A masterpiece of evolution – *Oecophylla* weaver ants (Hymenoptera: Formicidae)

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Abstract

Oecophylla species are among the most iconic tropical ants, but a broad review of their biology has been lacking. The two living species of *Oecophylla* are widespread in the Old World tropics and are similar in presenting the most sophisticated nest-building activities of all weaver ants. Workers draw leaves together, often forming long chains, and glue them together with larval silk. Chain formation promises to provide a major subject for the development of models of the self-organization of complex behavior. The colonies are very large and highly polydomous. Queens are predominantly though not exclusively once-mated and colonies are usually single-queened, but most Northern Territory (Australia) colonies are polygynous. The workers are highly polymorphic (seen also in a fossilized colony), show complex polyethism, and present a much-studied rich pheromonal repertoire for the colony's tasks. Colony odor is partly learned, showing a "nasty neighbor" effect in reactions to other colonies of this highly territorial ant, and partly intrinsic to each individual. The odor varies over time and differs between the nests of a colony. Not surprisingly, *Oecophylla* ants are hosts to a variety of inquilines, such as spiders, which mimic the colony odor to escape detection. In addition, a constellation of Homoptera benefit from ant protection, yet the activities of the ants in controlling pest species make these ants beneficial insects (they are also human food in some areas). We speculate that the existence of *Oecophylla* blocks other weaver ants from evolving highly complex social organization, an idea which could be tested with further knowledge on the timing of ant adaptive radiations.

Key words: Weaver ants, *Oecophylla*, self-organization, insect sociobiology, biogeography, colonymate recognition, nest-building, colony genetic structure, polygyny, polyandry, economic significance, review.

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Introduction

Ant researchers working in the Old World tropics will be familiar with weaver ants of the genus *Oecophylla*, justly described as one of the four pinnacles of ant social evolution (HÖLLDOBLER & WILSON 2009). By reviewing the current state of research concerning these ants, we hope to highlight their importance for understanding the evolution of ants and of sociality in general. By identifying the gaps in our current knowledge, we seek to provide some direction for future research on this important genus. The two currently recognised species (BOLTON & al. 2007) have very extensive ranges (Fig. 1) – *O. longinoda* occurs in a wide band across equatorial Africa, and *O. smaragdina* occurs in Sri Lanka and much of India through Indo-China and southern China to the Indomalayan region, northern Australia and Melanesia (COLE & JONES 1948). *Oecophylla smaragdina* has been the more intensively studied species, but as will become clear during our review *O. longinoda* is better known for some aspects. LOKKERS (1986, 1990) noted that in Australia their distribution is bounded jointly by temperature and humidity, and provided a formula said to hold for other regions as well, namely that the boundary to suitable territory is given by:

$$4.26 * \log(R) + 23.5 * \log(T_{min}) - 42.4 = 0$$

where R is average annual rainfall in mm and T_{min} is the mean minimum temperature in °C. Global warming is likely to lead to an expansion of the *Oecophylla* ranges.

Their prominent leaf nests (Fig. 2), glued ("woven") together with silk from the larvae, can readily be seen on many trees in open and closed forests, and their large colony sizes (often over 500,000 workers, LOKKERS 1990), polydomy, territoriality (HÖLLDOBLER & LUMSDEN 1980) and aggressive defenses make them hard to ignore. As we detail further below, aspects such as the high degree of cooperation required to build the leaf nests, the three-dimensional colony territories, huge colony sizes, and their extensive chemical repertoires make the species major subjects for evolutionary and ecological studies.

We sound a note of caution as to how many species of *Oecophylla* there are. Two are currently recognized, but with eight subspecies for *O. longinoda* and six for *O. smaragdina*, see BOLTON & al. (2007). In addition to the morphological variation implied by the recognition of subspecies, there is considerable variation between reports from the same species in such matters as the propensity to thelytoky (parthenogenesis in which females produce exclusively female offspring without fertilization, WHITE 1973), together
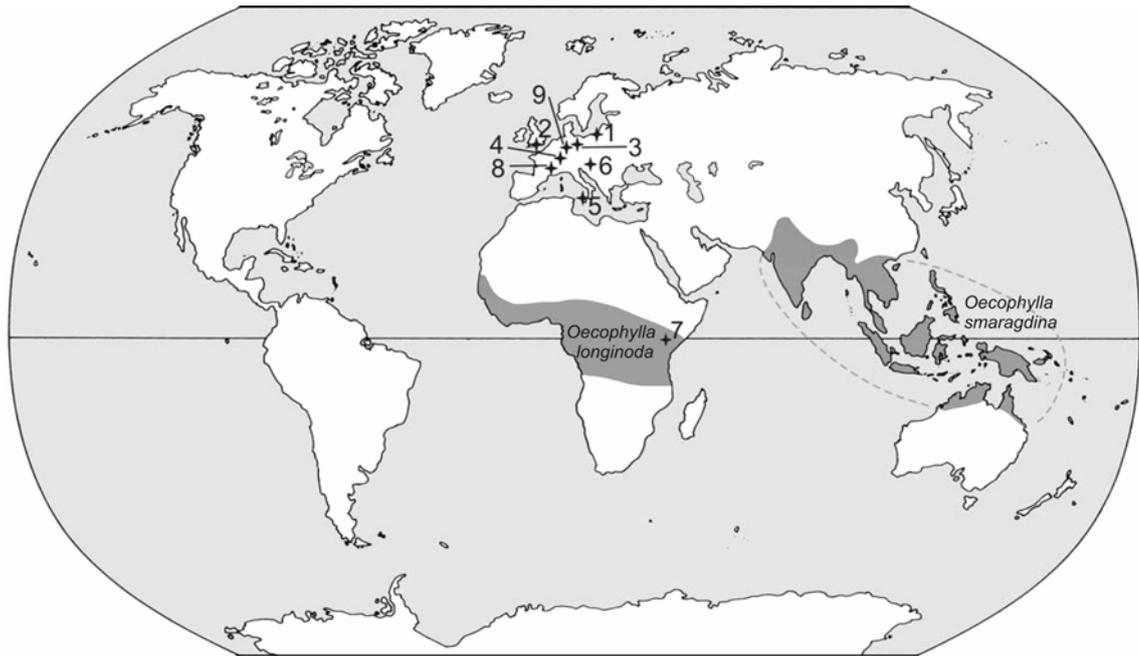
Fig. 1: Distributions of the two currently-recognized species of *Oecophylla*, and fossil sites (numbered, some numbers cover two nearby sites), from DLUSSKY & al. (2008), after LOKKERS (1986), by permission. Sympatric pairs of fossil species have been found twice – *O. brischkei* and *O. crassinoda* in the Eocene (Baltic amber, site 1) and *O. atavina* and *O. megarche* in the Oligocene (Isle of Wight, site 2), whereas the extant species are allopatric. Site 7 is where the fossil nest of *O. leakeyi* was found.

