

Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae)

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Abstract

Ant colonies are organized similarly to those of wasps and bees: reproductive altruism, age polyethism, and complex communication. Yet ants exhibit more species, much higher total biomass, and their lifestyles and diet are more diverse. Hence, factors additional to sociality must be involved in this evolutionary diversification. We argue that loss of flight permitted extensive changes in body size of ant workers and queens. Wingless helpers revolutionized colonial economy because they are cheaper to manufacture. Flightlessness also removed constraints on the evolution of dwarf workers (head width 1 mm or less); these exist in 229 / 286 ant genera examined but not in social wasps and bees. Miniaturisation involves simplification of tissues and organs (compound eyes, sting apparatus, ovaries, exoskeleton), and dwarf workers are cheaper per capita. Comparison of ovariole numbers in 106 genera indicates reduction of ovaries in dwarf workers, and complete loss in six genera of Ponerinae and eight genera of Myrmicinae. Body size influences trophic ecology, but also the pattern in which a colony's finite energy budget is "packaged", allowing increases in colony size if adaptive. Dwarf workers together with big queens enabled the evolution of claustral independent colony foundation that is predominant in three large subfamilies (Dolichoderinae, Formicinae and Myrmicinae). Winglessness allows this divergence of costs between workers and queens, but also novel activity schedules and adaptations for defence. Highly dimorphic queens and workers promoted the evolution of mosaic phenotypes (soldiers and ergatoid queens), which added to colonial complexity (MOLET & al. 2012 *The American Naturalist* 180: 328-341). We speculate that cheaper workers caused a shift away from a carnivorous diet to carbohydrates such as honeydew. Wasp and bee workers – infertile just as in ants – need to fly and this constrained extensive divergence from queens, which prevented bigger colonies. The winglessness of ant helpers maximized the benefits of having two morphological castes.

Key words: Body size, miniaturisation, morphology, colony foundation, flight, caste, queen, wasps, bees, Ponerinae, review.

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Introduction

There are few species of ants (at least 13000) compared with other insects (at least one million), yet ants are ubiquitous on earth. Ants inhabit all terrestrial habitats except polar regions, they play key ecological roles as predators, scavengers and herbivores, as well as being involved in mutualisms with many diverse organisms (insects, plants, fungi, ...) (HÖLDOBLER & WILSON 1990). This impressive ecological dominance contrasts with the other eusocial insects. The biomass of social bees, wasps and termites is much lower, a reflection of more restricted trophic niches. Social wasps (about 900 species) are predators of arthropods, social bees (about 1000 species) feed on nectar and pollen while termites (< 3000 species) have a cellulose diet (ROSS & MATTHEWS 1991, MICHENER 2007). The first ants were general predators, but feeding behaviour diversified considerably during their adaptive radiation (WILSON & HÖLDOBLER 2005, WARD 2006).

Ant colonies are organized similarly to those of wasps and bees: strict reproductive altruism, separation of helper tasks based on age polyethism, and complex communica-

tion. Yet ants have more diverse lifestyles and diets, hence, factors additional to sociality must be considered. One conspicuous difference is the extent of morphological divergence between reproductive and helper castes. All ants have wingless workers, and size dimorphism relative to queens is striking in many species (HÖLDOBLER & WILSON 1990). In contrast, only a minority of social bees and wasps have distinct morphological castes, and both queen and worker castes are winged, with only limited differences in body size (ROSS & MATTHEWS 1991, MICHENER 2007).

The vast majority of insects can fly, to disperse, forage widely and avoid predators. Evolving wingless helpers in the common ancestor of ants recast their way of life and led to a broad array of adaptations for foraging and colony defence. The winglessness of workers also had a decisive effect on the strategy of queens, who cut off their wings before founding their colonies. Ant queens fly only a few hours, but this once-in-a-lifetime event has great significance, to meet distantly related males (thus maximizing gene flow) and the opportunity to colonize new or dis-

Box 1: Ant workers are highly eccentric wasps.

Ant workers are modified aculeate wasps, and this ancestry is key for understanding some striking morphological adaptations. The evolution of Apocrita is characterized by the narrow waist formed between first and second abdominal segments. This constriction gives flexibility to the gaster, presumably for a more effective use of the ovipositor to pierce the exoskeleton of parasitized insects (WARD 2014). Gaster flexibility further increased in importance when the ovipositor of Aculeata (stinging wasps, bees and ants) became modified as a sting to inject venom.

Worker morphology is marked by both wasp ancestry and morphological divergence from winged queens:

Head: Prognathy (see text) caused substantial modifications away from wasps. Ant mandibles exhibit a broad diversity of shapes, which is not the case in wasps and bees. Moreover, head shape (round, square or triangular) influences the distance between mandible bases, with consequences on prey size. Powerful mandibles need big muscles, and these can constitute most of head volume (PAUL 2001), in soldiers for example. Mandibles are never specially adapted for brood care, but handling brood is an important constraint on the diversification of mandible shapes. This is clearly seen in *Polyergus*, where saber-shaped mandibles are viable only because brood is carried by the host workers (KUGLER 1979), while in *Mystrium voeltzkowi* workers have long snapping mandibles that seem unsuitable to carry brood, and such task is done by queens only (MOLET & al. 2007).

Redesigning the ant head also involved the antennae and the eyes. Antennae play important chemosensory and tactile functions whenever other ants or objects are encountered, and increasing scape length allows the antennal tips to project beyond the forward-pointing mandibles. Antennae are especially long in various formicoid genera, while in wasps and bees they are shorter and much less variable. Cuticular outgrowths of various anatomical origins make the antennal sockets much more complex than in vespid wasps. It is possible that this vital articulation needs better protection in ants because of life on six legs. However, movement of the scape is consequently restricted to a front-back fashion, with limited up-down motion (except in most Formicinae, Dolichoderinae and army ants) (KELLER 2008, 2011). This restriction is taken further in lineages where the retracted scape fits in an antennal "scrobe" or recess. As far as vision, eye size and placement vary tremendously. Worker eyes can be the same as flying queens', but they are often reduced (fewer ommatidia) whenever ground locomotion is based on chemical cues (GRONENBERG 2008). Some predatory species are capable of 3D vision, while eyes were lost in various microhabitats, e.g., litter, soil-dwelling or caves. Ocelli are typical of all flying insects, but they are retained in the workers of only a few lineages and apparently function in detection of light levels (e.g., NARENDRA & al. 2011).

Thorax (called "mesosoma" in all Apocrita): In Hymenoptera, both fore- and hindwings are powered by indirect flight muscles attached to the mesothorax only, hence, the mesonotum (dorsum of T2) is the most developed sclerite in ant queens (Fig. 1). Dorso-ventral wing muscles attach to the mesonotum, while the longitudinal muscles attach to internal cuticular projections ("phragma", plural "phragmata") of the mesonotum.

Winglessness in workers caused a dramatic re-structuring of the dorsal regions of the mesosoma (Fig. 1). The mesonotum is reduced due to the lack of wing muscles, and it is fused posteriorly to the vestigial metanotum (T3). The pronotum (T1) is always prominent because of the muscles powering the head (KELLER & al. 2014). Ventrally, the mesosoma supports the legs and is thus not modified in workers. The last segment (propodeum, A1) is unaffected by the lack of wing muscles and remains large because it accommodates the muscles powering the petiole (Fig. 1). The mesosoma is decisive for any mechanical operation involving the head and mandibles – lifting and carrying objects, digging, cutting, grabbing prey.

Leg length varies considerably (mainly femur and tibia) and is an obvious adaptation for running (long legs) or movement in narrow cavities (short legs). Both the tarsal claws (flexible hinges) and arolium (soft, movable cuticle bladder) are present in wasps, but they preadapt arboreal ants to hold on to smooth plant surfaces (FEDERLE & al. 2001).

