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A natural history of conspecific aggregations in terrestrial arthropods, with emphasis on cycloalexy in leaf beetles (Coleoptera: Chrysomelidae)

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Summary

Aggregations of conspecifics are ubiquitous in the biological world. In arthropods, such aggregations are generated and regulated through complex interactions of chemical and mechanical as well as abiotic and biotic factors. Aggregations are often functionally associated with facilitation of defense, thermomodulation, feeding, and reproduction, amongst others. Although the iconic aggregations of locusts, fireflies, and monarch butterflies come to mind, many other groups of arthropods also aggregate. Cycloalexy is a form of circular or quasicircular aggregation found in many animals. In terrestrial arthropods, cycloalexy appears to be a form of defensive aggregation although we cannot rule out other functions, particularly thermomodulation. In insects, cycloalexic-associated behaviors may include coordinated movements, such as the adoption of seemingly threatening postures, regurgitation of presumably toxic compounds, as well as biting movements. These behaviors appear to be associated with attempts to repel objects perceived to be threatening, such as potential predators or parasitoids. Cycloalexy has been reported in some adult Hymenoptera as well as immature insects. Nymphs of the orders Hemiptera (including Homoptera) as well as larvae of the orders Neuroptera, Coleoptera, Diptera, Hymenoptera, and, in a less circular fashion, the Lepidoptera, cycloalex. There are remarkable convergences in body form, life habit, and tendencies to defend themselves in the social larval Coleoptera, particularly chrysomelids, social larval Lepidoptera, and social larval Hymenoptera. In immature insects, the cycloalexing organisms can be arranged with either heads or abdominal apices juxtaposed peripherally and other conspecifics may fill in the center of the array. In the Chrysomelidae, the systematic focus of this review, species in the genera *Lema*, *Lilioceris* (Criocerinae), *Agrosteomela*, *Chrysophtharta*, *Eugonycha*, *Gonioctena*, *Labidomera*, *Paropsis*, *Paropsisterna*, *Phratora*, *Phyllocharis*, *Plagiodera*, *Platyphora*, *Proseicela*, *Pterodunga* (Chrysomelinae), *Coelomera* (Galerucinae), and *Acromis*, *Aspidomorpha*, *Chelymorpha*, *Conchyloctenia*, *Ogdoecosta*, *Omaspides* and *Stolas* (Cassidinae) are reported to cycloalex although cycloalexy in other taxa remains to be discovered. Other types of aggregations in insects include stigmergy, or the induction of additional labor, and epialexy, or the positioning of conspecifics organisms over the midvein or an elongated aspect of a leaf.

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Keywords
Behavior, aggregations, cycloalexy, cephaloperipheral cycloalexy (CPC), abdominoperipheral cycloalexy (APC), stigmergy, epialexy, Arthropoda, Hexapoda, Insecta, Chrysomelidae

It takes time to be recognized (PJ, about cycloalexy)

> JASB would like to dedicate this paper to his Masters in Science Thesis Advisor at the University of Puerto Rico (Río Piedras), Dr. Manuel José Vélez-Miranda, who died on October 28, 2012. Dr. Vélez, as we used to address him, generously taught a cadre of Puerto Rican scientists to love nature, to have broad scientific interests as well as curiosity, and to be hard workers in research as well as in education. I shall miss him but his light shall never die. As he used to say "*¡Joven aún*!"
>
> Forever young!

Introduction

Conspecific organisms tend to aggregate or clump. In arthropods, the most speciose of all animal phyla, such aggregations are generated and regulated through complex interactions, including chemical and mechanical as well as abiotic and biotic factors. Aggregations have been associated with facilitation of defense, thermomodulation, feeding, and reproduction, amongst others. Although the iconic aggregations of locusts, fireflies, and monarch butterflies come to mind, many other groups of arthropods also aggregate, as we shall illustrate in this paper.

In addition to the mere abundance in numbers, Pierre-Paul Grassé (1946, 1952, 1959a; Grassé and Chauvin, 1944) noted that some gregarious behaviors are influenced by the presence of conspecifics. He referred to those behaviors as the "group effect" or "group reactions", phrases he used more or less synonymously. Grassé considered that the "group effect" or "group reactions" included the dynamic behaviors whose expressions depend on the distribution of the organisms in time and/or space. In other words, somehow and under the influence of conspecifics, aggregating organisms can behave differently than when they are by themselves. According to Grassé, the mechanistic bases for the group effect include chemical, sonic, tactile, and visual cues. The importance of the group context in physiological, morphological, and behavioral changes is dramatically illustrated by the transformation of one of the best known insects, the relatively solitary grasshoppers into swarming locusts (Orthoptera: Acrididae). These changes are collectively known as the "Phase Theory", an idea proposed by the Father of Acrididology, Sir Boris Petrovich Uvarov, and supported by subsequent research during the 1930s to 1950s (Waloff and Popov, 1990).

This review paper consists of two parts. The first part is an overview of aggregations, emphasizing conspecific or homospecific groups of arthropods. There, we discuss the hypothesized functional significance of such aggregations and provide numerous examples from the literature as well as our observations from years of field experience. The second part of the review emphasizes one group effect behavior, cycloalexy, a form of circular, often defensive, gregariousness. There, we pay special interest to insects and, in particular, to chrysomelids, (Coleoptera). Others aggregation patterns, such as stigmergy and epialexy are also briefly discussed. As if simultaneously looking at an entity from different perspectives, this review has three objectives: (1) to review aggregating behaviors, with supporting examples from various taxa, (2) to review taxa, with supporting examples of relevant aggregating behaviors and (3) to review in more detail aggregations in one insect family, the Chrysomelidae, as the authors have expertise in this interesting group of insects.

This is a rather lengthy paper, hence we consider that some guidance to the reader is in order. We recommend reading this paper as follows. First, after reading up to here, browse the figures and tables to get an idea of the topics discussed in this paper. Second, if the reader wishes to learn more, s/he is welcomed to proceed to the section or sections of interest. The selection of examples represents a skewed sample of cases of which the authors are aware and find interesting. Although attempting to integrate the description of behaviors with their genetic or ecological underpinnings is a laudable, this is not the goal of this paper. Finally, although we are aware of heterospecific aggregations, they are not the subject of this review.

An overview of aggregations. What counts as a conspecific aggregation?

According to Bell et al. (2007), there is no unique answer to the question, "what is a conspecific aggregation?" Typically a group of conspecifics organisms is considered an aggregation, if they are in close proximity, or clumped, as contrasted to a randomly or a uniformly distributed group of organisms. How many individuals have to be together to be considered as an aggregation? For what percentage of their lives do organisms have to be in proximity? Interestingly, the ability to form aggregations varies within the life history of a species (Danks, 1994). Are there mechanisms that bring the organisms together? Once organisms aggregate, do they behave differently than when they are alone, showing Grassé's, "group effect"? A useful discussion of behavioral homologies is provided by Wenzel (1992). The examples we have chosen generally include dozens of organisms, regardless of how they come in close contact, the functional significance of the aggregation, etc. The images, sometimes represent one or just a few organisms of the many aggregating ones.

Impact of aggregations on humans

Aggregations of terrestrial arthropods are ubiquitous (Vulinec, 1990) and they are often responsible for many misfortunes worldwide (Pedigo, 2002). Some examples of aggregating arthropods include herbivorous pests, arthropods of medical importance (Lehane, 2005; Mullen and Durden, 2002; Rocky Mountain Region, 2010; Service, 2004), and nuisance in urban settings (Robinson, 2005) or gardens (Cranshaw, 2004), among others. Extreme aggregations, namely outbreaks or explosive increases in the population of conspecifics, have had impacts in human endeavors (e.g., Lockwood, 1997a,b). The opposite of outbreaks, namely crashes leading to extinction, have also been addressed (Lockwood, 2010). The negative impacts of aggregations are of greater concern in view of climate change and an ever-shrinking world due to commerce. In the United States alone, insects and pathogens are a major economic cost, much higher than those caused by fires, hurricanes, tornados, ice, landslides, etc. (Dale et al., 2001).

Figure 1. Aggregations in nature: a matter of perspective. A. Author JASB collecting at the San Leandro Bay Regional Shoreline, located near the Oakland International Airport, Alameda County, CA, USA. B. The plant of interest, located to the right of the transect on panel A, is a species of gum plant, *Grindelia humilis* Hooker & Arnott (Asteraceae). The brown leafy blotches represent leaf mines of a species of *Monoxia*. As the bird flies, these plants are highly aggregated but from the perspective of the herbivorous arthropod living on these clumps of host plants, the distribution of leaves probably looks closer to uniform in space. C. Collecting at the Kesterson Wildlife Refuge, Gustine, Merced County, CA, USA in the mid 1980s. The organisms of interest, two congeneric species of *Monoxia* (Coleoptera: Chrysomelidae: Galerucinae), were commonly found from the late spring to the fall, each species in a different host plants:

Aggregations of beneficial terrestrial arthropods are also vital for humans. For instance, many insects serve as pollinators. Others produce useful goods, such as honey and silk (Waldbauer, 2009). Some terrestrial arthropods serve as instruments of biological control (Hoy and Herzog, 1985; McEwen et al., 2001) and are tellers of time of death (Catts and Haskell, 1990). Finally, the fact that many species tend to aggregate facilitates rearing them *en masse* (King and Leppla, 1984).

Scientific approaches to the study of aggregations

Aggregations are studied scientifically in multiple ways. These research styles, briefly discussed below, as well as the biological phenomena themselves been studied, continue to contribute to shape suitable research questions. The first four approaches, listed below, emphasize contemporary, or here and now issues, by asking proximate questions.

One of those proximate approaches is to concentrate on the where and when, the description of the spatiotemporal aggregation (e.g., clumped, uniform, or random) of the organisms of interest. Depending on the question being asked, aggregations are examined at various levels of resolution or distance, each potentially yielding different kinds of valuable information (Figure 1).

Organisms can also be aggregated in time. For example, some aggregations approach the interphase between something attracting conspecifics (e.g., coccinellids that hibernate in a relatively small area) and simply high population densities (e.g., mayflies, cicadas, chironomids) where millions of conspecifics emerge at the same time and rapidly disperse. This fact, however, does not deny the existence of the aggregations and points towards factors that may be responsible for them.

A second flavor of the study of aggregations is the asking of what for, that is, to focus on their functional significance, such as defense, feeding, thermomodulation, nest building, reproduction, parental care, and numerous others (Figure 2).

A third tactic to understand aggregations is through how questions. This tends to be called the "mechanistic approach" and it focuses on the triggers after which a behavior occurs. Different mechanistic hypotheses have been proposed to explain the formation of aggregations in arthropods. One of the most commonly proposed hypotheses involves the use of semiochemicals, for mating, recruitment, foraging, group cohesion, etc. (Chapman, 1998; Eisner and Kafatos, 1962; Peng et al., 1999; Peng and Weiss, 1992; Städler, 1986). Aggregations can be induced by external stimuli, such as in groups of bark beetles (Curculionidae or Scolytidae, in older literature) that respond to kairomones emitted by injured hosts trees (Gillette and Munson, 2009), or they can be longer lasting assemblages possibly also resulting from chemicals or other factors

Figure 1. (*Cont.*) one species in a species of *Atriplex* (grayish green right where JASB is collecting); the other in *Suaeda fruticosa* Forssk. ex J. F. Gmelin in L. (reddish and panel D, both Chenopodiaceae). E. A clump of *Artemisia douglasiana* Besser (Asteraceae) in Meyer's Grade Road, Sonoma County, northern California. Note abundant blotches of a fourth species of *Monoxia*. Over 7000 host plant selection experiments (Santiago-Blay, unpublished data) demonstrate a relatively high host-specificity of all tested species of *Monoxia*.

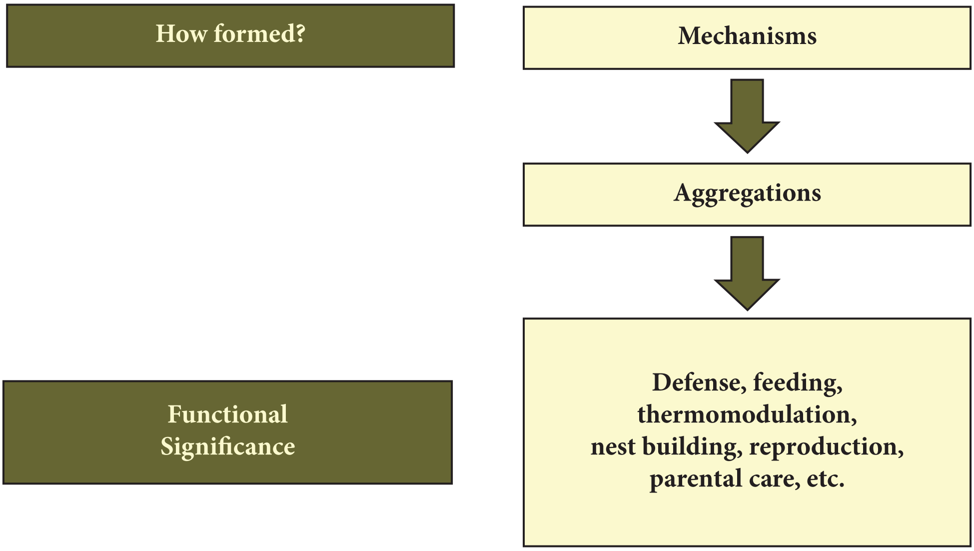

Figure 2. Two of the most commonly used approaches for the study of aggregations are by how they are formed (the mechanistic approach) and by functional significance of aggregations in the biological world. Other approaches for the study of aggregations are briefly discussed in the text. Separating survival from reproduction in the Functional Significance box has been omitted as both phenomena are intimately linked. Although many aggregating responses appear to be chemically (e.g., Shepherd et al., 2007) and/or mechanically mediated, in some cases there is limited experimental hypothesis-testing, particularly in cases of aggregations of relatively economically unimportant organisms.

(Figure 3). For instance, the widespread pest of some solanaceous crops, *Leptinotarsa decemlineata* Say, 1824 (Coleoptera: Chrysomelidae) is attracted to their hosts plants, such as potatoes, *Solanum tuberosum* L., tomatoes, *Solanum lycopersicum* L., and eggplants, *Solanum melongena* L. but *L. decemlineata* is rarely found in non-solanaceous plants even though there may be plenty in the immediate neighborhood for the beetles and larvae to choose from. A few examples of mechanistic explanations for aggregations follow.

A colossal body of literature exists on specific mechanisms purported to explain aggregations. Herein, we provide a few examples. Mechanical stimuli, such as body twitching and tapping have been observed during a pre-foraging phase and during processional movements of numerous insect larvae (Dajoz, 2000; Fletcher, 2007). Tapping may continue during foraging and also during the return of the larva to the group after some dispersion. In medically important triatomines (Hemiptera: Reduviidae), chemicals located in the feces appear to mediate their aggregations (Jurberg and Galvão, 2006). In aquatic insects, contact rates between stream-dwelling gyrinids (Coleoptera: Gyrinidae) or water striders (Hemiptera, *Gerris*, *Velia*, *Halobates*) increase with temperature (Vulinec and Kolmes, 1987). The weevil (Curculionidae), *Rhopalotria mollis* (Sharp, 1890), pollinator of *Zamia furfuracea* L.f. in Aiton

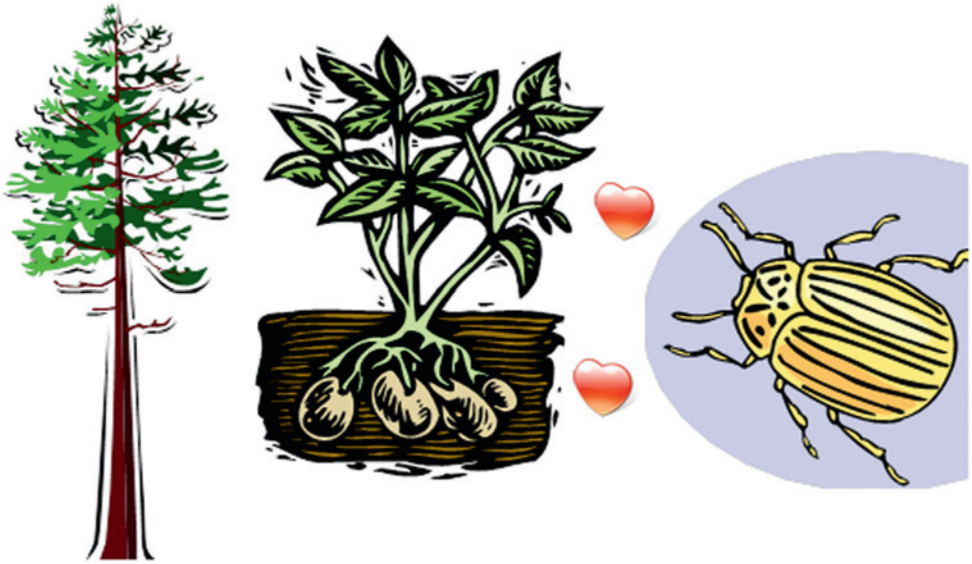

Figure 3. Feeding aggregations of Colorado potato beetles (and larvae, not shown), *Leptinotarsa decemlineata* Say (Chrysomelidae) are common in many parts of the world, including in author JASB's backyard in southern Pennsylvania, USA. Yet, hundreds of other plants species (represented by the tree to the left) are available within a few meters of the potato (*S. tuberosum*) plants and in those non-solanaceous plants, *L. decemlineata* is rarely found. The hearts represent the attraction of *L. decemlineata* to its host plant. Another example of this pattern was described by Santiago-Blay (1990) for *Monoxia* beetles (Chrysomelidae: Galerucinae) using host plant feeding experiments. Thousands of additional host plants feeding experiments using clip cages (Santiago-Blay and Blay-Sálomons, 2004) have been analyzed yielding similar results (Santiago-Blay, unpublished data). What are the chemical and mechanical bases for such attraction and feeding and not to the other easily available feeding possibilities? All images from Word's Clip Art.

(Figure 11G; Zamiaceae, note L.f. means *Linnaeus filius* or the son of Linnaeus, also known as Linnaeus the younger) could be attracted to 1,3-octadiene and linalool as male cones begin to open up (Pellmyr et al., 1991; Tang, 1993). The larvae of *Perga affinis* Kirby, 1882 (Hymenoptera) communicate with fellow larvae through tapping the substratum with the sclerotised abdominal apex and by twitching movements of the body. This helps maintaining cohesion of the group. Signaling by a solitary pergid larva produces a definite response in a group and tapping by larvae in a group makes a lone larva move faster (Fletcher, 2008). In social insects, such as termites, wasps, and bees, pheromones regulate numerous activities of the colony. Perhaps, aggregations enhance the collective environmental scanning as more sensors are added to the group (Vulinec and Miller, 1989; Watt and Chapman, 1998). The second and third approaches for the study of aggregations have contributed to the advancement of the field through experimental hypothesis testing.

A fourth style of proximate questions investigates the genetic bases of grouping, including the degree of genetic relatedness amongst the aggregating individuals, as in social animals, such as termites, wasps, ants and bees (Table 1). Longer term aggregations may result from two different causes: (1) the placement of the eggs or first instar

Table 1. Edward O. Wilson's (1979) classification of conspecific sociality into six categories. This table is generated by combining the presence or absence (two states) of three characteristics of sociality: overlapping generations, cooperative brood care, and reproductive castes. The authors are not aware, hence excluded from this table, whether two categories, which would complete the eight (2^3; — — + and + — +, respectively), exist. In those two categories, members of the reproductive castes would not be supported by other conspecifics taking care of the young or exhibit cooperative brood care. In contrast to solitary behavior, subsocial organisms take care of their own juveniles for a short time. Most cases of parental (usually maternal) care mentioned in this review fit the category of subsocial behavior. Communally behaving organisms share a common nest but do not exhibit cooperative brood care.

Degrees of sociality	Characteristics of sociality		
	Interacting overlapping generations	Cooperative brood care	Reproductive castes
Solitary, primitively subsocial, or communal	—	—	—
Intermediate subsocial I	+	—	—
Quasisocial	—	+	—
Intermediate subsocial II	+	+	—
Semisocial	—	+	+
Eusocial	+	+	+

larvae (L1) close to each other (cohort aggregations), or (2) from individuals belonging to multiple cohorts or generations that get together (affiliative aggregations, Bell et al., 2007). Importantly, however, complete genetic identity is not necessarily implied in cohort aggregations due to the likelihood of female using sperm from different males during fertilization (Wade, 1994) or from affiliative aggregations. In cockroaches, for example, Bell et al. (2007) reported greater genetic similarity among individuals of the German cockroach, *Blatella germanica* Linnaeus, 1767 sharing a building than between individuals living in different buildings.

