

20 • Social evolution in the Lepidoptera: ecological context and communication in larval societies

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ABSTRACT

We review key ecological and behavioral mechanisms underlying the origin and maintenance of larval sociality in the Lepidoptera. Using communication contexts of group defense, cohesion and recruitment as a framework, we relate social complexity among gregarious caterpillars to three patterns of foraging: patch-restricted, nomadic, and central-place. A review of the incidence of larval gregariousness in the Lepidoptera demonstrates that sociality is widespread in the order, occurring in twenty or more families representing thirteen ditrysian superfamilies, and it is likely to have evolved numerous times in response to different selective pressures. We specifically address the role of sociality in larval defense and resource use, with a focus on (1) signal enhancement in communication systems, (2) differential larval vulnerability, and (3) ant association. Larval Lepidoptera experience the greatest likelihood of mortality in the earliest instars; larval sociality enhances defensive and resource-exploitation signals in these instars, positively influencing survivorship and larval growth. Disease, predation and parasitism, nutrition, and inclusive fitness are discussed in terms of costs and benefits of group living. Finally, we identify two areas where additional research will contribute significantly to an understanding of social evolution in the Lepidoptera: (1) comparative phylogenetic studies, using ecological and communicative characters to trace the origins of caterpillar societies and transitions among them, and (2) larval behavior and ecology, focusing on kin discrimination abilities, assessment of colony genetic structure, and most importantly on the means and contexts of caterpillar communication.

INTRODUCTION

Sociality in the Lepidoptera is characterized by behaviors such as laying eggs in clusters, larval aggregation, and communal roosting by adults. By 'social', we refer to any system

in which individuals display reciprocal, cooperative communication (Wilson 1971). Wilson favored this definition partly on the grounds that 'the terms society and social must be defined quite broadly in order to prevent the arbitrary exclusion of many interesting phenomena' (Wilson 1971, p. 5). He stressed that a common denominator in the behavior of all social insects is communication.

While early investigators devised an elaborate classification of insect societies to match the diversity of their subject, an essential distinction was made between 'eusocial' and 'social' species. The term eusocial refers to species exhibiting three social attributes: overlapping generations, cooperative brood care, and reproductive division of labor. The combination of these characteristics is exhibited by complex, integrated societies marked by sophisticated communication systems and caste specializations, represented among the insects by the haplodiploid ants, many bees and wasps, some thrips and beetles, the diploid termites, and certain parthenogenetically reproducing aphids.

The recognition of eusociality was followed by the delineation of a social hierarchy based upon number and complexity of social attributes, with the eusocial species at its apex. This has had the unfortunate effect of infusing studies of social evolution with 'evolutionary ladder' thinking, as reflected in the moniker 'presocial' applied to social Lepidoptera and many other non-eusocial social insects. The term presocial is inappropriate not only because of its implicit teleological progression, but more importantly because it implies that these forms are not yet social, thereby equating the term 'social' with 'eusocial' in a way that underappreciates the complexity of many non-eusocial insect societies, including those of Lepidoptera.

Focussing on the communication criterion of sociality, the common ground that social caterpillars share with other social species is quickly apparent. Social complexity encompasses both signal repertoire (number of signals) and signal specificity (broadcast vs. personal). The simplest

signals are non-specific and group-directed, such as those of certain alarm pheromones; the most sophisticated signals are highly specific and often individually or caste-directed, such as the waggle-dance of the honey bee. Communication and cooperation in Lepidoptera are almost entirely confined to the simple, group-directed end of the spectrum. For example, communication for group cohesion in larval societies involves tactile signals or pheromone markers keeping individuals together, whereas insects such as wasps, bees and ants are capable of sophisticated kin recognition and discrimination in addition to simple group cohesion. Nevertheless, certain lepidopteran societies rival the eusocial insects in other respects, such as in the use of pheromonal foraging and recruitment trails.

Fitzgerald and Peterson (1988) and Fitzgerald (1993, 1995) have written recent reviews that discuss many of the ecological and behavioral correlates of lepidopteran sociality. These reviews developed a conceptual framework of understanding sociality in the Lepidoptera in terms of the nature of intra- and interspecific communication exhibited by different groups. We follow this same approach, and explicitly characterize lepidopteran sociality in terms of one or more of three communication contexts: defense, cohesion and foraging. We explicitly discuss the aggregation behavior of ant-associated caterpillars in the Lycaenidae, which have been overlooked in most reviews of lepidopteran sociality (Stamp 1980; Fitzgerald 1993; but see Kitching 1981). Our discussion is confined to sociality among larvae of Lepidoptera rather than adults, largely because sociality in the juvenile stages is far more common and more information is available concerning the behavioral ecology of gregarious juveniles.

We first characterize the levels of complexity observed in lepidopteran sociality, and classify these in terms of the communication contexts exhibited in each case. We then review the distribution of sociality in the Lepidoptera, and present a survey of species described as exhibiting some degree of sociality. The data suggest that gregariousness has evolved repeatedly in the order, and that it is associated in complex ways with such factors as larval host plant, presence of attendant ants, and the relative 'apparency' (visibility or detectability) of the taxa involved. Although considerable advances have been made in particular areas of higher lepidopteran phylogeny (see, for example, Scott 1985; Scott and Wright 1990; Minet 1991; Lee *et al.* 1992; Martin and Pashley 1992; Weller *et al.* 1994), the lack of well-resolved phylogenies at many lower taxonomic levels precludes a meaningful comparative study of these traits, and

we use these data to discuss selective pressures that may have been of particular importance in shaping sociality in the Lepidoptera, including signal enhancement, ant-association, and relatedness. Finally, we discuss the evolution of sociality and egg-clustering patterns in the Lepidoptera, and point to areas that require further research.

LEVELS OF COMPLEXITY IN LEPIDOPTERAN SOCIALITY

Adaptations evolved by caterpillars in response to ecological pressures include variability in coloration, such as crypsis, mimicry, and aposematism; acquisition of morphological armature, such as thick cuticles, spines or setae; association with ants; and behavioral modifications such as stem-boring, leaf-mining, leaf-rolling, and leaf-tying. Group-context communication, as the distinguishing feature of sociality in Lepidoptera, is yet another evolutionary response. Three main communication contexts which social Lepidoptera share with other social insects include: (1) alarm or group defense; (2) aggregation or group cohesion; and (3) foraging or resource use (indicating the location and quality of resources).

Fitzgerald and Peterson (1988) and Fitzgerald (1993) identify three levels of sociality in the Lepidoptera, essentially defined by their foraging behavior: patch-restricted, or static foragers, nomadic foragers, and central-place foragers. In each case, concomitant with changes in foraging behavior are changes in alarm and group defense, as well as signals employed in group cohesion. The subsets of social Lepidoptera represented in Fig. 20-1, and discussed below, are defined by the number of these communication characters; these demonstrate the range of social complexity found in the Lepidoptera. Communication signals unique to social species include those involved in promotion of group cohesion and coordinated resource use, both of which are relevant to group contexts only. Such signals are often chemical and serve to define the spatial limits or boundaries of the group and promote group cohesion (Fitzgerald and Costa 1986; Roessingh 1989, 1990) or aid in the location and evaluation of potential food (see, for example, Kalkowski 1966; Masaki and Umeya 1977; Weyh and Maschwitz 1978; Fitzgerald and Peterson 1983; Peterson 1987).

Social lycaenids that are also ant-associated, or myrmecophilous, exhibit a variety of forms of aggregation, although insufficient research has been conducted on either intraspecific communication among these caterpillars, or interspecific communication between caterpillars

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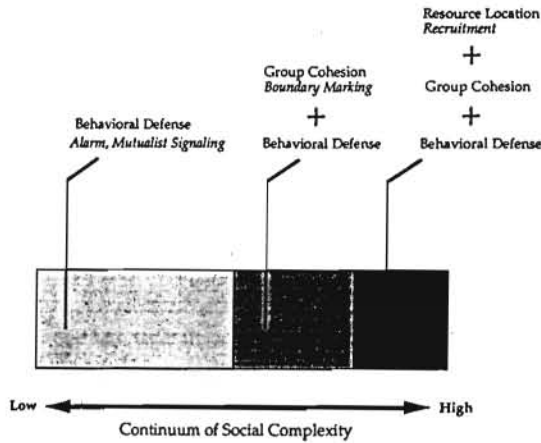


Figure 20-1. Lepidopteran social complexity. Complexity, indicated by intensity of shading, is defined in terms of communication characters: defensive, cohesion, and recruitment. Moving from low to high along the continuum, weakly or facultatively social species exhibit group defense only, more complex social species exhibit group cohesion in addition to group defense, and the most complex lepidopteran societies exhibit recruitment, cohesion, and defense. The continuum is intended to illustrate the range of extant lepidopteran social complexity, and does not represent explicit evolutionary transitions.

and ants, to be able to categorize fully the foraging behavior of many species. Signaling in gregarious ant-associated lycaenids primarily involves the use of ants in defense rather than as a foraging strategy, although the two are closely linked in that attraction of attendant ants may most obviously provide defense against predators and parasitoids, but, thus protected, these larvae are also free to select high-quality foliage and thermally beneficial zones on the host plant.

One question of interest is to what extent attendant ants are directly involved in aggregation of social Lycaenidae. Mathews (1993) demonstrated experimentally that larvae of the Australian lycaenid *Jalmenus evagoras* follow ant trails, and thus ants may play an important indirect role in the aggregation behavior of this species, or in the ability of the larvae to find high-quality food resources by avoiding predator harassment.

Patch-restricted foraging

Lepidoptera whose larvae exhibit patch-restricted foraging represent the most simple form of sociality in the order. Patch-restricted foragers are essentially static, feeding in

the same location throughout the larval stage. These species typically construct shelters and feed on leaves incorporated in the structure. As a result, their diet is often a mixture of nutritionally good and poor leaves. As food is exhausted, the shelter may be continually expanded (as in the fall webworm, *Hyphantria cunea*) or the patch occasionally abandoned (as with the palm leaf-skeletonizer, *Homaledra sabalella*). All social Lepidoptera are hypothesized to share the character of group defense, including active group-defensive behaviors such as thrashing and regurgitation (see, for example, Morris 1963; Myers and Smith 1978; Stamp 1984; Peterson 1986; Peterson *et al.* 1987) or attraction of attendant ants in gregarious myrmecophiles (see, for example, Pierce *et al.* 1987; DeVries 1990; Fiedler 1991). These characters are also exhibited by solitary species and, assuming that solitariness represents the plesiomorphic state, they are retained in social species, where their function can become amplified through aggregation. The static lifestyle of patch-restricted species obviates selection for communication beyond alarm signaling and perhaps marking group boundaries. Chemical markers are most commonly responsible for group cohesion, and may occur as a component of the silk deposited by these larvae, or may be applied to silk trails or other substrates by trail-marking glands (Fitzgerald 1993 and references therein).

Nomadic foraging

The next level of complexity in lepidopteran sociality is characterized by species whose larvae engage in nomadic foraging patterns, in which larvae move in groups or bivouacs from patch to patch. Nomads constitute perhaps the greatest number of social lepidopteran species; communication in most of these species appears to be chemically and visually mediated, and it is used in defense, cohesion, and in some cases local orientation to food. Group-cohesion signals are generally chemical in nature, and this use of marker pheromones is likely to be antecedent to resource-use functions such as trail-following and recruitment. Chemical marking and/or trail-following have been demonstrated in such diverse nomadic Lepidoptera as *Malacosoma disstria* (Fitzgerald and Costa 1986), *Euphydryas phaeton* (Stamp 1982), *Asterocampa clyton* (Stamp 1984), *Chlosyne lacinia* (Bush 1969; Stamp 1977), *Hemileuca lucina* (Capinera 1980), *Pieris brassicae* (Long 1955) and some species of *Euselasia* (P. J. DeVries, personal communication). Frequent site abandonment is characteristic of

nomadic species, and may represent an evolutionary response to predation (Heinrich 1979, 1993), depletion of local food reserves (Stamp and Bowers 1990a,b) or disease risk.

Larvae of the Australian lycaenid *J. evagoras* appear to follow a nomadic foraging pattern: larvae form loose aggregations composed of individuals of different age classes and presumably different genetic backgrounds, and they forage together diurnally on terminal foliage of their host plants (Common and Waterhouse 1981; Pierce *et al.* 1987). Larvae of this species are also known to produce vibrational calls (DeVries 1991); although these substrate-borne signals have mostly been discussed in terms of signaling to attendant ants (DeVries 1990, 1991) or deterring predators (Downey 1966; Downey and Allyn 1973), it is possible that they also play a role in intraspecific signaling and recruitment behavior.

Central-place foraging

The most sophisticated lepidopteran societies exhibit central-place foraging, and have the ability to communicate the location of food. Central-place foragers often construct shelters, but, unlike shelter-building patch-restricted foragers, they feed away from them. Movement between the nest and scattered feeding sites sets the stage for the most complex forms of communication found in the Lepidoptera, recruitment of colony mates to feeding sites. Recruitment involves keeping track of an initial foraging path or food location, usually by means of chemical trails which also convey this information to other larvae. Central-place foraging and trail-marking are also found in some solitary lepidopteran species such as the papilionid *Iphiclides podalirius* (Weyh and Maschwitz 1982) and the charaxine *Polyura pyrrhus* (Tsubaki and Kitching 1986), the larvae of which mark short trails between feeding and resting sites.

Recruitment communication in tent caterpillars improves foraging efficiency by expediting the discovery and use of patchily distributed, high-quality young leaves with relatively little search and exposure time (Fitzgerald and Peterson 1983; Fitzgerald and Costa 1986). Unlike some eusocial insects, eastern tent caterpillars do not carry food to the nest. Like eusocial species, however, they use the tent (nest) as a colony information center for communicating the location of food. Unsuccessful foragers periodically return to the tent; if a successful forager has deposited a recruitment trail, it is detected at the tent and followed to the feeding site (Fitzgerald and Peterson 1983).

Some unsuccessfully foraging larvae may also encounter a recruitment trail before reaching the tent; these trails are also effective in eliciting recruitment.

In a comparative study of trail-marking and trail-following in eastern (*M. americanum*) and forest (*M. disstria*) tent caterpillars, Fitzgerald and Costa (1986) showed that although both species possess trail-marking abilities and prefer trails deposited by fed vs. unfed larvae, only the fixed-base foraging pattern of *M. americanum* leads to recruitment of larvae to food-finds, since larvae return to the tent. By contrast, *M. disstria* often mark trails to a new resting site rather than back to their original site, which 'recruits' colony mates to the new site (promoting colony cohesion), but does not constitute resource-based recruitment. The trail-marking pattern of *M. disstria* may also lead to a higher incidence of colony fragmentation.

