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The hidden big predators of the Neotropics: The behaviour, diet, and impact of New World army ants (Ecitoninae)

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INTRODUCTION

There are more than 150 recognised species of New World army ants (Ecitoninae; Watkins 1976), distributed among five monophyletic genera (*Nomamyrmex*, *Eciton*, *Labidus*, *Neivamyrmex*, and *Cheliomyrmex*; Brady 2003; Brady & Ward 2005). Most of these species are strictly Neotropical in distribution, but a few species are found in the southern United States and northern Argentina (Watkins 1976). All Ecitoninae have the three defining characteristics of the 'army ant syndrome', which are a highly specialised wingless queen, nomadism, and obligate group-foraging (Brady 2003). They also share these characteristics with their sister taxa, the Dorylinae and Aenictinae from the Old World, but here we will focus solely on the Ecitoninae.

Army ant queens are distinct for two main reasons. First, they are permanently wingless and have a reduced, worker-like mesosoma. Second, they have an unusually large gaster capable of expanding to more than double its normal volume when the ovaries are fully active. This allows massive reproductive pulses of hundreds of thousands of eggs in as little as ten days (Rettenmeyer 1963; Schneirla 1971). Both of these characteristics make army ant queens well adapted to the nomadic lifestyle of their colonies.

Among the Ecitoninae, the pattern of nomadism can vary greatly. For instance, in *Eciton*, colonies follow a well-defined cycle of a nomadic phase followed by a statary (stationary) phase (Rettenmeyer 1963; Schneirla 1971; Teles da Silva 1977; Franks & Fletcher 1983). In the nomadic phase, which lasts approximately 16 days in all *Eciton* studied to date, colonies migrate to a new nest site almost every day and have a synchronised cohort of larvae. During this phase, the queen lays no eggs and has a contracted gaster, allowing her to run quickly within the emigration traffic. When the larvae reach maturity and start to pupate, the colony then enters the statary phase, lasting approximately twenty days, and in this time the pupae undergo metamorphosis and the queen's gaster expands dramatically, allowing her to lay a new batch of eggs. At the end of the statary phase, the synchronised cohort of pupae start to eclose into adults, the queen's gaster returns to its contracted state, and the eggs hatch into hungry first instar larvae, and the cycle repeats. At the opposite extreme are the members of the genus *Labidus*, which appear to lack synchronised brood cohorts, emigrate on an irregular schedule, and often nest in one location for a number of months (Rettenmeyer 1963) and references therein).

The foraging strategy of army ants is unusual among ants because instead of individuals finding food and then transporting it back to the nest or recruiting nestmates, army ants both seek-out and capture prey as a unified group (Rettenmeyer 1963; Schneirla 1971). Thus, when foraging activity begins, a large proportion of the colony leaves the colony together in search of prey. Group raids have the same basic properties in all species, with a densely populated raid front connected to the nest via a 'principal trail' of foragers shuttling back and forth. It is at the raid front that the prey is initially detected, and it is then overwhelmed, dismembered if necessary, and transported back to the nest. When workers are engaged in subduing prey and transporting, others simply take their place at the front and the raid continues to advance.

Despite the fact that all army ants use the same mode of foraging, the size, density of workers at the raid front, and the overall pattern of the raid can vary considerably among species (Rettenmeyer 1963). *Eciton burchellii* is well known for its conspicuous daytime raids that attract a great diversity of other animals, ranging from parasitic flies to birds (reviewed in Gotwald 1995), but this species is quite atypical. In fact, the raid front is so densely populated with workers in *E. burchellii* that it is considered one of only two species that produces a 'swarm raid'. All other Ecitoninae are generally referred to as 'column raiders' because their raid fronts are usually less densely populated and they can have a number of smaller fronts instead of one large one, as is usually seen in *E. burchellii*. As more army ants have been studied, however, it appears that there is no clear qualitative difference among swarm raids and column raids. Instead, it appears the width of the raid front and the density of workers varies continuously among species, with no clear divisions. For example, although it is easy to define a large raid by *E. burchellii* as a swarm, the raid fronts of small *E. burchellii* colonies are usually narrower and less densely populated than those of large colonies of the 'column raider' *Eciton hamatum*. Likewise, *L. praedator* is widely considered to be the only other swarm raiding species, but raid fronts of some *Neivamyrmex* species can be equally densely populated and display the same wave-like movement of workers described for *L. praedator* (Rettenmeyer 1963; Powell personal observation, see later for details), while *Labidus coecus* is said to have raids that are intermediate between column and swarm (Rettenmeyer 1963).

Aside from the basic understanding of the nomadic and group predatory behaviours of army ants, remarkably little is know about the particular foraging behaviour, diet, and impact of most species. This is because unlike the well-studied *E. burchellii*, which is active during the day and on the surface, the vast majority of the Ecitoninae are primarily active underground, or at night, or both (Rettenmeyer 1963; Schneirla 1971). Consequently, most species are very difficult to study and much of our understanding comes from chance encounters. The information collected during these encounters, however, can serve as a solid and vital base for more directed and quantitative studies of particular species in the future.

Here we review current knowledge on the local diversity, timing and strata use of raids and emigrations, diet, and impact of New World army ants. We also present new observations and data on these topics from Barro Colorado Island (BCI hereafter), which is a moist forest site in Panama, and from the reserve of the Clube Caça e Pesca Itororó – Uberlândia (CP hereafter), in the cerrado biome of Brazil. The observations from BCI are from a total of twenty-four months of fieldwork between 2001 and 2003, and were made mostly by S. Powell whilst working on the army ant genera *Eciton* and *Nomamyrmex*. The observations from CP were made by both of us during a preliminary two-month study.

