

Supplemental Information S1 - Supplementary Text

Species-level predation network uncovers high prey specificity in a Neotropical army ant community

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Review of army ant diets

By searching for army ant raids on the ground, this study focused on surface-raiding army ants and therefore does not represent the entire army ant community at La Selva. There are around 48 army ant species known for Costa Rica, a large part of which are known to occur in our study site (Longino 2010, Guénard et al. 2017). While we covered all *Eciton* and *Nomamyrmex* species, our study did only include few species of the speciose genus *Neivamyrmex*, and we were not able to retrieve prey from *Labidus*. The last comprehensive review about army ant diets was published more than 20 years ago (Gotwald Jr, 1995). We thus decided to present a brief literature review about Neotropical army ant diets, integrating studies published in the last three decades and the results obtained in the present study. We then also briefly review dietary preferences of Old World army ants. We restrict our literature review to the classical army ants in the subfamily Dorylinae (formerly the subfamilies Aenictinae, Dorylinae, and Ecitoninae; see Gotwald Jr, 1995 and Kronauer, 2009 for additional cases of army ant-like behavior in ants).

Neivamyrmex prey

Neivamyrmex is, after the Old World genus *Aenictus*, the most speciose doryline genus, consisting of 130 described species in the Neotropics (Borowiec, 2016). We were able to find two species of *Neivamyrmex* on a regular basis, *Ne. gibbatus* and *Ne. pilosus*. Both species are poorly studied. There are descriptions of *Ne. pilosus* prey by Rettenmeyer et al. (Rettenmeyer et al. 1983) who reported that this species raided ants of the genus *Crematogaster* in Panama. Indeed, *Crematogaster* also made up a large proportion of *Ne. pilosus* prey at La Selva. We discovered that *Ne. pilosus* additionally preyed on several species of *Tapinoma* and *Azteca*, the latter of which are known for their arboreal habits and close association with *Cecropia* trees (Longino, 2007). All prey species of *Ne. pilosus* have arboreal nesting habits – so raiding activity is expected to focus on arboreal zones. Notably, *Ne. pilosus* showed the highest level of prey specialization among army ants at La Selva, i.e. it had the most exclusive prey spectrum within the studied army ant community.

For the other common *Neivamyrmex* species at La Selva, *Ne. gibbatus*, Rettenmeyer provided a short commentary mentioning that its prey consisted of ant brood (Rettenmeyer, 1963). We

found quite diverse ant prey – 27 species - among *Ne. gibbatus* booty and made several observations on their raiding behavior. They seem to be rather generalist army ants (i.e. have a large prey diversity) and take a diversity of ants from the leaf litter and lower vegetation, such as fungus growers in the genera *Apterostigma* (Fig. 1) and *Cyphomyrmex*, species of *Pheidole*, *Nylanderia*, *Tapinoma* as well as *Aphaenogaster araneoides*.



Fig. 1 *Neivamyrmex gibbatus* raiding a nest of the fungus-grower *Apterostigma collare*.

We also detected two raids of *Ne. asper*. Since its description by Borgmeier (1955), nobody has published on the biology of *Ne. asper*, and no dietary information was previously known. *Neivamyrmex asper* preyed upon ants of the genera *Pheidole*, *Strumigenys*, and *Solenopsis*. The latter genus stands out, because it was not detected among the prey of other army ants, except of a single raid of *Ne. gibbatus*. This is surprising because at least 12 species of *Solenopsis* occur at La Selva – some of them at relatively high abundances (Longino, Coddington, & Colwell, 2002; see also discussion in main text).

Several studies about diets in other *Neivamyrmex* species exist. Miranda et al. (1980) studied the raiding behavior and quantitatively assessed the prey of two sympatric species in North America, *Ne. nigrescens* and *Ne. harrisi*. *Neivamyrmex nigrescens* preys primarily on species of *Pheidole*, while *Ne. harrisi* preys on *Solenopsis* ants. Other specialized *Neivamyrmex* species are *Ne. compressinodes* which preys primarily on *Wasmannia auropunctata* (Le Breton et al. 2007), and *Ne. rugosus* which is a specialized predator of *Trachymyrmex arizonensis* (LaPolla et al. 2002). Although *Neivamyrmex* remains a poorly studied ant genus, these studies, together with the results presented in the present study, indicate that many if not all *Neivamyrmex* species are specialist ant predators with little food niche overlap among sympatric species (see also Rettenmeyer et al., 1983).

