

MINI REVIEW

The life history continuum hypothesis links traits of male ants with life outside the nest

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Abstract

An ant society, headed by a mated queen, can live for decades. Male ants, in contrast, are generally assumed to be ephemeral sperm delivery vessels programmed to die hours after leaving the nest to mate. However, the events from dispersal to mate location have rarely been studied, and the links between male traits and the ecological demands of diverse mating systems remain poorly understood. Here, we propose that interspecific variation in the length of mating flights has generated a life history continuum for male ants, and that the previously proposed ‘male aggregating’ and ‘female calling’ mating syndromes represent the endpoints. We also provide the first evidence for systematic divergence in pre-mating traits between males that attract females to brief nuptial swarms (Male aggregation syndrome) and those that must survive while searching for patchily distributed females that signal with pheromones (Female calling syndrome). Specifically, female-calling males tend to have larger eyes and mandibles, but the length of the basal antennal segment (scape) appears relatively constant across body sizes. After exploring these patterns, we review evidence that key components of fitness like mating frequency vary across a male life history continuum, and then explore links between male traits and a colony’s per capita reproductive investment. Systematic variation in pre-flight provisioning of males relative to mating systems may have important ecological implications, given that ants are dominant consumers on a global scale, and colonies ultimately use large fractions of harvested resources to fuel reproduction.

“The body of the male ant is graceful in form, one might say emaciated. Its sense-organs, wings and genitalia are highly developed; its mandibles are... imperfectly developed, and in correlation with the head, are proportionately shorter, smaller and rounder than in females... Yet, the male type may present interesting modifications.” Wheeler (1910: 93)

“The evolution of male [ant] biology has been subject to few rigorous studies, and most questions concerning trends and optimality in its evolution remain unanswered.” Hölldobler & Wilson (1990: 155)

Mating in ants takes place early in life, soon after virgin queens and winged males disperse from natal nests. Males die following copulation, but live on as sperm stored by the queen who founds a society of females. These societies can live for decades, gradually using the sperm stored during this single mating event to produce many thousands of workers whose coordinated efforts can have profound ecological impacts. And, whereas female ants have long been model systems in biology, advancing concepts ranging from the evolution of eusociality to the optimization of foraging behavior (Wheeler, 1910; Hamilton, 1964; Wilson, 1971; Hölldobler & Wilson, 1990; Bourke & Franks, 1995), male ants have remained mysterious.

A variety of factors have caused this knowledge gap. First, male ants have bizarre traits. They often look nothing like female nestmates, with small heads, large eyes, and reduced architecture (Figure 1) that makes identification

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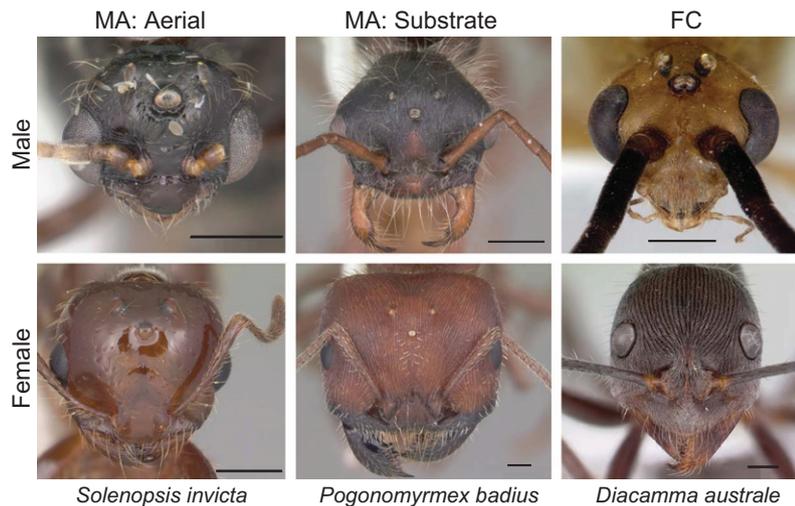


Figure 1 Representative male and reproductive female ants from opposite ends of the life history continuum. Although mating in female calling (FC) species invariably takes place on a surface, copulation in male aggregating (MA) species can occur on a surface or in the air. Male traits not only differ depending on their mating syndrome but they also generally look nothing like conspecific females. Scaling bars are 0.5 mm. All images courtesy of Antweb.org (see Table S1 for details).

difficult when captured outside the nest. Second, males are ephemeral. Their time in the nest is short, and being highly modified for a brief mating flight, they are relatively useless for the quotidian tasks of the colony. Third, they are elusive. Dispersal and copulation, and all the events in between, often occur in midair or cryptically on vegetation, making it difficult to observe male behavior, let alone understand the adaptive function of the males' traits. These unknowns impede our understanding of ants, dominant consumers across the planet whose colonies ultimately use harvested resources to fuel reproduction (Nielsen & Josens, 1978; MacKay, 1985; Tschinkel, 1993).