LOCAL ARMY ANY DIVERSITY

The simplest way to encounter army ants is to walk compacted hiking trails through intact tropical habitat during the day and at night. By doing this, one intersects the often long and conspicuous raid or emigration columns of army ants as they cross the trail. The compacted nature of the tail is particularly important because it forces subterranean species above ground, and this effect is even greater if the soil is very wet or near saturation. It is therefore not uncommon to see a column of army ants exit a hole on one side of a trail, cross it on the surface, and then return underground immediately on the other side. Like other large predators, army ants appear to be at low population density (Franks 1982; Britton et al. 1996), and significant distances often have to be covered to find just a few colonies, which is also facilitated by hiking pre-established trails. Using this simple method, detailed studies of army ants at a few sites in Central and South America suggest that intact moist or wet forest sites in the Neotropics may have as many as twenty sympatric army ant species (Rettenmeyer et al. 1983). It also appears that this approach can identify most of the species at a site in a relatively short period of time. For instance, in a six-month survey on BCI, Kaspari (1996) encountered nineteen species, and long terms records suggest that there are approximately twenty-three species at this site (Rettenmeyer 1963; Watkins 1976; Kaspari personal communication). With knowledge of raid patterns and average raid length, encounters on a regimented trail-walking schedule can also provide insight into the population density of particular army ant species, as Franks (1982) showed for *E. burchellii*.

All of the intensive studies of army ant diversity have been conducted in wet or moist tropical forest sites, and most of our general understanding of army ant biology comes from Barro Colorado Island. As such, less is known about army ant diversity and biology in other tropical systems. Perhaps one of the largest and most understudied of these other systems in the Brazilian savanna or 'cerrado'. This biome originally covered approximately 2 million km^2, representing around 22% of the landmass of Brazil and small areas of eastern Bolivia and northwestern Paraguay (Oliveira-Filho & Ratter 2002). Cerrado experiences a very pronounced dry season from April through September and the savanna structure means that at all times of year there is often little shade at ground level during the day. Not surprisingly, then, the diurnal, surface raiding *Eciton* or not found in this habitat (Watkins 1976; Powell & Baker personal observation), but many other species are (Watkins 1976).

In January and February of 2005, we walked a heavily compacted trail of approximately 2 km at CP. Walks were conducted an average of four times a week and all were started between 6 and 8 am. We encountered seven species from four genera (*Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex*) in a total of thirty-eight raids and two emigrations. We also located three subterranean bivouac sites by following raid columns a short distance off-trail. After approximately 10 am, and earlier on cloud-free days, the intensity of the sun broke up traffic on the columns and the army ants retreated underground. Given the sensitivity of all species to direct sunlight, it is likely that walking similar trails in cerrado at night would yield even higher species counts and activity rates. However, this preliminary survey demonstrates that like wet tropical forest, cerrado has both a diverse and active army ant community, but that it is not as apparent because there is essentially zero surface activity for most of the daylight hours.

STRATA USE AND TIMING OF RAIDS AND EMIGRATION

Eciton

There are nine described *Eciton* species for which the colonies have been found, and three more species that are described solely from males (Watkins 1976). In terms of strata use, existing data suggests that all *Eciton* raid and emigrate on the surface (Rettenmeyer 1963; Table 1), which is unusual or unheard of among the other Ecitoninae genera. Species other than *E. burchellii* and *E. hamatum* are sometimes referred to as subterranean (Schneirla 1971), but this really refers to their tendency to bivouac below ground (Rettenmeyer 1963; Schneirla 1971; Table 1). This can also result in the raid and emigration columns of these species being underground for short distances near the bivouac (Table 1). Among species, the size of the raid fronts can vary considerably, from the densely populated raid fronts of *E. burchellii*, which can be up to 10 metres wide, to the more sparsely populated raid fronts of species like *Eciton dulcium*, which rarely exceed 2 metres (Rettenmeyer 1963; Powell personal observation). Related to this, the traffic density along the 'principal trail' also varies considerably. In *E. burchellii*, traffic can be many ants wide, creating a conspicuous path over the litter, but in species with smaller raids, such as *Eciton dulcium*, traffic is rarely more than one ant wide and individuals are often widely spaced. Consequently, the principal trail of these species is much harder to follow. This is particularly true in areas with deep leaf litter because the narrow trail of ants can pass unhindered through the relatively large gaps in loose leaves in the top layer of the litter, periodically obscuring them from view.

The timing of raids can also differ markedly among *Eciton* species. However, all species complete a raid and an emigration within 24 hours when in the nomadic phase, and they may all start emigrations at approximately the same time, in late afternoon and the early evening (Rettenmeyer 1963; Table 1). On BCI, the raids of *E. dulcium*, *Eciton mexicanum* and *Eciton vagans* are nocturnal, with a quiescent period during the day. During the nomadic phase, colonies become active in the early evening and a raid column quickly extends out from the bivouac. Shortly after this, a new bivouac site is selected near the raid front and the emigration traffic starts to leave the old bivouac. During this time, there is continuous emigration traffic going form the old bivouac to the new one, but beyond this location, some raiding activity continues. Once the entire colony has arrived at the new site, raiding continues with renewed strength throughout the night. At dawn the raid retracts into the new bivouac and the colony is quiescent until the following night. This sequence is reversed in *E. burchellii* and *E. hamatum*, with diurnal raids and a quiescent period at night. When colonies are nomadic, the diurnal raids transition into a nocturnal emigration that is immediately followed by a quiescent period at the new site. The reason for this difference is not known, but we hypothesise that the larger colony sizes of *E. burchellii* and *E. hamatum* essentially force them to forage during the day. In all *Eciton*, the colony's brood and single queen are moved over the forest floor during an emigration. It is no surprise, then, that all species do this at night, to avoid possible predation pressure from the suite of visual predators that are active during the day. However, the largest colonies of *E. burchellii* and *E. hamatum* contain many hundreds of thousands of workers (Rettenmeyer et al. 1983; Franks 1985; Powell unpublished data), and emigrations can take up to twelve hours, so the last workers only arrive at the bivouac just before dawn (Franks 1985; Powell unpublished data). The daylight hours are therefore the only time within the 24-hour period that remains for *E. burchellii* and *E. hamatum* to conduct raids. In contrast, *E. dulcium, E. mexicanum, and E. vagans* colonies are relatively small and emigrations can be completed quickly (Rettenmeyer 1963; Powell unpublished data), so that many hours of raiding can still be conducted under cover of darkness. Nocturnal foraging appears to be preferable because during the day kleptoparasitic birds steal prey from both *E. burchellii* (Wrege et al. 2005) and *E. hamatum* (Powell personal observation).

