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Annual Review of Entomology

Correlates and Consequences of Worker Polymorphism in Ants

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Keywords

body size, division of labor, eusociality, life-history traits, ultimate and proximate mechanisms

Abstract

Body size is a key life-history trait influencing all aspects of an organism's biology. Ants provide an interesting model for examining body-size variation because of the high degree of worker polymorphism seen in many taxa. We review worker-size variation in ants from the perspective of factors internal and external to the colony that may influence body-size distributions. We also discuss proximate and ultimate causes of size variation and how variation in worker size can promote worker efficiency and colony fitness. Our review focuses on two questions: What is our current understanding of factors influencing worker-size variation? And how does variation in body size benefit the colony? We conclude with recommendations for future work aimed at addressing current limitations and ask, How can we better understand the contribution of worker body-size variation to colony success? And, what research is needed to address gaps in our knowledge?

INTRODUCTION

Body size is a fundamental life-history trait, influencing the reproduction and survival of an organism. Size affects all aspects of an organism's existence, including its metabolism, thermoregulation, locomotion, reproduction, longevity, and diet (92). Consequently, size plays an important role in determining how organisms interact with the biotic and abiotic components of their environments (92, 122). Size is often under strong directional selection (73), yet differences in body size are often pronounced in populations (26). Variation in size may result from a response to constraints and is subject to trade-offs, as is generally the case with life-history traits (122). For example, a reproducing organism may have to choose between investing in individual offspring size versus total offspring number (118).

For many organisms, body size is relatively easy to measure, allowing for quick and robust data sets (92). The causes and consequences of intraspecific variation in body size are commonly discussed in studies of life-history traits (40, 122), ecological physiology (26), and macroecology (26). Body size and its associated trade-offs have been the focus of biologists for decades with a majority of this work focused on solitary organisms (122). Eusocial organisms, however, are often missing from studies that examine how ecological factors influence intraspecific variation in traits (15) despite a long history of examining body-size variation in social insects (67, 78, 88, 125, 140).

Relative to solitary species, the study of reproductive investment in size in eusocial organisms is complicated by their reproductive division of labor. In eusocial organisms, reproduction is dominated by a queen caste, whereas other tasks within the colony are primarily performed by workers that are often sterile under typical colony conditions. This separation of reproductive and nonreproductive individuals may influence trade-offs thought to constrain the evolution of life-history traits such as size. In most ants, for example, workers no longer invest in characteristics related to dispersal, mating, and reproduction, and there is considerable variation in size between queen and worker castes. In approximately 13% of ant species (~16% of ant genera), the worker caste also exhibits considerable variation in size and shape (38, 55). Body size and its variation are both likely under strong selection and should therefore influence colony fitness through colony maintenance, survival, and reproduction (12, 100, 137). Inter- and intraspecific variation in body size may also influence ant community dynamics by influencing foraging behavior and prey selection (124), influencing competitive interactions (29), and mediating ant–plant mutualisms (25).

Variation in worker size within a colony can be influenced by several factors, including developmental and evolutionary constraints, larval nutrition, the social environment, and the abiotic and competitive environment of the colony (**Figure 1**). Variation in worker size within a single colony can be viewed as being associated with internal or external factors. For example, developmental mechanisms originate from within the colony, whereas the physical and competitive environments influence worker size externally. Additionally, internal and external factors may interact with each other. Larval nutrition and the social environment can both respond to and influence the competitive interactions a colony experiences.

In this review, we consider intraspecific variation in worker body size (i.e., worker polymorphism) from the perspective of both internal and external factors. We also identify proximate and ultimate causes of body-size variation where known, although research does not always differentiate between these mechanisms (27, 29). Explorations of proximate causes identify the genetic, developmental, or hormonal mechanisms responsible for variation in size. The ultimate explanations for worker body size typically attempt to explore the beneficial function of body-size variation and increasingly the history of body-size evolution, but these insights are rarely directly connected to impacts on colony fitness. Thus, we also highlight the current knowledge gaps in our understanding of worker body size in ants.
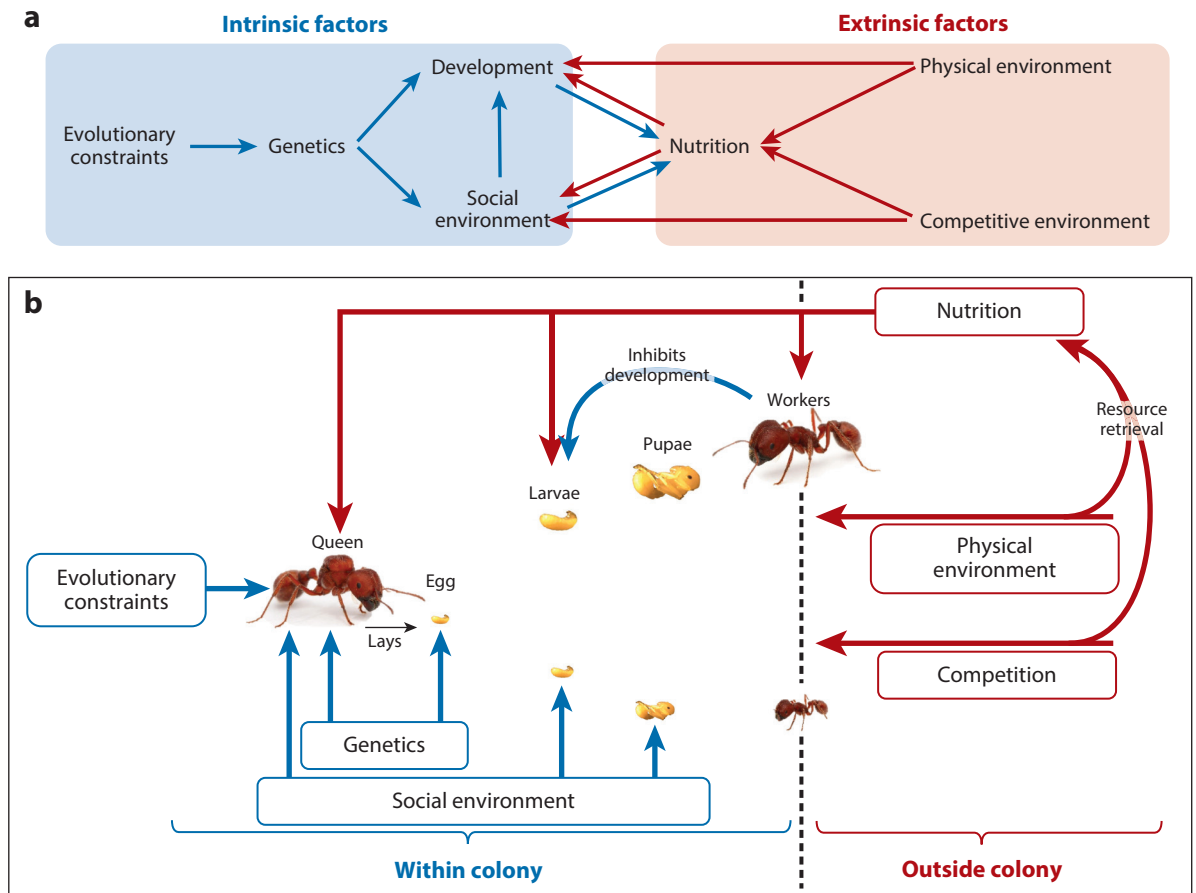
Figure 1

Worker body size and size distributions within a colony are influenced by a variety of factors from within and outside a colony. (*a*) The intrinsic factors we discuss include evolutionary constraints, genetic factors, and the social environment. The extrinsic factors include the physical environment, competition (e.g., colony defense, foraging), and nutrition. (*b*) These factors can also interact with one another at different stages of worker development and ultimately influence the development, survival, and longevity of different castes within a colony.

It is important to note that we do not comprehensively summarize the literature on variation in mean individual body sizes in species with monomorphic workers or on variation in colony size (e.g., the number of workers) across populations. Our review specifically addresses two questions: What is our current understanding of factors influencing worker-size variation? And how does variation in body size benefit the colony? Finally, we end with recommendations for future work aimed at addressing the current limitations in this field and ultimately ask the following: How can we better understand the contribution of worker body-size variation to colony success? What types of information or research are needed to address gaps in knowledge?