For instance, colonies provision queens for life after dispersal, with solitary founding species tending to have high fat stores (Keller & Passera, 1989) and wingless ergatoid queens having reduced flight muscles and associated production costs (Peeters & Molet, 2010). The number of reproductive females produced by a colony also trends lower in species where mating occurs inside or near the natal nest and reproductive females rely on sisters for colony founding (Peeters & Molet, 2010). However, we know little about how colony investment in males relates to the ecological demands of mating flights or the quality and mass of the sperm they deliver when mating.

Studies of male ants can also help reconstruct the unseen details of mating systems. For instance, although aerial copulation has not been directly observed in the leaf-cutter ant *Atta colombica* (Guérin-Méneville), Baer & Boomsma (2006) showed that males have genitalia

with recurved hooks and use a sawing behavior to anchor themselves inside a female. Although *A. colombica* females bear the scars of this conflict, it is males that receive injury in *Pogonomyrmex occidentalis* (Cresson). A bite from a queen signals the end of copulation, and some females retain pieces of broken male genitalia in their reproductive tracts (Nagel & Rettenmeyer, 1973). Moreover, elaborate courtship behaviors are generally absent in ants (Boomsma et al., 2005), but male size and shape can govern performance when scramble competition (common in surface-mating) governs access to females (e.g., *Pogonomyrmex* spp.; Davidson, 1982; Abell et al., 1999). After mating, male reproductive success is shaped by the quantity and quality of sperm (Wiernasz et al., 2001; Baer & Boomsma, 2004; Lawson et al., 2012), the chemistry of seminal fluids (den Boer et al., 2010), and the use of mating plugs (Robertson, 1995; Mikheyev, 2003; Boomsma et al., 2005). These dynamics suggest that both pre-mating and post-mating sexual selection can shape trait evolution in male ants, albeit in quite unusual ways as females do not remate later in life (Boomsma et al., 2005; Baer, 2011).

In contrast, we lack a synthesis explaining how pre-mating traits help males optimize performance during the critical window from dispersal to mate location. This dispersal window is generally assumed to be brief, but has rarely been measured. As we develop in more detail below, males likely lead complex lives outside the nest. This increases the opportunity for natural selection to shape

pre-mating traits and adds an ecological mating-system component to the analysis of male traits.

Our goal of linking male traits with life outside the nest is preliminary: mating systems of only a few of the over 12 000 ant species have been studied in detail (Baer, 2011). However, existing descriptions suggest a diversity of reproductive strategies. Males of *Eciton burchellii* (Westwood) (Franks & Hölldobler, 1987) and *Ophthalmopone* (= *Pachycondyla*) *berthoudi* Forel (Peeters & Crewe, 1986) must pass a gauntlet of workers when entering a foreign colony in pursuit of a wingless, non-dispersing queen; males of *Linepithema humile* (Mayr) often mate without dispersing (Keller & Passera, 1992); *Cardiocondyla* males often remain in the natal nest to control harems of females (Mercier et al., 2007); many *Mycocepurus smithii* (Forel) populations lack males altogether (Rabeling et al., 2011). Male ants also secure mates by using concave gasters to snugly affix onto females in *Myrmecaria opaciventris* Emery (Kenne & Dejean, 1998), by guarding pupating females still inside cocoons in *Hypoponera opacior* (Forel) (Foitzik et al., 2002), and by using chemical deception to avoid detection when searching for females in alien colonies in *Cardiocondyla obscurior* Wheeler (Cremer et al., 2002). Other males are hardly ephemeral – *Camponotus herculeanus* (L.) males can live a year inside the nest before dispersing (Hölldobler & Wilson, 1990). To manage this diversity, Hölldobler & Bartz (1985) proposed the mating syndrome concept, which outlined unifying themes in ant reproductive biology, and which we use to explore the evolution of male pre-mating traits.