Fig. 2: A leaf-nest of *Oecophylla smaragdina*, Cape Tribulation, North Queensland, Australia. Photo courtesy Alex Wild/myrmecos.net.

with, in *O. smaragdina*, marked phylogeographic structure (AZUMA & al. 2006) and big differences in microsatellite allele frequencies between Australia and Java (E.A. Schlüns, unpubl.). These differences in reports may reflect differences in biology between cryptic species (CROZIER 1970).

If *Oecophylla* species have an impressive present and their study a glorious future, they also have a rich past. Notable is the only intact fossil ant colony, of *O. leakeyi*, preserved in a lower Miocene deposit from Kenya (WILSON & TAYLOR 1964). *Oecophylla leakeyi* individuals were

larger than those of any other species, but present a similar allometry and bimodal size distribution to living species (WILSON & TAYLOR 1964). Eleven unequivocal fossil species are known, predominantly from mid-Eocene to Oligocene in Europe (DLUSSKY & al. 2008), speaking for significant climate change since then! On the basis of mitochondrial sequence divergence, AZUMA & al. (2006) estimate that the two living species diverged 11.3 - 13.3 million years ago, in the Miocene, and the groups they found for *O. smaragdina* diverged between 3.6 and 7.8 million years ago, a recency which may explain the similarity in their morphology and biology.

Social structure

Life cycle: The life cycle of an *O. smaragdina* colony starts with a mated queen finding a sheltered site for a first nest between leaves of a tree or shrub and laying a batch of about 35 eggs within 5 - 10 days after dealation / shedding her wings (LOKKERS 1990). Further brood development strongly depends on temperature. At 30°C LOKKERS (1990) found larvae emerging from about day eight. Pupae follow after day 17 and the first adult worker appeared after 28 days. These first workers are intermediate in size (LOKKERS 1990) to the distinct minor and major castes appearing later (COLE & JONES 1948). As soon as last-instar larvae arise (around day 15), they are used by the queen to seal the nest chamber with silk. Below 20°C and above 35°C brood development stalls mostly due to temperature sensitivity of the pupae, which inhibits colony growth in seasonal climates during the cooler months. One to three days after the first worker emerges the nest is opened through a hole and outside activity starts. Interestingly, LOKKERS (1990) did not find prey retrieved until five weeks after the nest was opened. As in many other ants, the survival rates of new colonies is very low (GREENSLADE 1971) because of high intra- and interspecific competition and disease. Those colonies surviving the founding stage will develop into colonies consisting of at least half a million individuals occupying several good-sized trees (HÖLLDOBLER & WILSON 1990). When the queen dies the workers activate their ovaries and produce a last set of male brood before the colony shrinks as worker numbers reduce over the following months (LOKKERS 1990). Worker reproduction may be delayed because even the queen's corpse may yield queen pheromones for up to half a year (HÖLLDOBLER & WILSON 1983a). GREENSLADE (1971) proposed an average colony life span of about eight years and synchrony of founding new colonies as the old ones die. New sexuals are produced during the wet season and released synchronously after heavy rainfall to take part in aerial swarm mating (in North Queensland, LOKKERS 1990; this locality is near the southern edge of the range and the situation is likely to differ elsewhere). There is a pronounced size dimorphism between the two sexes. The queens are a lot larger and heavier than the males. But we could not find any counts or biomass estimates so that sex allocation theory cannot yet be tested in this species.

The workers of *O. smaragdina* are highly polymorphic. WILSON (1953) showed that the change of head size and shape follows an unusual triphasic allometry with few intermediate sized individuals and the majors far out numbering the minors (Fig. 3). This species could therefore be a valuable model system to understand allometric changes
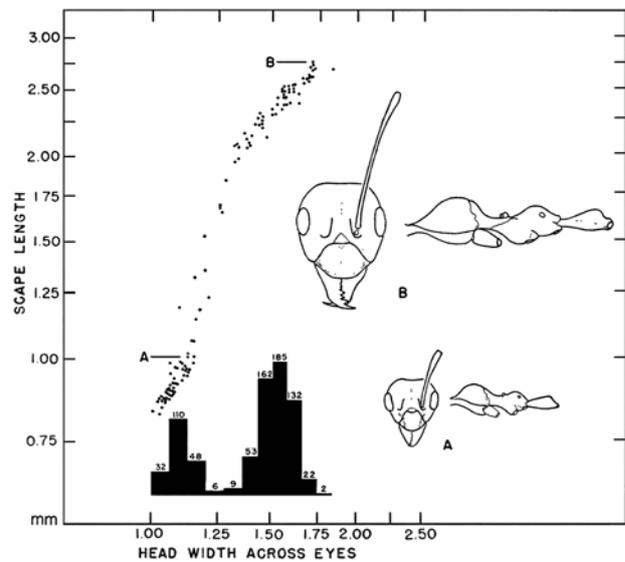

Fig. 3: *Oecophylla* species show a triphasic allometry, with this plot for *O. smaragdina* showing that the majors and minors have different slopes and are connected by intermediates. From WILSON (1953), by permission.

from a continuous to a dimorphic distribution of worker castes. The two worker castes show a clear division of labor with the minors staying inside the nest (caring for brood, etc.) and the majors performing outdoor tasks (e.g., foraging, defence) (HÖLLDOBLER & WILSON 1977c). HÖLLDOBLER (1983) also found age polyethism. Older workers are stationed in barrack nests along the colony periphery and act as guards and defenders. HÖLLDOBLER (1983) also described the territorial behavior of *O. smaragdina* as very similar to its sister species in tropical Africa using different cues for recruitment to new food or terrain, for marking their own territory, for long-range recruitment to intruders and for short-range recruitment to intruders or prey. As expected from demographic theory, CHAPUISAT & KELLER (2002) found that the minor workers live longer than the majors.

Depending on the climate, activity outside the nest occurs constantly in the wet tropics or in a diurnal pattern in the drier part of seasonal climates (LOKKERS 1990). In North Queensland, activity is seven times higher in the wet season than during the dry season and ceases completely below 12°C (LOKKERS 1990). While prey is brought in mainly during daylight hours (which perhaps reflects their excellent eye sight enabling a visual hunting technique), brood is transported after dark (LOKKERS 1990).

In North Queensland, the growth of a colony is highest during the wet season, when temperature, humidity and food availability (after flowering and leaf flushing of the trees and subsequently increased abundance of prey) are most suitable. Brood production then peaks and, following a lag of about a month, worker numbers increase to reach the maximum in March. During the wet season colonies tend to spread out through their territory and then contract to fewer and bigger nests during the dry months (LOKKERS 1990). While larvae are present at all times of the year, pupae are absent for three months in the cooler and drier season. The continuous presence of larvae may be favoured by selection to be able to weave at all times. Eggs and

very young larvae are kept in the same nest as the queen. Later older larvae are distributed throughout the colony.