Two major puzzles for evolutionary biology have been the genetic bases of behavior, including social behaviors as well as formation and maintenance of groups, in contrast to living as individuals. Group formation implies a suite of behaviors beyond those exhibited by the individual members. Evolution above the level of the individual implies that groups are more likely to be formed and maintained if such associations confer members of the group an average fitness, or reproductive advantage, greater than what they would each had if living as individuals, outside of the group of conspecifics. If the component members are genetically related, then, even if some individual members of the group are less likely to reproduce, thus less evolutionarily "fit", the overall fitness of this genetically-related group is enhanced and the behavior likely to be maintained. This preoccupation with the interphase of psychology and evolutionary biology, already present in mid to late 19th century Western European and American scholars (Santiago-Blay and Jolivet, in preparation), began getting theoretical underpinnings with the development of genetics later in the late 19th and early 20th century. The discovery that, like other traits, social behaviors can be inherited — else, how can behavioral changes be preserved over evolutionary time? — paved the way to

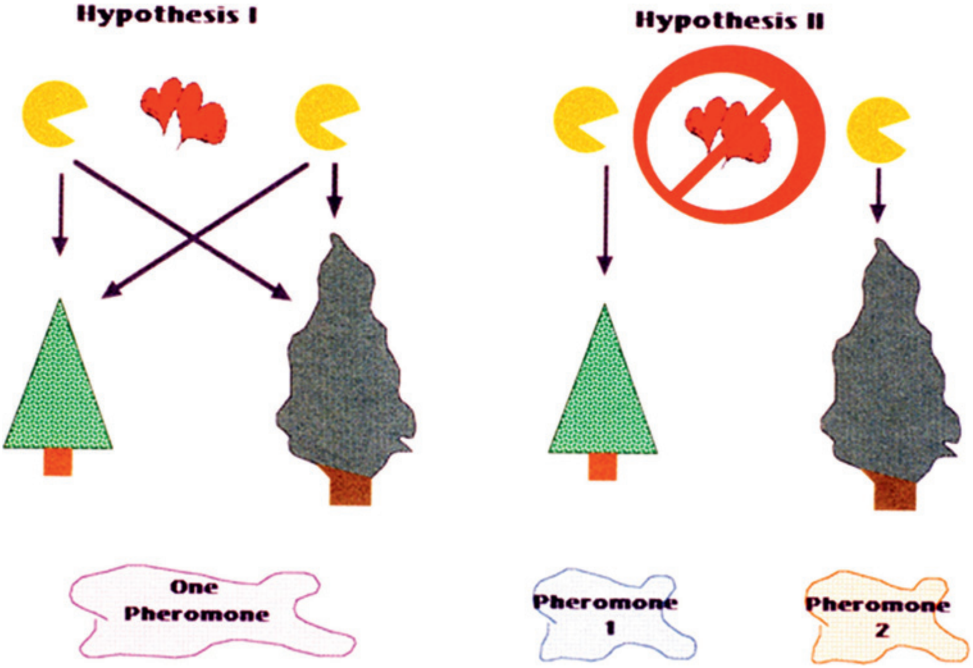

Figure 4. Chemical attraction to different host plants, amongst many other factors (Tilmon, 2008), has been suggested as a correlate of speciation, even if the host plants are sympatric. Data on chemical attractants can also be used for pest control. For an extensive discussion on speciation, see Coyne and Orr (2004). This figure was produced by C. Ayala and J. Sumortin, former undergraduate students doing research with author JASB in the mid-1990s at San Francisco State University. The image is herein reproduced with permission from both of them.

extraordinary research, beginning in the 20th century on social organisms (e.g., Billen, 1992; Bourke and Franks, 1995; Ross and Matthews, 1991; D.S. Wilson, 1980; E.O. Wilson, 1979). Thus, amongst others, numerous social behaviors, altruism, selfishness, etc. have been explained in standard evolutionary and genetic theory.

The fifth avenue to study aggregations draws from the explanations given for the four previous approaches and addresses more ultimate questions, the potential evolutionary significance of aggregations (Figures 4 and 5). What factors may have favored the evolutionary development of subsociality, namely, where a parent extends care for the young beyond the initial stage, such as egg or the first instar larva (L1)? According to E.O. Wilson (1975), four environmental factors may have helped select for parental investment beyond the egg: (1) a stable, structured habitat, (2) unusually stressful physical environment, (3) scarce, specialized resources, as those of many herbivorous, xylophagous, or coprophagous insects and (4) a high levels of predation.

Along with those factors, ever-shifting trade-offs, specific to every case, must also be considered. For instance, in cockroaches, aggregations of nymphs tend to accelerate development during this particularly vulnerable stage of development. Also, the effect of the group impacts numerous aspects of cockroach behavior, such as speed of flight reaction, circadian rhythm, and many others (Bell et al., 2007). On the other hand, the presence of a group also elicits a higher intensity of signals to potential predators, enhancing the probability of pathogen transmission and the likelihood of cannibalism, particularly if non-conspecific food items run low. Finally, when group living extends to parental care of the young, there are added costs associated with reduced mobility of the parent, including a drain of parents' food reserves, etc.

The strategy of grouping is not without trade-offs: the advantage larger groups may have (e.g., chemical or aposematic protection) needs to be balanced by the greater visibility or exposure that the larger group may have to natural enemies. There appears to be a trade-off in the larval behavior in a species of *Croesus* (Hymenoptera, Tenthredinidae), in which the larvae choose smaller host plants seemingly becoming less apparent.

Additional trade-offs include increased likelihood of pathogen spread, and increased risk of food shortage due to intense intraspecific food competition. In conifer-eating species of the Holarctic genus *Neodiprion* (Hymenoptera: Diprionidae), larvae feed communally and can reach outbreaks (Haack and Mattson, 1993; Larsson et al., 1993). When the larvae "feel threatened", they turn into "U"-shapes and regurgitate resinous compounds almost simultaneously, forming a "formidable regurgitating herd" (Costa, 2006). The exact chemical makeup of the compounds varies with the feeding site adding another variable to the mix. Furthermore, the effectiveness of the group effect defense varies with the type of predator: generally, it is relatively higher, although variable, against insect predators but relatively lower against vertebrate predators. Finally, there is also a trade-off between the potential defense function of the ingested resins and their effect on decreasing larval developmental rates.

Even if forming aggregations, whether they look like a ring or not, larvae are not invincible. For instance, adults of many Lebiidae (Carabidae), prey on cycloalexing chrysomelid larvae (Jolivet, personal observations). Although most chrysomelid larvae are unpalatable or toxic, some predatory stink bugs (Hemiptera: Pentatomidae) and ants appear to overcome those chemical defenses (Jolivet, personal observations). Generally, the cycloalexing larvae disperse to feed on foliage by night (or by day when resting at night), often moving in a procession, one behind the other, and recycloalex after foraging (Jolivet et al., 1990). In other words, cycloalexy is not necessarily associated with prolonged non-cycloalexing gregariousness.

A summary of some trade-offs involved in the development of aggregations is depicted on Figure 5.

Aggregations of conspecific organisms are common in life

Regardless of how we choose to study aggregations, groups of conspecifics are ubiquitous in life (Jolivet and Verma, 2005). One of the most spectacular aggregations in "lower" organisms is exhibited by cellular slime molds, *Dictyostelium discoideum* Raper, 1935 (Amoebozoa: Dictyosteliidae). Typically, *D. discoideum* cells are amoeboid and feed on bacteria. However, when food sources are scarce, *D. discoideum* cells aggregate and form a tiny slug-like structure that contains up to thousands of differentiating cells. This "slug" moves, stops, and undergoes one of the most spectacular transformations

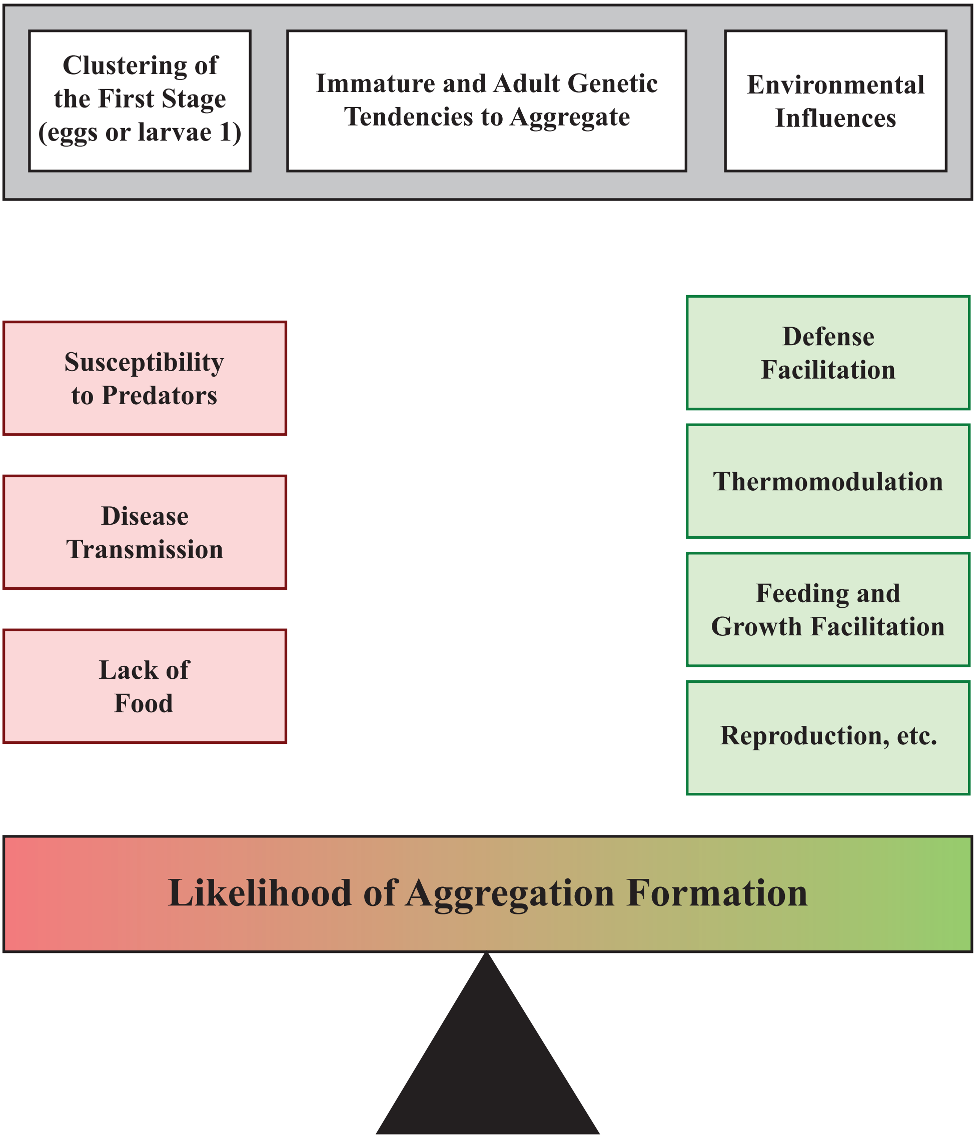

Figure 5. Broad causes of aggregations and some of their trade-offs, represented by a seesaw. Organisms can be aggregated because the mother arthropod leaves eggs or first stage immatures aggregated and/or genetic or environmental forces favor their becoming aggregated. Factors that tend to favor aggregation include (to the right, highlighted in green) defense facilitation, thermomodulation, feeding and growth facilitation, reproduction and others; those that are less likely to favor aggregations include (to the left, highlighted in pink) susceptibility of the group to predators, disease transmission, lack of food.

of the natural world, herein (Boner et al., 2010) videotaped. Once a *D. discoideum* "slug" stops, it forms a stalked, capitated structure whose apex has the spores-containing fruiting body. The cells that make the stalk die, or apoptose, yet the conspecific spores, located in the fruiting body, survive, and reinitiate the species life history (Anonymous, 2010).

On the other side of the animal phylogenetic tree, aggregations are also known to occur among vertebrates, such as muskoxen (*Ovibos moschatus* Blainville, 1818, Bovidae), birds (e.g., many species of Antarctic penguins), and many other vertebrates (Jolivet, 2004). Mammals living in confamilial groups under the siege of predators or strong winds, sometimes adopt a circular formation, known as cycloalexy, with the males generally on the periphery and the females and young generally inside. These behaviors are reminiscent of the westward bound American pioneers who, following the so-called "Manifest Destiny", sometimes placed the wagons in a circle (hence the idiom, "to circle the wagons") to defend themselves and their possessions against the attacking natives, whom they later systematically dispossessed.

Group territoriality is present in cooperative breeding birds, as with the Kagu (*Rhynochetos jubatus* J. Verreaux and Des Murs, 1860). This behavior seems to help protect these endangered animals (Theuerkauf et al., 2009). Cooperative breeding is also common in many other birds in the Australian region, as well as the Emperor Penguin, *Aptenodytes forsteri* Gray, 1844, in the Antarctic.

Arthropod aggregations in the fossil record (Figure 6)

Numerous examples of arthropod aggregations have been reported in the paleobiological literature (Boucot and Poinar, 2010). These cases suggest that many behavioral features we see today may have been in place for millions of years. Examples discussed therein include possible acridid aggregations, mass moth migrations, ant imago swarms, termite swarms, platypodid swarms, copulating insects, parental behavior and phoresy. An interesting example of possible eusociality in ants is discussed in Anderson (2006). On occasions, we have seen large aggregations of conspecific arthropods (e.g., ants or *Trigona* sp. stingless bees, Hymenoptera: Apidae) entombed in Dominican amber (approximately 15-20 Ma, Iturralde-Vinent, 2001; Iturralde-Vinent and MacPhee, 1996; see Vávra, 2006 for a proposed terminology on resiniferous exudates plant products). Interestingly, some species of extant *Trigona* sp. bees use exudates as structural materials for building their hives.

Could these ancient aggregations represent real cases of aggregation back millions of years ago? Caution is always granted to prevent falling into the potential intellectual traps of amber (Szwedo and Sontag, 2006) and other ancient matrices. In amber, one can look for the patterns of resin flow and evaluate whether the organisms where trapped within a relatively short time of each other. Another explanation, of course, is that the aggregated entombed individuals were actually not grouped but became terminally attracted to the sticky resin or to other objects stuck in the resin, such as prey items. Other examples of fossil aggregations in amber represented in Figure 6 include a termite (Isoptera) possible swarm, mites (Acari) phoresy on a platypodid (Coleoptera) beetle, a possible swarm of flies, copulating midges (Diptera), and mating moth flies (Diptera: Psychodidae).

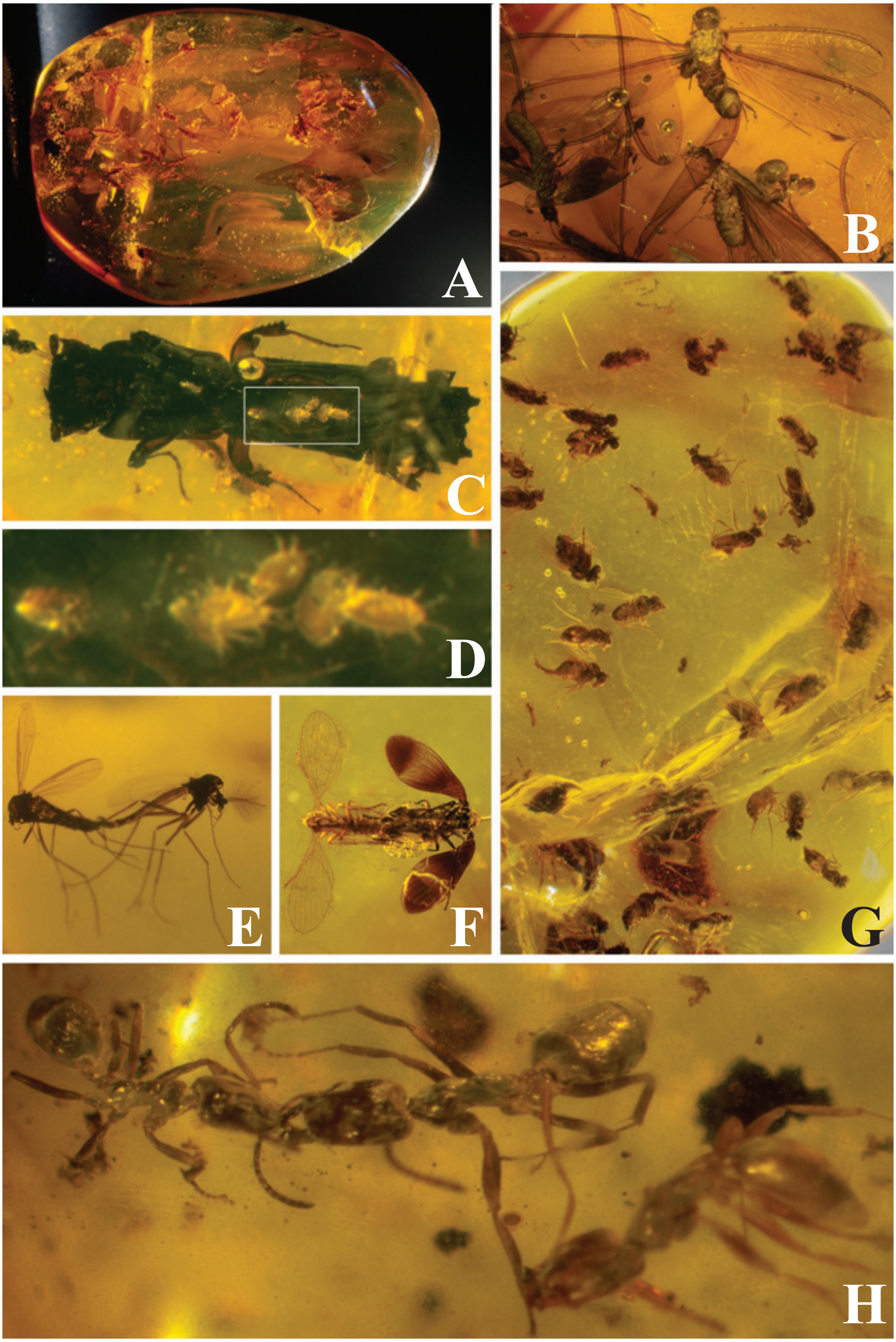

Figure 6. Aggregations of terrestrial arthropods in Dominican amber (approximately 15-20 Ma old). A–B. Termite possible swarm. C. Mites phoresy on a platypodid (Coleoptera), enlarged on panel D. E. Possible swarm of flies (Diptera). F. Copulating midges (Diptera: Chironomidae). G. Mating moth flies (Diptera: Psychodidae). H. Ants. All photographs taken by Patrick R. Craig (Monte Rio, CA, USA) and herein reproduced with his permission.

Even if the bodies of the fossilized arthropods are not available, sometimes one finds aggregated feeding marks of arthropod herbivores on host plants. However, in those instances we cannot easily ascertain whether one or more organisms caused the damage or, if more than one did it, whether they were aggregating when the damage was caused.

How do aggregations originate? Some explanations (Figures 7 and 8)

Many insects lay eggs in clutches. Other factors equal, this strategy saves the mother energy relative to what she would have to invest taking care of an otherwise dispersed

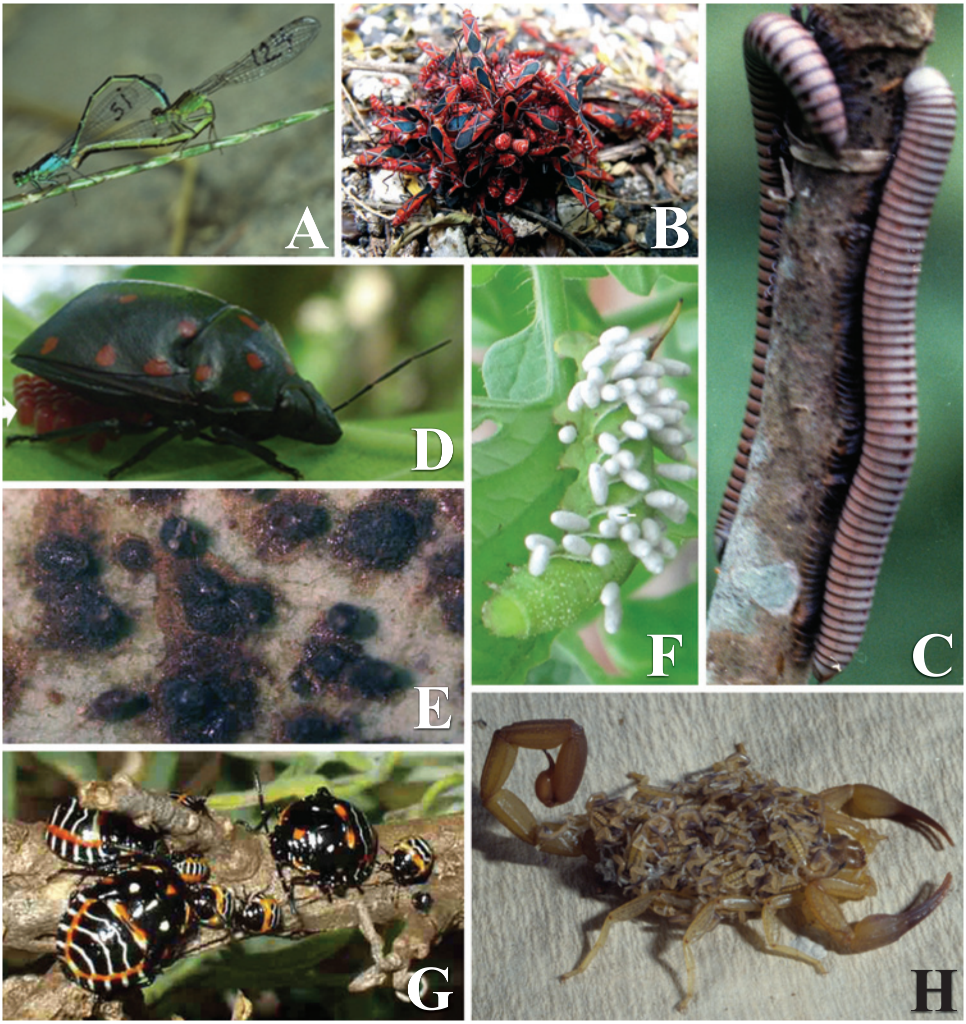

Figure 7. Arthropod aggregations related to courtship and early development. A. *Ischnura gemina* (Kennedy) (Odonata: Zygoptera) in the quasi-heart mating tandem, known as the wheel position, in Canyon, San Francisco, CA, USA. This species has a vulnerable conservation status. Note their sexually dimorphic coloration, male on the left, female on the right. In a humorous turn of events, Hafernik and

progeny. Right after hatching, the immatures tend to stay close together (Figures 7 and 8). Could it be that these immature individuals have not yet developed a sense of "self-identity", hence tactile and/or chemical signals of conspecifics are processed as part of the "self" via what Costa (2006) refers to as "self-referential pheromones"? The same hypothesis could also explain cases of larvipositing insects. For instance, when *Platyphora* sp. (Chrysomelidae) females larviposit on *Solanum* (Solanaceae) leaves, one by one, the larvae form a ring immediately following their deposition; mothers move away after laying the last larvae.

