

Recent advances in army ant biology (Hymenoptera: Formicidae)

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Abstract

Army ants are dominant social hunters of invertebrates and thereby play an integral role in tropical ecosystems. They are defined by a suite of evolutionarily interrelated physiological, behavioural and morphological traits, the army ant adaptive syndrome: they are obligate group predators, they frequently relocate their nests, and their permanently wingless queens found new colonies accompanied by workers. If this functional definition is applied rather than a taxonomic one, army ants have evolved repeatedly in distantly related groups of ants. In addition, army ants typically have extremely male-biased numerical sex-ratios, and the queens of the studied species are inseminated by many males. The aim of this review is to provide a synthesis of the most recent work on army ant biology, to outline an evolutionary scenario that connects the different aspects of army ant life-history, and to give some directions for future research.

Key words: Aenictinae, colony fission, Dorylinae, dorylomorph section, Ecitoninae, group predation, nomadism, review.

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Introduction

"Wherever they move, the whole animal world is set in commotion, and every creature tries to get out of their way" wrote the English naturalist Henry Walter Bates in the account of his journey to the New World tropics (BATES 1863). The ferocious predators he had in mind, however, were neither big cats nor birds of prey, but little insects, army ants, every single one of them not larger than a fingernail. And what sets the animal world in commotion is not the single ant, but the armies of ants, hundreds of thousands of individuals strong, that roam the forest floor in search of prey. Army ants have fascinated naturalists whenever they have come into contact with them, albeit that the details of their highly specialized life-history initially remained a mystery. This finally changed when researchers began to devote intense efforts into studying army ant biology in the first half of the last century. Most notably among the first studies are the works of T.C. Schneirla, curator at the American Museum of Natural History, who studied army ants in the Americas and Southeast Asia (summarized in SCHNEIRLA 1971); as well as those of Albert Raignier and Josef van Boven, who started out studying army ants while working as missionaries in Africa (RAIGNIER & VAN BOVEN 1955). The evolution and ecology of the highly specialized life-history of army ants will be the subject of this review. Two excellent overviews of army ant biology can be found in the early book by SCHNEIRLA (1971) and especially in the more recent book by GOTWALD (1995). In this contribution I will therefore attempt a synthesis of the most recent developments in army ant research after the publication of Gotwald's book.

The origin and diversification of army ants

The term "army ants" (or "legionary ants"; Box 1) does not refer to a taxonomically delimited group, but rather to ant

species that show a combination of certain interrelated behavioural and morphological traits. Most notably, army ants are obligate collective foragers and group predators, they are nomadic, and have highly specialized, permanently wingless queens (WILSON 1958a, GOTWALD 1995, BRADY 2003). This combination of traits has collectively been referred to as the army ant adaptive syndrome (GOTWALD 1995, BRADY 2003; Box 1). Furthermore, army ants typically have extremely male biased numerical sex-ratios and reproduce by colony fission. Although this syndrome, or parts thereof, also occurs in distantly related ant species, including members of the subfamilies Amblyoponinae, Cerapachyinae, Leptanillinae, Leptanilloidinae, Myrmicinae, and Ponerinae (see "The occurrence of army ant behaviour in other ants", below), the three subfamilies Aenictinae, Ecitoninae, and Dorylinae, which encompass most army ants, have been repeatedly referred to as the "true army ants" (e.g., WILSON 1964; Box 1). Given the functional definition and the phylogenetic heterogeneity of army ants, however, the usefulness of the taxonomically defined term "true army ants" seems questionable, due to the connotation that other army ants somehow differ qualitatively. Importantly, this connotation potentially blurs our appreciation of large scale evolutionary contexts. For the purpose of practicality I therefore use an explicitly taxonomically defined and connotation free abbreviation in this review, the "AenEcDo army ants" (Box 1), wherever I collectively refer to the subfamilies Aenictinae, Ecitoninae, and Dorylinae.

The AenEcDo army ants belong to the dorylomorph clade of ants (Box 1, Fig. 1), together with the subfamilies Aenictogitoninae, Cerapachyinae and Leptanilloidinae (BOLTON 1990, 2003, BRADY 2003, BRADY & WARD 2005, WARD 2007a, b, BOLTON & al. 2007, BRADY & al. 2006, MOREAU & al. 2006). While BOLTON (1990) assigned the

Box 1: Definitions and explanations of army ant related jargon.

AenEcDo army ant: a connotation free abbreviation that is introduced here to avoid the term "true" army ant. It collectively refers to species in the three subfamilies Aenictinae, Ecitoninae, and Dorylinae and is strictly taxonomically defined.

Army ant: any ant species with the army ant adaptive syndrome.

Army ant adaptive syndrome: a life-history characterized by group predation, nomadism, permanently wingless queens, and dependent colony founding.

Dichthadiiform ergatoid queen: the term dichthadiiform refers to a greatly enlarged gaster, an extreme case of physogastry (Fig. 4). The extent of physogastry, however, varies with reproductive output and colony size along a continuum. Therefore, while HÖLLDOBLER & WILSON (1990) defined dichthadiiform ergatogynes as being limited to army ants, I suggest that dichthadiiform queens should not be used in turn to define army ants (as, e.g., in BRADY 2003). The term ergatoid means worker-like. Although army ant queens look nothing like workers, they are permanently wingless and their mesosoma accordingly resembles that of workers rather than that of the winged queens of other species.

Dorylomorph section: a monophyletic group of ants encompassing the subfamilies Aenictinae, Aenictogitoninae, Cerapachyinae, Dorylinae, Ecitoninae, and Leptanilloidinae.

Driver ant: a term coined by SAVAGE (1847), only to refer to African *Dorylus* species of the subgenus *Anomma* that "drive" fleeing arthropods in front of epigaeic swarm raids. Because the same phenomenon also occurs in some New World army ants of the genera *Eciton* and *Labidus*, the term has generated confusion and usage should be avoided. Furthermore, it has been used inconsistently (e.g., GOTWALD 1974 also referred to the leaf-litter *Anomma* species as "driver ants").

Epigaeic: above ground; some army ants only hunt epigaeically, while others also nest epigaeically.

Group predation: hunting and retrieving of live prey in groups.

Hypogaeic: below ground / in the soil; most army ants both nest and hunt hypogaeically. Some species hunt in the leaf-litter and thereby are intermediate between epigaeically and hypogaeically hunting species.

Legionary ant: SCHNEIRLA (1971) used "legionary ant" to refer to "ponerine" species with army ant like behaviour. However, the term has since been used as a synonym for "army ant" (e.g., HÖLLDOBLER & WILSON 1990) and I therefore recommend that it be avoided.

Nomadic phase: phase in the colony cycle of phasic species where larvae are present and colonies frequently emigrate. In *Cerapachys biroi*, where colonies do not necessarily emigrate, the corresponding phase has been termed "foraging phase" instead, because colonies do not forage in the stately phase (RAVARY & JAISSON 2002).

Nomadism: nomadism in ants refers to the "relatively" frequent relocation of the entire colony. The term is somewhat loosely defined because many ant species occasionally move nests without being called nomadic.

Nonphasic: describes army ants that are not phasic. Nonphasic species had originally been called "Group B" species by SCHNEIRLA (1971).

Phasic: brood develops in distinct cohorts and colonies undergo stereotypical behavioural and physiological cycles. Phasic species had originally been called "Group A" species by SCHNEIRLA (1971).

