

Review article

Self-assemblages in insect societies

C. Anderson^{1,2}, G. Theraulaz³ and J.-L. Deneubourg⁴

¹ School of Industrial and Systems Engineering, Georgia Institute of Technology, Atlanta, GA 30332-0205, USA

² Current address: LS Biologie I, Universität Regensburg, Universitätsstrasse 31, D-93040 Regensburg, Germany, e-mail: carl.anderson@biologie.uni-regensburg.de

³ Laboratoire d'éthologie et cognition animale, CNRS, ERS 2382, Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse Cédex 4, France, e-mail: theraula@cict.fr

⁴ Center for Non-Linear Phenomena and Complex Systems, CP 231, Université Libre de Bruxelles, Boulevard du Triomphe, B-1050 Brussels, Belgium, e-mail: jldeneub@pop.vub.ac.be

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Summary. In insect societies, a number of very striking collective structures are formed by individuals linking themselves to one another. One such example is an army ant bivouac. These structures are termed self-assemblages and are part of a more general and important aspect of insect societies – intermediate-level parts – in which functional group-level adaptive structures are formed. These parts are, in a sense, the tissues and organs of complex insect societies. Here we review the natural history of self-assemblages in insect societies. We find that at least 18 different types of structure exist: bivouacs, bridges, curtains, droplets, escape droplets, festoons, fills, flanges, ladders, ovens, plugs, pulling chains, queen clusters, rafts, swarms, thermoregulatory clusters, tunnels, and walls. These self-assemblages are found in a variety of species of ants, bees, and wasps, but (as far as we are aware) not in termites. The function of these self-assemblages can be grouped under five broad categories which are not mutually exclusive: 1) defence, 2) pulling structures, 3) thermoregulation, 4) colony survival under inclement conditions, and 5) ease of passage when crossing an obstacle. The paucity of our knowledge concerning the factors that favour self-assemblage formation and the likely proximate mechanisms are highlighted.

Key words: Self-assemblages, chains, bivouacs, swarms, aggregation.

Introduction

Insect societies provide us with remarkable examples of sophisticated collective activity including nest construction, complex foraging strategies, and collective decision making (e.g. Deneubourg and Goss, 1989; Hölldobler and Wilson,

1990; Seeley, 1995; Bonabeau et al., 1999; Anderson and Franks, 2001; Camazine et al., 2001). Perhaps one of the most visually striking examples, but at the same time most understudied, are the physical structures comprised of individuals that have linked themselves to one another. These structures, which we term “self-assemblages,” which form when “individuals grip onto each other” (Lioni, 2000; Lioni et al., 2001), are a product of the process of self-assembly. For instance, an army ant bivouac is an adaptive structure comprised of many workers linked together and is therefore a self-assemblage.

Self-assemblages (hereafter SAs) are a potentially important aspect of insect societies because they are examples of what have been termed “intermediate-level parts” (Anderson and McShea 2001a, b; McShea and Anderson, in press) which are usually an easily identified and unambiguous characteristic of social complexity in insect societies. These structures are “intermediate” because they exist at a level intermediate to that of the individual and that of the colony. They are “parts” meaning that they are a set of strongly interacting components, which may be individuals or behaviours. Importantly, these parts exhibit a group-level functionality in that they exhibit properties not found in the individual components. For instance, as discussed below, army ants may form a living bridge across a gap. A single ant is too small to form such a structure, and the functionality – passage for the colony across the gap – only exists at the level of the group, in this case the structure, and not in the individuals. Thus, one can consider intermediate level parts as the tissues and organs of a complex insect society (see Wilson, 1985; Anderson and McShea, 2001a, b, in prep.). Self-assemblages are only one class of intermediate-level parts; others include groups and teams (sensu Anderson and Franks, 2001), the set of individuals tackling a partitioned task, nests, and the various structures that ants build away from the nest, and are

discussed in detail elsewhere (Anderson and Franks, 2001; Anderson and McShea, 2001 a, b, in prep.).

The primary aim of this study is to review the different self-assemblages currently known in insect societies; we catalog the types of structures that are observed, list the species in which they are found, and categorize the different classes of functions that they serve. It is unfortunate that we understand very little about the factors that favour self-assemblage formation and the proximate mechanisms by which they are formed. Thus, in a sense, the purpose of this review is to draw attention to these fascinating structures about which we know so little.

Self-assemblages in insect societies

Insect societies exhibit at least 18 different self-assemblages (Table 1). These include a range of structures and functions and are found in a variety of genera of ants, bees, and wasps, but, as far as we are aware, not in termites. (Possible reasons why self-assemblages are less likely to be found in termites are discussed later.) In this section we review these self-assemblages found in insect societies, concentrating on both structure and the likely adaptive benefits they convey to the colony.

We have tentatively arranged these self-assemblages in increasing order of overall “complexity.” Our definition of complexity has at least two components:

- 1) The arrangement of individuals – a formless random arrangement individuals is not crucial to function (e.g. an ant raft cluster, see below) is considered simpler than a SA with a definite structure and a particular (required) arrangement of individuals (e.g., ladder, see below).
- 2) How dynamic and adaptable the final structure is – a static structure (e.g., raft) is considered simpler than a dynamic structure that must adapt and change over time (in response to intrinsic or extrinsic factors) in order to function effectively (e.g., pulling chain, see below).

A third component, constraint, is discussed in the next section.

Clusters of individuals

Defensive doorways (“plugs”)

A number of species of ants, particularly in the (sub)genera *Colobopsis* and *Zacryptocerus*, and also some termites (Scheffrahn et al., 1998), have specially-shaped “phragmot-

ic” heads that they use to block nest entrances during nest guarding (Hermann, 1981). A single individual can block the entrance satisfactorily in some species, but in *Colobopsis truncatus* several workers may also link together to form a functional doorway to plug an entrance (Szabó-Patay, 1928; Wilson, 1971: 159–160; Fig. 1 a). It is currently not clear whether there is any division of labour within these “plugs” when a second row of one or more workers is present. If these latter workers have a different role from the front row workers, perhaps acting as a keystone lock, then this classifies as a “team” rather than a “group” (sensu stricto Anderson and Franks, 2001) and may classify as rather a sophisticated SA. As it stands, we suggest these plugs are the simplest SAs.

Rafts

When their nests are slowly flooded, a number of species are known to form rafts with individuals linking together to produce a floating knot of workers (Fig. 1 b). These species include *Solenopsis germinata* (Brazilian Pantanal and Colombian and Venezuelan Llanos; Jaffe, 1993), *S. invicta* (Southern USA; Wilson and Eads, 1949; Green and Hutchins, 1960; Morrill, 1974), *Camponotus compressus* (India; Hingston, 1922), *Lasius umbratus* (England; Donisthorpe, 1915), *Myrmica gallienii* (Germany; Münch and Engels, 1994), *Dorylus (Anomma) arcens* (W. Africa; Hingston, 1922). (Swimming balls of unspecified army ants and leaf-cutting attini were reported by Maidl, 1934 [cited in Buschinger and Maschwitz, 1984].)

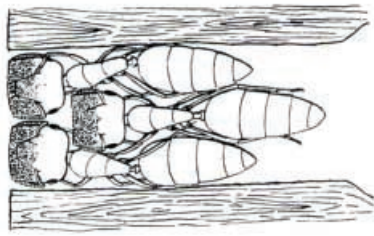
In some cases, these rafts consist solely of workers but in other case queens and brood may ride upon the raft (Morrill, 1974) (see also Münch and Engels, 1994: Table 1). Buschinger and Maschwitz (1984) state that during nest flooding in genera such as *Myrmica* and *Lasius*, clusters will form around the queen and brood at the top of grass stems or poles (see also Hoyt, 1996: p. 149). Presumably these will act as rafts if the water level rises sufficiently high to reach these clusters.