Ants of this species can dominate up to 50 to 75% of the trees in a given location depending on season (LOKKERS 1990). The expansion of a colony is generally limited only by the availability of trees and competition with other colonies of their own or a few other dominant ant species resulting in a mosaic of colonies across the landscape (HÖLLDOBLER 1983).

The genetic structure of colonies and populations: Studies of genetic colony structure and its causes and consequences have been fundamental to understanding not only the evolution of eusociality but also conflicts arising within colonies and their resolution (e.g., worker reproduction and sex allocation). In particular, the knowledge accumulating on deviations from the norm in genetic structure has helped in unravelling the factors mediating queen, worker and male behavior. Such deviations alter the structure of populations and may ultimately lead to diversification and speciation events (AVISE 2004).

The genetic structure of the archetypical ant colony is simple (CROZIER & PAMILO 1996). A single once-mated queen produces full-sibling workers and new female and male reproductives. Yet, due to relatedness asymmetries caused by male haploidy, various conflicts may arise among the different colony members. Differences from this archetypical breeding and mating behavior that alter relationship structure of colonies have thus gathered particular attention in order to gain insight into how kin selection and other forces might have shaped the life history and behavior of an ant species. *Oecophylla smaragdina* promises to be a very interesting study organism because its genetic colony structure deviates from the archetypical case and also varies among populations (SCHLÜNS & al. 2009). This is a rare case where colony relatedness is reduced by both polygyny and polyandry at levels specific to each population. Of three locations studied, one in Java maintains the highest relatedness among nestmates due to a very low incidence of both polygyny and polyandry. Two Australian populations tend to have greatly reduced colony relatedness and thus an increased intra-colonial genetic variation. Colonies in the Northern Territory are often polygynous and sometimes polyandrous and have therefore the greatest genetic variation (Fig. 4). Up to five unrelated queens were found to contribute equally to the worker offspring in a colony (SCHLÜNS & al. 2009). But this estimate is a minimum due to sample size and could well be higher. This finding confirms the observations of polygyny reported by PEETERS & ANDERSEN (1980) for incipient colonies and PENG & al. (1998) also for mature colonies (by nest dissections). After flying, queens found a colony together (PEETERS & ANDERSEN 1980), and continue living together in the same nest, probably until they die of natural causes. HÖLLDOBLER & WILSON (1977b) recorded swarm mating in *Oecophylla* ants, but VANDERPLANK (1960) wrote that males enter foreign nests and mate with virgin queens within. LOKKERS (1990) found many colony-founding queens, but never saw them leaving their natal nests, inferring that flights occur after dark. Given that these authors reported results from different localities, there is room for comparative studies between divergent sites. The finding (SCHLÜNS & al. 2009) that colony-founding queens are unrelated suggests that intranidal mating of relatives is quite unlikely, but does not distinguish between
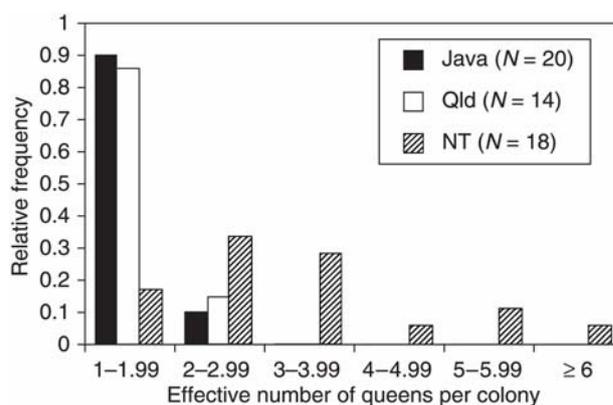

Fig. 4: Variation between localities in the effective number of queens in *Oecophylla smaragdina*, as determined from analyses of microsatellite analyses of 52 colonies from Australia and Indonesia, from SCHLÜNS & al. (2009), by permission.
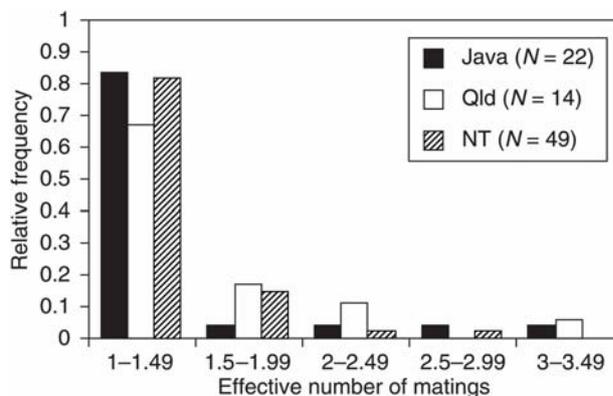

Fig. 5: Variation between queens of *Oecophylla smaragdina* of three localities in the effective number of matings, as inferred from worker microsatellite analyses of 85 colonies, from SCHLÜNS & al. (2009), by permission.

true swarm mating and the entry of males into foreign nests. Yet it is uncommon for unrelated queens to continue to cooperate after the first worker emergence (KELLER 1995, BERNASCONI & STRASSMANN 1999), because the selective advantage of greater competitiveness through faster initial growth and an advantage at raiding other new colonies wears off as competitors are eliminated. The colony lifespan reported for the Northern Territory of seven years (PENG & al. 2004) agrees with all nestmate queens stemming from the colony's founding, with no further queens added during the colony's life.

The queens in a polygynous Northern Territory colony live in the same nest but in different compartments (PENG & al. 1998). The small number of queens make it an example of oligogyny (HÖLLDOBLER 1962), and the probable territoriality suggests that it is a case of paragyny (PAMILO 1991).

In contrast to those in the Northern Territory, colonies in Queensland have an intermediate variability since they are often polyandrous and only sometimes polygynous. Queensland queens mate up to five times, sometimes with skewed contributions by the males (Fig. 5). This finding implies very different mating and colony-founding behavi-

ors in these three populations. Such a skew in male contributions in the production of new queens (as seen in the workers) could create different selection forces on males among populations with varying mating frequencies.

Although polygyny and polyandry each appeared to vary in incidence between locations, there was no correlation between the two. This indicates that within-colony genetic variation is not the only factor that influences queen number and multiple mating by queens in this species (SCHLÜNS & al. 2009).

A larger study covering a greater geographical range is needed to provide a stronger test for this hypothesis and to discover the trends in environmental parameters that drive these population differences.

In the populations where polygyny was rare, in the few cases it did occur reproduction was often skewed in worker production, making the colony functionally close to monogynous. In sharp contrast, colonies of the polygynous population in the Northern Territory rarely showed any skew. The mode of colony foundation was correlated with the queen number in mature colonies. PEETERS & ANDERSEN (1980) observed pleometrosis (multiple queens founding a colony together) in the Northern Territory, but other authors reported haplometrosis in Queensland (DODD 1902) and India (MAXWELL-LEFROY & HOWLETT 1909). This apparent contradiction is now resolved with the demonstration of population differences in queen number and that polygyny, when present, is functional. This makes *O. smaragdina* an excellent study system for the evolution of genetic variation within colonies.

