



Socioecology and Evolutionary Neurobiology of Predatory Ants

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Diet and social complexity are hypothesized to drive the evolution of the neuroarchitecture of the brain, but the relative impacts of foraging ecology and social organization have not been fully disentangled. Predatory ant species encompass generalists as well as specialists on remarkably narrow ranges of arthropod prey, and vary in strategy from solitary hunting to group raiding. Dietary differences and variation in individual or group predation appear to be correlated with the use of vision for navigation by solitary huntresses, the predominance of chemical signaling to organize group predation, and the structure, biomechanics, and sensorimotor control of the mandibles, and likely gustatory sensilla. Predatory ants provide the opportunity to separate the relative roles of diet and colony size and brain structure, and offer diverse novel systems to understand adaptive brain mosaicism and the neuronal regulation of predatory behavior. Here we discuss the socioecology of predatory ants and its influence on neuroanatomy.

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THE NEUROBIOLOGY OF PREDATION

Neuroethological and molecular studies of visual, olfactory, auditory, pheromonal, electrical, and mechanoreceptive sensory systems have identified circuitry underpinning predatory behavior in diverse animal clades (Sillar et al., 2016). Star-nosed moles (Catania, 2011), electric fishes (Sukhum et al., 2018), and bats (Genzel et al., 2018) are renowned models. Predator sensory systems generally reflect foraging ecology. Many predatory insects, for example, have large eyes to detect and pursue moving prey through interceptive or ambush hunting strategies. Optic lobe neurons tuned to the motion of small moving objects regulate predatory behavior (Wardill et al., 2015, 2017; Fabian et al., 2018; Nicholas et al., 2018; Nityananda et al., 2018; Supple et al., 2020). Predators may also exhibit morphological and anatomical adaptations to prey type (Martinez et al., 2018) and/or group hunting strategies (Lang and Farine, 2017; Bastos et al., 2021). Predatory behavior in ants evolved independently multiple times in virtually all major subfamilies, including basal clades (Rabeling et al., 2008; Ward, 2014) and most predatory genera are sociobiologically and ecologically diverse (Keller and Peeters, 2020). Predatory ants often show striking differences in diet—usually linked to differences in mandible morphology, biomechanics, motor, olfactory and likely gustatory systems—and social organization. An evolutionary approach can integrate studies of foraging ecology, social structure, morphological evolution, neuroanatomy, and neurophysiology.

MANDIBULAR MORPHOLOGY, SENSORY BIOLOGY, AND MOTOR CONTROL IN PREDATORY ANTS

The morphology of the mandibles—the primary appendages ants use like tools to manipulate their environment and capture prey—varies widely across taxa. Most ants, including some extinct and extant predatory species, have triangular, shovel-shaped mandibles, but those of many predatory species have extreme morphologies (**Figure 1**) and biomechanical adaptations to specialized diets

and prey-capture strategies (Brown and Wilson, 1959; Masuko, 1993, 2019, 2020; Dejean, 1997; Dejean and Dejean, 1998; Rabeling et al., 2012; Schmidt and Shattuck, 2014; Probst et al., 2015; Barden et al., 2020; Keller and Peeters, 2020). Predatory ant mandibles have associated neuronal mechanisms that, in some cases, control remarkably rapid closure. In trap-jaw ants, the mandibles can be cocked back (like a mousetrap) and then used to strike prey in as little as 0.33 ms. Bite force and speed of depend on mandibular muscle biomechanics and properties of the motor neurons that innervate them (Gronenberg, 1996; Just and Gronenberg, 1999). Trap-jaw mandibles typically have sensory trigger hairs that respond to prey contact with a high-frequency burst of action potentials and project into the subesophageal zone (SEZ; Gronenberg et al., 1998a,b; Gronenberg and Riveros, 2009), a brain compartment involved in sensorimotor control of the mandibles, mouthparts, feeding behaviors, and gustation. The motor and chemosensory information transduced by sensilla is eventually processed by the mushroom bodies (MBs) a higher-order brain compartment strongly linked to learning, memory, and behavioral plasticity (Fahrbach, 2006; Gronenberg, 2008; Wright, 2016). Gronenberg et al. (1993) first described how the sensory-motor reflex of the trap-jaw strike of predatory *Odontomachus* workers is controlled by mechanoreceptor trigger hairs with large, rapidly conducting axons in what is likely a monosynaptic connection with motor neurons. Comparative analyses of trap-jaw mechanisms, which have evolved independently in multiple ant genera, reveal convergent biomechanical and neurobiological traits (Gronenberg, 1996; Larabee et al., 2017). Mandible closure velocity in trap-jaw ants appears to differ among species due to phylogeny, physiology, and prey specialization (Larabee et al., 2017, 2018; Gibson et al., 2018). The study of mandible morphology and neurobiology (motor control and sensory capabilities) of predatory ants may thus shed light on the relationships of diet, prey recognition, hunting and prey-capture strategies, and brain organization. Additionally, brain compartments associated with feeding (e.g., SEZ) may scale allometrically with prey-catching strategies, prey specialization, and colony size (Kamhi et al., 2017; Miroshnikow et al., 2020).

