss the likely effect on our conclusions of using alternative phylogenetic arrangements. Unless otherwise stated we make the assumption that genera are monophyletic. Comments in systematic treatments like 'is closely related to' and 'is primitive' were interpreted to represent evolutionary relationships. The taxonomic groups, some important characteristics of the species in them, and the source of the phylogenetic arrangements are listed below.

Bombycoidea. Four families are included in our sample. The phylogenetic arrangement for Lasiocampidae is based on the taxonomy of Franclemont (1973). Our arrangement of Saturniidae follows Michener (1952) with the modifications made by Ferguson (1972). There is only one species of Endromidae, *Endromis versicolor*. The arrangement of Sphingidae follows the taxonomy of Hodges (1971). The Sphingidae have often been placed in their own superfamily. However Nielsen (1989) and Scoble (1991), for instance, place them in the Bombycoidea. We follow Kuznetzov & Stekolnikov (1985) and Minet (1994) concerning the relationship between the families, i.e. Lasiocampidae + (Sphingidae + (Endromidae + Saturniidae)), although they place Lasiocampidae in a separate superfamily.

Geometroidea includes one family, Geometridae. We have followed McGuffin (1967, 1972, 1977, 1981, 1989), who mostly used the larval characteristics to arrange the tribes and subfamilies of the Geometridae.

Noctuoidea is a large superfamily with five families represented in our sample. Arrangements follow Miller (1991) who based the phylogeny on larval and adult characters. The Lymantriidae has 2500 named species of worldwide distribution

(Schaefer, 1989), and arrangement was based on comments in Ferguson (1978). Lymantriidae is the likely sister group to Arctiidae (Ferguson, 1978). There is little phylogenetic information for Arctiidae and we use the taxonomy of Hodges *et al*. (1983). The small family Nolidae, with warningly coloured and solitary larvae, is sometimes considered as a subfamily of Noctuidae. Noctuidae is an enormous family, and the phylogeny is not well resolved (Kitching, 1984). Species were grouped into sub-families according to Hodges *et al*. (1983).

Hesperioidea contains a single family, Hesperiidae. Only three species from two genera are represented in our sample.

Papilionoidea, the sister group of Hesperioidea, contains four families, Papilionidae, Pieridae, Lycaenidae and Nymphalidae. We follow the phylogeny by Scott & Wright (1990) for the relationship between families and subfamilies, and Hancock (1983) concerning the relationships within Papilionini.

Analysis

First, each of the three characters coloration, defence and lifestyle, were reconstructed on the various trees derived from the systematic literature. We used MacClade 3.0 (Maddison & Maddison, 1992) for these reconstructions of ancestral states. The four states of the defence character were considered unordered. For one family, Notodontidae, chemical and physical defences were pooled into one state. This was done because this family has a lot of variation in the defence character, and optimizations based on four states gave rise to many of the ancestral branches being equivocal, making it difficult to separate between chemical/physical defence on one hand and leaf rolls/ties on the other.

After character reconstructions we carried out two separate analyses, both with lifestyle as the dependent character. In one analysis coloration was the independent character, and in the other defence was the independent character. The questions we ask are whether gregariousness is more likely to evolve in (1) branches with warning coloration than in branches with crypsis, and (2) branches with repellent defence than in branches that are cryptic and lack such defence.

The method that we use considers independent contrasts in the character regarded as independent, for instance coloration as in the example in Figure 1. Each contrast consists of sister groups carrying each of the states, e.g. warning and cryptic (Fig. 1). A contrast can also be formed from an unresolved group, polytomy, where both states occur (several examples in the Results). Contrasts are created by the procedure shown in Figure 1. Only contrasts that carry transitions in the dependent character, gregariousness, are further considered.

For each contrast, the proportion of branches that have a transition in the dependent character is calculated for each of the two states in the independent character. Following Sillén-Tullberg (1993) these proportions are based on branches which, according to character reconstructions, have a potential for such a transition (Fig. 1). Thus, all branches that carry the state solitary as well as branches for which an actual transition to gregariousness is inferred, have a potential for a transition to gregariousness. Branches for which the state gregariousness is maintained, however, are not considered to have a potential for a transition to gregariousness, and are consequently excluded from calculations (e.g. branches leading to taxa F and G in

Fig. 1). Neither would branches with reversals from gregariousness to solitary be considered to have a potential for a transition to gregariousness. It is very important that taxa of the different states of the independent character are resolved to the same degree in these calculations, since the degree of resolution affects the number of branches, and accordingly the calculated proportions (Sillén-Tullberg, 1993). Here, we have always used resolutions at the species level when calculating proportions. However, for illustration purposes in the figures we have used the genus level and lower only insofar as there is variation in a character. The number of species is always indicated for unresolved genera and the number of branches in a clade is 2*n*-1, where *n* is the number of species.

For each contrast we then consider which of the two states has the highest proportion of branches with transitions in the dependent character. The number of contrasts with the higher proportion of transitions per branch occurring in each of the two states of the independent character are then compared in a sign test (Zar, 1984: 386). For instance, the number of contrasts with the highest proportion of transitions occurring in branches with warning coloration is compared with the number of contrasts that have the highest proportion of transition in cryptic branches. We use one-tailed tests since there is no *a priori* reason to believe that

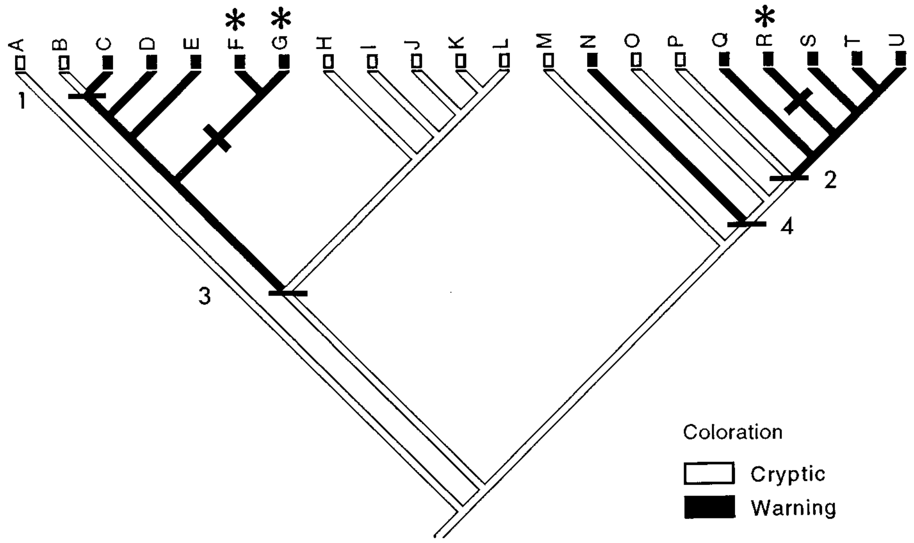

Figure 1. Example of contrast analysis for two discrete characters. The independent character, coloration, is shown reconstructed over a phylogeny with taxa A to U. The dependent character, with the states solitary and gregarious (asterisk), has been optimized and the two inferred transitions to gregariousness are shown as crossbars. Four contrasts can be created working from the tips (terminal taxa) to the basal branches of the phylogeny: (1) Taxon B-C with one cryptic and one warning colour banch, (2) P-U with one cryptic and nine branches with warning colour, (3) D-L with nine branches of each coloration, and (4) N-O with three cryptic and one warning colour branches. Thus, all the branches in contrast (1) are excluded from contrast (3), and, similarly, all the branches in contrast (2) are excluded from contrast (4). Contrasts (1) and (4) do not include transitions to gregariousness and are not further considered. In contrast (2) there are 0/1 cryptic and 1/9 warning colour branches with transitions to gregariousness. In contrast (3) there are 0/9 cryptic and 1/7 warning colour branches with transitions to gregariousness (note that the branches leading to F and G, respectively, are not included in this calculation since they are inferred to already carry the state gregarious, see text). In this example there are thus two contrasts, in each of which the proportion of branches with a transition to gregariousness is highest in the lineage with warning colour.

gregariousness is more likely to evolve in cryptic than in warning colour lineages, or more likely to evolve in cryptic lineages without repellent defences than in lineages with such defence.