Apart from studying the causes underlying the occurrence of polygyny and polyandry in only some populations, testing sex allocation theory and conflict resolution over male production will be interesting areas to explore in this species. Size differences between queens and males, the multiple mating of queens, and the occurrence of worker reproduction suggest a strongly male-biased numerical sex ratio in Australia, but possibly less in other, genetically less variable populations, as in Indonesia. Split sex ratios seem unlikely as in all reports known to us both males and females were found. A prediction from this is that worker reproduction (through males) is more prominent in the Australian populations.

Although workers in general do not contribute to the production of male brood, when the queen dies the worker-produced males are reared as a last effort to increase their fitness before the colony dies (CROZIER 1970, HÖLLDOBLER & WILSON 1983b).

A complex chemical world

Oecophylla has one of the most complex chemical repertoires among the ants, although most of the studies to date are of *O. longinoda*. Here we consider the role of pheromones in alarm and recruitment behavior, and the role of cuticular hydrocarbons (CHCs) in nestmate recognition.

Pheromones: Analysis of the glandular contents of *Oecophylla* has been restricted to *O. longinoda*. BRADSHAW & al. (1975, 1979b) described several secretions from the mandibular gland that seem to elicit alarm / attack responses of various intensities. Hexanal triggers alarm behavior, while 1-hexanol draws the ants towards the source; at closer range, 3-undecanone and 2-butyl-2-octanal elicit a bite response. BRADSHAW & al. (1979c) found both caste

differences and geographical and colonial variation in these mandibular gland contents.

An alarm response and various types of aggressive behavior are also elicited by the contents of the Dufours and venom glands in the ants' abdomens (BRADSHAW & al. 1979a). The main components, n-undecane and formic acid, appear to act synergistically to stimulate an attack response from major workers.

The sternal gland, identified for the first time in *O. longinoda*, appears to release a pheromone that is used for short range recruitment, inducing workers to gather into small clusters (HÖLLDOBLER & WILSON 1977c). The rectal gland appears to be the source of trail pheromones (HÖLLDOBLER & WILSON 1977c), but also of colony-specific territorial pheromones (HÖLLDOBLER & WILSON 1977a).

These studies are all based on *O. longinoda*. Similar behavioral patterns in *O. smaragdina* suggest a similar role for these glands in this species, but no comparable studies have so far been conducted. This may conceal some important differences between the species. Rectal discharges like those described for *O. longinoda* occur in *O. smaragdina*, although whether they serve the same function is unknown (HÖLLDOBLER 1983). OFFENBERG (2007) found a clear correlation between the density of these anal spots and worker activity, but this does not reveal anything about their function. However, OFFENBERG & al. (2004) found that the beetle *Rhyparida wallacei*, a prey item of *O. smaragdina*, preferred to feed on leaves that were free of these discharges, suggesting that they signalled the presence of the ants. It remains to be seen whether they also serve as a territorial signal for conspecifics.

Colonymate / kin recognition: Cuticular hydrocarbons (CHCs) are generally recognized to play a key role in insect recognition systems (HOWARD & BLOMQUIST 2005), including nest- or colonymate recognition in social insects (DANI 2006). Direct behavioral evidence for CHCs as nestmate-recognition cues has been found in several ant species (AKINO & al. 2004, TORRES & al. 2007, MARTIN & al. 2008).

Two main models have been proposed for understanding colony odor in social insects, the "gestalt" model, and the "individualistic" model (CROZIER & DIX 1979, CROZIER & PAMILO 1996). According to the gestalt model, individuals continually exchange chemical cues with other individuals, usually via trophallaxis (BOULAY & al. 2000) or allogrooming (SOROKER & al. 1998, LENOIR & al. 2001). This results in a more or less uniform odor across the colony, consisting of a blend of individual odors. According to the individualistic model, each individual retains its own odor, with little or no exchange between individuals taking place. The colony odor therefore consists of a greater or lesser variety of odors depending on the level of genetic and / or environmental diversity within the colony.

The gestalt model is now widely accepted as the general rule among eusocial insects (LENOIR & al. 1999). However, there are some indications that a perfect colony gestalt is not always realised. Many aggression bioassays reveal a range of responses by individuals towards the same intruder. BOULAY & al. (2000), for example, argued in favour of the gestalt model for *Camponotus fellah*, despite reporting that upon re-introduction to their colony of origin, workers that had been isolated from their colony for up to 40 days could be attacked by one worker and simultaneously

solicited for trophallaxis by another. Some individuals appear to make recognition errors when confronted with an intruder, while others do not, suggesting some degree of variation in the templates against which intruders are assessed. Furthermore, some "non-self" (TSUTSUI 2004) individuals from another colony are incorrectly recognised as "self" while others are not. This suggests some degree of variation in the signals borne by colony members, as well as in the templates against which they are assessed. In large colonies, perhaps with multiple queens and / or multiple queen-mating, or with heterogeneous microhabitat conditions across the range of the colony, complete mixing of the colony odor might be difficult to maintain. In the polydomous Australian meat ant, *Iridomyrmex purpureus*, for example, there appear to be both colony specific and nest (within colony) specific chemical signals (VAN WILGEN-BURG & al. 2006).

Early evidence for colonymate recognition in *O. smaragdina* is based on direct observation of the response of colony members to intruders from other colonies (HÖLL-DOBLER 1983), which is typically aggressive. HÖLLDOBLER (1983) found that the strength of aggressive response depended on where the intruder was found, with a stronger response elicited when the intruder was inside the territorial boundaries of the colony.

Most of what is known about the CHCs of *O. smaragdina* derives from a series of studies of the myrmecophilous salticid spider *Cosmophasis bitaeniata* that feeds on the larvae of *O. smaragdina*. ALLAN & al. (2002) found that *O. smaragdina* workers were more aggressive, and responded aggressively more frequently, towards filter papers soaked in CHC extracts of ants from alien colonies than to those soaked in extracts of ants from their own colony. ELGAR & ALLAN (2004) found that the CHC profile of *C. bitaeniata* resembled that of the larvae in the colony, rather than that of the workers. As larvae are easily exchanged between colonies (P.S. Newey, unpubl.), this suggests that the CHC profile of larvae (and, therefore, the spider) do not contain the signal used by workers to differentiate between colonymates and non-colonymates, despite the fact that the CHC profiles of larvae differed between colonies (ELGAR & ALLAN 2004), as did those of spiders (ELGAR & ALLAN 2006).