DIET, SOCIALITY, AND BRAIN EVOLUTION

Ecological brain theory hypothesizes that the behavioral and/or cognitive challenges of locating and processing food play a key role in brain evolution (Harvey et al., 1980; Goldman-Huertas et al., 2015; DeCasien et al., 2017; Lihoreau et al., 2019; Simons and Tibbetts, 2019). A high-quality (e.g., frugivorous) diet correlates with large brain size and expanded olfactory or visual systems in primates (Dunbar and Shultz, 2017; DeCasien and Higham, 2019). Social brain theory hypothesizes that brain size increases with group size and social complexity, due to cognitive challenges associated with increased conflict and cooperation (Dunbar and Shultz, 2017). Vertebrate societies are characterized by reproductive competition and social bonding, but eusocial insect workers are generally sterile. The applicability of social brain theory as developed for vertebrates to eusocial insects

has thus been questioned (Lihoreau et al., 2012; Farris, 2016). Here we use the term social complexity as a working concept consistent with Anderson and McShea (2001): socially complex ants have large colony size, worker polymorphism and division of labor, and collective foraging strategies. Dornhaus et al. (2012) further discuss how collective organization may scale with colony size. Empirical studies of eusocial insect brain evolution indicate increased social complexity may increase or decrease worker brain size in larger colonies depending on reproductive conflict and division of labor (Jaffe and Perez, 1989; Wehner et al., 2007; Riveros et al., 2012; Muscedere et al., 2014; O'Donnell et al., 2015, 2018; Kamhi et al., 2016; Godfrey and Gronenberg, 2019; DeSilva et al., 2021). Brain structure is also known to change with worker age (Seid et al., 2008; Muscedere and Traniello, 2012) or task specializations that may develop in large colonies (Amador-Vargas et al., 2015). Variation in diet, social organization, and behavioral polyphenisms in insects may be underpinned by neuroanatomical differentiation. Brain size in insects correlates with life history and diet (Farris and Roberts, 2005; Farris, 2008; Bouchebti and Arganda, 2020) and an increase in MB size, potentially supporting enhanced foraging-related navigation and memory (Sayol et al., 2020). At a cellular scale, the density of MB synaptic complexes (microglomeruli, MG) correlates with age, subcaste, task specialization or increase in behavioral repertoire (Groh and Rössler, 2011; Groh et al., 2014; Kamhi et al., 2017; Gordon and Traniello, 2018; Gordon et al., 2018), or requirements for higher-order processing involved in learning and memory (Li et al., 2017). Memory may be associated with a transient increase in MG density (Falibene et al., 2015). These latter studies are among the few suggesting a link between diet, social behavior, and brain evolution in insects. The relationship between diet and MB evolution remains poorly understood.

PREDATORY ANTS AS MODELS OF BRAIN EVOLUTION

Predatory behavior in ants evolved independently multiple times in virtually all major subfamilies, including basal clades. Predatory ants are widely distributed and sociobiologically and ecologically diverse. Workers are active predators, and species show striking differences in prey specialization, dietary breadth, and colony size (range from <10 workers [*Thaumatomyrmex* spp.] to 20 million [*Dorylus wilverthi*]), worker polymorphism, and division of labor. These ants thus have the potential to offer new insights into the relationship between social organization, diet, brain size, and mosaic structure. Army ants (Subfamily Dorylinae) are mass-foraging generalist or specialist predators that may form huge colonies of morphologically and behaviorally specialized workers (Kronauer, 2020; McKenzie et al., 2021). Predatory poneroid ants hunt alone or in groups and differ in diet and social complexity (Peeters, 1997; Ward, 2014; Hanisch et al., 2020). Solitary huntresses in some species broadly attack invertebrates whereas others specialize on termites, an energetically valuable clumped and sessile resource (Figure 1). The shift from randomly distributed prey to clumped prey involves changes in foraging behavior, resulting