RESULTS

The Appendix lists genera with larval gregariousness, warning coloration or repellent defence, and gives the total number of species in each family that are included in the study. Of the 825 species in the data set, 61 species (7%) feed gregariously for at least part of the larval stage (Appendix). All but 14 of these species are warningly coloured, and all but two have warning colour and/or defences such as long setae, spines, noxious chemical, leaf rolls or ties. Warning coloration and repellent defences are more widespread than the gregarious lifestyle, warning coloration occurring in 148 of the species (18%), and repellent defences in 227 species (28%). Warning colours and various types of defences are quite unevenly distributed, however. For instance, most members of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae have repellent defences, while the Sphingidae, Geometridae and Noctuidae are mostly cryptic, with smooth integuments and few reported chemical defences.

We will give a general account of each of the four superfamilies included in the analysis, with respect to the reconstruction of the three characters that we have investigated. Because of the size of the data set we will not show all the phylogenies. We will, however, show all the contrasts included in the analysis together with some other groups of special interest.

Bombycoidea

Larvae of most species of Lasiocampidae and Saturniidae are warningly coloured, whereas most species of Sphingidae are cryptic (Fig. 2A). All species of Lasiocampidae and Saturniidae have a physical defence, some of which combine this with a chemical defence, and species of *Ceratomia* in Sphingidae have a physical defence (Fig. 2B). The only species of Endromidae (*Endromis versicolora*) has a chemical defence and is cryptic. Gregariousness is inferred to have evolved twice in Lasiocampidae (*Eriogaster lanestris* and *Malacosoma*), once in Sphingidae (*Ceratomia catalpae*), once in Endromidae, and three times in Saturniidae (*Anisota-Dryocampa*, *Hemileuca-Automeris*, and *Pavonia*) (Fig. 2).

There are four contrasts based on coloration, three of which have a higher proportion of transitions to gregariousness in branches with warning coloration, and one with this proportion being higher in cryptic branches (Fig. 2A, Table 1). There are two contrasts in the defence character and both have a higher proportion of origins of gregariousness in branches with repellent defences (Fig. 2B, Table 2).

Geometroidea

Most species in this superfamily have no documented repellent defences and are cryptic (Appendix). We estimate that warning coloration has originated at least seven

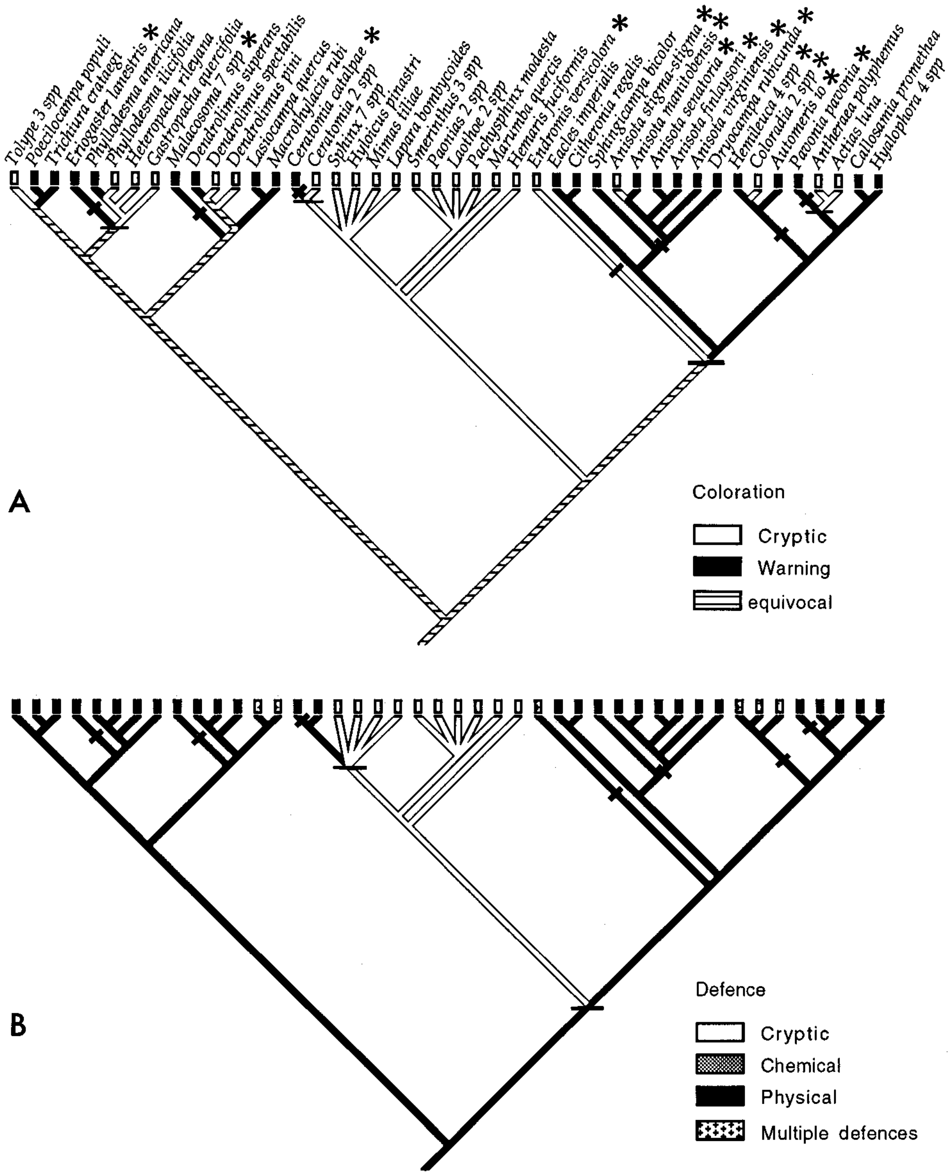

Figure 2. Phylogeny for Bombycoidea including Lasiocampidae (*Tolype-Macrothylacia*), Sphingidae (*Ceratomia-Hemaris*), Endromidae (*Endromis*), and Saturniidae (*Eacles-Hyalophora*). Gregarious taxa are marked by an asterisk and inferred transitions to gregariousness are shown by bars in the phylogeny. Reconstruction of (A) coloration and (B) defence. Contrasts that include a transition to gregariousness are denoted by a horizontal line. Thus, when calculating the proportion of branches with transitions to gregariousness in for instance the contrast including *Eriogaster-Gastropacha* in (A), it is important to note that the contrast including *Phyllodesma* has been excluded. Accordingly, for (A) there are three contrasts with the highest proportion of transitions to gregariousness in branches with warning coloration and one with the highest proportion in cryptic branches. For (B) there are two contrasts with the highest proportion of transitions to gregariousness in branches with repellent defence.

TABLE 1. Contrasts in the coloration character. The lineage with the higher proportion of transitions to gregariousness is indicated for each family or superfamily for which contrasts could be formed. Ho: Transitions to gregariousness equally frequent in the two types of branches or more frequent in cryptic branches. HA: Transitions to gregariousness more frequent in branches with warning coloration $P(1)=0.019$ (Sign-test)

	Contrasts with the highest proportion of transitions to gregariousness in branches with	
	Warning coloration	Crypsis
Bombycoidea		1
Sphingidae	1	
Lasiocampidae	1	
Saturnidae	1	
Geometroidea		
Geometridae	1	
Noctuoidea		
Notodontidae	3	1
Noctuidae	3	
	10	2

times in our sample. Repellent defences have evolved several times, and we estimate that physical defence has originated at least eight times, and leaf rolls or ties at least five times. Chemical defences are only reported for one species (Appendix). We infer only three origins of gregariousness, namely in *Ennomos subsignarius*, *Hydria prunivorata*, and *Hydriomena ruberata* (Appendix).