Rafts appear to be a survival strategy against (tropical) inundations in general, and especially during the rainy season in tropical low-lying areas, such as the Brazilian Pantanal, in which large areas may be regularly flooded (e.g., Jaffe, 1993). With queenless rafts, however, one must question whether these are simply clusters of dying ants rather than adaptive SAs.

Anti-predator “ovens”

Ono et al. (1987, 1995) report an unusual defensive behaviour in the Japanese honey bee (*Apis cerana japonica*) against attack from predatory hornets. The hornet *Vespa*

Figure 1. A selection of self-assemblages in insect societies. a) A plug of workers acting as a door in *Colobopsis truncata* (After Szabó-Patay, 1928). b) A raft of *Solenopsis invicta* in flood waters (© Bart D. Drees, Texas Fire Ant Project Coordinator). c) Balling in the Japanese honeybee *Apis cerana japonica* (© Masato Ono). d) A reproductive swarm in the honey bee *Apis mellifera* (© Scott Camazine). e) A thick wall of soldiers and other workers in the army ant *Dorylus wilverthi* (© Nigel R Franks). f) A curtain of the giant honeybee, *Apis dorsata* (© Thomas D. Seeley). g) An escape droplet in *Oecophylla smaragdina* (© Ulrich Maschwitz). h) and i) Droplets in *Linepithema humile* (= *Iridomyrmex humilis*) (© Guy Theraulaz). j) A bivouac in the army ant *Eciton burchelli* (© S. Powell). k) An exploratory bridge in *Oecophylla longinoda* (© Guy Theraulaz). l) and m) Pulling chains in *Oecophylla longinoda* (© Guy Theraulaz).



a



b



c



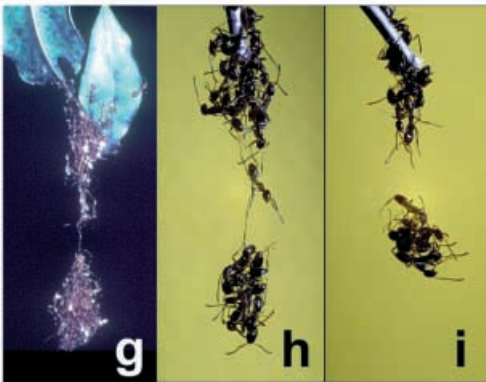
d



e



f



g

h

i



j



k



l



m

Table 1. Social insect self-assemblages classified by structure, that is, whether they are essentially 1D (one-dimensional), 2D, or 3D structures

Self-assemblage	Structure		
	Chain (1D)	Mesh (2D)	Cluster (3D)
Bivouac	•	•	•
Bridges	•	•	•
Curtains		•	
(Escape) droplets			•
Festoons	•	•	
Fills		•	•
Flanges	?	•	?
Ladders	•		
Ovens			•
Plug			•
Pulling chains	•	•	
Queen clusters			•
Rafts			•
Swarms			•
Thermoregulatory clusters			•
Tunnels		•	•
Walls		•	•

mandarina japonica has evolved a group predation strategy against other social bees and wasps. A scout hornet first marks the location of the site with a pheromone and other hornets will later attack the prey en masse. However, *A. cerana japonica* appears to have co-evolved to detect this marking behavior and may attack the lone scent-marking hornet en masse themselves. When this occurs, four or five hundred bees will form a tight ball around the hornet, a behaviour the authors term “balling” (Fig. 1c). The large number of bees and the compactness of the ball means that the internal temperature of the ball, i.e. the hornet’s “ambient” temperature, is raised sufficiently high to kill the hornet but not the bees. The lethal temperature for the bees is 48–50°C whereas for the hornet it is only 44–46°C. In effect, the ball is used to form an oven to cook the hornet. Ono et al. (1995) also suggest that an alarm pheromone, isoamyl acetate, whose evaporation is aided by the high temperatures, may act as a recruitment signal for other bees to join the structure. This species of bee reacts in a similar manner to attacks from a solitary hunting hornet, *V. simillima xanthoptera*, but the balls only consist of around 180–300 bees, but the effect is the same. Lastly, Ono et al. (1987) mention similar behaviour for the European honey bee, *Apis mellifera*, but little detail is provided.

Swarms

Various species of social bees and wasps reproduce by colony fission producing a reproductive swarm consisting of around half of the colony’s workers and one or more queens. The swarm cluster usually forms on a nearby tree branch and scouts search for a new nest site (Lindauer, 1955; von Frisch, 1967; Seeley and Morse, 1976; Jeanne, 1991; Camazine et

al., 1999; Fig. 1d). Whereas reproductive swarms are the result of natural colony growth, some swarms may be “absconding,” a colony response to disturbance – especially in the Africanized honey bee (Winston, 1992) – predation, or other unsatisfactory aspects of the current nest, such as leaks. In both swarm types the function is the same: to give the colony space and time to find a new nest site.

In honey bees, scouts leave the swarm, search for new nest sites, and report their findings using waggle dances (e.g., Seeley and Buhrman, 1999; Visscher and Camazine, 1999). The likely function of an absconding swarm is to keep the colony together and to protect the queen (from predators, parasites, and inclement weather). However, it is probable that an important additional function of a reproductive swarm is to separate its nest site selection process from the foraging process of its parent colony. This is because honey bee colonies swarm in summer when there is still forage available and the colony remnant left in the original nest will be continuing to forage using recruitment. Importantly, foraging and nest site selection both use the same signal – the waggle dance – and if nest site selection occurred within the original nest, dance followers would not know if a particular dancing scout were advertising a forage site or a nest site.

These structures adapt and change to produce thermoregulatory behaviour. During hot weather, inter-individual distances increase and channels form within the structure through which air circulates, sometimes aided by fanning bees (Heinrich, 1981; Winston, 1987; Camazine et al., 2001). Conversely, during cold weather, tight clusters form with a dense mantle of still bees (sometimes several bee layers thick), each with their head pointing inwards, and a less dense core in which fanning may occur (Seeley and Heinrich, 1981; Heinrich, 1993; Seeley, 1995). Such a structure protects the colony from lethal temperatures but also will reduce the rate at which the bees have to draw off their honey reserves to generate energy and heat.

Queen clusters

Queen retinues are observed in many species of ants, but they are particularly striking in *Eciton* army ants (e.g., see Schneirla, 1971: Fig. 10.3). When running along a trail, an *Eciton* queen is accompanied by a group of workers. If there is a delay or disturbance of some kind, e.g. due to rain or a gust of wind, the workers form a thick bolus around the queen (sometimes over 5 cm tall), presumably providing an increased level of protection (Rettenmeyer, 1963: pp. 311, 354; Schneirla, 1971: p. 111).

These clusters may, however, serve an additional function during colony fission. Although an *Eciton* colony generally produces around six new queens, at most only two succeed in taking over new daughter bivouacs (Franks and Hölldobler, 1987). The parent stately bivouac produces two raids in opposite directions, and in broad daylight the new queens run along one of the raids (Franks, 1989 a). Only one queen succeeds per raid and a new bivouac forms around her. Later, each raid becomes an emigration to a new

bivouac site with a single winning queen safely within. Extra queens seem to be held back by tight clusters of workers close to the old bivouac site (N.R. Franks, pers. comm.). It is possible that these clusters may serve as some sort of “holding cells” that prevent too many queens running along a trail; Schneirla (1971) notes that these clusters appear to generate some stability in the fission process. Additionally they may serve a protective role, in effect keeping the “insurance policy in the vault.” This remains to be tested but could be achieved by removing one, or both, of the new winning queens.

Balling behaviour in honey bees, *Apis mellifera*, has been described in which alien and unfavourable queens are surrounded by a ball of bees (Robinson, 1984; Winston, 1987; Lensky et al., 1991; Pettis et al., 1998). However, descriptions imply that it is more a case of the bees scrambling over each other in an attempt to reach the queen rather than an actual cage entombing the queen and preventing escape as in *Eciton*. As such, we do not consider such structures as SAs.