The idea of "self-referential pheromones" is reminiscent of a widely studied phenomenon in early human development. As the famous Swiss psychologist, Jean Piaget, argued, human infants at birth do not act as though they can discriminate self from non-self (Piaget, 1952; Vasta et al., 1999; Wozniak, pers. commun. to Santiago-Blay, March 2012). As Piaget put it, "the infant begins life in a state of profound egocentrism; that is, he literally cannot distinguish between himself and the outer world. The newborn and the young infant simply do not know what is specific to the self (one's own perceptions, actions, wishes and so on) and what exists apart from the self." Only slowly over the course of the first year do human infants develop the ability to distinguish sensory information generated by their own actions from that coming from the objects on which they act. This process eventually leads infants to acquire what Piaget referred to as "object permanence", or the recognition that objects continue to exist even when the child is not acting directly on them. The classic observation is that before approximately 8 months, if an object such as a toy is hidden from sight under a blanket, the infant will not search for the toy. After approximately 8 months, however, the infant will immediately remove the blanket to retrieve the toy.

Hypothesized functional significance of arthropod aggregations

Several explanations, such as defense, predator satiation, thermomodulation, enhanced work, or enhanced likelihood of reproduction, among others, have been offered as

Figure 7. (*Cont.*) Garrison (1986) report that marked male damselfly # 51 (a handwriting that could also be easily read as "SÍ", the affirmative "yes" in Spanish, native language of author JASB) had the highest frequency of mating, 15, in their study. Photographed and copyrighted by John Hafernik. C. *Anadenobolus arboreus* (DeSaussure, 1859) giant arboreal tree millipedes from Puerto Rico. Large numbers of these spirobolids and of *Rhinocricus parcus* Karsch, 1881 (Rhinocricidae) are seen in Puerto Rico during parts of the year (Santiago-Blay, unpublished observations). D. *Pachycoris klugii* Burmeister, 1835 (Hemiptera: Scutelleridae) female guarding her reddish eggs (arrow) laid on *Jatroph*a sp. (Euphorbiaceae) in a preserve wildlife reserve located in Domitila, Nicaragua. Photo courtesy of J.-M. Maes. E. *Manduca sexta* (Linnaeus, 1763) (Lepidoptera: Sphingidae) with eggs of an ectoparasitic wasp, possibly *Apanteles* sp. (Hymenoptera: Braconidae). Photograph by S. Shaffer, reproduced with permission. F. *Pseudacysta perseae* (Heidemann) (Hemiptera: Tingidae) eggs and early nymphs on avocado, *Persea americana* Mill (Lauraceae). Note aggregations of eggs, which are covered by a dark exudate produced by the mother lace bugs. Photograph by Irma Cabrera (Agricultural Experiment Station, Juana Díaz, Puerto Rico), herein reproduced with her permission. G. *Margantia histrionica* (Hemiptera: Pentatomidae) on bladderpod, *Peritoma arborea* Nuttall (Cleomaceae) at Madrona Marsh Preserve, Torrance, CA, USA. Photograph by Emile Fiesler (President, BioVeyda, Torrance, CA, USA). H. Adult female buthid scorpion, *Centruroides griseus* (C. L. Koch, 1845) (Arachnida: Scorpiones), an endemic Puerto Rico Region scorpion, with her 36 scorpionlings progeny.

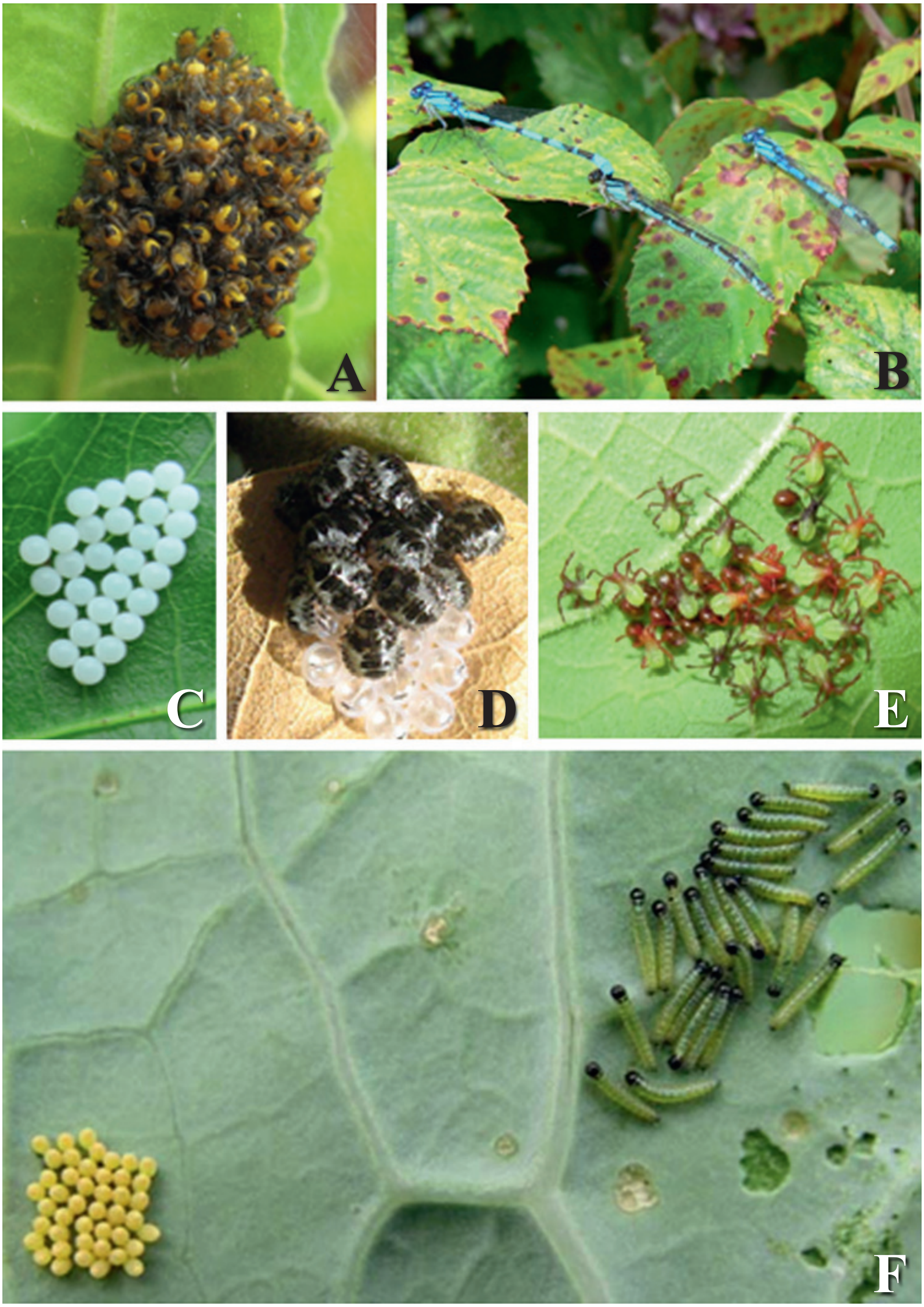

Figure 8. Arthropod aggregations related to courtship and early development. A. Recently-hatched, unidentified, spiderlings (Arachnida: Araneae). Photographed by Nic Franklin-Woolley near Tinsley, Sheffield, UK. © Copyright Nic Franklin-Woolley and licensed for reuse under Creative Commons Licence. Available online at http://www.geograph.org.uk/photo/1885539. Geograph image code, SK4090. Except for minor additions to enhance the scientific contents, the descriptions of all images

hypotheses for aggregations in arthropods. Yet, none of the hypotheses is a universal solution for all cases where conspecific arthropods group, as we discuss below.

Defense

Many arthropods, including soft-bodied larvae, constitute food for predators (Heinrich, 1994; Montllor and Bernays, 1993; Wesloh, 1994). Over evolutionary time, some lineages have evolved anti-predator chemical defenses (Bowers, 1994). Those chemicals originate through sequestration of materials from their host, whether plants or animals, or are manufactured from their building blocks, *de novo*. Could aggregations be related to the relative toxicity of the aggregants to potential attackers? In a number of cockroach aggregations, it seems that some individuals serve as sentinels and, upon a disturbance, emit chemical signals that alarm the rest of the congregation, presumably making it more difficult for predators to concentrate on a prey item (Bell et al., 2007). Conspecific groups of *Hylesia lineata* Druce, 1886 (Lepidoptera: Saturniidae) North American caterpillars, which also bear plenty of urticating setae, are typically gregarious and respond to sound or touch with sudden jerky movements (Fitzgerald and Pescador-Rubio, 2002, Pescador-Rubio, no date). Interestingly, chalcid wasps (Hymenoptera: Chalcididae), parasitoids of *Hylesia* caterpillars, also elicit the aggregation response, which has a protective, anti-predator function (Jolivet et al., 1990). Gregarious *Euproctis edwarsdi* (Newman, 1856) caterpillars (Lymantriidae) are endowed with dermatitis-causing setae. Likewise, gregarious *Phalena* sp. (Notodontidae) caterpillars defend themselves raising and curving their bodies into a “U”-shape, sometimes also regurgitate plant fluids.

Figure 8. (*Cont.*) herein reproduced from Creative Commons have been left as unchanged as possible. B. Unidentified damselflies (Odonata: Zygoptera) in premating tandem. Adult male, to the left, is holding the female’s thorax clasping her with his four terminal abdominal appendages. Fascinating, and at times hilariously anthropomorphic literature, reports the physical contacts between males and females as well as other males trying to disrupt courting pairs. Photographed by Brian Robert Marshall near to South Cerney, Gloucestershire, UK. © Copyright Brian Robert Marshall and licensed for reuse under Creative Commons Licence. Avaiable online at http://www.geograph.org.uk/photo/489790. Geograph image code, SU0696. C. Unidentified heteropteran eggs on a Rose of Sharon, *Hibiscus syriacus* L. (Malvaceae), leaf. Photograph by JASB. D. Newly hatched, unidentified, heteropteran nymphs (Hemiptera) with egg cases on the underside of a field maple, *Acer campestre* L. (Sapindaceae) leaf near to Saltwood, Kent, England, Great Britain. Photographed by Andy Potter “whilst waiting for the queue for a car parking ticket in the car park next to TR1435”. © Copyright Andy Potter and licensed for reuse under this Creative Commons Licence. Available online at http://s0.geograph.org.uk/geophotos/01/77/27/1772737_dc3f46bc.jpg Geograph image code, TR1436. E. Recently hatched unidentified heteropteran nymphs (Hemiptera) on a parsley, *Petroselinum crispum* (Mill.) Fuss (Apiaceae), leaf. Although the egg cases are no longer visible, the group still maintains a degree of cohesiveness that would soon end. Photograph by JASB. F. Eggs and just hatched larvae of *Pieris brassicae* (Linnaeus) (Lepidoptera: Pieridae), also known as the Cabbage White, feeding on *Crambe maritima* (Linnaeus) (Brassicaceae), the Sea Kale. Note larvae forming a tight array. Photographed by Andy Potter in a shingle environment next to the Millennium Seed Bank building at Wakehurst Place near to Ardingly, West Sussex, UK. © Copyright Andy Potter and licensed for reuse under this Creative Commons License. Available online at http://www.geograph.org.uk/photo/1009228. Geograph image code, TQ3331.

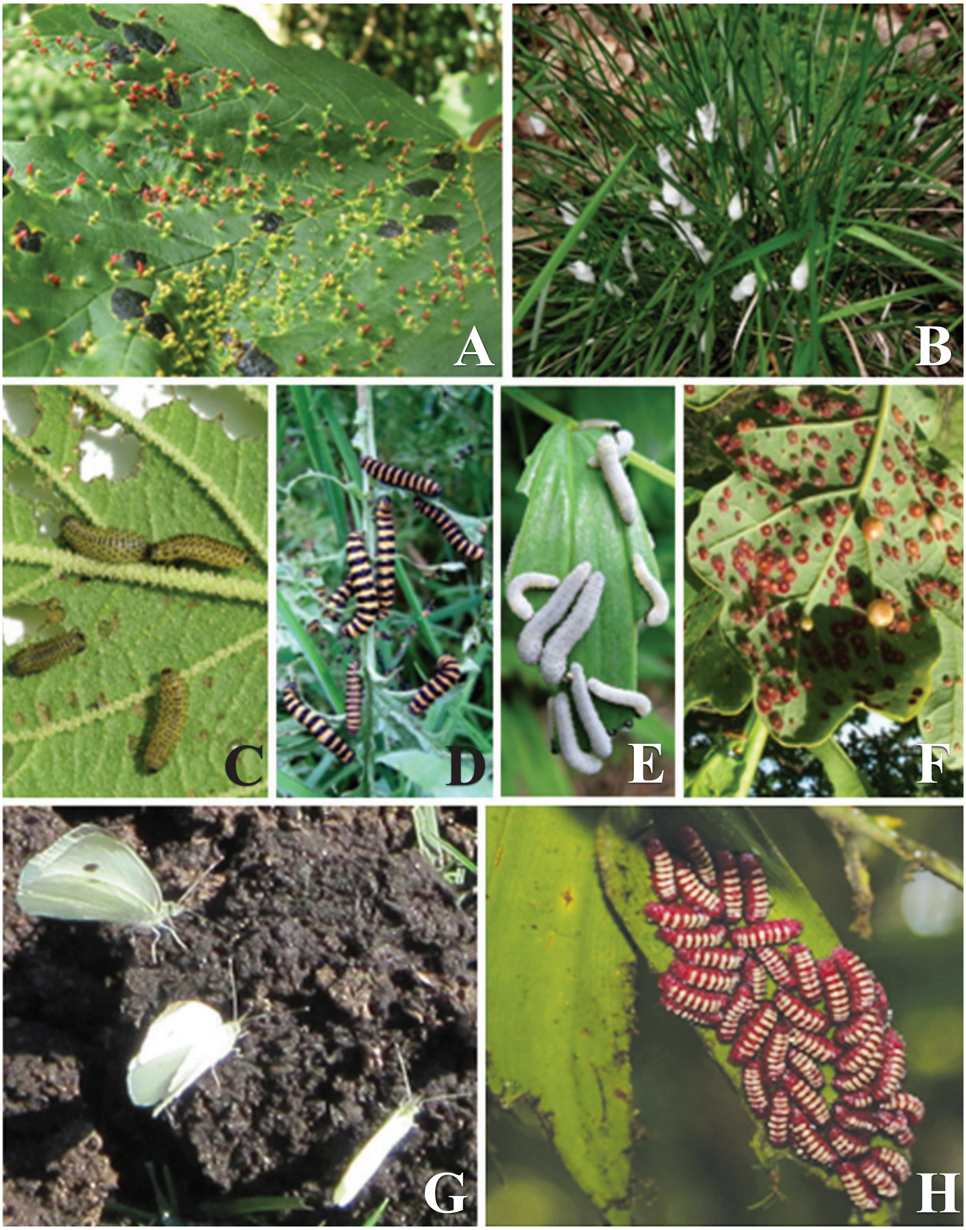

Figure 9. Arthropod aggregations related to feeding. A. Sycamore (*Acer pseudoplatanus* L, Sapindaceae) leaf with mite galls created by created by *Aceria macrorhynchus* (Nalepa, 1889) and tar spot fungus, *Rhytisma acerinum* Schwein, 1832. Photographed by Lairich Rig near Renton, West Dunbartonshire, UK. © Copyright Lairich Rig and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/919089. Geograph image code, NS3976. B. Spittlebugs (Hemiptera: Cercopidae) feeding and producing their characteristic foam that presumably keeps the nymphs in a relatively protected and thermally stable environment. Photographed by Jonathan Kingston near to Brown Edge, Staffordshire, UK. © Copyright Jonathan Kingston and licensed for reuse under Creative Commons

Does protection in a life history stage extends to a subsequent stage? In *Mnesampela privata* (Guenée, 1857) (Geometridae) the answer is no. In this taxon, caterpillars regurgitate phenolic compounds from their eucalypt host plants — perhaps kinos (Lambert et al., 2007) — and these constitute a form of chemical protection for the larvae. However, their subterranean pupae fall prey to Australian ravens (*Corvus coronoides* Vigors and Horsfield, 1827, Corvidae) and other birds.

Does protection against a guild, such as specialized parasitoids, extend to another guild, such as generalist parasitoids? In the species *Pryeria sinica* Moore, 1877 (Limacodidae), the answer is no. These gregarious and toxic adult North American moths deposit their eggs in clusters. Although only one specialized larval parasitoid has been reported, hence one would wrongly conclude that gregariousness "works", *P. sinica* larvae have its share of generalist predators (Costa, 2006).

Most importantly, is the presence of a defense action confer 100% protection against enemies? Costa (2006) describes the case of gregarious, mechanically defended egg clutches of the Australian Bag-shelter moth, currently known as *Ochrogaster lunifer* Herrich-Schäeffer, 1855 (Thaumetopoeidae). Experimental manipulation showed that the spiny scales deter egg predators and protect them against the rain. Once the caterpillars hatch, they benefit from shared defense, thermomodulation, and gregarious feeding (Figures 9-11).

Excellent examples of behavioral ecology of insect trench-cutting to overcome plant toxins have been reported by Becerra et al. (2009), Dussourd (2009), Helmus and Dussord (2005), and Oppel et al. (2009), among others. Sadly, sometimes chemical defenses are loosely referred to by the almost chemically meaningless term, "latex". An analogous situation is present in many plants which could be protected by all sorts of organic chemicals (see Lambert et al. (2008, 2010), for a brief review of plant exudates,

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Figure 9. (*Cont.*) License. Available online at http://s0.geograph.org.uk/geophotos/02/45/57/2455715_5f1d3c83.jpg. Geograph image code, SJ8955. C. *Pyrrhalta viburni* (Paykull, 1799) (Coleoptera: Chrysomelidae) larvae on *Viburnum lantana* L. (Adoxaceae). Photographed by M. J. Richardson near Morningside, Edinburgh, UK. © Copyright M. J. Richardson and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/1363569. Geograph image code, NT2470. D. Larvae of the Cinnabar moth, *Tyria jacobaeae* (Linnaeus, 1758) (Lepidoptera: Arctiidae) feeding on ragwort, *Jacobaea vulgaris* Gaertn. (Asteraceae) near Llanychaer, Pembrokeshire/Sir Benfro, UK. © Copyright "ceridwen" and licensed for reuse under Creative Commons License. Available online at http://s0.geograph.org.uk/geophotos/01/98/98/1989860_a52b8980.jpg. Geograph image code, SM9836. E. Larvae of the Solomon's Seal, *Polygonatum* (Asparagaceae), sawfly larvae, Phymatocera aterrima (Klug, 1816) (Hymenoptera: Tenthredinidae). Photographed by Walter Baxter near Galashiels, Scottish Borders, UK. © Copyright Walter Baxter and licensed for reuse under Creative Commons License. Available online at http://s0.geograph.org.uk/geophotos/01/38/73/1387379_9c9935b0.jpg. Geograph image code, NT4936. F. Three types of galls on oak, *Quercus* sp. (Fagaceae). The larger pale brown, spherical objects are Pea galls caused by Cynips divisa Hartig, 1840 (Hymenoptera: Cynipidae); four other types of galls are shown in this image. Photographed by Lairich Rig near Renton, West Dunbartonshire, UK. © Copyright Lairich Rig and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/1449701. Geograph image code, NS3976.