BODY-SIZE VARIATION IN ANTS

Ants are among the most diverse and successful organisms in terrestrial ecosystems. Their success is driven in part by their sophisticated division of labor. In addition to variation between reproductive

and nonreproductive castes (38), ants often exhibit pronounced structural variation within castes, with some taxa having novel castes, alternately referred to as discrete subcastes of either workers or queens (88, 140). For simplicity and accuracy, we use the term caste to refer to any morphologically distinct group of individuals within the colony. This diversity, even within a single colony, adds to the complexity of discussions of body size because it is both an individual trait and a colony-level trait. In polymorphic ants, worker size is phenotypically plastic, where eggs of a single genotype are responsive to environmental stimuli and result in alternative phenotypes. This plasticity has potentially contributed to ant diversification and speciation (93) and their ecological success (84).

The amount of variation observed in worker body size can broadly be categorized as monomorphic and polymorphic (**Figure 2**). Monomorphic workers display isometric morphological variation, limited body-size variation, or both (134, 140). Polymorphic workers display a sufficient range of adult variation to produce individuals of distinctly different proportions (134, 140). Worker polymorphism has historically been subdivided into discrete subcategories (e.g., monophasic, diphasic, triphasic, and others) (140) (**Figure 2**). However, polymorphism may be better viewed as conditions along a continuum. For example, while some species (e.g., most *Pheidole* and some *Eciton* and *Cephalotes*) have workers that are discretely dimorphic with considerable separation among castes (e.g., minors and majors) (88, 101, 105, 140), others (including some *Eciton* and *Cephalotes*) exhibit considerable inter- and intraspecific variation in the degree of discretization between minor and major worker subcastes (101, 105). Categorizing polymorphism can be challenging when based on the relative growth rates of body part pairs, and the relative growth relationships of different pairs of body parts may vary considerably within a single species (5, 16). Polymorphism may therefore be better characterized using approaches other than bivariate (i.e., pairwise) analysis (8, 35).

Polymorphism within the worker caste has evolved repeatedly (see the discussion below in the section titled Evolutionary Constraints) and is often associated with large colony size (5). The evolution of polymorphic workers is thought to determine colony efficiency and ultimately colony success (32, 88). However, little empirical evidence is available to support this view (7, 112). In the majority of cases that supports that body-size variation does improve colony fitness, these species have more than one distinct worker caste, with one often specialized for food retrieval, food processing, and/or colony defense (9, 100, 104). For these species, investment into different castes should directly influence colony survival, competitive ability, and reproduction (10, 100, 137).

INTERNAL DETERMINANTS OF BODY SIZE

In this section, we highlight intrinsic factors influencing body size. We use the terms internal or intrinsic to describe largely proximate or mechanistic factors that influence body size within the colony, including the role of genetics and development. By contrast, the next section highlights external or extrinsic features influencing worker body size, which largely describe ecological influences on body-size variation through interactions between a colony and its environment. Factors like nutrition and social environment may be the result of interaction between intrinsic and extrinsic factors, so we discuss these in a separate section. It is important to note that all the factors included in this review do not work singly, and interactions between factors are important in influencing body sizes within a colony (**Figure 1**). Much of the material in this section has been reviewed recently (6, 44, 52, 115, 120), so we have kept this section brief.

Heritable Factors

In most ants, castes are determined by environmental cues, specifically by the amount and type of nutrition received during larval development (133, 134). However, recent studies on hybrid
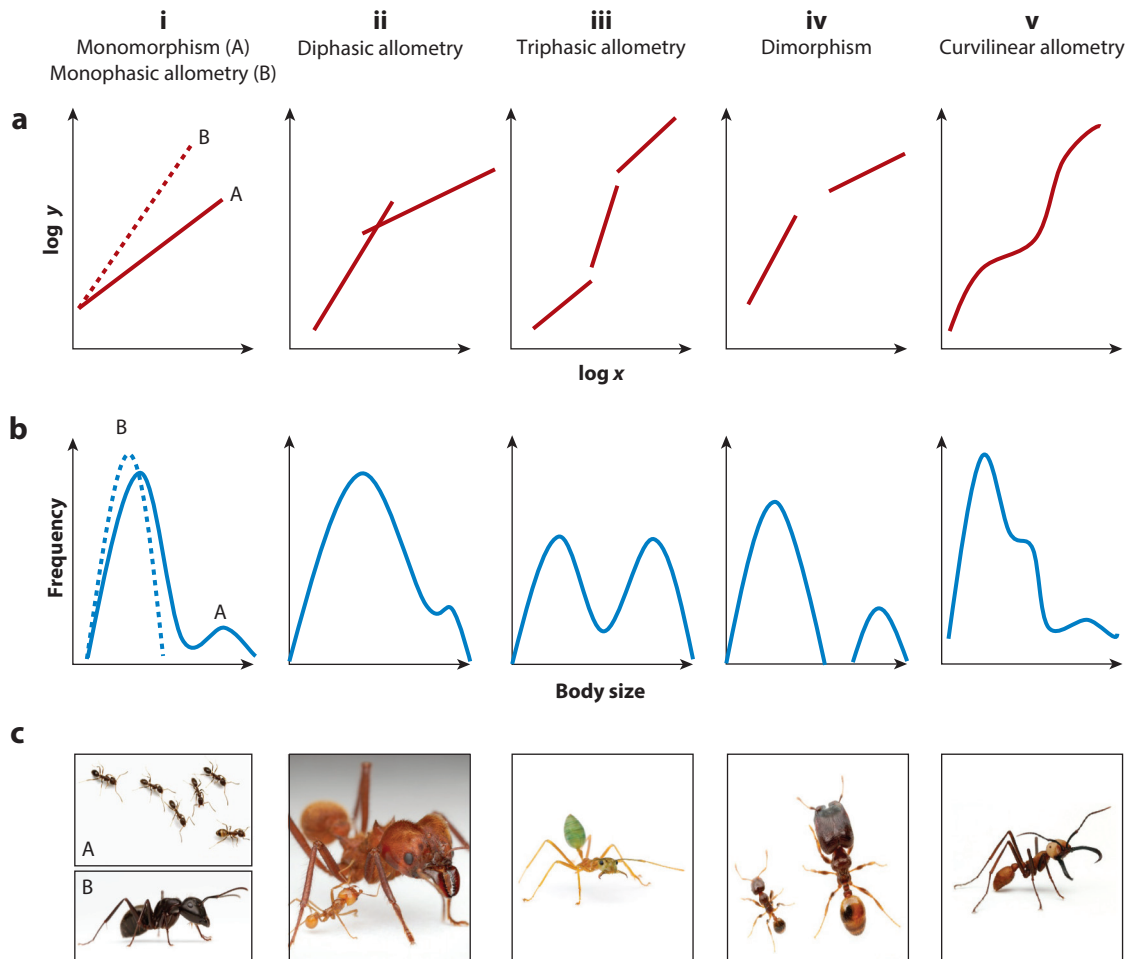
Figure 2

(*a*) Hypothetical examples of allometric growth curves (see 35, 88, 105, 134, 140, 141). (*a, i, line A*) Monomorphism is represented by an isometric growth curve (slope $= 1$), whereas (*a, i, line B*) monophasic allometric growth is nonisometric (slope > 1 or < 1). (*a, ii*) Diphasic allometry is represented by the intersection of two segments with different slopes. (*a, iii*) Triphasic allometry is represented by two breaks with three segments of different slopes (minors, medias, and majors). (*a, iv*) Complete dimorphism is represented by two distinct segments separated by a gap with no intermediates. (*a, v*) Curvilinear allometry includes nonlinear scaling of morphological features. (*b*) Example body-size distributions for ants with each allometric growth: *Linepithema humile* (*b, i, line A*), *Camponotus pennsylvanicus* (*b, i, line B*) (150), *Atta sexdens* (*b, ii*) (140), *Oecophylla smaragdina* (*b, iii*) (140), *Pheidole* sp. (*b, iv*) (140), and *Eciton hamatum* army ants (*b, v*). (*c*) Photos of species with each allometric growth curve: *L. humile* (*c, i, image A*), *C. pennsylvanicus* (*c, ii*), *A. cephalotes* (*c, i, image B*), *O. smaragdina* (*c, iii*), *Pheidole aberrans* (*c, iv*), and *Eciton burchellii* (*c, v*). Photos: copyright Alex Wild, used with permission.

lineages of *Pogonomyrmex* and *Solenopsis* spp. and a number of widely introduced tramp ant species (including *Vollenhovia emeryi*, *Wasmannia auropunctata*, *Paratrechina longicornis*, and *Anoplolepis gracilipes*) have shown that caste determination can be largely, if not entirely, genetically based (52, 115). There is also evidence for a genetic influence on body size through patriline identity in species with multiply mated queens. For example, research on polymorphic *Pogonomyrmex* (120), *Acromyrmex* (60), and *Eciton* spp. (64) suggests that worker body size may be influenced by the

genotype of the patriline (but see 39, 138). In multiple queen (polygyne) colonies, different reproductive queens may also produce differently sized workers (116). Genotype may therefore influence a developing ant larva's response to environmental stimuli, as observed in solitary organisms (34), resulting in a genetic influence on size.