Bridges, ladders, and walls

Army ants construct a number of different self-assemblages that aid their raids and emigrations by creating a smooth roadway when crossing difficult terrain. First, workers may form a living bridge across a gap. Such structures may bridge a significant distance, and may even form across water, in effect producing a pontoon. Schips (1920) describes an *Eciton burchelli* colony that crossed a river 12 metres wide using such a pontoon; however, this unusual behaviour needs to be confirmed independently. Savage (1847, 1849) and Bugnion (1924) report similar behaviour in *Dorylus* (*Anomma*) *arcens*. U. Maschwitz (pers. comm.) reports “extensive bridge formation in *Dolichoderus cuspidatus* and other *Dolichoderus* sp.” when leaving large feeding sites and during migration from a bivouac site.

Second, Schneirla (1971) reports that army ants may form “ladders” if the front of a swarm arrives broadside at the top of an overhanging bank. Overhanging strands form and are steadily lengthened by the addition of new workers to the bottom of the strands until the ground is reached. These ladders are then used by the rest of the colony and may stay in place for several hours until traffic over them eases off. Similar ladders and bridges are also observed in *Oecophylla* ants (Hölldobler and Wilson, 1978: fig. 10; Lioni et al., 2001; Fig. 1 k). Third, *Dorylus* spp. may form thick living walls, and sometimes even tunnels, along their trails (*D. laevigatus*, Weissflog et al., 2000; *D. wilverthi*, A. Sendova-Franks and N.R. Franks, pers. comm.; Fig. 1 e). A. Sendova-Franks (pers. comm.) reports that “The ants that made up the wall[s] tended to be the largest workers rearing in a threatening posture with open mandibles. Sometimes these walls were so thick that, they looked like the interwoven walls of a basket.” In addition, Rettenmeyer (1963: p. 432) cites W.J. Hanson’s observations of similar behaviour in *Nomamyrmex hartigi* and tunnels are also common in *Labidus praedator* (S. Powell, pers. comm.) Interestingly, during *Nomamyrmex esen-*

beckii emigrations, tunnels are formed entirely by the older individuals with callows carrying the larvae within (S. Powell, pers. comm.). The primary purpose of all these structures must surely be protection of the colony, principally the queen and brood.

Fourth, a number of other clusters that provide a smoother road surface, structures that have been termed “ramps,” “flanges,” and “fills,” are also known in army ants (Rettenmeyer, 1963: 330–331; Schneirla, 1971). Ramps form on rougher sections of the trail and produce a smoother rising roadway between uneven section of trail such as the step up from a rock to a vine (Schneirla, 1971: Fig. 12.1 a, b). Flanges, which are 10–15 mm wide in *E. mexicanum*, effectively widen the trail substrate (ibid.: Fig. 12.1 c, d; Rettenmeyer, 1963: p. 399). Fills, although not explicitly detailed in Schneirla (1971), presumably fill in potholes along the trail (see also Rettenmeyer, 1963: p. 331). The mechanisms by which some of the above structures form, is described in more detail later.

Dynamic meshes

Living curtains around combs

Two species of honey bee, the giant honey bee of southeast Asia (*Apis dorsata*) and the little honey bee (*A. florea*), nest in open spaces and cover the single comb with a blanket of bees (Morse and Laigo, 1969; Michener, 1974: Figs. 17.3 and 30.7; Dyer and Seeley, 1991; Fig. 1 f). (Similar behaviour is observed, albeit rarely, in *A. mellifera* (Michener, 1974: p. 203).) In *A. dorsata*, the blanket may consist of several layers of bees and contain at least 80% of the colony, and even as high as 95% in cooler weather (Morse and Laigo, 1969). In these “curtains,” each of the bees is regularly orientated, head up and facing the comb. *A. florea* curtains are less regularly orientated than *A. dorsata* (Michener, 1974: fig. 30.7) but are organised in a similar manner. These curtains clearly serve an important thermoregulatory role in which the internal “nest” temperate is closely regulated despite large variation in ambient temperature (e.g. Morse and Laigo, 1969; Michener, 1974). The curtains also serve to keep rain and wind off the comb. Additionally, the large number of visible workers may also serve as a visual deterrent, especially when combined with “abdominal shaking,” a wave of activity that passes over the blanket’s surface in which individuals thrust their abdomen more than 90 degrees upwards (Sakagami, 1960). Kastberger (1998; see also Kastberger et al. 1998) suggests that this response is (Nasonov) pheromone-mediated to prevent individual bees leaving the curtain to attack the predator. Finally, if the curtain receives a mechanical shock, “the bees of all layers extend themselves by stretching their legs and abdomens and activate their flight muscles. This doubles the thickness of the nest (‘increasing in size’) and produces a hissing sound like a snake (‘acoustic mimicry [sic]’)” (Kastberger, 1998). Thus, this SA exhibits an impressive array of functional adaptations.

Dynamic chains

Droplets and unstable chains

Buschinger and Maschwitz (1984) report that when a colony of *Oecophylla smaragdina* is raided by the Dolichoderine ant *Technomyrmex albipes*, clusters of thousands of workers (and brood) form a ball that eventually drops to the ground (Fig. 1 g). Unfortunately, nothing else is known about these structures.

Whereas *Eciton* and *Oecophylla* are known to form stable bridges (see below), *Linepithema humile* (= *Iridomyrmex humilis*) only forms unstable bridges (Bonabeau et al., 1998; personal observations) and also exhibits some interesting behaviour that may be related to such bridge building activity. In laboratory experiments, Theraulaz and colleagues (1996, 2001; Bonabeau et al., 1998) found that ants will congregate at the end of a rod and start to form a dangling chain. As more ants join, the chain becomes broader so that a knot of ants hangs below the rod. Eventually these dangling ants are only held by one or two links which break and the group of ants – up to 40 – falls as a drop (Fig. 1 h, i). Such droplets are remarkably similar to those observed in *Oecophylla* (above). Other chains soon develop and a dripping action is seen, rather like a leaky tap (Bonabeau et al., 1998).

The function of this behaviour is currently unknown but there are several possibilities. First, this behavior may simply be an artifact of the laboratory conditions. There is no evidence that this phenomenon is observed under natural conditions, but as far as we are aware it has not been the focus of attention of any studies. Second, it is possible that this phenomenon is related to exploratory behaviour or to escape behaviour, as in *Oecophylla*, but the ants did not happen to contain brood in the drops. Third and most likely, the ants may be attempting to form a bridge to the floor below but are simply inept, and so the chain repeatedly breaks generating the observed dripping process.

There are several lines of evidence that are suggestive of such an explanation. First, bridges, albeit unstable, have been observed in this species (personal observations). Second, bridges in other species form by individuals using their tarsal claws to hook onto other individuals (e.g., Schneirla, 1971). However, electron microscopy of *L. humile* reveals that their claws are much less well developed than those of *Oecophylla* (G. Theraulaz, unpubl. data). The likely reduced attachment ability of *L. humile* workers probably explains the large amount of movement within their bridges and clusters, and hence their instability.

Bivouacs

Unlike most ant species, many army ants do not live in subterranean or excavated nests but instead use temporary structures, “bivouacs,” formed from the bodies of the colony members themselves. These are primarily observed in epigeic (surface-adapted) genera such as *Aenictus* and *Neivamyrmex*, and perhaps most strikingly in the *Eciton hamatum* and *E. burchelli* (Rettenmeyer, 1963; Schneirla,

1971; Gotwald, 1995; Fig. 1 j) in which the bivouac may involve 150,000–700,000 workers forming a mass of workers a metre across (Wilson, 1971). “Simple” bivouacs (meaning a single layer of interlinked ants) have been reported in the ponerine army ant genus *Leptogenys* (*L. distinguenda*, Witte and Maschwitz, 2000, in prep.; *L. sp. 1*, Maschwitz et al., 1989; see also *L. diminuta*, *ibid.*: p. 314).