Petiole: Hallmark of the Formicidae, the petiole is a separate segment, thus more specialized than the waist of wasps. It is an adaptation for defence and prey capture, although the waist of wasps (a simple constriction) also allows manoeuvrability. The ant petiole varies in size and shape, reflecting the extent of muscular connections between thorax and gaster (HASHIMOTO 1996). An additional abdominal segment became modified as a post-petiole in various subfamilies, including Ecitoninae, Pseudomyrmecinae, and Myrmicinae. A post-petiole presumably further increases the flexibility between mesosoma and gaster. Petiole design enables the tip of the gaster to point forward or sideways, a behaviour often used aggressively, e.g., to sting prey, or to spray formic acid in Formicinae.

Gaster: Ants' gasters are generally similar to wasps, with only few exceptions (Proceratiinae). Both queens and workers are able to increase gaster volume considerably, by stretching the membranes connecting sclerites. Lack of flight (mated queens also) removes constraints on gaster expansion. This allows workers to store food inside the nest as well as transport honeydew and other sweet secretions.

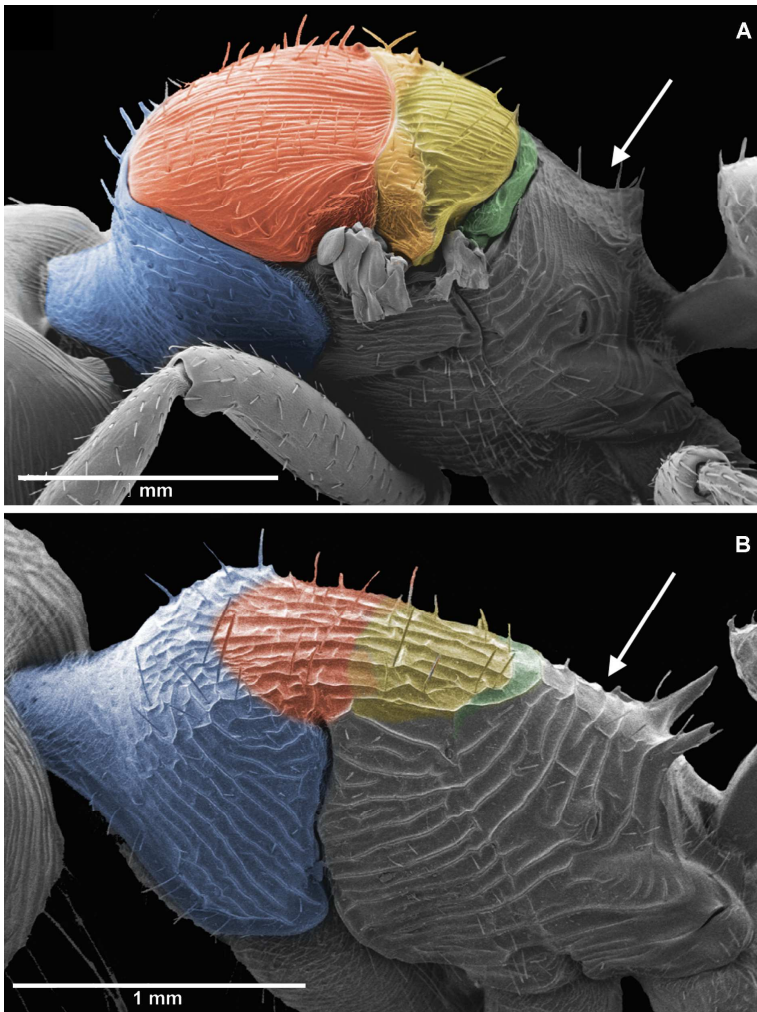


Fig. 1: Differences in thorax (mesosoma) structure between flying queen (A) and worker (B) in *Pogonomyrmex*. Dorsal sclerites are colour-coded: pronotum (T1) = blue; mesonotum (T2) = red-orange (scutum) and yellow (scutellum); metanotum (T3) = green; propodeum (A1) = arrow, no colour. Modified from PEETERS & al. (2012).

junct habitats. Aerial dispersal underlies the prevalence of ants in all ecosystems, and it is compatible with wingless workers because of polyphenism. Besides, a sizeable minority of ant species have lost winged queens and these disperse on foot with the workers, although males continue to fly and allow sufficient gene flow (reviewed in PEETERS 2012).

Using wasp workers for comparison, we try to distinguish adaptations of ant workers linked to (I) eusociality and age polyethism; (II) winglessness. We apprehend ant diversity by separating poneroid and formicoid subfamilies. A formicoid clade, not revealed by previous morphological studies, is very strongly supported by molecular data, meaning that all extant formicoids evolved from a single ancestor (MOREAU 2009, WARD 2014). Poneroids are a non-monophyletic group with all the subfamilies that arose from an earlier radiation. A broad comparative overview of poneroids and formicoids allows us to reconstruct major steps in the diversification of ant societies. We show that the lack of flight constraints allowed miniaturisation in many unrelated lineages, and ant workers can be considerably smaller than other social Hymenoptera. Such dwarf workers are cheaper per capita, and cost reduction enabled dramatic increases in colony size whenever it was adaptive or it opened up new lifestyles (e.g., army ant predation).

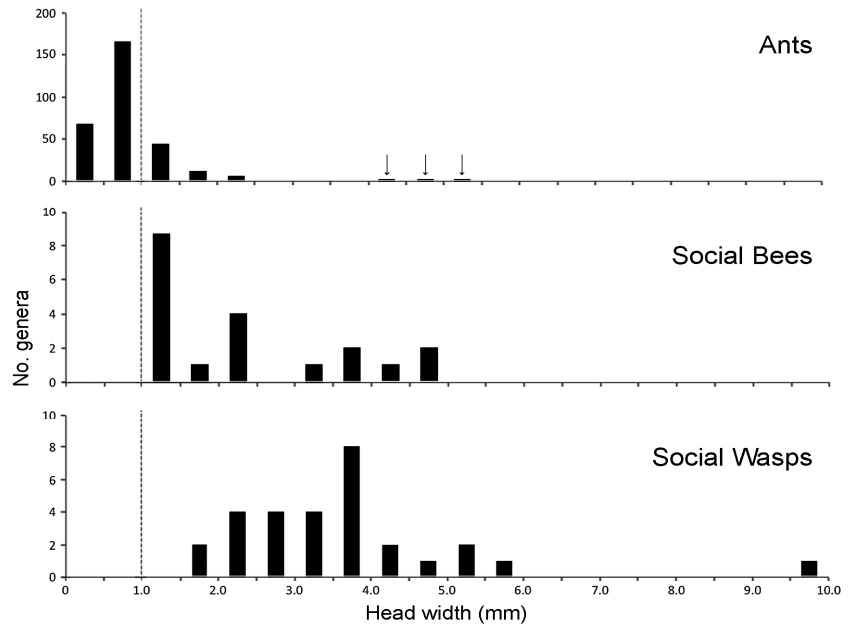
An ancestral commitment to ground-living

Ants (including all queens) perform their daily tasks on six legs, and this is reflected by winglessness (dealation in

the case of queens) as well as a shift to prognathy. Forward-pointing mandibles allow for effective manipulation of objects or prey, and result from a drastic reorganisation of head architecture (R.A. Keller & C. Peeters, unpubl.). Mandibles became multi-purpose tools that are assisted by specialized musculature in both head capsule (PAUL 2001) and prothorax (KELLER & al. 2014). The spatial relocation of mandibles implies vulnerability of the remaining mouthparts (i.e., maxillae and labium), accordingly all ants evolved a complex locking mechanism to protect these softer structures, and closure is tighter in the strictly predatory Amblyoponinae, Ponerinae and Dorylinae (KELLER 2008).

