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The flight ecology of ants (Hymenoptera: Formicidae)

Jackson A. HELMS IV



Abstract

Most of the world's ant species rely on flight for reproduction and dispersal, during a solitary phase in which colony fitness depends only on the survival of individual queens. Flight-related selection shapes ant physiology, such that queens and males fly for short durations but carry heavy loads due to the nutrient demands of mating and colony founding. Ants vary by four orders of magnitude in flight distance, with larger ants or those with lighter abdomens flying farther than smaller or heavier ones. Flight tradeoffs explain much variation in ant life history, including the temporal segregation of flight and egg production, the continuum of ant mating systems from male aggregation to female calling syndromes, and the evolution of alternate colony founding strategies. Flight performance also constrains range expansions or shifts in response to invasions or climate change. Flying queens and males act as dispersal vectors for pathogenic or symbiotic organisms, and are eaten in large numbers by aerial insectivores. By entering aerial food webs, flying ants help mediate the flow of energy and materials through ecosystems. They are also model systems for addressing several questions, including nutrient allocation tradeoffs and the evolution of reproductive polymorphisms.

Key words: Colony founding, dispersal, flight performance, Formicidae, mating flight, reproductive strategy, review, tradeoffs.

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Introduction

Most terrestrial animal species, including nearly all social insects, can fly (WAGNER & LIEBHERR 1992, DUDLEY 2000). They enter the air to forage, mate, evade predators, disperse, or perform other tasks. Even ants and termites, which have wingless worker castes, typically rely on flying individuals to mate and found new colonies (HÖLDOBLER & WILSON 1990, PEETERS & ITO 2001). In most of the world's 12,000 + ant species (BOLTON & al. 2006, ANTWEB 2017), males and queens fly to mate with individuals from other colonies, after which the queens locate nest sites and found new colonies (HÖLDOBLER & WILSON 1990, Fig. 1). Flightlessness among reproductive castes does occur, particularly among queens where it has evolved multiple times in over 50 genera (PEETERS 2012). But in almost all cases at least one flying reproductive caste remains – as either males or alternate queen morphs – so that flight remains the primary medium for mating and gene flow across the ants (ROSS & SHOEMAKER 1997, DOUMS & al. 2002, CLÉMENCET & al. 2005, BERGHOFF & al. 2008, PEETERS 2012).

Flight is also the only period when ants cease to be social and live instead as solitary individuals. Until young queens have found a nest site and begun laying eggs, the fitness of the incipient colony they represent hinges entirely on their own unaided survival. This is the deadliest phase in the life cycle, as queens are exposed to predation and adverse environmental conditions without the buffering effects of a cohort of workers, and over 99% of queens may die without founding a colony (NICHOLS & SITES 1991, GORDON

& KULIG 1996, PEETERS & ITO 2001, FJERDINGSTAD & KELLER 2004). The combination of solitary life, extreme mortality, and vital reproductive tasks results in strong flight-related selection (BUSCHINGER & HEINZE 1992, WIERNASZ & al. 1995, ABELL & al. 1999, WIERNASZ & COLE 2003, FJERDINGSTAD & KELLER 2004, SHIK & al. 2012, HELMS & KASPARI 2014, 2015).

The demands of flight help shape the immense ecological diversity among ants. Ants practice countless life history strategies, each of which entails different flight requirements (HEINZE 2008, PEETERS 2012). Flying queens vary by four orders of magnitude in body size and show substantial variation in wing size, flight muscle mass, and other aspects of flight morphology (PEETERS & ITO 2001, HELMS & KASPARI 2014, 2015). Similar variation exists among flying males (FORTELIUS & al. 1987, FJERDINGSTAD & BOOMSMA 1997, ABELL & al. 1999, SHIK & al. 2013). But how this variation impacts flight behavior is mostly unknown. This is partly due to the difficulty of studying ant flight – ants fly only once, under specific physiological and environmental conditions, and they are too small to easily track through the atmosphere. Recent advances, however, have begun to shed light on this inscrutable aspect of ant life.

Here, I review our current understanding of ant flight and suggest avenues of future work. Researchers have long recognized the dominance, diversity, and functional importance of ants in terrestrial environments (HÖLDOBLER & WILSON 1990, FOLGARAIT 1998, AGOSTI & al. 2000). Flying ants likely have a similar importance in aerial en-

Tab. 1: Ant flight performance estimates. In cases where references found a range of values, I report the maximum.