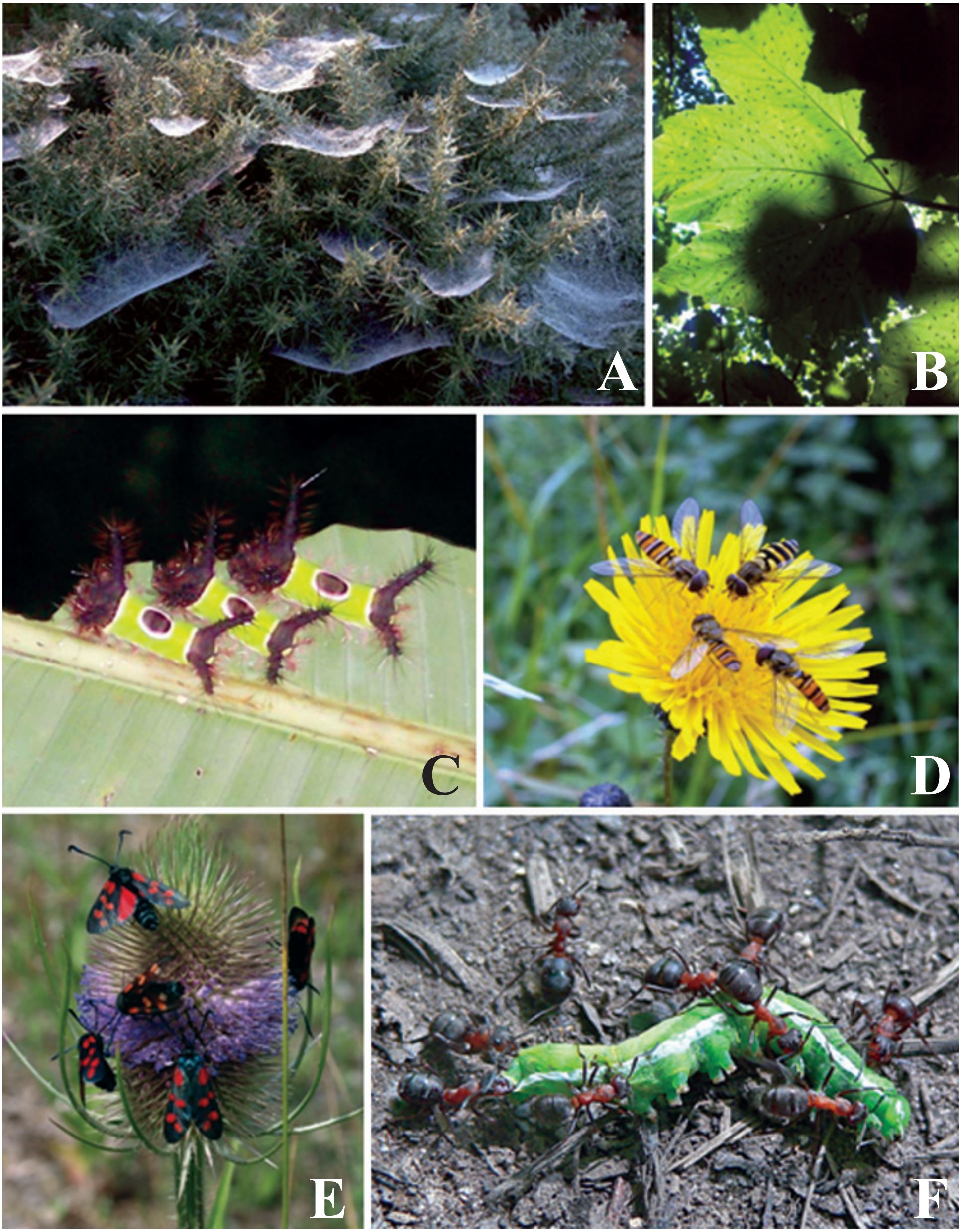

Figure 10. Aggregations of arthropods related to feeding. A. Spiders' webs on gorse, *Ulex* (Fabaceae). Photographed by John Comloquoy. Three kilometers from Maryburgh, Highlands, UK. © Copyright John Comloquoy and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/261408. Geograph image code, NH5156. B. Aphids on a Sycamore (*Acer pseudoplatanus* L, Sapindaceae) leaf. Photographed by David Lally near Bilborough, Nottingham, UK. © Copyright David Lally and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/1360829. Geograph image code, SK5240. C. Limacodid larvae, also known as saddleback or slug caterpillars, form feeding fronts, as shown in this photo of *Acharia hyperoche* (Dognin, 1914) taken by Roberto Cambra T. (Museo de Invertebrados G. B. Fairchild, Universidad de

and recent examples of exudates in other plant groups, such as conifers (Lambert et al., 2007b), Pinaceae (Lambert et al., 2007a), Fabaceae (Lambert et al., 2009), Myrtaceae (Lambert et al., 2007c) and rosids), yet plants are not immune from herbivore attack. Animals also have a share of maladies, regardless of their defenses.

In sum, toxic as well as non-toxic terrestrial arthropods aggregate. In this and other putative functions of aggregations, it is difficult to make broad generalizations because the biology and trade-offs of most aggregants have not been extensively documented. Examples of the difficulties of such studies are discussed in numerous works (e.g., Freeman and Herron, 1998; Rose and Lauder, 1996; Stearns and Hoekstra, 2000; Tollrian and Harvell, 1999).

Predator satiation

Could aggregations be an indirect defense mechanism of the group where some individuals of the group die, satiating predators for a short time, while the rest of the group moves forward, advancing to maturity? For instance, in toxic Pine processionary caterpillars, *Thaumetopoea pityocampa* (Denis and Schiffermüller, 1875) (Lepidoptera) as well as in caterpillars of the Hickory Tussock Moth or Hickory Halisidota, *Lophocampa caryae* Harris, 1841 (Arctiidae), larger groups of caterpillars have a reduced per capita predation than smaller groups (Costa, 2006). However, in some Brazilian toxic ithomiines (Lepidoptera), the butterflies are heavily preyed upon suggesting the predation satiation hypothesis may not be applicable in all cases (Pinheiro et al., 2008). Also, the aposematically-colored masses of monarch butterflies, *Danaus plexippus* (Linnaeus, 1758) (Lepidoptera: Nymphalidae) (Cech and Tudor, 2005; Smart, 1975, pp. 46-47), have been observed under attack by insectivorous birds (Fink et al., 1983) and ants. A magnificent video on Monarch butterfly, bee, and other aggregations in their full glory can be seen in Schwartzberg (2011). Climate change and deforestation put further pressure on populations of congregating monarchs in their overwintering ranges at higher elevations of central México.

Figure 10. (*Cont.*) Panamá, Panamá City, Panamá), taken in the Panama Canal Area, Cacao Plantation Road, October 3, 2004. "This species is common on palms, including species of *Socratea*. As far as I know they do not cycloalex. The same is true of a number of other Lepidoptera from at least six families." (Annette Aiello, Smithsonian Tropical Research Institute, personal communication to author PJ, March 2012). D. Hoverflies (Diptera: Syrphidae) on flower. Photographed by John Fielding near near to Upper Midhope, Sheffield, UK. © Copyright John Fielding and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/2002400. Geograph image code, SK2199. E. Burnet moths (Lepideoptera: Zygaenidae) on Teasel (*Dipsacus fullonum* L., Dipsacaceae). Photographed by Derek Harper Barton, Torbay, UK. © Copyright Derek Harper and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/1402279. Geograph image code, SX9066. F. Wood Ants, *Formica rufa* Linnaeus, 1761 (Hymenoptera: Formicidae) feeding on a lepidopteran larva. Photographed by Paul Dickson near Dunsford, Devon, UK. © Copyright Paul Dickson and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/1381268. Geograph image code, SX8088.

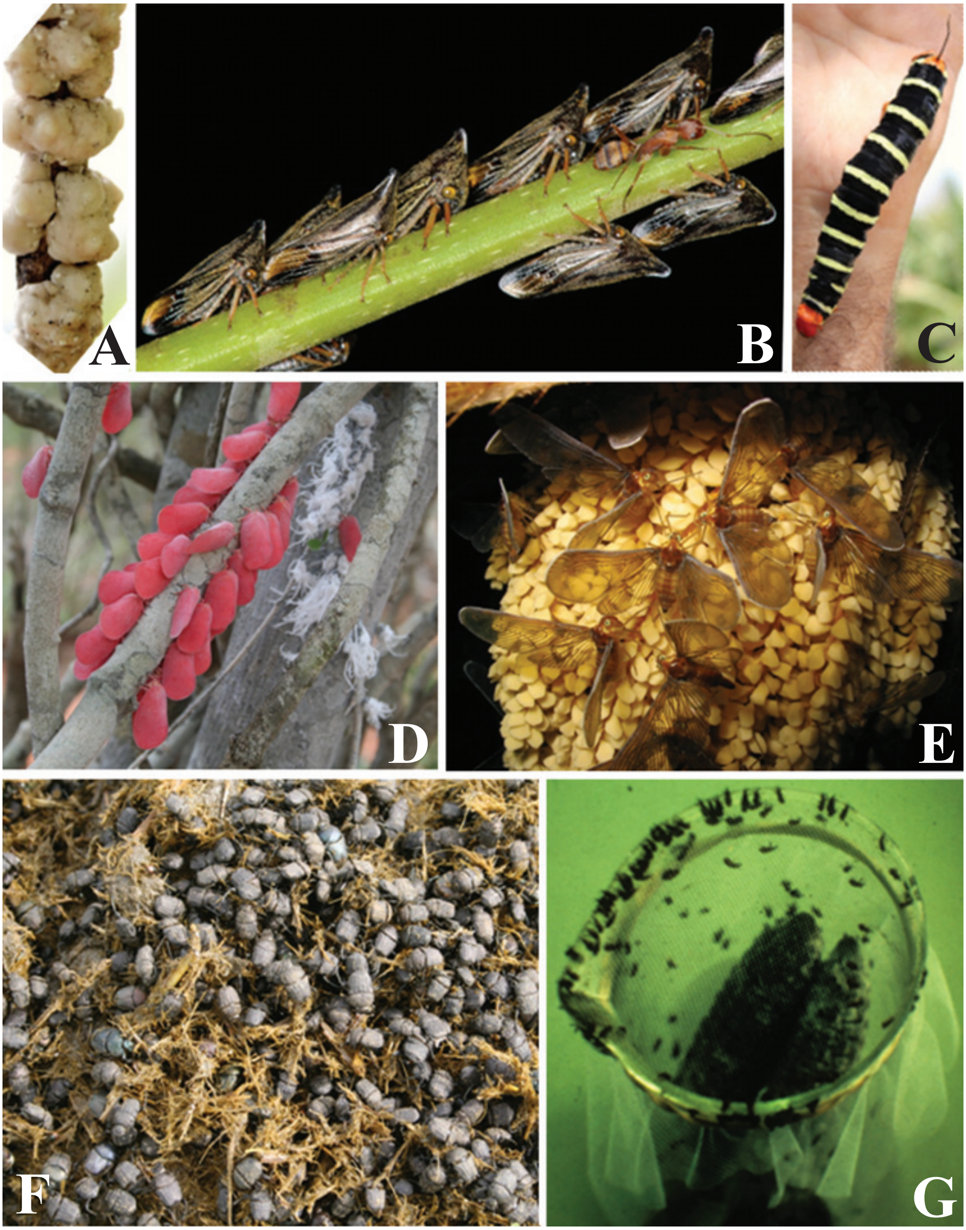

Figure 11. Aggregations of arthropods related to feeding. A. *Ceroplastes* sp. (Hemiptera: Coccidea). B. *Potnia* sp. (Hemiptera: Membracidae). Identification courtesy of T. James Lewis INBio (Instituto Nacional de Biodiversidad, Costa Rica. Photo courtesy of D. N. Proud. C. *Pseudosphinx tetrio* L. (Lepidoptera: Sphingidae). These Neotropical species is one of the most easily recognizable pests of *Plumeria* sp. (Apocynaceae) and form large defoliating aggregations. D. Malagasi flatbug, *Phromnia rosea*. Nymphs are white and bear long filaments. Photograph by Alberto Ballerio (Brescia, Italy). E. *Derbe* sp. (Hemiptera: Derbidae) on a palm inflorescence. Identification by L. O'Brien (California Academy of Sciences, San Francisco, CA, USA). Photographed by Samraat Pawar in 2003 at the Osa Peninsula, Sirena National Park, Costa Rica, herein reproduced with permission. F. Heterospecific

Feeding patterns and feeding facilitation

Where there is suitable food, there are usually those who want to partake. Some of those associations last only for the duration of the food, as in cases of butterfly aggregations in humid places (Smart, 1975), arthropods associated with carcasses, and many others. In cockroaches, aggregations serve to signal conspecifics of the presence of food (Bell et al., 2007).

Communally living organisms (Figure 12) display different feeding patterns. Costa (2006) describes three distinct feeding patterns in gregarious insects: (1) patch-feeding and retreat (to the commune) as in *Eriogaster lanestris* (Linnaeus, 1758), (2) nomadic, group feeding, with communal living, as in some species of *Arsenura* as well as *Eriogaster catax* (Linnaeus, 1758) and (3) foraging individually with a more permanent communal central living place, as in the Eastern USA tent caterpillar, *Malacosoma americanum* (Fabricius, 1793). Interestingly, some of these feedings styles may switch during development and within closely related taxa, even in the same individual host plant!

Regardless of the feeding pattern, in some social insects, being part of a group allows their larval members to "do better" under certain circumstances. This is the case of *Doratifera casta* Scott, 1904 (Limacodidae) caterpillars, which, when they aggregate in larger numbers do better in low-quality host-plants as compared to high-quality host plants (Costa, 2006). Not surprisingly, the thermal benefits that aggregations typically have, which the groups typically have, do not hold for tropical species. In *Plagiodera versicolora* (Laicharting, 1781) chrysomelines, as well as in sawflies, cycloalexy appears to facilitate feeding (Costa, 2006).

Thermomodulation or other environmental buffering (Figure 13)

Being poikilothermic organisms, arthropods do not have the same spectrum of physiological mechanisms to keep their internal body temperature within a given range that homoeothermic animals have. Nevertheless, a wide array of behavioral mechanisms has endowed arthropods with remarkable capabilities that approximate the feats of the so-called "warm bodied" animals. In addition to the benefits of aggregations, it appears that cycloalexy confers aggregants some other benefits. In *B. germanica* and *Gromphadorhina portentosa* (Schaum, 1853) Madagascar hissing cockroaches, aggregations reduce water loss (Bell et al., 2007).

Costa (2006) describes the fascinating case of *Hemileuca lucina* Henry Edwards, 1887 (Lepidoptera: Saturniidae) groups in northeastern United States. Specifically, in lukewarm temperatures, aggregating *H. lucina* caterpillars reach body temperatures of approximately 5°C warmer than single conspecific larvae and grow faster. Similar observations have been made for the pine processionary larvae, *T. pityocampa* (Costa,

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Figure 11. (*Cont.*) aggregation of feeding Scarabaeinae (Coleoptera: Scarabaeidae). Photograph by Alberto Ballerio (Brescia, Italy). G. *Rhopalotria mollis* (Sharp, 1890) (Coleoptera: Curculionidae) on *Zamia furfuracea* L.f. in Aiton (Zamiaceae) attracted to the cycad cones.

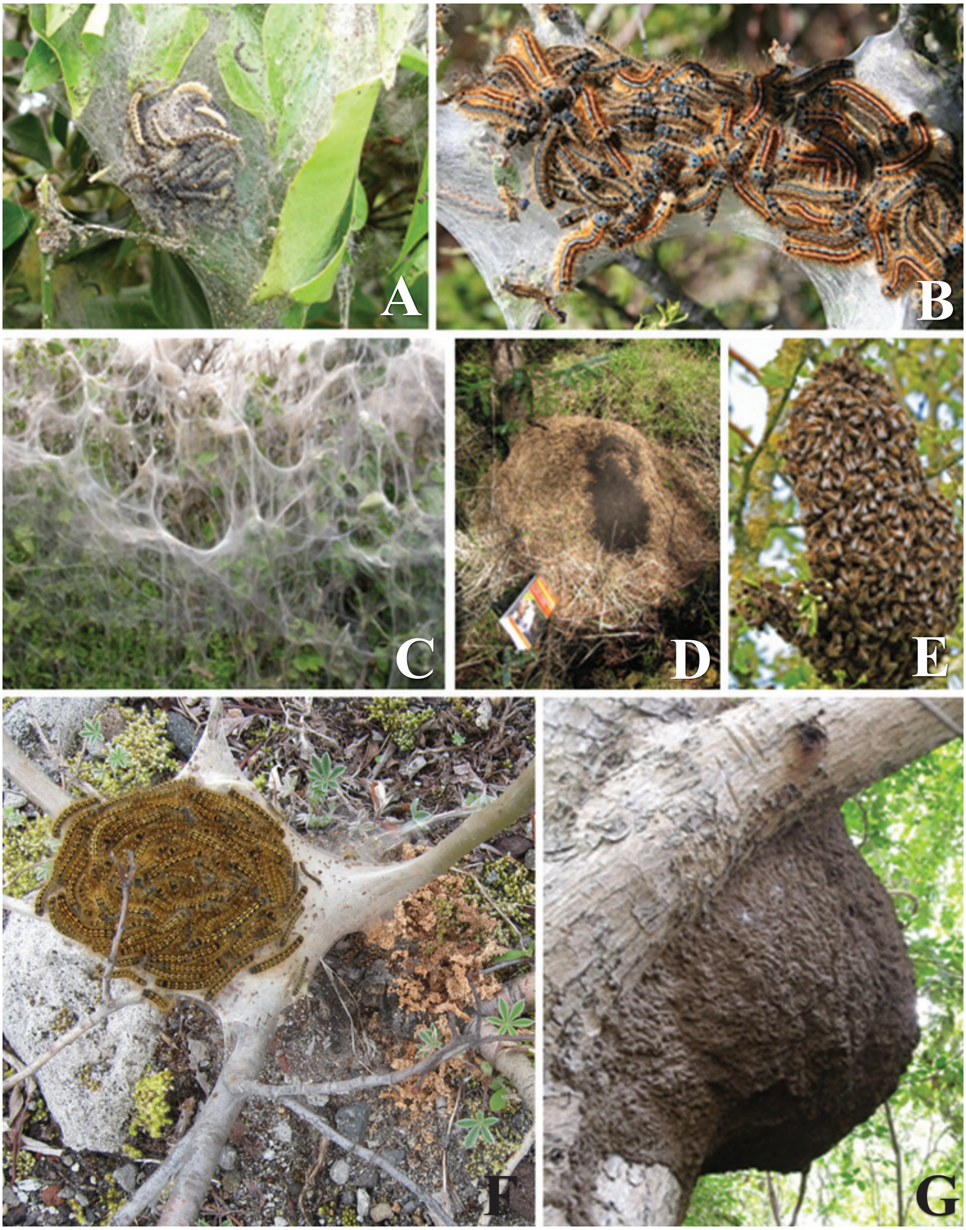

Figure 12. Arthropod aggregations related to communal living. A. Tent caterpillar webs, possibly *Yponomeuta cagnagella* (Hübner, 1813) (Lepidoptera: Yponomeutidae). Photographed by Penny Mayes near Milstead, Kent, UK. © Copyright Penny Mayes and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/178956. Geograph image code, TQ8959. B. Tent caterpillars, possibly *Malacosoma* sp. (Lepidoptera: Lasiocampidae). Photographed by Anne Burgess near Llanfairynghornwy, Isle of Anglesey/Sir Ynys Mon, UK. © Copyright Anne Burgess and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/1900793. Geograph image code, SH3293. C. A much greater aggregation of *Y. cagnagella* Photographed by Penny Mayes near Milstead, Kent, UK. © Copyright Penny Mayes and

2006). Interestingly, the early larval instars of *H. lucina* begin feeding on nitrogen-rich younger leaves of their *Spiraea* sp. (Rosaceae) host plants, further emphasizing that not every leaf in an individual plant is equally attractive to the herbivores. In *H. lucina* and in other saturniids, such as *Imbrasia belina* (Westwood, 1849), early instars, which have a smaller surface-to-area ratio for heat exchange relative to the larger instars, tend to aggregate more than later stages, which tend to be more solitary. These observations seem to support the thermomodulation hypothesis.