Stately phase: phase in the colony cycle of phasic species where pupae are present, eggs are laid, and the colony does not emigrate. "Stately" is an old English word meaning "settled".

True army ant: a term coined by WILSON (1964) to collectively refer to the subfamilies Aenictinae, Dorylinae, and Ecitoninae. Alternatively, the term "classical army ant" has been used (e.g., WITTE & MASCHWITZ 2000, BERGHOF & al. 2003a). Because both terms incorrectly seem to suggest that army ants outside these three subfamilies are not "real" army ants, they are not particularly useful and I recommend avoiding their usage.

dorylomorphs together with the subfamilies Leptanillinae and Ponerinae (the latter has been largely redefined in the meantime; BOLTON 2003, BRADY & al. 2006, MOREAU & al. 2006, WARD 2007b) to the poneroid group of ants, it has now become clear that the dorylomorphs indeed belong to the formicoid section, together with the large subfamilies Formicinae and Myrmicinae, among others (BRADY & al. 2006, MOREAU & al. 2006, WARD 2007b).

Recent evidence from DNA sequence data seemed to settle the long-standing quest for the evolutionary origin of army ants (BRADY 2003, MOREAU & al. 2006; Fig. 1). It suggested that the AenEcDo army ants comprise a monophyletic group within the dorylomorphs that originated some-

what over 100 million years ago on the ancient supercontinent Gondwana. With the subsequent break-up of Gondwana, army ants split into two major clades, the New World army ants (subfamily Ecitoninae) and the Old World army ants (subfamilies Aenictinae and Dorylinae). According to this scenario, the shared lifestyle would have evolved once in a single common ancestor of the AenEcDo army ants (BRADY 2003). This version has implicitly been challenged by BRADY & al. (2006), who estimated the age of the dorylomorph section to ca. 80 million years, with AenEcDo army ants being younger still, based on new molecular clock calibrations. This would mean that army ants in fact originated only after the break-up of Gondwana and pro-

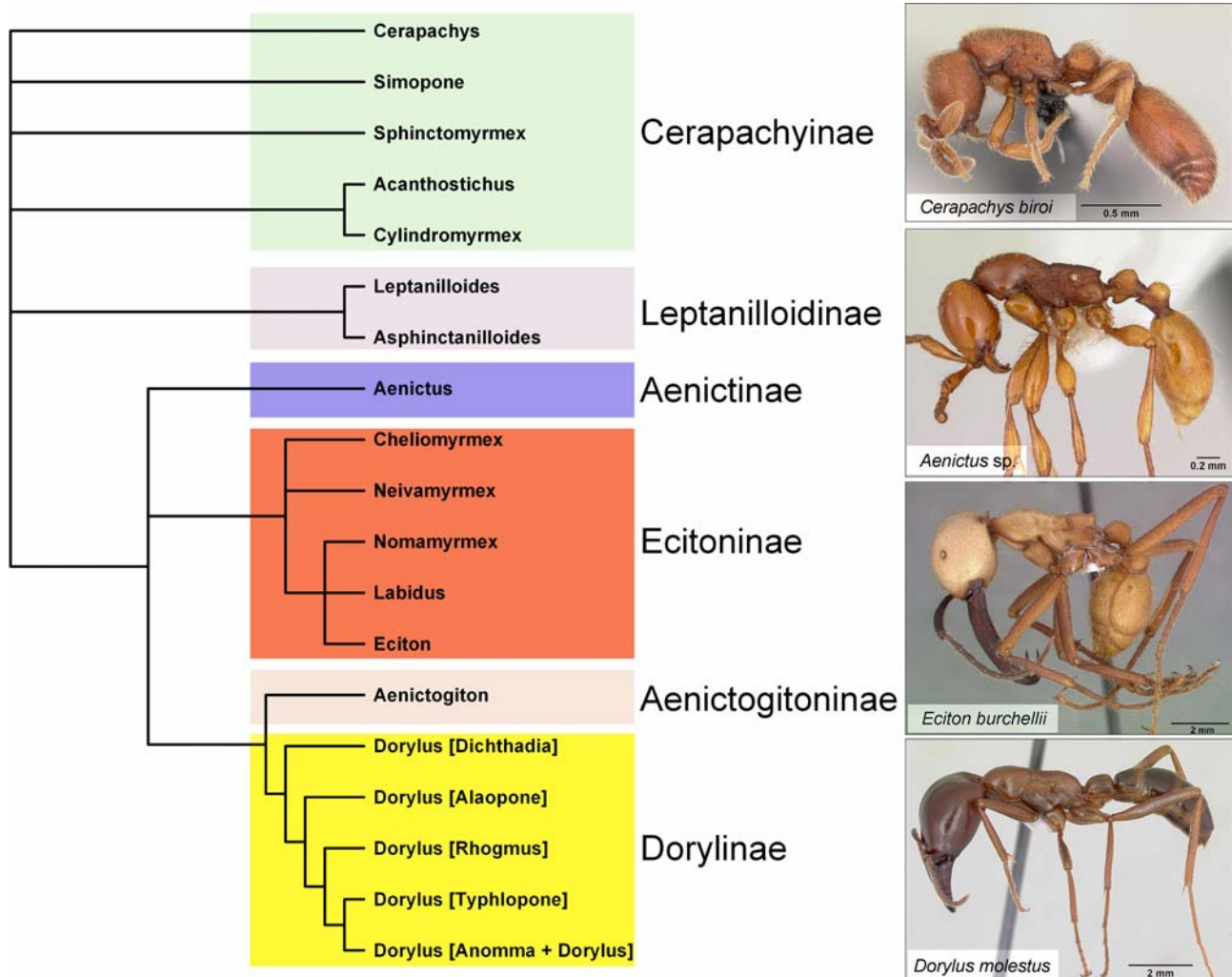


Fig. 1: The current understanding of the internal phylogeny of the dorylomorph section of ants, based on molecular and morphological studies (details are discussed in the text). Insert pictures are courtesy of AntWeb at www.antweb.org and April Nobile.

bably independently in the New World and the Old World. Furthermore, BRADY & al. (2006) added some key taxa to their molecular dataset, most notably the first sequenced specimen of the elusive subfamily Aenictogitoninae. In their phylogeny, Aenictogitoninae is unambiguously resolved as sister to Dorylinae (see also BRADY & WARD 2005), while *Cerapachys sexspinus* (formerly *Yunodorylus sexspinus*; subfamily Cerapachyinae) is sister to a clade comprising Aenictinae plus Ecitoninae (this latter relationship, however, did not receive unambiguous statistical support and was not recovered by MOREAU & al. 2006). Indeed, according to our current understanding, the highly diverse subfamily Cerapachyinae is paraphyletic (BRADY & WARD 2005, BRADY & al. 2006, MOREAU & al. 2006, WARD 2007b). Taken together, this tentatively suggests that adding additional Cerapachyinae taxa to the dataset might eventually break up the long basal branches to the three army ant subfamilies and disrupt AenEcDo army ant monophyly.