Subfamily Species	Sex	Duration (min)	Speed (m/s)	Altitude (m)	Distance (m)	Reference
Dolichoderinae						
<i>Azteca</i> sp.	F	–	–	–	400	BRUNA & al. (2011)
<i>Azteca ulei</i> FOREL, 1904	F	–	–	–	175	YU & al. (2004)
<i>Dorymyrmex flavus</i> McCOOK, 1880	F	–	–	105	–	HELMS & al. (2016b)
	M	–	–	111	–	HELMS & al. (2016b)
<i>Forelius pruinus</i> (ROGER, 1863)	Both	–	–	6	–	WARTER & al. (1962)
Formicinae						
<i>Camponotus ligniperda</i> (LATREILLE, 1802)	M	–	–	40	–	DUELLI & al. (1989)
<i>Camponotus pennsylvanicus</i> (DE GEER, 1773)	F	–	–	39	–	HELMS & al. (2016b)
<i>Colobopsis truncata</i> (SPINOLA, 1808)	Both	–	–	30	–	DUELLI & al. (1989)
<i>Formica lemani</i> BONDROIT, 1917	M	–	–	40	–	DUELLI & al. (1989)
<i>Lasius alienus</i> (FOERSTER, 1850)	F	–	–	7	–	BARTELS (1985)
	M	–	–	1	–	BARTELS (1985)
<i>Lasius bicornis</i> (FOERSTER, 1850)	M	–	–	70	–	DUELLI & al. (1989)
<i>Lasius brunneus</i> (LATREILLE, 1798)	F	–	–	70	–	DUELLI & al. (1989)
	M	–	–	150	–	DUELLI & al. (1989)
<i>Lasius carnolicus</i> MAYR, 1861	Both	–	–	150	–	DUELLI & al. (1989)
<i>Lasius flavus</i> (FABRICIUS, 1782)	M	–	–	100	–	DUELLI & al. (1989)
<i>Lasius fuliginosus</i> (LATREILLE, 1798)	Both	–	–	150	–	DUELLI & al. (1989)
<i>Lasius meridionalis</i> (BONDROIT, 1920)	M	–	–	150	–	DUELLI & al. (1989)
<i>Lasius mixtus</i> (NYLANDER, 1846)	F	–	–	100	–	DUELLI & al. (1989)
<i>Lasius neoniger</i> EMERY, 1893	F	–	–	22	–	HELMS & al. (2016b)
<i>Lasius niger</i> (LINNAEUS, 1758)	Both	–	–	150	–	DUELLI & al. (1989)
	M	–	–	200	–	CHAPMAN & al. (2004)
<i>Lasius umbratus</i> (NYLANDER, 1846)	Both	–	–	10	–	DUELLI & al. (1989)
<i>Petalomyrmex phylax</i> R.R. SNELLING, 1979	F	–	–	–	6000	DALECKY & al. (2007)
<i>Polyergus rufescens</i> (LATREILLE, 1798)	M	–	–	40	–	DUELLI & al. (1989)
Myrmicinae						
<i>Allomerus</i> sp.	F	–	–	–	150	YU & al. (2004)
<i>Aphaenogaster treatae</i> FOREL, 1886	Both	25	–	–	–	TALBOT (1966)
<i>Atta capiguara</i> GONÇALVES, 1944	Both	–	–	120	–	AMANTE (1972)
<i>Atta cephalotes</i> (LINNAEUS, 1758)	F	–	–	–	9700	CHERRETT (1968)
<i>Atta sexdens</i> (LINNAEUS, 1758)	M	140	1.57	–	11100	JUTSUM & QUINLAN (1978)
<i>Atta texana</i> (BUCKLEY, 1860)	Both	35	5.3	90	10400	MOSER (1967)
<i>Crematogaster decamera</i> FOREL, 1910	F	–	–	–	1103	TÜRKE & al. (2010)
<i>Crematogaster laevis</i> MAYR, 1878	F	–	–	–	90	BRUNA & al. (2011)
<i>Crematogaster laeviuscula</i> MAYR, 1870	F	–	–	76	–	HELMS & al. (2016b)
<i>Myrmecina graminicola</i> (LATREILLE, 1802)	M	–	–	20	–	DUELLI & al. (1989)
<i>Myrmica gallienii</i> BONDROIT, 1920	F	–	–	30	–	DUELLI & al. (1989)
<i>Myrmica rubra</i> (LINNAEUS, 1758)	M	–	–	40	–	HUBBARD & NAGELL (1976)
		–	–	5	–	DUELLI & al. (1989)
<i>Myrmica ruginodis</i> NYLANDER, 1846	F	–	–	70	–	DUELLI & al. (1989)
	M	–	–	150	–	DUELLI & al. (1989)
<i>Myrmica sulcinodis</i> NYLANDER, 1846	F	–	–	20	–	DUELLI & al. (1989)

Subfamily Species	Sex	Duration (min)	Speed (m/s)	Altitude (m)	Distance (m)	Reference
<i>Pheidole minutula</i> MAYR, 1878	F	–	–	–	30	BRUNA & al. (2011)
<i>Pogonomyrmex barbatus</i> (F. SMITH, 1858)	F	–	–	–	366	INGRAM & al. (2013)
<i>Solenopsis invicta</i> BUREN, 1972	F	–	–	240	16100	MARKIN & al. (1971)
	F	–	–	–	19300	BANKS & al. (1973)
	F	–	–	–	32200	WOJCIK (1983)
	F	60	1.5	–	5400	VOGT & al. (2000)
	F	79	–	–	7100	HELMS & GODFREY (2016)
	F	–	–	78	–	HELMS & al. (2016b)
	M	–	–	300	–	MARKIN & al. (1971)
	M	60	2	–	–	VOGT & al. (2000)
	–	–	88	–	HELMS & al. (2016b)	
<i>Temnothorax</i> sp.	F	–	–	119	–	HELMS & al. (2016b)
<i>Tetramorium caespitum</i> (LINNAEUS, 1758)	M	–	–	150	–	DUELLI & al. (1989)
<i>Tetramorium impurum</i> (FOERSTER, 1850)	M	–	–	150	–	DUELLI & al. (1989)
Unknown						
Unidentified ant	?	–	–	84	–	FREEMAN (1945)