In most ant bivouacs, the ants link their legs and bodies with their tarsal claws forming layer upon interlocking layer of chains and nets of workers. However, these bivouacs are not a disorganised mass of ants but exhibit structure; upon seeing an *Eciton* bivouac, Belt (1874) claimed “I was surprised to see in this living nest tubular passageways leading down to the center of the mass, kept open as if it had been formed of inorganic material.” Schneirla (1971: p. 58) identifies three types of bivouacs: cylindrical, curtain, and pouch. There are several aspects to their structure. First, there are chambers and galleries within the bivouac that contain the queen and brood (Schneirla, 1971: p. 55). (Rettenmeyer [1963: p. 302] cites T.C. Schneirla as finding that in *E. burchelli* and *E. hamatum* the brood are spatially organised within the bivouac, i.e. smallest larvae or eggs are found in the centre while the largest larvae are found at the periphery.) Second, larger workers often form the outer wall (Schneirla, 1971: p. 62 but this really needs to be quantified rigorously), at least overnight before the first set of raiders sets off at dawn (thus leaving a new wall of smaller ants; S. Powell, pers. comm.). This is probably because larger workers are stronger and better able to form effective attachments to other ants, they have longer legs, and they are also more resistant to desiccation than the smaller workers (Schneirla, 1971). When these differences exist between internal and external ants, this suggests a necessary division of labour within the structure, thus classifying bivouac formation as a “team task” rather than “group task” (sensu Anderson and Franks, 2001). Finally, the outer ants are generally orientated with head downwards (see Schneirla, 1971: Fig. 3.2), probably a result of the way that such bivouacs form (discussed later).

Schneirla (1971) proposes that bivouacs serve four functions: they are 1) centre of operations, 2) shelter, 3) incubator, and 4) a population reservoir. That these army ants form these structures (but some army ants do excavate nests in the soil) is likely an effective solution to their nomadic lifestyle in which a more “traditional” and permanent nest would be ineffective – by the time they had built a nest, they would be on the move again. However, these additional functions may also be important, independent of their nomadic lifestyle. For instance, the internal temperature of an *E. hamatum* bivouac was found to be 1–2°C higher and less variable than ambient temperature, both of which likely have a favourable effect upon brood development (Schneirla, 1971; Wilson, 1971; Franks, 1989b). Temperature regulation in the bivouac is probably achieved by creating or closing ventilation channels in the bivouac and by altering its overall shape to vary its surface area to volume ratio (Franks, 1989b and references therein). As such these adaptable SAs are relatively complex.

Pulling chains

Two examples of pulling chains in insect societies are known, each serving a different purpose. Morais (1994) reports an interesting example of a sit-and-wait group ambush strategy in the ant *Azteca cf. lanuginosa*. The ants line up along the underside margin of a leaf and wait until prey land upon the leaf. The ants then “rush” the prey and overcome it using sheer numbers of ants. Importantly, Morais (1994) reports that larger prey were sometimes overcome using a “cooperative ‘rope pulling’ technique” which supposedly provided additional power. Schneirla (1971: p. 85) describes similar behaviour in *Eciton burchelli* with “many chains of ants, formed by jaws gripping legs in series, all well anchored to the floor and pulling steadily.”

The second type of pulling chain is exhibited in *Oecophylla* during nest construction (Figs. 11, m). The workers form a nest by pulling leaves together then gluing them with larval silk (Ledoux, 1950; Hölldobler and Wilson, 1990: pp. 618–629). This process requires a great deal of cooperation: The leaves are both large and will normally be too stiff for a single ant to manipulate therefore bending over a leaf and holding it in position requires the combined effort of many ants. This is achieved in two ways: first, they may line up in a row along the margin of the leaf and all pull together. Second, they may also form a pulling chain self-assembly. When the gap to be bridged is longer than a single ant, individuals will form a chain and so work as a single unit, a part, to complete the task (Fig. 1j). In these nest-building chains, but not in bridges (Ledoux, 1950), the ants attach themselves to the ant in front by using their mandibles to grasp the other’s petiole (Fig. 11; see also Hölldobler and Wilson, 1983).

Festoons and pulling chains

During comb construction, honey bees (*Apis mellifera*) form chains of bees. Such chains are used for a variety of crucial functions. First, chains hang down over the area of comb under construction (Darchen, 1959a, 1962: Figs. 1–6). (In such a situation, these chains have been termed “festoons” (Hepburn, 1986).) It is hypothesised that this behaviour elevates the local temperature making the wax more malleable, thus aiding construction. They are also a source of wax for construction itself, and there is a strong correlation between the shape of the SA and the new section of comb (Darchen, 1959a; Hepburn, 1986). Second, chains linking adjacent combs are a source of long-range communication that ensure combs are parallel. When these chains are broken and separate clusters of comb-building bees exist, the pattern of combs in the nest may be highly disorganised (Darchen, 1959a). However, such problems may be corrected in that these chains are also used as true pulling chains. Such chains generate sufficient torque to pull the comb into its correct position (Darchen and Chauvin, 1962). This corrective behaviour requires a significant increase (2–3 °C) of the wax temperature, something generated by the festoons. The presence of cells in one comb facing the vertical section of another

comb appears to be the stimulus for such a rearrangement (Darchen, 1959b).

Factors that favour self-assemblages

What probable factors favour the formation of self-assemblages in insect societies? A dominant factor is certainly colony size: all the species listed in Table 2 have reasonably large colonies. SAs often require many individuals to form the structure; a ponerine ant colony with only a few tens of members may be severely limited in the structures it might be able to form (although some SAs such as pulling chains may only require a few individuals). Also, an individual “locked” into a living chain or wall represents a significantly larger proportion of colony resources in a small colony than a larger one. Additionally, a critical density of individuals, more likely in large colonies, may be required to initiate SA formation and growth. Thus, we conclude that SAs are generally, but not necessarily always, characteristic of a socially complex society (sensu Anderson and McShea, 2001a) in which SAs may be considered as intermediate-level parts.

Polymorphism, another characteristic of large socially complex societies, may also play a part. It may be the case that larger workers have both longer and thicker legs, which in turn may be able to sustain a larger force than smaller workers, thus favouring clustering (Rettenmeyer, 1963: p. 281). Polymorphism may also be associated with other important characteristics; for instance, the mantle of army ant bivouacs are formed by larger workers who are less prone to desiccation (e.g., Schneirla, 1971) than smaller ones. However, this of course may be optimisation of a structure rather than a factor favouring its evolution or construction.

Another factor in army ants in which the cause and effect are not clearly distinguished is their nomadic lifestyle. Whereas a large *Formica* wood ant colony may set up home in one spot for many years (and thus can invest in constructing a tailor-made nest) army ants are nomadic and so by the time they had constructed an inanimate nest they would likely have to move off again. Thus, a temporary home formed by the colony (probably a direct result of the limitation of sufficiently large natural nesting cavities) is an appropriate solution. However, there are other likely proximate cause of this lifestyle including local food limitation (Gotwald, 1995; Boswell et al., 1998).

Many termites spend a significant proportion, if not all, of their time underground. It is perhaps not entirely surprising then that termites, who have relatively much shorter legs than ants (possibly to aid manoeuvrability in narrow tunnels), are not observed to form self-assemblages; perhaps termites’ legs are just too short to link together with others. A major function of SAs (Table 2) appears to be as an anti-predator strategy. As mentioned above, *Apis dorsata* and *A. florea* curtains appear to act as a visual deterrent. Such a deterrence strategy is likely irrelevant for subterranean termites in which other tactics, such as blocking off tunnels (as individual plugs), are more effective. In addition, the linear galleries and foraging tunnels of many termites species may also disfavour SAs in termites.