There is only one contrast in the coloration character, with the transition to gregariousness taking place in the brightly coloured *Hydria prunivorata* in Hydriome-

TABLE 2. Contrasts in the defence character. The lineage with the higher proportion of transitions to gregariousness is indicated for each family or superfamily for which contrasts could be formed. Ho: Transitions to gregariousness equally frequent in the two types of branches or more frequent in cryptic branches. HA: Transitions to gregariousness more frequent in branches with repellent defence. $P(1)=0.002$ (Sign-test). The parenthesis indicates a contrast where the defence consists of leaf roll or tie

	Contrasts with the highest proportion of transitions to gregariousness in branches with	
	Repellent defence	Crypsis
Bombycoidea	1	
Sphingidae	1	
Geometroidea		
Geometridae	(1)	
Noctuoidea		
Notodontidae	2	
Noctuidae	2	
Papilionoidea		
Pieridae	1	
Nymphalidae	1	
	9	0

nini (Fig. 3A, Table 1). Similarly, there is only one contrast in the defence character, with the highest frequency of transitions to gregariousness occurring in the sister group with repellent defences (Fig. 3B, Table 2). Note, however, that in Hydriomenini defence consists of leaf ties.

Noctuoidea

In Notodontidae there is a lot of variation with regard to coloration, defences and lifestyle of larvae. Warning coloration is widespread in the family and the basal branches are equivocal with respect to coloration (Fig. 4A). Repellent defence occurs in the subfamilies Pygaerinae (physical defence in four and leaf ties in four other *Clostera* spp.), Notodontinae (physical defence in three *Furcula* spp. and chemical in *Cerura vinula*), Phalerinae (physical defence in the genus *Datana* and physical and chemical in *Phalera*), and Heterocampinae (chemical in *Lochmaeus manteo*, physical and chemical in *Schizura concinna*, physical in *Fentonia* and in *Stauropus*). Note that we have pooled chemical and physical defences in this family (see Material and methods) and that this state is inferred for the basal branches (Fig. 4B). Gregariousness has evolved

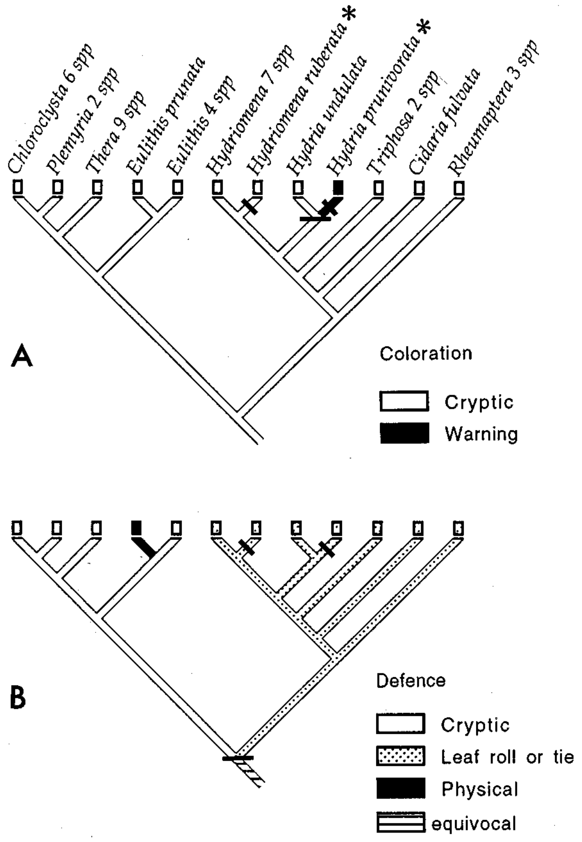

Figure 3. Phylogeny for a part of Hydriomenini (Larentiinae, Geometridae) with reconstruction of (A) coloration and (B) defence. In (A) there is one contrast with the highest proportion of transitions to gregariousness in branches with warning colour, and in (B) there is one contrast with the highest proportion of such transitions in branches with repellent defence (leaf ties).

at least once in the genus *Clostera* (occurs in five species, two of which have leaf ties and build tents), once in the group with the genera *Datana* and *Phalera*, once in the genus *Symmerista*, and once in *Schizura concinna* (Fig. 4).

For coloration there are three contrasts with the highest frequency of transitions to gregariousness in the warningly coloured, and one with the highest frequency in

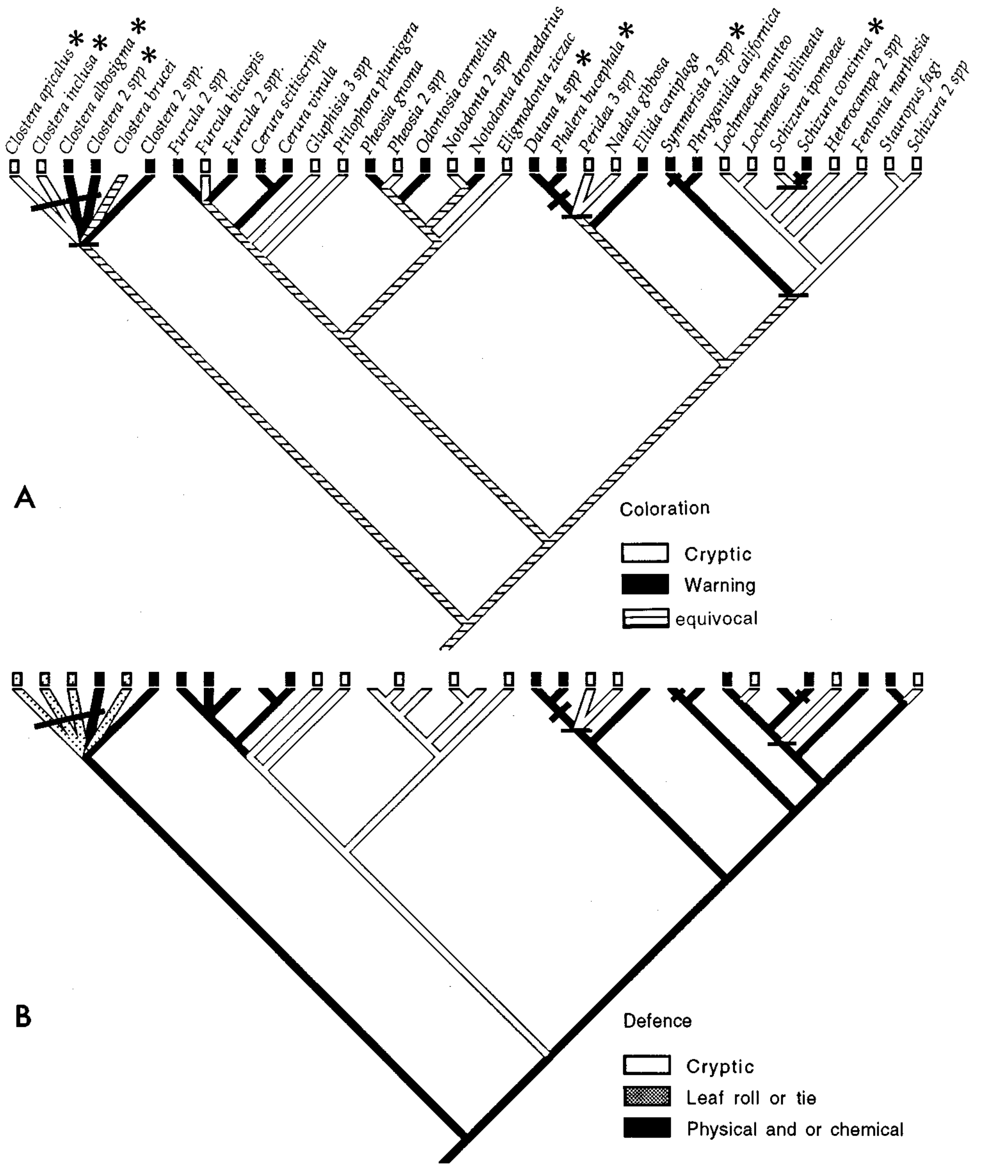

Figure 4. Phylogeny for Notodontidae (after Miller 1991) with reconstruction of (A) coloration and (B) defence. In (A) there are three contrasts with the highest proportion of transitions to gregariousness in warning colour branches, and one contrast, the genus *Clostera*, which has the highest frequency of transitions in cryptic branches. (Note, however, that the two characters Coloration and Lifestyle, respectively, are in conflict in this group, and that there may actually be only one transition to gregariousness in *Clostera*). In (B) there are two contrasts with the highest proportion of transitions to gregariousness in branches with repellent defence.

the cryptic sister group (Fig. 4A, Table 1). For defence there are two contrasts with transitions to gregariousness, both of which have the highest frequency in branches with repellent defences (Fig, 4B, Table 2).