The relative importance of genes regulating worker size varies on a continuum from largely genetically determined to predominantly environmentally controlled (115). The relative contribution of genetic factors on worker body size can also vary between castes of a single species (e.g., reproductive, major, minor) (120). Even in the absence of genetic caste determination, both genetic and epigenetic factors (such as maternal effects and DNA methylation) can affect a larva's response to environmental stimuli and therefore influence the development of body-size variation within a colony (4, 6, 60). For example, larval begging behavior can influence the amount of food obtained from workers and theoretically impacts size and even caste at development (6). The influence of genetics on body size through larval and worker behaviors may be pervasive (6).

Developmental Factors

Wheeler (133, 134) provides a thorough review of the developmental basis of worker body-size variation. Her work with *Pheidole bicarinata* reveals how juvenile hormone plays an integral role in controlling the timing of developmental periods and the critical size at which metamorphosis occurs, resulting in small minor workers and larger major workers (135). Workers can also regulate larval development by altering the flow of food, temperature, and pheromones within a nest, but the exact environmental stimuli eliciting a developmental switch remains unclear (134). Once present, majors can influence worker caste ratios in a colony by increasing the threshold level of juvenile hormone necessary for larvae to develop into majors through a contact pheromone (78, 133, 136). A recent developmental study by Rajakumar and colleagues (107) combined hormonal manipulation and gene expression to investigate how supermajors develop in the genus *Pheidole*. They created atypically large workers and concluded it is possible for species to generate morphological specialization based on genetic accommodation though selection of genes that control the frequency and form of expression (e.g., via the manipulation of juvenile hormone timing during sensitive periods or developmental switch points). Developmental research on worker variation is restricted to a few species (4, 107, 134) and is best described in the genus *Pheidole* (78). However, developmental regulation can vary in significant ways between different genera (4, 107, 134). Additional work is needed to uncover how morphological diversity is generated within a colony, particularly how existing variation in developmental pathways between queens and workers can be co-opted to generate novel phenotypes (84).

If it is relatively easy to manipulate body size during development, why do relatively few ant genera have a polymorphic worker caste? One proximate explanation as to why polymorphism has not evolved more frequently is that the regulation of some developmental pathways may be incompatible with producing variably sized workers (1). For example, systems with hormonal or pheromonal regulation of worker size, as observed in *Pheidole*, may be more amenable to worker-size variation than those without these social influences, which rely instead on queen control of larval nutrition (133). Early caste determination during larval development, which is associated with species with high worker-size variation, may increase the queen's influence on the reproductive status of offspring within the colony (38, 133). Moreover, in workers, resources typically devoted to tissue for dispersal or reproduction are free to be invested into other morphological features, allowing for variation and specialization among castes to evolve (84, 125, 133).

Evolutionary Constraints

Evolutionary constraints, characterized by macroevolutionary trends in morphology, have long been used to explain evolutionary patterns in body size. For ants, Hölldobler & Wilson (55) noted that, of the 297 described genera at the time, only 46 (15%) had polymorphic species. Although not explicitly in a phylogenetic context, they also mentioned the relative lack of worker polymorphism in the subfamily Ponerinae, with *Megaponera* as the sole polymorphic genus. This may have led to a false perception that worker polymorphism is primarily a trait of the formicoid clade (90). Two of the most diverse ant genera have either almost entirely dimorphic (*Pheidole*) or polymorphic (*Camponotus*) workers, suggesting that worker polymorphism may influence diversification rates or that transitions between monomorphism and polymorphism occur at unequal rates. However, studies on the evolution of morphology, particularly body size, need phylogenetic comparative methods to discern tempo and mode of trait evolution (119).

The first broad comparative analysis of worker variation used phylogenetic independent contrasts to test the predictions of potential mechanisms of worker variation (38). Although limited in their phylogenetic coverage (35 species, 22 genera), the authors found positive associations between worker variation, worker–queen dimorphism, and nest mate relatedness. More recently, Blanchard & Moreau (14) used a comprehensive phylogeny of 326 ant genera to examine trade-offs among defensive traits in ants. Coding 43 genera as polymorphic, they found that polymorphism is an evolutionarily labile trait but that it is not associated with variation in speciation rate in the absence of other characters (**Figure 3**).
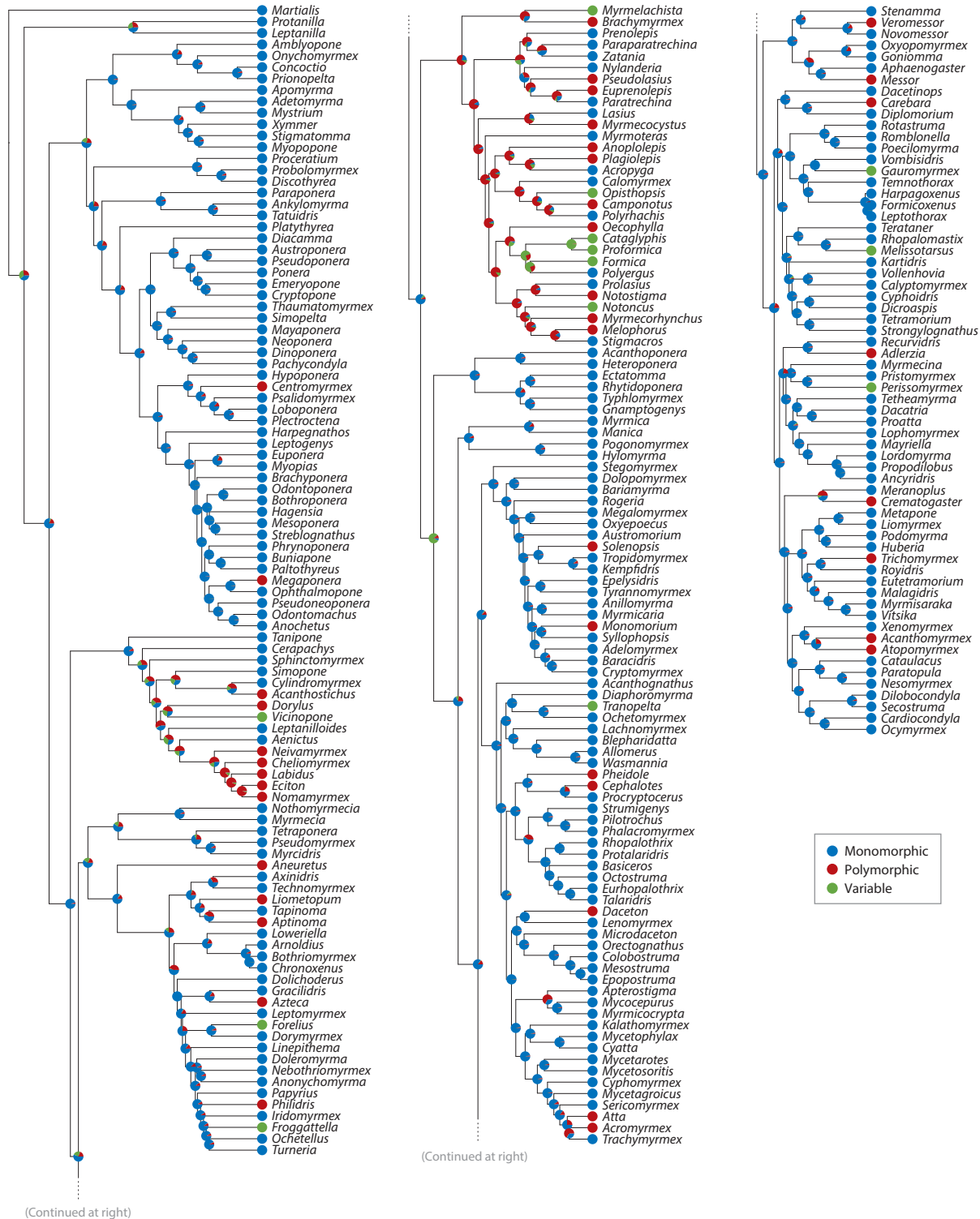
Not only is polymorphism significantly correlated with phylogeny at the generic level (14, 99, 114), but transitions from monomorphic to polymorphic workers may influence diversification rates (14). It is important to consider that worker polymorphism evolved repeatedly in ants and appears to be an evolutionarily labile trait (14). Expression of body-size variation in ants may therefore be largely driven by evolutionary history and subsequent selection for worker-size variation (91). Most evidence, however, suggests that ecological factors drive selection to ultimately determine the amount of worker-size variation within a nest (94, 99, 105, 114, 125).