Elective recruitment (recruitment based on individual assessment of food quality) has thus far been demonstrated in only two tent caterpillar species, *M. americanum* and *M. neustrium* (Fitzgerald and Peterson 1983; Peterson 1988), but it probably exists in other central-place foraging lasiocampids such as *M. californicum*, *Eriogaster lanestris* and *E. amygdali*, *Gloveria howardi*, and *Eutachytera psidii* (Fitzgerald 1993, 1995).

Ant-associated lycaenids that exhibit a form of central-place foraging include the Australian species *Paralucia auri-fera* (Cushman *et al.* 1994) and *Hypochrysops ignitus* (Common and Waterhouse 1981). These species are housed in earthen or thatch structures (called corrals or byres) constructed by their attendant ants, and are effectively central-place foragers since these structures are static 'nesting' sites. Larvae of these species often lay silken trails, which they follow during their nocturnal foraging bouts. For example, larvae of *Ogyris genoeveva* can use these silken highways to travel extremely rapidly from ant corrals at the base of the host tree to mistletoe feeding sites, sometimes several meters high in the boughs of the tree: relatively great distances from a caterpillar's perspective (Common and Waterhouse 1981). The degree of intra- and interspecific communication between larvae, and between larvae and ants, in these species remains to be investigated.

DISTRIBUTION OF SOCIALITY IN LEPIDOPTERA

We summarize in Table 20-1 key ecological and behavioral data gathered from the literature for social lepidopteran

species. Although it is not exhaustive and is likely to contain omissions, this table provides the most comprehensive overview of social Lepidoptera to date.

Inspection of Table 20-1 readily illustrates several points. First, sociality is a widespread phenomenon in the Lepidoptera, occurring in some twenty or more butterfly and moth families representing thirteen ditrysian superfamilies. The taxonomic distribution of social characters suggests that multiple origins of sociality are likely.

Second, social behavior does not correlate in any predictable way with physiological and ecological characteristics such as host specificity or voltinism. The lack of striking patterns of association underscores the point that sociality in the Lepidoptera is likely to have multiple origins, with different species coming to sociality by different paths. However, strong correspondence occurs within some sets of related characters: not surprisingly, shelter construction appears to be more commonly associated with both patch-restricted and central-place foraging, and less commonly with nomadic foraging. This pattern makes sense from a bioenergetic point of view, since silk proteins used in shelter construction are likely to be metabolically expensive, and the nomadic foraging pattern would lead to considerable waste. Central-place foraging, characterizing the most complex lepidopteran societies, is likely to have arisen from both ancestrally nomadic and patch-restricted foraging patterns, a shift reflecting a change in resource use. Such changes were accompanied by changes in the use of communication abilities such as trail-marking.

Certain traits also occur frequently in particular lineages; for example, ant-association is common in the Lycaenidae, and spiny structural defenses are typically observed in the Nymphalidae. Gregariousness in the Lycaenidae is almost entirely confined to ant associated, but otherwise relatively cryptic taxa, with at least two notable exceptions: a social species of Poritiinae has been described to have gregarious, hairy larvae, and larvae of neotropical *Eumaeus* species feed on cycads and sport bright red, aposomatic coloration.

Finally, Table 20-1 indicates that the largest gap in our knowledge of social Lepidoptera lies in the feature most essential to their sociality: communication. This has likely arisen because traits involving certain aspects of communication, especially behavior and physiology, are not always obvious and often must be experimentally demonstrated. On the other hand, features such as life cycle, host-plant use, and morphology are more readily measured or observed. In illustrating the taxonomic distribution of

sociality, in terms of which clades are social-rich and social-poor, which have a diversity of social systems, and which have a single system, Table 20-1 serves as a valuable reference point for framing phylogenetic hypotheses and identifying groups most in need of ecological, behavioral and systematic study; several such groups and questions are discussed in detail below.

COMMUNICATION IN THE CONTEXT OF CATERPILLAR ECOLOGY

We next consider selective pressures likely to have been important in the evolution of sociality. In particular, we relate the ecological contexts of communication to modes of larval defense and resource use, two key features of larval biology that mediate growth and adult fecundity, through a discussion of (1) signal enhancement in communication systems, (2) differential larval vulnerability, and (3) ant-association. These observations are integrated into a discussion of the costs and benefits of group living with respect to defense and resource use. Finally, we discuss social evolution in the Lepidoptera, treating the life-history and ecological factors shaping the characteristics of larval societies.

Signal enhancement

The communication-based benefits of sociality take several forms: defense, for example, may be enhanced through improved group-displays (Morris 1976; Shiga 1976; Stamp and Bowers 1988; Lawrence 1990) and shelter construction (Morris 1972a; Fitzgerald and Willer 1983; Damman 1987). Similarly, resource location and assimilation may be improved through a combination of behavioral thermoregulation (Morris and Fulton 1970; Seymour 1974; Capinera *et al.* 1980; Porter 1983; Knapp and Casey 1986; Casey *et al.* 1988; Joos *et al.* 1988) and cooperative or synchronized foraging (Ghent 1960; Fitzgerald 1976; Tsubaki 1981; Tsubaki and Shiotsu 1982; Casey *et al.* 1988; Fitzgerald *et al.* 1988).

The communication modes on which defense and resource use depend may in some cases be facilitated by group expression. A key quality of group contexts which may have favored sociality over solitary life-styles in many lepidopteran species is signal enhancement, a phenomenon wherein the effectiveness or efficiency of signaling improves as the number of individuals sending the signal increases.

Table 20-1. *Sociality in Lepidoptera*

Classification based on Kristensen (1984, 1991), Neilson (1989) and Neilson and Common (1991).

Classification	Species	Defenses ^a				Foraging pattern ^c	Shelter construc. ^d	Communication ^e				Host specific	Voltinism ^f	References
		Apo.	Struct.	Behav.	Ant Tended ^b			Chemical	Visual	Tactile	Acoustic			
TINEOIDEA														
Galacticidae	<i>Homadaula</i>	?	?	Y	N	PR	None	?	?	?	?	M	?	17
	<i>anisocentra</i>													
	<i>H. myriospila</i>	?	?	?	N	PR	L,S	?	?	?	?	M	?	11
YPONOMEUTOIDEA														
Heliodinidae	<i>Heliodines nyctaginella</i>	?	?	?	N	PR	L,S	?	?	?	?	M	?	11
	<i>H. roesella</i>	?	?	?	N	PR	L,S	?	?	?	?	O	?	11
Plutellidae	<i>Plutella</i> spp.	Y	?	Y	N	PR	L,S	?	?	?	?	?	?	68
Yponomeutidae														
Attevininae	<i>Atteva</i> spp.	Y	?	Y	N	PR	L,S	P	?	?	?	M/O	?	11; 38; 61
	<i>Prays lambda</i>	?	?	?	N	PR	S	P	?	?	?	M	?B	54
	<i>P. omicron</i>	?	?	?	N	PR	S	P	?	?	?	M	U	54
	<i>Euhypnometoides trachydeltus</i>	?	?	P	N	PR	S	P	?	?	?	M	U	54
	<i>Paraswammerdamia lutarea</i>	?	?	P	N	PR	S	P	?	?	?	?	?	22
	<i>Sariodoscelis</i> spp.	?	?	P	N	PR	S	P	?	?	?	M	?B	54
	<i>Yponomeuta cagnagellus</i>	Y	?	Y	N	PR	L,S	Y	?	?	?	M	U	35; 62; 63
	<i>Y. evonymellus</i>	?	?	P	N	PR	S	P	?	?	?	M	U	54
	<i>Y. internellus</i>	Y	?	P	N	PR	L,S	P	?	?	?	?	?	11
	<i>Y. kanaiellus</i>	?	?	P	N	PR	S	P	?	?	?	?	U	54
	<i>Y. malinellus</i>	?	?	P	N	PR	S	P	?	?	?	?	U	54
	<i>Y. multipunctellus</i>	Y	?	Y	N	PR	L,S	Y	?	?	?	M	U	38
	<i>Y. padella</i>	?	?	P	N	PR	S	P	?	?	?	?	?	22
	<i>Y. polystictus</i>	?	?	P	N	PR	S	P	?	?	?	M	U	54
	<i>Y. polystigmellus</i>	?	?	P	N	PR	S	P	?	?	?	M	?U	54
	<i>Y. pustulellus</i>	Y	?	P	N	PR	L,S	P	?	?	?	?	?	11
	<i>Y. rorrella</i>	?	?	P	N	PR	S	P	?	?	?	?	?	22
<i>Y. sociatus</i>	?	?	P	N	PR	S	P	?	?	?	M	U	54	
<i>Y. vigintipunctatus</i>	?	?	P	N	PR	L,S	P	?	?	?	M	M	54	
<i>Xyrosaris lichneuta</i>	?	?	P	N	PR	L,S	P	?	?	?	O	M	54	

GELECHIOIDEA

Coleophoridae	<i>Homaledra sabalella</i>	Y	?	?	N	PR	L,S	?	?	?	?	M	M	38
Ethmiidae	<i>Ethmia heliomela</i>	Y	?	?	N	PR	L,S	?	?	?	?	M	?	11
Oecophoridae														
Xyloryctinae	<i>Crypsicharis neocosma</i>	?	?	?	N	PR	L,S	?	?	?	?	M	?	11
COSSOIDEA														
Cossidae	<i>Culama</i> spp.	Y	?	?	N	PR	Under bark	?	?	?	?	O	?	11
	<i>Macrocyttara expressa</i>	?	?	?	N	PR	Under bark	?	?	?	?	M	?	11

TORTRICOIDEA

Tortricidae	<i>Argyrotaenia pulchellana</i>	?	?	?	N	PR	?	?	?	?	?	?	?	92
	<i>Archips cerasivoranus</i>	Y	Setae	?	N	PR	L,S	?	?	?	?	O	U	26; 38
	<i>A. fervidana</i>	Y	Setae	?	N	PR	L,S	?	?	?	?	O	?	38
	<i>Cryptoptila australana</i>	Y	?	?	N	PR	L,S	?	?	?	?	?	?	11

ZYGAENOIDEA

Limacodidae	<i>Ctenolita melanosticta</i>	Y	Sp	?	N	PR	None	?	?	?	?	O	?	94
	<i>Parasa lepida</i>	?	?	?	N	?PR	?	?	?	?	?	?	?	40
Zygaenidae	<i>Artona funeralis</i>	?	?	?	N	?Nom	None	?	?	?	?	?	?	36; 53
	<i>Pryeria sinica</i>	Y	?	?	N	Nom	S (1st inst)	?	?	?	?	M	U	81

PYRALOIDEA

Pyralidae														
Epipaschiinae	<i>Catamola thyrissalis</i>	?	?	?	N	PR	L,S	?	?	?	?	O	?	11
	<i>Macalla ebenina</i>	?	?	?	N	PR	L,S	?	?	?	?	M	?	11
	<i>M. pyrastris</i>	?	?	?	N	PR	L,S	?	?	?	?	M	?	11
	<i>Tetralopha robustella</i>	?	?	?	N	CP	L,S	?	?	?	?	M	U/M	32
Evergestinae	<i>Evergestis extimalis</i>	?	?	?	N	PR	S	?	?	?	?	O	U	31
	<i>E. pallidata</i>	?	?	?	N	PR	S	?	?	?	?	M	U	31
Galleriinae	<i>Meyriccia latro</i>	?	?	?	N	PR	S, flowers	?	?	?	?	M	?	11
	<i>Omphalocera munroei</i>	?	?	?	N	PR	L	?	?	?	?	M	M	16
Phycitinae	<i>Acrobasis consociella</i>	?	?	?	N	PR	L,S	?	?	?	?	M	U	31
Pyralinae	<i>Aglossa pinguinalis</i>	?	?	?	N	PR	S, debris	?	?	?	?	P	B	31
	<i>Ocrasa albidalis</i>	Y	?	?	N	PR	L,S	?	?	?	?	M	?	11
Pyraustinae	<i>Hyalobathra miniosalis</i>	?	?	?	N	PR	L,S	?	?	?	?	M	?	11
	<i>Mutuuraia terrealis</i>	?	?	Y	N	PR	S	?	?	?	?	M	U	31
	<i>Nomophila corticalis</i>	?	?	?	N	?CP	S	?	?	?	?	P	?	11
	<i>Paracorsia repandalis</i>	Y	?	?	N	PR	S	?	?	?	?	M	?	31
	<i>Pyrausta cespitalis</i>	?	?	?	N	PR	S	?	?	?	?	M	B	31
	<i>P. cingulata</i>	?	?	?	N	PR	S	?	?	?	?	O	?	31
	<i>Uresiphita reversalis</i>	Y	?	?	N	Nom	L,S	?	?	?	?	O	M	3

Table 20-1 (cont.)