vironments, which they enter in vast numbers (MARKIN & al. 1971, MORRILL 1974, KASPARI & al. 2001a, TORRES & al. 2001), and where they are eaten by predators and thereby transfer energy, nutrients, and contaminants to aerial food webs (WHITCOMB & al. 1973, HELMS & al. 2016a, HELMS & TWEEDY 2017). I therefore supplement the terrestrial view by looking upward and emphasizing the roles ants play in the air above our heads.

Flight physiology

Ant flight is characterized primarily by its short duration and the need to carry heavy loads, with the underlying mechanics similar to those in other insects. Ants probably experience Reynolds numbers – a dimensionless value that characterizes flight conditions and varies with body size and speed – from 100 to 1,000, well within the typical range for insects (DUDLEY 2000). They navigate to find mates and new nest sites using a combination of sight and pheromones (HÖLLDOBLER & HASKINS 1977, PEETERS 1997, NOORDIJK & al. 2008, PEETERS 2012, KING & TSCHINKEL 2016). They have correspondingly large eyes and antennae, particularly in males (SHIK & al. 2013, BOUDINOT 2015), and associated neural infrastructure like optic lobes, which can be up to 70 times larger in males than in conspecific workers (GRONENBERG & HÖLLDOBLER 1999). Flying ants of both sexes also possess well developed ocelli (PEETERS & al. 2012, SHIK & al. 2013, BOUDINOT 2015), which function in flight orientation and stabilization (KRAPP 2009). Nocturnal species may evolve larger ocelli, or larger ommatidia facets within their compound eyes (GRONENBERG & HÖLLDOBLER 1999), to compensate for darker flight conditions (e.g., queens of *Azteca instabilis* F. SMITH, 1862, LONGINO 2007). Ants differ from many other flying insects, however, in that they fly only once in their lives, almost always on a single day (HÖLLDOBLER & WILSON 1990). After this brief period, males die and females shed their wings and histolyze their flight muscles (HÖLLDOBLER

& WILSON 1990, PEETERS & ITO 2001). At the same time, female ants carry with them on their flights any nutrient reserves needed for founding a colony (KELLER & PASSERA 1989), and males carry a lifetime's supply of sperm for their potential mate (TSCHINKEL 1987, FJERDINGSTAD & BOOMSMA 1997, BAER 2011, DÁVILA & ARON 2017). The combination of short flights and heavy loads is reflected in queen and male physiology.

Like other hymenopterans, ants are thought to use glycogen for flight fuel, precluding long flights that would rely on high-energy fats (BEENAKKERS 1969, TOOM & al. 1976, JUTSUM & QUINLAN 1978, PASSERA & KELLER 1990, PASSERA & al. 1990, VOGT & al. 2000). Glycogen makes up only 1 to 10% of queen and male dry body weight and is depleted quickly after takeoff (TOOM & al. 1976, PASSERA & KELLER 1990, PASSERA & al. 1990, SUNDSTRÖM 1995). Ants are thus probably restricted to brief flights just sufficient to mate and disperse. Some females reduce flight time even further by attracting mates from the ground rather than searching for them in the air, and flying afterward only to locate nest sites (HÖLLDOBLER & HASKINS 1977, PEETERS & ITO 2001, PEETERS & ARON 2017). This energy conserving strategy likely entails increased nutrient demands for males, which may compensate by feeding after leaving the nest (SHIK & KASPARI 2009, SHIK & al. 2012, 2013). Flights may be as brief as one minute (TALBOT 1966, HELMS & GODFREY 2016), but there are few estimates of maximum flight duration (Tab. 1). Field observations (TALBOT 1966), calculations based on glycogen metabolism (VOGT & al. 2000), and timing of tethered flights (JUTSUM & QUINLAN 1978, MOSER 1967, HELMS & GODFREY 2016) yield maximum flight durations ranging from 25 to 140 minutes. More work is needed, however, to determine the extent of variation and its relation to morphology, nutrient allocation and life history.