Ant workers are not simplified queens (KELLER & al. 2014), they are highly specialized ground-dwelling insects that gather resources in a cost-efficient manner. In many lineages, workers are much smaller than conspecific winged queens, further highlighting their distinctness. Among flightless insects, ant workers have some of the more extremely reduced thoraces, reaching nearly complete fusion of all sclerites (Fig. 1). Together with forward-pointing heads, the combination of simplified thorax, elbowed antennae, and a petiole (Box 1) allow non-specialists to recognize ants across most human cultures (WARD 2006). Despite an extreme diversity in lifestyles, the morphology of ant workers is highly uniform (compared with morphology of e.g., beetles). Besides the shape of head and mandibles, body size (ranging from over 25 mm to 1 mm) is the most conspicuous variation among 13000 extant species.

Fig. 2: Head width as proxy for worker body size in ants (286 genera), social bees (21 genera), and social wasps (25 genera) (listed in Appendix S1). Maximum width of head capsule excluding eyes was measured in full-face view for the smallest species of each ant genus. In size-polymorphic species, the smallest worker was measured. Literature data were used for bees and wasps (such measures of head width usually include eyes).



Winglessness allows divergence of body size between workers and queens

Our views about caste evolution are based on several arguments that will be detailed hereafter:

1) Ant workers have lower manufacturing and metabolic costs than winged wasp workers. Moreover, ant workers show extreme reductions in size in many lineages. Dwarf workers (head width 1 mm or less) do not exist in social wasps and bees. Miniaturisation and associated simplifications in phenotypes led to even cheaper ant workers, especially in formicoids.

2) Compared with social wasps and bees, several ant lineages show huge size differences between queens and workers. This results from dwarf workers but also from queen specialization for increased fecundity (bigger gaster with numerous ovarioles) and independent colony foundation, ICF (bigger thorax with wing muscles that are enlarged relative to normal flying insects). Both smaller workers and substantial metabolic reserves are required for "claustral" ICF, i.e., founding queens do not forage outside the nest. Claustral ICF is unknown in social wasps and bees.

3) All insect colonies have a finite energy budget that can be allocated in different ways to produce either queens or workers, and both these show enormous interspecific variations in body size. Ant workers can be cheap while claustral queens are very expensive. This independence of costs between queens and workers enables novel strategies of caste "packaging", especially in formicoids. Colony sizes increased whenever this was selected for.

4) In social wasps and bees, queens and workers (both winged) do not diverge much in body size or per capita costs, hence options of caste allocation are limited. This hinders exploiting the benefits of two morphologically specialized castes.

5) The existence of dwarf workers and big queens in formicoid ants promoted the sporadic evolution of helper phenotypes with intermediate body size, such as a soldier caste.

Wingless workers are cheap labour

Obvious cost savings stem from the lack of wing muscles. These muscles are among the most metabolically active

tissues known, and constitute 22 - 46% of body mass in central-place foraging Hymenoptera (POLIDORI & al. 2013). Estimates are unavailable for ant queens, but per capita pre-emergence costs are high. Wingless workers are intrinsically cheaper to manufacture. In addition, wing muscles are expensive to maintain, because flying insects have resting metabolic rates about three times as large as non-fliers (REINHOLD 1999).

All social Hymenoptera exhibit age polyethism, and only the older workers forage away from the nests. In wasps, workers start to fly within a few days of emergence, which is vital in the event of nest relocation or escape from predators (MATSUURA & YAMANE 1990). Readiness for flight throughout adult life implies considerable maintenance costs, and these are eliminated in ant workers. Moreover, callow workers in ants are confined inside the nest and are not involved in defence. During nest emigrations they can simply walk along a pheromone trail or follow nest-mates. Young and old workers require different motor and sensory abilities, thus metabolic costs can be optimized better than in flying wasps. In *Harpegnathos saltator*, only older workers have functional poison gland secretions (HAIGHT 2012). In *Pheidole dentata*, workers emerge with incompletely developed mandible muscles, and these mature only later in life to bite and carry loads (MUSCEDERE & al. 2011). In *Camponotus floridanus*, the brain and mushroom bodies change physiologically according to age and task (GRONENBERG & al. 1996). Such age-related physiological adaptations make division of labour among wingless workers remarkably cost-efficient.

Another essential requirement for flight is compound eyes with high spatial acuity to measure distances and avoid obstacles. Like wing muscles, eyes must be fully operational in all adults. Eyes and associated neural networks are costly structures to manufacture and maintain, and there is strong evolutionary pressure to reduce them to the minimum needed for adequate function (NIVEN & al. 2007). In ants, young queens require many ommatidia for flying, but the brain and optic lobes shrink after mated queens dealate and move below ground (JULIAN & GRONENBERG 2002). Being pedestrian, ant workers have eyes that are strictly related to foraging needs, and they are free to diverge from conspecific queens if costs exceed the fitness

Box 2: Walking versus flying – cooperative transport in 2D or 3D.

Thousands of ant species (mostly formicoids) live in trees. Shifting from ground to arboreal life has a distinct meaning for pedestrian versus flying insects, an analogy with KASPARI & WEISER (1999): The 2D world of ant workers is dramatically expanded in trees, with a huge increase in the surface area over which to walk and forage (even within a small volume). Only large colonies have enough workers available to spread out and search for resources, e.g., dead arthropods or sweet secretions.

Cooperative transport has evolved multiple times in ants, with much variation in sophistication and effectiveness (CZACZKES & RATNIEKS 2013). Foraging on foot allows the cooperative retrieval of food items, but this is rare in arboreal species (YAMAMOTO & al. 2008). Big prey are usually cut up and smaller pieces are carried back by single workers. Social wasps behave similarly.

Let's imagine the hypothetical evolution of dwarf wasp workers: Many tiny flying insects cannot crowd around a prey and carry it, simply because wings become a handicap, a barrier to cooperation. Ants have no such problems because they can walk on top of each other, several layers thick. Cooperative behaviours differ between walking and flying insects for purely mechanical reasons.

benefits of better vision. Solitary predators such as *Harpegnathos*, *Myrmecia* and *Myrmoteras* have high spatial resolution (a few thousands of ommatidia per eye), while trail-following generalists have a few hundreds of ommatidia (GRONENBERG 2008).

Winglessness allowed the evolution of dwarf workers in many genera

Miniaturisation is one of the principal directions of evolution in insects (POLILOV 2015). Microinsects (adult body sizes smaller than 2 mm) show many reduced or simplified traits (e.g., cuticular structures, internal and sense organs), and this often corresponds to diminished abilities, such as poor flight and short adult lifespans, although muscles, nervous and reproductive systems are not compromised. Likewise, ant workers can have diminished phenotypes relative to conspecific queens, because their functions are complementary.

Using head width as proxy for body size, we compared workers from all three groups of social Hymenoptera (Appendix S1, as digital supplementary material to this article, at the journal's web pages). Our data indicate that only ants have heads 1 mm or less wide (Fig. 2). Such dwarf workers exist in 229 / 286 of genera in the sample we measured. In 71 of these genera, head width is < 0.5 mm (Appendix S1), corresponding to a total body length < 2 mm. Dwarf workers evolved across most ant subfamilies, but they are predominant in various formicoids (Appendix S1). In some genera (e.g., *Adetomyrma*, *Cardiocondyla*, *Hypoponera*, *Leptanilla*, *Nylanderia*, *Plagiolepis*), dwarf workers occur in all species, while they occur sporadically in other genera (e.g., *Aphaenogaster*, *Camponotus*). In some lineages with polymorphic workers, dwarf individuals correspond to the lowest body size (e.g., *Atta*, *Cataglyphis*).