Today, AenEcDo army ants are represented by 337 described species that are distributed throughout the world's tropics and the warmer periphery of the temperate zones, while they have failed to colonize areas with cold winters and are absent from many remote islands (Fig. 2; species

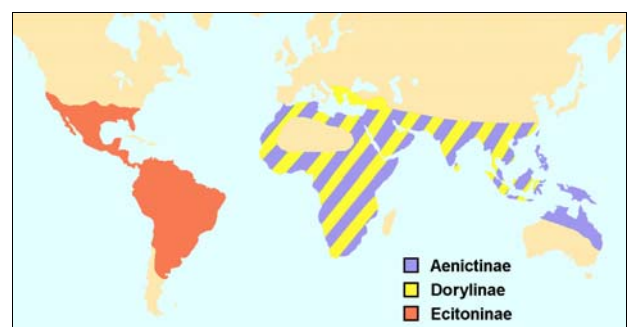


Fig. 2: The worldwide distribution of AenEcDo army ants (modified after GOTWALD 1995). The vast area where Dorylinae and Aenictinae overlap is hatched.

numbers are from the Hymenoptera Name Server version 1.5 retrieved on June 11 2008: http://atbi.biosci.ohio-state.edu:210/hymenoptera/nomenclator.home_page). The New World army ants are categorized in two tribes and five genera, and their systematics is comparatively well understood (BORGMEIER 1955, WATKINS 1976, BOLTON & al. 2007, WARD 2007b). The first tribe, Cheliomyrmecini, contains

the single genus *Cheliomyrmex* with four described species. *Cheliomyrmex* is a strictly tropical and subterranean genus and the colonies are rarely encountered. Therefore, the queens and many aspects of the life-history are still unknown. The workers are morphologically distinct from other Ecitoninae genera in that they do not possess a postpetiole. The first records of diet (O'DONNELL & al. 2005) and associated myrmecophiles (KISTNER & BERGHOFF 2006, BERGHOFF & FRANKS 2007) have only recently been published. The second tribe, Ecitonini, contains four genera. The genus *Neivamyrmex* is the most speciose army ant genus with 131 described species and the only one that regularly occurs in more temperate parts of North America. Some of the species, especially *N. nigrescens*, have been well studied, and a comprehensive review of the species occurring in the USA has been published recently (SNELLING & SNELLING 2007). The remaining three genera form a well supported clade (BRADY 2003, BRADY & WARD 2005). Two widely distributed species have been placed in the genus *Nomamyrmex* and some species of the genera *Labidus* (eight described species) and *Eciton* (12 described species) form the massive surface swarm raids that army ants are renowned for. The genus *Eciton* contains, with *E. burchellii* and *E. hamatum*, the best studied species in the entire group.

The Old World army ants are classified in two subfamilies, Dorylinae and Aenictinae, which each comprises a single genus, *Dorylus* (60 described species) and *Aenictus* (120 described species), respectively. A second genus, *Yunodorylus*, had been described as belonging to Dorylinae (XU 2000), but it has since been transferred to Cerapachyinae (BOLTON 2003), although its phylogenetic position remains somewhat ambiguous (BRADY & al. 2006). The genus *Dorylus* has been subdivided into six subgenera, *Dichthadia*, *Alaopone*, *Rhogmus*, *Typhlopone*, *Dorylus*, and *Anomma* (EMERY 1910). The most renowned representatives of the Dorylinae are the "driver ants" (Box 1) of the subgenus *Anomma*, which raid in massive swarms that cover the forest floor, similar to some *Labidus* and *Eciton* species in the New World. While the "driver ants" do form a clade, other species that have been assigned to *Anomma* and that hunt in the leaf-litter are in fact more closely related to some of the subterranean species of the subgenus *Dorylus* (KRONAUER & al. 2007a). This means that neither the subgenus *Dorylus* nor *Anomma* are monophyletic and therefore need to be redefined (KRONAUER & al. 2007a). The vast majority of species are found in Africa, but a few species occur in tropical Asia. The species-rank taxonomy of Dorylinae is presently in a state of disorder and a comprehensive taxonomic revision is badly needed.

The genus *Aenictus* contains mostly Asian species but also has a significant proportion of African representatives and ranges into northern Australia. While the Asian species have been treated comprehensively by WILSON (1964; several additional species descriptions and local identification keys have been published since), a similar effort is still lacking for the African species. Whether Dorylinae and Aenictinae arose in Africa or Asia, and when and how often they dispersed between the two regions, still remains an open question.

One major problem in the classification and nomenclature of army ants and their relatives stems from the difficulty of associating males with workers of the same species (BOLTON 2003). Males disperse on the wing from their

mother colonies and most species can be readily collected at light sources at night (e.g., LESTON 1979, BALDRIDGE & al. 1980, DO NASCIMENTO & al. 2004). However, only in some species have males been found together with workers before dispersal (Fig. 3A), and the association of the two castes remains elusive in the remaining species (BOLTON 2003). As a consequence, many army ant species have probably been described independently for males and workers and many species names will thus turn out to be redundant. This problem may now be partially overcome with the availability of molecular characters in ant taxonomy that can be used to associate the two forms if collected separately (BERGHOFF & al. 2003a, WARD 2007a, KRONAUER & al. 2007a, SCHÖNING & al. 2008a).

The army ant adaptive syndrome

Collective foraging and group predation

Army ants are formidable predators. Workers leave the nest in groups of up to several hundred thousand individuals in search for live prey, which they overwhelm and kill on the spot, partition if too large to carry, and transport back to the nest (Fig. 3B). Most species attack the colonies of other social insects and some are quite specialized in their prey spectrum (e.g., RETTENMEYER 1963, MIRENDA & al. 1980, FRANKS & BOSSERT 1983, GOTWALD 1995, HIROSAWA & al. 2000, LAPOLLA & al. 2002, BERGHOFF & al. 2003b, KASPARI & O'DONNELL 2003, POWELL & FRANKS 2006, LE BRETON & al. 2007, POWELL & BAKER 2008). Among the most spectacular combats between large societies are the attacks of the New World army ant *Nomamyrmex esenbeckii* on mature *Atta* leaf-cutting ant colonies (POWELL & CLARK 2004) and those of African *Dorylus* army ants on termite mounds (DARLINGTON 1985, SCHÖNING & MOFFETT 2007). In both cases the attacked societies themselves can number more than a million individuals with soldier castes specialized for colony defence, and the abandoned battle fields are often littered with corpses of both parties (POWELL & CLARK 2004). Some army ant species, on the other hand, are generalized predators that also attack and overwhelm solitary prey that is considerably larger than a single ant (RETENMEYER 1963, GOTWALD 1995, SCHÖNING & al. 2008b, POWELL & BAKER 2008). In most cases these will be large invertebrates like crickets, cockroaches and earthworms, but some army ants like the New World *Cheliomyrmex andicola* (O'DONNELL & al. 2005) and some *Dorylus* (*Anomma*) species (GOTWALD 1995) have been reported to occasionally prey on vertebrates.