Nomamyrmex

Nomamyrmex esenbeckii is primarily subterranean in its activities, but can conduct surface raids (Rettenmeyer 1963; Schneirla 1971). On BCI and at CP, surface raids were only encountered on heavily compacted trails (Powell & Clark 2004; Powell personal observation), even though more time was spent working off-trail. In all cases, the army ants were coming out of the ground on one side of the trail and on the other side either advanced a short distance along the surface before they attacked prey colonies, or returned underground. On three occasions on BCI, *N. esenbeckii* was seen coming out of the soil at the base of a tree and raiding prey colonies that were nesting at least 5 metres off the ground. These raids lasted less than thirty minutes, even though much brood was captured, and *N. esenbeckii* always returned underground. At CP, surface activity was particularly high, with twenty-one raid columns and two emigrations encountered in two months. We attribute this to the fact that the census was conducted in the wet season and the soil of the trail was close to saturation, thus forcing the army ants to the surface more often. On BCI and at CP, *N. esenbeckii* always moved their surface raid column underground wherever possible during long periods of prey retrieval (Powell & Clark 2004; Powell & Baker personal observation). This was true near the site of surface raids as well as persistent sections of raid column that crossed the trail and were presumably far from the raid front. *N. esenbeckii* raids were encountered at both day and night on BCI and when large prey colonies were successfully attacked, prey retrieval continued day and night, lasting over thirty-five hours on one occasion (Powell & Clark 2004). At CP, raid columns were active at night and in the morning, until the sun broke through continuous clouds cover. Two raid columns were seen after noon at CP, but these were on very overcast days with 100% cloud cover. This suggests that daytime surface activity of *N. esenbeckii* is curtailed in the cerrado by the strong sun and lack of shade.

On BCI, emigrations were also seen during the day and night, which is no surprise as the only complete emigration to be studied lasted over twenty-one hours (Rettenmeyer 1963). All four of the emigration columns that we encountered on BCI were only above ground for two metres or less as they crossed a trail, and workers built partial or complete tunnels over the column with their bodies (Fig. 1). Two *N. esenbeckii* emigrations were encountered at CP at dawn and like surface raid activity at this site, they ceased when the morning sun broke through the clouds. This suggests that in the cerrado, emigrations that are forced to the surface at any point may be suspended during the day. In all six emigrations, *N. esenbeckii* appeared to have synchronised brood cohorts, with emigration traffic having either many callow workers and micro-larvae, or more uniformly coloured workers and a brood of well-developed larvae. Pupae were never seen during any of the emigrations. These observations support the idea that *N. esenbeckii* has cyclic brood production and nomadic and statary phases similar to *Eciton* and *Neivamyrmex*.

Nomamyrmex hartigii, the only other member of this genus, appears to be more subterranean than *N. esenbeckii*. Foraging columns of this species have rarely been seen above ground and some encounters have only occurred because soil covering otherwise hidden raid columns was disturbed (references in Rettenmeyer 1963).

Labidus

There are four described species of *Labidus* for which colonies have been found, and four more species described from males only. *L. praedator* and *Labidus coecus* are the best understood *Labidus* species and will be the focus here. The most notable difference among them, based on current knowledge, is in their raid activity. *L. praedator* conducts large and conspicuous surface raids that have a width and worker density that rivals or surpasses that of *E. burchellii*. *L. praedator* raids are, however, less directed than those of *E. burchellii* and the principal trail is always moved underground, or covered by soil tunnels as the raid front advances. Raids can occur at both night and day, but appeared be larger and more densely populated at night on BCI, particularly during the dry season. One curiosity is that even the largest *L. praedator* raids may be quite short lived, usually lasting from just a few minutes to around an hour before they retreat underground (Rettenmeyer 1963; Powell & Baker personal observation). They may, however, re-emerge from the ground in a nearby area shortly after. This is a strong contrast to the similarly large raids of *E. burchellii* that progress steadily over the forest floor in an approximately straight line for ten hours or more (Franks & Fletcher 1983). Given the strong subterranean tendencies of *L. praedator*, it is likely that they also raid underground, supplementing the often-spectacular surface raids

The timing and duration of *L. praedator* emigrations is hard to assess as they have been seen very rarely and they are always underground or covered by soil tunnels. Given the apparent size of *L. praedator* colonies (Rettenmeyer 1963), however, emigrations are likely to take significantly longer than in *Eciton* and may take more than twenty-four hours. *L. praedator*, and perhaps other *Labidus* species, also appears to have asynchronous brood production, which is not true for other Ecitoninae (Rettenmeyer 1963). We observed three emigrations on BCI, all visible for less than half a metre above the surface, and the emigration column contained larvae, pupae, and bright yellow callow workers, which supports the observations of other authors (Rettenmeyer 1963 and references therein). Seven subterranean bivouacs of *L. praedator* were also located on BCI, and two were lightly excavated to reveal mixed broods of larvae and pupae as well as many callow workers, as seen in emigrations. All of these bivouacs were beneath large trees or logs and were identified by the large amount of loose excavated soil around these structures. Light disturbance of the soil caused thousands of workers and some exceptionally large soldiers to erupt from the ground. Three of these bivouacs were monitored and two persisted for just over two months before emigrating.