Nomamyrmex prey

Nomamyrmex is a common and widespread genus in Central and South America and forms the sister clade to *Eciton* (Borowiec 2019; Brady et al. 2014). There are two described species in this genus, *No. esenbeckii* and *No. hartigii*, both of which were detected in this study. Little is known about *No. hartigii*. This species seems to have a subterranean lifestyle and is thus hard to find (Borgmeier, 1955). According to Rettenmeyer there are reports that this species preys on termites (Rettenmeyer, 1963). We found it only once carrying *Pheidole* brood.

The prey of *No. esenbeckii* is better known. This species is the only army ant capable of raiding the mature colonies of *Atta* leafcutter ants (Powell & Clark, 2004; Sánchez-Peña & Mueller, 2002; Souza & Moura, 2008; Swartz, 1998). There are also reports and video coverage of such raids from La Selva (Longino, 2007; Bruce 2017, pers. comm.), but none of the ten raids we encountered contained *Atta* brood. Instead, *No. esenbeckii* booty often consisted of *Sericomyrmex amabilis*, another common fungus farming ant with much smaller colony sizes than *Atta* (Ješovnik & Schultz, 2017). In addition, *Pheidole* was found regularly and in one instance also *Acromyrmex*, *Camponotus* and *Pachycondyla*. Our prey collection design, which was blind to the raided nest site, suggests that *Atta* might not be the most common prey of *No. esenbeckii*, at least at La Selva (10 spatio-temporally independent collection events, 149 collected prey items, 22 identified prey items). While raids on *Atta* nests are certainly the most conspicuous raiding events of this species, our prey collection questions if *Atta* is the main prey species of *No. esenbeckii*. We believe that further research collecting prey items in a standardized way from returning raiding columns (blind to the raided nest) is necessary to systematically identify prey specificity and dietary niche preferences of *No. esenbeckii*, and to evaluate the dependency on *Atta* species (which might also geographically differ). We observed twice that raiding columns went up a tree (*Camponotus* sp. 1: nest-site approx. 2 m above ground; *Acromyrmex octospinosus*: nest-site >10m above ground). Arboreal hunting in *No. esenbeckii* on *Camponotus* has been described once before, and those authors also recorded raids on *Odontomachus* and termites (Souza & Moura, 2008). Taken together, *No. esenbeckii* seems to have a rather broad prey spectrum, probably with a preference for fungus farming ants.



Fig. 11 *Nomamyrmex esenbeckii* worker carrying an *Acromyrmex octospinosus* pupa.

***Eciton* prey**

Eciton is perhaps the best studied genus of Neotropical army ants (Borowiec, 2016). At La Selva, we found six sympatric *Eciton* species, and for most of them we compiled a good dataset on their diet. Our results show that all species are specialized ant predators and that food niche overlap is very limited.