The workers of many ant species are exceptionally small among the Aculeata. Dwarf workers do not exist in social wasps and bees (Fig. 2; Appendix S1); this is true when considering either body length or head width (the latter overestimates body size in flying insects because of the compound eyes). *Microstigmus* (Crabronidae) that hunt collembolans are the smallest social wasps, while stingless and allodapine bees are smallest. The lack of dwarf wasps and bees suggests the importance of flying constraints for

central place foragers. Food must be transported in flight which may be incompatible with pronounced reduction in body size (parasitic wasps are tiny but need only to fly between hosts). In addition, close cooperation among dwarf flying individuals may be ineffective (Box 2). The Bethyloidea, solitary and wingless, are among the tiniest Aculeata (EVANS 1978), confirming that flight loss can allow miniaturisation.

Assuming that winglessness removes proximate constraints on the evolution of dwarf workers in ants, why is this adaptive? Body size affects the food types that can be exploited, and selective pressures appear to be mostly ecological. Dwarf workers can be specialised predators on tiny soil arthropods like collembolans and mites, a vast resource (e.g., MASUKO 2009). Dwarf workers are matched for size with many aphids and scale insects, allowing for efficient manipulation. Body size affects the way that organisms perceive the surface of the earth (KASPARI & WEISER 1999). Tiny size opens up new niches: soil interstices, leaf litter or inside the stems of live plants. Such microhabitats can be both foraging grounds and nesting sites, and indeed dwarf queens exist also. Species with dwarf workers can become involved in mutualistic associations (cleptobiosis) with dramatically larger ants, e.g., *Strumigenys* and *Platythyrea* (YÉO & al. 2006). Invasive ants are often smaller than native congeneric species, highlighting the importance of worker body size and colony size during interspecific fights (MCGLYNN 1999).

All organisms are faced with the evolutionary dilemma of producing either a few expensive offspring, or many cheaper ones. This dilemma is much more complex in social insects (for ants, see MOLET & al. 2008) because (I) resources are allocated to either queen or worker castes, (II) queen-worker dimorphism differs considerably across species, (III) new queens disperse while new workers remain in natal colonies, hence increased allocation to workers produces bigger colonies, which is a key ecological parameter. Like caste allocation, body size is often a compromise between ecology and colonial economy. Colonies have finite energy budgets, and decreasing manufacturing costs of workers allows to produce more of them (however, smaller workers probably have higher mass-specific metabolic costs, SHIK 2010). In social insects, ex-

tensive cooperation between workers outside the nest allows marked reductions in body size (Box 3).

BOURKE (1999) gave an alternative explanation for body size, arguing that smaller workers give the queen a greater monopoly over egg production. Given the determining influence of body size on food regimes and other ecological parameters, we think it unlikely to be outweighed by the resolution of colonial conflicts.

Queen-worker differences in size allow the evolution of claustral foundation

Many social Hymenoptera start new colonies independently (ICF), and the queen phenotype is under intense selection during this solitary stage (dependent colony foundation occurs in many other species; CRONIN & al. 2013, and below). Independent founding species are either non-claustral or claustral. Non-claustral ICF occurs in social wasps and bees, poneroid ants and a minority of formicoids, while claustral ICF is restricted to the three most important formicoid subfamilies (Dolichoderinae, Formicinae and Myrmicinae). As we will show, this pattern of occurrence matches closely the extent of size dimorphism between queens and workers.

Non-claustral foundresses must forage during several weeks to feed their first workers. In all poneroids and a proportion of formicoids, queens have worker-like neck muscles (KELLER & al. 2014), and they can hunt outside the nest just like workers. Body size differences between queens and workers are small in non-claustral species, with two consequences: (I) Foundresses need to produce first offspring that are almost the same size as themselves; (II) foundresses have little metabolic reserves, and wing muscles provide insufficient amino acids to rear the first larvae. Foraging by queens until the first workers take over may be associated with a low success rate, although no data are available. In social bees and wasps, queens cannot use their wing muscles as a food store, hence they must forage even more than in ants. However, the first offspring of bees and wasps can be much smaller than subsequent offspring.

In sharp contrast, claustral foundresses can rear their first brood of workers without outside food. They carry large metabolic reserves (fat and specialized storage proteins), and the wing muscles are hyperdeveloped to carry this extra load (HELMS & KASPARI 2015). Importantly, claustral species have workers that are much smaller than queens, including dwarf workers in many species, and thus much fewer resources are needed to feed them to adulthood (PEETERS & MOLET 2009). In addition, "nanitics" (workers smaller than the average) can be reared in the first brood, and their accelerated development allows foraging to begin earlier. Claustral ICF is thus a derived trait associated with a pronounced divergence between queen and worker phenotypes. It relies on a colonial strategy of heavy reproductive investment prior to dispersal, and this is energetically possible only in populous colonies.

A majority of ant species are claustral (reviewed in KELLER & al. 2014), but none of the social bees and wasps. Non-claustral ICF is the basal condition among formicoids, e.g., subfamilies Ectatomminae, Heteroponerinae, Myrmeciinae and Pseudomyrmecinae. Its occurrence in some Formicinae (e.g., *Cataglyphis*, *Myrmoteras*, *Polyrhachis*, ...) and Myrmicinae (e.g., *Acromyrmex*, *Messor*, *Pogono-*

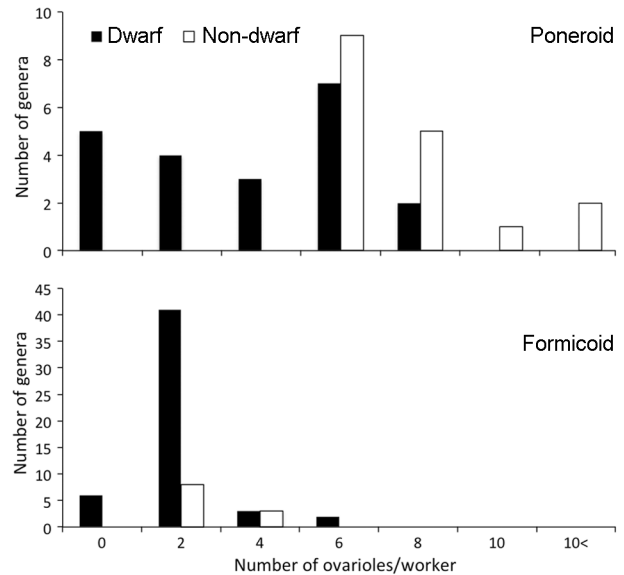


Fig. 3: Relationship between body size and ovariole numbers in workers from 34 poneroid and 61 formicoid genera ("dwarf" defined as head width < 1 mm). In genera with more than one species dissected, the lowest number is included.

myrmex, ...) may be either basal or a reversal. Size dimorphism between queens and workers is low in all these non-claustral species. If successful, queen foraging can produce more first workers, unlike claustral species where demography of the first brood is limited by metabolic reserves.

Dwarf workers have reduced ovaries?