Table 2. Social insect self-assemblages classified by function (a–e). Some assemblages may have several functions and so are placed in more than one category; thus, placement of a particular assemblage in a category does not necessarily represent its supposed primary function. The function(s) of *Linepithema humile* SAs is not clear and thus is placed in parentheses

Function	Species	Reference	Function	Species	Reference
a) Anti-predator / anti-parasite			c) Thermoregulation		
Bivouacs	Various army ant species	e.g. Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1995; Witte and Maschwitz, 2000	Bivouacs	Various army ant species	Rettenmeyer, 1963; Schneirla, 1971; Franks, 1989b; Gotwald, 1995; U. Maschwitz, pers. comm.
Curtain	<i>Apis florea</i> and <i>A. dorsata</i>	Michener, 1974; Dyer and Seeley, 1991; Kastberger, 1999	Curtain	<i>Apis florea</i> , <i>A. dorsata</i>	Morse and Laigo, 1969; Michener, 1974
(escape) Droplets	<i>Oecophylla smaragdina</i> , <i>Linepithema humile</i> (= <i>Iridomyrmex humilis</i>)	Buschinger and Maschwitz, 1984; (Theraulaz et al., 1996; 2001; Bonabeau et al., 1988)	Swarms	<i>Apis mellifera</i>	Heinrich, 1993; Seeley, 1995
Oven	<i>Apis cerana japonica</i>	Ono et al. 1987, 1995	Thermoregulatory clusters	<i>Apis mellifera</i>	Heinrich, 1993; Seeley, 1995
Plug	<i>Colobopsis truncatus</i>	Szabó-Patay, 1928	d) Survival under inclement conditions		
Queen clusters	<i>Eciton</i> spp.	Rettenmeyer, 1963; Schneirla, 1971	Bivouacs (mantle shields against rain)	Various army ant species	N.R. Franks, pers. comm.
Swarms	Swarm-founded bees and wasps	e.g. Lindauer, 1955; Jeanne, 1991; Seeley, 1995	Thermoregulatory clusters (against temperature extremes)	<i>Apis mellifera</i>	Heinrich, 1993; Seeley, 1995
Walls and tunnels	<i>Eciton</i> spp., <i>Dorylus</i> spp., <i>Nomamyrmex hartigi</i>	Rettenmeyer, 1963; Weissfloget al., 2000; A. Sendova-Franks and N.R. Franks, pers. comm.	Swarms (against desiccation)	As in a) above	As in a) above
			Rafts (against flooding)	<i>Camponotus compressus</i> , <i>Dorylus (Anomma) arcens</i> , <i>Lasius umbratus</i> , <i>Myrmica gallienii</i> , <i>Solenopsis invicta</i> , <i>S. saevissima</i> ,	Donisthorpe, 1915; Hingston, 1922; Wilson and Eads, 1949; Green and Hutchins, 1960; Morrill, 1974; Jaffe, 1993; Münch und Engels, 1994
b) Pulling			e) Ease of passage or crossing		
Pulling chain (foraging)	<i>Azteca cf. lanuginosa</i>	Morais, 1994	Bridges (and “pontoons” when over water), ladders, ramps, and fills	Various surface-adapted army ants, <i>Dolichoderus</i> spp., <i>Oecophylla longinoda</i>	Savage, 1847, 1849; Schips, 1920; Bugnion, 1924; Leodux, 1949; Schneirla, 1971; Hölldobler and Wilson, 1978; Lioni et al., 2001; U. Maschwitz, pers. comm.
Pulling chain (foraging?)	<i>Eciton burchelli</i>	Schneirla, 1971	Rafts	As in d) above	As in d) above
Pulling chain (nest construction)	<i>Oecophylla</i> , <i>Apis mellifera</i>	Darchen, 1959a; Hölldobler and Wilson, 1990	Escape droplets	<i>Linepithema humile</i> (= <i>Iridomyrmex humilis</i>)	Theraulaz et al., 1996; Bonabeau et al., 1988

A very important adaptation, or perhaps *pre*-adaptation (exaptation), favouring SAs are the recurved tarsal claws (and also in some ant species, tarsal arolia, e.g. Wojtusiak et al., 1995) that individuals use to link with one another. A highly-recurved claw will form a more effective link than a less recurved one (which may slip under force). Referring to army ants, Rettenmeyer (1963: p. 454) claimed that “I do not believe the opposed recurved tarsal claws were developed with the evolution of such clustering because similar claws are present on many species of nondoryline ants including Ponerinae.” However, as described earlier, clustering, chains, and bivouacs are known in ponerines and other nondorylines such as *Oecophylla*. Highly-recurved tarsal claws may certainly have evolved under

selection for other uses such as an effective strategy to capture or dismantle prey or to cling to vertical surfaces such as tree trunks, and only later found an alternative use in SAs.

A second adaptation or *pre*-adaptation favouring SAs is that some army ants, when stretched, become motionless – “workers seem to become immobilized as a physiological reaction to being stretched” (Schneirla, 1971: p. 272). Such inactivity may have at least two benefits. First, it might increase the probability that a SA “seed,” i.e. a stimulating configuration of individuals, will remain in place long enough to attract new individuals (Schneirla, 1971). Second, it may increase the stability of the SA, i.e. prevent premature disassembly.

Assembly and disassembly in SAs

The way that SAs form may often determine the orientation of the individuals within the SA. For instance, in an *Eciton* chain or ladder, new individuals arrive at the top of the chain from the attachment point (e.g., log, rock etc.) and run downwards over the surface of the chain and attach themselves at the bottom. (A possible rule may be “continue to run downwards until there is no more chain left, then hang from the end.”) Consequently, the individuals are almost always oriented head-downwards (e.g., Schneirla, 1971: Fig. 3.2). (However, Schneirla (1971: p. 55) does suggest that unspecified tests show “that the placement of [the tarsal claws] and the weight of ants pulling on other ants rather than a general behavioral disposition ... explain why workers fastened into a bivouac wall usually hang head downward”.) Contrast this with *Apis dorsata* and *A. florea* curtains in which the bees fly toward the structure facing it, joining at the bottom and hence attach head upwards. Michener (1974) states this is the busiest part of the structure with many bees coming and going. Honey bee swarms, in which new bees may arrive on just about any part of the SA's surface, are much less organised and oriented. For instance, a new arrival may land on the branch from which the swarm hangs and walk onto the swarm, or it may land directly on the swarms' surface and wander over the surface before attaching; thus, this reflects perhaps this cluster's more simple structure compared to most of the other SAs we have considered.

Schneirla (1971: p. 272) describes the formation of flanges and fills. Small workers are “repeatedly bumped and overrun” and drop out of the emigration or raiding process by huddling in clusters; they “stretch out with tarsal claws anchored to leaf edges and similar places or to the protruding legs of nestmates already clustered, then lie motionless in place except for slight vibrations of antennae.” He suggests that the continual tactile stimulation of numerous ants passing over the SA keeps the individuals immobilised. It is only when the traffic has ceased, and thus the inhibitory stimuli are no longer present, that the SA disassembles.

Unfortunately, this is almost the sum total of our knowledge of the proximate mechanisms by which SAs form and disassemble. In some cases, data exist on the global dynamics of some of the SAs, e.g. rate of growth of a chain or bivouac, or the probability of joining or leaving an *Oecophylla* chain of a certain size (Lioni et al., 2001). In other cases we have some inkling of why bivouacs form in a particular location, e.g. *Eciton* bivouacs often appear to form where the local density of ants is increased at dusk where two trails of returning ants meet at a junction (Schneirla, 1971). Lastly, O. Sandler (cited in Darchen, 1959a) shows that both the queen, who acts as a nucleus, and the substrate properties (e.g. smooth versus rough) and shape (e.g. horizontal versus sloping) greatly influence where a swarm hangs within a nest. Unfortunately, despite these insights, virtually nothing is known regarding the rules, signals, and cues used by individuals in SA formation or the physical constraints these structures are under (e.g. Darchen, 1959a; Schneirla, 1971); these are the most important avenues for future research.