The most conspicuous species of this genus is *E. burchellii*. Due to their wide distribution range and large swarm raids, this species has received the most scientific attention among army ants (Borowiec, 2016; Gotwald Jr, 1995; Rettenmeyer, 1963). Its life history is very well known, and there are several studies about its diet (e.g., Gotwald Jr, 1995; Scott Powell & Franks, 2006a; Rettenmeyer, 1963; Sazima, 2017). For instance, Franks investigated its prey biomass intake and the identity of many prey items (Franks, 1980). Our results show that *E. burchellii* is a specialist predator of *Camponotus* ants, which is in accordance with literature records (Franks, 1980; Powell & Baker, 2008; Scott Powell & Franks, 2006b). This species is also a generalist predator of various arthropods, which has been more thoroughly investigated than their ant prey. A few records even reported vertebrate prey (Sazima, 2017). *Eciton burchellii* had the highest proportion of non-ant prey in our study (see below) supporting the idea that the diet of classical swarm raiding species includes a higher proportion of non-ant invertebrate prey in Neotropical army ants (Gotwald Jr., 1995). Kaspari *et al.* (2011) studied forest floor patches and assessed their arthropod composition before and after raids of the swarm-raiding army ant species *E. burchellii* and *Labidus praedator*. Surprisingly, *E. burchellii* had little impact on leaf litter arthropod communities compared to *L. praedator*. It was suggested that *E. burchellii* is less effective in leaf litter predation, allowing prey to escape. Our study suggests an alternative explanation for this result; despite the fact that *E. burchellii* had the largest amount of non-ant prey of all studied species, most of its prey still consisted of other ants (80% of incidence data; 93% of all collected prey items; Supporting information S2), primarily of arboreal *Camponotus* species. A study by Vieira & Höfer (1994) analyzed the prey spectrum of *E. burchellii* at La Selva, but their study focused mostly on spider species and ants were not further identified. They concluded that ants make up 23% (median) of prey in two hours of sampling. Various explanations could conceivably explain the different proportions of ant prey in *E. burchellii* diets detected in our study and the study by Viera & Höfer - for instance the different sampling methods or seasonal differences.

Another rather well-known species is *E. hamatum*, a common diurnal column raider. Temporary prey caches are common along raiding columns in this species (Fig. 3). Powell *et al.* (2011) determined the biomass prey intake of *E. hamatum*, which was similar to that reported for *E. burchellii* (Franks, 1980). The most common prey species in that study was *Acromyrmex octospinosus*, which was encountered in 25% of the observed raids and made up 23% of the total prey biomass (range of seven different colonies 9% - 36%; see also Rettenmeyer *et al.*, 1983). Being present in 24% of prey collections at our study site, we confirmed that *Acromyrmex* is a very common prey taken by *E. hamatum*.



Fig. 3 Prey cache of *Eciton hamatum* filled with brood of *Pheidole*.

The biology of the remaining *Eciton* species is poorly known (Powell & Baker, 2008; Rettenmeyer *et al.*, 1983) - with one notable exception: a detailed prey assessment of an *Eciton* community was published by Powell & Franks in 2006. They sampled prey of the following four *Eciton* species on Barro Colorado Island, Panama: *E. burchellii*, *E. hamatum*, *E. dulcium* and *E. mexicanum*. This study focused on the most common prey genera and lacked species-level identifications. Our results match the reported prey preferences for all four species remarkably well (Table 1). However, some notable differences were detected: *Pheidole* is lacking as common prey item in Panama, while in our study it is the most common prey for *E. mexicanum* and *E. hamatum*. While *Ectatomma* was also found as prey of *E. mexicanum* in our study (~4% of raids), it was far less common than in Panama (68%). We cannot disentangle whether differences in dietary preferences between these studies can be attributed to regional differences in prey preferences, prey species abundance or to different sampling techniques. It would certainly be a valuable avenue for future research to investigate how flexible interaction links in army ant-prey networks are across tropical regions.

Tab. 1 Dietary preferences of army ants in Panama and Costa Rica. Shown are the three most common prey genera. Note that our percentages are calculated with relative incidence, while Powell & Franks used relative abundances. Sample size is given as total prey number. *The genera *Mayaponera* and *Neoponera* were known as *Pachycondyla* until the last taxonomic revision (Schmidt & Shattuck, 2014) and might be included in *Pachycondyla* in the study of Powell & Franks (2006b).