EXTERNAL DETERMINANTS OF BODY SIZE

In this section, we explore research examining how external factors, or ecological interactions, influence body-size variation in workers within and between colonies. These include potential proximate and ultimate influences from the abiotic environment, the competitive environment, food availability and quality, and the social environment (including colony size). Ultimately, our goal is to understand how extrinsic factors independently influence body size and also through interactions with intrinsic factors, such as genetics, development, and evolutionary history.

Abiotic Environment

The physical environment can have strong influences on morphological variation in insects. Photoperiod and temperature are important cues influencing the timing of larval development (74, 96) and survival (2). Worker size also influences resistance to environmental stresses, including heat (23, 131), cold (53), and desiccation (57, 66). In seasonal climates, temperature and photoperiod can be important cues to determining colony production of workers (74) and the timing of the production of reproductive castes (18). Moreover, temperature can impact the speed of larval development, with published optimal ranges from 24°C to 32°C (see 96). However, there is little direct evidence that temperature impacts size variation in ants. For example, in *Solenopsis invicta* temperature during larval development does not appear to influence worker body size (22).

Martialis	Stenamma
Protanilla	Veromessor
Leptanilla	Novomessor
Amblyopone	Oxyopomyrmex
Onychomyrmex	Goniomma
Concoctio	Aphaenogaster
Prionopelta	Messor
Apomyrma	Dacetinops
Adetomyrma	Carebara
Mystrium	Diplomorium
Xymmer	Rotastruma
Stigmatomma	Romblonella
Myopopone	Poecilomyrma
Proceratium	Vombisidris
Probolomyrmex	Gauromyrmex
Discothyrea	Temnothorax
Paraponera	Harpagoxenus
Ankylomyrma	Formicoxenus
Tatuidris	Leptothorax
Platythyrea	Terataner
Diacamma	Rhopalomastix
Austroponera	Melissotarsus
Pseudoponera	Kartidris
Ponera	Vollenhovia
Emeryopone	Calyptomyrmex
Cryptopone	Cyphoidris
Thaumatomyrmex	Dicroaspis
Simopelta	Tetramorium
Mayaponera	Strongylognathus
Neoponera	Recurvidris
Dinoponera	Adlerzia
Pachycondyla	Myrmecina
Hypoponera	Pristomyrmex
Centromyrmex	Perissomyrmex
Psalidomyrmex	Tetheamyrma
Loboponera	Dacatria
Plectroctena	Proatta
Harpegnathos	Lophomyrmex
Leptogenys	Mayriella
Euponera	Lordomyrma
Myopias	Propodilobus
Brachyponera	Ancyridris
Odontoponera	Meranoplus
Bothroponera	Crematogaster
Hagensia	Metapone
Mesoponera	Liomyrmex
Streblognathus	Podomyrma
Phrynoponera	Huberia
Buniapone	Trichomyrmex
Paltothyreus	Royidris
Megaponera	Eutetramorium
Ophthalmopone	Malagidris
Pseudoneoponera	Myrmisaraka
Odontomachus	Vitsika
Anochetus	Xenomyrmex
Tanipone	Acanthomyrmex
Cerapachys	Atopomyrmex
Sphinctomyrmex	Cataulacus
Simopone	Paratopula
Cylindromyrmex	Nesomyrmex
Acanthostichus	Dilobocondyla
Dorylus	Secostruma
Vicinopone	Cardiocondyla
Leptanilloides	Ocymyrmex
Aenictus	
Neivamyrmex	
Cheliomyrmex	
Labidus	
Eciton	
Nomamyrmex	
Nothomyrmecia	
Myrmecia	
Tetraponera	
Pseudomyrmex	
Myrcidris	
Aneuretus	
Axinidris	
Technomyrmex	
Liometopum	
Tapinoma	
Aptinoma	
Loweriella	
Arnoldius	
Bothriomyrmex	
Chronoxenus	
Dolichoderus	
Gracilidris	
Azteca	
Leptomyrmex	
Forelius	
Dorymyrmex	
Linepithema	
Doleromyrma	
Nebothriomyrmex	
Anonychomyrma	
Papyrius	
Philidris	
Iridomyrmex	
Froggattella	
Ochetellus	
Turneria	

Myrmelachista
Brachymyrmex
Prenolepis
Paraparatrechina
Zatania
Nylanderia
Pseudolasius
Euprenolepis
Paratrechina
Lasius
Myrmecocystus
Myrmoteras
Anoplolepis
Plagiolepis
Acropyga
Calomyrmex
Opisthopsis
Camponotus
Polyrhachis
Oecophylla
Cataglyphis
Proformica
Formica
Polyergus
Prolasius
Notostigma
Notoncus
Myrmecorhynchus
Melophorus
Stigmacros
Acanthoponera
Heteroponera
Ectatomma
Rhytidoponera
Typhlomyrmex
Gnamptogenys
Myrmica
Manica
Pogonomyrmex
Hylomyrma
Stegomyrmex
Dolopomyrmex
Bariamyrma
Rogeria
Megalomyrmex
Oxyepoecus
Austromorium
Solenopsis
Tropidomyrmex
Kempfidris
Epelysidris
Tyrannomyrmex
Anillomyrma
Myrmicaria
Monomorium
Syllophopsis
Adelomyrmex
Baracidris
Cryptomyrmex
Acanthognathus
Diaphoromyrma
Tranopelta
Ochetomyrmex
Lachnomyrmex
Blepharidatta
Allomerus
Wasmannia
Pheidole
Cephalotes
Procryptocerus
Strumigenys
Pilotrochus
Phalacromyrmex
Rhopalothrix
Protalaridris
Basiceros
Octostruma
Eurhopalothrix
Talaridris
Daceton
Lenomyrmex
Microdaceton
Orectognathus
Colobostruma
Mesostruma
Epopostruma
Apterostigma
Mycocepurus
Myrmicocrypta
Kalathomyrmex
Mycetophylax
Cyatta
Mycetarotes
Mycetosoritis
Cyphomyrmex
Mycetagroicus
Sericomyrmex
Atta
Acromyrmex
Trachymyrmex

Monomorphic (blue)
Polymorphic (red)
Variable (green)

(Continued at right)

(Continued at right)

Using a nearly global biogeographical analysis of worker body size, Kaspari (67) found that workers in warmer climates tend to be smaller than those in colder climates. Temperature may be important in determining how colonies invest in worker size for species from climates with greater extremes in temperature (10, 23, 148). Differences in size and resistance to environmental stress may impact how ants compete by influencing the timing and location of foraging. For example, in a tropical rainforest in Costa Rica, smaller ant species tend to forage in moist microclimates, whereas species with large body sizes forage in a variety of microclimates (66). Thus, species with smaller workers potentially experience more interspecific interactions than species with larger workers (66). Worker polymorphism may therefore allow colonies to forage in a variety of microclimates simultaneously (24). Worker-size variation may also reduce foraging niche overlap within a habitat (23, 75, 114) and produce a resilient worker force (20, 23, 131).