Investing little in flight fuel allows ants to maximize investment in other tissues necessary for mating and colony

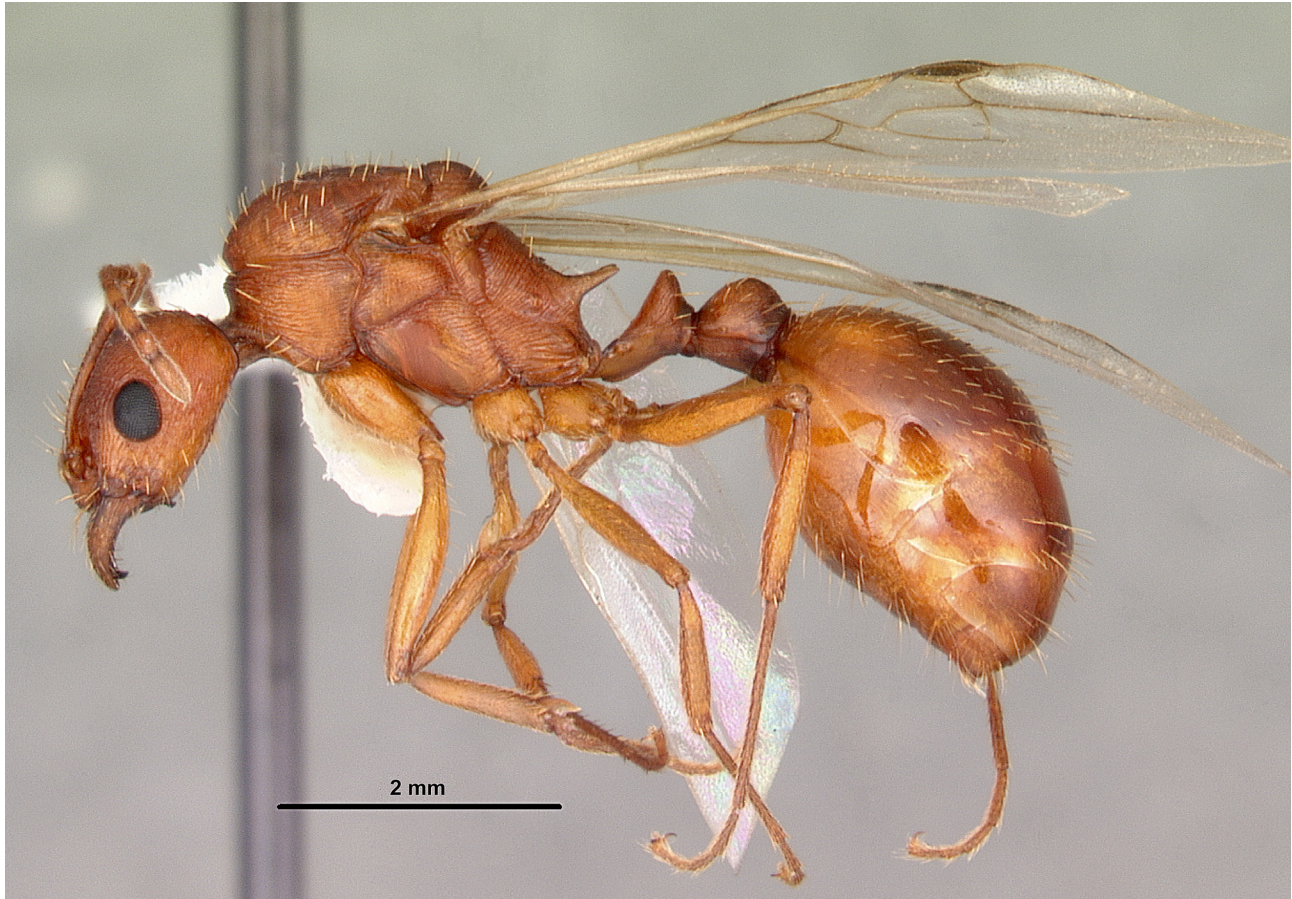


Fig. 1: In most ant species, males and young queens have wings and fly to find mates or disperse to new nest sites (pictured, *Aphaenogaster flemingi* queen, photographer April Nobile, from www.AntWeb.org).



Fig. 2: Flying ants often carry heavy abdomens packed with nutrient reserves for founding colonies (queens) or sperm for fertilizing potential mates (males). Some of them, such as male *Dorylus* driver ants, are among the largest ants in the world (photo by Alex Wild, with author in background).

founding (Fig. 2). Before flying, queens build up abdominal reserves of fats and storage proteins, which can make up over 60% of their body weight (PEAKIN 1972, BOOMSMA & ISAACS 1985, NIELSEN & al. 1985, KELLER & PASSERA 1989, MARTINEZ & WHEELER 1994, WHEELER & MARTINEZ 1995, WHEELER & BUCK 1996, HAHN & al. 2004, HELMS & KASPARI 2015). Males likewise produce large amounts of sperm (FJERDINGSTAD & BOOMSMA 1997, WIERNASZ & al. 2001, BAER 2011), and both

sexes develop massive flight muscles to carry the burden (VOGT & al. 2000, PEETERS & ITO 2001, HELMS & KASPARI 2015). Males of *Camponotus americanus* MAYR, 1862 reduce abdominal burdens before flight by voiding their gut contents (WILSON 1971), and other ants may do the same. Some queens nevertheless have abdominal nutrient loads so extreme they push theoretical limits of flight. They carry burdens of up to ~ 7 mg per mg of flight muscle (HELMS & KASPARI 2015), which would be impossible for most other insects (average maximum across insects ~ 5.5 mg/mg, average among non-ant hymenopterans 4.6 mg/mg, MARDEN 1987, 2000). How they manage this feat, and what morphological and physiological adaptations it entails, are unknown. At the same time, the discrete partitioning of tissues towards different tasks – glycogen and muscle for flight versus fats, storage proteins, and sperm for reproduction – makes ants ideal systems for studying nutrient allocation tradeoffs (HELMS & KASPARI 2014, KELLER & al. 2014).