Mating syndromes have distinct flight ecologies

Hölldobler & Bartz (1985) defined two mating syndromes: male aggregation (MA) and female calling (FC). Male aggregation mating flights are generally synchronized within populations, with males forming massive, but ephemeral swarms (e.g., <5 min in *Aphaenogaster treatae* Forel; Talbot, 1966) that attract winged females. The largest MA swarms rank among the most dramatic events in insects. Moments before takeoff, nest entrances are a flurry of activity, with reproductives preparing to fly, some mating near the nest entrance (Harmon, 1993), workers frantically pulling others back into the nest, and diverse predators harvesting many just after taking flight (Warter et al., 1962; Levin et al., 2009). Males typically disperse first, forming swarms from 1 m above the ground in *Lasius alienus* (Foerster) (Bartels, 1985), to 40 m in *Myrmica laevinodis* Nylander (Hubbard & Nagell, 1976), to over 200 m in *Solenopsis invicta* Buren (Markin et al., 1971). Male aggregation swarms vary greatly in size, containing from <100 to many thousands of ants and are

usually, but not always, male dominated (Wilson, 1957; Eberhard, 1978).

Female calling mating flights, in contrast, occur at low densities when virgin queens disperse and then use pheromones to attract males. In *Formica montana* Wheeler, a lone female walks a short distance from the natal nest, perches on low vegetation, arches her gaster in the air, and remains motionless until a male approaches flying upwind 1 m above the ground with rapidly probing antennae (Kannowski & Johnson, 1969). The scale of FC mating events ranges from one calling female in *F. montana*, to 500 in *Pseudomyrmex ferruginea* F. Smith (Janzen, 1967). Male and female dispersal likely ranges from closely timed in FC species like *Cataglyphis cursor* (Fonscolombe) (Lenoir et al., 1988) and *Temnothorax pergandei* (Emery) (Heinze et al., 1995), to decoupled in *Gnamptogenys menadensis* (Mayr) (Gobin et al., 2001) and *Rhytidoponera metallica* (Smith) (Haskins, 1978). At the extreme, mating opportunities are likely to be completely unpredictable in *Dinoponera quadricaps* Kempf, where females only start calling when the α -breeder (i.e., gamergate) has died or disappeared (Monnin & Peeters, 1998). Similar asynchronous phenologies are common among species in tropical forests (Kaspari et al., 2001a; Torres et al., 2001) and suggest either a continuous supply of free-living males searching for calling females, or continuous dispersal of ephemeral males from natal nests.

A life history continuum in male ants

The potential for male trait divergence under the distinct flight ecologies of the MA and FC syndromes remains largely unexplored. We posit that male life histories have evolved along a central axis – the duration of mating flights. Although males are known to live from days to up to a year in the nest before dispersing (e.g., *M. laevinodis*; Wheeler, 1910), recent evidence suggests this variation also extends to life outside the nest. Specifically, male life span appears linked to mating syndromes, with swarming MA males dying hours after leaving the natal nest, but searching FC males living weeks to months outside the nest when provided energy-rich nectar in laboratory experiments (Shik & Kaspari, 2009). Male starvation tolerance further appears independent of body size and thus the size-dependent balance between energy storage and energy consumption (Shik et al., 2012), suggesting that the typical physiological correlates of longevity (e.g., body size, metabolic rate; Peters, 1983) do not apply to male ants.

We propose the ‘life history continuum’ hypothesis (LHC) as an alternative to the assumption that male ants are uniformly ephemeral sperm delivery vessels programmed to die soon after dispersing (Shik et al., 2012).

The LHC builds on the observation that MA males generally die after a brief mating swarm, and holds that FC males must survive to locate calling females at low densities – a journey that may take days or possibly even weeks. Because MA species tend to initiate mating flights at a characteristic hour of the day and time of the year (Kannowski, 1959; Hölldobler & Bartz, 1985; McCluskey, 1992), the LHC predicts that the pre-mating traits of MA males reflect the ecological conditions at dispersal (e.g., enhanced visual systems for night fliers; Narendra et al., 2011). In contrast, given the more continuous nature of female availability for FC species (Haskins, 1978; Hölldobler & Bartz, 1985; Kaspari et al., 2001b), the FC male must be more of a generalist, with traits adapted to a broader range of ecological challenges.