Worker size may also be a response to the physical structure of the habitat. Habitat structure (e.g., vegetation, leaf litter) can directly impact the microclimate and ultimately impact worker survival and foraging success (66, 149). The physical structure of a habitat can also restrict foraging success, determining worker foraging speed (61) and load size (108). Therefore, in restrictive physical environments, smaller ants can move more easily (69), but larger ants are potentially more efficient at retrieving larger food items (108). Colonies with variably sized workers can potentially take advantages of both strategies (75, 114) and have the flexibility to deal with a wider breadth of resources and conditions (29, 43). For example, the transition from subterranean foraging to aboveground foraging in *Dorylus* army ants is associated with an increase in worker size and morphological variation (75, 114). The combination of a specialized transport caste and smaller individuals in the army ant *Eciton burchellii* allow prey-retrieval teams to dynamically form and disband, overcoming frictional interactions with the leaf litter that otherwise slow prey delivery (104).

Enemy Environment

Ants are reasonably viewed as their own worst enemies, and body size is known to play a critical role in competitive and predatory interactions among ants (reviewed in 31, 124). The most intense competitive interactions are typically focused at the site of rich food resources, or at the nest with the goal of usurping the nest structure. Predation, in contrast, is focused on gaining access to the nest for the purpose of consuming its contents. In any enemy interaction among ants, the opportunity for social combat is critical in determining how body size will influence the outcome. Lanchester's Laws of Combat, a body of theory developed to predict the outcome of human battles, has been repurposed to provide useful qualitative and explicit quantitative predictions about the outcomes of social combat in ants (3, 42) across a range of competitive and predatory interactions (e.g., 95, 102). Qualititively, when the combat arena forces a series of one-on-one battles, such as in the confines of nest tunnels, the side with the best individual fighters is predicted to win. In contrast, when combat occurs in an open area, where many-on-one interactions are possible, then the side that is numerically superior is expected to win regardless of individual fighting abilities. Of course, individual fighting ability in ants is closely associated with body size and body size–related traits, such as mandible and head size. Concordantly, selection associated with social combat appears to have been a strong and recurrent pressure on the evolution of polymorphism in ants, including the evolution of a functionally specialized and large soldier caste.

←——

Figure 3

Ant phylogeny with body-size variation in ant worker castes labeled as monomorphic (*blue*), polymorphic (*red*), or variable (*green*). Node pie charts represent frequency of ancestral state occurrence for polymorphism based on stochastic character mapping (redrawn from Reference 14).

In the foraging arena, the evolution of body-size variation can provide both a numerous worker caste for combat in open areas and larger, more capable fighters for spatially constrained combat scenarios. This dual combat function of polymorphism is well illustrated in a number of taxa. For example, the small, fast workers of *Pheidole* species can be critical in locating and numerically dominating rich food resources, and then soldiers defend the resources against subsequent usurpation attempts by competitors (147). Similarly, *Atta* leaf-cutting ants recruit small workers to intra- and interspecific territorial incursions in the open (137) but recruit soldiers to the front line of defense against nest attacks by the army ant *Nomamyrmex esenbeckii* (102). In this same interaction, *N. esenbeckii* raiders, which have a broad worker-size range but no distinct soldier, commit their largest fighters to the front line, where they engage in head-to-head battles with the *Atta* soldiers. Furthermore, the numerous smaller individuals on both sides shift the combat scenario to a many-on-one attack whenever one of their large combatants manages to pull its opponent behind the frontline (102).

At the nest, usurpation pressure from nest-site competitors appears to be associated with soldiers morphologically specialized for entrance-blocking defense (phragmosis). The genus *Cephalotes*, commonly known as turtle ants, provides an extreme example of this caste morphotype: Soldiers have armored heads, which they use to block the entrances of arboreal cavity nests, and there are a number of distinct soldier morphotypes within this group (30). Recent work has established that soldiers primarily defend against usurpation pressure from nest-cavity competitors (100). Moreover, specialization on naturally occurring cavity entrances that better fit the head of one soldier is associated with the evolution of more specialized soldier morphotypes in this group (99, 101). Remarkably, a similar soldier morphotype for entrance blocking has evolved in at least four other polymorphic ant lineages, including *Carebara* (37), *Tetraponera* (130), *Pheidole* (146), and *Colobopsis* (50). This remarkable functional convergence suggests that the same interaction between nest usurpation pressure and specialization on a highly defendable nesting resource may have selected for this aspect of worker body-size variation repeatedly in ants, although the enemy ecology for most is not well known. Moreover, recent theory suggests the possibility that this pattern can be the product of strong disruptive selection from intense nest-site competition in sympatry (94).

In contrast to the convergent evolution of blocking soldiers that defend against nest usurpation, intense predation pressure at the nest from other ants appears to be associated with fighting soldiers. This is especially true with respect to predation pressure from army ants, which specialize in consuming other ants (105, 109) and are diverse and abundant in tropical and subtropical systems (68, 87). In the best-documented interactions, soldiers display both rapid recruitment to army ant attack and specialized defensive strategies (58, 102). Although the adaptive role of fighting soldiers in defending against army ants is clear, the extent to which army ant predation has driven soldier evolution is currently unclear. This is especially true for the diverse genus *Pheidole*, whose soldiers provide a defensive function across a range of enemy ant contexts (58, 147). Studies that address the trajectory of soldier evolution with respect to different ant enemies and defensive contexts can therefore be seen as an important focus for future work.

The role of other kinds of enemies in the evolution of ant body-size variation is currently unclear. Nevertheless, a couple of striking examples appear to be associated with pressure from vertebrate predators. In another case of remarkable functional convergence, *Cataglyphis bombycina* and most members of the genus *Eciton* have soldiers with sickle-shaped mandibles that are effective at puncturing vertebrate flesh (31, 83). Yet even in these conspicuous examples, ecological data supporting this expected enemy interaction is lacking; no specialized predator has been identified in either taxon. A suite of vertebrate predators may exert suitable pressure to drive the evolution of this type of defensive body-size variation, or at least maintain it, but again data on opportunistic vertebrate predation pressure in these taxa is lacking.

Resource Utilization

Body size plays a central role in resource utilization in ants, by dictating the size of food items that can be harvested and the dimensions of preexisting nesting resources that can be occupied (i.e., nests that are not excavated from scratch by the ants). The acquisition of food items many times larger than individual ants appears to be dictated by the transition from solitary foraging to collective foraging strategies (31). Nevertheless, body size can place bounds on the size of items that individuals can transport and process (reviewed in 31, 124). Likewise, for ants that nest in any kind of preexisting cavity, body size places a lower bound on the cavities that they can use: Cavities or cavity entrances of a given size simply prevent access to ants of a larger size. Moreover, if resource defense is tightly coupled with body size, it may also dictate the upper bound of the nest resources that can be utilized effectively. Body-size variation within a species can therefore have profound implications for the resources a colony can use, and these interactions are likely to be important drivers of body-size evolution across taxa.

Size matching between ant size and a food item is a common theme in the interaction between body size and load size in polymorphic ants. Although this association can be weak in some taxa and ecological contexts (e.g., 9, 132), it is consistent and pronounced in others (e.g., 104). Numerous factors may interact to determine the extent to which size matching is present across contexts, including (a) the extent to which load size can be manipulated by the ants (e.g., cut versus captured food items), (b) the mode of carrying [e.g., carry versus dragging (9) or overhead versus below body (35)], and (c) the time constraints to foraging. Indeed, the combination of a lack of control over load size, beneath-the-body transport, and the demands of high-speed retrieval may explain the extreme size matching commonly seen in army ants (104). Furthermore, transport of particular load types is associated with the presence of a discrete transport caste in *Eciton* army ants (105), providing colonies with the capacity to carry loads that are beyond the capabilities of the standard worker caste (104).