Especially *E. burchellii*, *E. hamatum*, *L. praedator*, and some *Aenictus* and *Dorylus* (*Anomma*) species hunt epigaeically (Box 1), and their raids are therefore easily observed. Based on their epigaeic activity, standardized methods have been devised to estimate colony densities (FRANKS 1982, SCHÖNING & al. 2005a, VIDAL-RIGGS & CHAVES-CAMPOS 2008). Based on his detailed studies of *E. hamatum* and *E. burchellii*, SCHNEIRLA (1934) described two basic types of epigaeic raiding pattern for the two species, column and swarm raiding, respectively. In *E. hamatum*, a base column which connects the nest to the raid, branches into smaller narrow columns which terminate in groups of advancing workers on the lookout for social insect colonies. In *E. burchellii*, on the other hand, a dense ant carpet



Fig. 3: (A) A winged male of *Labidus praedator* in the emigration column of its colony. Workers are carrying pupae. (B) A team of *Eciton vagans* workers transports a prey ant, *Pachycondyla* sp., back to the nest. Note the two myrmecophilous *Cephaloplectus* beetles hitching a ride. (C) Synchronized larvae during the foraging phase in a nest of *Cerapachys biroi*. (D) A *Simopelta pergandei* queen walks in an emigration column while workers carry the brood.

initially spills out from the bivouac, flushing out a diverse array of arthropods. Where prey has been encountered, smaller columns are left behind in the swarm's wake and coalesce into the base column, thereby retaining a connection with the bivouac. However, column and swarm raids do not represent discrete categories as evidenced by intermediate raiding patterns in other species and variations among differently sized colonies of the same species (SCHNEIRLA 1934, GOTWALD 1995, FRANKS 2001). Systematic quantifications and data on additional species are therefore needed to assess how exactly raiding pattern, group size, and prey spectrum are interrelated.

The traffic on army ant trails often resembles rush hour in human cities, but an apparent overall order emerges from relatively simple and local rules that are followed by individual ants. A stable three-lane system with minimal congestion is formed on *E. burchellii* trails, where inbound ants occupy the central lane. This pattern is due to a combination of the tendency of every single worker to move towards the highest concentration of trail pheromone (which is in the centre of the trail), and an asymmetry in interactions between out- and inbound ants (with outbound ants being more likely to turn around after head-on collisions) (COUZIN & FRANKS 2003).

Above ground raiders are especially exposed to variable climatic conditions and face the risk of desiccation. *E. burchellii* raids avoid open patches with higher temperatures (MEISEL 2006), but at the same time, raid densities of above ground raiders decrease with altitude and associated lower temperatures (O'DONNELL & KUMAR 2006). To observe an army ant surface raid really is an amazing experience. In *E. burchellii*, large soldiers with sabre shaped mandibles guard the raiding columns. Subsoldiers, a specialized porter caste with long legs that allow the ants to carry even big and bulky items slung beneath their body, transport prey back to the nest (POWELL & FRANKS 2005, 2006). Army ants readily form teams in which workers collaborate to carry prey items that would be too large or heavy for a single ant (Fig. 3B). These teams typically consist of a large front runner, often a subsoldier, which is assisted by smaller workers that prevent the prey item from dragging (FRANKS & al. 2001, POWELL & FRANKS 2005). Such teams are superefficient, in that they together can carry prey items heavier than what the members combined could carry if working alone (FRANKS & al. 1999). Gaps in the way of the swarm are bridged by chains of living ants that cling together, and rough terrain is mended by single ants that motionlessly serve as pothole plugs (POW-

ELL & FRANKS 2007). The ant swarm is accompanied by ant following birds, a specialized guild in tropical forests that feed on the arthropods that attempt to flee from the approaching army (SWARTZ 1997, 2001, CHAVES-CAMPOS 2003, WILLSON 2004, BRUMFIELD & al. 2007, KUMAR & O'DONNELL 2007, CHAVES-CAMPOS & DEWOODY 2008, PETERS & al. 2008). It has been shown recently that these birds actually parasitize the ants by significantly reducing the success of raids (WREGE & al. 2005). In turn, certain butterflies are attracted to the ant swarms, which indirectly provide a reliable resource of mineral rich bird droppings (RAY & ANDREWS 1980). Diverse parasitic flies perch on leaves or hover above the swarm front and occasionally dart down at a fleeing cricket or cockroach to deposit their eggs or larvae on the body of the escapee, while others steal prey from the ants (GOTWALD 1995).

Unlike the epigeaic surface swarm raiders, most army ants are poorly known because they forage in the soil, largely hidden from the human observer. However, some are attracted to oil and nut-based baits (WEISSFLOG & al. 2000, O'DONNELL & al. 2007) and this method has been recently used to intensively study one of the strictly hypogaeic (Box 1) army ants for the first time. *Dorylus (Dichthadia) laevigatus* is one of the few *Dorylus* species that occur in Southeast Asia (WILSON 1964). Nests are entirely subterranean, without any above-ground signs of excavations (BERGHOFF & al. 2002a). Unlike any of the epigeaic species, *D. laevigatus* constructs subterranean trunk trail systems that can be stable for several months (BERGHOFF & al. 2002b). Originating from these trunk trails, the smallest workers conduct exploratory column raids, and upon prey encounter construct tunnels to allow the passage of larger workers (BERGHOFF & al. 2002b). Tentative results suggest that the impact on local arthropod communities is less severe than that of epigeaic army ants, which probably allows this species to employ the same hunting ground sustainably for extended periods of time (BERGHOFF & al. 2003b).

Nomadism

Army ants do not construct permanent nests as do other ants. Instead, they form clusters of living ants clinging together in partially excavated subterranean cavities, or suspended from logs or trees in species with above ground nesting. These so called "bivouacs" (SCHNEIRLA 1933) are relocated frequently and emigrations to new nesting sites can cover around a hundred metres. In the species with the largest colonies, like some *Dorylus (Anomma)* species, emigrations can take several days. Two types of nomadic ants have been distinguished, "phasic" and "nonphasic" species (SCHNEIRLA 1971, GOTWALD 1995; Box 1).

The former group includes the New World army ants *E. burchellii*, *E. hamatum*, and *N. nigrescens*, as well as some Asian *Aenictus* species (SCHNEIRLA 1971). In these phasic species, brood is produced and develops in distinct, regularly spaced, and partially overlapping cohorts. Two alternating phases of colony behaviour and physiology can be distinguished: one in which the colony contains larvae (the nomadic phase; Box 1), and one in which the colony contains pupae and eggs (the stately phase; Box 1) (Fig. 4). Emigrations only occur during the nomadic phase, when food demanding larvae are present. In *E. burchellii*, the best studied species, the stately phase lasts for 20.4 days on

average and the bivouac is typically constructed at well protected sites, several metres above ground in trees or inside hollow logs. During the nomadic phase, which lasts for 14.3 days on average, bivouacs are more exposed and colonies emigrate almost every night. The durations of both phases are largely fixed, with a variation of maybe one day (SCHNEIRLA 1971, TELES DA SILVA 1977a, b, KRONAUER & al. 2007b). The queen becomes highly physogastric during the stately phase and lays a batch of eggs that hatch towards the end of this phase into a new cohort of developmentally synchronized larvae. During the nomadic phase, however, the queen is contracted and can walk in the emigration columns (Fig. 4).

"Group B" or nonphasic species include the studied *Dorylus (Anomma)* species, and possibly all Dorylinae (BERGHOFF & al. 2002a, SCHÖNING & al. 2005a). The available data also suggest that *Labidus* species might be nonphasic (RETTENMEYER 1963, FOWLER 1979, POWELL & BAKER 2008). *Dorylus* queens do not undergo the extreme physiological cycles of *Eciton* and *Aenictus* queens, and the brood is therefore not strictly synchronized in their development. In these species, single emigrations are separated by stately intervals of highly variable length (RAIGNIER & VAN BOVEN 1955, LEROUX 1982, SCHÖNING & al. 2005a). Colonies of *D. (Anomma) molestus*, for example, can stay in a nest for three to 111 days (median 17 days), which means that nomadic behaviour is not tightly coupled to a brood developmental cycle (SCHÖNING & al. 2005a).