As a first test of the LHC framework, we review evidence of differences in morphological, physiological, and chemosensory pre-mating traits of male ants that swarm (MA) or search (FC). We combine this with the first analysis of male traits across mating syndromes, using published descriptions of mating events to identify the syndrome (Table S1) and omitting species where the mating syndrome was ambiguous [e.g., *Paltothyreus tarsatus* Fabricius was described as FC by Villet et al. (1989) and as MA by Peeters et al. (2013)]. We only use species if trait data could be gathered from at least one specimen or an image from the Antweb portal (www.antweb.org). In some cases, we estimated traits from congeners assumed to have the same mating syndrome (Table S1). We examined scaling relationships between male traits and body size (estimated as head width; HW), using least squares mean regressions on log-transformed values to estimate the slope (b) and intercept (a) in the scaling equation $\log(\text{trait}) = \log(a) + b \log(\text{HW})$. We then used analysis of covariance (ANCOVA) to test for differences in these parameters across mating syndromes.

Linking male traits and mating syndrome ecology

As described above, when flight times are predictable, male visual systems likely reflect those prevailing conditions. Narendra et al. (2011) compared visual traits across four MA species of *Myrmecia* and found that low-light flying males of *Myrmecia nigriceps* Mayr have the highest relative eye area with 50% more ommatidial facets than conspecific workers. However, male *Myrmecia* also pair large eyes with relatively small facets, and likely have lower resolving power than female alates (Narendra et al., 2011). Male ants also tend to have larger ocelli than female alates, with this dimorphism being extreme in night flying species (Cody & Watkins, 1986; Moser et al., 2004; Narendra et al., 2011). More generally, although eye size is known to

scale differently with body size across species of birds (allometry, $b < 1$; Brooke et al., 1999) and bees (isometry, $b \approx 1$; Jander & Jander, 2002), the general result is that nocturnal species similarly have exceptionally large eyes for their size ($a_{\text{nocturnal}} > a_{\text{diurnal}}$). As a first step in comparing visual systems between mating syndromes, we compare the scaling of male eye size.

We expected that whereas male eye length (EL) is closely tied to body size (HW) for FC species, it depends more on dispersal hour for MA species. However, dispersal time was lacking for most species in the dataset, so we simply tested whether EL was more tightly correlated with HW for FC species than for MA species. Although MA species included both diurnal and nocturnal dispersers, EL was as tightly linked to HW for this syndrome ($R^2 = 0.86$) as it was for FC males ($R^2 = 0.93$). Eye length did scale differently across mating syndromes (Table 2), with a slope approaching isometry ($b = 1.03$; Table 1) for FC males and allometry for MA males ($b = 0.83$; Table 1) (Figure 2A). It will be important to add temporal niche into this analysis, but this preliminary result suggests that the eyes of MA males are under relaxed selection to increase proportionately with body size.

Sensory adaptations are rooted in information processing systems, which we predict are more developed in FC males given the complex decision making needed to avoid predators and find food while searching for a mate. The mushroom body in ant brains, thought to control advanced social behaviors and learning, generally tends to be reduced in males, which may reflect the ‘hard-wired’ nature of male ant behavior (Gronenberg, 2008). However, although males tend to have smaller brains than reproductive females, a variety of species, including searching FC males of *Ectatomma ruidum* (Roger) have larger optic lobes, antennal lobes, and central bodies than workers (Gronenberg & Hölldobler, 1999; Gronenberg, 2008). In addition, given that small worker ants (<0.9 mg) tend to have brains comprising ca. 15% of body mass (Seid et al., 2011), it will be interesting to explore scaling of brain size in male ants, given that their heads are frequently much smaller than conspecific reproductive females (Figure 1). Moreover, the energetic costs of fueling brains equipped for extended survival outside the nest may involve, as of yet, undiscovered trade-offs.