Most species of Arctiidae and Lymantriidae are brightly coloured (Fig. 5A), and all have a physical defence, sometimes combined with a chemical defence (Fig. 5B). There are two transitions to gregariousness in the Lymantriidae (in *Dasychira* and in

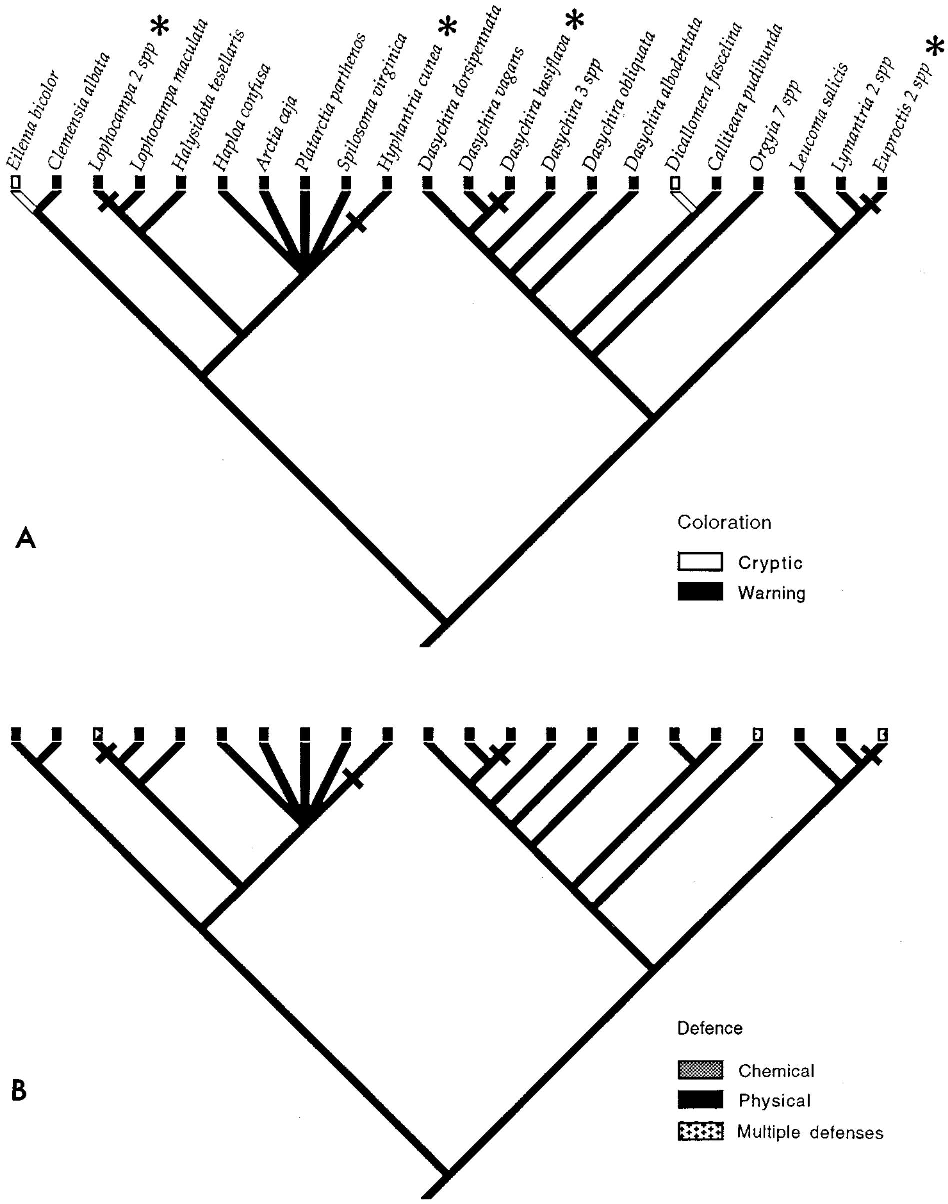

Figure 5. Phylogeny for Arctiidae (*Eilema-Hyphantria*) and Lymantriidae (*Dasychira-Euproctis*), with reconstruction of (A) coloration and (B) defence. There are two transitions to gregariousness inferred for each of the two families but there are no contrasts with a difference in transitions to gregariousness for either of the two independent characters.

Euproctis), and two transitions in Arctiidae (in *Lophocampa* and in *Hyphantria*). However, we could not form any contrasts with transitions to gregariousness in either the defence or the coloration character.

The family Noctuidae consists mainly of cryptic, solitary species without any other documented defence. However, there are scattered occurrences of repellent defence, warning colours and gregariousness in our sample of this huge family. Gregariousness has evolved in the cryptic *Catocala concinna* (Catocalinae) and two species of *Nycteola* (Sarrothripinae) which have leaf ties. It has evolved twice in Acronictinae (*Moma alpium* and *Acronicta rumicis*), and once in Hadeninae (*Orthosia miniosa*).

Three contrasts could be formed in the coloration character, two in Acronictinae, and one in the genus *Orthosia* in Hadeninae, and all three contrasts have the highest frequency of transitions to gregariousness in branches with warning coloration (Fig. 6A, Table 1). Two contrasts could be formed for the defence character, both in Acronictinae, each of which has the highest frequency of transitions to gregariousness in the sister group with repellent defences (Fig. 6B, Table 2).

Hesperioidea *and* Papilionoidea

The only family in Hesperioidea, Hesperiidae, is represented by two genera (*Epargyreus* and *Erynnis*), the species of which are cryptic and defended by leaf rolls (Fig. 7).

In our sample of Papilionoidea, warning coloration is estimated to have evolved once in Papilionidae (*Pterourus eurymedon*), once in Pieridae (*Aporia crataegi*), and once or twice in Nymphalidae (*Polygonia-Nymphalis* and *Limenitis camilla*) (Fig. 7A). The majority of species have various sorts of repellent defences (Fig. 7B). Gregariousness

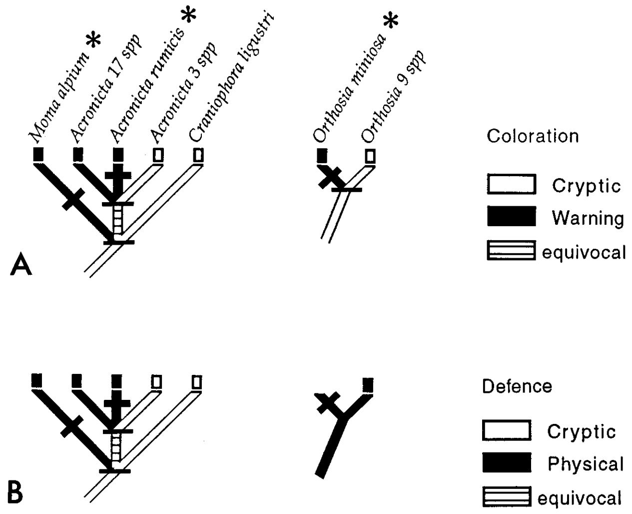

Figure 6. Phylogeny for Acronictinae and for the genus *Orthosia* (Hadeninae), in Noctuidae. Reconstruction of (A) coloration and (B) defence. In (A) there are three contrasts with the highest proportion of transitions to gregariousness in branches with warning colour, and in (B) there are two contrasts with the highest proportion of transitions to gregariousness in branches with repellent defence.