We will however venture the following predictions, which are certainly testable; it probably only requires detailed behavioural observations. We suggest that the more organised and complex a structure, the more well-defined are the proximate rules used in its formation, and that individuals are subject to greater constraint. That is, in a simple cluster such as a swarm or a raft, individuals anywhere on the surface are free to leave the structure at any time; their neighbours are mostly beneath them and they do not have the weight of others pulling them onto the SA. In short, they can simply unhook themselves and leave (and vice versa when joining). Contrast this with a more organised *Eciton* ladder suspended from a branch. Probably the most adaptive dimension of growth is its length (with an appropriate increase in its basal attachment; Lioni et al., 2001). Individuals should therefore join at the dangling end. However, consider the restrictions an individual in the middle of the chain is under. It is stretched out by the weight of the rest of the chain below. It would have to lift all of the chain below to unhook itself – ants do not have claws they can be retracted like those of cats. Suppose an individual was able to unhook itself; in a thin ladder, this would cause all of the chain below to fall to the ground, clearly not an adaptive behaviour. Thus, the only place that individuals can, and should, join and leave a thin chain is the non-attached end. This is what we mean by constraint. (Perhaps immobility when stretched is an adaptive behaviour to prevent costly mid-chain unhooking errors in SAs.) In summary, we suggest that in one-dimensional structures – chains – assembling and disassembling is most likely at just one end; in two-dimensional structures – meshes – this is probably constrained to some of the perimeter, and in three-dimensional structures – clusters – it may occur on just about the whole surface.

Discussion

In this study, we have reviewed the natural history of self-assemblages in insect societies. We find that such structures exist in a variety of species of ants, bees, and wasps but not, as far as far as we are aware, in termites. These SAs exist in a variety of forms (Table 1) and are used for a variety of functions (Table 2) and conceptually form a continuum of complexity, ranging from low constraint static clusters to high constraint dynamic chains. In Table 2, we tentatively group SA functionality under five broad categories that are not mutually exclusive: 1) defence, 2) pulling structures, 3) thermoregulation, 4) colony survival under inclement conditions, and 5) ease of passage when crossing an obstacle. It is clear that these structures, even if only used rarely, play an important role in colony life.

In attempting to understand why SAs have evolved, it is instructive to inspect Table 2 and ask the question: could these functions be achieved without self-assembly? In almost all cases, the answer is no. Such strategies, including bridge crossing, thermoregulation, and bivouac formation would be impossible without self-assembly. Thus, we can conclude that these intermediate level parts do convey a new level of

functionality not available to simpler societies (sensu Anderson and McShea, 2001 a). In short, complex insect societies do new things that simpler societies cannot. For some functions, SAs are not strictly necessary but would certainly be favoured for colony cohesion and survival after the function is completed. That is, it is conceivable that, when attacked, *Oecophylla* workers could jump off a branch individually, rather than in a droplet, and survive. However, this will make it harder for the colony to stay together and reform afterwards. (In the case of *Linepithema*, droplet formation may be related to their exploratory and foraging behaviour, which involves a high density of individuals [Deneubourg et al., 1990].) Similarly, nest site selection in a swarm will be easier if the individuals remain together in a cluster, and individual ants can swim, but a raft maintains colony cohesion. (Brood, however, may not survive as well as when they ride upon a raft.) Finally, queen clusters and plugs may not strictly require a SA, a cluster of unlinked individuals such as in honey bee balling may also achieve the goal, but elevated coordination and connectivity, as in SAs, will probably enhance functionality.

We see that Table 2 is dominated by three genera – *Apis*, *Eciton*, and *Oecophylla* – in which the same species utilises self-assembly for several different functions. It is possible that self-assembly evolved in a species for a single key function, e.g. bridge crossing, but this new-found ability opened the door for other functions using this mechanism, e.g. pulling chains for foraging and construction. An alternative non-mutually-exclusive possibility is that different tasks within a species are under similar constraints (e.g. many different *Oecophylla* tasks are tackled in trees), and so can each be solved with a similar mechanism, self-assembly. As might be expected, it is the simplest structures (relatively static clusters) such as swarms and rafts that are found in the greatest diversity of genera and species. Such structures may possibly evolve rather easily as a byproduct of a basic instinct, e.g. during flooding “carry brood to the nearest and highest point” such as atop a grass stem, which will create an elevated local density of individuals. It is not hard to imagine how this might then translate into a linked cluster of individuals. More complex SAs, however, such as pulling chains in which necessary coordination is greater, presumably were harder to evolve. If this and the above arguments are true, we suggest that *Azteca cf. lanuginosa*, a species in which only pulling chains are currently known, may reveal additional SAs upon closer inspection. In short, if it has the ability to form chains then it should have the ability to form (and probably uses) other simpler SAs. Only detailed behavioural observations are required to test this hypothesis.

One factor that seems to unite the species with the greatest diversity and complexity of SAs is that they are relatively surface-adapted and more importantly, spend a significant amount of time off the ground in trees and bushes. Such behaviour, as found in *Eciton*, *Oecophylla*, and also *Azteca*, might well favour mechanisms that enable them to travel from one branch to another (bridges), to escape quickly without having to use the main stem or trunk (escape droplets) and coping with topological constraints such as prey capture

on narrow branches (pulling chains). Additionally, Schneirla (1971) suggests that for army ants at least, the surface-adapted species tend to have relatively longer legs, which might also favour SAs. As mentioned earlier, a final but likely very important factor is colony size: SA complexity is probably a function of the available individuals available to form a structure and possibly also of polymorphism (a factor generating interindividual differences in morphology and size), a trait correlated with colony size (see Anderson and McShea, 2001 a).

Clearly, there is a paucity of information about the proximate mechanisms by which SAs form and adapt to changing circumstances and need. We suspect that in most cases self-organisation (Camazine et al., 2001) is involved, but as Sendova-Franks and Franks (1999) point out, self-assembly may occur with or without such a mechanism (see also Anderson, 2002). A key ingredient of self-organisation is positive feedback (Bonabeau et al., 1997; Camazine et al., 2001; Anderson, 2002) and in most cases SA formation almost certainly requires such a mechanism. For a structure to grow relatively quickly from some initial seed or nucleus, it must be attractive to other individuals, perhaps using a feedback mechanism similar to that found in *Oecophylla longinoda* chain formation: the probability that a new individual will enter the chain increases with current chain size (Lioni et al., 2001). Such a mechanism can quickly enhance the stability of the structure. Positive feedback is also a key element in collective decision making. This is particularly relevant to SAs as several stimulating nuclei may be present (Lioni, 2000; Lioni et al., 2001), e.g. various small *Eciton* strands within a locality (Schneirla, 1971), but it is most adaptive that a single SA forms. An additional positive feedback mechanism that will amplify the growth of one strand over any others is a visual stimulus to which the chain is growing. In *Oecophylla*, such stimuli increase the hanging time (the duration an ant spends at the end of the chain before departing) compared to chains without such a stimulus (Lioni et al., 2001) and so chain growth is faster, and competition among chains fiercer. Competition, in conjunction with positive feedback, among nuclei or proto-SAs will likely not only result in a single site selection but favourable differences will be amplified to select also the better of the sites.

Self-assemblages are only well documented in insect societies. However, similar structures exist in other social groups (e.g. ball of aphids soldiers around a predator [Aoki, 1987]); aggregation of harvestmen (Wagner, 1954 cited in Eibl-Eibesfeldt, 1975)]. Three factors likely contribute to the rich diversity and prevalence of SAs in insect societies. First, high relatedness, and thus degree of kin selection, favour the cooperative behaviour necessary for SA formation; it is likely that only a high inclusive fitness would favour individuals being locked into the centre of a wall or bridge. Second, larger animals, which require a relatively larger and heavier supporting skeletal system (Schmidt-Nielsen, 1984), will presumably have greater difficulties in supporting the weight of other individuals in a SA. Third, and likely most important, social insects are often found in very high local densities. In summary, the most promising candidates in which to find

SAs are those taxa in which we find these three characteristics: *high local density* (resulting from large colony size) of *small and highly-related* individuals.