Polymorphism among foragers may also allow for transport teams, which further increase the functional capabilities of the colony for food retrieval (reviewed in 5). In the cases where load size is determined by the ants prior to retrieval, body size may also dictate the size of the load produced, as is the case in the mechanics of leaf fragment cutting in leaf-cutting ants (28, 144). Size matching in the foraging arena is also not necessarily limited to load production and transport. In a novel example, *E. burchellii* workers size match their bodies to potholes in the foraging substrate, providing a smoother and faster surface for their nest mates to run over (106).

Following the retrieval of food items, worker body-size variation can also play an integral role in food processing inside the nest. Large individuals or discrete castes that specialize in milling seeds are particularly widespread in polymorphic taxa. For example, specialized seed-milling individuals have evolved independently multiple times in the major caste of *Pheidole* ants (56), which often play a functional role as soldiers. Large seed-milling individuals have also evolved independently in other genera, including *Messor* (9), *Pogonomyrmex* (128), and *Solenopsis* (142). Small ants in polymorphic species can also have an important part in food processing. For example, in *Atta* leaf-cutting ants, smaller individuals process leaves and garden fungal hyphae (143). In a number of other taxa, the smallest individuals are most common in the nest and adopt a functional role as nurses (41, 143), which can be seen as the final step in the food-processing chain, from resource acquisition to effective delivery to developing offspring.

As already addressed in the section titled Enemy Environment, polymorphism is closely associated with nest defense in some taxa. However, in cases where the largest individuals defend the colony by blocking the nest entrance, polymorphism can also be connected directly with the acquisition of shelter resources. In the best-studied example, turtle ants rapidly deploy specialized

soldiers to new nests in the process of colony expansion (103) and preferentially occupy those that match the head of their soldiers' armored head discs (99–101). Moreover, the variation in the size of utilized entrance holes is correlated with soldier polymorphism across species, suggesting that the acquisition of shelter resources is dictated by the polymorphic range of the larger defensive caste (101). The extent to which the range of shelter resources tracks the range of ant body size in other taxa is currently unknown. Nevertheless, it may be a convergent trend in those taxa with the same soldier morphotype.

As a final step in the chain of resource utilization, from acquisition to the production of new ants, body-size variation can also be associated with novel methods for long-term food storage. In perhaps the most well-known and striking example, larger individuals in some members of the genus *Myrmecocystus* are used as living storage vessels for liquid food (110). They then provide the nutrition through regurgitation to other colony members as needed. The same replete function has evolved convergently in other taxa via diverse mechanisms. For example, the large and discrete soldier caste of *Colobopsis* also serves as a storage caste, via the accumulation of fat and water (51). Adding a third mechanism for food storage and distribution, a large caste in *Crematogaster smithi* produces unfertilized trophic eggs that are primarily fed to developing larvae (54). The extent to which these storage functions of larger individuals represent primary drivers of polymorphism or secondary adaptations in existing larger ants in polymorphic lineages remains unknown. How widespread such mechanisms for food storage are across the ants has yet to be addressed, but it is perhaps most likely to be seen in other polymorphic taxa where the largest individuals spend the majority of their lives inside the nest.

FEEDBACK BETWEEN INTRINSIC AND ECOLOGICAL FACTORS

Many factors linked to body-size variation are the result of interactions between intrinsic and extrinsic conditions. For example, the relative roles of nutrition and a colony's social environment on body size can vary based on demography and feedback between environmental and internal factors.

Nutrition

Nutrition has long been considered an important factor determining the body size of insects (133, 134). Access to balanced protein and carbohydrate-based resources is essential for larval development (33, 139), and sufficient quantities are necessary to invest into larger-bodied workers because they require greater investment in biological building materials (36, 111). Moreover, in many species, nutrition and development are linked (134). For example, nutrient provisioning can alter juvenile hormone levels, and with sufficient provisioning, larvae can develop into workers of larger sizes (133) and resource availability alters colony investment in worker body size and body-size distributions within a colony (81, 139).

Body size is not only influenced by the overall amount of food received but also by nutritional quality. The use of stable isotopes allows researchers to estimate the relative proportions of carbohydrate and protein investment into worker pupae. In *Pogonomyrmex badius*, nitrogen-to-carbon ratios were higher for major than minor workers and highest for queens (121). The ratio of carbohydrates and proteins may also affect individual worker survival and overall colony size (33, 139). Specifically, colonies reared on high-protein diets tend to be smaller than colonies reared on more balanced diets (33). Small colonies, in turn, may have an impact on body sizes of workers within the nest through changes in foraging success or through social interactions (see the section titled Social Environment below). We should therefore expect to find interactions between the food availability, foraging success, and colony investment into worker size. In a test of this theory,

McGlynn & Owen (81) found an increase in soldier pupa production (e.g., change in worker subcaste ratios) of *Pheidole flavens* colonies in food-supplemented forest plots compared to forest plots not supplemented with food.

Colonies may change larval nutrition in response to shifts in food availability or adjust the food flow within a colony (111, 134). Changes in climate and temperature likely influence the size and type of food resources available (113), and changes in photoperiod and temperature may serve as reliable cues to a change in quality or quantity of food resources. The seasonal availability of food resources may constrain how and when colonies invest in worker size. For example, when resources are abundant, seed-harvesting *Veromessor pergandei* colonies produce larger workers than they do during periods of reduced seed availability (111). Colonies may also invest in the production of larger workers in anticipation of seasonal food scarcity as larger-bodied workers may serve as living food stores (repletes) (77, 129); repletes can help colonies survive periods of starvation (51) and are likely important components of colony fitness in seasonal climates.

Changes in food availability (e.g., differing climates, seasons, etc.) may also influence worker proficiency in food retrieval and defense (36, 88). Colonies with access to sufficient food resources of the appropriate quality may invest in larger workers or workers with specialized morphologies that can further improve task efficiency and colony fitness. Seasonal variation in resource availability could therefore result in colonies shifting investment into workers to improve foraging success. However, because ants show sufficient behavioral plasticity and cooperative foraging to respond to environmental changes, body size within a colony may not change in response to seasonality or food availability (9, 124). Selection may also favor stable investment in a certain body-size range and proportion of discrete castes that can best meet the full range of environmental challenges the colony faces simply because of the mismatch between relatively long development times from egg to adult and fast shifts in environmental conditions (88, 103). Currently, changes in a colony's investment in worker size relative to seasonal variation in resources remain largely untested.

Social Environment

Social environment within a colony can have large impacts on the variation of body sizes within a colony. By social environment, we mean factors that are directly related to the colony's traits and ontogeny as a whole. These include, but are not limited to, the age and size of a colony, the social form of the colony (e.g., monogyne versus polygyne), the worker caste distribution, and influences of pheromone control that are related to any of the aforementioned factors. For example, in many ants, body-size distribution changes as the colony ages and grows. Specifically, it may take many years for long-lived colonies to start producing the largest workers (13, 126, 127, 145). In many species, recently founded queens initially produce nanitic workers, which are smaller than those produced later in life (55, 126). Flexibility in worker production based on age is advantageous because smaller workers are energetically less costly for a nonforaging queen to produce during the early founding stages of colony growth (98). Subsequently, as colonies continue to grow and more workers are produced, the production of larger workers (majors) increases (126, 127). This pattern has been well described in *S. invicta* (126) and is also seen in many species of *Pheidole* (59), *Pogonomyrmex* (65), and the long-lived colonies of *Atta* (145).

Queen number may also be an important determinant of body-size variation in ants (38, 45). In the red imported fire ant, *S. invicta*, colonies can occur in two social forms, single-queen (monogyne) and multiple-queen (polygyne) colonies. Generally, the distribution of worker sizes is greater in monogyne colonies than in polygyne colonies (46). Variation in *S. invicta* social form is associated with allelic differences at the general protein-9 (GP-9) locus. Monogyne colonies have GP-9 *BB* queens, whereas polygyne colonies have GP-9 *Bb* queens (the genotype GP-9 *bb* is

largely lethal) (71). Queens in monogyne colonies tend to be larger and more fecund than those in polygyne colonies (70, 71). Interestingly, during development, monogyne and polygyne queens differ little in weight and fat content (70). However, cross-fostering experiments revealed that mature queens (postmetamorphosis) in monogyne colonies weighed more and had a greater fat content than those from polygyne colonies (70). This exemplifies the synergistic nature of intrinsic influences on body size in ants. Here, the genotype at GP-9 (and its closely linked genes) plays an important role in determining queen phenotype and the number of queens in the colony. In turn, queen number influences the social environment and the body sizes of workers and new reproductives (both males and queens) produced by the colony.