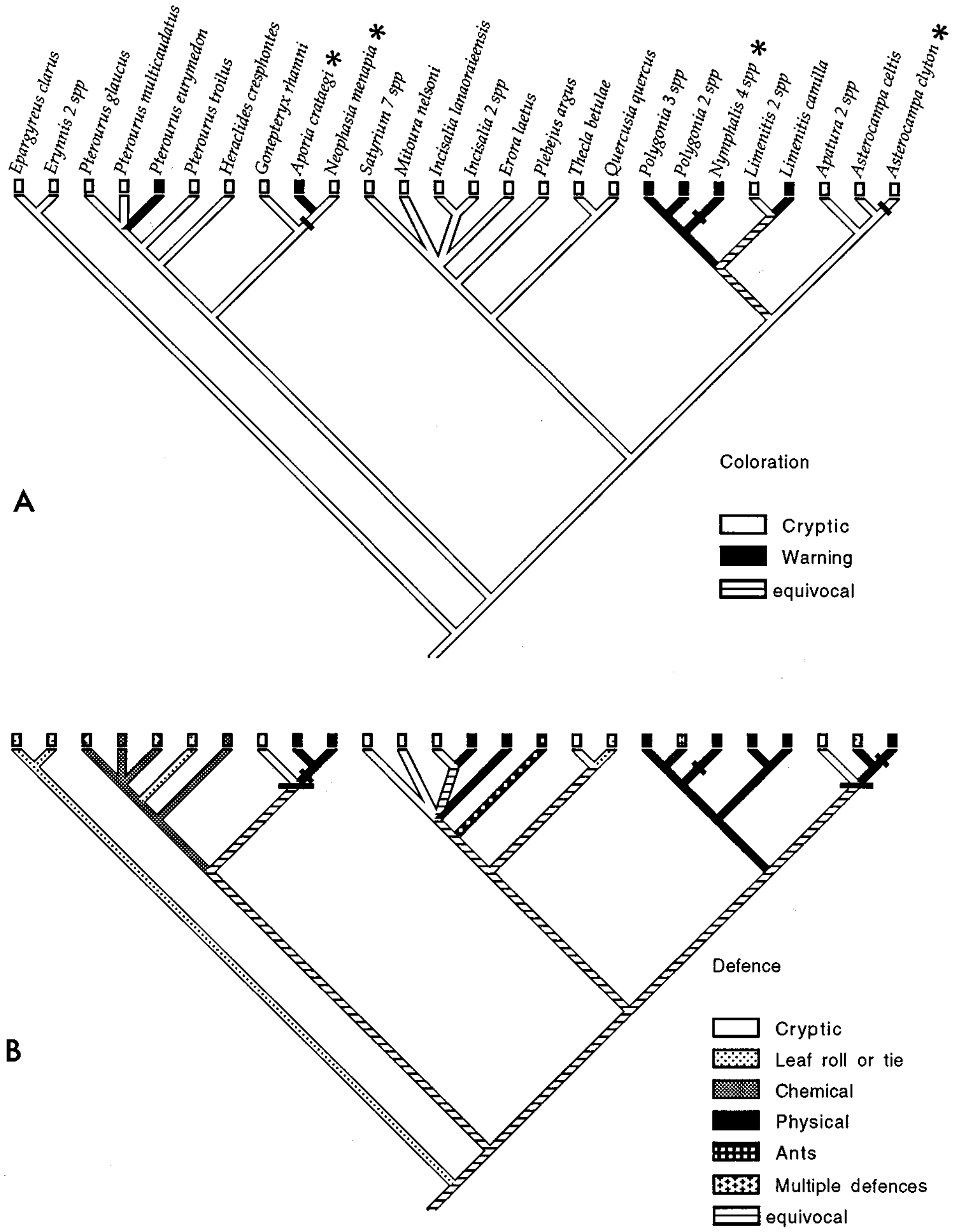

Figure 7. Phylogeny for Hesperioidea (*Epargyreus-Erynnis*) and Papilionoidea (*Pterourus-Asterocampa*). Reconstruction of (A) coloration and (B) defence. In (A) there is either a contrast with the highest proportion of transitions to gregariousness in branches with warning coloration or in branches with cryptic coloration, depending on the state in the two equivocal branches (up to *Limenitis*). Because of this uncertainty we do not include any contrast for coloration from this phylogeny in the analysis. In (B) there are two contrasts with the highest transition proportion in branches with physical defence. There is also a possible contrast including Nymphalinae (*Polygonia-Limenitis*), but this depends on the state of other branches that are equivocal, so this possibility has not been included in the analysis.

has evolved once in Pierinae (*Aporia-Neophasia*), once in the genus *Nymphalis* (Nymphalinae), and once in *Asterocampa clyton* (Apaturinae).

No contrast was accounted for in the coloration character due to equivocal branches (Fig. 7A). In the defence character there are two contrasts, both of which have the highest frequency of origins of gregariousness in branches with physical defence (Fig. 7B, Table 2).

Summary of results

For the coloration character there are 12 contrasts (Table 1), 10 of which have the highest frequency of transitions to gregariousness in the warning colour branches and two that have the highest frequency in the cryptic branches. The probability of this happening by chance is $P(1) = 0.019$ (Sign-test).

For the defence character, there are nine contrasts with the frequency of transitions to gregariousness being higher in the sister group with repellent defences than in the cryptic sister group, and zero contrasts with the reverse condition (Table 2). The probability of this happening by chance is $P(1) = 0.002$ (Sign-test). One of the contrasts included defence in the form of leaf ties and if we include only the eight contrasts with the physical or chemical defence the pattern is still significant ($P(1) = 0.004$).

DISCUSSION

In this study most origins of repellent defence or warning colour take place in lineages for which a solitary lifestyle is inferred. This is in accordance with results from previous studies (e.g. Sillén-Tullberg, 1988), supporting the idea that these traits have mostly evolved through individual, not kin selection. However, there is an increased likelihood for a gregarious lifestyle to evolve in lineages with repellent defence or warning coloration, although it should be noted that most such lineages do not evolve larval gregariousness at all. In previous analyses of butterfly larvae, warning coloration has been used as a cue for repellent defences (Sillén-Tullberg, 1988, 1993) the rationale being that Batesian mimicry seems to be most common in adult insects (e.g. Edmunds, 1974), not in larvae. In the present study repellent defence has been used as a character in its own right.

How do we explain the observed pattern? First, theoretical considerations indicate that the presence of repellent defence may effect the evolution of gregariousness in insects. This is so because a dilution effect may be attained through predator satiation due to limited predation on distasteful prey (Sillén-Tullberg & Leimar, 1988). However, warning coloration is also likely to facilitate gregariousness, because the detection risk may already be substantial for a brightly coloured individual and may therefore not increase much with gregariousness (Sillén-Tullberg & Leimar, 1988). In the present study most taxa with repellent defences also have warning coloration and it is therefore difficult to separate the effects of secondary defences and of coloration per se. However, in our phylogenies there are several instances of both origination and maintenance of gregariousness in defended lineages without warning coloration.

The method that we have used in this paper is based on independent contrasts in an independent character, the states of which are compared with respect to transitions in a dependent character. We consider this a rigorous method for investigating the correlation between two discrete characters after these have been reconstructed using parsimony. However, when characters are not tightly correlated (see discussion in Björklund, 1991), so that change in one character does not necessarily lead to change in the other character, the method requires a large data set in order to see a significant pattern.