In the structures formed by self-assembly as we have reviewed here, one sees a new level of complexity arising, a new hierarchical level above that of the individual. The structures introduce a new topology to the colony by which we mean the creation of supra-individual colony structures such as droplets, curtains and chains. In some cases we see differentiation and sorting of the structures' subcomponents (workers) so that a "histology" reminiscent of tissues is observed (discussed in detail in C. Anderson and D.W. McShea, in prep.). For example, the compact and regularly-oriented array of individuals in an *Apis* curtain protects the colony beneath from inclement weather and is functionally similar to epithelial tissue (ibid.). Such patterns and results will probably not be a surprise to researchers working on morphogenesis at the cellular level. Indeed, in this area many experiments show that self-assembly plays a key role in morphogenesis; examples include the restoration of a multicellular organism or tissue from a homogeneous mix of dissociated cells (Steinberg, 1993) and the aggregation and subsequent differentiation of individuals in social amoebae (Bonner, 1967; Gadagkar and Bonner, 1994). Thus, self-assembly is a beautiful example of a similar organisational mechanism operating at very different biological levels.

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References

- Anderson, C., 2002. Self-organization in relation to several similar concepts: are the boundaries to self-organization indistinct? *Biol. Bull.*: in press.
- Anderson, C. and N.R. Franks, 2001. Teams in animal societies. *Behav. Ecol.* 12: 534–540.
- Anderson, C. and D.W. McShea, 2001a. Individual versus social complexity, with particular reference to ant colonies. *Biol. Rev.* 76: 211–237.
- Anderson, C. and D.W. McShea, 2001b. Intermediate-level parts in insect societies: adaptive structures that ants build away from the nest. *Insectes soc.* 48: 291–301.
- Aoki, S., 1987. Evolution of sterile soldiers in aphids. In: *Animal Societies: Theories and Facts* (Y. Itô, J.L. Brown and J. Kikkawa, Eds.), Japan Scientific Societies Press, Tokyo. pp. 53–65.
- Belt, T., 1874. *The Naturalist in Nicaragua*. John Murray, London. 306 pp.
- Bonabeau, E., G. Theraulaz, J.L. Deneubourg, S. Aron and S. Camazine, 1997. Self-organization in social insects. *Trends Ecol. Evol.* 12: 188–193.
- Bonabeau, E., M. Dorigo and G. Theraulaz, 1999. *Swarm Intelligence: From Natural to Artificial Systems*. Oxford University Press, New York. 307 pp.
- Bonabeau, E., G. Theraulaz, J.L. Deneubourg, A. Lioni, F. Libert, C. Sauwens and L. Passera, 1998. Dripping faucet with ants. *Phys. Rev. E* 57: 5904–5907.
- Bonner, J.T., 1967. *Cellular Slime Molds* (2nd Ed). Princeton University Press, Princeton. 149 pp.
- Boswell, G.P., N.F. Britton and N.R. Franks, 1998. Habitat fragmentation, percolation theory and the conservation of a keystone species. *Proc. R. Soc. Lond. B* 265: 1921–1925.
- Bugnion, E., 1924. L'Oecophylle de Ceylan (*Oecophylla smaragdina* F., sous fam. Camponotinae For.). *Bull. Soc. Zool. Fr.* XLIX: 422–456.
- Buschinger, A. and U. Maschwitz, 1984. Defensive behavior and defensive mechanisms in ants. In: *Defensive Mechanisms in Social Insects* (H.R. Hermann, Ed.), Praeger Scientific, New York. pp. 95–150.
- Camazine, S., P.K. Visscher, J. Finley and R.S. Vetter, 1999. House-hunting by honey bee swarms: collective decisions and individual behaviors. *Insectes soc.* 46: 348–360.
- Camazine, S., J.L. Deneubourg, N.R. Franks, J. Sneyd, G. Theraulaz and E. Bonabeau, 2001. *Self-organization in Biological Systems*. Princeton University Press, Princeton. 524 pp.
- Darchen, R., 1959a. Les techniques de construction chez *Apis mellifica*. *Ann. Sci. Natl. Zool.* 12: 113–209.
- Darchen, R., 1959b. Un des rôles des chaînes d'abeilles: la torsion des rayons pour les rendre parallèles entre eux. *Ann. Abeille* 3: 193–209.
- Darchen, R., 1962. Observation directe du développement d'un rayon de cire. Le rôle des chaînes d'abeilles. *Insectes soc.* 9: 103–120.
- Darchen, R. and R. Chauvin, 1962. Observations directes de la torsion des rayons par des chaînes d'*Apis mellifica*. *C. R. Acad. Sci.* 254: 1–3.
- Deneubourg, J.L. and S. Goss, 1989. Collective patterns and decision-making. *Ethol. Ecol. Evol.* 1: 295–311.
- Deneubourg, J.L., S. Aron, S. Goss and J.M. Pasteels, 1990. The self-organizing exploratory pattern of the Argentine ant. *J. Insect Behav.* 3: 159–168.
- Donisthorpe, H.St.J.K., 1915. *British Ants, Their Life-History and Classification*. William Brendon & Son, Plymouth. 379 pp.
- Dyer, F.C. and T.D. Seeley, 1991. Nesting behavior and the evolution of worker tempo in four honey bee species. *Ecol.* 72: 156–170.
- Eibl-Eibesfeldt, I., 1975. *Ethology: The Biology of Behavior*. Holt, Rinehart and Winston, New York. 625 pp.
- Franks, N.R. and B. Hölldobler, 1987. Sexual competition during colony reproduction in army ants. *Biol. J. Linn. Soc.* 30: 229–243.
- Franks, N.R., 1989a. Army ants: a collective intelligence. *Am. Sci.* 77: 139–145.
- Franks, N.R., 1989b. Thermoregulation in army ant bivouacs. *Physiol. Entomol.* 14: 397–404.
- Frisch, von K., 1967. *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge. 566 pp.
- Gadagkar, R. and J.T. Bonner, 1994. Social insects and social amoebae. *J. Biosci.* 19: 219–245.
- Gotwald, W.H., 1995. *Army Ants: the Biology of Social Predation*. Cornell University Press, Ithaca, New York. 302 pp.
- Green, H.B. and R.E. Hutchins, 1960. Laboratory study of toxicity of imported fire ants to bluegill fish. *J. Econ. Ent.* 53: 1137–1138.
- Heinrich, B., 1981. The regulation of temperature in the honeybee swarm. *Sci. Am.* 244: 147–160.
- Heinrich, B., 1993. *The Hot-blooded Insects: Strategies and Mechanisms of Thermoregulation*. Harvard University Press, Cambridge. 601 pp.
- Hepburn, H.R., 1986. *Honeybees and Wax*. Springer-Verlag, Berlin. 205 pp.
- Hermann, H.R., 1981. Defensive mechanisms in the social Hymenoptera. In: *Social Insects, Vol. II* (H.R. Hermann, Ed.). Academic Press, New York. pp. 77–197.
- Hingston, R.W.G., 1922. *Problems of Instinct and Intelligence*. The Macmillan Company, New York. 296 pp.