Army ant species	Panama (Powell & Franks 2006)	Costa Rica (this study)
<i>Eciton burchellii</i>	96% <i>Camponotus</i> N = 380	48% <i>Camponotus</i> 20% Non-Ant 13% <i>Pheidole</i> N = 467
<i>Eciton hamatum</i>	23% <i>Acromyrmex</i> N = 38,872	35% <i>Pheidole</i> 24% <i>Acromyrmex</i> 16% <i>Trachymyrmex</i> N = 530
<i>Eciton mexicanum</i>	68% <i>Ectatomma</i> 18% <i>Pachycondyla</i> * N = 100	19% <i>Pheidole</i> 16% <i>Mayaponera</i> * 12% <i>Pachycondyla</i> * N = 436
<i>Eciton dulcium</i>	53% <i>Odontomachus</i> 47% <i>Pachycondyla</i> * N = 450	58% <i>Pachycondyla</i> * 27% <i>Odontomachus</i> 8% <i>Neoponera</i> * N = 162
<i>Eciton vagans</i>	not available	28% <i>Odontomachus</i> 23% <i>Pheidole</i> 11% <i>Aphaenogaster</i> N=782
<i>Eciton lucanoides</i>	not available	26% <i>Camponotus</i> 19% <i>Trachymyrmex</i> 11% <i>Nylanderia</i> N=126

Eciton lucanoides is rare at La Selva, and nothing was previously known about its prey spectrum. Rettenmeyer et al. pointed out that its prey spectrum is most similar to that of *E. hamatum* (Rettenmeyer et al., 1983). We cannot confirm this. *Eciton lucanoides* had a surprisingly high diversity of prey species, most notably of the genera *Camponotus*, *Trachymyrmex* and *Nylanderia*. However, similar to *E. hamatum*, the species was also found preying on social wasps.

We frequently detected raids of *E. vagans* in the study area. Its prey habits were poorly described. Rettenmeyer et al. described that *E. vagans* takes *Odontomachus* and other ponerines as prey (Rettenmeyer et al., 1983). We can confirm that *Odontomachus* was common and showed additionally that it raided *Pheidole* and *Aphaenogaster* among many others. *Eciton vagans* seemed to prefer arboreal nesting species and it was one of the most generalist army ant species, indicated by a low species-level specialization within the predator-prey network.

With six species, our study covered half of the hitherto described *Eciton* species (Borowiec, 2016). Since most of the Neotropical army ant research has been done in Central America, studies on *Eciton* species occurring exclusively in South America are rare to non-existent (Gotwald Jr, 1995). Few descriptions from older literature are available (Borgmeier, 1995; Rettenmeyer et al., 1983). Probably the best records are available for the South American species *E. rapax*, which has been shown to prey primarily on other ants (Burton & Franks, 1985; Kazan, 1972), and field observations suggests that they additionally take bumblebees and wasps on occasions (Kazan, 1972; Ramírez & Cameron, 2003). Remarkably, Kazan even identified prey to the species level. He reported that prey consisted mostly of ponerine ants (genera: *Odontomachus*, *Neoponera*, *Pachycondyla*), formicine ants (genera: *Camponotus*, *Gigantiops*) and dolichoderine ants (genus: *Dolichoderus*) (Kazan, 1972). Notably, this food spectrum differs considerably from the *Eciton* species studied at La Selva; for example, none of the studied army ant species raids on both *Odontomachus* and *Camponotus*.

***Labidus* prey**

The genus *Labidus* consists of seven described species (Borowiec, 2016), two of which are known to occur at La Selva. Both species, *L. praedator* and *L. coecus*, are probably common, but exhibit a largely underground lifestyle which makes them difficult to detect without using underground baits. Because of high colony densities these species probably play an important ecological role, which, however, remains to be studied in more detail (Kaspari & O'Donnell, 2003; O'Donnell et al., 2004). *Labidus coecus* has a subterranean lifestyle and is frequently reported to not just eat other arthropods, but also plant parts such as fruit and seeds (e.g. Powell, 2009; Longino, 2010). In contrast, *L. praedator* and *L. spinoides* are also known to exhibit conspicuous above-ground swarm raids similar to those of *E. burchellii* (Borgmeier, 1955; Hoenle, 2018, pers. obs.). Their diet is described to be more generalistic, taking a variety of arthropods and infrequently also plant parts in *L. praedator* (Borgmeier, 1955; Viera & Höfer, 1994; Monteiro et al., 2008). Kaspari et al. (2011) reported a significant reduction in abundance of leaf-litter arthropods after a *L. praedator* raid has passed, and Viera & Höfer (1994) quantified their prey items at La Selva, which contained nearly no ants. There are also reports of *L. praedator* raiding ants of the genera *Camponotus*, *Pheidole* and *Solenopsis* in Paraguay (Fowler, 1979). The degree of dietary specialization in *Labidus* remains poorly quantified, but