Many of the most inferred ancestral families of Hymenoptera, collectively placed in the Symphyta, also thermomodulate (Costa, 2006). For instance, at higher ambient temperatures, the larvae of many species of *Perga* larvae raise their abdomens allowing for behavioral thermomodulation through their exoskeleton. Also, the anal segment of these larvae can secrete a fluid which they sponge on co-aggregating conspecifics resulting in evaporative cooling, just as in sweating humans. Another benefit for *Perga affinis* aggregating larvae, is their higher body temperature, being higher in larger groups than in smaller ones. Larvae with higher body temperatures grow faster, and gain more in body weight. Heavier larvae were found to be more successfully pupating than lighter ones (Fletcher, 2009). Adult mayflies, flies, and many other species of insects can also thermomodulate.

Reproduction and care of the young

Most land arthropods reproduce sexually and this is usually accomplished through copula or intromission of a male-produced structure (e.g., spermatophore) into the female genital tract. Obviously, aggregations enhance the likelihood of finding mates but it is by no means a guarantee that the likelihood of mating for each individual male will be increased because of aggregating. In elegantly simple experiments, summarized by Bailey (1991), sound-producing male *Anurogryllus arboreus* T. J. Walker, 1973 (Orthoptera; Gryllidae) shorttailed crickets, where released in two possible forest scenarios: as a group, potentially forming a "chorus", or as individuals or "soloists (see also Brown and Wayne, 1997). Then, individual females where released in consecutive

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Figure 12. (*Cont.*) licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/178948. Geograph image code, TQ8959. D. Large ant (Hymenoptera: Formicidae) hill. Photographed by Dave Croker. Five kilometers from Bronaber, Gwynedd, UK. © Copyright Dave Croker and licensed for reuse under Creative Commons License. Available online at http://www.geograph.org.uk/photo/1237731. Geograph image code, SH6729. E. Photographed by Nic Franklin-Woolley near Tinsley, Sheffield, UK. © Copyright Nic Franklin-Woolley and licensed for reuse under Creative Commons License. Available online at http://s0.geograph.org.uk/photos/41/64/416400_f213e398.jpg. Geograph image code, SK4090. F. Western Tent Caterpillar, *Malacasoma californicum* (Packard) *pluviale* (Dyar) (Lepidoptera: Lasiocampidae) attacking *Salix sitchensis* Sanson ex Bong. (Salicaceae) and *Alnus viridis* (Chaix.) D.C. (Betulaceae) at Mount St. Helens, WA, USA. Photograph by J. Bishop (Washington State University, Vancouver, WA, USA) in July 2012. Herein reproduced with his permission. Large pile of frass comes from colony of stem boring weevils, *Cryptorhynchus lapathi* (Linnaeus, 1758) (Coleoptera: Curculionidae). G. *Nasutitermes* sp. (Isoptera: Termitidae), photographed by JASB during the summer 2012 in Fajardo, Puerto Rico.

Figure 13. Arthropod aggregations related to resting and thermoregulation. A. *Hexagenia* adult mayflies (Ephemeroptera: Ephemeridae) resting. Photograph by Dr. Lynda Corkum (University of Windsor, Canada). Available online at http://www.epa.gov/med/grosseile_site/indicators/images/hexagenia.jpg. Used by permission from Dr. John Hartig (United States Fish and Wildlife Service). B. *Dolycoris baccarum* (Linnaeus, 1758) (Hemiptera: Pentatomidae) aggregated on *Arbutus andrachne* Linnaeus (Ericaceae), commonly called Greek Strawberry Tree, a shrub or tree that grows in soils rich with silt in Mediterranean grove mountain tops in northern Israel. Photographed and herein reproduced by permission from Eran Levin (Tel-Aviv University, Israel). C. *Harmonia axyridis* (Coleoptera: Coccinellidae) clustered in my garage in Carman, Manitoba, Canada. Photographed and herein reproduced by permission from John Gavloski (Manitoba Agriculture, Food and Rural Initiatives Crops Branch). D. Flies appearing to be thermoregulating, "flies on about thirty flies on the south-facing side of this tree".

nights and their mate choice tallied. Although females walked to the aggregating chorusing males by a nearly 2:1 ratio, soloists males also got some matings. In other words, aggregating is not a 100% guarantee of reproductive success.

In dragon- and damselflies, insects often considered as solitary, aggregations do happen. Sometimes, male and female odonatans of all ages move together, by the millions as part of migrations where new areas are colonized, with the assistance of convergently ascending winds (Corbet, 1999). In smaller aggregations of odonatans, noncopulating males are attentive to pairing conspecifics, waiting for opportunities to disrupt the copulating pair to have their own mating chance, as in the Odonata (dragon- and damselflies, Figure 8B), a group of insects not usually associated with mating aggregations. McCafferty (1981) mentions "swarm feeding", "which involves aggregating prey insects and predator dragonflies".

On the other side of the spectrum, in mayflies, hepialid moths, numerous dipterans, etc., large groups of flying adults, called leks, form and from them, copulating pairs emerge. Typically, leks are mating aggregations. However, there are other likely generators of leks, such as resource availability not related to the immediacy of mating. In other works, such aggregations not related to mating are known as swarms (Godfray, 1994). In other arthropods, calling males do not aggregate in space, or lek (used as a verb). Instead, they spree (to form a spree), that is, form aggregations in time, not in space (Bailey, 1991).

Once females are ready to oviposit, they have to make choices: how to allocate eggs to oviposition sites? Female *Neodiprion* (Hymenoptera: Diprionidae) divide their reproductive output in different pine needles, often ovipositing next to other female's eggs. Consequently, groups of eggs are actually of mixed maternal origin. This social oviposition, according to Costa (2006), may lead to larval aggregations. The cohesiveness of the larval group is maintained through chemical and mechanical inputs. Sometimes, grasshopper oviposition is clustered, with hundreds of females lying almost simultaneously in a small patch (Stauffer and Whitman, 1997).

Aggregations can also serve as nurseries. In cockroaches, aggregations not only reduce the likelihood of desiccation, increases the rate of development through group effects, food, an inoculum of digestive microbes, but also younger aggregants may learn valuable survival lessons from more experienced conspecifics (Bell et al., 2007).

A circular, or quasi-circular, larval aggregation, or cycloalexy, is often, but not always, linked to parental care (Gilbert and Manica, 2010). For instance, in *Hypolimnas anomala* (Wallace, 1869) (Lepidoptera: Nymphalidae), rare butterflies from Guam, adult females stand over the first-instar larvae, which tend to be aggregated in a closely packed cluster (Nafus and Schreiner, 1988). Likewise, mother cassidines often care for their young larvae and, as far as we know, the father is not involved in parental care of aggregated larvae, but this needs to be confirmed.

Figure 13. (*Cont.*) Photographed by Albert Bridge, Minnowburn, Belfast, UK. © Copyright Albert Bridge and licensed for reuse under Creative Commons Licence. Available online at http://www.geograph.org.uk/photo/2635625. Geograph image code J3268.

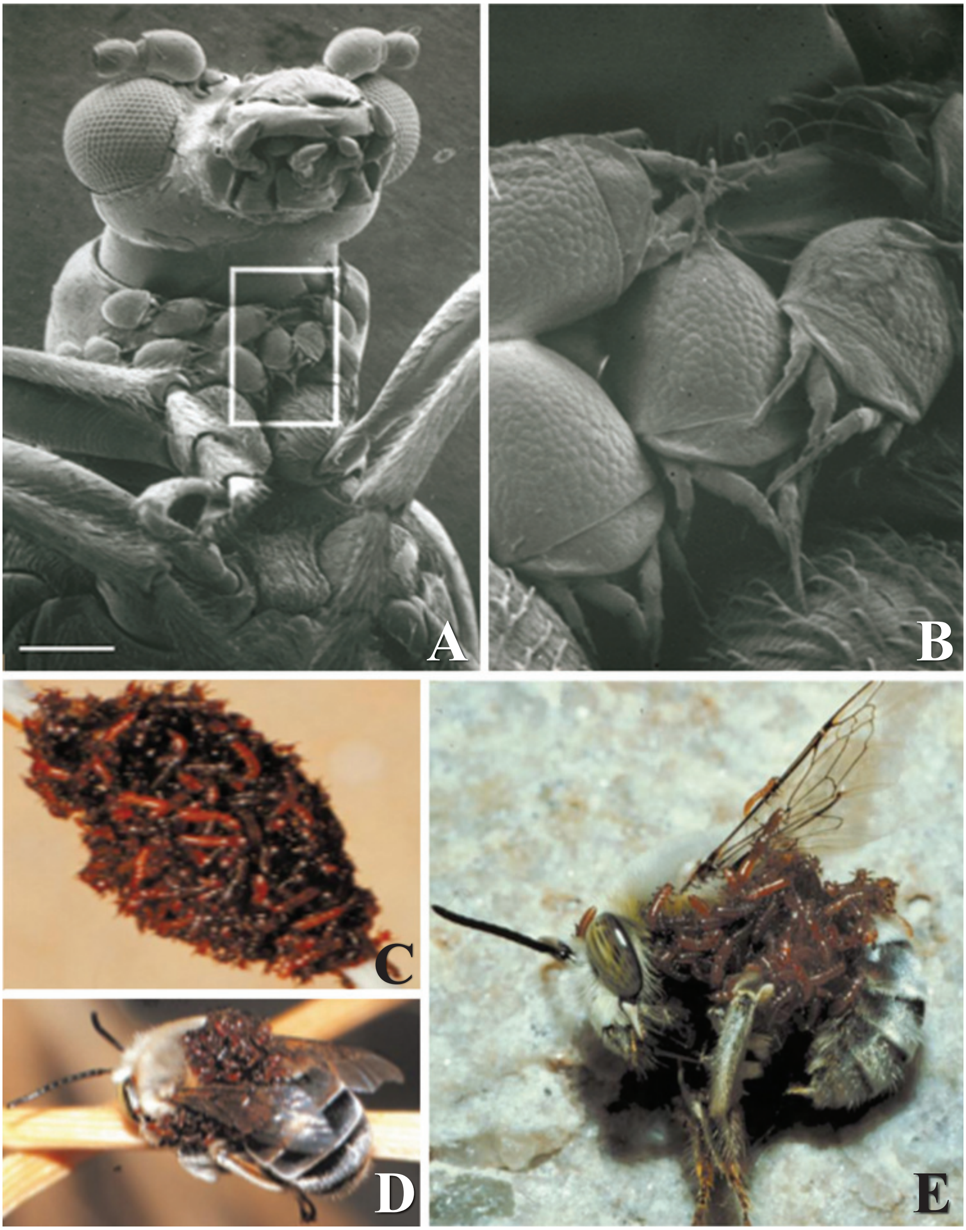

Figure 14. Aggregations related to phoresy. A–B. Deuteronymphs or hypopi of *Ancyranoetus virkkii* Fain and Santiago-Blay, 1993 (Acari: Histiostomatidae) on *Lema nigripes*. (Weise, 1885) from Puerto Rico. Scale bar on A = 250 µm. B. Enlargement of insert on A. C. Aggregating *Meloe franciscanus* Van Dyke (Coleoptera: Meloidae) larvae, called triungulins, on a branch (Kelso Sand Dunes, San Bernardino County, CA, USA). D. *Hapropoda pallida* (Timberlake) (Hymenoptera: Apidae) female bee loaded with *M. franciscanus* triungulins, which have been sexually transmitted to her by parasitized conspecifics males (E note to Jorge, lower left, orange background). C–E Photographed and copyrighted by John Hafernik (Hafernik and Saul-Gershenz, 2000).

Phoresis and other escapes (Figures 14 and 15)

Hafernik and Saul-Gershenz (2000) report the fascinating case of *Meloe franciscanus* Van Dyke, 1928 (Coleoptera: Meloidae) larvae, called triungulins, that aggregate mimicking the *Hapropoda pallida* (Timberlake, 1937) female bees they parasitize. Terribly confused *H. pallida* males attempt to mate with the larval aggregation, pick them up, and then transfer the triungulins to female *H. pallida* bees, like a sexually transmitted disease (Figure 14C–E).

Another fascinating case of aerial transport, mass-feeding larvae of *Scopelodes contracta* Walker, 1855 (Lepidoptera: Limacodidae) cut the apex of the petiole of their host plants gently "parachuting" to the ground where they usually escape predatory ants and cocoon (Yamazaki, 2010, Figure 15A–B).

Ultimate explanations, fitness

Do aggregants benefit from an increased fitness by forming part of a group? Group living may enhance the likelihood of survival through sharing of labor (e.g., care of progeny, search of food, maintenance and protection of the living quarters, etc.), as well as increased likelihood of reproductive encounters. Costa (2006) points out that in *Malacosoma americanum*, there is little genetic relatedness amongst older members of a larval commune, let alone members of different tents, or larvae in a single tree. To make it worse, Alexander (1974), quoted by Fletcher (2009), wrote that "there are no automatic or universal benefits to group-living".

What are the evolutionary costs to develop and maintain such defenses? If there is plasticity within the defense, what are the genetic and infrastructural (receptors and chemicals) costs of such plasticity? What are the costs associated with developing, maintaining and operating the defenses? Once the defenses are established, are there costs related to its interaction with the environment?

Figure 15. Aggregations related to escape. Feeding (A) and parachuted (B) larvae of *Scopelodes contracta* Walker, 1855 (Lepidoptera: Limacodidae). Images kindly provided by Kazuo Yamazaki (Osaka City Institute of Public Health and Environmental Sciences, Osaka, Japan).

Figure 16. A. *Coenobita clypeatus* (Fabricius, 1787), the Caribbean hermit crab. Millions of individuals that sometimes mass migrate to inland forests, Available online at http://www.riledupjournal.com/Blog/TabId/64/PostId/1079/crab-migration.aspx. B. An aggregation of *Nelima elegans* (Weed, 1889) (Opiliones: Phalangioidea: Sclerosomatidae) harvestmen observed on a wet rocky outcrop on the bank of a stream located on Glen Burney Falls trail, near the town of Blowing Rock in western North Carolina, USA. C. Juvenile harvestmen, possibly *Phalangium opilio* Linnaeus, 1758 (Opiliones: Phalangioidea: Phalangiidae), under a decomposing tree log at Toft Point State Natural Area, Door County, WI, USA. Although adults were also collected from the area, the species identification of the juveniles cannot be 100% confirmed because juveniles are difficult to identify to species. Exuvia attached to the rough surface are also visible.

Additional examples of aggregations in arthropods

Many other examples of conspecifics' gatherings abound in the living world, including the most speciose of all extant animal phyla, the Arthropoda, the taxonomic target of this paper. In this section, we provide additional examples of such aggregations. We have organized this portion of the paper taxonomically.

Aggregations of arthropods have been studied in crustaceans (e.g., isopods, Hornung, 1990, 2011; Hornung and Warburg, 1995a,b, 1996; Figure 16A), arachnids (e.g., social spiders, Foelix, 2011; opilionids (Figures 16B-C); scorpionlings being transported by their mother (Figure 7H); spiderlings emerging from a cluster of eggs (Figure 8A)), myriapods (millipedes, centipedes, symphylans, and pauropods), as well as insects. The scene entitled *The spider attack*, in *Chamber of Secrets*, Episode 2 of the widely popular *Harry Potter* movies, etched into our collective imagination the concept of spider aggregations, albeit exaggerated. The Acari, a universe by themselves, can reach colossal proportions in the numerous microhabitats they inhabit (Krantz and Walter, 2009; Walter and Proctor, 1999).

Diplopoda or millipedes

Millipedes are frequently recorded as "swarming" (Blower, 1957; Hopkin and Read, 1992; Kania and Tracz, 2005; Voigtländer, 2005; Youngstead, 2011), often with hundreds or thousands of moving individuals. The following anecdote is representative of those swarms. "Each July for the past three or four years my house has been infested by house millipedes [*Oxidus gracilis* (Koch, 1847) (Figure 16D, Paradoxosomatidae) and an unidentified species of *Uroblaniulus* (Parajulidae)]. From what I have read, they do not reproduce in the house. I sweep up thousands of them for about a month. I have tried to seal the baseboards, spray around the house, and other solutions, such as cleaning the floors with alcohol, etc. They come back and I cannot figure how they are getting in. Within five minutes after I sweep some up and the room is clean, I see a half dozen more. I thought maybe they were laying eggs, but I doubt it. I can see them on the sides of my house sometimes also. The thing that puzzles me the most is how they seem to appear out of nowhere. I don't see them coming in from the ventilators, areas around the doors, etc. Is there some kind of entomological explanation for their appearance? They are otherwise harmless, but annoying" (Anonymous to Santiago-Blay, personal communication, 2011). Stories like this are supported by scientific research, some of which is described below.

Figure 16. (*Cont.*) "The yellow spheres are resin droplets seeping out of the underside of the decomposing wood. This piece of the log was stuck in the ground a couple of inches. When the log was turned over there was a small cavity underneath and that's where I observed the juveniles and the resinous substance. Given that little is known regarding the life history of many harvestmen species and that most observations of diet and foraging are anecdotal, it is possible that the harvestmen were feeding on the resin (not observed). It is also possible that they were just using this small dark microhabitat as a shelter (rather than a food source)." Images B and C, as well as quote, courtesy of D. N. Proud, with permission. D. *Oxidus gracilis* (Koch, 1847) (Diplopoda: Paradoxosomatidae), a common tropical and temperate millipede found in aggregations worldwide.

The first and second instar larvae of the British polydesmids, *Polydesmus coriaceus* Porat, 1871 and *Brachydesmus superus* Latzel, 1884 remain together in feeding flocks (Blower 1969, additional examples offered; Harding, in Blower, 1969) as do the first three instars of *Strongylosoma pallipes* (Seifert, 1932). The immature instars of several species of African paradoxosomatid polydesmids form tight swarms (Lewis, 1971a). In Puerto Rico, mostly adult paradoxosomatids *Asiomorpha coarctata* (DeSaussure, 1860) and *Chondromorpha xanthotricha* (Attems, 1898) are commonly observed in large numbers in urban households (Santiago-Blay and Vélez, 1985) as are other Puerto Rican millipedes (Santiago-Blay, personal observations and Canáls, personal communication to Santiago-Blay). Highly toxic species of *Polyconoceras* (Spirobolida: Rhinocricidae) aggregate in New Guinea and the natives stay away from them (Jolivet, 1970a,b; Hudson and Parsons, 1997). Once a train in Thailand was stopped when the tracks where seen to be covered with millions of unidentified millipedes (Jolivet, 1971a). Costa (2006) reports that platydesmids cycloalex with their head pointing towards the center of the semi-circular aggregation (abdominoperipheral cycloalexy).

These observations suggest that pheromones could be regulating millipede swarms. For instance, in three Nigerian species of paradoxosomatids, most swarms comprise only one instar, suggesting the presence of pheromones synchronizing molting and/or swarming (Lewis, 1971a). West African female *Sphenodesmus sheribongensis* Schiøtz, 1966 have been observed in a hole in the ground surrounded by six males, hinting that the female released a sex pheromone (Lewis, 1971b). In laboratory studies, Bellairs et al. (1983) showed that the poylydemoid millipede's, *Streptogonopus phipsoni* Pocock, 1892, relative degree of aggregation depends on the concentration of benzaldeyde. Hopkin and Read (1992) report that males of *Glomeris marginata* (Villers, 1789) produce a pheromone.

Chilopoda or centipedes

Chilopods have been occasionally reported aggregating. These groups appear to form in environmentally suitable habitats, whether as places to hide, feed, etc. (e.g., *Cryptops hortensis* Leach, 1814 from Madeira and possibly the Azores and the Canary Islands, Whitehead, 2004; *Scolopendra cingulata* Latreille, 1829 in northern Iraq (Lewis, 2001); *Strigamia* (= *Scolioplanes*) *maritima* (Leach, 1817) in the Isle of Man, Blower, 1957; Barber to Santiago-Blay, personal communication 2011). Lewis, quoting from the original sources, wrote "The large black centipede [*Scolopendra cingulata*] was present at a density of one per meter of road length. All were crossing from north to south and the crossing time was about mid-morning. There were certainly sufficient numbers of the centipede to make me think at the time that it was some kind of migration." Experiments on *Lithobius forficatus* (Linnaeus, 1758) and *L. variegatus* Leach, 1814 show that homing behavior is exhibited by some, but not all, individuals, intimating that pheromones might be involved (Lewis et al., 1992). The coxal organs of lithobiomorph centipedes suggest their involvement in pheromone production (Littlewood, 1983a, 1983b, 1988, 1991; Littlewood and Blower, 1987).

Hexapoda or insects and their allies

Many examples of aggregations exist in the hexapod world, the most abundant creatures of the modern world, with an estimated 5-10 million species (or more), most undescribed. The aggregating groups may consist of a handful of organisms, as in webspinners (Embioptera) or in angel insects (Zorapterans), thousands of specimens, such as cassidines (Chrysomelidae) on an island beach (Théodoridès, 1946), or millions of specimens that appear briefly and then vanish, as in the case of locust or mayfly (Ephemeroptera) aggregations. Herein, more examples are noted.