Classification	Species	Defenses ^a			Ant Tended ^b	Foraging pattern ^c	Shelter construc. ^d	Communication ^e				Host specific	Voltinism ^f	References
		Apo.	Struct.	Behav.				Chemical	Visual	Tactile	Acoustic			
GEOMETROIDEA														
Geometridae														
Diptychinae	<i>Venilioides inflammata</i>	Y	Y	Y	N	PR, Nom	S (1st- 2nd inst.)	?	?	?	?	M	?	75
Ennominae	<i>Mnesampela lenaea</i>	?	?	?	N	?	L,S	?	?	?	?	?	?	11
	<i>M. privata</i>	?	?	?	N	?	L,S	?	?	?	?	M	?	11
	<i>Zerenopsis leopardina</i>	Y	?	Y	N	PR	S (1st- 2nd inst.)	?	?	?	?	M	?	94
Larentiinae	<i>Hydria prunivorata</i>	Y	?	Y	N	PR	L,S	?	?	?	?	M	U	66
Oenochrominae	<i>Naxa seroaria</i>	?	?	?	N	PR	S	?	?	?	?	?	?	96
URANIOIDEA														
Uraniidae														
Epipleminae	<i>Epiplema</i> spp.	N	?	?	N	PR	S	?	?	?	?	?	?	2
HESPERIOIDEA														
Hesperiidae	<i>Hidari irava</i>	?	?	?	N	PR	L,S	?	?	?	?	M	?	40
PAPILIONOIDEA														
Lycaenidae														
Polyommatainae	<i>Anthene emolus</i>	N	None	?	Y	Nom	None	?	?	?	?	?	?	24
	<i>A. lycaenoides</i>	N	None	?	Y	Nom	None	?	?	?	?	P	?	12
Poritiinae	<i>Poritia erycinoides</i>	?Y	Set	?	N	Nom	None	P	?	?	?	?	?	64
	<i>P. sumatrae</i>	N	Set	?	N	Nom	None	?	?	?	?	?	?	95
Riodininae	<i>Emesis lucinda</i>	N	None	?	N	?Nom	None	?	?	?	?	O	M	91
	<i>Euselasia cafusa</i>	N	None	?	N	?Nom	None	?	?	?	?	O	M	91
	<i>E. mystica</i>	N	None	?	N	?Nom	None	?	?	?	?	O	M	91
	<i>E. rhodogyne</i>	N	None	?	N	?Nom	None	?	?	?	?	O	M	91
	<i>Hades noctula</i>	Y	None	?	N	?Nom	None	?	?	?	?	O	M	91
	<i>Melanis pixie</i>	Y	None	?	N	?Nom	None	?	?	?	?	O	M	91
Theclinae	<i>Acrodipsas</i>	N	None	?	Y	Nom	None	?	?	?	?	Parasites?	?	12
	<i>myrmecophila</i>													
	<i>Arhopala</i>	?	?	?	Y	Nom	None	?	?	?	?	?	?	98
	<i>pseudocenta urus</i>													
	<i>Axiocerses bambana</i>	N	None	?	Y	CP	L,S	?	?	?	?	M	B/M	10
	<i>Crudaria leroma</i>	N	T	?	Y	?Nom	None	?	?	?	?	M	U/M	10
	<i>Drupadia theda</i>	?	?	?	Y	Nom, ?CP	L,S	?	?	?	?	?	?	92

	<i>Eumaeus atala</i>	Y	Set	?	N	Nom	None	?	?	?	?	O	M	35; 69
	<i>E. minijas</i>	Y	Set	?	N	Nom	None	?	?	?	?	O	M	35; 69
	<i>Hypochrysops delicia delicia</i>	N	None	?	Y	Nom	None	?	?	?	?	M	?	12
	<i>H. ignitus ignitus</i>	N	None	?	Y	CP	Byre	?	?	?	?	P	?	12
	<i>H. epicurus</i>	N	None	?	Y	Nom, CP	None	?	?	?	?	M	?	12
	<i>H. cyane</i>	N	None	?	Y	Nom, CP	None	?	?	?	?	M	?	12
	<i>H. miskini</i>	N	None	?	Y	Nom, CP	None	?	?	?	?	M	?	12
	<i>Ogyris amaryllis meridionalis</i>	N	Set	?	Y	Nom	None	?	?	?	?	M	?	12
	<i>O. genoeveva</i>	?	None	?	?Y	?Nom	None	?	?	?	?	?	?	97
	<i>Jalmenus evagoras</i>	N	None	?	Y	Nom	None	?	?	?	Y	O	M	12; 91
	<i>J. icilius</i>	N	None	?	Y	Nom	None	?	?	?	Y	O	M	12; 91
	<i>J. icinus</i>	N	None	?	Y	Nom	None	?	?	?	Y	O	M	12; 91
Nymphalidae														
Argynninae	<i>Phalanta</i> spp.	?	Sp	?	N	?Nom	?	?	?	?	?	P	?	49
Apaturinae	<i>Asterocampa celtis</i>	?	Ceph. Sp.		Y	N	Nom	None	?	?	?	M	M	48; 69; 72
	<i>A. clyton</i>	?	Ceph. Sp.		Y	N	Nom	None	?	?	?	O	M	48; 69; 72
Brassolinae	<i>Brassolis isthmia</i>	?	?	Y	N	CP	L,S	P	?	?	?	O	B	20; 89
Heliconiinae	<i>Heliconius doris</i>	Y	Sp	?	N	Nom	None	?	?	?	?	M	?	19
	<i>H. sapho leuce</i>	Y	Sp	?	N	Nom	None	?	?	?	?	M	?	19
	<i>H. hewitsoni</i>	Y	Sp, H	?	N	?	None	?	?	?	?	M	?	19
	<i>H. xanthocles</i>	Y	Sp	?	N	Nom	None	?	?	?	?	M	M	52
Ithomiinae	<i>Hypothyris euclea valora</i>	Y	?	?	N	?Nom	None	?	?	?	?	M	?	19
	<i>H. lycaste callispila</i>	Y	?	?	N	?Nom	None	?	?	?	?	M	?	19
	<i>Mechanitis polymnia isthmia</i>	Y	T	?	N	?Nom	?	?	?	?	?	?	?	19
	<i>M. lysimnia doryssus</i>	Y	T	?	N	?Nom	?	?	?	?	?	?	?	19
	<i>M. menapis saturata</i>	Y	T	?	N	?Nom	?	?	?	?	?	?	?	19
Melitaeinae	<i>Anthanassa frisia frisia</i>	Y	Set, Sp	?	N	PR, ?Nom	?	P	?	?	?	?	?	9
	<i>Chlosyne gabbi</i>	Y	Sp	?	N	Nom	?	P	?	?	?	O	U	69
	<i>C. gorgone</i>	Y	Sp	?	N	Nom	?	P	?	?	?	O	U	69
	<i>C. hoffmanni</i>	Y	Sp	?	N	PR, Nom	S	P	?	?	?	O	U	69
	<i>C. janais harristii</i>	Y	Sp	?	N	Nom	?	P	?	?	?	?	?	19
	<i>C. lacinia</i>	Y	Sp	Y	N	Nom	?	Y	?	?	?	O	M	5; 19; 69; 70
	<i>C. leanira</i>	Y	Sp	?	N	PR, Nom	S	P	?	?	?	O	U	69
	<i>C. melanarge</i>	Pr	Sp	?	N	Nom	?	P	?	?	?	M	?	18

Table 20-1 (cont.)

Classification	Species	Defenses ^a			Ant Tended ^d	Foraging pattern ^e	Shelter construc. ^f	Communication ^g				Host specific	Volitinism ^h	References	
		Apo. Struct.	Behav.	Tended ^d				Chemical	Visual	Tactile	Acoustic				
Melitaeinae	<i>C. nyx</i>	Y	Sp	?	N	Nom	?	?	?	?	?	?	O	U	69
	<i>C. pallia</i>	Y	Sp	?	N	Nom	?	?	?	?	?	?	O	U	69
	<i>Euphydryas aurinia</i>	Y	Sp	Y	N	PR, Nom	S	P	?	?	?	?	P	?	60; 80
	<i>E. chalcidona</i>	Y	Sp	?	N	PR, Nom	S	P	?	?	?	?	P	U	69
	<i>E. colon</i>	Y	Sp	?	N	PR, ?Nom	L,S	P	?	?	?	?	O	?	35; 69
	<i>E. gynthis</i>	Y	Sp	?	N	PR, ?Nom	S	?	?	?	?	?	?	?	92
	<i>E. debilis</i>	Y	Sp	?	N	PR, ?Nom	S	?	?	?	?	?	?	?	92
	<i>E. editha</i>	Y	Sp	?	N	Nom	?	P	?	?	?	?	P	U	69
	<i>E. gillettii</i>	Y	Sp	?	N	PR, Nom	L,S	P	?	?	?	?	P	U	69
	<i>E. idana</i>	Y	Sp	?	N	PR, ?Nom	S	?	?	?	?	?	?	?	92
	<i>E. intermedia</i>	Y	Sp	?	N	PR, ?Nom	S	?	?	?	?	?	?	?	92
	<i>E. matura</i>	Y	Sp	?	N	PR, ?Nom	S	?	?	?	?	?	?	?	92
	<i>E. wolfsbergerti</i>	Y	Sp	?	N	PR, ?Nom	S	?	?	?	?	?	?	?	92
	<i>E. phacton</i>	Y	Sp	Y	N	PR, ?Nom	S	P	?	?	?	?	P	U	71; 69
	<i>Eucisia alsima</i>	Y	Sp	Y	N	Nom	?	?	?	?	?	?	M	?	19
	<i>Melitaea cinxia</i>	Y	Sp	Y	N	PR, Nom	S	?	?	?	?	?	O	U	8; 80
	<i>M. diamina</i>	Y	Sp	Y	N	PR, Nom	S	?	?	?	?	?	?	?	92
	<i>M. phoebe</i>	Y	Sp	Y	N	PR, Nom	S	?	?	?	?	?	?	?	92
	<i>Melitaea astertia</i>	Y	Sp	?	N	PR, Nom	S	?	?	?	?	?	O	U	92
	<i>M. atalanta</i>	Y	Sp	?	N	PR, Nom	S	?	?	?	?	?	O	U	7; 80
	<i>M. aurelia</i>	Y	Sp	?	N	PR, Nom	S	?	?	?	?	?	O	U	92
	<i>M. britomartis</i>	Y	Sp	?	N	PR, Nom	S	?	?	?	?	?	O	U	92
	<i>M. partenoides</i>	Y	Sp	?	N	PR, Nom	S	?	?	?	?	?	O	U	92
<i>M. varia</i>	Y	Sp	?	N	PR, Nom	S	?	?	?	?	?	O	U	92	
<i>Physcides</i> spp.	?	Sp, T	?	N	Most Nom	?	?	?	?	?	?	M, ?O	?	4; 69	
<i>Poladytes minuta</i>	Y	Sp	?	N	?	?	?	?	?	?	?	O	M	69	
<i>Tarnaris myops</i>	?	Set, H	?	N	?Nom	?	?	?	?	?	?	?	?	12	
<i>Acroca andromacha</i>	Y	Set, H	?	N	Nom	?	?	?	?	?	?	O	?	12	
<i>andromacha</i>	Y	Sp	Y	N	PR, Nom, L, S	?	?	?	?	?	?	M	U	8; 80	
<i>Aglais urticae</i>	Y	Sp	?	N	?CP	?	?	?	?	?	?	M	U	8; 80	
<i>Araschnia leucana</i>	Y	Sp	?	N	Nom	?	?	?	?	?	?	M	B	8	
<i>Cethosia gemhesilia</i>	Y	Sp	?	N	Nom	?	?	?	?	?	?	M	?	12	
<i>pakshia</i>	Y	Sp	?	N	Nom	?	?	?	?	?	?	M	?	12	

	<i>C. cydippe chrysippe</i>	Y	Sp	?	N	Nom	?	?	?	?	?	M	?	12
	<i>Doleschallia</i>													
	<i>bisaltide pratipa</i>	Y	Sp	?	N	?Nom	?	?	?	?	?	O	?	14
	<i>Hamadryas</i>	Y	Sp	?	N	Nom	?	?	?	?	?	O	M	69
	<i>amphinome</i>													
	<i>H. fornax</i>	Y	Sp	?	N	Nom	?	?	?	?	?	O	M	69
	<i>Hypolimnas</i> spp. (most)	Y	Sp	?	N	Nom	?	?	?	?	?	P	?	12; 49
	<i>Inachis io</i>	Y	Sp	Y	N	PR, Nom	S	?	?	?	?	M	U	8; 80
	<i>Mynes goeffroyi guerini</i>	Y	Set, Sp	?	N	?Nom	?	?	?	?	?	O	?	12
	<i>Nymphalis antiopa</i>	Y	Sp	Y	N	Nom	None	?	?	?	?	O,P	M, B	38; 69
	<i>N. californica</i>	Y	Sp	?	N	?Nom	None	?	?	?	?	O	U, M	69
	<i>N. milberti</i>	Y	Sp	?	N	PR, Nom	L,S	?	?	?	?	P	M	35; 69
	<i>N. polychloros</i>	Y	Sp	Y	N	?PR, ?CP	L,S	?	?	?	?	P	U	8; 80
	<i>N. va u-album</i>	?	Sp	?	N	PR, Nom	?	?	?	?	?	P	U	35;69
	<i>N. xanthomelas</i>	?	?Sp	?	N	?	?	?	?	?	?	?	?	96
	<i>japonica</i>													
	<i>Salamis cacta</i>	?	Sp	?	N	?Nom	?	?	?	?	?	M	?	49
	<i>Symbrenthia</i>	?	Sp	?	N	?Nom	?	?	?	?	?	O	?	14
	<i>lilaea luciana</i>													
Satyrinae	<i>Dioriste</i> spp.	?	H	?	N	?Nom	?	?	?	?	?	M	?	19
	<i>Megeuptychia antonoe</i>	?	H	?	N	?Nom	?	?	?	?	?	M	?	19
Papilionidae														
Papilioninae	<i>Battus polydamus</i>	Y	O	Y	N	Nom	None	?	?	?	?	O	M	69
	<i>Papilio anchisiades</i>	N	O	Y	N	Nom	None	?	?	?	?	O	M	69; 90
	<i>idaeus</i>													
	<i>P. demolion demolion</i>	Y	O	Y	N	Nom	None	?	?	?	?	M,O	?	14
	<i>P. pelaus</i>	N	O	Y	N	Nom	None	?	?	?	?	?	?	4
	<i>Parnassius apollo</i>	Y	O	Y	N	Nom	None	?	?	?	?	?	?	85
	<i>Zerynthia polyxena</i>	Y	O	Y	N	Nom	None	?	?	?	?	?	?	67
Pieridae	<i>Anaphaeis java</i>	?	?	?	N	?	?	?	?	?	?	O	?	93
Pierinae	<i>Ascia monuste</i>	Y	?	?	N	Nom	?	?	?	?	?	P	M	69
	<i>Aporia crataegi</i>	Y	Set	?	N	CP, Nom	?	?	?	?	?	O	?	80
	<i>A. hippia japonica</i>	?	?	?	N	?	?	?	?	?	?	?	?	96
	<i>Catasticta</i> spp.	?	Set	Y	N	?	?	?	?	?	?	O	?	19
	<i>Colotis amatus</i>	?	?	?	N	Nom	?	?	?	?	?	M	?	49
	<i>C. phisadia</i>	?	?	?	N	Nom	?	?	?	?	?	M	?	49
	<i>Delias harpalyce</i>	Y	?	?	N	PR	S	?	?	?	?	M	B	12
	<i>D. hyparete metarete</i>	Y	Set	?	N	?	?	?	?	?	?	O	?	14
	<i>D. ninus ninus</i>	Y	Set	?	N	?	?	?	?	?	?	O	?	14
	<i>Eucheira socialis</i>	Y	None	Y	N	CP	S	P	?	?	?	M	U	39; 82

Table 20-1. (cont.)