Reproductive ecology

The link between flight and reproduction in ants, and tradeoffs between the conflicting demands of each, are captured in three flight-related hypotheses that explain much of the variation in ant life histories (Tab. 2). First, the oogenesis-flight syndrome hypothesis (JOHNSON 1969) views the temporal partitioning of dispersal and egg production across the ants as a consequence of the energetic costs of flight muscles. Second, the life history continuum hypothesis (SHIK & al. 2012, 2013) links variation in ant mating systems to male flight demands. Finally, the

Tab. 2: Ant reproductive strategies and predicted flight traits.

Reproductive strategy	Queen traits	Male traits
(A) Mating		
Male aggregation	Pre-mating flight, often at high altitudes, followed by post-mating dispersal flight Large eyes and ocelli	Brief flights, often at high altitudes Short life outside nest Reduced mandibles Eyes and ocelli larger in aerially mating versus surface mating species
Female calling	Brief or absent pre-mating flight Some species flightless	Long searching flights at low altitudes Longer life outside nest Well developed mandibles for refueling More complex sensory & neural apparatus
(B) Colony Founding		
Dependent colony founding (flightless queens)	Wingless (ergatoid) or with reduced wings (brachypterous), or fertile workers (gamergates) May have reduced eyes	Same as above for female calling males
Claustral founding (queens do not feed during founding period)	Heavy abdomens Low flight muscle ratios High abdomen drag Larger wings to compensate for loads Ovaries develop after flying Adaptations for extreme load bearing Shorter flight duration & distance?	Mostly unknown if and how male flight traits vary with colony founding strategy
Non-claustral founding (queens hunt, found colonies in nests of ants or termites, or feed on symbiotic fungi or insects)	Lighter abdomens High flight muscle ratios Low abdomen drag Smaller wings Social parasites may develop ovaries before flying Longer flight duration & distance?	Mostly unknown if and how male flight traits vary with colony founding strategy

found or fly hypothesis relates variation in queen flight ability to abdominal nutrient loads and colony founding (HELMS & KASPARI 2014, 2015). These complementary hypotheses address different aspects of ant flight, from development and histolysis of flight muscles to sex-specific flight behaviors and the evolution of alternate reproductive strategies.

Like many insects, ant queens display an oogenesis-flight syndrome, in which the high energetic costs of egg production and flight muscles lead to tradeoffs between the two (JOHNSON 1969, HARRISON 1980, MARDEN 2000). This results in dispersal and egg production taking place at different life stages, as queen ovaries do not usually develop until after they have finished flying and have histolyzed their flight muscles (KELLER & PASSERA 1988, 1990, TSCHINKEL 1988). An apparent exception is the facultatively parasitic fire ant *Solenopsis invicta* BUREN, 1972 (and potentially other parasitic species, BUSCHINGER 1986, 2009), in which some queens found colonies inside conspecific nests and exploit unrelated workers into rearing their offspring (TSCHINKEL 1996). Queens pursuing this parasitic strategy become fecund before flying, possibly to increase their attractiveness to workers and likelihood of adoption by host colonies (TSCHINKEL 1996). They compensate, however, by foregoing abdominal nutrient reserves that would otherwise allow them to found colonies independently (TSCHINKEL 1996, HELMS & GODFREY 2016). Male ants may experience a similar spermatogenesis-flight syndrome, as they stop producing sperm before reaching maturity (HÖLLDOBLER & WILSON 1990), the only exceptions being flightless males of some *Cardiocondyla* species (HEINZE & HÖLLDOBLER 1993).

Ant mating systems vary in the relative flight demands of males and females, captured by the male life history continuum (SHIK & al. 2012, 2013). Species at one extreme of this continuum practice male aggregation, in which males and females both fly to mate in synchronized aerial mating swarms (HÖLLDOBLER & BARTZ 1985). At the other extreme, species may practice female calling, in which queens on the ground use pheromones to attract flying males, and only afterwards leave to find a nest site (HÖLLDOBLER & HASKINS 1977, HÖLLDOBLER & BARTZ 1985). Female calling species thus limit energetic costs and mortality risk for queens by shifting the burden of mate location onto males, while reserving queen flight only for dispersal or doing away with it altogether (PEETERS & ITO 2001, PEETERS & ARON 2017). The continuum of male flight demands – from a single short swarming flight to long searching flights for scattered females – shapes several aspects of male biology (SHIK & al. 2012, 2013). Males of female calling species may have a more complex sensory and neural apparatus for detecting scattered females (GRONENBERG & HÖLLDOBLER 1999), are more likely to have functional mandibles with which to feed and refuel for repeated flights (SHIK & KASPARI 2009), have more opportunities for multiple matings (e.g., LENOIR & al. 1988), and may live several days or weeks outside the nest (SHIK & KASPARI 2009).