Flight is costly relative to walking; a volant male outside the nest for an extended period likely has to refuel at some point (Shik et al., 2012). Males of *Formica lugubris* Zetterstedt use 77% of their carbohydrate stores during a single mating flight (Passera et al., 1990), while male *Atta sexdens* (L.) nearly exhaust their carbohydrate stores during only 100 min of flight (Jutsum & Quinlan, 1978). We posit that plant nectar is the key resource enabling extended

Table 1 Results from least squares mean regression for scaling of eye length (EL), mandible length (ML), and scape length (SL) with head width (HW) for male ants from the male aggregating (MA) and female calling (FC) mating syndromes, using the scaling equation $\log(\text{trait}) = \log(a) + b \log(\text{HW})$. n denotes the number of species in analysis, CI confidence interval

Mating syndrome	Trait	n	MS model	MS error	F	R ²	a ± SE	b ± SE	95% CI of b
Male aggregation	EL	32	1.02	0.01	189.66	0.86	-0.44 ± 0.01	0.83 ± 0.06	0.70–0.96
	ML	32	2.39	0.02	154.09	0.84	-0.43 ± 0.02	1.26 ± 0.10	1.06–1.46
	SL	32	2.51	0.10	25.66	0.46	-0.38 ± 0.06	1.29 ± 0.26	0.77–1.81
Female calling	EL	14	1.19	0.01	165.35	0.93	-0.37 ± 0.02	1.03 ± 0.03	0.86–1.20
	ML	14	1.01	0.03	30.36	0.72	-0.50 ± 0.05	0.95 ± 0.17	0.57–1.33
	SL	14	0.28	0.03	8.24	0.41	-0.58 ± 0.05	0.50 ± 0.17	0.12–0.88

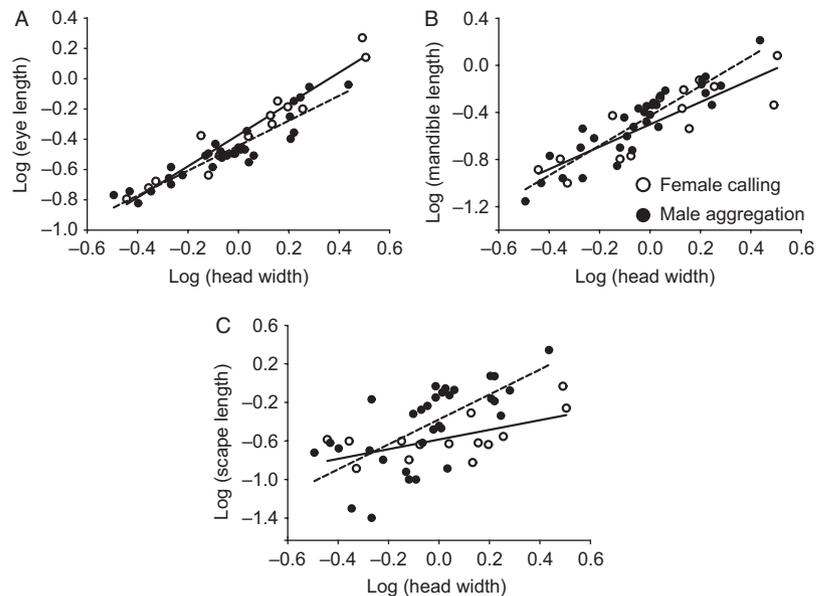


Figure 2 Scaling of (A) eye length, (B) mandible length, and (C) scape length with head width for male ants of the male aggregation (MA) and female calling (FC) mating syndromes.

searching periods, given that male flight is fueled primarily by stored carbohydrates (Peakin, 1964; Jutsum & Quinlan, 1978; Passera et al., 1990; Vogt et al., 2000). Males may also forage to avoid desiccation, given that water loss during flights is also considerable (Vogt et al., 2000). Studies of male digestive physiology will help test the idea that searching FC males are better equipped to feed outside the nest than swarming MA males. As a first test for feeding differences, we compared male mandibles across mating syndromes.

Robust mandibles are found on males that fight (Heinze & Hölldobler, 1993) and compete for access to females (Abell et al., 1999), although most males, especially aerially mating species, have small falcate ('strap-like') mandibles (Hölldobler & Wilson, 1990) (Figure 1). However, mandible morphology also reflects feeding behavior in ants, and we reason that whereas feeding FC males uniformly have developed mandibles, such mandibles are only found in MA males when they enhance copulation success. Indeed,

the relationship between mandible length and head width is approximately isometric in FC males ($b = 0.95$; $R^2 = 0.72$), but larger MA males tend to have relatively longer mandibles ($b = 1.26$; $R^2 = 0.84$) (Figure 2B). This result suggests that for larger MA males, the task of grasping females during aerial copulation becomes more challenging. However, this hypothesis represents a starting point given the paucity of knowledge on the physics of midflight copulation, and the as of yet unknown ecological functions of mandibles in free-living males.