L. coecus is more subterranean in its activities than *L. praedator* (Rettenmeyer 1963; Powell personal observation) and its foraging behaviour is therefore harder to observe. However, on BCI and at CP densely populated raid fronts were seen moving through the loose topsoil, but never entirely on the surface, like those of *L. praedator*. Thus, the soil appeared to be alive with army ants over a relatively wide area, but it was difficult to delimit the edge of the raid and therefore its dimensions. Numerous raid columns were also seen at both locations and like those of *L. praedator*, they were covered with soil tunnels so that the ants were only visible when the tunnels were disturbed. Based on the encounters with raid fronts and covered raid columns with prey laden workers, *L. coecus* appears to raid at all times of day. This was also corroborated by monitoring raid activity along soil-covered raid columns coming from two subterranean bivouacs sites at CP. Like the *L. praedator* bivouacs on BCI, both *L. coecus* bivouacs were at the base of large trees and had large amounts of excavated soil around the base. In contrast, however, both *L. coecus* bivouacs at CP were beneath fruiting trees (see later for details). We have never seen an *L. coecus* emigration, but like *L. praedator*, *L. coecus* appears to have asynchronous brood and an irregular emigration pattern (Rettenmeyer 1963). Both *L. coecus* bivouacs at CP were well established when they were discovered and persisted at their respected sites for just under two months.

Neivamyrmex

Neivamyrmex is by far the most diverse genus in the Ecitoninae with 126 described species. Existing data suggests that all species bivouac below ground and are primarily active at night, but that they can vary considerably in strata use during raids and emigrations (Rettenmeyer 1963; Schneirla 1971; Mirenda et al. 1980; LaPolla et al. 2002; Powell & Baker personal observation). Many species have a tendency to conduct raids on the surface at night, and in some cases they can be impressive. For instance, one raid column of *Neivamyrmex gibbatus* that was encountered on BCI was approximately six ants wide, and it terminated in a densely populated raid front of about 2 metres in width. Moreover, the ants moved from side to side in synchronised waves within the front, as is often seen in *L. praedator*. Rettenmeyer (Rettenmeyer 1963) reported similarly wide columns and 'miniature swarms' for *N. gibbatus* on BCI. *Neivamyrmex pilosus* can also conduct impressive surface raids (Rettenmeyer 1963; Schneirla 1971; Powell & Baker personal observation) and we have seen them climb over 5 metres up trees in search of prey. Ultimately, however, all the surface raids of *Neivamyrmex* species witnessed by us and by other authors retreated into the ground, often after just a few minutes after they emerged (Rettenmeyer 1963; Schneirla 1971). Many more species of *Neivamyrmex* are likely to raid only underground or in the interface between the litter and soil, as only short sections of raid column are usually encountered above ground.

Of the five *Neivamyrmex* emigrations we witnessed on BCI, all were at night and only visible at the surface for short distances, and to our knowledge no true surface emigrations have been reported for Neotropical *Neivamyrmex*. Interestingly, however, some *Neivamyrmex* found in the southwestern United States raid and emigrate primarily or entirely above ground at night (Mirenda et al. 1980). Why these *Neivamyrmex* differ in their strata use from those in the

Neotropics is not known, but it may be due to lower predation pressure in the desert grassland habitats where this occurs.

Cheliomyrmex

There are four recognised species of *Cheliomyrmex*, and the genus as a whole appears to be the most subterranean of all the Ecitoninae. Its foraging and emigration patterns are therefore virtually unknown (Rettenmeyer 1963; Gotwald 1995). Indeed, all that can be gleaned from the literature is that *Cheliomyrmex* rarely leaves the ground, and that they cover their columns with soil tunnels when they do, as is common for *Labidus*. Interestingly, *Cheliomyrmex* workers may occasionally erupt from the ground in pursuit of escaping prey (O'Donnell et al. 2005).

ARMY ANT DIET

While the diet of the majority of army ant species remains unknown, existing data suggest that, with a few notable exceptions, New World army ants are primarily or exclusively predators of other ants. Moreover, each army ant appears to specialise on one or two genera of prey species, or, in extreme cases, a single prey species.

Eciton

Within the genus *Eciton* there are some species that are strict ant predators and others that have an expanded diet that includes other social insects and arthropods. A recent quantitative study of *Eciton* diet on BCI showed that *E. dulcium* eats only ponerine ants from the genera *Odontomachus* and *Pachycondyla*, while *E. mexicanum* specialises on ants from the genus *Ectatomma* (Powell & Franks In Press). In addition to these two species, *E. rapax* may also be a specialist predator on poneroid ants (Rettenmeyer et al. 1983). *E. hamatum* also eats primarily ants, but supplements its diet with large social wasps. Interestingly, on BCI *E. hamatum* preys on *Acromyrmex* leaf-cutting ants more than any other ant genus, but in Ecuador they specialise on formicine species in the genera *Gigantiops* and *Camponotus* (Rettenmeyer et al. 1983; Powell & Franks In Press). This suggests that the prey specialisation of some army ants may vary among populations. The last species for which detailed diet data exist is *E. burchellii*. Although this species is famed for its large raids and has a reputation for eating all that gets in its way, 50% of its diet is ant prey (Franks 1983) and on BCI 96% of this ant prey is from the genus *Camponotus* (Powell & Franks In Press). The remaining proportion of the diet of *E. burchellii* comes from social wasps and large litter-dwelling arthropods like cockroaches, spiders and scorpions. This shows that even the *Eciton* species with the most generalised diet still eats more ants than anything else.

Nomamyrmex

Prey records indicate that *N. esenbeckii* is a strict ant specialist, but more importantly this species is the only army ant that is a confirmed predator of *Atta* leaf-cutting ants (Rettenmeyer et al. 1983; Swartz 1998; Sánchez-Peña & Mueller 2002; Powell & Clark 2004). Moreover, *N. esenbeckii* does not target only young and relatively defenceless colonies. They also successfully attack massive mature colonies with large soldiers (Fig. 2), and are capable of capturing tens if not hundreds of thousands of brood items (Powell & Clark 2004). Of equal importance is that this predator-prey interaction has been reported from Mexico, Costa Rica, Panama, and Brazil, and collection records suggest that the geographical range of *N. esenbeckii* perfectly overlays that of *Atta*.