Recent work on colonymate recognition has focussed on laboratory-based behavioral studies and the use of near-infrared reflectance spectroscopy (NIRS) to determine colony odor. The latter involves generating absorption spectra in the near-infrared, from about 4000 per cm to 12500 per cm (wavenumber). Functional groups in molecules have characteristic vibration frequencies within certain sections of this range (SCARFF & al. 2006) and this provides a broad picture of the chemical "signature" of any scanned sample. The method lacks the chemical specificity of Gas Chromatography / Mass Spectroscopy, which is generally used to determine the CHC profile of a colony, but is attractive because it is rapid and inexpensive: a sample can be scanned in less than a minute.

NEWEY & al. (2008b) found that NIRS could be used to differentiate between colonies of *O. smaragdina* and also between nests within colonies. This indicates that, while there are differences in odor between colonies, there are also significant differences within colonies, suggesting that there is, at best, only an imperfect colony gestalt in this species.

However, additional analysis of spectra (NEWEY & al. 2009a) indicates that the differences between colonies occur mainly in the locations and widths of certain peaks, while differences between nests within colonies occur mainly in the amplitudes of peaks. Thus intra-colonial differences do not necessarily obscure inter-colonial differences. Intra-colonial variation may result from limited exchange of workers between nests. HÖLLDOBLER (1983) found that workers in the "barrack" nests at the edges of colonies demonstrated a high degree of site fidelity. This may also be true of workers in other nests: perhaps there is some degree of fidelity to the nest in which the worker first eclosed. This remains to be tested.

Overall, NIRS assigned 76.5% of workers to the correct colony (of four) (NEWEY & al. 2008b). This finding indicates that there is likely to be some overlap in odor between colonies, a result supported by CHC analysis (ELGAR & ALLAN 2006). This might also be expected to result in recognition errors, with some intruders mistakenly identified as colonymates. NEWEY & al. (2008a) demonstrated that the level of aggression shown towards intruders from different colonies varied significantly, with some colonies showing very little aggression towards intruders from some alien colonies. In fact, the level of aggression increased linearly as the spectral distance between colonies, as measured using NIRS, increased (NEWEY & al. 2008a). Similar results have been obtained for other social insects when measuring the chemical distance between colonies using CHCs (SUAREZ & al. 2002, KAIB & al. 2004, D'ETTORRE & al. 2006, FOITZIK & al. 2007). Furthermore, in *O. smaragdina* the level of aggression expressed towards different intruders from the same alien colony also showed a great deal of variability, suggesting that there may be considerable variation in either the odor or recognition template even between individuals in the same nest. Recent research suggests both that some ants are consistently more aggressive than others (CROSLAND 1990) and, more significantly, that individuals may assess intruders using templates based on their individual odor, rather than the colony odor (P.S. Newey & al., unpubl.). This diversity of templates may serve to provide the colony with defence against intruders from a range of conspecific colonies, in that workers may vary in which intruders they most readily detect.

It has been demonstrated in several ant species that colony odor is not fixed, but changes over time, as in *Solenopsis invicta* (see VANDER MEER & al. 1989), *Temnothorax lichtensteini* (see PROVOST & al. 1993), *Cataglyphis iberica* (see DAHBI & LENOIR 1998), *Formica truncorum* (see NIELSEN & al. 1999), *Aphaenogaster senilis* (see LENOIR & al. 2001), and *Linepithema humile* (see SUAREZ & al. 2002). Using NIRS, NEWEY & al. (2009b) showed that colony odor in *O. smaragdina* also exhibited temporal variation. However, they also demonstrated that the spectra of nests from the same colony, when separated for up to three months, changed in parallel with each other (NEWEY & al. 2009b). The level of aggression between separated nests did not increase significantly over that time period, although the frequency of trophallaxis did increase. Imperfect exchange of CHCs between nests within a polydomous colony could lead to incompatibility between nests if the odors diverged sufficiently. In polygynous colonies, this could result in colony budding, but in monogynous colonies this is not possible, and would result in loss of colo-

nial integrity. The parallel changes in separated colony fragments of *O. smaragdina* suggest that there is an underlying mechanism, probably genetic, preventing radical divergence between nests. This may be a necessary adaptation for a species with very large polydomous colonies, but with only a single queen. It would be interesting to see whether this is also the case in other populations of *O. smaragdina* in which polygyny has been reported (PENG & al. 1998, SCHLÜNS & al. 2009).

Colonymate recognition in *O. smaragdina* probably also has a learning component. Colonies are more aggressive towards intruders from neighboring colonies, with which they have presumably had prior contact, than they are towards intruders from more distant colonies (P.S. Newey & al., unpubl.). This is the opposite of the "dear enemy" effect (FISHER 1954), and might be termed the "nasty neighbor" effect (MULLER & MANSER 2007). This could reflect either a difference in the capacity to recognise intruders, or a differential response to intruders depending on their colony of origin. Our research indicates that colonies are both more aggressive towards individuals, and aggressive towards a higher proportion of individuals, from neighboring colonies than from distant colonies (P.S. Newey, unpubl.). This suggests that there is both a behavioral and a perceptual component to this effect. The behavioral component is clear from the fact that, among individuals towards which an aggressive response occurred, this response was greater towards intruders from neighboring colonies. The perceptual component is indicated by the fact that a smaller proportion of workers from distant colonies than from neighboring colonies elicited any level of aggressive response. While we cannot completely rule out the possibility that recipients made a behavioral decision to treat some workers from a colony aggressively and some non-aggressively, it seems more likely that the difference was the result of misidentification. We found no evidence that intruders from distant colonies were avoided rather than engaged in conflict, as might have been expected if they were recognised as alien conspecifics. Furthermore, workers from recipient colonies were more likely to engage in grooming or trophallaxis with workers from unfamiliar than from familiar colonies. We therefore conclude that intruders from distant colonies are more likely to be misidentified as colonymates than workers from neighboring colonies; in addition, when intruders are correctly identified as alien conspecifics, they are greeted with a more aggressive response when they originate from a neighboring colony than when they originate from a more distant colony. It seems clear from this that experience plays an important role in the ability of weaver ants to differentiate between self and other, and in determining the level of aggression directed towards those identified as other. HÖLLDOBLER (1983) also suggested that workers might become sensitised to heterospecific enemies.

Oecophylla smaragdina colonies appear to possess an incomplete colony gestalt odor, with limited exchange of workers between nests resulting in significant intra-colonial variation. However, this variation seems to be limited by an underlying mechanism that prevents the odor between nests from drifting too far apart. This is certainly aided by some exchange of chemicals between nests. Colonies also show considerable variation in their capacity to identify intruders from different colonies. However, as contact between widely separated colonies is unlikely, with an

Fig. 6: Workers of *Oecophylla smaragdina* form chains to pull leaves together in nest-building, from HÖLLDOBLER & WILSON (1990), by permission.

occasional stray representing no real threat, colony defences seem to be directed towards the more immediate threat posed by neighboring colonies, with whom they are likely to compete for resources, and against whom they need to defend an extensive territory.