Ancestral hexapodans

Traditionally, Collembola (or springtails), Protura, and Diplura have been considered the most ancestral groups within the extant Hexapoda. These orders are typically associated with humid microenvironments and, under some circumstances, can reach enormous populations, as in the cases of the springtails *Hypogastrura viatica* (Tullberg, 1872) and *Folsomia sexoculata* (Tullberg, 1871). Within the Insecta proper, the jumping bristletails (Archaeognatha: Machilidae) and the bristletails (Thysanura) aggregate in favorable littoral microhabitats (Joose, 1976).

Paleopteroid orders

Ephemeroptera. This unique order of relatively ancestral insects has the peculiarity of having a pre-adult winged stage, called sub-imago. In some groups, the aquatic stages, known as nymphs or naiads, aggregate in large enough numbers, to be useful as biological water quality indicators, as in the case of *Hexagenia* spp. (Ciborowski, 2009). Small to immense aggregations of the winged insects are common in temperate regions for just a few days giving name to the order (McCafferty, 1981). The adults do not feed. Adults mate and oviposit, completing their life history (Campbell, 1987; Edmunds et al., 1976).

Odonata. Not surprisingly, as the immature stages are aquatic, adult dragon- and damselflies tend to be abundant close to aquatic environments. As their lives as naiads, or nymphs, come to an end, they climb onto emergent vegetation and can be seen exiting from their exuvia and, later on, basking in groups (Paulson, 2012). Numerous mark-and-recapture studies as well as direct observations have demonstrated that intense male-to-male competition is common in this order.

Neopteroid orthopteroid orders

Gregariousness is fairly common in the orthopteroid orders, including, alphabetically, Blattodea, Dermaptera, Embiidina, Isoptera, Mantodea, Orthoptera, Phasmatodea, Psocoptera, and Zoraptera. In some of these taxa, parental care is present.

Blattodea. Cockroaches, a group with 4,500 described species, are commonly seen (and reared) in large groups and have many strongly gregarious species. Many are reared at college and university laboratories for teaching and research purposes. Indeed, author JASB did not particularly enjoy being around the American cockroach, *Periplaneta americana* (Linnaeus, 1758), before becoming an entomologist but he needed to overcome such feelings when he became a teaching assistant for the laboratory of Insect Morphology at the University of California, Berkeley. There, Professor Rudolph L. Pipa reared large numbers of *P. americana* and there was no way out for JASB. A few years later, the largest colonies of big insects author JASB has seen are cockroaches, in the mid to late 1980s at a research facility in Ohio State University, Columbus, OH, USA.

As a group, maternal or biparental care of the young in the Blattodea, including group nesting, is ubiquitous (Bell et al., 2007). A basic parent-offspring interaction is ovoviviparity, the retention of the egg case, guaranteeing a longer care for the developing progeny. After hatching, some species of roaches exhibit brooding behavior, that is, the ephemeral (typically less than a day) association (not only for feeding) of mother and newly born progeny. Whether in a nest or burrow, or out in the open, a number of cockroaches exhibit prolonged maternal (rarely biparental) behavior where the mother expels substances from her abdominal apex that serves as food for the young and/or provided a place where the nymphs can cling to, that is the provision of board and/or room (Table 8.4 in Bell et al., 2007).

The size of a group can vary enormously. In the viviparous Pacific Beetle Cockroach, *Diploptera punctata* (Eschscholtz, 1822), for example, groups of 2-8 adults and 5-8 nymphs are common, whereas in *B. germanica* groups can reach 100 000 roaches in apartments (Bell et al., 2007). In many species, gregarious behavior tends to be more common in the earlier nymphal stages although the pattern is different in cave species. Pheromones appear to be a factor in cockroach aggregations, however, numerous other stimuli, such as vision, sound, touch, smell, temperature, degree of illumination, light, humidity, and others are important.

Dermaptera. Earwigs, as they are commonly known, are often found in small groups, under covers. Author JASB commonly found aggregations of a dozen or so earwigs under sources of food intended for squirrels in his former home located in southwestern Virginia, USA. Also, he has seen them inside rotting sunflower stems. Parental behavior is also widespread in this order (Costa, 2006).

Embiidina (or Embioptera). This small, tropical order of insects, commonly called webspinners, includes cryptic gregarious forms. They tend to live in aggregations under bark of decaying trees, under rocks, leaf litter, etc. There, apterous females invest considerable time taking care of the progeny (Ananthasubramanian, 1957; Edgerly et al., 2002).

Isoptera. An order with approximately 2600 described species, termites are closely related to roaches (Blattodea) and to mantids (Mantodea). Termites are notorious social insects whose behaviors appear to form a continuum with the Blattodea (Edwards and Mill, 1986; Bell et al., 2007). Termites aggregate to support the division of labor in the colonies, including reproduction, feeding, and defense (Abe et al., 2000; Edwards and Mill, 1986). Contrary to the mantids and to the other major eusocial order, the Hymenoptera (e.g., ants, wasps, and bees), both the roaches and termites communicate extensively through vibration and chemistry, including trail following and kin recognition. Both cockroaches and termites build nests although in termites, the architectural skills are taken to a much higher level of ability.

Mantodea. Praying mantids lay they eggs in hardened clusters, called oothecae. A few species in this order have been reported as guarding their developing brood (Costa, 2006).

Orthoptera. Numerous families of Orthoptera *sensu stricto*, form groups, and some species form large swarms (Capinera et al., 2004; Lockwood, 1997a,b, 2010). Some of those aggregations involve migrations and are tightly connected with endogenous (e.g., hormonal) and exogenous (e.g., photoperiod, temperature, etc.) changes (Dingle, 1974; Stengel, 1974). Parental care has been noted in the Gryllotalpidae and the Gryllidae.

Phasmatodea. This group of insects includes the walking sticks. Some species, however, are aposematically colored and spray defensive compounds suggesting a possible benefit of forming groups, even if they are ephemeral, and possessing defense mechanisms.

Psocoptera. In some species of barklice (or booklice, as those among our libraries, are called), communal oviposition has been noted (Costa, 2006).

Neopteroid hemipteroid orders

Gregariousness is fairly common in the hemipteroid orders, including the Hemiptera and the Thysanoptera.

Hemiptera. This order currently includes between 50 000 and 80 000 described species. Many adult true bugs and their allies, such as lace bugs (Tingidae, Figure 7E), stink bugs (e.g., Brown marmorated stink bugs, *Halyomorpha halys* Stål, 1855 Pentatomidae), cicadas, maternally-caring Membracidae (both formerly placed in the paraphyletic order Homoptera) aggregate in great numbers (Maguire, 2010). Egg guarding and maternal care of the young are fairly common in the Hemiptera (Monteith, 2006; Roth et al., 2006). In some of these groups, nymphal aggregations have partial ring-like shape. As in the Orthoptera, some aggregations of hemipterans are related to migrations (Caldwell, 1974). Periodical cicadas (Hemiptera: Cicadidae) (Jolivet, 2004) tend to aggregate by millions every so many years. After intense male-male competition (Cooley and Marshall, 2001; Heliövaara et al., 1994), oviposition takes place, and the rest of the life history proceeds in the darkness of the soil where nymphs feed on roots. Numerous other groups in the Hemiptera also form aggregations. For instance, in the fulgoroids, members of the Flatidae (Figure 11D) and Derbidae (Figure 11E) aggregate (O'Brien, 1982; O'Brien to Santiago-Blay, personal communication, September 2012). In the Stenorrhyncha, the diluted sugary honeydew produced by aphids attests to the power of insect aggregations. Aggregations in scale insects (Miller and Davidson, 2005) are very common (Figure 11A) and often difficult to detect by the untrained eyes as these insects often do not resemble insects at all. Not surprisingly, scale insects are amongst the most common insects that enter new places through ports of inspection.

Thysanoptera. Thrips are fascinating small insects, with approximately 5000 described species. Many of them tend to live in groups and many are important economical pests (Ananthakrishnan, 1984). In a number of species of *Frankliniella*, males have pheromones that assist in conspecifics aggregations (Kirk and Hamilton, 2009;

Cabrera to Santiago-Blay, personal communication, October 2012). A number of species of thrips exhibit different degrees of sociality, including communal egg masses, females guarding egg clutches, and males guarding guarding females. In species of the subfamily Phlaeothripinae (Phlaeothripidae), known as gall thrips, a soldier caste is present (Costa, 2006).

Neopteroid holometabolous orders

The bulk of the insect world is holometabolous and this mega-assemblage of species includes the four most speciose orders of modern insects, namely the Coleoptera, Diptera, Lepidoptera, and the Hymenoptera.

Coleoptera. Perhaps the most iconic aggregations in this megaorder, containing approximately 400 000 described species, are those of fireflies (Lampyridae), which are often associated with reproductive behavior. Clearly, many aggregations in the Coleoptera are chemically mediated (e.g., bark beetles, Wood et al., 1986) although sonic communication can also be important (Crowson, 1981).

Other aggregations are known among many beetles but, in most cases, the phenomena await reasonable explanations. Examples of such aggregations include *Calosoma* (Coleoptera: Carabidae) in Canada (Crins, 1980), Staphylinidae (Orousset, 1993; Smith and Webb, 1999) in France and England, hibernating Coccinellidae in Africa, Asia, and North America (Jones, 1999), Scarabaeidae (hatching cockchaffers, *Melolontha* in Europe or New Guinea, adult *Stenotarsus subtilis* Arrow, 1920 (Coleoptera: Endomychidae) on two trees, a palm (Aracaceae or Palmae) and a species of Burseraceae, in Barro Colorado Island, Panama (Denliger, 1994; Roubik and Skelley, 2001). Female fungus beetles, *Pselaphacus giganteus* (Germar, 1824) (Erotylidae), gather her young larvae into a neat pile — instead of the larvae arranging themselves, as in cycloalexy — before searching for food in Trinidad (Preston-Mafham, 1993). *Gonocephalum* (Coleoptera: Tenebrionidae) in north Africa, and millions of *Mesomorphus* beetles (Coleoptera: Tenebrionidae) congregate over few dozens of trees in Phu Kae, Thailand in August-September 1970 (Jolivet, 1971). In the chrysomeline leaf beetle, *Timarcha*, adults rest and aggregate under leaves of *Thymelaea hirsuta* L. (Thymelaeaceae) in north Africa during the night. Then, in the morning they disperse during day time activity (Jolivet, 1999b).

Diptera. A megaorder with some 120 000 described species. Adults of numerous families of nematoceran flies tend to congregate in huge numbers, sometimes synchronizing their emergence from the pupa (McCafferty, 1981). Other dipteran families that form large groups include the chironomids (Ferrington et al., 2008; Hashimoto, 1976), the so-called "non-biting flies" (but see Azar and Nel, 2012) as well as chaoborids aggregate in flight and on the ground by large numbers over fresh (Central African lakes; Jolivet, 1972-1973) and salty bodies of water (Linley, 1976). Mosquitoes (Culicidae) are notorious for forming huge larvae, pupal, and adult aggregations (Al-Amin et al., 2011; O'Meara, 1976), which increases their notorious medical and veterinary importance. Huge aggregations of flies (e.g., *Sophophora*, Drosophilidae or flesh flies; Sarcophagidae, associated with decaying animal matter; true fruit flies or Tephritidae, Aluja and Norrbom, 2001) are commonly seen over their sources of food.

Lepidoptera. In this insect megaorder with approximately 175 000 species, aggregations often begin with the eggs, which tend to be laid in clusters. Therefore, it is not surprising to see aggregations of newly hatched caterpillars. Feeding aggregations in larval Lepidoptera have long been documented (Gibson, 1902) and are known in many larval groups, including Zygaenidae, Arctidae, Limacodidae (Figure 9C, Yamazaki (2010, 2011)), sub-social Lepidoptera, such as tent caterpillars (*Malacosoma*, Lasiocampidae, Figure 12), as well as in the Nymphalidae (Smart, 1975, pp. 36-37). *Caligo* sp. (Nymphalidae Brassolinae) larvae also feed together in Nicaragua (Maes to Santiago-Blay, personal communication, April 2012). Sometimes, quasi circular aggregations of Lepidoptera and Neuroptera larvae can be observed around a twig or a trunk where the available background surface makes the shape of the larval aggregation distorted.

Amongst California (USA) moths, swarming has been observed in moths, such as *Eriocraniella aurosparsella* (Walsingham) Eriocraniidae, several species with greatly enlarged eyes in the Adelidae, *Amydria arizonella* Dietz (Acrolophidae), and *Glyphipterix fenisea* Heppner (Glyphipterigidae) (Powell and Opler, 2009). Feeding aggregations in adult lepidopterans are also well known and entomologists frequently use this propensity to create baited traps (Wagner et al., 2011). Many species of butterflies have also been observed drinking watery materials other than nectar, including manured water and, like a colleague in entomology once told me, seemingly "enjoying every bit of it" Recently, we were made aware of an interesting grouping of butterflies, possibly *Colias* sp. (Pieridae, see http://youtu.be/UDO619ngBtI). Of these butterflies, the videographer, Mr. William Martínez (Villalba, Puerto Rico) said (translation by author JASB), "I was driving to the home of a friend. Far away, in an abandoned place close to the road, there were the butterflies. From afar, they looked like leaves. As I approached them in my car, I realize the leaves were actually butterflies and I turned around. I could not believe was I was seeing. There were over 100 of them. I just placed my cell phone over a rock and let it videotape while the butterflies surrounded me… What was in there? What kept them together? I do not know but it was an experience that I shall never forget." (Martínez to Santiago-Blay, personal communication, October 2012). Moths and butterflies also aggregate for reproductive purposes forming leks. This is the case of ghost moths (Hepialidae, McCabe and Wagner, 1989), where males chemically "call" females, perhaps using an androconium-emitted pheromone.

Sometimes, aggregations of Lepidoptera larvae appear to have a defensive function. For instance, one of us (PJ) has often observed unidentified noctuid caterpillars grouping on leaves of unidentified Melastomataceae in Vietnam. The larvae stand up and agitate their heads when someone approaches the host plants on which they live.

Trichoptera. McCafferty (1981) mentions two specific swarming types in adult caddisflies. In species of *Ceraclea*, swarming involves a horizontal zigzag near the surface of the water and they orient themselves parallel to the shoreline. Other taxa (e.g., species in the genera *Mystacides* and *Oecetis*), swarm with a vertical movement, just like ephemeropterans.

Hymenoptera. This insect megaorder, with over 130 000 described species, contains the other quintessential groups of social insects, namely bees (Butler, 1609; Michener, 2007; Seeley, 2010), wasps and ants (Hölldobler and Wilson, 1990). It is not the purpose of this review to elaborate on the social life of hymenopteran social insects but, instead, we will focus on quasi-circular group defense. Cycloalexing in tenthredinoid larvae have been known for decades (Wheeler and Mann, 1923; Azevedo Marques, 1933) and the functional significance of such aggregations has been described elsewhere in this paper. On occasions, parasitic Hymenoptera larvae and pupae cycloalex on their host, as depicted by Wagner et al. (2011, p. 28). Likewise, adult parasitic Hymenoptera have been reported to hibernate (Quickle, 1997), presumably owing to pheromones, or aggregate to host find (Godfray, 1994; Jervis and Kidd, 1996). The functional significance of some of aggregations in parasitic Hymenoptera remains to be discovered (Quickle, 1997).

One lesser studied behavior is the tendency of some pergids to mass migrate, pupating *en masse* (Costa, 2006). The toxins of some pergid larvae, such as the South American *Perreyia fulvipes* Konow, 1899 are retained by the soil-dwelling pupae causing lethal liver failure to swine and cattle within two days upon their ingestion. An even more amazing behavior is the communal pupation of several species of *Dielocerus* (Hymenoptera: Argidae). In these species, the larvae spin a communal nest (or nidus, Costa, 2006, p. 639) in which they pupate communally.

In addition, feeding, defense, and reproductive aggregations are well-known in many social Hymenoptera. For instance, coordinated group ambush allows *Azteca* ants to capture large mobile prey (Morais, 1994). The vast number of amazing behaviors of eusocial insects (Table 1), such as ants, bees, and wasps have been extensively documented (Figure 12E and 12G).

Convergences and divergences amongst some larvae of social insects

There are remarkable convergences in body form (eruciform, namely relatively straight, podous), life habit (herbivory of all sorts), and tendencies to defend themselves in groups, be they aggregations or cycloalexy, in the social larval Coleoptera, particularly chrysomelids, social larval Lepidoptera, and social larval Hymenoptera. Also, when disturbed, these aggregating larvae tend to regurgitate presumably repellent or toxic substances.

Interestingly, social Lepidoptera display a wide array of feeding strategies (patch-feeding and retreat, nomadic, group feeding, with communal living, and foraging individually with a more permanent communal central living place). Of those three, the last one has not yet been discovered in the social Hymenoptera.

There are variations in the degree of parental care for social insect larvae. For instance, gregarious Lepidoptera tend to lack maternally caring forms, whereas in gregarious Hymenoptera, such as the Pamphilidae, Argidae, Tenthridinidae, and Pergidae, maternal care of the larvae is commonly displayed.

Aggregations in the Chrysomelidae (Coleoptera)

In this section of the paper, we summarize published literature on aggregations of leaf beetles (Chrysomelidae) and include some of our unpublished observations. Our remarks are organized by stage in their life history, namely, eggs, larvae, pupae, and adult.

Eggs

In oviparous leaf beetles, eggs are often laid in batches — even if such behavior may at first seem maladaptive (Desurmont et al., 2009) and frequently toxic. For instance, Gregoire (1988) has reported that the hispine *Cephaloleia consanguinea* Baly, 1885 uncovered eggs are laid in groups. In tortoise beetles (Cassidinae), eggs are sometimes provided with a protective cover, such as an ootheca, or with feces, as in *Timarcha* (Chrysomelinae). Unprotected eggs are open to attack by predators and parasitoids, and a percentage of eggs are destroyed, but for an egg in a group, the probability of being parasitized/predated upon is smaller than if it were isolated.

Larvae

In numerous larval chrysomelids, it appears that group feeding increases the likelihood or survival by mechanically weakening the host plants, as in *Chrysophtharta agricola* (Chapuis, 1877) (Chrysomelinae) on *Eucalyptus nitens* (Deane and Maiden) Maiden (Myrtaceae) (Nahrung et al., 2001). Panamanian *Macrohaltica jamaicensis* (Fabricius, 1792) (Galerucinae: Alticini) larvae and adults aggregate in the central mountains of Panamá, over large *Gunnera* (Gunneraceae) leaves (Eberhard et al., 1993). In Nicaragua, *M. jamaicensis* aggregates in huge numbers, hundreds of individuals on some plants in an area and not a single individual nearby. Interestingly, some of those aggregations — perhaps reproductive (not feeding) ones – have been seen on *Lycopodium* (Maes to Santiago-Blay, personal communication, April 2012).

Pupae

Sometimes, cassidine pupae remain in cycloalexy in South America (Jolivet, personal observations). Images of cycloalexing immatures, including pupae of the cassidine *Aspidimorpha* (*s. str.*) *miliaris* (Fabricius, 1775) are provided in Borowiec and Świętojańska, 2011). The latter reference, as well as Borowiec (1999) are also excellent sources for names, authorships, and years in tortoise beetles.

Adults

Often, adult chrysomelids are found in large numbers, feeding on their host plants. The Colorado potato beetle, *Leptinotarsa decemlineata* (Chrysomelinae) sometimes aggregate in flight and at rest. Author Santiago-Blay has seen leaf-mining species of *Monoxia* in the western USA and numerous other species of chrysomelids aggregate by the dozens to hundreds over their host plants (Figure 1). Aggregations of adult tortoise beetles *Physonota caudata* Boheman, 1854 (Cassidinae) (Flowers, 1991) in the Americas produce a sound when potential predators approach.

In a ten-year-long study, Wade (1994) discussed the biology of the chrysomelid beetle, *Plagiodera versicolora* (Laicharting, 1781). There, he reported that, in spite of multiple matings by females, the genetic similarity amongst larvae in a group is relatively high. As compared to solitary individuals, keeping close proximity in a larval feeding group increases survivorship through two mechanisms: (1) increased likelihood of food sharing and (2) by increased growth rate through mutual stimulation.

It appears that feeding aggregations of adult *Aulacoscelis* (Aulacoscelinae (Santiago-Blay, 2004a, 2008) or Aulacoscelidinae (International Commission of Zoological Nomenclature, 2010) for discussion on spellings of this group, the later was favored by the ICZN) (Windsor et al., 1999) and/or Languridae (Coleoptera) over *Zamia* cycads (Zamiacae) leaves in tropical America represent a case of feeding facilitation on relatively hard leaves. Once the sharp mandibles of adult *Aulacoscelis* (Santiago-Blay, 2004a,b) pierce a leaf, other beetles move in for the feast. The selective advantage offered to individuals living in groups may relate to overcoming plant defenses, such as hardness. Also, adult "aulas", as JASB likes to call them, bleed reflexively (Prado et al., 2011, 2012) and must form a formidable defense barrier to potential predators.