Since we needed a large sample of taxa we have made a trade-off concerning our demands on the systematic literature on which we base phylogenetic relationships. Thus, for many groups we have based relationships on taxonomic, not cladistic studies. It is thus important to ask whether alternative systematic studies, preferentially based on cladistic analyses, would force us to change the conclusions from this study. In our sample we inferred a total of 26 transitions to gregariousness. Of these 18–19 were inferred to take place in branches with warning coloration, and 24 in branches with some kind of repellent defence, respectively. Thus, major changes in phylogenetic relationships among taxa would lead to contrasts having a different composition than in our study, but would not lead to more transitions to gregariousness in cryptic branches lacking repellent defences. Thus, unless there were, for example, a drastic reduction in the number of contrasts with transitions to gregariousness, which we have no a priori reason to believe, it is unlikely that results would deviate much from those in the present study. The problem with inadequate phylogenetic information in correlation studies might also be dealt with using a simulation approach, as proposed by Losos (1994) for continuous characters. However, this approach may be problematic with a data set as large as in the present study.

Since butterflies have been subjected to previous analyses of coloration and life-style based on a much larger set of species (Sillén-Tullberg, 1988, 1993) it might be objected that Papilionoidea should not be included again in the present study. However, we do not see this as a problem. First, there was no contribution of contrasts from Papilionoidea in the final test of the coloration character, and, secondly, the defence character has not been analyzed in previous studies.

It should be emphasized that our sample includes tree-feeding species only. The constraints facing tree-feeders are quite different from those of herb-feeding species, which use plants that can generally only support a few larvae. In such species females must spread eggs over many plants, or must find continuous patches of the host plant, or be highly polyphagous. Thus, on this basis, we expect fewer herbaceous feeders to be gregarious. On the other hand, because openness of habitat is more common for herb-feeders and because the evolution of repellent defences should be positively correlated with the probability of discovery by predators (e.g. Bakus, 1981; Pasteels, Gregoire & Rowell-Rahier, 1983), gregariousness, insofar as it is associated with such defence, could be expected to be more common in herb-feeders. Thus, it would be interesting to compare the evolution of gregariousness in herb- and tree-feeders.

Although aggregations of larvae may have other advantages apart from deterring predators, such as physiological amelioration (thermoregulation or reduced water loss), or increased foraging efficiency, interactions with natural enemies are likely to be the most universal function (Vulinec, 1990). However, Young (1983) suggested that leaf toughness and spatial distribution of host plants are more important than predation. Studies comparing predation on gregarious and solitary species that would help resolve this issue are few. Sheehan (1991) compared parasitism rates of Lepidopteran species with hairy and smooth integuments, and with gregarious or solitary lifestyles. Hairy and gregarious species were frequency collected, because many of these species have outbreaks (Hunter, 1991). They also have higher parasitism rates, particularly by generalist parasitoids, probably because they are easier to find. If defences and warning coloration decrease mortality rates, it must be mortality from predators (which were not studied by Sheehan, 1991) rather than parasitoids. Many studies indicate an advantage of large group size in reducing mortality in gregarious species (e.g. Damman, 1987; Lawrence, 1990; Stamp & Bowers, 1990; Wade & Breden, 1986), but how these mortality rates compare to those of solitary species feeding in comparable conditions is unknown.

In conclusion, our study based on independent contrasts shows that gregariousness in tree-feeding macrolepidopteran larvae is more likely to evolve in lineages with repellent defence, and is more likely to evolve in lineages with warning coloration than in such with cryptic coloration. This means that, as a rule in this group of organisms, the evolution of repellent defence and warning coloration precedes that of gregariousness. Theoretically, both repellent defences and warning coloration increase the likelihood for gregariousness to evolve, but because of strong intercorrelation between the two traits it is hard to discern their separate effects.

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REFERENCES

Bakus GJ. 1981. Chemical defense mechanisms on the Great Barrier Reef, Australia. *Science* **211:** 497–498.

Bernays EA, Cornelius ML. 1989. Generalist caterpillar prey are more palatable than specialists for the generalist predator *Iridomyrmex humilis. Oecologia* **79:** 427–430.

Björklund M. 1991. Evolution, phylogeny, sexual dimorphism and mating system in the grackles (*Quiscalus* spp.: Icterinae). *Evolution* **45:** 608–621.

Bolte KB. 1990. Guide to the Geometridae of Canada (Lepidoptera). VI. Subfamily Laurentiinae 1. Revision of the genus *Eupithecia. Memoirs of the Entomological Society of Canada* **151:** 1–253.

Buckler W. 1896. *The larvae of British butterflies and moths.* London: The Ray Society.

Carter JD. 1984. *Pest Lepidoptera of Europe.* Dordrecht: Dr W. Junk Publishers.

Cott HB. 1940. *Adaptive coloration in animals.* London: Methuen.

Damman H. 1987. Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology* **68:** 88–97.

Edmunds M. 1974. *Defence in Animals.* Harlow: Longman.

Emmet AM, Heath J. 1991. *The Moths and Butterflies of Great Britain and Ireland. Vol. 7(2). Lasiocampidae-Thyatiridae with life history chart of the British Lepidoptera.* Colchester: Harley Books.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125:** 1–15.

Ferguson DC. 1972. *The moths of America north of Mexico including Greenland. Fascicle 20.2. Bombycoidea: Saturniidae.* London: EW Classey & RBD Publications.

Ferguson DC. 1978. *The moths of America north of Mexico including Greenland. Fascicle 22.2. Noctuoidea: Lymantriidae.* London: EW Classey & Wedge Entomological Research Foundation.

Fisher RA. 1930. *The genetical theory of natural selection.* Oxford: Clarendon.

Fitzgerald TD. 1993. Sociality in caterpillars. In: Stamp NE, Casey TM, eds. *Caterpillars.* New York: Chapman & Hall, 372–403.

Franclemont JG. 1973. *The moths of America north of Mexico including Greenland. Fascicle 20.1. Mimallonoidea: Mimallonidae and Bombycoidea: Apatelodidae, Bombycidae, Lasiocampidae.* London: EW Classey & RBD Publications.

Furniss MM, Carolin VM. 1977. *Western forest insects*. USDA Forest Service Miscellaneous Publication 1339.

Garland T Jr, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42:** 265–292.

Grafen A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London Series B* **326:** 119–157.

Hancock DL. 1983. Classification of the Papilionidae: A phylogenetic approach. *Smithersia* **2:** 1–48.

Harvey PH, Pagel MD. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

Harvey PH, Bull JJ, Pemberton M, Paxton RJ. 1982. The evolution of aposematic coloration in distasteful prey: A family model. *American Naturalist* **119:** 710–719.

Hodges RW. 1971. *The moths of America north of Mexico including Greenland. Fascicle 21. Sphingoidea: Hawkmoths.* London: EW Classey and RBD Publications.

Hodges RW, Dominick T, Davis DR, Ferguson DC, Franclemont JG, Munroe EG, Powell JA. 1983. *Check list of the Lepidoptera of America North of Mexico including Greenland*. London: EW Classey & Wedge Entomological Research Foundation.

Higgins LG, Riley ND. 1970. *Europas fjärilar*. Stockholm: Almqvist & Wiksell.

Hunter AF. 1991. Traits that distinguish outbreaking and non-outbreaking Macrolepidoptera feeding on northern hardwood trees. *Oikos* **60:** 275–282.

Hunter AF. 1995. Ecology, life history, and phylogeny of outbreak and nonoutbreak species. In: Cappuccino N, Price PW, eds. *Population Dynamics: New Approaches and Synthesis*. San Diego: Academic Press, 41-64.

Järvi T, Sillén-Tullberg B, Wiklund C. 1981. Individual versus kin selection for aposematic coloration: a reply to Harvey and Paxton. *Oikos* **37:** 393–395.