Behavioral complexity, cooperation and masterful building

Perhaps one of the most distinctive behavioral attributes of *O. smaragdina* involves the manner in which nestmates of multiple castes (including larvae) cooperate to construct arboreal silk nests. Workers form living chains to cross gaps and bring leaves together at the work site (Fig. 6). Additional workers then hold final instar larvae in their mandible at the work sites (Fig. 7), and use the silk produced by the larvae to fasten together leaves to form the nest walls (HÖLLDOBLER & WILSON 1977b). Together, workers and larvae act as a living moveable sewing machine, a skill considered to play a significant role in the ability of *Oecophylla* to achieve such large colonies and ecological dominance (HÖLLDOBLER & WILSON 1990).

Green tree ants as arboreal builders: The nests of *Oecophylla* have attracted attention for many years. The habitation of arboreal nests constructed of leaves glued together with "white material" appears to have been first noted by BANKS (unknown date of online publication) during James Cook's voyage to Australia in the late 18th century. Later studies of *O. smaragdina* determined that the white material used was larval silk, and described how workers can form chains to bring together leaf material to construct their arboreal nests (RIDLEY 1894, and DOFLEIN 1905

Fig. 7: An *Oecophylla smaragdina* worker stimulates a larva to produce a silk thread which is passed back and forth over the gap to fasten the leaves together, from Hölldobler & Wilson (1983b), by permission.

cited by Hemmingsen 1973). These studies were followed with more general ones of the ecology of both extant *Oecophylla* species, *O. smaragdina* (see Cole & Jones 1948) and *O. longinoda* (see Way 1954).

Nest building involves both the preparation of the substrate and the gluing of the substrate together with larval silk. Workers combine to form living chains. Leaves in close proximity can be drawn together through the actions of multiple individuals aligning themselves along leaf perimeters and pulling the edges together, or via the formation of living chains, that bridge gaps and are shortened to draw leaves together (Hölldobler & Wilson 1977b). Nest weaving involves workers holding larvae and initiating silk production through a series of complex behavioral interactions at the work site (Hölldobler & Wilson 1990). A division of labor involving nest weaving is likely, though the actual details are uncertain. Some studies of *O. longinoda* have reported that only major workers hold spinning larvae (Hölldobler & Wilson 1990), while others report that both minor and majors are involved, though the sites of weaving can be different (minors inside nests, majors outside, Hemmingsen 1973). Only final-instar larvae appear to be involved in silk production: Larvae allocate all of their silk to the colony nest (they pupate without cocoons), and they possess relatively larger silk glands and a more modified external silk apparatus than the larvae of other ant species (figure 2 in Hölldobler & Wilson 1983b).

Cooperation between larvae and adults in weaving: Male larvae have silk glands that are relatively smaller than those of female larvae (Wilson & Hölldobler 1980). Wilson & Hölldobler (1980) suggest that this sex difference may reflect the lower levels of relatedness of males than females to other nestmates: males may have less incentive to cooperate in nest building than females. However, we now know that this difference is smaller than was then thought in *O. smaragdina,* as shown by Schlüns & al. (2009), and a comparison with non-social Hymenoptera might prove instructive because in such cases there can be no differential selection on gland size due to sociality.

Comparison with other weaving ants: The incorporation of silk into nests is known from a number of ant species, but the source of this silk is often uncertain. Silk has been described in the earthen nests of some *Temnothorax* (Myrmicinae, Baroni Urbani 1978) but the source of this silk is unknown. Struck by the resemblance of *Technomyrmex bicolor* nests to "miniature" ones of *Polyrhachis*, Jacobson & Forel (1909) suggested that this dolichoderine ant is also a weaver, but this seems unlikely. The terrestrial nests of *Melissotarsus emeryi* contain silk strands produced from specialized glands in the hypostoma of the workers, but *M. emeryi* is the only known ant in which workers can produce silk (Myrmicinae, Fisher & Robertson 1999). Arboreal silk nests are produced by *Dolichoderus sulcaticeps* (Dolichoderinae, Maschwitz & al. 1991), but the silk is from spiders (Rohe & Maschwitz 2003).

The use of larval silk in arboreal nests appears to be limited to three genera within the Camponotini: *Camponotus, Polyrhachis* and *Oecophylla.* Weaving has likely evolved independently four times, twice in *Camponotus* (subgenera *Dendromyrmex* and *Karavaievia*) and once each in the other genera (Johnson & al. 2003), but further studies are needed. Recent research on the nesting habits of the genus *Polyrhachis* suggests that nesting habits can be much more variable than previously thought (Robson & Kohout 2007). Nest location (arboreal or terrestrial) and the inclusion of silk in nests can be variable within individual species, and the presence or absence of cocoons varies between species within the genus. The use of spider rather than larval silk is known in some *Polyrhachis* species (Robson 2004) and suspected in others (Robson & Kohout 2008), and the use of non-larval silk may provide an explanation for observations mentioned above of silk nests in *Temnothorax.*

Hölldobler & Wilson (1983b) place *Oecophylla* at the top of three levels of sophistication in the weaver-ant life style. The first grade is occupied by species of *Camponotus* (*Dendromyrmex*). *Dendromyrmex* larvae contribute to nest architecture by emitting silk in the nest, but they are neither held nor manipulated by workers (Wilson 1981). The second grade comprises various *Camponotus* (*Karavaievia*) and *Polyrhachis* species in which workers hold larvae which emit silk to fill the spaces between leaves and other structural elements, but do not otherwise adjust the substrate (Maschwitz & al. 1985). The third grade is represented solely by *Oecophylla*, in which the silk-producing larvae are always held by workers, the larvae do not pupae in cocoons and alone among all weaving ants, the workers extensively adjust the substrate by pulling leaves together (Hölldobler & Wilson 1983b).

Hölldobler & Wilson (1983b) note that the two lower levels of weaver ant organization show how the high level of sophistication achieved by *Oecophylla* could have evolved, while filling in little about the actual details. Hölldobler & Wilson (1983b) also discuss two hypotheses on why not all weaver ants have achieved the level shown by *Oecophylla*. The first hypothesis is that all weaver-ant lineages are indeed evolving to the *Oecophylla* level, but that a combination of extinctions and new originations of weaving mean that there are always species further back

on the path. The second hypothesis is that species at the three grades are more or less in a stable state – that the level each has reached is appropriate for it given its ecological niche. We incline to the second hypothesis. Thus, honey bees such as *Apis mellifera* have a much more elaborate social organization than bumble bees, but the life cycle of the latter bees enables them to survive in higher latitudes than can honey bees (GOULSON & SPARROW 2009). However, given that there are no fossil *Dendromyrmex* (see BOLTON 2003) and that the sole *Polyrhachis* fossil is quite recent (Upper Mioncene; WAPPLER & al. 2009), we cannot be sure of the dates of origin of the weaver ants in these groups.