It seems plausible that nomadism evolved concurrently or shortly after group predation in order to escape depletion of the local food resources and to exploit new hunting grounds (WILSON 1958a, FRANKS & FLETCHER 1983, GOTWALD 1995). Nomadism is generally thought to evolve in ant species that rely on spatiotemporally unstable and unsustainable food sources. A recent non-army ant example is the Southeast Asian ant *Euprenolepis procera*, which is specialized on naturally growing mushrooms (WITTE & MASCHWITZ 2008). In nonphasic army ants, food shortage may still also be the proximate cause of irregular emigrations (unless emigrations are triggered by other external causes such as predator attacks (SCHÖNING & al. 2005a, but see RAIGNIER & VAN BOVEN 1955) while in phasic species the situation is more complicated. For phasic species, Schneirla (reviewed in SCHNEIRLA 1971) suggested that external factors had little influence on the colony cycle and advanced his "brood stimulation hypothesis". According to this hypothesis, stimulation from the eclosing callow workers triggers the onset of the nomadic phase, which is later sustained by stimulation from the developing larvae. Once the larvae pupate and this stimulation ceases, the colony enters the stately phase.

One finding that supports this contention is that *E. burchellii* colonies that raise reproductive larvae, which develop faster than worker larvae, have shorter nomadic phases (SCHNEIRLA & BROWN 1950, KRONAUER & al. 2007b). However, to test the regulation of the army ant cycle experimentally has been difficult. TOPOFF & al. (1980) conducted a brood transfer experiment in *N. nigrescens* and tentatively showed that callow emergence can initiate emigrations even in the absence of larvae. A big advance in understanding cyclic regulation in ants finally came from studies of the army ant like species *Cerapachys biroi*, which has small colonies of a few hundred workers. *C. biroi* is a

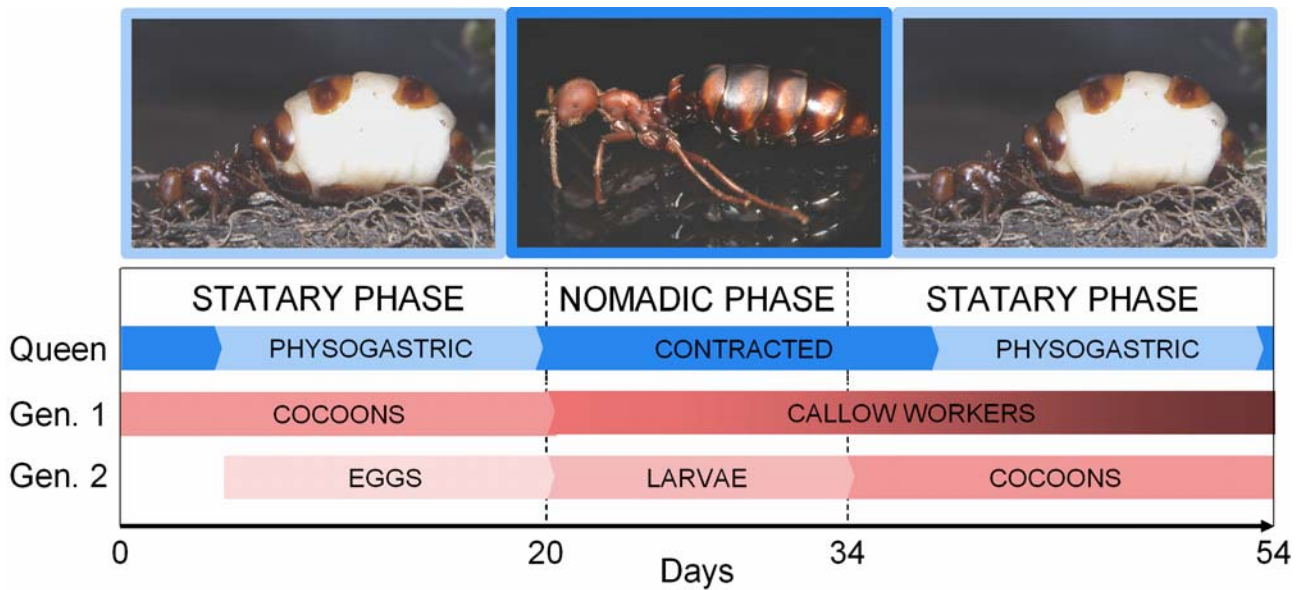


Fig. 4: A schematic representation of the phasic cycle of an *Eciton burchellii* colony. Two subsequent worker generations are shown (Gen. 1 and Gen. 2). The photographs show the queen at the peak of the statory and the nomadic phase.

queenless species in which workers reproduce parthenogenetically (TSUJI & YAMAUCHI 1995, RAVARY & JAISON 2004) and colonies undergo phasic cycles (RAVARY & JAISON 2002; Fig. 3C): During the statory phase, which lasts for 18 days, a colony contains pupae, while the workers develop their ovaries, lay worker destined eggs, and forego foraging. When the callows eclose and the eggs hatch simultaneously, the colony enters the foraging phase, during which workers do not reproduce, but hunt for ant brood to feed their developing larvae. The foraging phase lasts for 16 days. Using brood transfer experiments, RAVARY & al. (2006) first established that the cycle does not follow an endogenous rhythm, but is indeed controlled by brood stimulation. They then showed that, contrary to Schneirla's earlier model (SCHNEIRLA 1971) larval stimulation plays a pivotal role in eliciting and sustaining the foraging phase, while the effect of callow workers is transient. To what extent this system is representative for army ants in general remains to be investigated, especially because queen and worker functions are not separated in *C. biroi*.

At this point it seems important to make the distinction between the nomadic phase and actual emigrations. As has become clear, the colony cycles of the studied phasic species are largely independent of factors other than brood development. However, while emigrations only occur during the nomadic phase, their frequency and regularity could still be influenced directly by external factors such as food availability. TOPOFF & MIRENDA (1980a, b) and TOPOFF & al. (1981) indeed showed that overfeeding *N. nigrescens* colonies reduces and in some cases even entirely suppresses emigrations during the nomadic phase, but that it does not alter the duration of the nomadic phase *per se*, e.g., by accelerating larval development or by promoting continuous egg-laying by the queen.

Army ant queens

Queens of epigaic *Dorylus* species are the biggest ants on Earth, with a total body length of more than five centimetres. During their life they lay an estimated quarter of a

billion eggs (RAIGNIER & VAN BOVEN 1955, KRONAUER & BOOMSMA 2007a), which probably makes them the record holders in the insect world. To accomplish this, they store close to a billion sperm in their spermatheca (KRONAUER & BOOMSMA 2007a). These outstanding reproductive capacities serve to maintain the huge colony sizes of up to ten million individuals (LEROUX 1982). The queens of other army ants are somewhat smaller, but are still highly specialized egg layers. Typically, army ant colonies are headed by a single queen. The only known exception is the North American species *Neivamyrmex carolinensis*, where several reproductively active queens are present in probably all colonies (RETTENMEYER & WATKINS 1978, KRONAUER & BOOMSMA 2007b). Because army ant colonies cannot be kept for extended periods in the laboratory and are difficult to follow in the field, it is not exactly known how long a queen normally lives. Mark and recapture studies on Barro Colorado Island, however, have established that *Eciton* queens can live more than four years (SCHNEIRLA 1971). AenEcDo army ant queens have been described as dichthadiiform ergatogynes (Box 1).