Classification	Species	Defenses ^a					Communication ^c					Host specific	Voltinism ^e	References
		Apo.	Struct.	Behav.	Ant Tended ^b	Foraging pattern ^c	Shelter construc. ^d	Chemical	Visual	Tactile	Acoustic			
Pierinae	<i>Eurema blanda</i>	?	Set	?	N	?	?	?	?	?	?	M,O	?	95
	<i>Hesperocharis crocea</i>	?	Set	?	N	?	?	?	?	?	?	O	?	19
	<i>Neophasia menapia</i>	No	Set, T	?	N	Nom	?	?	?	?	?	O	U	21; 69
	<i>N. terlooti</i>	No	Set, T	?	N	Nom	?	?	?	?	?	M	B	21; 69
	<i>Pereute</i> spp.	?	Set	?	N	?	?	?	?	?	?	?	?	19
	<i>Pieris brassicae</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	P	51; 80
BOMBYCOIDEA														
Eupterotidae														
	<i>Rhabdosia patagiata</i>	N	?Set	?	N	CP	S	?	?	?	?	O	?	79
	<i>Hyposoides</i> spp.	?	Set	?	N	?CP	S	P	?	?	?	?	?	59
Panacelinae	<i>Panacela lewinae</i>	?	Set	Y	N	CP	S	P	?	?	?	P	?	11
	<i>P. nyctopa</i>	?	Set	Y	N	Nom	?	P	?	?	?	P	?	11
	<i>P. pilosa</i>	?	Set	Y	N	CP	S	P	?	?	?	P	?	11
Lasiocampidae														
Lasiocampinae														
	<i>Bombycomorpha bifascia</i>	Y	Set	Y	N	Nom	?	P	?	Y	?	?O	M	78
	<i>Catalebeda cuneilinea</i>	Y	Set	?	N	PR	?	?	?	Y	?	M	?	94
	<i>Eriogaster amygdali</i>	?	?Set	?	N	CP	S	P	?	?	?	O	?	77
	<i>E. arbusculae</i>	N	Set	?	N	CP	S	Y	?	?	?	?	?	65
	<i>E. catax</i>	N	Set	?	N	CP	S, Nom	Y	?	?	?	?	?	57; 92
	<i>E. lanestris</i>	N	Set	?	N	CP	S	Y	?	?	?	P	?	7; 86
	<i>E. philippi</i>	Y	Set	?	N	CP	S	P	?	?	?	M	?	76
	<i>E. rimicola</i>	?	?	?	N	?Nom	None	P	?	?	?	?	?	57; 92
	<i>Eutachyptera psidii</i>	?	?	?	N	CP	S	P	?	?	?	M	U	13; 29
	<i>Gloveria howardi</i>	?	?	?	N	CP	S	P	?	?	?	M	?	29
	<i>Macrothylacia rubi</i>	Y	Set	?	N	Nom	None	?	?	?	?	?	?	57; 92
	<i>Malacosoma alpicolum</i>	Y	Set	?	N	Nom, ?CP	S	P	?	?	?	P	?	29
	<i>M. americanum</i>	Y	Set	Y	N	CP	S	Y	?	Y	?	O	U	27; 74
	<i>M. californicum</i>	Y	Set	Y	N	CP	S	P	?	Y	?	O	U	74
	<i>M. castrensis</i>	Y	Set	Y	N	Nom, ?CP	S	P	?	?	?	P	U	30
	<i>M. constrictum</i>	Y	Set	Y	N	CP, Nom	S (molting)	P	?	?	?	M	U	74
	<i>M. distria</i>	Y	Set	Y	N	Nom	None	Y	?	Y	?	P	U	25
	<i>M. franconium</i>	Y	Set	?	N	Nom, ?CP	S	P	?	?	?	P	?	30
	<i>M. incurvum</i>	Y	Set	Y	N	CP	S	P	?	?	?	O	U	74

	<i>M. luteum</i>	Y	Set	Y	N	?Nom	?	P	?	?	?	P	?	30
	<i>M. neustria</i>	Y	Set	Y	N	CP	S	Y	?	?	?	O	U	58
	<i>M. tigris</i>	Y	Set	Y	N	CP, Nom	S (molting)	P	?	?	?	M	?	74
	<i>Rhinobombyx cuneata</i>	N	?Set	?	N	PR	?	?	?	Y	?	M	?	94
	<i>Schausinna regia</i>	Y	Set	?	N	PR	S	?	?	Y	?	O	?	55
Endromidae	<i>Enromis versicolora</i>	N	N	?	N	Nom	None	?	?	?	?	M	U	3a
Lemoniidae	<i>Sabalia tippelskirchi</i>	Y	?	Y	N	PR	?	?	?	?Y	?	?M	?	28; 56
Saturniidae														
Ceratocampinae	<i>Anisota senatoria</i>	Y	T,H	?	N	Nom	?	?	?	?	?	P	U, B	33; 38
	<i>A. stigma</i>	Y	T,H	?	N	Nom	?	?	?	?	?	P	U, B	38
	<i>A. virginensis</i>	Y	T,H	?	N	Nom	?	?	?	?	?	P	U, B	38
	<i>Dryocampa rubicunda</i>	Y	T,H	?	N	Nom	?	?	?	?	?	P	U, B	38
	<i>Hemileuca lucina</i>	Y	Spiny	T	Y	N	Nom	?	Y	?	?	M	U	15; 73
	<i>H. oliviae</i>	Y	Spiny	T	Y	N	Nom	?	Y	?	?	?	?	6
	<i>Hylesia lineata</i>	N	Sp	Y	N	Nom, CP	L,S	P	?	?	?	P	B	37
	<i>H. acuta</i>	N	Sp	Y	N	CP	L,S	P	?	?	?	O	U	87
	<i>Samia cynthia</i>	Y	T	?	N	Nom	?	?	?	?	?	O	?	2
Ludiinae	<i>Holocerina smilax</i>	Y	Sp	?	N	PR	?	?	?	?Y	?	P	?	94
	<i>Micragone ansorgei</i>	Y	Sp	?	N	PR	?	?	?	?Y	?	O	?	94
	<i>Vegetia dewitzi</i>	Y	Sp	?	N	PR	?	?	?	?Y	?	M	?	94
Saturniinae	<i>Bunaea alcinoe</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	42; 94
	<i>B. aslauga</i>	Y	Sp	?	N	PR	?	?	?	?	?	O	?	94
	<i>Cinabra hyperbicus</i>	N	Sp	?	N	PR	?	?	?	Y	?	M	?	94
	<i>Circula spp</i>	Y	T	?	N	None	?	?	?	?	?	P	M	54a
	<i>Cirina forda</i>	Y	?	?	N	PR	?	?	?	Y	?	O	?	46; 56
	<i>Copaxa denda</i>	Y	Set, Sp	?	N	Nom	None	?	?	?	?	O	?	88
	<i>C. escalentei</i>	Y	Set, Sp	?	N	Nom	None	?	?	?	?	O	?	88
	<i>C. mazaorum</i>	Y	Set, Sp	?	N	Nom	None	?	?	?	?	O	?	88
	<i>C. multifenestrata</i>	Y	Set, Sp	?	N	Nom	None	?	?	?	?	M	?	88
	<i>C. rufinans</i>	Y	Set, Sp	?	N	Nom	None	?	?	?	?	O	?	88
	<i>Eochroa trimenii</i>	Y	?	Y	N	PR	?	?	?	?Y	?	M	?	94
	<i>Gyanisa maja</i>	N	Sp	?	N	PR	?	?	?	Y	?	O	?	44; 94
	<i>Imbrasia belina</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	94
	<i>I. carnegiei</i>	Y	Sp	?	N	PR	?	?	?	Y	?	O	?	94
	<i>I. cytherea</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	94
	<i>I. ertli</i>	Y	?	?	N	PR	?	?	?	Y	?	O	?	94
	<i>I. guenzii</i>	Y	Sp	?	N	PR	?	?	?	Y	?	M	?	94
	<i>I. hecate</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	41; 94
	<i>I. hoehnelii</i>	Y	?	?	N	PR	?	?	?	Y	?	O	?	47; 94
	<i>I. macrothyris</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	94

Table 20-1 (cont.)

Classification	Species	Defenses ^a				Ant Tended ^b	Foraging pattern ^c	Shelter construc. ^d	Communication ^e				Host specific	Voltinism ^f	References
		Apo.	Struct.	Behav.					Chemical	Visual	Tactile	Acoustic			
Saturniinae	<i>I. petiveri</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	94	
	<i>I. rhodophila</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	45; 94	
	<i>I. tyrrhea</i>	Y	?	?	N	PR	?	?	?	Y	?	P	?	94	
	<i>I. wahlbergi</i>	Y	Sp	?	N	PR	?	?	?	Y	?	P	?	94	
	<i>I. zambesina</i>	Y	Sp	?	N	PR	?	?	?	Y	?	O	?	94	
	<i>Lobobunaea acetes</i>	N	?	?	N	PR	?	?	?	?Y	?	?P	?	94	
	<i>L. angasana</i>	N	?	?	N	PR	?	?	?	?Y	?	P	?	94	
	<i>L. phaedusa</i>	N	?	?	N	PR	?	?	?	?Y	?	?P	?	94	
	<i>Melanocera dargei</i>	Y	Sp	?	N	PR	?	?	?	?Y	?	O	?	94	
	<i>M. menippe</i>	Y	Sp	?	N	PR	?	?	?	?Y	?	P	?	43; 94	
	<i>Opodiphthera engaea</i>	?	?Set	?	N	Nom	?	?	?	?	?	O	?	11	
	<i>O. loranthi</i>	Y	Set	?	N	Nom	?	?	?	?	?	O	?	11	
	<i>Pavonia pavonia</i>	Y	S	?	N	Nom	None	?	?	?	?	P	U	3a	
	<i>Pseudaphelia apollinaris</i>	Y	?	Y	N	PR	?	Y	?	?	?Y	?	M	?	94
	<i>Pseudobunaea irius</i>	N	?	?	N	PR	?	?	?	?	Y	?	O	?	94
	<i>P. tyrrhena</i>	N	?	?	N	PR	?	?	?	?	Y	?	M	?	94
	<i>Rohaniella pygmaea</i>	N	?	?	N	PR	?	?	?	?	Y	?	M	?	94
	<i>Tagoropsis flavinata</i>	Y	?	Y	N	PR	?	?	?	?	Y	?	M	?	94
	<i>Ubaena fuelleborniana</i>	Y	Sp	?	N	PR	?	?	?	?	?Y	?	O	?	94
	<i>Urota sinope</i>	Y	?	?	N	PR	?	?	?	?	?Y	?	M	?	94
<i>Usta terpsichore</i>	Y	?	Y	N	PR	?	?	?	?	?Y	?	O	?	94	
<i>U. wallengrenii</i>	Y	?	Y	N	PR	?	?	?	?	?Y	?	M	?	94	
NOCTUOIDEA															
Arctiidae															
Arctiinae	<i>Amerila astreus</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	?	2	
	<i>Baroa siamica</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	?	2	
	<i>Cretonotos transiens</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	?	2	
	<i>Euchaetis egle</i>	N	?	?	N	Nom	?	?	?	?	?	M	?	17	
	<i>Halisidota caryae</i>	N	?	?	N	Nom	?	?	?	?	?	O	?	50	
	<i>Hyphantria cunea</i>	Y	Set	Y	N	PR	L,S	Y	?	?	P	?	P	U,M	83; 38
	<i>Lemyra</i> spp.	Y	Set	?	N	Nom	?	?	?	?	?	M	?	2	
	<i>Nyctemera</i> spp.	Y	Set	?	N	Nom	?	?	?	?	?	M	?	2	
	<i>Tyria jacobaeae</i>	Y	?	?	N	Nom	?	?	?	?	?	M	?	50; 92	

	<i>Pericallia galactina</i>																
	<i>trigonalis</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	?				2
	<i>Spilosoma</i> spp.	Y	Set	?	N	Nom	?	?	?	?	?	M	?				2
Ctenuchinae	<i>Syntomeida epilais</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	T				38
Aganaiidae	<i>Asota</i> spp.	Y	Set	?	N	Nom	?	?	?	?	?	M	?				2; 11
	<i>Neochera</i> spp.	Y	Set	?	N	Nom	?	?	?	?	?	M	?				2
	<i>Euplocia membliararia</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	?				2
	<i>Anagnia subfascia</i>	Y	Set	?	N	Nom	?	?	?	?	?	M	?				2
Lymantriidae	<i>Calliteara</i> spp.	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Carriola ecnomoda</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Cassidia peninsularis</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Cobanilla marginata</i>																
	<i>phaedra</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Dura alba</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Euproctis</i> spp. (many)	Y	Set	?	N	Nom, ?CP	L,S	?	?	?	?	O,P	U				2; 8; 92
	<i>Ilema vaneeckei</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Imaus munda</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>collettei</i>																
	<i>Leucoma impressa</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Locharna limbata</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Lymantria</i> spp.	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Numenes contrahens</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Redoa micacea</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Rhyptoses humida</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Scarpona ennomoides</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
	<i>Sitria denudata</i>	Y	Set	?	N	Nom	L,S	?	?	?	?	P	?				2
Noctuidae																	
Chloephorinae	<i>Camptoloma</i>	?	?	?	N	?	?	?	?	?	?	?	?				96
	<i>interiorata</i>																
Notodontidae	<i>Datana major</i>	Y	?	?	N	Nom	None	?	?	?	?	O	U,B				38
	<i>D. ministra</i>	Y	?	Y	N	Nom	None	?	?	?	?	P	U,B				38
	<i>D. integerrima</i>	Y	Set	?	N	Nom	None	?	?	?	?	O	U				38
	<i>Ichthyura inclusa</i>	N	?	?	N	CP	L,S	?	?	?	?	M	U,B				38
	<i>Phalera assimilis</i>	?	?	?	N	?Nom	None	?	?	?	?	?	?				96
	<i>P. bucephala</i>	Y	?	?	N	Nom	None	?	?	?	?	?	?				57; 92
	<i>P. bucephaloides</i>	Y	?	?	N	Nom	None	?	?	?	?	?	?				57; 92
	<i>P. sundana</i>	N	Set	?	N	Nom	None	?	?	?	?	?	?				2
	<i>Symmerista canicosta</i>	Y	?	?	N	Nom	None	?	?	?	?	M	U				38
Oenosandridae	<i>Oenosandra</i> spp.	?	?	?	N	Nom, CP	?	?	?	?	?	M	?				11; 68
Thaumetopoeidae	<i>Anaphe panda</i>	?	Set	?	N	?CP	S	P	?	?	?	O	?				59
	<i>A. reticulata</i>	?	Set	?	N	?CP	S	P	?	?	?	O	?				59
	<i>Cynosarga ornata</i>	?	?	?	N	?	?	?	?	?	?	M	?				11

Table 20-1. (cont.)