Kitching IJ. 1984. An historical review of the higher classification of the Noctuidae (Lepidoptera). *Bulletin British Museum of Natural History (Entomology)* **49:** 153–234.

Kuznetzov VI, Stekolnikov AA. 1985. Comparative and functional morphology of the male genitalia of the Bombycoid moths (Lepidoptera, Papilionomorpha: Lasiocampoidea, Sphingoidea, Bombycoidea) and their systematic position. *Trudy zoologicheskogo Instituta, Leningrad* **134:** 3–48.

Lawrence WS. 1990. The effects of group size and host species on development and survivorship of a gregarious caterpillar *Halisidota caryae* (Lepidoptera: Arctiidae). *Ecological Entomology* **15:** 53–62.

Leimar O, Enquist M, Sillén-Tullberg B. 1986. Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. *The American Naturalist* **128:** 269–490.

Losos JB. 1994. An approach to the analysis of comparative data when a phylogeny is unavailable or incomplete. *Systematic Biology* **43:** 117–123.

Maddison WP. 1990. A method for testing the correlated evolution of 2 binary characters: are gains and losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44:** 539–557.

Maddison WP, Maddison DR. 1992. *MacClade 3.0: Analysis of phylogeny and character evolution*. Sunderland MA: Sinauer.

Martins EP, Garland T Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45:** 534–557.

McGuffin WC. 1967. Guide to the Geometridae of Canada (Lepidoptera). I. Subfamily Sterrhinae. *Entomological Society of Canada Memoir* **50**.

McGuffin WC. 1972. Guide to the Geometridae of Canada (Lepidoptera). II. Subfamily Ennominae. 1. *Entomological Society of Canada Memoir* **86**.

McGuffin WC. 1977. Guide to the Geometridae of Canada (Lepidoptera). II. Subfamily Ennominae. 2. *Entomological Society of Canada Memoir* **101**.

McGuffin WC. 1981. Guide to the Geometridae of Canada (Lepidoptera). II. Subfamily Ennominae. 3. *Entomological Society of Canada Memoir* **117**.

McGuffin WC. 1989. Guide to the Geometridae of Canada (Lepidoptera). II. Subfamily Ennominae. 4. *Entomological Society of Canada Memoir* **138**.

McGugan BM. 1958. *Forest Lepidoptera of Canada. Vol. 1*. Ottawa: Canada Department of Agriculture Publication 1034.

Michener CD. 1952. The Saturniidae (Lepidoptera) of the western hemisphere: Morphology, phylogeny and classification. *Bulletin of the American Museum of Natural History* **98:** 335–501.

Miller JA. 1991. Cladistics and classification of the Notodontidae (Lepidoptera: Noctuoidea) based on larval and adult morphology. *Bulletin of the American Museum of Natural History*. **204:** 1–226.

Minet J. 1994. The Bombycoidea: Phylogeny and higher classification (Lepidoptera: Glossata). *Entomologica Scandinavica* **25:** 63–88.

Nielsen ES. 1989. Phylogeny of major Lepidopteran groups. In: Fernholm B, Bremer K, Jörnvall H, eds. *The hierarchy of life*. Amsterdam: Elsevier, 281–294.

Nothnagle PJ, Schultz JC. 1987. What is a forest pest? In: Barbosa P, Schultz JC, eds. *Insect outbreaks*. New York: Academic Press, 59–80.

Nylin S, Wedell N. 1994. Sexual size dimorphism and comparative methods. In: Eggleton P, Vane-Wright RI, eds. *Phylogenetics and ecology*. London: Academic Press, 253–280.

Pasteels JM, Gregoire JC, Rowell-Rahier M, 1983. The chemical ecology of defense in arthropods. *Annual Review of Entomology* **28:** 263–289.

Prentice RM. 1962. *Forest Lepidoptera of Canada. Vol. 2.* Ottawa: Canada Department of Forestry Bulletin 128.

Prentice RM. 1963. *Forest Lepidoptera of Canada. Vol. 3*. Ottawa: Canada Forestry Branch Department Publication 1013.

Purvis A. 1991. *Comparative analysis by independent contrasts (C.A.I.C.). A statistical package for the Apple Macintosh*. Version 1.2.

Ridley M. 1983. *The explanation of organic diversity: the comparative method and adaptations for mating*. Oxford: Oxford University Press.

Rose AH, Lindquist OH. 1984. *Insects of eastern pines*. Ottawa: Canadian Forestry Service Publication 1313.

Rose AH, Lindquist OH. 1985. *Insects of eastern spruces, fir and hemlock*. Ottawa: Canadian Forestry Service Technical Report 23.

Rose AH, Lindquist OH. 1992. *Insects of eastern larch, cedar and juniper*. Ottawa: Canada Forestry Service Technical Report 28.

Schaefer PW. 1989. Diversity in form, function, behaviour and ecology: An overview of the Lymantriidae (Lepidoptera) of the world. In: Wallner WE, McManus KA, eds. *Lymantriidae: A comparison of features of New and Old World tussock moths*. United States Department of Agriculture Forest Service General Technical Report NE-123, 1–20.

Scoble MJ. 1991. Classification of the Lepidoptera. In: Emmet AM, Heath J, eds. *The moths and butterflies of Great Britain and Ireland. Vol. 7*. Colchester: Harley Books.

Scott JA. 1986. *The Butterflies of North America*. Stanford: Stanford University Press.

Scott JA, Wright DM. 1990. Butterfly phylogeny and fossils. In: Kudrna O, ed. *Butterflies of Europe. Vol. 2. Introduction to Lepidopterology*. Wiesbaden: AULA-Verlag, 152–208.

Sheehan W. 1991. Host range patterns of hymenopteran parasitoids of exophytic Lepidopteran folivores. In: Bernays EA, ed. *Insect-plant interactions Vol. III*. Boca Raton, FL: CRC Press, 209–248.

Skou P. 1986. The Geometroid moths of North Europe. *Entomonograph* **6:** 1–348.

Sillén-Tullberg B. 1988. Evolution of gregariousness in aposematic butterfly larvae: A phylogenetic analysis. *Evolution* **42:** 293–305.

Sillén-Tullberg B. 1993. The effect of biased inclusion of taxa on the correlation between discrete characters in phylogenetic trees. *Evolution* **47:** 1182–1191.

Sillén-Tullberg B, Bryant EH. 1983. The evolution of aposematic coloration in distasteful prey: An individual selection model. *Evolution* **37:** 993–1000.

Sillén-Tullberg B, Leimar O. 1988. The evolution of gregariousness in distasteful insects as a defense against predators. *American Naturalist* **132:** 723–734.

Stamp NE, Bowers MD. 1990. Variation in food quality and temperature constrain foraging of gregarious caterpillars. *Ecology* **71:** 1031–1039.

Stokoe WJ, Stovin GHT. 1948. *The caterpillars of British moths including the eggs, chrysalids, and food plants. Vol. 1 & 2*. London: Frederick Warne & Company.

Vulinec K. 1990. Collective security: Aggregation by insects as a defense. In: Evans D, Schmidt JO, eds. *Insect defenses*. Albany NY: State University of New York Press, 251–288.

Wade M, Breden F. 1986. Life history of natural populations of the imported willow leaf beetle, *Plagiodera versicolora* (Coleoptera: Chrysomelidae). *Annals of the Entomological Society of America* **62:** 503–506.

Young AM. 1983. On the evolution of egg placement and gregariousness of caterpillars in the Lepidoptera. *Acta Biotheoretica* **32:** 43–60.

Zar J. 1984. *Biostatistical Analysis*. 2nd ed. London: Prentice-Hall International.