Mating and reproduction by colony fission

The permanent lack of wings in army ant queens has one important corollary: they do not go on mating flights. Instead, young army ant queens mate inside their natal colony with foreign males that disperse on the wing. Like the queens of other social Hymenoptera, army ant queens mate only shortly after they have eclosed from the pupae (KRONAUER & BOOMSMA 2007a). The reproductive colony undergoes fission during which the worker force splits into two roughly equal parts (RAIGNIER & VAN BOVEN 1955, SCHNEIRLA 1971, GOTWALD 1995). Colony reproduction by fission is rare among the eusocial Hymenoptera, and is confined to army ants, honeybees, stingless bees and a few other taxa mainly in the ant subfamily Ponerinae (PEETERS & ITO 2001). Colony fission, as opposed to colony budding, involves monogynous societies that raise very few young queens (gynes), and young colonies are independ-

ent (BOURKE & FRANKS 1995, PEETERS & ITO 2001). Prior to fission, which occurs approximately every three years (FRANKS 1985), colonies of the army ant *E. burchellii* produce a reproductive brood, and eventually around six gynes and three- to four thousand males eclose (SCHNEIRLA 1971). Of these six or so gynes, all but one or two (if the old queen is superseded) are left behind in the process of colony fission and die. The highly male biased numerical sex-ratios, which, at first sight, differ strikingly from the expected equal investment into both sexes (FISHER 1930), are found in all army ants and in other species that reproduce by colony fission. A possible reason is that, at most, two young queens will head the new colonies, and producing significantly more gynes would be a waste of resources. Males, on the other hand, take part in the population level competition for mating opportunities so that a colony should produce as many males as possible (CRAIG 1980, BULMER 1983, BOURKE & FRANKS 1995). Also, if the workers that accompany a young queen are regarded as part of the colony investment in that queen (HAMILTON 1975, MACEVICZ 1979), the total investment in queens versus males is far less male biased. The main allocation problem in fissioning species is then between allocating resources to workers that accompany the two queens, versus males (PAMILO 1991, BOURKE & FRANKS 1995). Measuring sex-allocation in other fissioning species such as honeybees is rather complicated because males are produced continuously and colonies invest significantly into nest construction and other resources (e.g., honey combs, which have to be partially counted towards the investment into young queens) (PAGE & METCALF 1984). Army ants, especially those with smaller colonies, might therefore be a simpler model system for future empirical studies of sex-investment in fissioning species (see MACEVICZ 1979 and FRANKS 1985 for preliminary analyses).

The development of neutral genetic markers for a variety of army ant species (*Aenictus dentatus*, by KRONAUER & al. 2007c; *Aenictus laeviceps*, by HAMAGUCHI & al. 2007 and KRONAUER & al. 2007c; *Dorylus molestus*, by KRONAUER & al. 2004a; *Eciton burchellii*, by DENNY & al. 2004a; and *Neivamyrmex nigrescens*, by KRONAUER & al. 2007c) has helped to elucidate some of the corollaries and consequences of the idiosyncratic life-history of army ants. First, dependent colony founding by fission is directly reflected in the genetic structure of army ant populations. In *E. burchellii*, mitochondrial loci that are only inherited via queens, show much stronger differentiation between populations than nuclear loci, which are also inherited via the dispersing males (BERGHOFF & al. 2008).

Second, it has become apparent that all investigated army ant queens mate with an exceptionally large number of males, typically between 10 and 20, which results in offspring of mixed parentage (polyandry) (DENNY & al. 2004b, KRONAUER & al. 2004b, KRONAUER & al. 2006a, KRONAUER & al. 2007d). The adaptive value of this derived mating system, which has repeatedly evolved from monandry in distantly related groups, such as leaf-cutting ants, *Pogonomyrmex* harvester ants, and honeybees, is still hotly debated (CROZIER & FJERDINGSTAD 2001, HUGHES & al. 2008a). Polyandry is the ancestral mating system in AenEcDo army ants and seems to be an integral part of the army ant adaptive syndrome (KRONAUER & al. 2007d). While polyandry increases the genetic variance within sin-

gle colonies, it also decreases the variance between colonies, as queens increase their "sample size" of alleles in the population by mating with more males.

Increased genetic variance within colonies has been suggested to be adaptive in some cases for a variety of reasons (reviewed in CROZIER & FJERDINGSTAD 2001). For example, because genetically diverse colonies might be more resistant to parasites (van BAALEN & BEEKMAN 2006, HUGHES & BOOMSMA 2006), or because genetic diversity might facilitate the evolution of task specialization, which in turn leads to increased colony homeostasis (OLDROYD & FEWELL 2007). Both factors could be important in army ants. First, their colonies harbour an astonishing number and diversity of myrmecophilous arthropods, many of which are probably mainly parasitic. Reproduction by colony fission and the lack of an independent founding phase furthermore makes it difficult for new colonies to shed parasites once they have become established in the mother colony. This means that large parasite populations can persist over a long time in army ant colonies and directly co-evolve with their hosts. Second, many army ants have large societies with complex systems of division of labour. Their temporary nests, and especially the bivouacs of above-ground nesting species, are subject to environmental perturbations such as temperature fluctuations, similar to honeybee swarms (FRANKS 1989). One assumption of the hypothesis that genetic diversity can lead to more effective division of labour and thereby greater colony homeostasis, is that individuals with different genetic makeup differ in their propensity to perform a certain task or to develop into a certain caste (OLDROYD & FEWELL 2007). That this can be the case in army ants has been shown for *E. burchellii*, where members of a given worker caste (i.e., soldiers, subsoldiers, majors, and minors) tend to belong to different full-sister subfamilies (JAFFÉ & al. 2007).

Decreased genetic variance between colonies will make polyandry adaptive if, for any trait with a genetic basis, the "average" colony performance is sufficient for colony success (PAGE 1980, SHERMAN & al. 1988, KRONAUER & al. 2007d, RUEPPELL & al. 2008). Such traits could, e.g., be fitness load from diploid male production, or, again, parasite resistance and efficiency of division of labour. Single mating by queens maximizes the variance between colonies for such a trait, and thereby maximizes the proportions of colonies that perform extremely well and extremely badly, respectively. Single mating is therefore the best strategy under circumstances where only colonies that perform extremely well survive. This could for example apply to most species with independent colony founding, where the vast majority of young queens die during the founding phase. Multiple mating by queens, on the other hand, decreases the proportions of such extreme colony phenotypes. Multiple mating is therefore the best strategy under circumstances where only colonies that perform extremely badly die. This hypothesis seems especially suitable to account for the evolution of polyandry in fissioning species like honeybees and army ants, where colonies never go through the highly risky phase of independent colony founding (PAGE 1980, SHERMAN & al. 1988, KRONAUER & al. 2007d, RUEPPELL & al. 2008).

Under each scenario a reversal to low mating frequencies under polygyny is predicted, as long as there is some cost associated with mating multiply (KRONAUER & BOOMS-

MA 2007b, HUGHES & al. 2008b). The reason is that polygyny is more efficient than polyandry in increasing genetic variance within colonies and decreasing genetic variance between colonies. The single polygynous AenEcDo army ant, *Neivamyrmex carolinensis*, nicely meets this prediction: it is the only species where queens have reverted from strict polyandry to mating only once or twice (KRONAUER & BOOMSMA 2007b).