On BCI, we have also seen *N. esenbeckii* raiding, *Acromyrmex* leaf-cutting ants, *Pheidole*, *Camponotus*, and *Odontomachus*, totalling seven observations. However, this compares to nineteen observations of raids on *Atta* (Powell & Clark 2004), so *N. esenbeckii* may specialise on *Atta* more than any other group of ants. At CP, we encountered twenty-one raid columns of *N. esenbeckii* between January and February 2005, and prey was present in the column on fourteen of these occasions. Prey samples included, *Atta*, *Acromyrmex, and Camponotus,* but nine samples were primarily or exclusively of *Atta* prey. In addition, it was possible to track eight of the nine columns containing *Atta* prey to the site of the raid, and 50% were against mature colonies with mounds over five metres. Again, this suggests that *N. esenbeckii* specialises on *Atta* more than on any other group of ants and successfully raids both young and mature colonies. The similarities in *N. esenbeckii* diet and raid activity on BCI and at CP bolsters the hypothesis that *N. esenbeckii* predation is both significant and common throughout *Atta*'s range, particularly given the great geographical separation between the two sites and the dramatic differences in habitat type.

Diet data for *N. hartigii* is extremely scarce, but the few records that exist suggest that this species may specialise more than any other Ecitoninae on termites (references in Rettenmeyer 1963). If this is true, predation on such abundant prey may mean that *N hartigii* is actually a common and widespread species, and that it is just rarely encountered because of an exclusively subterranean lifestyle.

Neivamyrmex

Much like *Eciton, Neivamyrmex* species appear to be primarily or exclusively ant predators, but none have diets as generalised as that of *E. burchellii.* For instance, on BCI we encountered *N. pilosus* with prey nine times, and on all occasions the prey was from the genus *Crematogaster*. On three occasions the prey-laden army ants were encountered as they were coming down a tree, after just raiding an arboreal *Crematogaster* nest. Rettenmeyer et al. (1983) also reported that *N. pilosus* specialises exclusively on *Crematogaster* on BCI. The same authors also report that in Ecudaor, *Neivamyrmex pseudops* and *Neivamyrmex diana* specialise on *Pseudomyrmex*. Like *Crematogaster, Pseudomyrmex* is arboreal, suggesting that these two species of *Neivamyrmex* also climb low vegetation or trees in search of their prey. In total, all six species of *Neivamyrmex* we have encountered on BCI and all four encountered at CP have had only ant prey.

Temperate *Neivamyrmex* also appear to have retained a strong or exclusive specialisation on ants. For instance, ants comprised 85% of the diet of *Neivamyrmex nigrescens* in a desert grasslands community in New Mexico, and over 50% of the prey was from the genus *Pheidole* (Mirenda et al. 1980). In the same community, *Neivamyrmex harrisi* preyed exclusively on *Solenopsis xyloni*. Also in the southwestern Unites States, *Neivamyrmex rugulosus* is known to raid *Pheidole desertorum* and the fungus gardening ant *Trachymyrmex arizonensis* (LaPolla et al. 2002).

Labidus

Labidus species appears to have the most generalised diet of all the Ecitoninae. Although both *L. praedator* and *L. coecus* prey on ants and other arthropods, much like *E. burchellii*, they also have a strong preference for certain plant material (Rettenmeyer 1963). This is best illustrated by our observations at CP on two *L. coecus* colonies. Both bivouacked below fruiting trees for nearly two months and consumed the fallen fruits continuously during that time (fig. 3b). When a new fruit fell to the ground, thousands of workers were recruited to the site and while some stripped the fruit of its flesh, others excavated soil from beneath it. The result, after many days of activity, was that a fruit was completely stripped of its flesh, and the seed was partially or completely buried. The workers appeared incapable of penetrating the seed, so it is assumed that it was unharmed. A number of buried seeds were marked, and while other animals dug some up, others stayed buried for at least one month after the army ants departed. This suggests that in the cerrado, *L. coecus* may help reduce seed predation and fungal infection, and help increase seed germination, as has been suggested for fungus gardening ants (Leal & Oliveira 1998).

It is important to note, however, that while the fruits were being consumed, both colonies regularly sent out raids at both day and night. Prey samples taken near the bivouac contained a lot of ant brood and pieces of large arthropods, including spiders, and both adult and juvenile Lepidoptera (Fig. 3a). This prey is consistent with the diet observations made by Rettenmeyer on BCI, and similar to prey records for *L. praedator*. Like other authors (Rettenmeyer 1963; Schneirla 1971), we have seen *L. praedator* take a mixture of ants and other arthropods, which includes a lot of spiders, scorpions, cockroaches, and isopods. Based on these general observations, *L. praedator*, *L. coecus* and *E. burchellii* appear to have considerable overlap in their diet. This is interesting because they often occur in the same habitat, as on BCI. It is likely, however, that there is some partitioning of prey resources among species, based on prey size or type. Quantitative studies of the diet of these three species would be a valuable focus for future work, both within sites and among site. It would be particularly interesting to know if the diet of a focal species expands in any way when one or both of the other species is absent.