Male ants have diverse chemosensory adaptations, even though they often lack metapleural glands (Brown, 1968; Hölldobler & Engel-Siegel, 1985; Yek & Mueller, 2011), as well as a sting and thus glands associated with the sting apparatus (Hölldobler & Engel-Siegel, 1982). For instance, army ant males must enter foreign nests in search of queens, and have highly developed abdominal glands possibly to advertise their quality to queen-retinue workers (Franks & Hölldobler, 1987). Dispersing *C. obscurior*

males chemically disguise themselves as virgin queens to avoid conflict with wingless resident males (Cremer et al., 2002). Males also produce diverse semiochemicals with unclear functions (Brand et al., 1973; Blum, 1981; Adams et al., 2010), but little is known about how they detect queen pheromones, given that volatile signals remain relatively unstudied in ants (d'Ettorre & Lenoir, 2010). Traits enhancing olfaction are likely to be especially developed in FC males, like *R. metallica* (Hölldobler & Haskins, 1977) that must detect single calling queens at long distances. As a first step in comparing chemosensory traits of MA and FC males, we examine the length of the basal antennal segment, known as the scape. As we collected data from full-face images that often cut off antennal segments (e.g., Figure 1), scape length (SL) was considered a more reliable way of comparing antennae across species than either the number or length of antennal segments.

The scaling of SL with HW differed significantly between mating syndromes (Table 2). Although larger MA males had increasingly long scapes ($SL \approx HW^{1.29}$; $R^2 = 0.46$), SL only weakly increased with HW among FC males ($SL \approx HW^{0.50}$; $R^2 = 0.41$) (Figure 2B). The low R^2 of both relationships (Table 1) suggests that scapes more freely respond to selective pressures than either EL or ML. To explain this result, we propose that scape length in FC males is mediated by a trade-off between the benefits of extending antennae away from the head (i.e., detecting female calling pheromone) and the costs (e.g., risks of antennal damage or diminished flight performance). This assumes that pheromone detection is weak in the thin (≤ 1 mm; Oke, 1978) boundary layer surrounding the ant's head, and that the thickness of this boundary layer is constant across all body sizes. If so, whereas FC males have uniformly long scapes that keep antennae an optimal distance from the head, large MA males have relatively longer scapes, given the benefits for pheromone detection combined with life spans that are too short to realize the costs. Rapid female detection may be especially useful for surface-mating MA males where it pays to initiate, and not react to, a mating scum. Regardless of the mechanism, the result that disproportionally long scapes appear adaptive for MA species, but not in FC species, begs further study.

Mating syndromes and male mating frequency

Male ants are typically assumed to mate once during a single brief mating event (although as we describe below, this assumption is often violated), given that they are unable to produce new sperm as adults (Hung & Vinson, 1975; Keller & Passera, 1992; Wheeler & Krutzsch, 1992), and often discharge all their sperm in a single mating

Table 2 Results of ANCOVAs testing differences in the size (measured by head width, HW) dependence of traits for males that differ in mating syndrome (MS), i.e., that acquire mates by swarming (male aggregating) or searching (female calling). All data are log-transformed prior to analysis

Trait	Factor	d.f.	Type III SS	F	P
Eye length	Head width	1	2.21	374.34	0.0001
	Mating syndrome	1	0.05	7.96	0.007
	HW*MS	1	0.03	4.62	0.04
	Error	42			
Mandible length	Head width	1	3.14	152.44	0.0001
	Mating syndrome	1	0.05	2.51	0.12
	HW*MS	1	0.06	3.09	0.09
	Error	42			
Scape length	Head width	1	2.06	25.92	0.0001
	Mating syndrome	1	0.42	5.22	0.03
	HW*MS	1	0.40	5.08	0.03
	Error	42			

attempt (e.g., *Formica polyctena* Foerster; Hölldobler & Bartz, 1985). However, copulation ranges from suicidal in *Diacamma rugosum* (Le Guillou) (Fukumoto et al., 1989) and *D. quadriceps* (Monnin & Peeters, 1998) where male gasters are dismembered following copulation, to repeated copulations over an extended life span in the nest in some *Cardiocondyla* species where males produce sperm as adults (Heinze & Hölldobler, 1993). Multiple mating attempts can also be promoted by extremely female-biased operational sex ratios (Boomsma et al., 2005), especially when males can dominate access to these females inside the nest (Yamauchi et al., 1991; Foitzik et al., 2002; Allard et al., 2008). Here, we propose that FC males also have more opportunity for multiple mating attempts.