it seems that they possess a diet niche with much fewer ant prey species than other Neotropical army ants.

***Cheliomyrmex* prey**

Species of the genus *Cheliomyrmex* have been rarely observed, which might be attributed to their subterranean lifestyle. There is only one study describing two occasions of food retrieval by *Cheliomyrmex andicola*. This report described that *C. andicola* workers fed on a snake cadaver and actively killed a giant earthworm (O'Donnell et al. 2005).

Old World army ants

As described above, most Neotropical army ants are specialized ant predators – but what about the army ants of the Old World? In the following literature review, we will briefly characterize the diets of Old World army ants.

The best studied army ant taxon besides *Eciton* is the genus *Dorylus*. Members of this genus are distributed in the Afro-tropics, with some species expanding into Southeast Asia (Borowiec, 2016). Most species are subterranean, but a few species (formerly the subgenus *Anomma*; Kronauer et al., 2007) are known to form large, conspicuous above-ground raids. During these raids arthropod prey and even occasionally vertebrates are overwhelmed (Gotwald Jr, 1995). There are many accounts of surface raiding *Dorylus*, and all seem to indicate that ants as prey are rather uncommon (Gotwald Jr, 1995; C. Schöning, Njagi, & Kinuthia, 2007). Interestingly, another abundant group of social insects, the termites, seem to be common prey at least for some subterranean *Dorylus* species (Berghoff et al., 2003; Caspar Schöning & Moffett, 2007). Despite a broad food spectrum in the generalist surface raiders, Schöning et al. (2007) discussed dietary differences in two *Dorylus* species, in that *D. molestus* preyed commonly on earthworms, while *D. wilverthi* did not. The authors speculated that this might be attributed to different swarm-raiding behaviors (*D. molestus* shows more digging behavior than *D. wilverthi* during raids).

The genus *Aenictus* is with 183 described species the most speciose genus of all army ants, and in its diversity somewhat the Old World equivalent to the New World genus *Neivamyrmex* (Borowiec, 2016). *Aenictus* species are small and monomorphic. As is the case for most army ants, little is known about the diets of different *Aenictus* species. Several studies indicate that they are also predominantly if not exclusively ant specialists. Rościszewski and Maschwitz (1994) studied sympatric *Aenictus* in the Malay Pasoh forest reserve, and concluded that they differed in their food preference due to differences in spatial niche and different body size preferences of prey ants. Hirosawa et al. (2000) systematically collected prey items of *A. laeviceps* and *A. gracilis* near Mt. Kinabalu, Borneo, and identified them to morphospecies level. They confirmed that there is only little prey overlap between the two species. Similarly, Hashimoto & Yamane (2014) collected prey items from four sympatric *Aenictus* on Borneo, Lambir Hills NP. Species differed in their foraging stratum and preferred prey of different size, resulting in little food niche overlap among the four *Aenictus* species. While the data on *Dorylus* diets are too sparse to conclude anything with certainty, the prey specialization of *Aenictus* ants is very similar compared to the results of the present study (niche differentiation in diets and stratum preferences).

Conclusion

We conclude that the diets of most army ant species are unknown, and for those for which we found information the descriptions are often of descriptive nature and systematic assessment of diets are rare. Ants seem to be the main prey target of army ants. In fact, ant predation might represent the ancestral condition in the entire subfamily Dorylinae (Borowiec, 2016; e.g., Naoto & Dobata, 2018). We hope our study will inspire future research to uncover more information about the ecology of this fascinating group of ants.

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