Classification	Species	Defenses ^a					Shelter construc. ^d	Communication ^e				Host specific	Voltinism ^f	References
		Apo.	Struct.	Behav.	Ant Tended ^b	Foraging pattern ^c		Chemical	Visual	Tactile	Acoustic			
Thaumetopoeidae	<i>Discophlebia catocalina</i>	?	?	?	N	?Nom	?	?	?	?	?	M	?	11
	<i>Epanaphe</i> spp.	?	Set	?	N	?CP	S	P	?	?	?	O	?	59
	<i>Epicoma dispar</i>	?	?	?	N	Nom	?	?	?	?	?	P	?	11
	<i>Ochrogaster</i> spp.	?	Set	?	N	CP	S	P	?	?	?	M	?	11
	<i>Oenosandra boisduvalii</i>	?	?	?	N	CP	Under bark	P	?	?	?	M	?	11
	<i>Thaumetopoea pinivora</i>	Y	?	?	N	CP,PR	L,S	Y	?	?	?	?	?	92
	<i>T. pityocampa</i>	Y	?	?	N	CP,PR	L,S	P	?	Y	?	M	U	1; 8; 23
	<i>T. processionea</i>	Y	?	?	N	CP,PR	L,S	Y	?	?	?	M	U	8
	<i>Trichiocercus sparshalli</i>	?	?	?	N	CP	Under bark	P	?	?	?	M	?	11
Thyretidae	<i>Metarctia meteus</i>	?	?	?	N	Nom	?	?	?	?	?	O	B	78

^a Defenses: Apo. = aposematic; Struct. = structures; Behav. = behavioral; Y = yes; N = no; P = probably; Set = setae; Sp = spines; H = horns; T = tubercles; O = osmeterium.

^b Ant-tended: Y = yes; N = no.

^c Foraging pattern: PR = patch-restricted; Nom = nomadic; CP = central-place.

^d Shelter construction: L = leaves; S = silk.

^e Communication: Y = yes; N = no; P = probably.

^f Host-specificity: M = monophagous; O = oligophagous; Poly = polyphagous.

^g Voltinism: Uni = univoltine; B = bivoltine; T = trivoltine; Multi = multivoltine.

Sources: (1) Balfour-Browne 1925; (2) Barlow 1982; (3) Bernays and Montllor 1989; (3a) Brookes, 1991; (4) Brown and Heineman 1972; (5) Bush 1969; (6) Capinera 1980; (7) Carlberg 1980; (8) Carter 1982; (9) Chermock and Chermock 1947; (10) Clark and Dickson 1971; (11) Common 1990; (12) Common and Waterhouse 1981; (13) Comstock 1957; (14) Corbet *et al.* 1992; (15) Cornell *et al.* 1988; (16) Damman 1987; (17) Dethier 1959a; (18) Dethier 1959b; (19) DeVries 1987; (20) Dunn 1917; (21) Edwards 1897; (22) Emmet 1979; (23) Fabre 1916; (24) Fiedler and Maschwitz 1989; (25) Fitzgerald and Costa 1986; (26) Fitzgerald and Edgerly 1979; (27) Fitzgerald and Peterson 1983; (28) Fontaine 1975; (29) Franclemont 1973; (30) de Freina and Witt 1987; (31) Goater 1986; (32) Hertel and Benjamin 1979; (33) Hitchcock 1961; (34) Hoebeke 1987; (35) Howe 1975; (36) Iwao 1968; (37) Janzen 1984; (38) Johnson and Lyon 1988; (39) Kevan and Bye 1991; (40) Khoo *et al.* 1991; (41) Lampe 1982a; (42) Lampe 1982b; (43) Lampe 1983a; (44) Lampe 1983b; (45) Lampe 1984; (46) Lampe 1985a; (47) Lampe 1985b; (48) Langlois and Langlois 1964; (49) Larsen 1991; (50) Lawrence 1990; (51) Long 1955; (52) Mallet and Jackson 1980; (53) Mizuta 1968; (54) Moriuti 1977; (54a) Naumann 1995; (55) Oberprieler 1993; (56) Oberprieler 1995; (57) Patocka 1980; (58) Peterson 1988; (59) Pinhey 1975; (60) Porter 1982; (61) Robinson *et al.* 1994; (62) Roessingh 1989; (63) Roessingh 1990; (64) Rosier 1951; (65) Rougeot and Viette 1983; (66) Schultz and Allen 1975; (67) Schweizerischer Bund für Naturschutz 1987; (68) Scoble 1992; (69) Scott 1986; (70) Stamp 1977; (71) Stamp 1981a; (72) Stamp 1984; (73) Stamp and Bowers 1988; (74) Stehr and Cook 1968; (75) Staude 1994; (76) Talhouk 1940; (77) Talhouk 1975; (78) Taylor 1949; (79) Taylor 1950; (80) Thomas and Lewington 1991; (81) Tsubaki 1981; (82) Underwood 1994; (83) Warren and Tadic 1970; (85) Weidemann 1988; (86) Weyh and Maschwitz 1978; (87) Wolfe 1988; (88) Wolfe 1993; (89) Young 1985; (90) Young *et al.* 1986; (91) P. J. DeVries, personal communication; (92) K. Fiedler, personal communication; (93) J. Holloway, personal communication; (94) R. G. Oberprieler, personal communication; (95) M. W. Tan, personal communication; (96) H. Yoshimoto, personal communication; (97) N. E. Pierce, personal observations; (98) K. Fiedler and U. Maschwitz, unpublished observations.

Defensive signals and survivorship

The idea of defensive-signal enhancement through gregariousness has been explored in many theoretical and empirical studies. Guilford (1990) points out that the details of predator-prey interactions are key to understanding the evolution of aposematic coloration. In an early discussion of possible 'predator conditioning' by gregarious larvae, Edmunds (1974) argued that predators adversely affected by ingesting one individual in a group learn to associate their resultant condition with the color patterns exhibited by adjacent larvae. Several theoretical and empirical studies have shown that vertebrate predators can learn to associate distastefulness with conspicuous coloration (see, for example, Brower 1958; Gittleman *et al.* 1980; Gittleman and Harvey 1980; Harvey *et al.* 1982; Roper and Redston 1987). Gregariousness could increase the contact rate between predators and aposematic prey, thereby facilitating predator association of warning coloration with unpalatability (Tinbergen *et al.* 1967; Smith 1974; but see Wiklund and Järvi 1982). Considerable theoretical work has addressed the importance of density-dependence and kin selection in the evolution of aposematism (see, for example, Fisher 1958; Harvey *et al.* 1982; Guilford 1985; Leimar *et al.* 1986; Mallet and Singer 1987).

Several studies have explored the effectiveness of group-displayed antipredator behaviors in larvae of Lepidoptera and symphytan Hymenoptera. Group displays generally include defensive regurgitation of noxious compounds and/or vigorous thrashing or flicking of the body (see, for example, Prop 1960; Lyons 1962; Myers and Smith 1978; Stamp 1984; Cornell *et al.* 1987; Peterson *et al.* 1987). Although it has often been suggested that aposematic coloration is also more effective in deterring predators in grouped vs. solitary situations (see, for example, Eisner and Kafatkos 1962; Young 1978; Pasteels *et al.* 1983), Vulinec (1990) points out that there is as yet no experimental evidence directly supporting this claim. Based on studies with gregarious and solitary aposematic caterpillars and bird predators, Sillén-Tullberg (1988, 1990) reports essentially no immediate or 'automatic' benefit accruing to gregarious vs. solitary prey, since gregariousness has initial costs in the form of increased predation risk per capita (*cf.* Cooper 1992). Insofar as clustering renders aposematic signals more apparent to visually hunting predators capable of such association, it may be expected to increase the efficacy of the aposematic defense. Although myrmecophilous lycaenid species do not appear to exhibit high levels of defensive thrashing (Malicky 1970), the

efficacy of chemical and/or acoustic signals in attracting ant attendants that deter predators is improved in a group context, a pattern observed in both larvae and pupae of gregarious species (Pierce and Elgar 1985; Pierce *et al.* 1987; DeVries 1991).

Other evidence suggesting the importance of defensive-signal enhancement in the evolution of gregariousness and sociality comes from trait-distribution patterns and comparative phylogenetic analysis of some groups. In her review of insect aggregation and its defensive significance, Vulinec (1990) argues that aggregation evolved after other modes of defense such as chemical or structural predator deterrents. Aggregation may thus be seen as an adaptation that increases the effectiveness of signals inherent in warning coloration or structural defenses. This view is supported by the phylogenetic studies of Sillén-Tullberg (1988, 1993) and Sillén-Tullberg and Leimar (1988), who used comparative analyses to show that aposematic coloration in butterfly evolution probably precedes gregariousness. Sillén-Tullberg (1988) states that '...unpalatability is an important predisposing factor for the evolution of...larval gregariousness in butterflies'. Gregariousness is thus seen to amplify pre-existing antipredator signals in many aposematic butterflies, a conclusion supported by reanalysis (Sillén-Tullberg 1993) for the effects of biased characters on comparative studies. The presence of many gregarious non-aposematic lepidopteran and hymenopteran larvae (Table 20-1) suggests, however, that aposematism is not a prerequisite for gregariousness, but rather facilitates social evolution.

In summary, the evidence supports the idea that defensive signals are augmented in their expression, and therefore functional effectiveness, in group contexts. The defensive signals of social larvae are not merely directed at predators, but also include a pheromonal, tactile, or visual signal broadcast to the group and acting to coordinate defense.

Foraging signals and resource use

Social facilitation of feeding through foraging-related signals may occur in several ways: (1) by trail-based chemical communication, often exhibited by central-place foragers such as tent caterpillars and other lasiocampids (Fitzgerald 1976; Fitzgerald and Gallagher 1976; Weyh and Maschwitz 1978; Fitzgerald and Edgerly 1979; Carlberg 1980; Fitzgerald and Peterson 1983; Peterson 1987); (2) via synchronization of group feeding schedules (Fitzgerald 1980; Casey *et al.* 1988; Fitzgerald *et al.* 1988); (3) through orientation to group feeding sites (Stamp 1981a); and

(4) via group-enhanced establishment of feeding sites (Ghent 1960; Mizuta 1968; Shiga 1976; Tsubaki 1981; Tsubaki and Shiotsu 1982).

Efficiency of central-place foraging is improved as group size increases (see, for example, Fitzgerald and Costa 1986). Since rate of location and communication of resources to colony mates depends upon the number of searching individuals, group foraging efficiency will increase with number of foragers up to a point where density-dependent factors cause it to level off. As a result of information-sharing, central-place foragers capable of recruitment communication reduce average individual search and exposure time, thereby increasing overall survival probability and growth rate of colony members.

Feeding synchronization and group orientation to feeding sites may increase growth rate by raising overall activity levels (Long 1953) or by contributing to the consumption of high-quality food by recruitment to such food patches. Stamp and Bowers (1990a), for example, observed greater survivorship and smaller variance of biomass in larger vs. smaller groups of the saturniid *Hemileuca lucina*. In some species, such as eastern tent caterpillars, group foraging schedules may actually constrain individual feeding frequency, although these caterpillars still grow faster in a social context (Fitzgerald 1993).

As with defensive signals, enhancement of foraging-related signals involved in recruitment increases with the number of potential signalers: the rate of information exchange increases with the number of communicators. However, unlike defense where a signal is simply spreading through the group, recruitment-signal enhancement is manifested as decreased time taken for the average group member to locate food. Enhancement means, in this context, improved foraging through cooperative location of food, improvement stemming from the group-expression of search and recruitment behavior.

Caterpillar castes

Many social insects exhibit morphological or behavioral castes dividing the reproductive and labor effort of the colony. There have been no reports of morphological castes in caterpillar societies; this is not surprising insofar as such castes are generally found in long-lived or clonally reproducing social species. Several authors have, however, explored the possibility of polyethism in various social Lepidoptera. Wellington (1957, 1965) first raised the possibility of behavioral castes in his studies of intracolony foraging variation among *Malacosoma californicum pluviale* larvae. Wellington

(1957, 1965) reported that many colonies are composed of relatively 'active' (type I) and 'inactive' (type II) larvae, apparently determined by the amount of yolk deposited in the egg; the type I larvae act as foraging 'leaders' while the type II larvae are 'followers', collectively creating a division of labor. Analyses of other *Malacosoma* species, however, failed to detect any consistent behavioral foraging differences among colony mates (Laux 1962; Franz & Laux 1964; Greenblatt 1974; Greenblatt & Witter 1976; Myers 1978; Shiga 1979; Edgerly & Fitzgerald 1982). Papaj & Rausher (1983) reanalyzed Wellington's (1965) data and found his conclusion of polyethism unsupported.

It thus appears likely that any behavioral variation among tent caterpillars of a given colony is stochastic and does not constitute even a weak division of labor. This conclusion is consistent with Edgerly & Fitzgerald's (1982) observation that *M. americanum* activity levels are normally distributed within colonies. A study of the saturniid *Hemileuca lucina* found that individual levels of activity also vary with age (Cornell *et al.* 1988). Responses to variables such as nutrition and disease are also likely to result in behavioral variation within colonies.

Some authors have treated social facilitation as a weak division of labor in some species (e.g. group-facilitated breaching of plant cuticular defenses by 'biter' larval castes (Ghent 1960; Iwao 1968; Tsubaki 1981)). Insofar as there is no consistent behavioral specialization among larvae, however, facilitation is stochastic and therefore does not reflect behavioral caste differentiation.