Microinsects often show simplification in internal organs (POLILOV 2015), so what about the ovaries of dwarf workers (i.e., head width 1.0 mm or less)? A comparison of ovariole numbers in a sample of 106 genera belonging to all major subfamilies indicates clear trends in the reduction of worker ovaries relative to queens (F. Ito & C. Peeters, unpubl.). In a majority of poneroids, workers have as many ovarioles (usually six or eight) as queens (Fig. 3). Dwarf workers tend to have fewer ovarioles, and they lack ovaries in six genera, i.e., *Anochetus* (at least four species), *Brachyponera* (all species), *Hypoponera* (all species), *Leptanilla* (three species), *Leptogenys* (three species) and *Myopias emeryi* (VILLET & al. 1991; F. Ito & C. Peeters, unpubl.). In *Probolomyrmex dammermani*, both workers and queens are dwarf and have two ovarioles (ITO 1998). In most formicoids, workers have only two ovarioles (Fig. 3), even though body size is large in several genera. Workers with more ovarioles are mainly confined to Ectatomminae, Myrmeciinae and Pseudomyrmecinae, but also social parasites in Formicinae and Myrmicinae (HEINZE 1996). Among genera with dwarf workers, ovaries have been completely lost in at least eight genera of Myrmicinae, i.e., *Cardiocondyla*, *Carebara* (including *Pheidologeton*), *Monomorium*, *Pheidole*, *Solenopsis*, *Strumigenys*, *Tetramorium* and *Vollenhovia*. In Dolichoderinae and Formicinae however, dwarf workers without ovaries are unknown (note that *Linepithema* workers have four ovarioles, in contradiction with WILSON & NOWAK 2014). Retention of ovaries by workers is adaptive to produce either males or trophic eggs involved in food exchange (e.g., GOBIN & al. 1998).

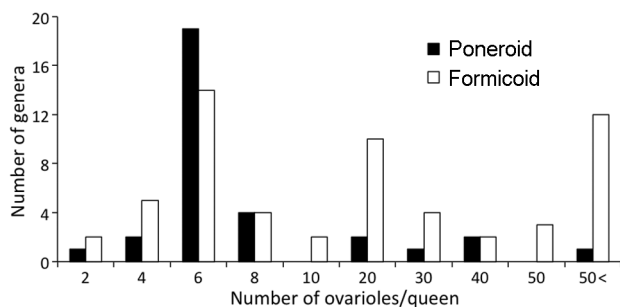


Fig. 4: Frequency distribution of ovariole numbers in queens from 32 poneroid and 58 formicoid genera. In genera with more than one species dissected, the lowest number is included.

In social wasps and bees, workers lacking reproductive organs are unknown.

What is the effect of body size on the presence of a spermatheca, which is a complex structure necessary for long-term sperm storage? Only a small proportion (less than 200 species) of poneroids have workers that can mate and produce diploid offspring (MONNIN & PEETERS 2008), but workers in many other poneroid species retain an incomplete spermatheca (it cannot be found in some species with dwarf workers) (GOBIN & al. 2008). Importantly, workers in formicoid subfamilies completely lack a spermatheca, except some Ectatomminae and Myrmeciinae. Wasp and bee workers all have a spermatheca (GOTOH & al. 2008), except *Apis* (GOTOH & al. 2013).

Concerning queens, increased ovariole number is a remarkable characteristic of ants, because most social bees and wasps do not show caste differences in ovaries (*Apis* is one exception) (F. Ito & C. Peeters, unpubl.). More ovarioles means that more eggs can develop and mature concurrently. Among formicoids, some queens are highly fecund (exceeding 100 ovarioles), but other species have queens with few ovarioles (Fig. 4). Conversely, the queens of a few poneroids have many ovarioles, reaching 30 or even 60.

Large queen-worker dimorphism and increased colony sizes

Several extant poneroid ants have queens and wingless workers that are almost the same size, while others exhibit limited divergence (PEETERS 1997). The continuum in queen-worker dimorphism is much greater in formicoids: little in Ectatomminae and Myrmeciinae (PEETERS 1997), very pronounced in a majority of Dolichoderinae, Dorylinae, Formicinae and Myrmicinae. Extreme divergence evolved repeatedly and convergently from ancestors in which workers and winged queens are similar in body size. Different manufacturing costs underlie queen-worker divergence, as evidenced by similar dry weights for poneroid queens and workers (Fig. 5, such basic data are surprisingly scarce in the literature, TSCHINKEL 2011). Among formicoids, queen-worker differences in dry weights vary considerably, but they are very high in several genera, many of them with dwarf workers (Fig. 5). In at least 14 genera (Appendix S2), queens weigh as much as 10 - 50 \times as workers (not dwarf in all species). But in other formicoids, queens weigh only 2 - 5 \times as much as workers, ICF may be non-claustral and colonies do not exceed a few thousands. In

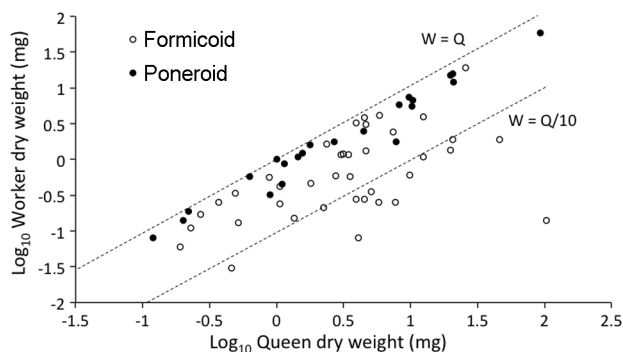


Fig. 5: Differences in dry weights between queen and worker castes in 20 poneroid and 39 formicoid species (listed in Appendix S2). Two grid lines indicate lack of caste dimorphism ($W = Q$) and queens that are ten times heavier than workers ($W = Q / 10$).

wasps, maximum caste dimorphism occurs in some species of *Vespa*, *Dolichovespula*, and *Vespula*, but queens are never more than twice the size of workers, and colonies have just over 1000 workers (maximum number of cells is ca. 4500, reaching 10,000 - 15,000 cells in *Dolichovespula*) (MATSUURA & YAMANE 1990).

WILSON (2003) described *Pheidole* workers as a "throw-away caste - small, light, cheaply manufactured, short-lived and lacking ovaries". This description seems valid for dwarf workers in many genera from Dolichoderinae, Dorylinae, Formicinae and Myrmicinae. In general, Formicinae and Myrmicinae workers weigh much less than poneroid workers (Box 3). As explained elsewhere, miniaturisation has been associated with reduction of several traits (e.g., cuticular structures, compound eyes, sting apparatus, ovaries). *Pheidole* workers can have less than 20 ommatidia per eye, enough to obtain some visual information (RAMIREZ-ESQUIVEL 2012). In species with size-polymorphic workers, a correlation exists between body size and ommatidia number, and the latter match the requirements for different tasks (GRONENBERG 2008).

An aspect of the reduction of manufacturing costs in some formicoids was revealed by a histological study of cuticle thickness, comparing 33 species from six subfamilies. There was a clear trend from the heavy exoskeleton of Ponerinae to a thinner one in Dolichoderinae, Formicinae and Myrmicinae (C. Peeters, M. Molet & J. Billen, unpubl.). Nonetheless various formicoids have a thick cuticle as an adaptation for specific lifestyles, e.g., *Calyptomyrmex*, *Cataulacus*, *Cephalotes*, *Meranoplus* (Myrmicinae), *Echinopla*, and *Polyrhachis* (Formicinae). Cuticle is an expensive resource at colony-level. Given age polyethism, the drawbacks of a thinner cuticle (desiccation, protection, ...) are only relevant at the end of workers' lives, when they become active outside the nest. Hence producing workers with a cheaper exoskeleton may be selected in a social context. The thinner cuticle of an individual equals minuscule cost savings, but these are considerably amplified in populous colonies. All ant workers have a reduced mesonotum (dorsum of second thorax segment) because it no longer functions for attachment of wing muscles (Box 1). In some formicoids, this segment is considerably tapered, e.g., *Aphaenogaster*, *Myrmecia*, *Myrmoteras* and *Oecophylla*, as opposed to most Ponerinae where the entire thorax remains bulky. It is a moot point that this remodelling

Box 3: Just six legs or ten times six legs?