Queen biology is further shaped by the found or fly hypothesis, which posits a tradeoff between flight and colony founding mediated by abdominal nutrient loads. Flying queens vary in their abdominal nutrient reserves, both within species (HELMS & KASPARI 2014) and among castes or species practicing different colony founding strategies

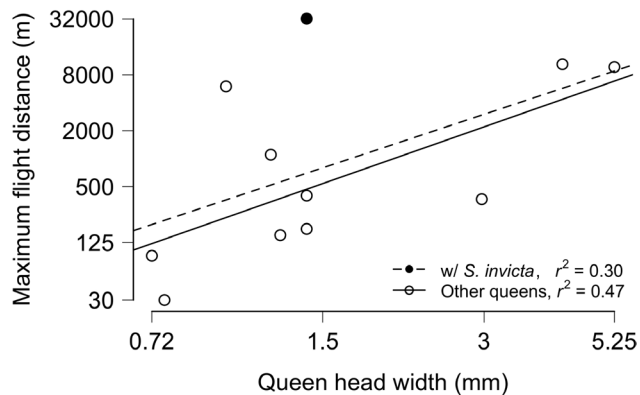


Fig. 3: Ant queen flight distance increases with body size. Both axes are log scale. Solid circle shows *Solenopsis invicta* queens. The solid regression line excludes *S. invicta*, the dotted line includes all species.

(KELLER & PASSERA 1989, KELLER & ROSS 1993a, b, HAHN & al. 2004, HELMS & KASPARI 2015, HELMS & GODFREY 2016). Claustally founding queens, for example, which do not feed during the founding period, have abdominal fat reserves totaling at least 40% of their body weight, while queens that parasitize host colonies carry virtually no extra nutrients (KELLER & PASSERA 1989, HELMS & KASPARI 2015). Heavier abdomens increase a queen's ability to survive the founding period (MINTZER 1987, NONACS 1992, BALAS & ADAMS 1996, BERNASCONI & KELLER 1996, 1999, JOHNSON 1998, 2001, ADAMS & BALAS 1999) or to produce more workers (TSCHINKEL 1993, WAGNER & GORDON 1999, LIU & al. 2001, DEHEER 2002). But extra loads also adversely impact flight morphology by reducing flight muscle ratios and increasing drag (DUDLEY 2000, HELMS & KASPARI 2014, 2015, HELMS & GODFREY 2016), thereby reducing flight endurance (MARDEN 2000, HELMS & GODFREY 2016), maneuverability (MARDEN 1987, 2000, VOGT & al. 2000), and the ability to fly at high altitudes (DILLON & al. 2006, SRYGLEY & DUDLEY 2008, HELMS & al. 2016b). Heavier queens may thus incur costs in reduced dispersal distance (FORTELIUS & al. 1987, SUNDSTRÖM 1995, RÜPEL & al. 1998, LACHUAD & al. 1999), predator evasion (FJERDINGSTAD & KELLER 2004), or mating success (DAVIDSON 1982, FJERDINGSTAD & BOOMSMA 1997, WIERNASZ & al. 1995, VOGT & al. 2000, WIERNASZ & COLE 2003). Claustally founding species compensate for some effects of heavier abdomens by evolving larger wings, but still suffer from heavy loads and higher drag during flight (HELMS & KASPARI 2015, HELMS & GODFREY 2016). A similar tradeoff may occur in males, in which heavy sperm loads increase fertilization potential but can hinder the ability to fly and locate mates (FJERDINGSTAD & BOOMSMA 1997, WIERNASZ & al. 2001).

An emphasis on flight would help resolve several further questions in ant reproductive ecology. The basics of copulation remain a mystery for most ants, especially male aggregating species that mate in the air (BAER 2011, SHIK & al. 2013). Mating has never been witnessed, for example, in the intensively studied fire ant *S. invicta* (TSCHINKEL 2013). Studying ants in flight would illuminate this process, as well as the dynamics of mate choice, mating frequency, and sexual selection and conflict (DAVIDSON 1982, CROZIER & PAGE 1985, REICHARDT & WHEELER 1996, BAER 2011, BARTH & al. 2014, WINSTON & al. 2017). Some potential sexually selected traits