Chain formation as an experimental system: Social insects play a key role in advancing our understanding of how complex systems solve problems, via the relative ease with which they can be experimentally manipulated and the diversity of problems they solve on a daily basis. Comprised of relatively simple individuals, as a group they display a "collective intelligence that seems far beyond the capabilities of single individuals" (BONABEAU & al. 1997). A new science has emerged that develops problem-solving algorithms inspired by the behaviors of social insects and recognizes biologists as "providers" of innovative ideas (BONABEAU & al. 2000, DORIGO & STÜTZLE 2004). Exemplary studies of real-life problem solving such as the manner in which colonies of honey bees and ants select new nest sites (PRATT & al. 2002, SEELEY & VISSCHER 2004) and the foraging of ants (DENEUBOURG & al. 1983, BEEKMAN & al. 2001, BURD & al. 2002) have naturally lead to advances in our understanding of more general principles such as social insect nest-site selection (FRANKS & al. 2002), teamwork (ANDERSON & FRANKS 2003, SUMPTER 2006), self-assembly (ANDERSON & al. 2002), foraging behavior (SUMPTER & PRATT 2003), colony organization (BONABEAU & al. 1997), group decision making (DETRAIN & DENEUBOURG 2008, PASSINO & al. 2008) and cognition (SEELEY & al. 2006). These, in turn, have lead to significant advances in our ability to find optimal solutions to problems facing humans, such as traffic flow (DUSSUTOUR & al. 2004), communication networks (BONABEAU & al. 2000, DORIGO & STÜTZLE 2004) and clustering algorithms for internet searches (SCHOCKAERT & al. 2007). An example of the impressive extent to which insects can be used to solve practical problems involves allowing live insects to cohabit with robots to optimize the problem solving capabilities of the combined group (HALLOY & al. 2007).

Studies of the building behavior of *Oecophylla* promise to contribute significantly to our understanding of problem solving in complex systems and the production of collective systems through self-assembly. Building on earlier studies of the organization of group behavior (SUDD 1963), recent studies have demonstrated how population size and individual probabilities of entering or leaving chains explain much of the observed dynamics of chain formation in *Oecophylla* (LIONI & al. 2001, LIONI & DENEUBOURG 2004). Despite the amazing ability of *Oecophylla* workers to form "bridges, ladders, pulling chains and droplets" we know little of the proximate mechanisms underlying these behaviors (ANDERSON & al. 2002). The behavior in which *Oecophylla* workers form groups that hang then drop from the end of branches, for example, resembles water dripping from a leaky tap (BONABEAU & al. 1998).

Associations – friends and enemies

Oecophylla smaragdina has some interesting relationships with other fauna. The parasitic and mutualistic associations that other species have with weaver ants is probably worth a review of its own. Here we will only consider some of the more important and interesting of these.

Enemies: One of the most closely studied relationships is with the predatory spider, *Cosmophasis bitaeniata*, which is both a visual and a chemical mimic of the ant. This salticid spider feeds on the ant larvae and appears to be quite comfortable inside ant nests, although it tends to avoid direct contact with major workers (ALLAN & ELGAR 2001). The CHC profile of the spider most closely resembles that of the larvae in the host colony (ELGAR & ALLAN 2006), and is almost certainly obtained either through eating or handling its prey (ELGAR & ALLAN 2004). Although the CHC profile of larvae varies between colonies, colonies readily accept larvae from alien conspecific colonies. This means that spiders are likely to be able to move between colonies, although they appear to have more success acquiring larvae from minor workers in their host colony than from minor workers from other colonies (ELGAR & ALLAN 2006). The difference appears to be the result of changes in the behavior of the spider rather than of the ants, as no change in activity was recorded by workers in the presence of spiders from colonies other than their own (ELGAR & ALLAN 2006). *Oecophylla smaragdina* are also host to *Myrmarachne* spiders, which show a large measure of independence in their speciation pattern from the wide range of host ants they mimic (CECCARELLI & CROZIER 2007).

The larvae of two lycaenid butterflies, *Liphyra brassolis* and *L. grandis*, feed exclusively on larvae of the weaver ant (BRABY 2000). The larvae of *L. brassolis* are flat and broadly oval (PIERCE & al. 2002), and their tough exterior probably protects them from the ants (BRABY 2000). Whether any chemical mimicry is also involved is not known. However, nests sometimes contain several of these large and conspicuous predators and the workers exhibit no obvious reaction to their presence (P.S. Newey, unpubl.), suggesting that some chemical disguise may also be in effect. Most ant / lycaenid associations appear to be mutualistic to some degree, and these predatory associations are among only 37 confirmed cases worldwide of ant-parasitic lycaenids (DANIELS 2004).

Friends: The larvae of many lycaenid butterflies secrete ant-appeasement substances or attractants, as well as sugary food solutions, from epidermal glands. These enable them to live within the protection of ant nests. Within Australia, the larvae of eight species of lycaenid butterflies are attended by weaver ants. *Arhopala centaurus*, *A. madytus*, *A. micale*, *Hypolycaena phorbas*, and *Anthene seltuttus* are obligate myrmecophiles, tended exclusively by weaver ants (BRABY 2000). *Anthene lycaenoides* and *Nacaduba berenice* are facultative myrmecophiles attended by a range of ant species including weaver ants (BRABY 2000), while *Theclinesthes miskini* has been recorded as associated with weaver ants only once (BRABY 2000). *Anthene emolus*, an obligate myrmecophile associated exclusively with weaver ants in south-east Asia, also appears to give off alarm pheromones when disturbed, to which the ants respond (FIEDLER & MASCHWITZ 1989). Whether or not this is true of other lycaenids is not known. These associa-

Fig. 8: *Oecophylla smaragdina* workers congregating on a dead Forest Kingfisher (*Todiramphus macleayii*), courtesy David Browning.

tions are mutualistic because the larvae acquire some protection from predators, and are also carried to food sources at some stages in their development (FIEDLER & MASCHWITZ 1989), while ants receive food that is rich in carbohydrates.

Weaver ants also derive food from a range of other insect species that excrete solutions rich in sugars, amino acids and other nutrients. In the Solomon Islands *O. smaragdina* is reported to attend at least nine species of sedentary Homoptera (GREENSLADE 1972). BLÜTHGEN & FIEDLER (2002) identified trophobionts from seven families (excluding lycaenids) associated with weaver ants at a rainforest site in far north Queensland, Australia. Although ant / trophobiont associations are generally assumed to be mutualistic, evidence of benefits to the trophobionts appears to be largely anecdotal (HÖLLDOBLER & WILSON 1990). Early studies yielded conflicting evidence concerning the extent to which ants provided protection for trophobionts (WAY 1963). More recent evidence suggests that protection from parasitism is one likely benefit in some relationships. For example, trophobiotic associations with two ant species, *Camponotus brutus* and *Myrmicaria opaciventris*, reduce egg parasitism in *Caternaultiella rugosa* (Heteroptera: Plataspidae) (GIBERNAU & DEJEAN 2001). There is some evidence that *O. longinoda* reduces the level of parasitism among the homopterans it attends (WAY 1963). Both *Oecophylla* species also transport homopterans to suitable feeding locations (WAY 1963). The degree to which

these associations are obligate or exclusive between species is largely unknown, although some weaver ant associations with Homoptera may be exclusive, or nearly so (WAY 1963). In general there is a paucity of detailed studies of weaver ant / trophobiont associations other than those involving lycaenids.