- Hölldobler, B. and E.O. Wilson, 1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 3: 19–60.
- Hölldobler, B. and E.O. Wilson, 1983. The evolution of communal nest-weaving in ants. *Am. Sci.* 71: 490–499.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard University Press, Cambridge. 732 pp.
- Hoyt, E., 1996. *The Earth Dwellers*. Simon & Schuster, New York. 310 pp.
- Jaffé, K., 1993. Surfing ants. *Fla. Entomol.* 76: 182–183.
- Jeanne, R.L., 1991. The swarm-founding Polistinae. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca, New York. pp. 191–231.
- Kastberger, G., 1999. Mechanisms of colony defence in giant honeybees. In: *Social Insects at the Turn of the Millennium, Proc. 13th Int. Congr. IUSSI, Adelaide* (M.P. Schwarz and K. Hogendoorn, Eds.), Flinders University Press, Adelaide. p. 244.
- Kastberger, G., G. Rasputnig, S. Biswas and O. Winder, 1998. Evidence of Nasonov scenting in colony defence of the giant honeybee *Apis dorsata*. *Ethol.* 104: 27–37.
- Ledoux, A., 1950. Recherche sur la biologie de la fourmi fileuse (*Oecophylla longinoda* Latr.). *Ann. Sci. Nat. Zool.* 11: 313–409.
- Lensky, Y., P. Cassier, S. Rosa and D. Grandperrin, 1991. Induction of balling in worker honeybees (*Apis mellifera*) by “stress” pheromone from Koschewnikow glands of queen bees: behavioural, structural and chemical study. *Comp. Biochem. Physiol.* 100A: 585–594.
- Lindauer, M.L., 1955. Schwarmbienen auf Wohnungssuche. *Z. vergl. Physiol.* 37: 263–324.
- Lioni, A., 2000. Auto-assemblage et transport collectif chez *Oecophylla*. Unpublished Ph.D. Thesis, Université Libre de Bruxelles, Belgium.
- Lioni, A., C. Sauwens, G. Theraulaz and J.L. Deneubourg, 2001. Chain formation in *Oecophylla longinoda*. *J. Insect Behav.* 14: 679–696.
- Maschwitz, U., S. Steghaus-Kovac, R. Gaube and H. Hänel, 1989. A South East Asian ponerine ant of the genus *Leptogenys* (Hym., Form.) with army ant life habits. *Behav. Ecol. Sociobiol.* 24: 305–316.
- McShea, D.W. and C. Anderson, 2002. The modularization of the organism. In: *Modularity: Understanding the Development and Evolution of Complex Natural Systems* (W. Callebaut and D. Raskin-Gutman, Eds.), MIT Press, Cambridge. In press.
- Michener, C.D., 1974. *The Social Behavior of the Bees*. Harvard University Press, Cambridge. 404 pp.
- Morais, H.C., 1994. Coordinated group ambush: a new predatory behavior in *Azteca* ants (Dolichoderinae). *Insectes soc.* 41: 339–342.
- Morrill, W.L., 1974. Dispersal of red imported fire ants by water. *Fla. Entomol.* 57: 39–42.
- Morse, R.A. and F.M. Laigo, 1969. *Apis dorsata* in the Philippines. *Monogr. Philippine Assoc. Entomol.* 1: 1–96.
- Münch, W. and W. Engels, 1994. Vorkommen der Moor-Knotennameise *Myrmica gallienii* im Riedgürtel des Federsees (Hymenoptera: Myrmicidae). *Entomol. Gener.* 19: 15–20.
- Ono, M., I. Okada and M. Sasaki, 1987. Heat production by balling in the Japanese honeybee, *Apis cerana japonica* as a defensive behavior against the hornet, *Vespa simillima xanthoptera* (Hymenoptera: Vespidae). *Experientia* 43: 1031–1032.
- Ono, M., T. Igarashi, E. Ohno and M. Sasaki, 1995. Unusual thermal defence by a honeybee against mass attack by hornets. *Nature* 377: 334–336.
- Pettis, J.S., L.C. Wescott and M.L. Winston, 1998. Balling behaviour in the honey bee in response to exogenous queen mandibular gland pheromone. *J. Apic. Res.* 37: 125–131.
- Rettenmeyer, C.W., 1963. Behavioral studies of army ants. *Univ. Kansas Sci. Bull.* 64: 281–465.
- Robinson, G.E., 1984. Worker and queen honey bee behavior during foreign queen introduction. *Insectes soc.* 31: 254–263.
- Sakagami, S.F., 1960. Preliminary report on the specific difference of behaviour and other ecological characters between European and Japanese honeybees. *Acta Hymenopterologica* 1: 171–198.
- Savage, T.S., 1847. On the habits of the “drivers” or visiting ants of West Africa. *Trans. R. Entomol. Soc. Lond.* 5: 1–15.
- Savage, T.S., 1849. The driver ants of West Africa. *Proc. Acad. Nat. Sci. Phila.* 4: 195–200.
- Scheffrahn, R. H., J. Krčec, N.-Y. Su, Y. Roisin, J.A. Chase and J.R. Mangold, 1998. Extreme mandible alteration and cephalic phragmosis in drywood termite soldier (Isoptera: Kalotermitidae: *Cryptotermes*) from Jamaica. *Fla. Entomol.* 81: 238–240.
- Schips, M., 1920. Über Wanderameisen. *Naturw. Wochschr., N. F.* 19: 618–619.
- Schmidt-Nielsen, K., 1984. *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge. 241 pp.
- Schneirla, T.C., 1971. *Army Ants: a Study in Social Organization* (H. Topoff, Ed.). Freeman, San Francisco. 349 pp.
- Seeley, T.D., 1995. *The Wisdom of the Hive*. Harvard University Press, Cambridge, Mass. 295 pp.
- Seeley, T.D. and S.C. Buhrman, 1999. Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* 45: 19–31.
- Seeley, T.D. and R. Morse, 1976. The nest of the honey bee (*Apis mellifera* L.). *Insectes soc.* 23: 495–512.
- Seeley, T.D. and B. Heinrich, 1981. Regulation of temperature in the nests of social insects. In: *Insect Thermoregulation* (B. Heinrich, Ed.), John Wiley & Sons, New York. pp. 159–234.
- Sendova-Franks, A. and N.R. Franks, 1999. Self-assembly, self-organization and division of labour. *Phil. Trans. R. Soc. Lond. B.* 354: 1395–1405.
- Steinberg, M.S., 1963. Reconstruction of tissues by dissociated cells. *Science* 141: 401–411.
- Szabó-Patay, J., 1928. A kapus-mangay. *Termesztudományi Közlöny*, Budapest. pp. 215–219.
- Theraulaz, G., A. Lioni, F. Libert, E. Bonabeau and J.L. Deneubourg, 1996. Dynamique de formation des grappes et des chaînes chez la fourmi d’argentine *Linepithema humile*. *Actes Coll. Insectes soc.* 10: 175–178.
- Theraulaz, G., E. Bonabeau, R. Solé, C. Sauwens, A. Lioni, F. Libert, J.L. Deneubourg and L. Passera, 2001. Model of droplet formation and dynamics in the Argentine ants (*Linepithema humile* Mayr). *Bull. Math. Biol.* 63: 1079–1093.
- Visscher, P.K. and S. Camazine, 1999. Collective decisions and cognition in bees. *Nature* 397: 400.
- Weissflog, A., E. Sternheim, W.H.O. Dorow, S. Berghoff and U. Maschwitz, 2000. How to study subterranean army ants: a novel method for locating and monitoring field populations of the South East Asian army ant *Dorylus (Dichthadia) laevigatus* Smith, 1857 (Formicidae, Dorylinae) with observations on their ecology. *Insectes soc.* 47: 317–324.
- Wilson, E.O., 1971. *The Insect Societies*. Harvard University Press, Cambridge. 548 pp.
- Wilson, E.O., 1985. The sociogenesis of insect societies. *Science* 228: 1489–1495.
- Wilson, E.O. and J.H. Eads, 1949. A report on the imported fire ant *Solenopsis saevissima* var. *richteri* Forel in Alabama. Alabama Department of Conservation. 53 pp.
- Winston, M.L., 1987. *The Biology of the Honey Bee*. Harvard University Press, Cambridge, Mass. 281 pp.
- Winston, M.L., 1992. *Killer Bees: the Africanized Honey Bee in the Americas*. Harvard University Press, Cambridge. 162 pp.
- Witte, V. and U. Maschwitz, 2000. Raiding and emigration dynamics in the ponerine army ant *Leptogenys distinguenda* (Hymenoptera, Formicidae). *Insectes soc.* 47: 76–83.
- Wojtusiak, J., E.J. Godzińska and A. Dejean, 1995. Capture and retrieval of very large prey by workers of the African weaver ant, *Oecophylla longinoda* (Latreille 1802). *Trop. Zool.* 8: 309–318.