The current distribution of worker body sizes can also influence future investment in body size. In some *Pheidole*, major workers tend to show a reduced efficacy in brood care (82), and the presence of majors in a colony can suppress the development of larvae into more majors (133, 136). Experiments that artificially remove castes from laboratory colonies can lower the rate of worker production (12, 97), brood survival (82), and the development of early- and late-instar larvae (97). The mechanism by which body sizes vary as a result of differences in social environment may be attributable to differences in food availability (21, but see 97), queen pheromone control (47), and the influence of cues that come directly from specific worker castes (136). Finally, the strong influence of ecological factors, such as temperature (10, 127) and competition (89), on the social environment within a colony highlights the interconnectedness of factors determining worker body size.

ASSESSING ADAPTIVE BENEFIT OF BODY-SIZE VARIATION

Different approaches to assessing the adaptive benefits of body-size variation can be effectively combined within or across studies. Nevertheless, by far the most common approach is to assess the efficiency of task completion by a focal ant size relative to other colony members and to determine how these size-related differences scale up to influence overall colony efficiency (reviewed in 31, 55). Efficiency is defined here as some measure of the rate of task throughput. This approach was established by the ergonomic theory of caste formulated by Oster & Wilson (88). The theory seeks to explain the adaptive evolution of body-size variation, including distinct castes, within a framework of optimization of task handling and work throughput within the colony, in much the same way that a factory production line might be optimized. This approach is inherently appealing within the context of the widespread factory-like division of labor in insect societies (55). The general prediction in such studies is that the adaptive benefits of body-size variation should be detectable as efficiency gains in the focal individuals versus in other colony members (e.g., 9, 82, 97, 104, 144). In laboratory studies of the ergonomic efficiency of body size, the focal task or tasks are often simply any tasks that the focal size class participates in, without explicit knowledge of the ecological contexts under which they usually perform the tasks or the importance of the tasks for colony fitness.

A second approach to assessing the adaptive benefits of body-size variation, far less common than focusing on efficiency, is to assess the functional performance of the focal size range of individuals in contrasting ecological contexts (e.g., 100, 104, 106). This approach is derived not from the long-standing emphasis on collective ergonomic efficiency in social insect research (88) but from the broader functional ecology literature that focuses on novel functional capabilities in particular ecological contexts (reviewed in 62, 63). The general prediction here is that the focal individuals provide an adaptive benefit if they are found to perform a function maximally under the ecological conditions they face most often. Critically, the function they perform must have some known benefit to colony fitness. This approach, unlike the emphasis on efficiency,

therefore requires knowledge of the species' range of natural ecological interactions and the direct involvement of the focal ant size in them. The focus in data collection is not on a metric of rates of task throughput relative to other individuals, but on the maximal functional capabilities of the focal ant size across a range of ecological contexts.

The final general approach to assessing the adaptive benefit of body-size variation is to directly link the presence of body-size variation with some measure of colony fitness. With this approach, task efficiency or performance may not be addressed directly. Instead, body-size range is manipulated, and the effects of this manipulation on fitness are tracked (e.g., 12, 13). The general prediction here is that if the existing body-size variation is adaptive, any change in that body-size variation should result in a detectable change in colony fitness. Nevertheless, direct metrics of fitness remain challenging in ant research. Across all studies, a true measure of fitness, meaning representation in the next generation, is extremely challenging (but see 48). This is due to the extended life history of ants, often with many years before reproductive maturity is reached, and the subsequent wide dispersal of reproductive units (reviewed in 55). Instead, fitness is typically measured by some meaningful proxy. Arguably, the best-case scenario for a fitness proxy in ants is a measure of the number and quality of reproductive units the colony produces. Beyond these measures, the best proxy may vary with taxa. For example, measuring the rate of worker production (e.g., 12, 97) may be a meaningful proxy for fitness in taxa that reach reproductive maturity at small colony sizes, where each additional worker represents a greater proportional increase in the workforce. Regardless, we know little about the relationships between worker number and reproductive output within and across taxa (but see 100, 127).

Beyond measures of reproduction and growth, meaningful proxies of colony fitness can only be reasonably assessed from intimate knowledge of the biology of the focal taxa. They may include any level of colony-level performance beyond the individual-level performance of the focal size class of individuals, such as nest size or number (e.g., 100, 127), or submeasures of reproduction and growth, like larval growth rates and survival (e.g., 82). Nevertheless, it must be acknowledged that the further one moves from direct measures of fitness, the less reliable these proxies become. In ant research in particular, complexity in colony structure and life history often results in sharp trade-offs between convenience and directness of fitness measures. Further development of reliable and tractable metrics of colony fitness in polymorphic taxa would therefore be a valuable focus for future work.

CONCLUSIONS AND FUTURE DIRECTIONS

The primary goals of this review are to recognize the internal and external factors that are associated with worker body size in polymorphic ant species and to identify proximate and ultimate explanations for worker body-size variation where possible. We also review how body-size variation can benefit colonies. We find that the genetics and development of morphologically distinct castes in workers are areas that have received considerable attention. However, a limitation of this literature is that we do not yet have functional analyses at the genetic level. More quantitative data is also needed to describe the amount of variation in worker body size within and between species (49). Additionally, we need to improve our understanding of how ecology influences colony investment in worker body size and colony fitness.

In pursuing a more complete understanding of the intrinsic and extrinsic factors, and their individual proximate and ultimate causes, we will be able to more completely identify the roles of phenotypic plasticity and developmental controls in shaping possible patterns of body-size variation, and understand how body size responds to abiotic and biotic pressures. Moreover, phylogenetic analyses of variation in worker body size will also be particularly important for

testing hypotheses relating to the evolution and maintenance of worker polymorphism in ants. Below we highlight a few priority areas for future research.

Does Variation Generally Lead to More Efficient Division of Labor?

Colony investment into worker size and number is hypothesized to be related to colony performance, typically assessed as efficiency and ultimately as colony success (32, 88). However, few studies go so far as to measure the impact of worker-size variation on measures of colony fitness (7, 112). Those species for which experimental work has demonstrated benefits of worker-size variation typically have at least one novel morphological worker caste (e.g., soldiers), with that caste specialized for food retrieval, food processing, storage, and/or colony defense (9, 77, 100, 104, 129). Considering the importance of these roles, even a slight increase in benefit at the cost of additional investment into these castes should have a disproportionally positive influence on colony survival, competitive ability, and reproductive output (10, 100, 137).

Research supporting a general relationship between size variation and increased efficiency is limited, and the lack of resounding support for such a relationship may occur for a number of reasons. First, evolutionary history and associated developmental mechanisms may constrain worker-size variation (133, 134). Second, morphological variation among workers may appear as a result of selection on different traits such as queen–worker development (84, 133) rather than because of fitness gains associated directly with worker-size variation. Third, behavioral plasticity (11, 19, 29, 86) and group foraging behavior (124) may play more important roles in determining colony success than morphological variation. Fourth, we may lack reliable metrics for estimating colony efficiency or fitness based on body size (10, 23, 50, 97, 112). Finally, many metrics of worker-size efficiency are applied outside of the ecological context in which they evolved and to which they are putatively adapted.

Assessing metrics of efficiency under a range of natural contexts provides a more ecologically relevant test of the adaptive efficiency gains that workers of a given size or caste are predicted to yield (100). By identifying the metrics useful for estimating colony efficiency or fitness, we can start to develop more tractable experimental systems for addressing how and if worker-size variations impact colony fitness. Examples of useful approaches include manipulating physical caste ratios for long periods of time (e.g., many years) or creating single-cohort colonies to control for age-related division of labor (e.g., 19). Such experimental approaches might finally begin to empirically test the models for body-size variation proposed decades ago by Oster & Wilson (88). Although difficult, conducting these experiments under field conditions would be ideal for determining the fitness consequences (e.g., reproductive output) of such manipulations.