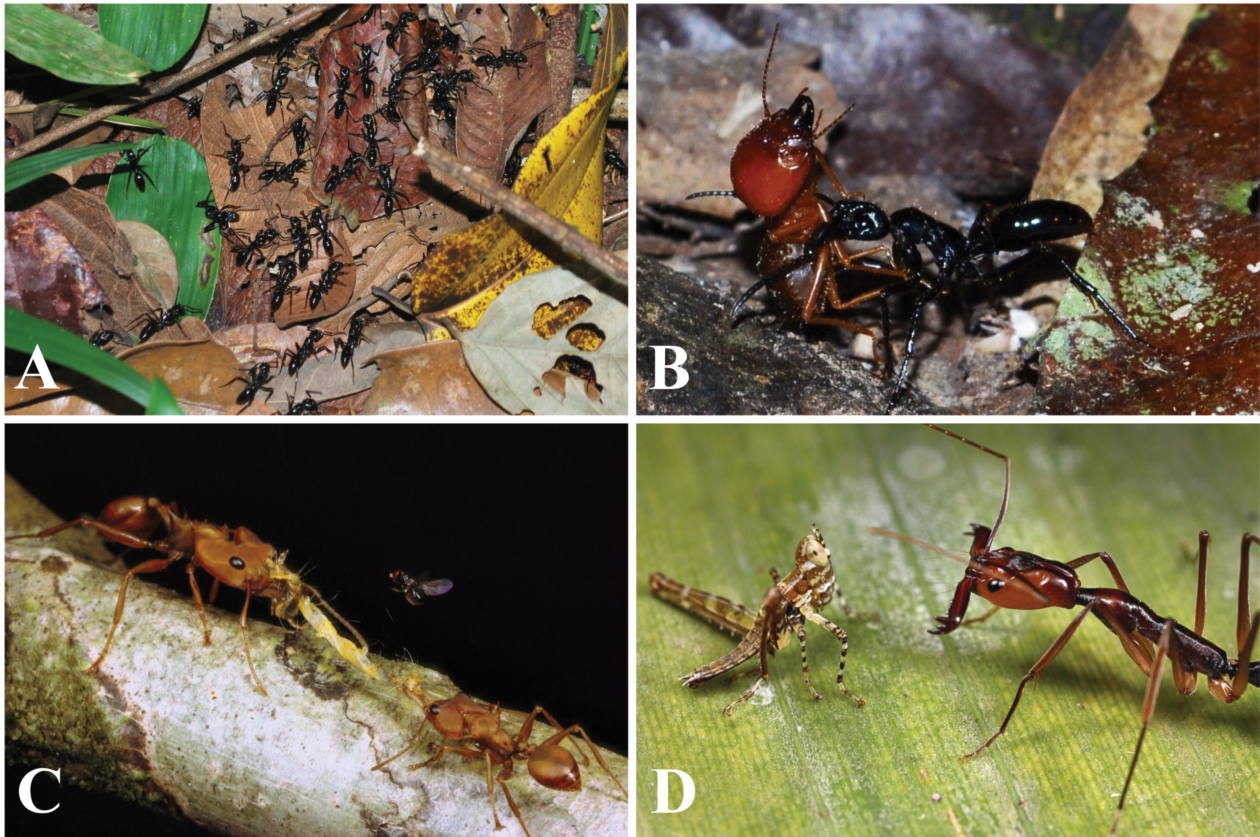


FIGURE 1 | Predatory behavior in ants. **(A)** Group foraging in *Neoponera commutata*, a specialized predator of termites, and **(B)** prey retrieval. **(C)** *Dacetone armigerum* workers retrieving prey. **(D)** *Odontomachus*, a trap-jaw ant.