Social behavior and larval vulnerability

Non-ant-associated lepidoptera

The larval stage of Lepidoptera is a period of great risk and vulnerability to mortality factors such as predation, desiccation, and starvation. Some instars, however, are likely to be at greater risk than others. We next explore the idea of shifting vulnerability and its relevance to signal enhancement and caterpillar sociality. In what ways do social characters influence larval defense and growth? Several studies on larvae of Symphyta and Lepidoptera have considered the effects of larval size and grouping on survivorship and fecundity. The importance of survivorship is obvious; moreover, fecundity and mating success in the Lepidoptera are often intimately tied to larval size at pupation (Scriber and Slansky 1981; Haukioja and Neuvonen 1985, 1987; Barbosa *et al.* 1986; Boggs 1986; Wickman and Karlsson 1989; Haukioja 1993; Reavey 1993).

Larval size. Relative body size has been used as the basis for determining survival probability in various organisms (Stamp and Bowers 1991). Relative sizes of predators and prey are important determinants of predation levels, as both predator classes and their search modes change as larvae grow (Montllor and Bernays 1993). Early-instar larvae are usually attacked by invertebrate predators such as ants, spiders, stinkbugs and parasitoids (Ayre and Hitchon 1968; Morris 1972a,b; Tilman 1978; Evans 1983; Stamp 1986; Stamp and Bowers 1991), whereas mid- to late instars contend with larger invertebrate predators such as vespid wasps (Rabb and Lawson 1957; Morris 1976; Stamp and Bowers 1988; DeVries 1991) and vertebrate predators such as birds (Dempster 1967; Morris 1972a; Witter and Kulman 1972; Knapp and Casey 1986; Bernays and Montllor 1989; Heinrich 1993).

With respect to larval defense, bigger may be better for a variety of reasons. First, larger caterpillars have a narrower range of predators, since smaller, solitary assailants are often readily rebuffed (Sullivan and Green 1950; Morris 1963; Evans 1982). Second, in shelter-building species, incipient shelters are more easily penetrated by vertebrate or invertebrate predators than are the larger, stouter-walled shelters of older caterpillars. Third, it is often not until later instars that structural and chemical defenses constitute an effective defense. The spines or setae of structurally defended species are proportionately small and poorly developed in newly eclosed larvae, and many chemically defended species require time to accumulate secondary compounds. Such defense phenology may explain why many larvae are cryptic in early instars and only later display aposematic coloration or conspicuous clustering, a pattern observed in many animal species (Booth 1990). These observations suggest that the earliest larval instars are generally more vulnerable than later instars; we describe this early-instar period as a 'vulnerability window'. Early instars are also likely to be more vulnerable to abiotic mortality factors, such as drowning in rainstorms, freezing, or desiccation.

Larval grouping. Group-enhanced growth rates have been reported in a number of symphytan and lepidopteran larvae, including *Neodiprion* spp. (Ghent 1960; Lyons 1962; Henson 1965; Tostowaryk 1972), *Hyphantria cunea* (Watanabe and Umeya 1968; Morris 1976), *Malacosoma* spp. (Shiga 1976; Damman 1987; Peterson 1987), *Pryeria sinica* (Tsubaki 1981; Tsubaki and Shiotsu 1982), and *Halisidota caryae* (Lawrence 1990). It is difficult to disentangle the relative importance of different group-derived factors

influencing growth rate in social species. Since growth is a metabolic process, social characters or their byproducts that affect the location, feeding frequency, and assimilation of resources may be subject to increased efficacy as group size increases. For larvae, socially facilitated feeding may enhance growth rates in several ways: (1) overcoming plant structural defenses (Young and Moffett 1979; Ghent 1960; Tsubaki and Shiotsu 1982; Young 1983); (2) coordinating foraging (Stamp 1981a; Peterson 1987; Casey *et al.* 1988); or (3) constructing group shelters, which may create a favorable microclimate (Fitzgerald 1980; Fitzgerald and Willer 1983; Fitzgerald *et al.* 1988). Recruitment, a form of social facilitation, may improve foraging and growth rate (Peterson 1987) such that larvae more quickly exit the early-instar vulnerability window.

Other observations. Additional observations suggestive of differential vulnerability of larval instars include age-related changes in social behavior of larvae, and 'artificial' increase of egg-batches by adults. The integrity of social groups often erodes over the course of the larval stage, such that the penultimate or ultimate instars abandon the social group and become solitary, or the colony fragments into smaller units (see, for example, Carlberg 1980; Tsubaki and Yamamura 1980; Tsubaki 1981; Porter 1982; Hansen *et al.* 1984a,b; Cornell *et al.* 1987; Pierce *et al.* 1987; Fitzgerald *et al.* 1988; Stamp and Bowers 1988; Lawrence 1990). This phenomenon has been attributed to an easing of selective pressures favoring aggregation in early instars (Chansigud 1964) or the increased food requirements of older larvae (Dethier 1959a,b; Porter 1982).

Considering that age-related independence is exhibited by many social species even when food appears to be abundant (Tsubaki 1981; Fitzgerald *et al.* 1988), it is likely that early pressures to function as an integrated, cooperative unit are counterbalanced by other factors as the larvae age, such as increased vulnerability to pathogens or predators. Late-instar increases in the cost:benefit ratio stemming from aggregation is consistent with the view that social behaviors are of greatest importance among early instars, which are both most vulnerable to predators and face the greatest hurdles in finding food and establishing feeding sites. For these species, the major benefits of social behavior occur during the early stages of colony growth (Fitzgerald 1993), and the mechanism leading to late-instar abandonment of the colony is likely to vary between species. Hochberg (1991a) points out that there are few instances of solitary early-instar larvae that

preferentially associate when older, although one exception appears to be the pine webworm *Tetralopha robustella*, which solitarily mines pine needles in the first few instars and spins small communal tents in later instars (Hertel and Benjamin 1979; Johnson and Lyon 1988).

A second observation concerns oviposition pattern. A positive effect of group size on defense and resource use may make it advantageous for some species to oviposit near existing egg masses, thereby increasing group size at eclosion. Such an oviposition pattern has been observed in several social lepidopteran species (see, for example, Morris 1972b; DeVries 1977; Stamp 1981b; Fitzgerald and Willer 1983; Pierce and Elgar 1985), despite the fact that larger egg clusters sometimes suffer higher rates of parasitism (Stamp 1981b). An interesting mode of increasing batch size is 'social oviposition', in which at least two females simultaneously oviposit eggs in a cluster. This phenomenon has been observed in several species of *Heliconius* butterflies (Turner 1971; Mallet and Jackson 1980), and may be a consequence of resource limitation (i.e. uncommon or ephemeral resources are best exploited by batch laying) or represent a means of increasing group size. Benson *et al.* (1976) report a *Heliconius* cluster of over 800 eggs, a number Mallet and Jackson (1980) attribute to multiple females. To the degree that larval survival or growth rate improves with group size, adjacent or synchronous oviposition suggests that colony family structure is unimportant under some conditions relative to the need for rapid growth or enhanced defense.

Ant-associated Lepidoptera

The twofold advantage of appeasing ants that might themselves be potential predators, and attracting attendant ants that can serve as protective guards against predators and parasitoids, has been essential in the evolution of ant-associated Lepidoptera, especially those conforming to our definition of social Lepidoptera (Hinton 1951; Downey 1962; Ross 1964; Malicky 1970; Pierce and Mead 1981; Pierce and Eastal 1986; Fiedler 1991; Wagner 1993). In particular, Atsatt (1981a) argued that selection for 'enemy-free space' (Askew 1961; Gilbert and Singer 1975; Lawton 1978) has led to the elaborate mutualistic relationships exhibited by many ant-tended lycaenids; this may be especially true of social species. The concept of 'enemy-free space' can likewise be applied to the evolution of other ant-tended gregarious insects such as aphids and membracids in the Homoptera (see, for example, Way 1963; Nault *et al.* 1976; Wood 1977; McEvoy 1979; Bristow 1984).

Differences between lycaenids such as the social Australian species *Falmenus evagoras* (whose caterpillars are tended by ants from the first instar) and other species such as the North American solitary lycaenid *Glauopsyche lygdamus* (whose larvae are not strongly attractive to ants until the third instar) suggest that the cost : benefit ratio differs significantly between species for early instars. The dorsal organ, a gland producing sugary secretions, does not develop until the third instar in many lycaenids and riodinids (Clark and Dickson 1956; Ross 1964; DeVries 1988; Fiedler 1991). Production of secretions to appease and reward ants is expensive, and selection should favor the evolution of ant association only when the benefits of tending ants outweigh the costs of their attraction and maintenance. Selection favors early ant-association in *F. evagoras*, and alternative means of larval defense (such as crypsis and burrowing in flower buds) in *G. lygdamus*. Differences between species may be generated by a number of selective forces, including host-plant quality, pressure from predators or pathogens, and availability of alternative means of defense.

In the context of ant-mediated defense of plants, the period of greatest vulnerability to herbivores is thought to occur with the onset of foliar nectar production in ant-protected plants (Tilman 1978; O'Dowd 1979), although larvae of myrmecophilous riodinid butterflies may benefit from both feeding on leaves and drinking from the extrafloral nectaries of their hostplant (DeVries and Baker 1989).

In summary, the probability of mortality in larval Lepidoptera is generally greatest in the earliest instars. Within a given instar, larger groups generally suffer lower per capita mortality rates than smaller groups. Plots of hypothetical, generalized survivorship curves exhibit a general trend from concave-up to concave-down with increasing group size (Fig. 20-2). Group size improves survivorship through concomitant effects on body size and growth rate: early-instar vulnerability to predators and desiccation is inversely related to body size; group size (or simply social context) may increase growth rate, which in turn determines rate of passage to larger, less vulnerable instars.

SOCIAL EVOLUTION IN LEPIDOPTERA: COSTS AND BENEFITS OF LIVING IN LARVAL SOCIETIES

Costs of sociality

Group-living may lead to several types of cost to individuals, including (1) increased conspicuousness to predators, (2) increased transmission rates of pathogens, and

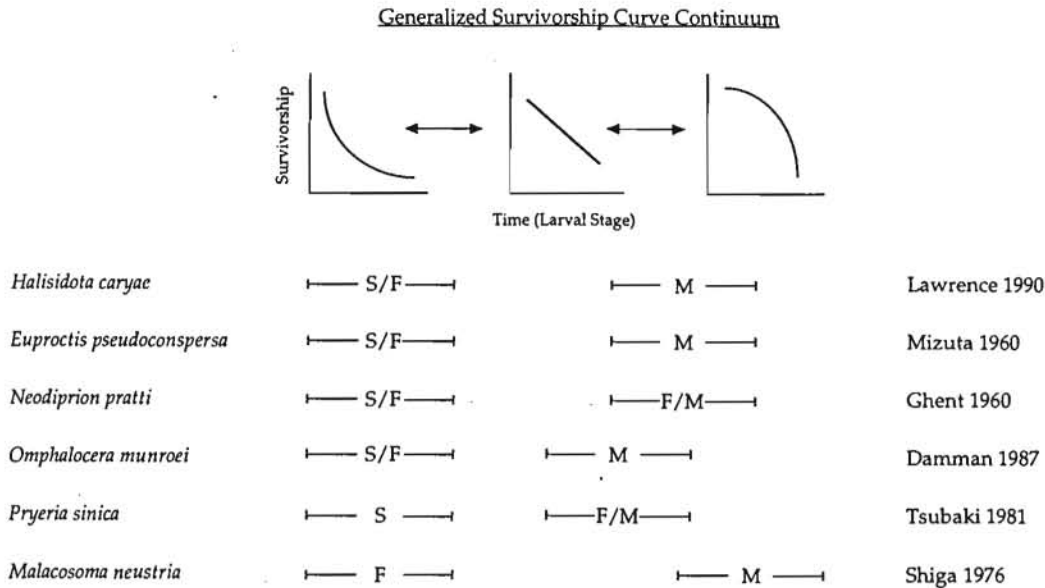


Figure 20-2. The influence of group size on survivorship in some social Lepidoptera and Symphyta. Three survivorship curves are illustrated as points along a continuum. For purposes of comparison, larval colonies are divided into group-size classes (S = solitary, F = few, M = many); in some cases, 'many' is used to denote intact, natural colonies. Bars for each species and group size are positioned relative to the survivorship curve continuum. Larger groups tend to experience better survivorship as a result of the greater defensive and/or feeding capacity of aggregated individuals. Enhanced group survivorship in some species is in part attributable to accelerated larval growth.

(3) nutritional deficiency under conditions of resource limitation and ensuing competition. Factors leading to fitness trade-offs often interact in a complex fashion; for example, predators and parasites can reduce fitness directly through mortality and indirectly by interfering with feeding and metabolism. Thus, it is most convenient to divide trade-offs into two sections: (1) disease, and (2) predators, parasites, and nutrition.

Disease

Temporal and spatial gregariousness can incur costs through density-dependent controls. Survivorship of social species is reduced, for example, by group-enhanced risk of contracting disease (see, for example, Bucher 1957; Payne *et al.* 1981; Hochberg 1991a,b) or by attracting certain types of predator and parasite (see, for example, Stamp 1981a,b; Knapp and Casey 1986; Pierce *et al.* 1987; Hieber and Uetz 1990; Rosenheim 1990). The role of disease costs in insect social evolution is understudied relative to that of predation, perhaps because the effects of the two are difficult to disentangle (diseased individuals may be less able to

defend themselves against predators). Pathogens are likely to have played a role in shaping sociality in some Lepidoptera, notably in cases where disease risk is influenced by foraging pattern (and hence social complexity).

Another important disease factor is mode of transmission. Pathogens such as certain *Bacillus* bacteria that are transmitted by physical contact pose a greater risk for social groups than those such as polyhedrosis viruses that must be ingested to infect the host. Hochberg (1991a) found that an increase in disease resistance with larval age is more frequently observed in gregarious than in solitary lepidopteran species, which suggests that viruses have historically exerted a selective pressure on social caterpillars.

Predators, parasites and nutrition

Some of the best-studied costs of sociality include conspicuousness to predators and resource competition. Predators that employ foraging strategies involving repeated return to successful foraging sites or intensified searching in the immediate area where prey are encountered place aggregated prey at increased risk relative to solitary prey

(Taylor 1977a,b; Vermeij 1982; Kareiva and Odell 1987; Vulinec 1990). When resources are limiting, aggregation can also incur costs due to increased intraspecific competition and indirect effects on predation. Colonies may deplete their food supply under conditions of high local population density, forcing larvae to abandon the host plant in search of alternative hosts and potentially resulting in significant mortality (Dethier 1959a,b; Chew 1977; Tsubaki and Shiotsu 1982; Stamp 1984).