Males are known to resume flying after the first copulation or attempt multiple copulations with the same or different partners in diverse FC species like *F. montana* (Kannowski & Johnson, 1969), *P. tarsatus* (Villet et al., 1989), *C. cursor* (Lenoir et al., 1988), *Leptothorax gredleri* Mayr (Obserstadt & Heinze, 2003), and *Gnamptogenys striatula* Mayr (Allard et al., 2008). Moreover, recent insights into the flight ecology of the FC species *E. ruidum* suggest that if males are capable of multiple ejaculations, they may be able to spread mating attempts among multiple sexual females. First, even though an *E. ruidum* male cannot produce new sperm after dispersing, he matures with ca. 200 000 sperm, which is likely orders of magnitude more than a singly mated queen would

require to reach a mature colony size of a few hundred workers (Shik et al., 2012). Second, laboratory experiments show that an *E. ruidum* male can survive a month after dispersing if provided energy-rich nectar (Shik & Kaspari, 2009), suggesting that matings can be spread over time. More generally, whereas large colony sizes may select for multiple mating in ant queens (e.g., Crozier & Page, 1985; Hughes et al., 2008), the small colony sizes of many FC species may present greater opportunities for males to distribute their sperm across multiple queens. Given that species differ in relative sperm discharge per mating event (Kronauer & Boomsma, 2007), it will be important to examine whether physiological capacity for male multiple mating varies among FC species based on average colony size.

There are several ways by which males of MA species could also have multiple mating opportunities. First, males of *Meranoplus peringueyi* Emery (Robertson & Villet, 1989), *M. opaciventris* (Kenne & Dejean, 1998), and *Paratrechina (Nylanderia) flavipes* (Smith) (Ichinose, 1994) can return to a swarm after mating. Second, males of *Myrmica ruginodis* Nylander (Elmes, 1991), *Myrmica americana* Weber (Kannowski & Kannowski, 1957), and several *Pogonomyrmex* species (Nagel & Rettenmeyer, 1973; Davidson, 1982) can persist for days after the initial swarm by clustering in vegetation or overhanging rocks. Third, males of *A. colombica* and *A. cephalotes* have sperm reservoirs that may enable multiple matings (Baer & Boomsma, 2006). Fourth, multiple male mating in the field has been observed in the species *P. badius* (Hölldobler & Wilson, 1990). Clearly, more studies of male dispersal are needed to understand the extent to which the MA stereotype of males dying soon after a single mating is actually correct.

Male investment costs across a life history continuum

Gyne-male cost ratios, based on dry mass, have been critical for studying queen-worker conflict over sex allocation (e.g., Trivers & Hare, 1976), but these may underestimate the energetic costs of male production and maintenance (Boomsma et al., 1995). Consistent differences in the size of male eyes, mandibles, and scapes across mating syndromes (Figure 2) may add an additional wrinkle by influencing male production costs across the ant phylogeny, much like colony founding strategy has influenced queen provisioning (Peeters & Molet, 2010). However, pre-dispersal maintenance costs may be more difficult to predict. Across species, male energy demands are accurately predicted by body mass (Metabolic rate \approx Body mass^{0.67}; Shik et al., 2012), which implies that larger

males have lower mass-specific requirements. Male body size can also increase intraspecifically with a colony's total reproductive output (e.g., *Pogonomyrmex desertorum* Wheeler; Davidson, 1982), and across species with colony size (Shik, 2008). However, male maintenance costs also vary in idiosyncratic ways, given that some disperse soon after eclosion whereas others must be fed over many months (Hölldobler & Wilson, 1990). Males may also feed far less than nestmate female alates; male *S. invicta* are known to increase in mass by only 6% from eclosion to dispersal, whereas female alates can increase by 275% (Tschinkel, 1993).