in an apparent decrease in use of vision (e.g., ommatidia size and/or number) for navigation by solitary workers to chemical signaling to organize group predation (Hölldobler and Traniello, 1980; Mill, 1984; Dejean and Lachaud, 2011; Jelley and Barden, 2021; Sosiak and Barden, 2021). These differences in hunting and prey-capture strategies, as well as the involvement of different sensory modalities in prey localization (Masuko, 1990; Gronenberg and Tautz, 1994; De la Mora et al., 2008), are associated with changes in behavioral demands for prey recognition, foraging communication, and foraging-task specialization (Schmidt and Overal, 2009) that will be reflected in volumetric changes in functionally specialized brain compartments. Other socioecological traits (activity pattern, nesting and foraging habits, foraging range, and prey distribution) are associated with morphological adaptations such as eye and antenna size, and sensilla type and density, and in turn linked with prey selection, diet, and brain mosaicism (Menzi, 1987; Polidori et al., 2012; Narendra et al., 2013; Ramirez-Esquivel et al., 2014; Bulova et al., 2016; Wittwer et al., 2017; Heinze et al., 2018; McKenzie et al., 2021). Prey olfactory detection and discrimination likely depend on the diversity of sensillae and receptors, and their neuronal projections into individual antennal lobe glomeruli that vary in

size and number (Couto et al., 2005; van der Woude and Smid, 2016). These characteristics make predatory ants useful models to understand how dietary shifts may have shaped colony size and complexity, individual and group behavior, and brain and sensory system structure.

COMPARATIVE AND PHYLOGENETIC ANALYSES

Species that vary strongly in diet, predatory strategy, and social complexity can be compared to identify selective influences on brain mosaicism and synaptic architecture. For example, *Neoponera laevigata* is a specialized group-predator of termites: workers are polymorphic, colonies are relatively large (~1,500) and nomadic (Downing, 1978). In contrast, workers of the sister species *N. apicalis* are monomorphic generalist predators that forage solitarily and form small colonies (~200 workers; Schmidt and Shattuck, 2014). Other species that differ socioecologically include *N. villosa* (large colonies, generalist diet) and *Leptogenys langi* and *Stigmatomma pallipes* (small colonies, specialist diet). The influences of social organization and diet on brain compartment scaling and MG densities can thus be distinguished

given that species have small or large colony size and generalist or specialist diets. Brain compartment volume variation of the [MBs], the optic [OL], the antennal lobes (AL; visual and olfactory information processing, respectively), and the SEZ can then be assessed to test the following hypotheses:

- If colony size and associated increases in social interactions, rather than diet, drive brain evolution, then species with large colonies with either generalist or specialist diets are hypothesized to have allometrically large MBs to process social information.
- If diet has a primary influence on brain evolution, then workers of prey-generalist species with both small and large colonies will have large MBs compared to specialist species (higher demands for navigational skills involving learning and memory [MB elaboration and increased MG density] in prey-generalist species; prey-specialist species depend on chemical signaling during foraging).
- Species with generalist diets that vary in behavioral and/or cognitive demands for prey recognition and navigation are predicted to have similar compartmental scaling in the OLs and ALs, and MG densities in large and small colonies (macroscopic and synaptic neuroanatomy are independent of colony size).
- Prey-specialist species will have reduced OL and increased AL size and a decrease in MG density in association with relative demands for processing visual (MB collar) and olfactory (MB lip) information, respectively.
- Prey-generalist species will have larger SEZ and a higher diversity and size of AL glomeruli (need to discriminate among prey).
- If the interaction of diet and colony size influence brain size evolution, then workers of prey-generalist species with large colonies will have allometrically large MBs (higher demands on sensory and behavioral functions).
- Neuroanatomical scaling and socioecology can be mapped phylogenetically to identify patterns of brain evolution. Detailed cellular analyses can be informed by and benefit from this broad analysis.

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CONCLUSION

Our understanding of the relationship between diet, sociality, brain size, compartmental scaling, synaptic architecture, and other neuroethological underpinnings of behavior can benefit from studies of predatory ants. Integrated sociobiological, ecological, morphological, neurobiological, transcriptomic, and genomic research is needed to understand the evolution of individual and group predatory strategies. Brain evolution can thus focus on the behavioral ecology of predation. Studies of morphological evolution can be integrated with sensory biology and motor control of the mandibles as well as the scaling of olfactory specialized brain centers. The characterization of olfactory sensilla and their receptors on the mandibles, other mouthparts, and antennae, and investigation of AL glomeruli size and distribution are needed to understand mechanisms of gustation and their relationship with diet preference, prey identification, and prey-capture strategy. Additionally, we can infer whether gains and losses in neuroarchitecture are significantly associated with clades bearing particular individual worker and social traits and dietary habits.

AUTHOR CONTRIBUTIONS

FA, MM, and JT: conceived, wrote, and edited the manuscript. JT: secured funding. All authors contributed to editing the article and approved the submitted version.

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