Trade-offs are often manifested in the foraging pattern of social larvae. Many studies have considered the effects of such factors as predation, food quality, temperature regime, and resource use on caterpillar foraging and developmental patterns, providing measurements of variables such as mortality, developmental rate, mass at pupation, fecundity, etc., in both the laboratory and the field (see reviews by Hassell and Southwood 1978; Scriber and Slansky 1981; Wickman and Karlsson 1989; Montllor and Bernays 1993; Stamp 1993). These studies indicate that larvae exhibit maximum growth rates when feeding on high-quality resources under thermally optimal, 'enemy-free' conditions (Brower 1958; Holloway and Herbert 1979; Price *et al.* 1980; Schultz 1983). Such conditions are rarely met in the natural world; how and why do larvae deviate from a hypothetical foraging optimum?

Suboptimal conditions include unfavorable climate, low host-plant quality, and predation, often interacting in a complex and interrelated manner (Stamp 1993). Although environmental conditions, plant defenses and leaf quality are recognized as important selective forces, predation risk may have a more immediate effect in influencing the exposure of herbivores to these forces. For example, predation has been hypothesized to play a key role in selecting for caterpillar activity at suboptimal temperatures (such as nighttime foraging to escape diurnal predators) (Heinrich 1979, 1993; Schultz 1983; Fitzgerald *et al.* 1988), and a large body of evidence indicates that predation can constrain host-plant choice as well as the quality of leaves consumed on a chosen plant. In a series of studies on *Hemileuca lucina*, Stamp and Bowers (1988, 1990a,b, 1991) demonstrated that harassment by vespid wasp predators reduced caterpillar growth and survivorship by interfering with caterpillar feeding; larvae were frequently induced to move to the shaded host-plant interior where only poor, mature leaves were available. The harassment phenomenon has also been observed in the ecology of other insects, including tent caterpillars (Knapp and Casey 1986), odonates (Heads 1986) and hemipterans (Sih 1980, 1982). In other studies, predation pressure was implicated

in the preference for nutritionally inferior, old, or damaged leaves by the oecophorid leaf-roller *Diurnea fagella* (Hunter 1987) and the leaf-tying pyralid *Omphalocera munroei* (Damman 1987) because of the greater defensive potential of these leaves as shelters.

Benefits of sociality

Passive defense and growth effects

It is often difficult to separate communicative and non-communicative factors that affect group defense and resource use. Passive or non-communicative mechanisms contributing to defense include 'group dilution effects' (Hamilton 1971; Turner and Pitcher 1986; Sillén-Tullberg and Leimar 1988; Lawrence 1990; Wrona and Dixon 1991) and early warning against predators (Treherne and Foster 1980, 1981, 1982; Vulinec 1990). Group dilution refers to the 'safety in numbers' concept, whereby a given individual is less likely to be taken by a predator when standing with a group than when alone (Hamilton 1971). In principle, the bigger the group, the more effective the dilution effect. Exceptions to this pattern have been reported, however. For example, Stamp (1981a,b) found that medium-sized groups of larval *Euphydryas phaeton* experienced lower rates of parasitism than smaller and larger groups. Conversely, Subinprasert and Svensson (1988) observed that the smallest and largest egg clutches of *Laspeyresia pomonella* had high survivorship compared with medium-sized clutches. In general, however, both survival probability and growth rate tend to be positively correlated with colony size up to a certain point (Evans 1982; Porter 1983; Stamp and Bowers 1988), a phenomenon that is the product of both protective mechanisms and accelerated developmental rates.

Inclusive fitness effects

Genetic mechanisms may play a role in the evolution of cooperation, but there are almost no genetic studies of social lepidopteran species. The selective strength of ecological pressures may be (or historically have been) severe enough to favor cooperation regardless of genetic relatedness between interactants. Indirect fitness will be greater than zero whenever patterns of mating and sperm utilization result in family structure (kinship) within groups. In Lepidoptera, the greatest degree of family structure, full sibships, obtains when colonies are derived from a single batch of eggs (i.e. comprise a single matriline) and the ovipositing female has mated once or uses sperm from one male.

One way to determine the likely importance of kin selection in the evolution of social behavior is to establish whether mechanisms either preserving or undermining group family structure exist, since family structure is integral to the operation of kin selection. Kin discrimination may be the most common mechanism preserving family structure (Fletcher and Michener 1987), whereas structure is undermined by adjacent or synchronous oviposition by mixing family groups (if ovipositing females are unrelated).

In the only study to date addressing kin discrimination in a social caterpillar, Costa and Ross (1993) inferred a lack of kin discrimination among eastern tent caterpillars from their observations of eroding family structure. This erosion occurs through stochastic fusion and fission of unrelated colonies foraging together on the same tree. Despite mixing, however, mating and oviposition in this species set up conditions of both high relatedness within colonies and low colony density on trees, effectively preserving some family structure throughout the larval stage. Thus, insofar as indirect fitness is consistently greater than zero, it is likely to have played some role in *M. americanum* social evolution. The important point is that inclusive fitness effects may result from overt behavioral mechanisms or may be byproducts of behavior and population biology.

Sawfly larvae belong to a group in which inclusive fitness effects are most likely, yet are among the least complex 'caterpillar' societies. In theory, inclusive fitness effects are more readily realized in sawflies because of the relatedness asymmetry of the haplodiploid sex determination system of Hymenoptera; such asymmetries are thought to be key in the evolution of eusocial hymenopteran societies (Wilson 1975; Trivers and Hare 1976). Social communication and interaction in larval sawfly societies is apparently limited to group alarm and defense, and group cohesion. To our knowledge, there are no examples of recruitment communication in sawflies, although a few patch-restricted species construct silken structures. These include species in the pamphiliid genera *Neurotoma*, *Acantholyda* and *Cephalcia*, various members of which are called the 'web-spinning' or 'pine-webbing' sawflies (Peterson 1962; Johnson & Lyon 1988). Many gregarious sawflies are aposematic and exhibit the characteristic sawfly group-defensive behavior of rearing and regurgitating.

Signal enhancement and cooperation

Some authors view predation and parasitism as the major selective force leading to social evolution in insects and

other animals (see, for example, Hamilton 1971; Michener 1974; Pulliam and Caraco 1984; Turner and Pitcher 1986; Inman and Krebs 1987; Strassmann *et al.* 1988). Others, focussing primarily on the behavior of larvae in the Symphyta and Lepidoptera, have stressed the importance of social facilitation in feeding (Ghent 1960; Shiga 1976; Tsubaki and Shiotsu 1982; Young 1983). As discussed above, sociality can simultaneously facilitate passive and active defense, thermoregulation, and foraging efficiency in both ant-associated and non-ant-associated contexts. None of these selective factors are mutually exclusive; the most important factor in social evolution in the Lepidoptera is likely to be the enhancement of signals that collectively bear on both group defense and resource use, perhaps providing rapid growth through the vulnerable early larval stages.

DISCUSSION

Lepidopteran social evolution: factors and scenarios

Life history and ecology

No single feature of the ecology, development, genetics, or behavior of social Lepidoptera sets them apart from other social taxa. Ecological factors such as host specificity and voltinism are not consistent predictors of social behavior (Table 20-1), and there appear to be no unusual genetic attributes of Lepidoptera that favor cooperation in the sense that this group lacks the relatedness asymmetry of haplodiploidy and the genetic identity of parthenogenesis. None the less, we identify a suite of life-history and ecological traits collectively shaping and uniquely defining sociality in the order.

Table 20-2 summarizes the key behavioral, life-history, and ecological characteristics of social insects and arachnids. Comparing the social forms of these groups, important similarities and differences are apparent. Virtually all social forms exhibit group, or at least family, defense and cohesion, and communication by tactile or chemical means is nearly universal. Ecological conditions such as predation and resource distribution has resulted in interesting parallels between social Lepidoptera and other social taxa. For example, patch-restricted foragers, found among such diverse taxa as aphids, termites, caterpillars, sawflies and embiids, live in or on their food; recruitment communication, associated with patchy resource distribution, is found in the ants, bees, wasps, caterpillars and termites.

Table 20-2. *Life-history and communication characteristics of social insects and arachnids*

Life-history defines generationally the relationship of social interactants (e.g., parent-parent, parent-offspring, sib-sib). Societies are further shaped by ecological factors influencing defensive and foraging traits. Lepidopteran societies lack parental interaction; communication occurs within larval cohorts, and includes the contexts of foraging, group defense, and group cohesion. See text for discussions of foraging patterns, group defense, and group cohesion. Brood care is broadly defined as defense and/or feeding of immatures by one or both parents.

Taxon	Brood care	Perennial	Foraging Pattern ^d			Group defense	Group cohesion	Nestmate recognition	Modes of communication ^b
			PR	Nom	CP				
Hymenoptera (Eusocial)	Yes	Many	?	Many	Most	Yes	Yes	Yes	V, C, T, A
Hymenoptera (Symphyta)	No ^c	No	Yes	Yes	No	Yes	Yes	?	?V, ?C, ?T
Lepidoptera	No ^d	No	Many	Many	Some	Yes	Yes	?	?V, C, T, A
Coleoptera ^e	Yes	Yes	Yes	No	No	Yes	Yes	?	?C, ?T, A
Thysanoptera	Yes	No	Yes	No	No	Yes	?	?	C
Hemiptera ^f	No	No	Yes	No	No	Yes	?	?	C
Psocoptera	No	Yes	Yes	Yes	No	?	Yes	?	T, ?C, ?A
Zoraptera	No	Yes	Yes	No	No	No	Yes	No	?C, T
Embioptera	Yes	Yes	Yes	No	No	No	?	?	?C, ?T
Dictyoptera ^g	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	C, T
Araneae	Yes	Yes	Yes	No	No	Yes	Yes	?	C, T

^a PR = patch-restricted; Nom = nomadic; CP = central-place.

^b V = visual; C = chemical; T = tactile; A = acoustical.

^c See Dias (1975, 1976, 1982) and Morrow *et al* (1976).

^d For an exception, see Nafus and Schreiner (1988).

^e Passalidae.

^f Aphididae.

^g Isoptera.

In defensive terms, social Lepidoptera lack soldier castes, but share group-defensive displays with gregarious sawflies and pleometrotic Hymenoptera.

Among the many taxon-specific differences, two general features are apparent. First, the demographic structure of social insect colonies is defined generationally, splitting into those with overlapping generations and those comprising a single-generation cohort. The former colonies are usually perennial or multivoltine; the latter tend to be univoltine. This distinction is important because demographic composition determines the possibility of such social traits as parental care. Second, the communication complexity of social insect colonies is related to foraging pattern. Life-history traits delimit the essential structure and composition of insect societies while ecological factors provide the selective regime favoring particular types of social interactions.

Lepidopteran societies are among the simplest of social insects in terms of demographic composition (typically single-generation) and lifespan (usually annual), while in many cases sharing communication features of more complex social species (such as recruitment). The route of social evolution in many social insects is hypothesized to have begun with a maternal care phase, subsequently elaborated with morphological or behavioral specialization among siblings cooperating in the care and rearing of brood. Lepidopteran adults rarely interact with larval aggregations (but see Nafus and Schreiner 1988), typically abandoning their eggs after perhaps concealing or coating them with accessory-gland secretions or abdominal setae. The absence of adults in most lepidopteran societies also means that they tend to be ephemeral, since eggs are not replenished and the colony exists only as long as the

larvae take to mature. The relative simplicity of lepidopteran societies follows from the general lack of parental care or even parental presence, as the parent-offspring communication and reproductive-based cooperation found in many other social taxa are precluded.

Resource use appears to be a factor shaping social complexity in this order. Social interactions beyond alarm and defense are unnecessary for species living in or on abundant resources. For many larvae, seemingly-abundant host-plant leaves are not equally acceptable. Often, larvae can survive on only the youngest foliage (see, for example, Fitzgerald and Peterson 1983; Peterson 1987; Fitzgerald 1993); such leaves are patchily distributed on the host plant, and their exploitation depends on frequent movement or recruitment. The correlation of central-place foraging (and recruitment communication) with patchy resources is quite general among social insects, exhibited by members of such taxonomically widespread social groups as ants, bees, wasps, termites, and butterfly and moth larvae.

The difference in foraging, trail-marking, and trail perception between eastern and forest tent caterpillars, two of the best-studied social lepidopteran species, illustrates how shifts in foraging and communication directly relate to social evolution in this order. As discussed above, these closely related species mark trails before and after feeding. The prefeeding trails are termed 'exploratory trails' (Fitzgerald and Peterson 1983) and may be homologous to the 'personal trails' of trail-marking solitary species (see, for example, Weyh and Maschwitz 1982; Tsubaki and Kitching 1986). Both eastern and forest tent caterpillars deposit postfeeding trails as well. The crucial difference in the social complexity of these species lies in their use of post-feeding trails: the fixed base (tent) of eastern tent caterpillars provides a predictable communication center, setting up conditions for recruitment. By contrast, the postfeeding trails of forest tent caterpillars are as likely to lead to a new resting site as to the site of origin, undermining the use of these trails in recruitment communication.

One scenario for social evolution in Lepidoptera involves the context-elaboration of trail-marking: ancestrally solitary species may have used trails to keep track of food-sites. In groups, trail-marking may initially have played an identical 'personal' function, with group-cohesion simply stemming from mutual marker-recognition. Natural selection may have subsequently favored communication through changes in trail perception (e.g. preference for trails left by colony-mates) and behavior (e.g. repeated return to a fixed base). Over evolutionary

time, group-enhanced expression of defensive and resource-based signals may have further aided to integrate larvae into a cohesive society. The change from simple webbing to nests reflects elaboration from a purely protective use to a more or less permanent, stable retreat, which simultaneously serves as an information center for foraging-related communication.

Evolution of oviposition patterns

Non-ant-associated caterpillars. Fitzgerald and Costa (1986) and Fitzgerald and Peterson (1988) suggested a general evolutionary pathway for social evolution in the Lepidoptera whereby oviposition patterns facilitating larval encounters were selectively favored as a result of benefits accruing to larvae in chance groupings. In this scenario, the initial benefits of grouping were passive, perhaps involving such factors as predator dilution effects, amplified aposematic signals, and enhanced thermoregulation. This scenario implies that larval success has selectively favored batch oviposition in the Lepidoptera, although eggs may incipiently have been loosely clustered if not specifically batch-laid, as a result of resource limitation.