Ponerinae workers are generally large insects, weighing 5.3 mg on average (range 0.14 - 21.2 mg, sample of 16 genera listed in Appendix S2). Formicinae workers are much smaller, weighing 1.45 mg on average (range 0.15 - 3.9 mg, sample of 11 genera), and Myrmicinae workers weigh 0.39 mg on average (range 0.06 - 1.19 mg, sample of 14 genera). Roughly speaking, one ponerine worker equals the weight of four formicine workers, or 14 myrmicine workers. But this ratio can exceed 300 if we select species at extremes of the ranges. This disparity is also true within species exhibiting worker polymorphism – in *Carebara diversa*, one big soldier weighs the same as 100 dwarf workers. So much for manufacturing costs.

In all insect societies, the number of autonomous units (i.e., six legs) is a critical ecological parameter – units search for food independently but can cooperate during prey capture or transport. The evolutionary shift from a few units to many tiny units is affected by foraging needs and colonial economy. Ants are the greatest scavengers because so many units are available to patrol simultaneously.

Ant biomass is extremely difficult to measure reliably (i.e., extrapolation and guesswork), and is anyway not a good measure of ecological dominance. The importance of ants lies in their amazing prevalence and dominance, and their ability to exploit many trophic systems. It's all about the number of foragers active outside the nest, looking for different kinds of food.

of the worker thorax represents convergent attempts to optimize the cost of a wingless aculeate wasp. Ant workers also save cuticle inside the thorax, because the phragmata (see Box 1) no longer exist as a result of losing wing muscles (KELLER & al. 2014).

Comparing brood time schedules across poneroids and formicoids hints at quicker development among the latter (KIPYATKOF & LOPATINA 2015). Eggs to adults takes 2 - 3 months in poneroids, but this is shortened almost by half in various formicoids. The scant data in the literature do not allow us to determine the effect of phylogeny, nonetheless it can be expected that dwarf workers develop quicker. Besides, various microinsects are characterized by extremely short adult lifespans (e.g., few days in braconid wasps). In ants, longevity is generally correlated with body size: Smaller workers live shorter in *Solenopsis invicta* (e.g., CALABI & PORTER 1998). Longevity needs to be investigated in dwarf ant workers.

Together with queen adaptations for higher fecundity, lower per capita costs of workers allowed colony size to increase by several orders of magnitude in various formicoids (e.g., HÖLLDOBLER & WILSON 1990, KASPARI & VARGO 1995). Colonies exceeding 10^5 or 10^6 workers are unknown in social wasps and bees, even though colony biomass may be similar. In many ant species, populous colonies are associated with dwarf workers. This is however, not always the case, especially in poneroids. For instance, two species with head width < 0.5 mm (*Probolomyrmex dammermani* and *Prionopelta kraepelini*) have colonies of 14 and 60 workers, respectively (ITO 1998, ITO & BILLEN 1998). Several poneroids with heads < 1.0 mm (e.g., *Brachyponera nakasuji*, *Discothyrea* sp. from Java, *Hypoconera*, *Myopias emeryi*, *Mystridium camillae*) have a few hundred workers or less in colonies. Among formicoids, *Gnamptogenys cribrata* has head width of 0.5 mm and colonies average 27 workers (ITO & GOBIN 2008), while tropical twig-dwelling *Pheidole* colonies consist of less than 50 workers. Most of these species also have miniaturised queens with limited fecundity. Thus performance benefits linked to life inside plant stems, in leaf litter or underground are sufficient to select for dwarf size.

Ant workers: cheap but very effective labourers

The evolutionary trend of miniaturisation in ant workers has not affected their effectiveness as ground labourers. Winglessness brought about selection pressures for increased diversity in defence strategies.

(1) Defence adaptations: An important function of flight is to escape predators. Wingless ant workers are inherently vulnerable (especially to other ants), except that they evolved defence adaptations generally absent in social wasps and bees. Solitary hunting wasps use the sting to paralyse the prey on which they will oviposit, however, social wasps subdue their prey with mandibles and the sting functions for defence instead, e.g., *Dolichovespula*, *Vespa* and *Vespa* (IWATA 1976, MATSUURA & YAMANE 1990). Because social bees and wasps can fly to escape predators, their sting is often used against large vertebrates intent on stealing brood in their nests (MATSUURA & YAMANE 1990). In ants, mandibles and sting are important tools for defence, especially against vertebrates, while volatile chemicals are often used against ant enemies (KUGLER 1979). Mandibles are also used to bite or stun prey, e.g., trap jaws. Spines on thorax or petiole are common in some formicoid lineages and confer passive protection against vertebrate predators (BUSCHINGER & MASCHWITZ 1984), while social wasps and bees lack spines. Other defence techniques include a thickened cuticle, camouflage, death-feigning and cliff jumping (reviewed in HÖLLDOBLER & WILSON 1990: tab. 10-3).

Poneroids and some formicoids (e.g., Dorylinae except *Dorylus* (KELLER 2011), Myrmeciinae) have a long and manoeuvrable sting that can pierce arthropod cuticle and inject poison gland secretions. Dacetine ants (Myrmicinae) use their mandibles to catch prey which is then stung (e.g., MASUKO 2009). In Dolichoderinae and a proportion of Myrmicinae, the sting apparatus is variously reduced in strength and size (less muscles, simpler and less sclerotized components) (KUGLER 1979), and the sting is extruded merely to release volatile secretions. In Formicinae the sting is lost and formic acid is sprayed at opponents. Non-stinging ants often have biting mandibles with well-

developed muscles, or even a soldier caste with hyper-developed heads almost filled with mandible muscles.

In parallel with the reduced importance of the sting, chemical weaponry was enriched in myriad ways across formicoid subfamilies, often in concert with collective defence behaviours (HÖLDOBLER & WILSON 1990). An array of exocrine glands produce repellent compounds, and most of these glands are absent in wasps. Sternal, anal and even metapleural glands produce toxic substances in different lineages (KUGLER 1979, PASSERA & ARON 2005, BILLEN & al. 2011), and the functions of other glands remain unstudied. In *Lasius spathepus*, large mandibular glands produce strongly smelling substances that make ants unpalatable to treefrogs (TANIGUCHI & al. 2005). In *Crematogaster striatula*, Dufour's gland secretions released on the protruded sting function to paralyze termite prey without direct contact, to recruit nestmates in the vicinity and to repel competing ant species (RIFFLET & al. 2011). Thus the same pheromones can function for defence and recruitment. However, many species release alarm pheromones from the mandibular glands which function exclusively to increase the number of defenders in one spot.

Availability of numerous workers underlies the defensive strategy of many species, and the death of hundreds of defenders is sustainable at colony-level. During intra- and interspecific fights in ants, smaller workers always lose against larger workers in one-to-one encounters, but in group-group encounters, bigger teams of workers usually win irrespective of body size (MCGLYNN 1999). The combination of numerous workers and a few specialized, bigger soldiers is another winning formula in various ants, e.g., many *Pheidole*.

(2) Activity schedules: Insects need optimal body temperatures to fly. Bees and wasps must generate metabolic heat to activate their flight muscles, and this constrains their foraging schedule, e.g., *Bombus* (HEINRICH 1993). In temperate climates, this thermal regulation is energetically costly. Various species of wasps and bees can adapt their window of activity to either high or low ambient temperatures, but not both. By doing away with flight, ant workers are released from this constraint and can fulfil a huge variety of foraging needs. For example, specialized hunters have temporal schedules that match their prey's. Patterns of temporal activity are an important parameter allowing species with similar diets to coexist.