What Are the Evolutionary Patterns of Body Size and Body-Size Variation in Ants?

E.O. Wilson (141) asked whether relative abundance is associated with specific morphological or behavioral traits in ants. Although he found no general relationships, he noted that the two most species rich genera, *Camponotus* and *Pheidole*, are both polymorphic (141). While quantitative data regarding the variation within and among species are limited, databases dedicated specifically to ant traits and metrics exist (e.g., **https://antweb.org**, **http://globalants.org/**, **http://antbase.org/**) and provide opportunities for compiling and storing data associated with ant morphological variation. These data in conjunction with the recent development of robust phylogenies describing the relationships among most ant genera (17, 85) will allow for a careful examination of how body size and its variation relate to a wide variety of factors (including diversity, abundance, and

dominance) while controlling for evolutionary history. To our knowledge, relatively few recent studies have used comparative analysis to link ecological and worker morphological variation (56, 80, 99, 101, 105, 114). In using a comparative approach, we can develop a broader understanding of the relationship between ecology and worker body-size variation.

How Do Internal and External Factors Feedback to Promote Variation in Body Size?

Most examinations of body-size variation focus on either intrinsic or extrinsic factors. Even for ecological studies, there have been few holistic attempts to simultaneously measure the relative contribution of many factors. Experiments that covary temperature and nutrition to determine their relative impacts on foraging behavior and caste differentiation would be a good start. Similarly, more research quantifying community ecological factors on body size, such as the presence of conspecifics or the general influence of the competitive environment, is still needed. Ultimately, this will help bridge the gap between single-species patterns and community ecological approaches that seek to explain how ant assemblages form in nature based on interactions between body size and climatic, metabolic, or biogeographic factors (66, 72, 79).

Future research should take advantage of ant species with polymorphic workers that live over a wide geographic range so natural variation in biotic and abiotic factors can be utilized (**Figure 4**). The black carpenter ant, *Camponotus pennsylvanicus* (native to North America), or a number of introduced species, including *Solenopsis geminata*, *S. invicta*, *Pheidole megacephala*, *P. fervens*, *C. planatus*, and *C. sexguttatus*, provide good models for this approach as they have wide geographic distributions, are common in both urban and natural environments, and are easy to maintain in the lab, allowing for experimental manipulations and reciprocal transplant experiments (123).

Concluding Remarks

Body size is one of the most important life-history traits as it directly affects an organism's metabolism, thermoregulation, locomotion, reproduction, abundance, longevity, and diet (69, 92). Understanding determinants of body-size variation in ants is no trivial task. The complexity arises because of the division of labor and the presence of novel castes in some species. This suggests that the relative importance of extrinsic and intrinsic factors on worker body size varies within and between species (49, 116). This may explain why the vast majority of research examining body size is focused on solitary organisms (122) and relatively little work is done using social insects (16, 49, 88) or colonial organisms (117). Given the ecological dominance of ants in terrestrial environments (55, 76), failing to examine the factors influencing within- and among-colony body-size variation limits our understanding of body size roles in insect ecology. There exists a substantial amount of information about the factors influencing body size in ants, but there is much left to discover.

With the increasing availability of genomic data for ants (44), we are entering an exciting era for understanding the genetic, molecular, and developmental basis for body-size variation in ants. Using these tools, we have started to develop a deeper understanding of the interplay of multiple factors regulating size variation within polymorphic ant species (4, 78). Despite this growing understanding of the proximate causes of the expression of specialized castes or variation in worker size within nests, we still know very little about the ultimate causes of worker-size variation. Future work is required to explore and experimentally test how variation in body size both within and among colonies contributes to variation in fitness. This will require both extensive new ecological data to establish the natural and putative adaptive context of body-size variation, as well as field- and laboratory-based experimental studies that test adaptive function.
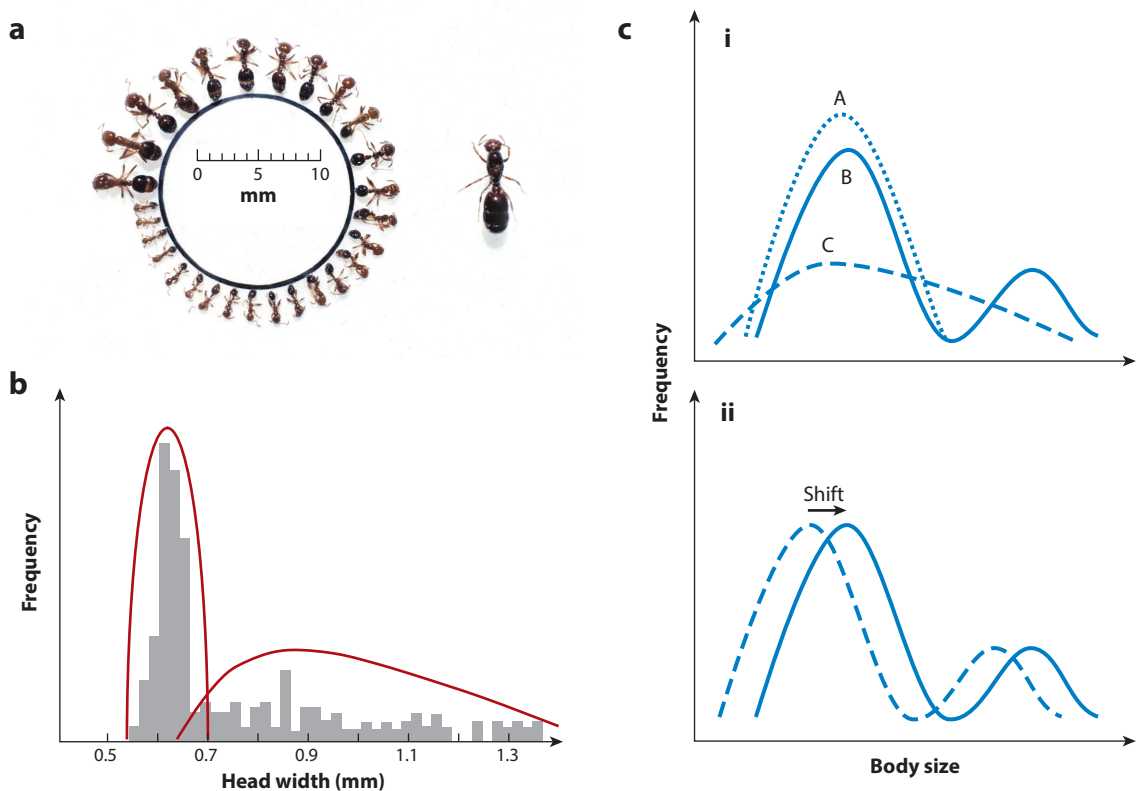
Figure 4

An example of a polymorphic ant species that is distributed over a large geographic area in which colonies experience a wide range of abiotic and biotic conditions. Species such as the red imported fire ant are ideal for comparative and experimental approaches to investigate proximate and ultimate factors influencing body-size variation in workers. (*a*) Continuous distribution of worker body size of the red imported fire ant, *Solenopsis invicta*. Workers encircle the scale of the photo and a queen is located to the right of the panel for scale. Photograph by S.D. Porter, US Department of Agriculture, Agricultural Research Service (used with permission). (*b*) Worker-size distribution can be categorized by two distinct subpopulations (*red lines*), one of a large number of relatively small workers located to the left on the frequency distribution graph and the other of a small number of medium- to large-sized workers to the right on the frequency distribution graph (redrawn from Reference 126). (*c*) Colonies of *S. invicta* can potentially control investment in worker size and shift worker distributions. (*c, i*) For example, they could opt to invest the same energetic resources into many small workers [*A* (*dotted line*)]; many small and a few large workers [*B* (*solid line*)]; or a relatively even number of workers of all sizes [*C* (*dashed line*)]. All three distributions would have the same mean worker body size. (*c, ii*) Colonies may instead evenly shift fixed worker-size distributions (and the mean) depending on environmental or colony conditions.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

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