The inverse pathway was proposed by Hebert (1983), who suggested that the evolution of egg-clustering evolved in response to energetic considerations related to adult feeding habits, and that once egg-clustering evolved, group-favorable behavior and communication could be selected. The crux of Hebert's (1983) argument is the positive correlation of egg-clustering with reduced or absent adult mouthparts. However, this correlation largely occurs along taxonomic lines, and the two characters may be phylogenetically non-independent. In addition, there are many examples of batch oviposition by species capable of feeding as adults.

Courtney (1984) and Stamp (1980) studied batch versus single oviposition in butterflies, and reached different conclusions regarding the evolution of egg clustering. Courtney (1984) argued that the most important benefit to batch-layers is greater fecundity resulting from reduced adult search time, whereas Stamp (1980) argued for protection against desiccation and enhanced defense among other benefits, noting that most species ovipositing in clusters have at least some aposematic larval instars, and many have aposematic eggs. In our view, defensive and larval foraging benefits are probably of greatest importance to the evolution of batch oviposition. It is difficult to evaluate the energetic arguments, since experiments linking fecundity and lifetime reproductive success to oviposition

pattern are lacking. The occurrence of aposematic eggs argues for a defensive function, though here, too, experiments evaluating egg predation rates for aposematic vs. non-aposematic batched and singleton eggs are lacking.

Ant-associated caterpillars. Lycaenid gregariousness leads to enhancement of defensive alarm signals just as in non-ant-associated larvae, and it is possible that ant attendance in general permits foraging on high-quality food under thermally beneficial conditions by deterring predators. Because obligately myrmecophilous lycaenids are dependent upon both suitable host plants and attendant ants for survival, resource limitation may have played an important role in the evolution of aggregation behavior in these species. Females of certain myrmecophilous taxa have been shown to use ants and conspecific larvae as cues in oviposition (Atsatt 1981b; Pierce and Elgar 1985; Mathews 1993); in some cases, females deposit larger egg batches in the presence of ants (Atsatt 1981b). Larval vulnerability combined with patchy distribution on limited resources may thus have given rise to active aggregation, in a scenario similar to that proposed by Fitzgerald and Costa (1986). Kitching (1981) pointed out that egg-clustering in lycaenids is often observed in obligate myrmecophiles, especially in Australia, and argued that a causal relationship between the two is likely.

Larval aggregation in ant-tended lycaenids may have played a role in the evolution of species-specificity in lycaenid-ant interactions. Any ant species whose workers are sufficiently good tenders that larvae survive and develop will receive enhanced oviposition by butterflies, because ovipositing females of the aggregating lycaenids are attracted to conspecific larvae. If a particular ant is a consistently strong tender, then selection may favor recognition by ovipositing females of that ant species (by visual or olfactory cues), even in the absence of conspecific larvae (Elgar and Pierce 1988). This may account for the high degree of species-specificity in ant association observed among Australian lycaenids whose larvae aggregate. A curious feature of the Lycaenidae that deserves mention with respect to the evolution of aggregation behavior is that many of the species whose larvae are solitary are also cannibalistic; an important precondition to aggregation behavior in the Lycaenidae is absence of cannibalistic behavior.

Sociality in ant-associated Lepidoptera is, unlike non-ant-associated species, attributable to a particular defensive strategy: employing ant attendants for protection from predators and parasitoids. Because the ants

themselves are aggregated, and the lycaenids must rely upon the coincidence of ants and host plants, limitation of both defense and food availability has promoted sociality in these taxa. The rare occurrence of social species amongst the Poritiinae suggests that the trait may have been lost and regained several times.

This 'defensive route' of social evolution is undoubtedly shared by many social Lepidoptera that do not associate with ants, the defenses of which include refuge shelters and chemical and structural deterrents. The ant-associated species are remarkable in employing ants as their primary defense.

Scenarios for lepidopteran social evolution

Batch oviposition is necessary but not sufficient to ensure social interaction. In this sense whether ancestral Lepidoptera laid eggs singly or in batches may not be as important as the selective milieu in which the eggs were laid. Eggs may be deposited in batches owing to adult energetic limitations, resource patchiness, or for unknown historical reasons, but the grouped larvae may disperse, behave antagonistically (e.g. cannibalism) or remain spatially associated upon eclosion. The selective regime experienced by particular species may favor one or the other response; initially 'passive' associations may then experience selective pressures leading to disruption or elaboration of social behaviors. For example, once grouped, larvae are more conspicuous to predators, and increased predation may select for dispersal or socially mediated defenses such as protective webbing or leaf-tying, or coordinated anti-predator behavior.

In attempting to understand the evolution of sociality in Lepidoptera, as well as the transitions between social forms, it is important to note that resource use is intimately connected to foraging pattern. We suggest that nutritional and defensive needs jointly determine the particular pattern of sociality and foraging for a given species. Nomadic (N), patch-restricted (PR) and central-place (CP) foraging hold very different implications for both nutrition and defense: wandering larvae (N and CP foragers) can choose which leaves they eat, seeking profitable patches. Patch-restricted foragers have less choice, feeding on their shelter from within if it is constructed of leaves (e.g. *Hydria prunivorata*) or, if constructed of silk, expanding their shelter to engulf nearby leaves as food becomes exhausted (e.g. *Hyphantria cunea*). In defensive terms, leaf-tying PR foragers rely on their shelter and are often cryptically colored, whereas those inhabiting silken structures

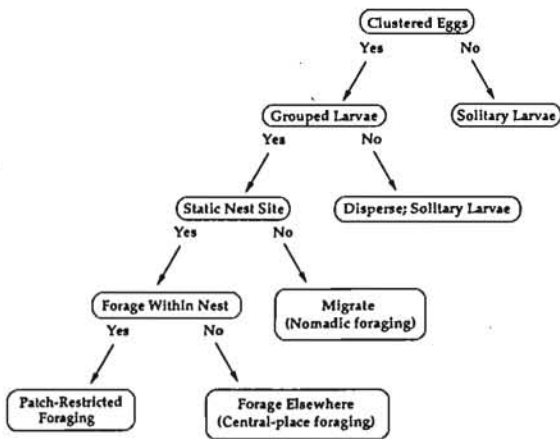


Figure 20-3. Heuristic summary of character states relevant to lepidopteran sociality, presented as a series of either/or options: eggs are deposited singly or in batches, larvae in batched clutches may disperse or group, grouped larvae nest in place or migrate, and larvae nesting in place forage *in situ* (expanding their patch as food is exhausted) or forage elsewhere (returning to the nest site following each foraging bout). This diagram is not intended as an explicit evolutionary scenario.

are often chemically and structurally defended, as N and CP foragers often are (although this needs testing for many groups).

The differences in foraging and defensive ecology of lepidopteran social classes lend themselves to an analysis of social evolution through phylogenetic hypothesis-testing. Fig. 20-3 is a heuristic chart of social states: eggs are deposited either singly or in batches; if in batches, larvae may either disperse or group; grouped larvae either remain in place or migrate; and larvae remaining in place either forage *in situ* (continually expanding the spatial bounds of the patch as food is exhausted) or forage elsewhere (returning to the nest site following each foraging bout). Note that this chart is not intended as an evolutionary scenario; rather, it summarizes the relevant states and their relationships, serving as a starting point for framing such scenarios. Following the framework presented in Fig. 20-3, we divide social-evolutionary hypotheses into two groups: (1) hypotheses concerning the evolution of gregariousness from solitary ancestors; and (2) hypotheses concerning the evolution of particular social states and transitions among these states once gregariousness is achieved. This division is made for convenience, as the two groups are actually part of a continuum.

Social evolution from solitary ancestors. The only way in which solitary caterpillars systematically differ from social caterpillars is in their solitariness; solitary species, like their social relatives, may be aposematic, sequester and/or regurgitate toxic chemicals, be spiny, hairy, diurnal, nocturnal, uni- or multivoltine, be host-specific or feed broadly. Crypsis is the most apparent lifestyle or character-state consistently differing in frequency between solitary and social caterpillar species, although this depends on how some social species, such as many leaf-tying PR foragers, are scored. Many PR species are certainly not aposematic, if not cryptic *per se*. None the less, clear examples of crypsis and mimicry occur throughout the solitary Lepidoptera and have no counterpart among social species (e.g. twig-mimicking geometrids, leaf-edge-mimicking notodontids, cryptic catocaline noctuids).

Morphological and behavioral defensive and foraging traits such as possession of spines or leaf-tying may be phylogenetically correlated (Table 20-1), suggesting that some ancestral traits may in some cases 'predispose' the evolution of certain social forms over others in a given clade. In other words, have particular solitary lifestyles given rise to particular social lifestyles, or vice versa? For example, are aposematic N foragers consistently derived from ancestrally cryptic or aposematic solitary foragers? Are PR foragers living within webbed leaves derived from solitary leaf-tiers? An important factor leading to different PR strategies may have been ancestral body size. Leaf-tying is observed in a diversity of solitary microlepidoptera, a behavioral trait that was likely to have been preserved and elaborated in a social context. Larger body sizes require active foraging because food is likely to become exhausted locally, leading to either N or CP social systems.

Societies marked by N or PR foraging may be more likely to have evolved from solitary ancestors before CP foraging societies, since the former possess fewer social characters (group cohesion and defense). The solitary to N transition requires simple batch oviposition and group cohesion cues. The transition to PR requires the development of one of two shelter-building classes: leaf structures or silk structures. These 'routes' of social evolution hold different implications for resource use and defense. The question of whether aposematic, chemically defended ancestors more likely to give rise to N foragers could be tested in groups exhibiting the full range of social interactions (solitary plus the three social systems) by mapping foraging or social pattern onto independently generated phylogenies.

Good candidate groups for such analyses, once reliable and largely complete lower-level phylogenies are known, are the Pyraloidea and the Pierinae (see Table 20-1).

Branching order of species typified by different states permits inference of the most likely transitions within a given clade, whether those transitions entail a gain or loss of social characters. The North American pamphiliid sawfly genus *Cephalcia*, for example, has ten species, five of which are gregarious web-spinners; the solitary species construct silken tubes for shelter and the gregarious species are PR foragers (Johnson & Lyon 1988). Knowledge of the phylogenetic branching order of these species could be used to determine whether sociality in this group has arisen from solitary ancestors or vice versa, or whether there has been a more complex pattern of gain and loss of social characters.

Transitions between lepidopteran social forms. Once sociality has arisen, all transitions are possible, though some may be more likely than others. A shift from N to either CP or PR foraging, for example, involves a gain of shelter-building behaviors, but CP foraging also requires the extra step of some form of chemical bookkeeping to relocate the shelter. Trail-marking pheromones are often subsequently used for recruitment in CP foragers. The same analysis described above for exploring the solitary to social transition could also be used to ask whether CP foraging arises from N or PR foraging systems, or vice versa, in particular clades. Groups with a range of social forms (e.g. Saturniidae or Thaumetopoeidae, with solitary as well as different social systems represented) hold special promise for this approach.

Focussing on the relationship between nutritional requirements and sociality, we predict that within-host diet breadth will vary with foraging pattern, and thus with social form. CP foragers such as tent caterpillars are often 'leaf specialists' that recruit preferentially to young, newly expanding foliage, whereas PR foragers tend to be leaf generalists in the sense that their feeding is confined to patches of foliage varying in age and nutritional quality. For a given group, host selection and growth experiments, or simple observation, can establish whether member species are leaf specialists or generalists; the co-occurrence of leaf specialization and CP foraging can then be statistically tested by mapping host-use states onto independently derived phylogenies.

Moreover, the evolutionary order of leaf specialization and CP foraging in a given lineage can be useful in inferring whether resource use was more important than defense in the evolution of CP foraging in that lineage,

because the food of leaf specialists is patchily distributed and more efficiently exploited through recruitment communication whereas leaf generalists are presented with an abundance of food. CP foraging in the absence of leaf specialization suggests a defensive role for the nest structure.

There are many other social-evolutionary scenarios that may be tested phylogenetically. For example, we expect shifts in foraging or social pattern to be accompanied by shifts in defense. In other words, are some defenses characteristic of certain foraging or social patterns, such as crypsis with leaf-tying, or aposematism with silk shelter-building or nomadic foraging? There are also patterns worthy of investigation *within* social classes; are there consistent ecological, behavioral or morphological differences between different PR strategies (i.e. leaves vs. silk)?

AVENUES FOR FURTHER INQUIRY

We identify two complementary areas requiring further research. First, comparative phylogenetic approaches will help to assess coincidence of social and ecological characters, as well as patterns of gain and loss of social characters. Several specific questions in need of attention were discussed in the previous section, ranging from the evolution of sociality from solitary ancestors to transitions among social forms and correlated changes in other life-history, defensive or behavioral traits. There are many groups marked by both solitary and social species, often with all three social systems (e.g. Lycaenidae, Nymphalidae, Pierinae, Lasiocampidae, Pyraloidea, Thaumetopoeidae, several saturniid subfamilies); (see Table 20-1). These groups can be used to address the relationship between solitary lifestyles and the social forms to which they are most likely to give rise, notably the importance of solitary defensive and host-use patterns in shaping these parameters in social species. The same taxa can simultaneously serve as focal points for investigations of evolutionary transitions among social forms. Shifts between N, PR and CP foraging are expected to exhibit clade-specific patterns, but may also entail predictable correlated shifts in defense and host use.

Second, a great deal of empirical research is necessary to fill in the gaps in our knowledge of larval ecology and behavior. The characters defining lepidopteran sociality must be better understood before we will be in a position to apply this knowledge to the slowly but steadily accumulating phylogenetic data. The most critical of these characters concern communication mechanisms and the

types of larval interactions mediated by communication. Significantly, the communication abilities of the vast majority of social Lepidoptera are altogether unknown, as is the ecological context of such communication (e.g. to what degree do narrow host (or *intra*host) requirements influence the evolution of recruitment communication by creating conditions of patchy resource distribution?). Finally, in terms of behavioral interactions mediated by communication, very little is known about genetic relatedness and kin discrimination abilities of colonymates. Such information is integral to evaluating the potential importance of inclusive fitness and kin selection in the maintenance and evolution of caterpillar societies; this avenue of research is virtually unexplored in the Lepidoptera compared with the wealth of such studies on eusocial Hymenoptera and other social groups.

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