Cheliomyrmex

Diet data for *Cheliomyrmex* is scarce. However, *Cheliomyrmex andicola* has been seen killing and cutting flesh from a snake and a giant earthworm (O'Donnell et al. 2005). This suggests that members of this genus may be the only Ecitoninae to attack and eat relatively large, soft-bodied prey. Indeed, the only other Ecitoninae that kill small vertebrates are *E. burchellii* and *L. praedator*, but this is exceptionally rare and they are never consumed because these army ants appear to be incapable of removing portions of flesh (Rettenmeyer 1963; Powell personal observation). Moreover, the diet of *C. andicola* appears to be remarkably similar to members of the Old World army ant genus *Dorylus*, and these taxa also share unusual mandible morphology for cutting flesh (O'Donnell et al. 2005). As suggested by O'Donnell et al (2005), this may be important for understating the relationship between diet and the evolution of the army ant group-foraging strategy. However, the interpretation differs depending on the hypothesised phylogenetic relationships among the Ecitoninae and their relationships to the Old World army ant genera. If *Cheliomyrmex* is the sister taxon of the other Ecitoninae genera and most closely related to *Dorylus* in the Old World (Brady 2003), then the army ant foraging strategy may be an adaptation to preying on large prey (O'Donnell et al. 2005). However, if *Neivamyrmex* is the sister taxon to all other Ecitoninae and most closely related to the *Aenictus* in the Old world (Brady & Ward 2005), which are ant specialists (Gotwald 1995), then army ant group-foraging may be an adaptation to preying on other ants. This would then suggest that the similar diet of *Cheliomyrmex* and *Dorylus*, and the associated cutting mandibles, has evolved convergent in the New World and Old World.

IMPACT OF ARMY ANT RAIDS

Data on the impact of army ant raids at the level of the prey colony, population, or community are scarce. However, the few quantitative studies that have been conducted suggest that army ant predation is significant at all levels.

At the level of the colony, general observations suggest that army ant raids usually crop prey colonies, removing a significant proportion of brood, but not killing the colony outright (Rettenmeyer et al. 1983). This may be a product of the evacuation strategy adopted by most ants when under attack, whereby every adult grabs as many brood items as they can carry and seeks refuge outside the nest. The army ants then take the remaining brood with little resistance, and the workers and queen of the prey colony return to raise a new brood when the army ants have gone.

For example, this strategy is used by fungus gardening ant *T. arizonensis* when raided by *N. rugulosus*, and although it results in the loss of around 75% of a colony's brood, the adults are not injured and return to the nest once the army ant have moved on (LaPolla et al. 2002). In contrast, prey species with very large colonies may actively defend against army ant attack, and this can result in a greater range of possible outcomes to a raid. This strategy is perhaps best illustrated by *Atta* leaf-cutting ants, which vigorously defend themselves against raids by *N. esenbeckii* (Fig. 2; Powell & Clark 2004). While mature *Atta* colonies can successfully repel the army ants, or limit the extent of the raid, they can also suffer massive brood loss and adult mortality, and in some cases be killed outright (Powell & Clark 2004).

We have also seen the active defence strategy used by the aggressive and highly polymorphic *Camponotus sericeiventris* when under attack by *E. burchellii* on BCI. This suggests that active defence may be a common strategy for aggressive, large-colony species. However, it may drive an arms race between predator and prey, with the impact of raids conditionally determined by the fine balance between attack and active defence strategies. Thus, if a particular prey species defends itself, the army ants may be selected to take all they can when a raid is successful, instead of quickly cropping the colony's brood, to get the maximum payoff from a large and costly raid. Certainly, it seems that *N. esenbeckii* will empty an *Atta* colony of brood over many hours if they get the opportunity (Powell & Clark 2004). Whereas *N. esenbeckii* raids on species that abandon the nest are quick and result in little adult mortality on either side (Powell & Baker personal observation).

If army ant raids are significant at the level of the prey colony, is it then important to know if this translates into significant population-level effects for particular prey species and an important impact on the ant community as a whole. To address these topics, it is necessary to understand the frequency of army ant raids and if their effects are lasting. While data of this kind are scarce, there is good initial evidence that army ant raids can be both frequent and have long lasting effects.

Kaspari and O'Donnell (2003) estimated that army ant raids might occur at a frequency of 1.22 raids per m^2 per day. This number sums for all of the army ants within a community, so it means is that each m^2 has an average of more than one raid of some army ant species passing through it each day. Due to the specificity of the diet of most army ants, this does not necessarily mean that each m^2 is raided each day, but this quantitative estimate does provide good evidence that army ant raids should be considered common events. The frequency with which areas are raided by one particular army ant species may also be high. For instance, Franks and Bossert (1983) showed with simulations based on detailed movement data that approximately 50% of BCI is raided within an eight month period by *E. burchellii*. While this raid frequency may seem relatively low, it is important to remember that it takes approximately 2-3 months from egg to adult ant in most species, so colonies may barely recover normal worker production before they are raided again. Although limited, these studies suggest that army ant raids are common, but how long do the effects last and what are the consequences?

Army ant raids may have two lasting effects on ant populations and communities. First, they may reduce the number and size of established colonies, altering the population density of particular species and the community composition. Indeed, Franks and Bossert (1983) showed that *E. burchellii* raids maintain ant diversity in the leaf litter by selectively removing certain species, allowing numerous others to invade the open patches. In essence, *E. burchellii* raids initiate a process of succession in the litter ant community, with diversity increasing after a raid and then decreasing over a number of months as the more competitively dominant species take over. Second, army ants may reduce the reproductive output of established colonies, and therefore the number of new colonies that are founded, by taking the sexual broods of prey species. While there is no quantitative data to support this hypothesis, army ants routinely take sexual brood from their prey when it is present in the nest (Powell personal observation).

CONCLUSIONS

For ant biologists working in the Neotropics, there are three key aspects of army ant biology that should be remembered. First, most tropical systems are likely to have a diverse and active army ant community, but most species are partly or exclusively subterranean and nocturnal. The diurnal surface-active species are highly atypical for the group. This means that a rich army ant community is always present, but rarely visible.

Second, most New World army ants are primarily or exclusively specialist predators of other ants, although the exact diet of most species is not known. When conducting field studies that may be sensitive to the presence or absence of natural predators, a myrmecologist should therefore ask the following question: does my study species have an army ant predator that attacks beneath my feet during the day and while I sleep at night?

Third, most New World army ants are likely to have a significant impact on the particular species that they raid. This is likely to translate into significant regulatory pressure at the population level and on the ant community as a whole.