The succession of old queens by young queens during colony fission makes army ant colonies theoretically immortal. However, because army ants cannot rear emergency queens in the case of queen loss, the death of the queen under most circumstances will also mean the death of the colony. Queen loss can occur for example due to an accident (mainly during emigrations), illness, predator attack, or simply old age (e.g., LEROUX 1979). Two possible alternatives to plain colony death after queen loss exist. First, queenless colonies have been observed to fuse with neighbouring colonies (SCHNEIRLA & BROWN 1950). This would increase the inclusive fitness of the workers, if these were related to the colony they fuse with. Second, it is conceivable that workers in queenless colonies produce haploid eggs from which they raise males. Although the successful production of worker derived adult males has not been documented for army ants, it has been found that workers of *D. wilverthi* can lay eggs that develop into male larvae after queen loss (RAIGNIER 1972) and workers of *E. burchellii* possess functional ovaries (WHELDEN 1963). These observations have also prompted studies on the percentage of males in queenright colonies. In both *D. molestus* (KRONAUER & al. 2006b) and *E. burchellii* (KRONAUER & al. 2007b) the genotyped males were sons of the colony queen and not of the workers. Whether workers forego reproduction in the first place, or whether worker reproduction is actively policed, still remains to be investigated.

The occurrence of army ant behaviour in other ants

None of the defining army ant traits is restricted to the AenEcDo army ants. In fact, one or more of these traits are found in several, distantly related ant taxa and some species seem to combine all behavioural and morphological adaptations that characterize army ants (WILSON 1958a, GOTWALD 1995, BRADY 2003). The large colonies of the Asian ponerine ant *Leptogenys distinguenda* are headed by a single physogastric and ergatoid queen, emigrate frequently, and workers engage in mass foraging as general predators (MASCHWITZ & al. 1989, WITTE & MASCHWITZ 2000, 2002). Another example is the New World ponerine genus *Simopelta*. Workers forage in columns and attack colonies of other ants, the queen is a permanently wingless dichthadiigyne, and colonies have been repeatedly observed during emigrations (GOTWALD & BROWN 1966; Fig. 3D). Other species that resemble army ants are, e.g., *Leptanilla japonica* (subfamily Leptanillinae; MASUKO 1990), *Pheidologeton diversus* and *P. silenus* (subfamily Myrmicinae; MOFFETT 1988a, b), *Onychomyrmex hedleyi* (subfamily Amblyoponinae; MIYATA & al. 2003), as well as the ponerines *Leptogenys nitida* (DUNCAN & CREWE 1994), *Pachycondyla marginata* (LEAL & OLIVEIRA 1995) and *P. analis* (formerly *Megaponera foetens*; LONGHURST & HOWSE 1979). The most recent molecular phylogenies have raised the possibility that the Leptanillinae are the sister group to all other extant ants (BRADY & al. 2006, MOREAU

& al. 2006). This surprising result would imply that an army ant like lifestyle arose very early in ant evolution, or might even have characterized the ancestor of all living ants. However, this result should be taken with caution as the position of Leptanillinae on the ant tree of life remains rather uncertain (BRADY & al. 2006).

Of special interest to our understanding of army ant evolution are the remaining species in the dorylomorph section of ants, the closest relatives to the AenEcDo army ants (Fig. 1). Unfortunately, studies on the life-history of these species are still exceedingly sparse. The subfamily Leptanilloidinae presently contains two neotropical genera, *Leptanilloides* (eight described species) and *Asphinctanilloides* (three described species) (BRANDÃO & al. 1999, LONGINO 2003, DONOSO & al. 2006). Information on the biology of this group had been virtually non-existent until the recent discovery of entire colonies, the queens, and the winged males (BRANDÃO & al. 1999, WARD 2007a, DONOSO & al. 2006). Larvae develop in synchrony, which suggests that colonies are phasic (BRANDÃO & al. 1999, DONOSO & al. 2006). A colony of *L. nomada* has been observed on a nightly emigration, and workers carried larvae in the typical army ant fashion: slung underneath the body (DONOSO & al. 2006). One colony of *A. anae* has been observed preying on an unidentified arthropod and foraging in columns, which suggests group predatory behaviour (BRANDÃO & al. 1999). The recently described queens of *L. nubecula* are permanently wingless, which means that they do not participate in mating flights and most likely found new colonies accompanied by workers (DONOSO & al. 2006). Interestingly, two different gyne morphs have been found in a single colony (the only Leptanilloidinae gynes that are known so far; DONOSO & al. 2006): A "real" gyne, which is about 25% larger than the workers and possesses compound eyes, and several ergatoid gynes, which resemble workers but have ovarioles and an enlarged gaster. Given this finding of queen polymorphism, the sociobiology of the species will certainly be very interesting, although it remains unclear how representative it is for Leptanilloidinae as a whole.

The subfamily Cerapachyinae is presently organized in the three tribes Acanthostichini (with the single genus *Acanthostichus* and 23 species), Cerapachyini (with the genera *Cerapachys* (84 species), *Simopone* (16 species), and *Sphinctomyrmex* (22 species)), and *Cylindromyrmecini* (with the single genus *Cylindromyrmex* and 13 species). Cerapachyinae is most likely not a monophyletic group (BRADY & WARD 2005, BRADY & al. 2006, MOREAU & al. 2006, WARD 2007a, b). All studied Cerapachyinae are myrmecophagous and raid the nests of other ant species (WILSON 1958b, HÖLLDOBLER 1982, BUSCHINGER & al. 1989, TSUJI & YAMAUCHI 1995). Unlike AenEcDo army ants, but similar to many ponerine army ants, at least some Cerapachyinae initially send out individual foraging scouts that then recruit additional workers to food sources in an act of group predation (HÖLLDOBLER 1982, BUSCHINGER & al. 1989). Prey and brood are carried under the body in the typical army ant fashion (HÖLLDOBLER 1982, BUSCHINGER & al. 1989) and some species have been observed to relocate the nest frequently under laboratory conditions (BUSCHINGER & al. 1989). The studied *Cerapachys* and *Sphinctomyrmex* species show synchronized brood development, which again indicates phasic colony cycles

(WILSON 1958b, HÖLDOBLER 1982, BUSCHINGER & al. 1989, RAVARY & JAISSON 2002). Otherwise, this subfamily is very diverse in life-history and colony organization. Some species of *Cerapachys*, *Simopone* and *Sphinctomyrmex* have ordinary winged queens with large eyes, while others have blind subdichthadiiform queens (BUSCHINGER & al. 1989, FISHER 1997). Colonies of *C. turneri* contain one or two ergatoid queens (HÖLDOBLER 1982) and *S. cf. steinheili* is functionally polygynous, also with ergatoid queens (BUSCHINGER & al. 1989). Colonies of *C. biroi*, on the other hand, are queen-less and workers reproduce parthenogenetically as has been described above. Species with permanently wingless queens are likely to found new colonies accompanied by workers. Cerapachyines also show diverse nesting habits, with some living in preformed plant cavities (FISHER 1997) and others being entirely subterranean (TSUJI & YAMAUCHI 1995).

Finally, the afrotropical subfamily Aenictogitoninae, with the only genus *Aenictogiton* (seven described species), still remains somewhat a mystery, as it is unique among ant subfamilies in that it is only known from males. Both morphological (BRADY & WARD 2005) and molecular data (BRADY & al. 2006) show that *Aenictogiton* is the sister taxon to *Dorylus*. This suggests that *Aenictogiton* may indeed qualify as a true army ant, but only the eventual discovery of *Aenictogiton* colonies with workers and queens will show to what degree their behaviour resembles other army ants.