2 a. High and / or low temperatures: Because they walk on the substrate, ant workers live in a different microenvironment from wasps and bees. KASPARI & al. (2015) discussed how surface temperatures are critical for the activity limits of small insects. Boundary layer microclimates near surfaces can superheat relative to the air above (HEINRICH 1993). The broad range of body sizes exhibited by ants offers a wide range of thermal tolerances in the same ecosystem. In a Panama assemblage of 88 species exhibiting a 1000-fold span of body sizes, tiny ants experienced boundary layer climates dictated by convection, while larger ants experienced cooler air but increased solar radiation (KASPARI & al. 2015).

In both deserts and cold regions, ants dig underground nests to escape harsh conditions, and foraging activity can be highly seasonal. Desert specialists (e.g., *Cataglyphis*, *Melophorus*, *Ocymyrmex*) have physiological adaptations as well as long legs, and they often become active once

ground temperature is too high (45°C) for other insects (GEHRING & WEHNER 1995). Other species can forage in a broad range of temperatures, e.g., Argentine ants can be active between 5 to 35°C in western Japan (TOUYAMA & al. 2004).

2 b. Day and / or night: In tropical regions where temperatures remain high at night, numerous ant species continue foraging activities (YAMANE & al. 1996 in Borneo, KASPARI & WEISER 2000 in Panama; F. Ito unpubl., in Japan and Malaysia). A literature survey indicates 29 species in 16 genera that are day-active, 21 species (11 genera) that are night-active, and 98 species (43 genera) are active night and day (24h foraging). Interestingly, *Nothomyrmecia* is strictly nocturnal but only on cold nights (5 - 10°C), which suggests avoidance of competitors (HÖLDOBLER & TAYLOR 1983).

Many ants forage in the dark because workers can orientate on the ground with chemical trails. However, workers in some nocturnal species have highly specialised compound eyes allowing for visual navigation. In *Polyrhachis sokolova*, solitary foragers are active day and night (i.e., during low tides), and ommatidia show various adaptations to cope with the dramatic variation in ambient light intensity (NARENDRA & al. 2013). Using the ground plan of insect eyes, several ants evolved workers with eyes that are well-adapted for both diurnal and nocturnal lifestyles. No other insects have such opposed requirements, and anyway 24h foraging activity makes no sense for solitary insects. 24h foraging is the sum of the activities of different individuals, hence each worker must be equipped for both day and night vision. Such 24h ants are valuable partners for mutualistic plants and insects, providing effective defence against enemies and herbivores.

24h foraging is unknown in social wasps and bees. A few tropical species independently evolved nocturnal habits, e.g., *Apoica*, *Megalopta*, *Provespa* and *Xylocopa* (ROUBIK 1989, MATSUURA & YAMANE 1990), but foragers fly only during a few hours of dim light (after sunset, or full moon). *Vespa crabro* foragers collect tree-sap on oak trees during day-time, and continue 3 - 4 hours after sunset (MATSUURA & YAMANE 1990). Nocturnal bees and wasps use visual cues during flight, with eyes and ocelli showing similar specialisations (WARRANT 2008) as in ants. This indicates that the lack of 24h foraging in social wasps and bees is not caused by sensory constraints, but rather ecological specialization for either night or day. Thus ants and termites are the only social insects that realized the full potential of non-stop foraging.

Dwarf workers and big queens promote the evolution of additional helper phenotypes

Many ants have monomorphic workers, and division of labour is based on age differences only. Other ants have morphologically diverse helpers, and these do not exist in wasps and bees (except one stingless bee, GRÜTER & al. 2012). Helpers with bigger body size include both polymorphic workers (same growth rules but small and large individuals differ in shape due to allometry) and soldiers having morphological traits absent in workers (discussed in MOLET & al. 2014). This intra-colonial variation in helper size and shape evolved repeatedly and convergently across ant lineages. Soldiers are mostly restricted to Dorylinae, Formicinae and Myrmicinae (at least 25 genera, C. Peeters

& F. Ito, unpubl.). Size-polymorphic workers occur more widely, including a few poneroids (PEETERS & MOLET 2010) and *Myrmecia* (e.g., HIGASHI & PEETERS 1990, DIETEMANN & al. 2002).

Bigger helpers are not always associated with populous colonies. For example, *Acanthomyrmex ferox* colonies have 25 ± 11 workers and 2.6 ± 1.5 soldiers with specialized mandibles and enormously enlarged muscles to crush fig seeds (GOBIN & ITO 2000). In *Cephalotes*, soldiers evolved different head shapes to block nest entrances of varying diameters (i.e., phragmosis) (POWELL 2008). In other genera having dwarf workers, additional helpers perform functions where large size is an advantage. *Pheidole* workers have a vestigial sting and lack toxic defensive chemicals (energetically expensive), instead the strength and mandibles of soldiers underlie colony defence (WILSON 2003).

Bigger helpers increase the efficiency of division of labour in colonies, yielding fitness gains that offset higher manufacturing costs (OSTER & WILSON 1978). This is particularly true if bigger helpers can combine trophic functions with defence or heavy lifting. *Acanthomyrmex* soldiers not only have a specialized head but their ovaries are queen-like and produce numerous trophic eggs (GOBIN & ITO 2000). Repletes in other genera have hypertrophied fat bodies or a distended crop filled with glucose-rich liquid (WHEELER 1994), thus the larger gasters typical of both soldiers and major workers are adaptive for food storage. Ant repletes innovate by using their own bodies, unlike various bees that store food in wax cells (in wasps, the larvae function as repletes). Such repletes are possible because of winglessness. Similarly, big heavy heads make soldiers unsuited for flying.

MOLET & al. (2012) pointed out that soldiers are often mosaics of workers and winged queens, and hypothesized that existing developmental programs can be reshuffled to generate novel castes. The bigger the size dimorphism between workers and winged queens, the more possibilities to develop mosaics – and some can be helpful for the colony. In social wasps and bees, winged queens and winged workers are too similar in phenotype and development costs, consequently a mosaic cannot contribute much to colony fitness. This is also true of poneroids and formicoids with limited caste divergence.

Wingless workers make it possible to evolve permanently wingless queens

In contrast to species having queens that are specialized solitary founders, many other ants use dependent colony foundation (DCF) whereby queens are continuously helped by nestmate workers. Such queens are no longer totipotent and rely on workers to feed and protect their brood (PEETERS 2012). Since queens disperse on foot together with workers, wings are no longer required (unlike wasps and bees in which queens and workers fly during DCF), and wing muscles can be lost to reduce costs. "Ergatoid" (worker-like, referring to the simplified thorax caused by lack of wing muscles) and "brachypterous" (short-winged) queens occur sporadically across poneroids and formicoids (PEETERS 2012). The exception is subfamily Dorylinae where most species have ergatoid queens; these can be giant in *Dorylus* and *Eciton* because of no flying constraints. Queens involved in DCF are often produced in small numbers,

but extra workers are needed for successful founding. Because ant brood is readily transported, unlike in wasps and bees, colony fission is very efficient in ants (CRONIN & al. 2013), and DCF strategies contribute as much as clausal ICF to their evolutionary success.

Cheaper workers make it profitable to shift diet?