Economic significance

Oecophylla smaragdina is not only ecologically important, as one of the dominant species in the forest canopies of northern Australia and south-east Asia (BLÜTHGEN & STORK 2007, DAVIDSON 2007), but is also of considerable economic importance as a biological control agent, as food and medicine, and also as a potential pest itself.

Biological control agent: Written records indicate that *Oecophylla smaragdina* was recognised in China as a biological control agent as early as 304 A.D. (VAN MELE 2008). Recent research has demonstrated its effectiveness in controlling several pests in mango orchards (PENG & CHRISTIAN 2004, 2005, 2006, BLÜTHGEN & STORK 2007, DAVIDSON 2007, PENG & CHRISTIAN 2007), cashew plantations (PENG & al. 1999, 2005), citrus orchards (VAN MELE & CUC 2000, VAN MELE & al. 2002), coconut plantations (KUMARESAN 1996) and cocoa plantations (WAY & KHOO 1989, 1991). For example, weaver ants, combined with soft chemical applications, reduce the numbers of Jarvis's fruit fly, *Bactrocera jarvisi*, in mango plantations, compared with treatment by chemical insecticides, signifi-

cantly reducing the level of rejected fruit (PENG & CHRISTIAN 2006).

Food and medicine: Throughout south-east Asia, weaver ants are a significant commercial product. In Java the larvae and pupae of weaver ants are harvested and sold as food for song birds or as fishing bait (CÉSARD 2004). Small larvae (either of workers or early instar queens) are preferred as bird food. In the markets, 1 kg of larvae sells for between US$3.5 and US$5.00 (CÉSARD 2004). In Thailand, large queen larvae and pupae are harvested as a food product for human consumption (SRIBANDIT & al. 2008). This not only provides food for the family, but also as much as 30% of the total family income for collectors (SRIBANDIT & al. 2008). In parts of India the workers themselves are consumed, and even used in the making of chutney (OUDHIA 2002)!

Extracts from the ants are used by Indian traditional healers to treat a range of common maladies (OUDHIA 2002). Weaver ants are also reportedly used by indigenous Australian women to produce a remedy for colds and flu (WATSON 2002).

Pest: Although generally regarded as beneficial within the agricultural industry, *O. smaragdina* can also sometimes be regarded as a pest, being an opportunistic and aggressive feeder (Fig. 8). Even when the benefits of weaver ants to the quality of mango fruit are acknowledged, the ants are still often regarded as a nuisance pest during harvesting (SINZOGAN & al. 2008). The use of weaver ants as a biological control agent on coffee plantations in Sri Lanka has reportedly been abandoned for just this reason (CÉSARD 2004).

Outlook

It is our impression that research into the living *Oecophylla* species has been uneven. The glandular contents are better known in *O. longinoda*, and *O. smaragdina* has been more studied for behavior, population structure and colony structure. The two species are generally regarded as very similar, but are estimated to have separated over 10 million years ago (AZUMA & al. 2006) and surprises may result from work making them equally well-known. Further, the importance of these species to insect sociobiology makes them worthwhile subjects for exhaustive study to test for the presence of sibling species (SCHLICK-STEINER & al. 2009); given the very large ranges involved it is likely (CROZIER 1981) though not certain (WARD 1989) that such sibling species do occur. Thus, TAYLOR (2008) considers that *O. longinoda* comprises several cryptic species. Discovery that there are more species than currently recognized would place apparent geographic variation in biology in a new light.

Oecophylla species present a tractable system for studying a complex behavior, namely the construction of the leaf nests. How this cooperative system is controlled, and the degree to which it differs between the species, are fruitful subjects for future study. Combination of such studies with further molecular phylogenetic studies may allow identification of correlates in habitat or sociality mediating these complex behaviors.

Oecophylla species have unusual economic potential for ants, not only in their interactions with beneficial and pest insects, but also in medicinal terms. Although it is likely that in many places their use as biological control agents has been superseded by the use of insecticides, increasing reluctance to deploy large-scale biocide application means that the use of *Oecophylla* species in biological control should be re-examined.

Zusammenfassung

Arten der Gattung *Oecophylla* gehören zu den bekanntesten Ameisen in den Tropen, jedoch fehlt bis heute ein breiter Überblick über ihre Biologie. Die zwei heute lebenden *Oecophylla*-Arten sind in den Altwelttropen weit verbreitet und ähneln sich in dem komplexesten Nestbauverhalten aller Weberameisen. Arbeiterinnen ziehen Blätter zusammen, was oft mit dem Bilden langer Ketten verbunden ist, und kleben sie mit der Seide ihrer Larven aneinander. Die Kettenbildung verspricht ein wichtiges Themengebiet für die Entwicklung von Modellen zur Selbstorganisation komplexen Verhaltens zu bieten. Die Kolonien sind sehr groß und hochgradig polydom. Die Königinnen sind meist, jedoch nicht immer, einfach verpaart und die Kolonien normalerweise monogyn, außer im Northern Territory (Australien), wo sie polygyn sind. Die Arbeiterinnen sind stark polymorph (wie schon bei einer fossilisierten Kolonie dokumentiert) und zeigen einen komplexen Polyethismus und ein viel untersuchtes, reichhaltiges Pheromonrepertoire für die verschiedenen Aufgabenbereiche der Kolonie. Der Koloniegeruch, teils erlernt und teils jedem Individuum intrinsisch, weist in den Reaktionen gegenüber anderen Kolonien dieser hochgradig territorialen Ameise einen "nasty neighbor"-Effekt auf. Der Geruch verändert sich mit der Zeit und unterscheidet sich zwischen Nestern einer Kolonie. Es ist nicht überraschend, dass *Oecophylla*-Ameisen Wirte einer Reihe von Inquilinen sind (wie z.B. Spinnen), die den Koloniegeruch imitieren, um einer Entdeckung zu entgehen. Zusätzlich profitieren verschiedene Homopteren vom Schutz der Ameisen, dennoch eignen sich diese Ameisen auf Grund ihres Verhaltens als Nutzinsekten zur Schädlingskontrolle. In verschiedenen Regionen werden sie auch vom Menschen gegessen. Wir spekulieren, dass die Existenz von *Oecophylla* die Evolution hochkomplexer sozialer Organisation bei anderen Weberameisen verhindert, eine Idee, die mit größerem Wissen über die zeitliche Abfolge von adaptiven Radiationen innerhalb der Ameisen getestet werden könnte.

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