APPENDIX

Macrolepidopteran taxa with larvae that are gregarious, warningly coloured and/or have repellent defences. For each family and genus, the total number of species included in the study are listed, as well as the number of species that are gregarious, warningly coloured, and/or have repellent defences

	No. of species	Gregarious	Warning coloration	Repellent defences
Lasiocampidae	**23**	**9**	**16**	**23**
Macromphalinae				
Poecilocampa populi	1	0	1	1
Trichiura crataegi	1	0	1	1
Gastropachinae				
Eriogaster lanestris	1	1	1	1
Phyllodesma spp.	2	0	2	2
Lasiocampinae				
Malacosomatini				
Malacosoma spp.	8	8	8	8
Lasiocampini				
Lasiocampa quercus	1	0	1	1
Macrothylacia rubi	1	0	1	1
Dendrolimus spp.	3	0	1	3
Endromidae	**1**	**1**	**0**	**1**
Endromis versicolora	1	1	0	1
Sphingidae	**23**	**1**	**2**	**2**
Sphinginae				
Ceratomia spp.	3	1	1	2
Lapara bombycoides	1	0	1	0
Saturniidae	**24**	**13**	**19**	**24**
Citheroninae				
Eacles imperialis pini	1	0	1	1
Citheronia regalis	1	0	1	1
Sphingicampa bicolor	`1	0	1	1
Dryocampa rubicunda	1	1	1	1
Anisota spp.	5	5	4	5
Hemileucinae				
Hemileuca spp.	4	4	4	4
Coloradia spp.	2	2	0	2
Automeris io	1	0	1	1
Saturniinae				
Saturniini				
Pavonia pavonia	1	1	1	1
Attacini				
Callosamia promethea	1	0	1	1
Hyalophora spp.	4	0	4	4
Geometridae	**363**	**3**	**17**	**32**
Archierinae				
Archieris spp.	3	0	0	2
Ennominae				
Abraxini				
Abraxas spp.	2	0	2	1
Semiothisini				
Semiothisa spp.	32	0	2	1
Bistonini				
Phigalia titea	1	0	1	1
Lycia spp.	6	0	3	0
Erannis spp.	3	0	2	0
Apocheima spp.	2	0	0	2
Gonodontini				
Odontopera bidentata	1	0	0	1
Campeini				
Campaea margaritata	1	0	0	1
Hylaea fasciaria	1	0	1	0

APPENDIX (continued)

	No. of species	Gregarious	Warning coloration	Repellent defences
Geometridae (continued)				
Ennominae (continued)				
Ennomini				
Ennomos subsignarius	1	1	0	0
Ourapterygini				
Nepytia umbrosaria	1	0	0	1
Larentiinae				
Hydriomenini				
Eulithis prunata	1	0	0	1
Hydria prunivorata	1	1	1	1
Hydriomena spp.	8	1	0	4
Rheumaptera spp.	4	0	0	3
Triphosa dubitata	1	0	0	1
Entephria caesiata	1	0	1	1
Philereme spp.	2	0	0	2
Asthenini				
Euchoeca nebulata	1	0	1	0
Hydrelia sylvata	1	0	1	1
Asthena albulata	1	0	1	1
Operophterini				
Operophtera spp.	4	0	0	3
Eupithecini				
Eupithecia tenuiata	1	0	0	1
Chloroclystis spp.	3	0	0	2
Lobophorini				
Acasis viretata	1	0	1	1
Notodontidae	**62**	**14**	**22**	**23**
Pygaerinae				
Clostera spp.	8	5	5	8
Notodontinae				
Dicranurini				
Furcula spp.	7	0	2	3
Cerura vinula	1	0	0	1
Notodontini				
Notodonta dromedarius	1	0	1	0
Ptilodon capucina	1	0	1	1
Odontosia carmelita	1	0	1	0
Pheosia gnoma	1	0	1	0
Phalerinae				
Phalera buccephala	1	1	1	1
Datana spp.	4	4	4	4
Dioptinae				
Phryganidia californica	1	0	1	0
Nystaleinae				
Symmerista spp.	3	3	3	0
Heterocampinae				
Heterocampini				
Lochmaeus manteo	1	0	0	1
Schizura concinna	1	1	1	1
Stauropini				
Stauropus fagi (Tribe unknown)	1	0	0	1
Nerice bidentata	1	0	0	1
Oligocentriia lignicolor	1	0	0	1
Arctiidae	**14**	**4**	**9**	**11**
Arctiinae				
Callimorphini				
Haploa confusa	1	0	1	1
Arctiini				
Spilosoma virginica	1	0	1	1
Hyphantria cunea	1	1	1	1

APPENDIX (continued)

	No. of species	Gregarious	Warning coloration	Repellent defences
Arctiidae (continued)				
Arctiinae (continued)				
Arctiini (continued)				
Platarctia parthenos	1	0	1	1
Arctia caja	1	0	1	1
Phaegopterini				
Halysidota tesellaris	1	0	1	1
Lophocampa spp.	4	3	3	4
Lymantriidae	**23**	**3**	**15**	**23**
Orgyinae				
Dasychira spp.	8	1	2	8
Calliteara pudibunda	1	0	1	1
Orgyia spp.	7	0	7	7
Leucoma salicis	1	0	1	1
Lymantriinae				
Euproctis spp.	2	2	2	2
Lymantria spp.	2	0	2	2
Nolidae	**4**	**0**	**3**	**3**
Meganola spp.	2	0	2	2
Nola spp.	2	0	1	1
Noctuidae	**250**	**5**	**33**	**62**
Herminiinae				
Palthis angulalis	1	0	0	1
Rivulinae				
Diphthera coenitoba	1	0	1	1
Sarrothripinae				
Nycteola spp.	2	2	0	2
Pantheinae				
Panthea spp.	4	0	1	3
Colocasia spp.	3	0	1	3
Chararda deridens	1	0	0	1
Acronictinae				
Moma alpium	1	1	1	1
Acronicta spp.	33	1	18	16
Amphipyrinae				
Apameini				
Enargia spp.	3	0	0	3
Parastichtis suspecta	1	0	0	1
Ipimorpha spp.	3	0	0	3
Hyppa rectilinea	1	0	1	0
Amphipyrini				
Amphipyra spp.	5	0	0	3
Dicycla oo	1	0	0	1
Cosmia spp.	4	0	1	2
Cucullinae				
Xylenini				
Xylena spp.	5	0	2	0
Aporophyla lutulenta	1	0	1	0
Lithophane spp.	20	0	3	0
Eupsilia spp.	3	0	0	3
Agrochola spp.	6	0	0	2
Xanthia spp.	6	0	0	2
Brachylomia spp.	3	0	0	2
Drybotodes eremita	1	0	0	1
Psaphidini				
Brachionycha sphinx	1	0	0	1
Hadeninae				
Lacanobia spp.	3	0	1	1
Orthosia spp.	12	1	1	5
Egira spp.	4	0	0	1

APPENDIX (continued)

	No. of species	Gregarious	Warning coloration	Repellent defences
Noctuidae (continued)				
Noctuinae				
Graphiphora spp.	2	0	0	1
Chloephorinae				
Earias clorana	1	0	0	1
Dilobinae				
Diloba caeruleocephala	1	0	1	1
Hesperiidae	**3**	**0**	**0**	**3**
Pyrginae				
Epargyreus clarus	1	0	0	1
Erynnis spp.	2	0	0	2
Papilionidae	**5**	**0**	**1**	**5**
Papilioninae				
Papilio spp.	5	0	1	5
Pieridae	**3**	**2**	**1**	**2**
Pierinae				
Aporia crataegi	1	1	1	1
Neophasia menapia	1	1	0	1
Lycaenidae	**15**	**0**	**0**	**5**
Eumeninae				
Strymonini				
Incisalia spp.	3	0	0	2
Erora laetus	1	0	0	1
Theclinae				
Quercusia quercus	1	0	0	1
Polyommatinae				
Plebejus argus	1	0	0	1
Nymphalidae	**16**	**6**	**9**	**14**
Nymphalinae				
Polygonia spp.	5	0	4	5
Nymphalis spp.	4	4	4	4
Limenitinae				
Limenitini				
Limenitis spp.	3	0	1	3
Apaturinae				
Asterocampa spp.	2	2	0	2