An intriguing difference between ants versus social bees and wasps is the higher diversity in ant diets. Social wasps are predators, with no reports of scavenging or regular honeydew feeding (ROSS & MATTHEWS 1991). Social bees consume nectar and pollen, a high-energy proteinaceous food needed by larvae (MICHENER 2007). Exceptions to this monotony in diet are very few: Some stingless bees in the Amazon feed on dead meat (ROUBIK 1989), *Vespa* consume fruits and tree sap, *Vespula* scavenge sun-dried fishes and squids in coastal villages (MATSUURA & YAMANE 1990). In obvious contrast are the ants, including predators on invertebrates (both generalists and specialists), predators on ant brood, scavengers, herbivores (honeydew and sweet plant secretions), granivores and fungivores. Why are ants more evolutionarily flexible in their diet? First we need to realize that this is characteristic of some formicoids only, i.e., Dolichoderinae, Formicinae and Myrmicinae. Poneroids are strict carnivores, and only few species collect honeydew (e.g., *Odontomachus*, *Paraponera*). A proportion of formicoids are predominantly predators although their diet includes insect carcasses, sweet secretions and honeydew. There is evidence that evolutionary shifts of diet can occur readily, requiring only behavioural and physiological modifications: In arid regions of Australia, species in the morphologically conservative genus *Melophorus* (Formicinae) are mostly generalist predators and scavengers but include specialist predators of termites and *Iridomyrmex* brood, seed harvesters and honeydew collectors (ANDERSEN 2007).

All social Hymenoptera are central place foragers: Food is located at various distances from the nest and then carried back. The metabolic costs of foraging are tightly linked to the energetics of locomotion. Flapping flight is very expensive, and flight metabolic rates are about 10× the rates for running insects of similar size (NIVEN & SCHARLEMANN 2005). Although walking is cheaper than flying, foraging on foot is not cheaper than aerial foraging. Indeed, flying insects can move over large distances or difficult terrain very effectively. NIELSEN (2001) considered three components in the energetics of foraging in *Rhytidoponera aurata*: resting metabolism (i.e., while motionless), cost of locomotion and cost of carrying a load. All three components are influenced by body size, hence a shift to dwarf workers may affect the benefit-to-cost ratios of different diets. Body size of workers is seldom considered amongst the many factors determining protein:carbohydrate intake targets. Dwarf workers have higher maintenance costs (see SHIK 2010) that may explain high intake targets of carbohydrates such as honeydew.

Conclusions: Ant success due to sociality or wingless helpers?

Flight had a pivotal role in the formidable diversification of insects. Aerial dispersal remains of prime importance in ants (queens and males), but ecological dominance is based on wingless workers that prevail numerically across

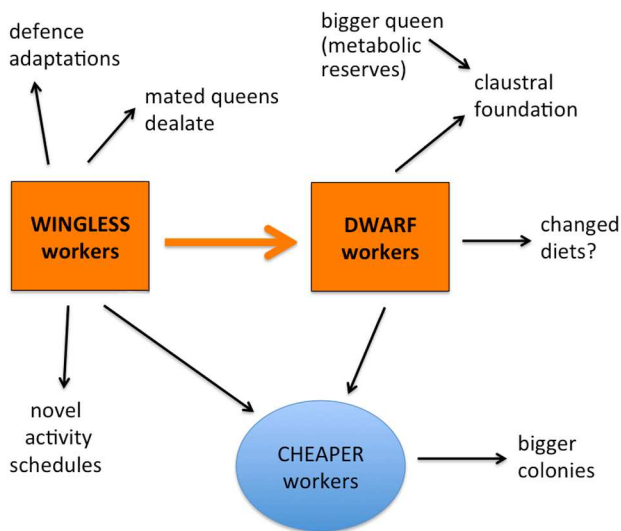


Fig. 6: Consequences of winglessness and dwarfism, and interactions between these.

the entire clade. This union of flying and walking is unequalled among insects. The first ants evolved on the ground (as evidenced by prognathous heads), and aculeate morphology became adapted for non-flying helper roles (Box 1). Extensive divergence between flying queens and wingless workers evolved repeatedly, unlike social wasps and bees where caste divergence is curbed by flying constraints. Nonetheless, caste dimorphism is moderate in many poneroid and formicoid ants. This highlights the importance of further adaptations that became possible once wings had been lost (Fig. 6). In particular, general properties of insects make miniaturisation a widespread evolutionary option, and many ants took advantage of this. Microinsects generally exhibit reduced structures, and simplified morphology (eyes, thorax, ovaries) is appropriate for workers that are infertile and interdependent with queens. Ant workers live longer than most solitary insects, but they are short-lived relative to conspecific queens. This difference is inherent to age polyethism and mortality associated with foraging outside the nest, so workers can be designed more cheaply than queens. Workers do not require a flight thorax with specific biomechanical properties, thus the exoskeleton became thinner. Savings in manufacturing and maintenance costs are often minute, but they are greatly magnified in colonies with thousands or more workers. Developmental costs are also reduced in ants, with cocoons becoming thinner from Ponerinae to Formicinae, and eliminated in Dolichoderinae and Myrmicinae. To summarize, per capita costs of ant workers have been reduced without compromising their effectiveness.

Dwarf workers exist across poneroids and formicoids, but only in some of the latter are they associated with bigger queens and huge colonies. This suggests that dwarfism evolved initially for ecological reasons, and was used subsequently as a blueprint to increase colony size. Dwarfism can be an adaptation for solitary hunting on restricted prey, e.g., in Ponerinae and Dacetini, and this is incompatible with populous colonies. Many other lineages have dwarf workers that scavenge or collect honeydew. Winglessness removed constraints on the reduction of body size, and cooperative foraging means that dwarf workers are viable.

Ants, bees, and wasps all experimented with sociality for many millions of years, driven by ecological benefits of cooperation that are enhanced by close relatedness (BOOMSMA 2009). Some lineages are left as relicts of one stage or another, while other lineages broke through successive evolutionary barriers. Focusing on morphological differences among female adults, we recognize three types of colonies in eusocial Hymenoptera: (a) All adults are morphologically equal, i.e., bees, wasps, ants with gamergates; (b) queen and worker castes are distinct, but diverge little in size, i.e., bees and wasps (winged workers), a proportion of ants (wingless workers); (c) castes diverge strongly in body size, i.e., some Dolichoderinae, Dorylinae, Formicinae, Myrmicinae. Queens and workers of similar body sizes occur in poneroids, many formicoids and social wasps, and all show parallels in general biology: non-claustral ICF, a mainly carnivorous diet, colonies of a few thousands or less. It is a sharp divide with formicoids having dwarf workers, much bigger claustral queens and often colonies with tens of thousands or more. Future studies may show that formicoids with dwarf workers form the bulk of ecologically dominant ants. WILSON (2003) attributed much of the evolutionary success of *Pheidole* to the cheap dwarf workers functioning in symbiosis with bigger soldiers. However, *Camponotus* and *Polyrhachis* both radiated into hundreds of species without dwarf workers (although queen-worker dimorphism in weight is remarkable). This emphasizes that body size is paramount in ant biology, and readily selected.

Termites are also social insects with wingless (and often dwarf) helpers. However, termites are hemimetabolous: Immatures develop gradually into adults, without metamorphosis. For this reason the developmental basis of polyphenism is completely different (e.g., KORB & HARTFELDER 2008). Since all immatures participate in colony labour, age-related variations in body size cause division of labour. The phenotype of termite "workers" contrasts sharply with the wingless workers in ants, because the latter are adults with fixed morphology. Hence, hemimetaboly restricts complex patterns of caste allocation in termites.

Cheaper helpers are arguably the very basis of ant success, and all the emphasis cannot be placed on sociality only. Our size and weight data are preliminary but help reveal definite patterns in evolution. Such data on the "characters of eusociality" are easily obtained but scarce in the literature (TSCHINKEL 2011). Although numerous and varied adaptations are responsible for the evolutionary and ecological success of ants, we suggest that changes in body size of queens and workers were decisive. With the initial condition of large workers closely resembling their queens, as in many Ponerinae (Box 3), dwarf workers were often selected to determine activities outside the nest as well as the demography of colonies. Wingless workers permitted to benefit fully from morphologically specialized castes, unlike in social wasps and bees.

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