For potential students of army ant biology, there is a great deal to do. While existing data suggests that the Ecitoninae are likely to be one of the most ecologically important groups of big predators in the Neotropics, the biology of most species is completely unknown. One of the main goals for future army ant research is therefore to collect quantitative data on the behaviour, diet, and impact of many more species. This can then be used as a foundation for more detailed quantitative and experimental studies of the ecological role of this remarkable group of ants.

REFERENCES

Brady, S. G. 2003 Evolution of the army ant syndrome: The origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 6575-6579.

Brady, S. G. & Ward, P. S. 2005 Morphological phylogeny of army ants and other dorylomorphs (Hymenoptera: Formicidae). *Systematic Entomology* **30**, 593-618.

Britton, N. F., Partridge, L. W. & Franks, N. R. 1996 A mathematical model for the population dynamics of army ants. *Bull. Math. Biol.* **58**, 471-492.

Franks, N. R. 1982 A new method for censusing animal populations: the number of *Eciton burchelli* army ant colonies on Barro Colorado Island, Panama. *Oecologia* **52**, 266-268.

Franks, N. R. 1983 Ecology and population regulation in the army ant *Eciton burchelli*. In *The ecology of a tropical forest: Seasonal rhythms and long-term changes* (ed. E. G. Leigh, Jr., A. S. Rand & D. M. Windsor), pp. 389-395. Oxford: Oxford University Press.

Franks, N. R. 1985 Reproduction, foraging efficiency and worker polymorphism in army ants. In *Experimental behavioral ecology and sociobiology: in memoriam Karl von Frisch,1886-1982*, vol. 31 (ed. B.Holldobler & M.Lindauer), pp. 91-107. Sunderland, Mass.: Sinauer Associates.

Franks, N. R. & Bossert, W. H. 1983 The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In *Tropical rain forest: ecology and management. Special Publication of the British Ecological Society No. 2* (ed. S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 151-163. Oxford. xii + 498 p.: Blackwell Scientific Publications.

Franks, N. R. & Fletcher, C. R. 1983 Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado, Panama. *Behav. Ecol. Sociobiol.* **12**, 261-270.

Gotwald, W. H., Jr. 1995 *Army ants: the biology of social predation*. The Cornell series in arthropod biology. Ithaca, New York: Cornell University Press.

Kaspari, M. 1996 Litter ant patchiness at the 1-m(2) scale: Disturbance dynamics in three Neotropical forests. *Oecologia* **107**, 265-273.

Kaspari, M. & O'Donnell, S. 2003 High rates of army ant raids in the Neotropics and implications for ant colony and community structure. *Evol. Ecol. Res.* **5**, 933-939.

LaPolla, J. S., Mueller, U. G., Seid, M. & Cover, S. P. 2002 Predation by the army ant *Neivamyrmex rugulosus* on the fungus- growing ant *Trachymyrmex arizonensis*. *Insect. Soc.* **49**, 251-256.

Leal, I. R. & Oliveira, P. S. 1998 Interactions between fungus-growing ants (Attini), fruits and seeds in cerrado vegetation in southeast Brazil. *Biotropica* **30**, 170-178.

Mirenda, J. T., Eakins, D. G., Gravelle, K. & Topoff, H. 1980 Predatory behavior and prey selection by army ants in a desert-grassland habitat. *Behav. Ecol. Sociobiol.* **7**, 119-127.

O'Donnell, S., Kaspari, M. & Lattke, J. 2005 Extraordinary predation by the Neotropical army ant *Cheliomyrmex andicola*: Implications for the evolution of the army ant syndrome. *Biotropica* **37**, 706–709.

Oliveira-Filho, A. T. & Ratter, J. A. 2002 Vegetation physiognomies and woody flora of the cerrado biome. In *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (ed. P. S. Oliveira & R. J. Marquis), pp. 91-120. New York: Columbia University Press.

Powell, S. & Clark, E. 2004 Combat between large derived societies: A subterranean army ant established as a predator of mature leaf-cutting ant colonies. *Insect. Soc.* **51**, 342 - 351.

Powell, S. & Franks, N. R. In Press Ecology and the evolution of worker morphological diversity: A comparative analysis with *Eciton* army ants. *Functional Ecology.*

Rettenmeyer, C. W. 1963 Behavioral studies of army ants. *Univ. Kans. Sci. Bull.* **44**, 281-465.

Rettenmeyer, C. W., Chadab-Crepet, R., Naumann, M. G. & Morales, L. 1983 Comparative foraging by neotropical army ants. In *Social insects in the tropics. Volume 2* (ed. P. Jaisson), pp. 59-73. Paris. 252 p.: Université Paris-Nord.

Sánchez-Peña, S. R. & Mueller, U. G. 2002 A nocturnal raid of *Nomamyrmex* army ants on *Atta* leaf-cutting ants in Tamaulipas, Mexico. *Southwestern Entomologist* **27**, 221-223.

Schneirla, T. C. 1971 *Army ants. A study in social organization. (Edited by H. R. Topoff.)*. San Francisco: W. H. Freeman & Co.

Swartz, M. B. 1998 Predation on an *Atta cephalotes* colony by an army ant, *Nomamyrmex esenbeckii*. *Biotropica* **30**, 682-684.

Teles da Silva, M. 1977 Behaviour of the army ant *Eciton burchelli* Westwood (Hymenoptera: Formicidae) in the Belem region. I. nomadic-statary cycles. *Anim. Behav.* **25**, 910-923.

Watkins, J. F., II. 1976 *The identification and distribution of New World army ants (Dorylinae: Formicidae)*. Waco, Texas: Baylor University Press.

Wrege, P. H., Wikelski, M., Mandel, J. T., Rassweiler, T. & Couzin, I. D. 2005 Ant birds parasitize foraging army ants. *Ecology* **86**, 555-559.