such as male body size, mandible morphology, and mating plugs (DAVIDSON 1982, BAER 2011, SHIK & al. 2013), probably impact flight performance and may interact with dispersal selection. Dispersal concerns likely also influence tradeoffs in total colony reproductive effort, by shifting the optimum investment in quantity versus per capita mass of queens and males (SHIK 2008). Flight related selection likewise plays a role in the evolution of reproductive polymorphisms, since alternate reproductive strategies entail corresponding dispersal differences (ROSS & KELLER 1995, SUNDSTRÖM 1995, RÜPEL & HEINZE 1999, HEINZE & KELLER 2000, HELMS & BRIDGE 2017). Alternate flight behaviors can drive differences in gene flow and population genetic structure among ants practicing different social systems (PAMILO & al. 1992, CHAPUISAT & al. 1997, ROSS & SHOEMAKER 1997, LIAUTARD & KELLER 2001, ROSS 2001, SUNDSTRÖM & al. 2005). In an extreme case, species may evolve polymorphisms where one queen type mates in high altitude swarms and founds colonies independently, while a second parasitic or dependent type mates near the ground before entering conspecific host nests (BOURKE & FRANKS 1991, ROSS & KELLER 1995, BOOMSMA & NASH 2014). If queen type is heritable and their flight patterns drive disruptive selection on males to specialize in mating with one of the two types, it may lead to assortative mating between parasitic genotypes, reproductive isolation from the host population, and sympatric speciation (BUSCHINGER 1986, 2009, WEST-EBERHARD 2005, BOOMSMA & NASH 2014, LABELING & al. 2014, LEPÄNEN & al. 2016).

Dispersal, invasions, and range shifts

Available estimates of ant flight performance reveal dramatic variation (Tab. 1). Maximum flight distance varies over four orders of magnitude from only 30 meters in the obligate plant-ant *Pheidole minutula* MAYR, 1878 (see BRUNA & al. 2011) to over 30,000 meters in the fire ant *Solenopsis invicta* (see WOJCIK 1983, but see TSCHINKEL 2013). Flights can be as short as one minute or last over two hours (JUTSUM & QUINLAN 1978, HELMS & GODFREY 2016), occur at maximum speeds of 1.5 to 5.3 meters per second (MOSER 1967, VOGT & al. 2000), and reach altitudes from 1 to 300 meters above the ground (BARTELS 1985, MARKIN & al. 1971). Much variation remains to be discovered. We lack, for example, flight performance estimates for any ponerine ants, which are one of the most speciose subfamilies and display substantial variation in reproductive ecology (PEETERS & ITO 2001). At the same time, we know little about how flight performance scales up to affect phenomena like invasions or the ability of species to shift their ranges in response to climate change.

Ant dispersal distance probably varies with body size since larger species have faster flight speeds and lower mass-specific metabolic demands (RAYNER 1988, DUDLEY 2000, DARVEAU & al. 2005, GREENLEAF & al. 2007). To test this I compared maximum queen flight distance to head width, a standard measure of body size. Head widths were obtained from AntWeb (ANTWEB 2017), and both distance and head widths were log-transformed to meet normality assumptions. When queen measurements were unavailable, I used major worker head widths (*Azteca ulei* FOREL, 1904, *Pheidole minutula*) or those of queens or majors from similar congeneric species (*Azteca* sp., *Allomerus* sp.), or estimates based on the ratio between queen and worker head width in congeneric species (*Crematogaster laevis* MAYR, 1878). Larger species tended to fly farther (\log_{10} distance = $1.92 * \log_{10}$ head width + 2.56, $P = 0.08$, $r^2 = 0.30$, Fig. 3), es-

pecially when ignoring extreme distance *S. invicta* queens (\log_{10} distance = $2.03 * \log_{10}$ head width + 2.37, $P = 0.03$, $r^2 = 0.47$). Additional variation in flight performance is explained by life history. Consistent with the found or fly hypothesis, for example, body weight accounts for nearly 90% of variation in maximum flight altitudes among male aggregating species (HELMS & al. 2016b). Lighter species are better able to fly in low density air or take advantage of rising air currents (DUDLEY 2000, DILLON & al. 2006), such that the heaviest ant species fly only 40% as high as the lightest (HELMS & al. 2016b). Similarly, within *S. invicta*, queens with the heaviest abdomens fly only 40% as fast and for 5% as long as the lightest ones (VOGT & al. 2000, HELMS & GODFREY 2016). Taken together, the patterns suggest that larger species can fly farther than small ones, but perhaps at lower altitude, and that among similarly sized queens those with lighter abdomens can probably fly longer and higher.

Outside of human transport (BERTELSMEIER & al. 2017), flight is the primary mechanism of range expansion in most ants. By increasing rates of spread and the probability of colonizing new areas, superior flight ability may contribute to a species' invasiveness. Queens from invasive populations of *Solenopsis invicta* fly farther than any other ant for which estimates are available (Tab. 1). On the other hand, the invasion process itself may lead to the evolution of better dispersal ability through selection and assortative mating (PHILLIPS & al. 2008, HILL & al. 2011). Dispersal is selected for during range expansion due to the availability of vacant habitat outside a species' current range (HELMS & BRIDGE 2017), and mating events at the range boundary are likely to be between high dispersal genotypes, reinforcing selection for superior dispersal. Since dispersal in ants is tied to reproduction, range shifts in response to changing environments may also drive evolutionary changes in reproductive ecology. In polymorphic ants practicing alternate life histories, selection favors more dispersive reproductive strategies in new populations at expanding range edges versus in a range interior (DALECKY & al. 2007, HELMS & BRIDGE 2017). At the same time, reproductive strategy likely constrains the ability to track shifting habitats in response to climate change (COLWELL & al. 2008). Social parasites or obligate plant mutualists, for example, may be unable to rapidly shift their ranges, since they cannot colonize areas lacking suitable host populations (BRUNA & al. 2005, HELMS & BRIDGE 2017). Similar dispersal dynamics likely affect the genetic and demographic rescue of isolated populations or the persistence of species in habitat fragments (VEPSÄLÄINEN & PISARSKI 1982, VAN DYCK & MATTHYSEN 1999, BRUNA & al. 2005, 2011, MORRISON 2016).