In a preliminary study, Windsor and Choe (1994) suggested that "subsociality evolved more than once within the Cassidinae (Coleoptera: Chrysomelidae), possibly as a convergent adaptation to life on exposed, enemy infested, leaves of fast-growing tropical vines." More experimental research needs to be done on sociality in chrysomelids.

Cycloalexy or (quasi)circular defensive aggregations

The word "cycloalexy", is derived from the Greek, *kuklos* (κὑκλος) and *alk-* (or *alek-*) (αλκ- or αλεκ-). The word *kuklos* means ring or circle. On the other hand, *alk* (*or alek-*), has several meanings, including "to fight an enemy", "to push away", as well as "to protect to defend", or "to help". Whether the rules of linguistics (morphology or semantics) for the creation of new words from Greek were followed, or whether the resulting words are eloquent or visually appealing, the intention of the creators of the published term, cycloalexy, was "to protect" or "to defend by forming a circle". Although it appears that Andrade (1981) refers to a circular defense strategy in insects (Galerucinae) for the first time, Jolivet created the noun, cycloalexy, in 1987 when he and the late French dipterist, Loïc Matile (Muséum national d'histoire naturelle, Paris, France) were discussing Grassé's group effect. A year later, cycloalexy was formally defined as "the attitude adopted at rest by some insect larvae, both diurnal and nocturnal, in a tight circle, when the heads or ends of the abdomen are juxtaposed at the periphery, with the remaining larvae at the center of the circle" (Vasconcellos-Neto and Jolivet, 1988, 1989, 1994). Additional observations on cycloalexy in Chrysomelidae were made by Jolivet in 1985 around Viçosa University and later on Universidade Estadual de Campinas (UNICAMP) both in Brazil, mostly on *Coelomera* spp. (Galerucinae) larvae feeding on *Cecropia* spp. (Urticaceae), on *Platyphora* sp. (Chrysomelinae) larvae feeding on *Solanum* spp. (Solanaceae), and on unidentified cassidine larvae feeding on unidentified Convolvulaceae. Following the formal description of the concept, many observations were made worldwide (e.g., Weinstein, 1989; Jolivet et al., 1990). In this review, we are using cycloalex as root for the verb, to cycloalex (e.g., some insects are cycloalexing) and as an adjective (e.g., cycloalexic formation, see also Jolivet, in Capinera, 2008).

Examples in insects (Figures 17 and 18)

Taxonomic and geographic distribution

Cycloalexy is uncommon and sporadically distributed among insect groups. The phenomenon has been reported in adult Hymenoptera as well as immature insects, including nymphs of the orders Hemiptera, as well as larvae of Neuroptera (Ascalaphidae), Coleoptera (Chrysomelidae and Curculionidae), Diptera (Ceratopogonidae, Figure 17E), Hymenoptera (Tenthredinidae), some rare ants (*Conomyrma* spp. and *Myrmecocystus* spp.) (*Trigona* sp., Figure 17F) and, in a less circular fashion, the Lepidoptera (Noctuidae (Figure 17A), Sphingidae and Saturniidae). In the Chrysomelidae (Figure 18), cycloalexy has been reported in the subfamilies Criocerinae, Chrysomelinae, Galerucinae, and Cassidinae, and in one genus in *Phelypera* (Curculionidae) (Jolivet and Maes, 1996).

Cycloalexy tends to be more common in the tropics but is also found in temperate regions (e.g., *Plagiodera*, *Gonioctena*, both chrysomeline chrysomelids, and sawflies (Hymenoptera: Symphyta) Figure 17D). Meyer-Rochow (1972) described the phenomenon among Australian *Paropsis* (Cassidinae) chrysomelids and sawflies.

Cycloalexic formations have also been reported in organisms that lack obvious chemical defenses. For example, some larval saturniids, such as *Lonomia electra* Druce, 1886 in tropical America, aggregate in circular formations (Fitzgerald, personal communication to author PJ); are amongst the most burning larvae in the Saturniidae (Maes to Santiago-Blay, personal communication, April 2012). Other gregarious saturniids, such as *Arsenura armida* (Cramer, 1779) (Figure 17A-B) are non-toxic. They rest by day on the trunk of the food plant in an irregular, oval group and use a trail pheromone for procession, approximately in single file formation (Costa et al., 2003; Jolivet and Verma, 2005). Larval insect processions were described by the great French naturalist Jean-Henri Fabre over a hundred years ago (Santiago-Blay and Shaffer, 2004).

Anecdotal accounts supporting the defensive role of cycloalexy come from observations of what happens when a ring is in peril. Some Nicaraguan aggregating saturniid larvae answer to noise. If a human claps his/her hands, all the larvae move together (Maes to Santiago-Blay, personal communication, April 2012). Before a ring is broken altogether, some members of the ring vibrate, as if they were "agitated". When the circle is broken, predators, such as ants (Hymenoptera: Formicidae) or stink bugs (Hemiptera: Pentatomidae) can easily prey on the relatively isolated chrysomelid larvae. *Coelomera* spp. (Galerucinae) and *Phelypera distigma* (Boheman, 1842) (Curculionidae) larvae fall prey to unidentified predatory pentatomids (Hemiptera) and ants (Formicidae) following the breaking apart of a ring (Jolivet, personal observations).

Acording to Kudo and Ishibashi (1996), cycloalexy appears to be more efficient against insect predators than parasitoids. For example, trigonalyid (Hymenoptera: Trigonalyidae) parasitoids, such as *Taeniogonalos venatoria* Riek, 1962 seem to be repelled by the ring, perhaps by what appears to be a "threatening posture" of the cycloalexic larvae. However, by depositing eggs nearby, which are later swallowed by host sawfly larvae, trigonalyid wasps successfully avoid confronting the defensive ring (Weinstein, 1989, 1991). Although parasitoids, such as *Westwoodia* sp. (Ichneumonidae)

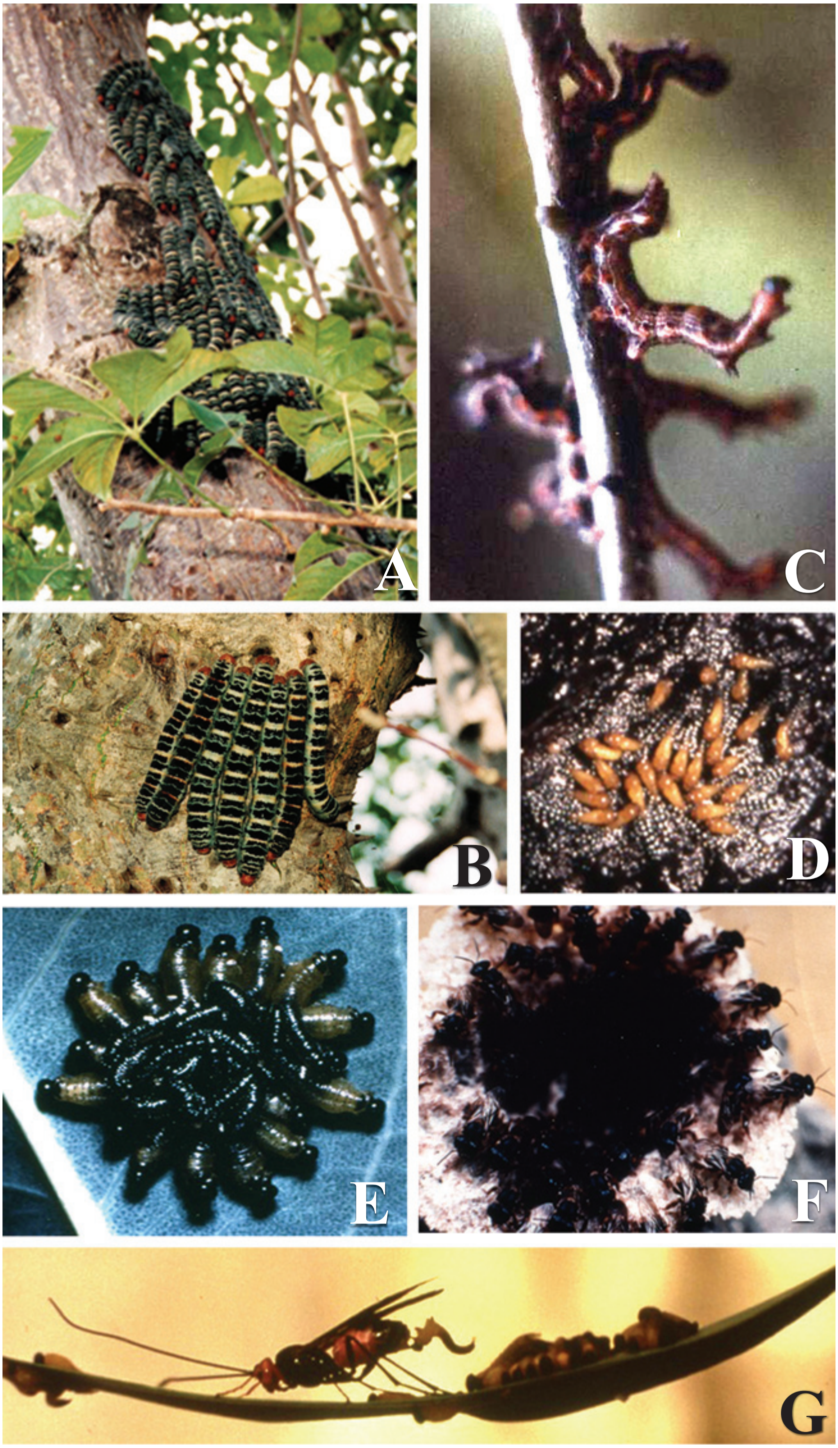

Figure 17. Cycloalexy amongst insects. A–B. *Arsenura armida* (Cramer, 1779) (Lepidoptera: Saturniidae) larvae resting in a less than circular aggregation in an unidentified tree trunk in Nicaragua. Photos by A. Somarriba Siezar, courtesy of J.-M. Maes, herein reproduced with Maes' permission. Author P. J. has

have been observed attacking the cycloalexing Hymenoptera, thus far, they have not been reported attacking cycloalexing Chrysomelidae.

What happens inside the ring? Is there altruism among subsocial cycloalexing larvae, such as members of the Pergidae (Hymenoptera) or Chrysomelidae (Coleoptera), as larvae on the periphery of the ring are more exposed to the risk of predation than the inner ones? In chrysomelids, there are member exchanges between the outer and the inner circle larvae (Jolivet, personal observations). Exchanges between the inner and the outer cycloalexing larvae have been studied by Weinstein and Maelzer (1997) for the Australian sawfly *Perga dorsalis* Leach, 1817 (Hymenoptera: Pergidae). In an elegant example of experimentalism, the outer individuals in a cycloalexic group of *P. dorsalis* were paint-marked — the paint had no effects on the spitfires, as these larvae are called in Australia — and their positions recorded in consecutive nights. Interestingly, about 20% of the cycloalexing larvae were found to preferentially occupy ring's periphery even after breaking the ring to lead in their nocturnal foraging expeditions. These "leaders" often occupied the anterior and posterior – also considered leadership by the authors - positions of these larval "pelotones" as they moved in their feeding *tour de eucalypts*. When a cycloalexic group of *P. dorsalis* is attacked by a predator, such as hymenopteran parasitoids, all the larvae (not just the ones in the periphery) became greatly agitated, regurgitated, made biting movements, as well as moved their heads and abdominal apices, all suggesting a defensive value for the aggregation. Several adaptive explanations for the consistency in leadership behaviors are plausible, but the ideas need to be tested. Also, could there be small genetic differences between the consistent leaders and the consistent followers? Fletcher (2009) studied the benefits of aggregation in the gregarious larvae of the Australian sawfly, *Perga affinis*. She noted that mortality was significantly higher among solitary than aggregating larvae.

Location of cycloalexy and variations of the circle

Commonly, a cycloalexic group is formed on a leaf but it may also be formed, in a less than circular shape, on a petiole, a stem, or a tree trunk. Formation of a nearly perfect

Figure 17. (*Cont.*) seen *A. armida* in oval cycloalexy on an unidentified tree trunk during the day on Ilha de Maracca, Roraima, Amazon River, Brazil. Wagner (2005, p. 243) depicts a similar looking yet smaller group of *Callosamia promethea* Drury, 1773 saturniid larvae feeding on the underside of leaves. C. Unidentified noctuid (Lepidoptera) caterpillars grouped on a stem of a species of *Mussaenda* (Rubiaceae) displaying a "seemingly menacing" attitude. Photographed by P. Jolivet in Tam Dao mountain range of Vietnam. Note the remarkable posture similarity between this species and *Croesus latitarsus* Norton, 1862 (Hymenoptera: Tenthredinidae) on *Betula* sp. or birch (Betulaceae) depicted in Wagner (2005, p. 12). D. Young larvae of *Perga dorsalis* (Hymenoptera: Pergidae) in cycloalexy on a leaf of a *Eucalyptus* sp. in Australia. Photographed by Philip Weinstein, herein reproduced with permission (see also Codell and Raffa, 1993). E. *Forcipomyia fuliginosa* (Meigen, 1818) (Diptera: Ceratopogonidae) larvae in cycloalexy on a coffee tree (*Coffea arabica* L., Rubiaceae) in Costa-Rica. Photographed by Willis Wirth, herein reproduced with permission. F. *Trigona* sp. (Hymenoptera: Apidae) stingless bees forming a ring as they surround the entrance of their nest in Viçosa University, Minas Gerais, Brazil. Photo by P. Jolivet. G. Young larva of *Perga dorsalis* apparently biting the ovipositor of a *Westwoodia* sp. (Hymenoptera: Ichneumonidae), a parasitoid in Australia. Photographed by Philip Weinstein, herein reproduced with permission. Images C–G reproduced with permission of the Editor of Nouvelle Revue d'Entomologie (Nouvelle Série).

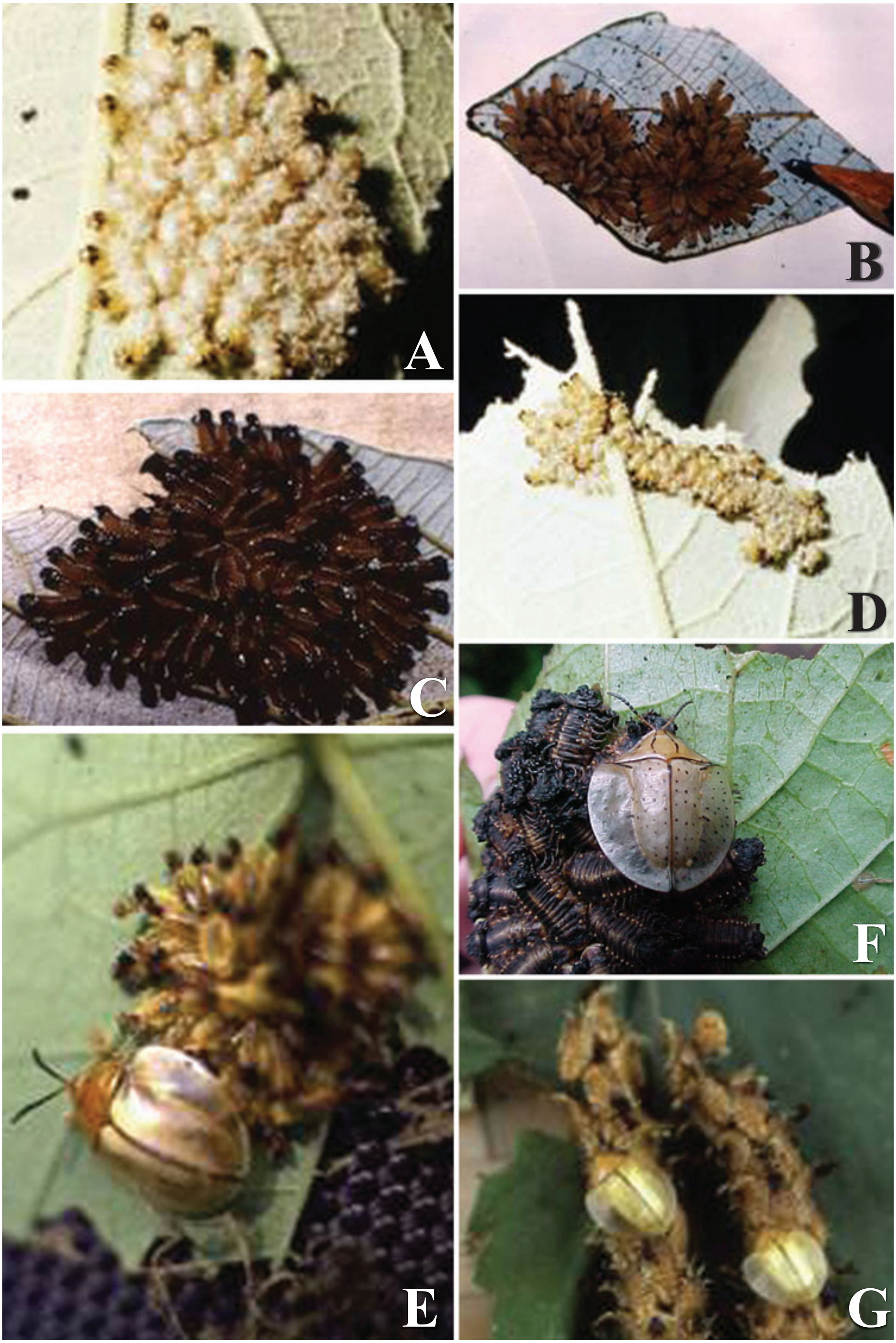

Figure 18. Cycloalexy among Coleoptera Chrysomelidae. A. *Platyphora conviva* (Stål, 1858) (Chrysomelinae). One ring circle. National Park of Itatiaria, Rio de Janeiro, Brazil. Photo by P. Jolivet. B. *Coelomera raquia* Bechyně, 1956 (Galerucinae). Duplication of the ring by the larvae themselves.

circle may be seen in larvae and, exceptionally, in pupae of species of *Forcypomyia* (Diptera: Ceratopogonidae) that live in Central American cacao (*Theobroma cacao*, L., Malvaceae) plantations. These creatures cycloalex with their heads pointed towards the center (Hinton, 1955; Saunders, 1924; Young, 1984). Ants and bees (e.g., *Trigona*), sometimes appear to protect the entrance to a hive by cycloalexing around the opening of their nest, with heads pointing towards the potential intruders (Figure 17F, see also Koedam et al., 1996). Typically, cycloalexy is circular but the circle may divide into two or three when larvae have grown. On the other hand, aggregations of ascalaphid neuropteran larvae, *Ascaloptynx furciger* (McLachlan, 1891), around a branch are a form of cycloalexy (Henry, 1972).

Cycloalexy well after hatching: formation and defensive reactions

The larvae of the processionary Neotropical weevil (Curculionidae), *Phelypera distigma (*Boheman, 1842), travel during the night in a loose procession along a branch of their host tree, *Guazuma ulmifolia* Lam. (Sterculiaceae) (Jolivet and Maes, 1996; Costa et al., 2004; Fitzgerald et al., 2004). When larvae lose tactile contact with the larva immediately ahead of them, they rely on a trail pheromone, which lasts some four hours. The larvae secrete the pheromone from the posteroventral surface of their abdomen. When resting, the larvae of *P. distigma* rearrange themselves in perfect circular formations. The cycloalexic formations maximize the amount of body contact in an aggregate and allow tactile signals to radiate rapidly through the group. Larvae of *P. distigma* readily bite and regurgitate, when disturbed by potential predators. Apparently, larvae of *Phelypera schuppeli* (Boheman, 1834) from Brazil, as well as the other thirteen species of *Phelypera* cycloalex (Diniz and Morais, 1996).

Among the Hymenoptera, larvae of tenthredinoids, such as toxic Gondwanan *Perga dorsalis*, *Perga affinis* Kirby, and others pergids arrange themselves in an oval mass — keeping physical contact with each other — and, when disturbed by the smallest tactile stimulus, they eject a liquid and raise their heads or abdomens seemingly for defense, as do chrysomelid cycloalexic larvae. Before reuniting, a group of dispersed conspecific pergid larvae communicate using low frequency vibrations by tapping the leaves with their uropod (Lewis, 1836; Evans, 1934; Carne, 1962; Weinstein, 1991).

Among the Symphyta, the Argidae show semisocial behavior in Brazil, with maternal care and cycloalexy (Souza Dias, 1975, 1976). Parental care and larval grouping has been known among sawflies for a long time (Froggatt, 1890; Wheeler and Mann,

Figure 18. (*Cont.*) Bernardo, Goias, Brazil. Later on it will divide into three rings. Photo by P. Jolivet. C. *Coelomera lanio* (Dalman, 1823) (Galerucinae). First instar larvae in a cycloalexic ring, starting to divide. Serra do Japi, São Paulo, Brazil. Photo by P. Jolivet. D. Platyphora conviva (Chrysomelinae). Larvae on line on a leaf. Feeding on the National Park of Itataria. Rio de Janeiro, Brazil. Photo by P. Jolivet. E. *Omaspides tricolorata* (Boheman, 1854) (Cassidinae). Mother protecting larvae in a cycloalexy ring on an unidentified species of *Ipomoea* (Convolvulaceae) in Serra do Japi, São Paulo, Brazil. Photo by P. Jolivet. F. *Acromis sparsa* (Boheman, 1854). Photo by L. Huez, courtesy of J.-M. Maes, herein reproduced with Maes' permission. G. *Paromaspides sobrina* (Boheman, 1854) (Cassidinae). Mothers guarding their cycloalexic larvae over a stem of an unidentified species of *Ipomoea* (Convolvulaceae). Photo by P. Jolivet. Images A-E, G reproduced with permission of the Editor of Nouvelle Revue d'Entomologie (Nouvelle Série).