Next steps

At this point, we hope to have convinced the reader that male ants are more than ephemeral 'flying sperm missiles' and are worthy of the intense and productive eco-evolutionary studies of queens. The hypotheses we propose will survive or fail as more comparative studies of male traits reconstruct the unseen details of ant mating systems (e.g., Baer & Boomsma, 2006). Female calling, although thought to be ancestral in ants, will provide models for such studies having repeatedly evolved from MA as a solution to a variety of diverse challenges, including (1) species with small colonies where mates can be hard to find because so few are produced (Bourke & Franks, 1995); (2) social parasites where females attract males to patchily distributed host nests (Bourke & Franks, 1995); (3) species where sexual workers (gamergates) attract foreign males to the nest (Haskins, 1978; Peeters & Crewe, 1986; Monnin & Peeters, 1998; Gobin et al., 2001); (4) colonies with non-flying (ergatoid) queens (Peeters & Molet, 2010; Peeters, 2012); and (5) species in tropical forests where asynchronous flight patterns are common (Kaspari et al., 2001b; Torres et al., 2001). It will be important to explore male trait convergence among FC species that have followed these varied evolutionary pathways.

The mating syndrome paradigm is also not without limitations. For instance, it places emphasis on the mechanisms of locating sexual partners, and may not reliably predict female and male dispersal distances (e.g., Peeters & Molet, 2010). More field observations will be required to demonstrate that the MA and FC mating syndromes are truly groups of diagnostic symptoms consistently occurring together. In the meantime, Peeters & Molet (2010) suggest an alternative framework focused on how the mode of colony founding [queens independent or dependent (DCF) on an existing workforce] shapes many attributes of ant societies, including the behavior of males outside the natal nest.

'Dependent colony founding' ergatoid queens deserve special consideration given that they occur among unrelated species in over 50 genera (Peeters, 2012). These non-dispersing queens require searching males and set the stage for unique adaptations. For instance, males of *P. berthoudi* appear able to detect pheromones emanating from subterranean nests containing receptive gamergates (Peeters & Crewe, 1986), whereas males of *Pachycondyla analis* (Latreille) [formerly *Megaponera foetens* (Fabricius)] locate conspecific colonies by following pheromone trails laid by workers when hunting termites (Longhurst & Howse, 1979). In many species, these males must then gain entrance inside the nest, often passing through a hostile workforce (Ward, 1981; Peeters & Crewe, 1986). It will be interesting to explore whether these males use chemical disguises to smooth the entry process as in *C. obscurior* (Cremer et al., 2002). Mating frequency may also vary in predictable ways, given that a few males can inseminate potentially >100 gamergates in subterranean nests of the polygynous ant *P. berthoudi* (Peeters & Crewe, 1986), but males in the monogynous species *Pachycondyla sublaevis* (Emery) only mate with the most behaviorally dominant gamergate (Ito & Higashi, 1991). A more general conclusion is that long-lived searching males are likely far more common than currently assumed, given that factors like colony fission and budding, which promote DCF, are widespread across the ants.

Recent reviews have further documented the wellspring of fascinating morphological (Boudinot, 2013) and chemical (Baer, 2011) copulatory adaptations in the male ant arsenal. These traits may have surprising impacts on flight ecology if they constrain other aspects of dispersal. For instance, *A. colombica* males with larger sperm complements may have reduced flight performance (Fjerdingstad & Boomsma, 1997), and males of *Camponotus americanus* Mayr are known to void gut contents and fill gasters with air before dispersing, which likely improves flight performance, but may also reduce post-flight longevity (Wilson, 1971). The potential for trade-offs between flight and copulatory performance represents yet another promising avenue to study the ecology and evolution of male ants.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Data used to compare male traits across the male aggregation (MA) and female calling (FC) mating syndromes, representing 47 species from 35 genera. The mating behaviors of ‘species’ are described in the ‘mating syndrome source’ and the trait data were taken from a conspecific or congeneric ‘specimen’ listed in the ‘specimen source’. The traits, measured in mm, were head width (HW), eye length (EL), mandible length (ML), and scape length (SL). Trait data were not available for some of the species with known mating syndromes (indicated by *), so we used specimen data for congeners assumed to have the same mating syndrome. We provide the image identification code when these trait data were from antweb.org. Under ‘specimen ID’, CASENT specimens are from antweb.org, and MEK specimens are from collection of M. Kaspari. NA, no data available; A, average measurements taken from the literature where sample size was not provided.