How to become an army ant

A simple plausible scenario for the evolution of army ants has been suggested by WILSON (1958a) and extended by HÖLDOBLER & WILSON (1990): first, group predatory behaviour evolves in species that prey on large arthropods or attack colonies of other social insects – prey that cannot be overwhelmed by single foragers. While raiding parties are initially recruited upon prey encounter, raids then evolve to become more massive and to be initiated autonomously. As a second step, or concurrently with the first, nomadism evolves to avoid depletion of local food resources. Increases in colony size then make group predation more effective, while effective group predation in turn can sustain larger colonies. Colony size therefore increases as the group predatory / nomadic lifestyle becomes more sophisticated and evolves to extremes in species that secondarily expand their food spectra to become generalized predators. Generalized army ant predators typically hunt above ground, and evolutionary transitions to a more epigeic life-style are thought to be accompanied by marked changes in overall worker morphology (SCHÖNING & al. 2005b, KRONAUER & al. 2007a). Colony fission and permanently wingless queens probably evolve concurrently with the first two steps as group predation becomes obligate. The reason is that single foundresses or the tiny worker forces of incipient colonies cannot engage in group predation to promote colony survival and growth (FRANKS & HÖLDOBLER 1987, BOURKE & FRANKS 1995, GOTWALD 1995). Similar to colonies of bee and wasp species that reproduce by fission and can disperse on the wing, the nomadic life-style of army ants also leads to a much greater dispersal of daughter colonies than is the case in less mobile fissioning or budding ant species. This in turn weakens local resource competition between related colonies and thereby selection against colony fission.

Highly male-biased numerical sex-ratios and obligate multiple mating by queens in monogynous species then possibly evolve as a corollary of colony fission as has been outlined above, but additional comparative data are needed.

The question remains why some army ants are phasic, while others are not. GOTWALD (1988) reckoned that the phasic lifestyle had evolved secondarily from nonphasic army ants. The above review, however, suggests that, while phasic broods arose repeatedly and early in army ant evolution, the nonphasic lifestyle could also represent a reversal in the Dorylinae and *Labidus*. Nonphasic broods might have become adaptive in the Dorylinae as they evolved a more sustainable way of hunting and thereby reduced the necessity to emigrate regularly. The idea that broad prey spectra and sustainable resource exploitation might weaken or even circumvent the necessity to emigrate is also supported by *Pheidologeton* ants which employ stable trunk trails and do not emigrate frequently (MOFFETT 1988a, b). Phasic broods could be adaptive if it would be impossible or costly to carry pupae in the emigrations, due to their shape or size. Although some species, like *D. molestus*, are incapable of carrying large reproductive larvae and pupae (SCHÖNING & al. 2005a), phasic species will readily carry worker pupae when disturbed and pupae are normally present in the first emigration of an *E. burchellii* nomadic phase (TELES DA SILVA 1977b, KRONAUER & al. 2007b). Measures of energetic costs for transporting brood at different stages, however, are presently not available for army ants. Alternatively, it could be impossible for reproductively active queens to walk or be carried in the emigration columns. This is certainly the case for species like *E. burchellii*, but cannot be a decisive factor in other phasic species like *C. biroi*, where workers share reproduction and do not become immobile during the starchy phase. A third possibility is that raids and emigrations are costly and a phasic lifestyle in many cases minimizes the absolute amount of raids and emigrations necessary. The reason could be that army ants feed on fresh prey which is a patchy food source and cannot be stored indefinitely, while it may be overabundant for a short time after successful raids. It might therefore be adaptive to temporally restrict the presence of food demanding larvae and thereby the necessity to raid and emigrate. Clearly, the adaptive value of phasic colony cycles is presently not well understood.

Conclusions

While our knowledge and understanding of army ant biology has greatly increased since the last comprehensive overview by GOTWALD (1995), the available information is still largely limited to a few fairly easily accessible species that have been studied in great detail. However, for the vast majority of army ants, even the most basic life-history parameters such as prey-spectrum and mode of hunting, emigration patterns, reproductive biology and colony cycles, remain unknown, let alone their ecological impact and interactions with other organisms. The relevance of army ants to ecosystem functions is one important area that certainly deserves further study, as their role may well be pivotal but remains poorly understood globally. Any given site in the Neotropics typically harbours around ten Ecitoninae army ant species alone, and at some locations every given square metre of forest floor is hit by one army ant raid each day on average (O'DONNELL & al. 2007). To

obtain a more complete picture it will be important to understand how resources are partitioned between species in different army ant guilds (RETTENMEYER & al. 1983) and how army ants affect prey abundance and biodiversity (FRANKS & BOSSERT 1983, OTIS & al. 1986, VIEIRA & HÖFER 1994, KASPARI & O'DONNELL 2003, O'DONNELL & al. 2007). Extremely diverse communities of myrmecophiles (e.g., KISTNER 1982, WITTE & al. 2008) and swarm-followers are dependent on army ants and, especially in Africa, several large vertebrates like chimpanzees regularly rely on army ants as a food source (e.g., SCHÖNING & al. 2007, 2008c). In times of intense anthropogenic change it will therefore be crucial to study the resilience of army ant populations to habitat alteration, fragmentation, and climate change to allow for efficient conservation planning (PARTIDGE & al. 1996, BOSWELL & al. 1998, ROBERTS & al. 2000, SCHÖNING & al. 2006, BERGHOF & al. 2008). Furthermore, despite immense efforts and advances in recent years, the phylogeny of dorylomorphs and other army ants is still not definitely resolved. A complete understanding of the numerous independent evolutionary transitions towards an army ant lifestyle, combined with detailed studies of a larger number of strategically chosen species within and outside the dorylomorphs is badly needed. Such data should make large scale comparative analyses feasible in the future in order to evaluate the evolutionary scenario outlined above and to reconstruct the sequence and causality of events in army ant evolution.

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Zusammenfassung

Wanderameisen sind dominante soziale Jäger von Invertebraten, wodurch sie eine wesentliche Rolle in tropischen Ökosystemen spielen. Sie zeichnen sich durch eine Reihe von evolutionär zusammenhängenden Besonderheiten ihrer Physiologie, des Verhaltens und der Morphologie aus, dem sogenannten adaptiven Wanderameisensyndrom: Sie jagen obligatorisch in Gruppen, sind nomadisch, und ihre dauerhaft ungeflügelten Königinnen gründen neue Kolonien in Begleitung von Arbeiterinnen. Wendet man diese funktionelle Definition statt einer taxonomischen an, dann sind Wanderameisen mehrmals in phylogenetisch nicht verwandten Ameisengruppen entstanden. Außerdem ist das numerische Geschlechterverhältnis bei Wanderameisen normalerweise extrem männchenlastig, und die Königinnen der untersuchten Arten sind obligat polygam. Das Ziel dieser Abhandlung ist es, einen Überblick über die jüngsten wissenschaftlichen Ergebnisse zu Wanderameisen zu verschaffen, ein evolutionäres Szenario zu umreißen, welches die unterschiedlichen Aspekte ihrer spezialisierten Biologie in Zusammenhang bringt, und einige Anregungen für zukünftige Forschung zu geben.

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