Table 2. Genera of Chrysomelidae reported to cycloalex, their geographical distribution, and selected references.

Subfamily (-inae), genus, and, if noted, specific epithet. In all cases, genera and species are followed by the author, year	Geographical distribution	Selected references
Criocerinae		
Lema apicalis Lacordaire, 1845	southern Brazil	Medeiros, 1991; Medeiros et al., 1996
Lema reticulosa Clark, 1866	southern Brazil	Medeiros, 1991; Medeiros et al., 1996
Lilioceris nigropectoralis (Pic, 1928)	Taiwan	Chi-Feng Lee, pers. commun. to author PJ, 2008
Lilioceris formosana Heinze, 1943	Taiwan	Chi-Feng Lee, pers. commun. to author PJ, 2008
Chrysomelinae		
Agrosteomela Gistl, 1857	India, Himalaya	Jolivet and Verma, 2011
Chrysophtharta Weise, 1901	Australia	De Little, 1981
Eugonycha Chevrolat, 1843	Brazil	Vasconcelos-Neto and Jolivet, 1994
Gonioctena Chevrolat, 1837	Holarctic	Vasconcelos-Neto and Jolivet, 1994
Labidomera suturella Chevrolat, 1844	Central America	Choe, 1989; Daccordi and LeSage, 1999
Paropsis Olivierwe, 1807	Australia	Vasconcelos-Neto and Jolivet, 1994 ; Selman, 1994
Paropsisterna Motschulsky, 1860	Australia	Jolivet and Verma, 2011
Phratora Chevrolat, 1837	Holarctic	Vasconcelos-Neto and Jolivet, 1994
Phyllocharis undulata (L., 1763)	Indonesia, southeastern Asia, New Guinea, Australia	Mohamedsaid, 2008. Probably the larvae of all congenerics and many other members of the Paropsini cycloalex.
Plagiodera Chevrolat, 1837	Worldwide, except Australia and the West Indies	Vasconcelos-Neto and Jolivet, 1994; Wade, 1994
Platyphora Gistel, 1857	Neotropical	Vasconcelos-Neto and Jolivet, 1994
Proseicela Erichson, 1847	Central and South America	Medeiros, 1991
Pterodunga Daccordi, 2000	Australia	Reid et al. 2009
Galerucinae		
Coelomera Chevrolat, 1837	Neotropical	Vasconcelos-Neto and Jolivet, 1994. Larvae closely related to *Coelomera* need to be observed closely for possible cases of cycloalexy.

(*Continued*)

Table 2. (*Cont.*)

Subfamily (-inae), genus, and, if noted, specific epithet. In all cases, genera and species are followed by the author, year	Geographical distribution	Selected references
Cassidinae		
Acromis Chevrolat, 1836	Central and South America	Windsor, 1987; Windsor and Choe, 1994
Aspidomorpha Hope, 1840	Old World tropics	Verma, 1992
Chelymorpha Chevrolat, 1837	New World	Vasconcelos-Neto and Jolivet, 1988
Conchyloctenia Spaeth, 1902	Africa	Heron, 1992, 1999
Ogdoecosta Spaeth, 1909	Central America and Mexico	Romero-Nápoles, 1990
Omaspides Chevrolat, 1836	Neotropical	Windsor and Choe, 1994; Freiro-Costa and Vasconcellos-Neto, pers. comm. to author PJ, 1994; Freiro-Costa, 1995
Stolas Billberg, 1820	Central and South America	Windsor and Choe, 1994; Vasconcelos-Neto and Jolivet, 1994

If species not noted, based on Seeno and Wilcox (1982), with modifications.

1923). Weinstein (1988, 1989) has observed what looks like a case of altruistic suicide of a larva of a pergid by biting the ovipositor of a parasitoid wasp.

Trigona (Apidae) bees sometimes cycloalex outside at the entrance of their nests, apparently protecting their colony (Figure 17F) (Jolivet et al., 1990). The same phenomenon has been observed in *Conomyrma* and numerous other ants, bees, and wasps (Vespidae), seemingly to protect the colony from invaders.

Cycloalexy among the Chrysomelidae (Table 2 and Figure 18)

Although chemical defenses are widespread in the Chrysomelidae (Chaboo, 2011; Prathapan and Chaboo, 2011), defensive cycloalexy is less common. Among the Chrysomelidae, cycloalexy has been reported in four subfamilies (Chrysomelinae, Galerucinae, Cassidinae, and Criocerinae) but it probably occurs in other subfamilies. Also, often cycloalexy is related to maternal care (Jolivet, 1999a).

Eggs

Many chrysomelids, such as species of *Chrysomela* and *Phratora* (Chrysomelinae), deposit their toxic eggs in clusters (Jolivet and Verma, 1987b, 2002). As we have discussed, egg association appears to be associated with the formation of aggregations.

Larvae

Many genera of chrysomelids have cycloalexing larvae. How is the larval group formed and maintained? In subsocial chrysomelids, like *P. versicolora*, leaf geometry is an important determinant of the cycloalexic group shape. Not surprisingly, in more elongated leaves, the group becomes more elongated, looking closer to a phalanx (*sensu* Wade, 1994) or a line (*sensu* Selman, 1994). Interestingly, experimental studies to evaluate the survivorship costs of defensive secretions by larvae of *P. versicolora* were inconclusive (Wade, 1994). Could the leaf chemistry of the different species of *Salix* (Salicaceae) upon which *P. versicolora* feeds constitute an important factor on the relative survivorship of the larvae, regardless of their ability to group?

Tapping is directly related to the maintenance of arthropod aggregations (Meyer-Rochow, 1972). In the Paropsini (Chrysomelidae) that live on *Eucalyptus* (Myrtaceae) leaves as in pergid sawflies (Hymenoptera), tapping is used for intraspecific communication and for recruiting lost larvae. For example, Jolivet (2004) has frequently observed larvae of Chrysomelidae fighting unidentified pentatomoids (Hemiptera) and ants (Hymenoptera), often successfully, as long as the circle is not broken. The behaviors that have been inferred as possibly having a defensive functional significance against predators or parasitoids include, coordinated movements, such as the adoption of seemingly threatening postures, regurgitation, and biting movements (Jolivet, 2004).

If larvae form groups, sometimes biologists do not report whether the larvae have heads or abdomens at the periphery of the ring. In either position the larval heads, make threatening movements against potential predators and readily bite as well as regurgitate (Jolivet, personal observations).

i. CPC: Cephaloperipheral cycloalexy or cycloalexy with heads at the periphery of the circle: species of Lema, Lilioceris *(Criocerinae), and* Platyphora conviva *(Chrysomelinae)*

In the criocerines, *Lema reticulosa* Clark, *L. apicalis* Lacordaire, 1845 and a third species of *Lema* in Brazil, larvae hatch from an egg mass and readily form large cycloalexic groups in which they remain until the end of their second instar (Medeiros et al., 1996). According to Chi-Feng Lee (personal communication to author PJ), *Lilioceris nigropectoralis* (Pic, 1928) and *Lilioceris formosana* Heinze, 1943 cycloalex in Taiwan.

Many species of *Platyphora* (Chrysomelinae) are viviparous, that is, larvae are not surrounded by chorion at birth (Bontems, 1988 and Bontems, personal communication to author PJ). Larva are surrounded by a chorion at birth are said to be ovoviviparous. Adults and larvae *P. conviva* (Figure 18A and 18D) eat hard leaved *Solanum* (Solanaceae) shrubs, like many – but not all – species of *Platyphora*. Some species of *Platyphora* also feed on more distantly related (Angiosperm Phylogeny Group, 2009) Central American trees in the family Apocynaceae.

Platyphora conviva larvae congregate in circles, with only a few larvae in the center of the circle, on the abaxial side of leaves. Adult *P. conviva* are viviparous and larviposit one by one for about one hour, thereafter the larvae begin cycloalexing immediately, with the circle modified as more larvae are larviposited. The adult takes to an exposed position on the upper, or adaxial, surface of the leaf and never contacts the larvae again. On the other hand, the larvae cover themselves with hairs taken from the underside of the leaf as do more solitary larvae of Chlamisinae. When the larvae are disturbed, the peripherally-positioned larvae raise their front legs and open their mouths in a "menacing-looking" display. A gastric secretion derived from their host plants is ejected through the mouth. If disturbed further, these larvae attempt to bite the attacker. If the circle is broken, the larvae fall easy prey to pentatomids and ants (Jolivet, personal observations). However, at dusk and during the night, when ants and pentatomids do not attack the larvae, the circle breaks and the chrysomelids larvae position themselves in a row and feed along the edge of the leaf. The circular pattern is readopted each morning and maintained during the daylight hours. When molting, the larvae adopt their defensive posture but do not remain in a circle. New hairs are stripped off from the leaves to replace those lost with the exuvium. In contrast, adult *Platyphora fasciatomaculata* (Stål, 1857) lay large groups of small first instar larvae that immediately display vigorous cycloalexic behavior, forming tight circles on the underside of leaves of *Solanum mauritianum* Scopoli (Solanaceae) in Brazil (Medeiros et al., 1996). If disturbed, the larvae regurgitate, swing the body side by side or up and down, and make biting movements, as do most *Platyphora* larvae.

ii. APC: Abdominoperipheral cycloalexy or cycloalexy with abdomens on outside of circle. Coelomera spp. *(Galerucinae) and cassidines*

Andrade (1981), in Brazil, was the first to study the relationships of *Coelomera* (Figure 18B and 18C) with *Cecropia* plants. The 35 species of the tropical American genus *Coelomera* (Galerucinae) have cycloalexic larvae on *Cecropia* trees (Jolivet, 1987a, 1988b; Vasconcellos-Neto and Jolivet, 1989, 1994), however, cycloalexy is not associated with parental care. Depending on the species, *Coelomera* may oviposit in oothecae placed inside a *Cecropia* stem or under the leaves. The eggs are deposited inside the stems only if it lacks *Azteca* eggs or ants (Jolivet, 1992, Jolivet and Salinas, 1993). The competing *Azteca* queen ant opens the prostoma on the stem in two hours but it takes female *Coelomera ruficornis* Baly, 1865 twelve hours to do the same (Andrade and Carauta, 1982; Andrade, 1981, 1984). After getting out from the hole, the female *Coelomera* seals the opening and the larvae will have to reopen to get out when they hatch. The defense is mainly directed at *Azteca* ants which are also symbiotic with *Cecropia* trees. The 70 or so emergent larvae form first one ring, then two or three rings when they have grown. When disturbed, the larvae raise their abdomens, which are protected by a supra-anal shield, and eject a fluid from the anus. The rings are nocturnal resting formations under leaves, the larvae feeding by day. The formation persists during molting and is rearranged for disposition of old exuviae adherent to the substrate (Jolivet, 1988b).

Cycloalexy has been reported in a wide array of cassidines (Cuignet et al., 2008) where it is often associated with parental care. For example, the tropical American larvae of *Chelymorpha infecta* Boheman, 1854 (= *Chelymorpha informis* Spaeth, 1928) (Cassidinae) exhibit cycloalexy on the adaxial surface of species of *Ipomoea* (Convolvulaceae) leaves. They cycloalex during the night and mainly in defense against *Pseudomyrmex* ants. The species is interesting because the disturbed larvae rear up in successive waves, waving the abdominal furca. When the larvae grow, they cycloalex around the stems of the host plants as flat areas on the leaves are insufficient. Many other cassidines also cycloalex. As in other cases of cycloalexy with maternal care, females often lay on the eggs, and before the ring made out of larvae forms on the leaf, the mother is long gone (Goidanich, 1956; Jolivet, 1988a; Windsor and Choe, 1994). According to Windsor (1987), *Acromis sparsa* (Boheman, 1854) larvae assemble as a tight knot of bodies, either encircling the stem or forming a flat rosette on the adaxial — or underside — portion of *Ipomoea* (Convolvulacae) leaves. *Omaspides tricolorata* (Boheman, 1854) (Figure 18E) and *Paramospides sobrina* (Figure 18G) have an elaborate defensive behavior, combining female parental care and larval cycloalexy (Vasconcellos-Neto, personal communication to author PJ). In India, cycloalexy has been described in the cassidine *Aspidomorpha miliaris* (Verma, 1992, 1996). When resting, larvae of this tortoise beetle form compact oval groups, with their abdominal ends pointing to the periphery on the abaxial surface of leaves of *Ipomoea carnea* Jacquelin (Convolvulaceae). When such an aggregate is disturbed, the larvae curve their abdomens upward in a seemingly threatening posture. Additionally, Nakamura and Abbas (1987, 1989, 1992) noted that when cycloalexing Sumatran larvae of *A. miliaris*, which live on *Ipomoea carnea* Jace. (Convolvulaceae), are about to pupate, they disperse and suffer a steep rise in mortality. The latter observation further supports the hypothesis that cycloalexy is associated with larval defense. Heron (1992, 1999) has reported cycloalexy in two South African cassidines, *Conchyloctenia punctata* (Fabricius, 1787) and *Aspidomorpha puncticosta* Boheman, 1854. Both the species live on *Ipomoea* and the larvae of both, when at rest, cycloalex tightly on the abaxial surface of leaves, the outer larvae with their caudal ends towards the periphery. As in the Indian population of *A. miliaris*, the larvae of these South African cassidines maintain themselves in a tight row of gregariousness organisms along the leaf margin, even when feeding, moving away from it as the edge of the leaf is eaten away (Verma, 1992).

The cycloalexic bond does not always last the entire larval stage (Wade, 1994). For instance, the cycloalexic larval groups of *Conchyloctenia punctata*, which are circular to oval, appear to weaken after the third instar when some larvae may become solitary (Heron, 1992, 1999). In contrast to cycloalexic *Aspidomorpha puncticosta*, the larvae of South African *Aspidomorpha submutata* Weise, 1899 remain solitary (Heron, 2008).

Many other cases of this most common "abdomens out" cycloalexy are known among the Chrysomelidae but, as far as we are aware, no detailed study has been published. Cycloalexy has been reported from eleven genera of Chrysomelinae: *Gonioctena* Chevrolat, *Plagiodera* Chevrolat, *Phratora* Chevrolat, *Paropsis* Olivier, *Paropsisterna* Motschulsky, *Chrysophtharta* Weise, *Platyphora* Gistel, *Proseicela* Erichson, *Eugonycha* Chevrolat, *Labidomera* Chevrolat, and *Phyllocharis* Dalman. The list is far from complete and more Paropsini may cycloalex (Simmul and deLittle, 1999). Furthermore, not all congeneric species or confamilial genera are cycloalexic or even gregarious (de Little, 1981). Apparently, all species of *Gonioctena* show different gradations of maternal care and cycloalexy in the Holarctic (Kudo and Hasegawa, 2004; Kudo and Ishibashi, 1995; Kudo et al., 1995). *Gonioctena rufipes* (DeGeer, 1775) (Chrysomelinae; there are several spellings in use for "DeGeer"), which lives on poplar (*Populus*, Salicaceae) leaves in Europe, cycloalexes and shows maternal care. Also, *Labidomera suturella* Guérin Meneville, 1838 larvae, *Platyphora selvae* Daccordi, 1994 (cf., Reid et al., 2009) are gregarious with maternal care (Choe, 1989).

Among the Paropsini, some larvae remain gregarious throughout the larval stages, such as *Paropsis atomaria* Olivier, 1807 (Simmul and de Little, 1999) while others, such as *Paropsisterna tigrina* (Chapuis, 1877), *Paropsisterna bimaculata* (Olivier, 1807, formerly *Chrysophtharta bimaculata* Olivier, 1807), and *Paropsis charybdis* Stål, 1860 may disperse in small groups or live individually, following the first or second instar. The Australian Paropsini (Chrysomelinae), which feeds on *Eucalyptus* (Myrtaceae) or *Acacia* (Fabaceae) trees, includes many cycloalexic species, such as those in the genera *Chrysophtharta* and *Paropsis*. Interestingly, some of the cycloalexic aggregations of paropsine chrysomelids, which secrete hydrogen cyanidae (HCN) when disturbed and are useful devices in entomological "killing jars", include larvae of different instars and can be heterospecific (Selman, 1994). *Phyllocharis undulata* (Linnaeus, 1763) (Chrysomelinae), which lives in the island of Lombok (Indonesia) and feeds on *Clerodendrum inerme* (L.) (Verbenaceae), has larval cycloalexy, with abdomens juxtaposed at the periphery (Mohamedsaid, 2008).

Many South American chrysomeline genera are viviparous, some of them cycloalexic and some of those cycloalexic forms also have maternal care. However, there are always exceptions. For instance, *Platyphora quadrisignata* (Germar, 1824) feeding on *Solanum variabile*, lays isolated larvae, which do not group into rings. Among the *Platyphora*, which live on trees, the biology is totally unknown.

In Australia, Reid et al. (2009) described ring-forming behavior among larvae of *Pterodunga mirabile* Daccordi, 2000 where the subsociality is combined with maternal care. It seems that many other related genera of Chrysomelinae are subsocial in Australia and should display cycloalexy in the larval stage. In Taiwan, *Agrosteomela chinensis* (Weise, 1922) female, a viviparous species, lays 16 to 20 larvae, which seem to be gregarious (Bontems and Lee, 2008). Perhaps, the larvae are cycloalexic and as in the case with sawflies, heterospecific aggregations are possible (Weinstein, 1989; Selman, 1994).

Stigmergy or induced communal labor by conspecifics

The group effect, as per Grassé (1959b), plays a role in the social regulation among termites (Isoptera), as well as wasps, bees, and ants (Hymenoptera). The word "stigmergy" comes from the Greek words *stigma* (στίγμα) stigma, which means mark or sign, and *ergon* (ἔργον), which means work or action. Hence, stigmergy is the incitation of additional labor in conspecifics through a mark or sign of such of work previously accomplished (Hölldobler et al., 2009). Stigmergy involves behavioral positive feedback loops. For instance, the cooperation seen in weaver ants, *Oecophylla* spp. (Hymenoptera) to build nests from green leaves, in web-spinning sawfly larvae (Pamphilidae) and *Malacosoma* spp. (Lasiocampidae) caterpillars to build their silken homes, as well as in many activities in eusocial insects, are examples of stigmergy. The "wisdom of the crowds" is the result of a complex hierarchical organization regulated through intricate chemical pathways among eusocial organisms (Grassé, 1946, 1952, 1959a, 1959b; Grassé and Chauvin, 1944).

Figure 19. Aggregations related to epialexy. A. Larvae of the European Pine Sawfly, *Neodiprion sertifer* (Geoffroy) (Hymenoptera: Diprionidae). Image, taken approximately in May 2002 in Mansfield, CT, USA, was originally used in Anonymous (2008) and it is herein reproduced with permission from R. S. Cowles (The Connecticut Agricultural Experiment Station). According to Cowles (pers. commun. to Santiago-Blay, April 2012), "by the next year, the sawflies had killed the pine tree through defoliation". B. Epialexing *Endromis versicolora* (Linnaeus, 1758) (Lepidoptera: Endromidae). Image kindly provided by Andre Lequet (Nantes, France), lepidopterist, insectes-net.fr, herein reproduced with permission.

Epialexy or resting aggregations (Figure 19A-B)

Another form of aggregation, frequent in tropical America, is epialexy, a term author PJ coined with Joao Vasconcellos-Neto (Jolivet and Verma, 2012). The word, epialexy, is derived from two Greek words, epi (ἐπί), which means "on", and *alk* (*or alek-*), whose meaning we described in the cycloalexy section. This behavior, which is common in Lepidoptera larvae, consists of organisms located on the midvein or a similar more medially-located elongated structure of a plant after devouring most of the leaf blade.

Prop (1960) mentions a similar case among larval *Diprion sertifer* (Geoffroy, 1785) (Hymenoptera: Tenthredinidae) congregated over pine needles in The Netherlands. Costa (2006, p. 652) illustrates larvae of *Neodiprion lecontei* (Fitch, 1858) (Hymenoptera: Diprionidae) aggregated over needles of *Pinus virginiana* Mill. (Pinaceae) but they can be signaling to each other or defoliating their host plants (see http://www.ct.gov/caes/cwp/view.asp?a=2823&q=377886). JASB has frequently seen unidentified caterpillars on the midvein or branchlets of otherwise eaten celery, *Apium graveolens* L. (Apiaceae), leaves. We are not aware of a biological significance for this type of aggregations on elongated structures.

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