	E. mexicanum	***E. dulcium***	***E. vagans***	***E. hamatum***	***E. burchellii***
Period of raid activity	Nocturnal (22)	Nocturnal (69)	Nocturnal (6)	Diurnal (>100)	Diurnal (>100)
Raid stratum	Surface*	Surface*	Surface*	Surface	Surface
Emigration start time	7-10 pm (7)	7-10 pm (16)	7-10 pm (3)	4-10 pm (>100)	4-10 pm (>100)
Emigration stratum	Surface*	Surface*	Surface*	Surface	Surface
Bivouac location	Underground (8)	Protected / Underground (22)	Protected / Underground (4)	Exposed / Protected (>100)	Exposed / Protected (>100)

Table 1. Colony-level behaviour of five *Eciton* species on Barro Colorado Island, Panama. Period of raid activity defines the period when most raiding is conducted. However, nocturnal raids may start just before dusk and end in the early morning, while diurnal raids may start just before dawn and end in the early evening. Bracketed numbers indicate the number of observations. The asterisk indicates that the surface emigration and raid columns of these species can go underground for a short distance near the bivouac when it is partially or entirely underground. In all cases where this was seen, the subterranean or well-protected bivouac was located within 10m of the hole where the army ant column went underground. A protected bivouac location is one where the bivouac is hidden in a log or tree cavity that is above ground or partially buried.

Figure 1. An emigration column of the army ant *Nomamyrmex esenbeckii*. The emigration traffic is covered by a partially complete tunnel made of army ant workers that are linked together. Notice that millipedes, which is an obligate associates of the colony, move in the emigration traffic and are untouched by the army ants.

Figure 2. A raid by the army ant *Nomamyrmex esenbeckii* against a mature colony of the leaf-cutting ant *Atta laevigata*. As reported by Powell and Clark (2004), the leaf-cutting ants recruited large numbers of soldiers, which have massive heart-shaped heads, to block the advance of the army ants. This creates a distinct 'frontline' to the interaction, where the largest fighters from both sides engage each other in combat.

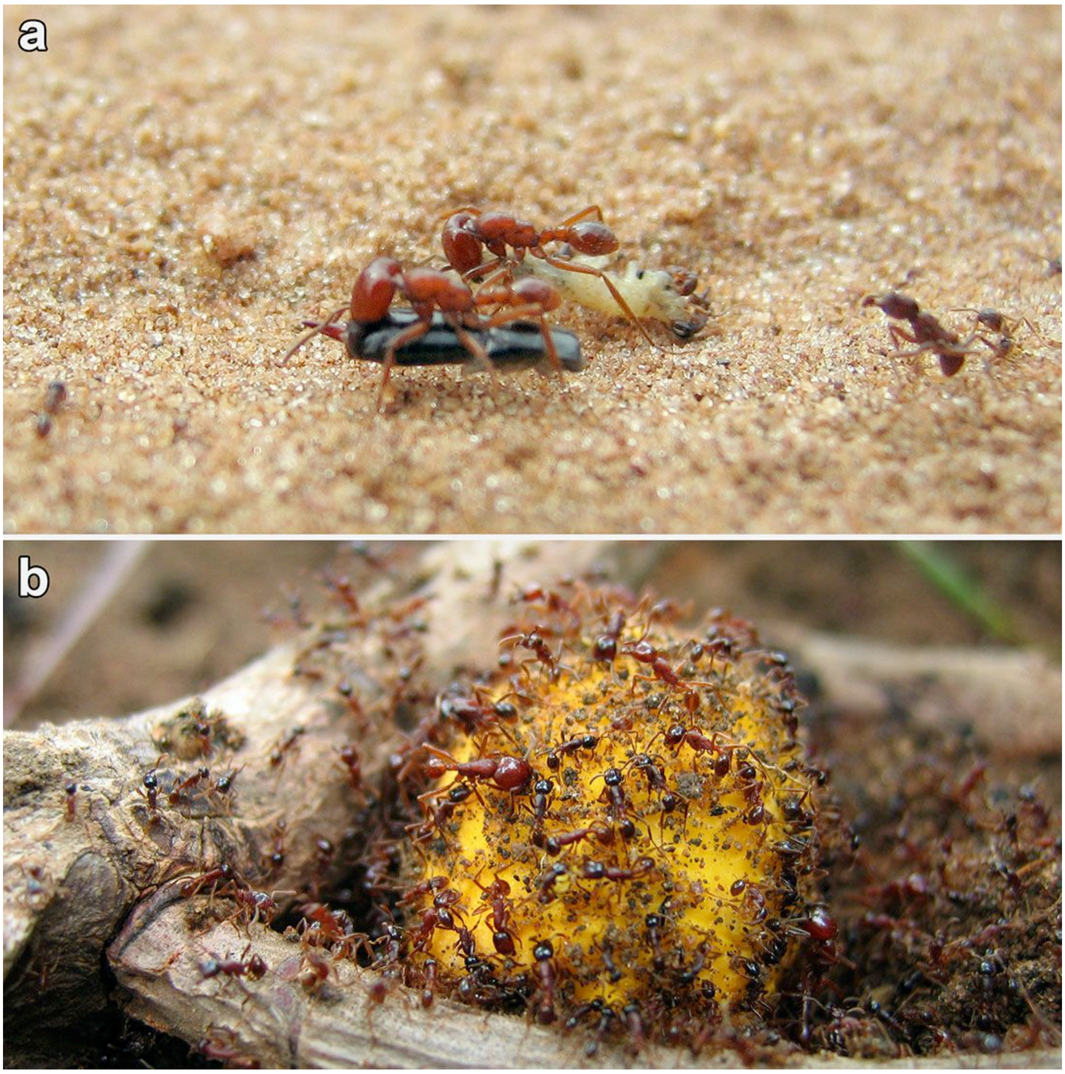

Figure 3. The varied diet of the army ant *Labidus coecus*. **a**, Large workers transport arthropod prey back to the nest situated below a fruiting Pequi tree *(Caryocar brasiliense)*. **b**, Workers at the nest site consume fruit that has fallen from the tree, partially burying it in the process.