Many gaps remain in our understanding of the physical process of ant flight. The role of wind in dispersal, for example, has yet to be measured for any ant. Ants are often unable to fly in strong winds at ground level, with winds as slow as 1 to 3 meters per second sufficient to preclude takeoff (TALBOT 1966, MARKIN & al. 1971, BALDRIDGE & al. 1980, BOOMSMA & LEUSINK 1981, STAAB & KLEINEIDAM 2014). Once airborne, however, some species may take advantage of high altitude winds to increase flight distance, and prevailing winds may bias dispersal direction (ROSS & SHOEMAKER 1997). Some long distance records are likely due to wind-aided dispersal (e.g., *Atta cephalotes* (LINNAEUS, 1758), on a small island, CHERRETT 1968, and *S. invicta* on offshore oil rigs, WOJCIK 1983). But underlying flight ability still plays a key role, as farther or higher flyers would be

better able to exploit such winds (SRYGLEY & DUDLEY 2008, HELMS & al. 2016b).

Interspecific interactions and aerial food webs

Ants on the ground interact with a diverse array of predators, pathogens and symbionts (HÖLLDOBLER & WILSON 1990), and the same is true for flying ants in aerial environments. Because queens leave one colony to found another, they are ideal dispersal vectors for pathogenic fungi and bacteria (ESPADALER & SANTAMARIA 2012, HO & FREDERICKSON 2014) or for arthropods that inhabit ant nests. At least five species of phoretic mites (Acari: Scutacaridae), for example, occur on the bodies of flying queens and males of the fire ant *Solenopsis invicta* (see EBERMANN & MOSER 2008). In an extreme case, cockroaches in the genus *Attaphila* live in fungus gardens of *Atta* leaf-cutter ants and disperse by clinging to flying queens (PHILLIPS & al. 2017). Larval male twisted-wing insects (Strepsiptera: Myrmecolacidae) often parasitize winged queens and males, although it is unclear whether the ants serve as dispersal vectors (KATHIRITHAMBY & JOHNSTON 1992, 2004). Some ants actively carry symbionts with them on mating flights. Queens of *Aphomyrmex afer* EMERY, 1899, *Tetraoponera binghami* (FOREL, 1902), and multiple *Acropyga* species, for example, carry between their mandibles or on their bodies gravid mealybugs (Hemiptera: Pseudococcidae) with which to start a honeydew-producing herd in their new nest (KLEIN & al. 1992, GAUME & al. 2000, JOHNSON & al. 2001). Tree-dwelling *Tetraoponera* and *Crematogaster* queens may likewise carry starter cultures of nest-lining fungi (BAKER & al. 2017), as do *Atta* queens for their fungus gardens (AUGUSTIN & al. 2011). Many co-dispersing species likely incur flight performance costs in their hosts due to heavier loads or increased drag, making them potentially useful systems for studying tradeoffs in the evolution of symbioses.

Flying ants are also eaten in large numbers by aerial predators. Queens and males are attractive prey because they are relatively defenseless, contain large nutrient reserves, and often occur in dense aggregations (WHITCOMB & al. 1973, HELMS & al. 2016a). Dozens of ant species can fly over a single location in different seasons, times of day, and flight altitudes, providing a diverse menu for predators (DUELLI & al. 1989, KASPARI & al. 2001a, b, TORRES & al. 2001, DUNN & al. 2007, HELMS & al. 2016b). Many dragonflies, bats, and birds capture ants during flight (WARTER & al. 1962, WHITCOMB & al. 1973, BALDRIDGE & al. 1980, ORLOWSKI & al. 2014, HELMS & al. 2016a), and some swifts (Apodidae) and swallows (Hirundinidae) may specialize on them, with flying ants constituting up to 30 to 80% of their diet (HESPENHEIDE 1975, LAW & al. 2017). Queens of the fire ant *Solenopsis invicta*, for example, are the primary prey for nesting Purple Martins (*Progne subis* LINNAEUS, 1758, Hirundinidae) in the southern USA, which double their foraging efficiency by targeting fire ants instead of other insects (HELMS & al. 2016a). By distributing terrestrially derived resources to aerial predators, flying ants thus help mediate the flow of energy and materials through ecosystems. This includes toxins like methylmercury, which may be transferred from aquatic to aerial food webs by *S. invicta* queens and other ants (HELMS & TWEEDY 2017). More work is needed, however, to measure ant inputs to aerial food webs, and to determine whether predator-prey interactions in the air influence population dynamics on the ground.

Conclusion

Flight is a brief but critical phase in the life cycle of nearly all ant species. The hazards of solitary life, and reliance on flight for reproduction and dispersal, create a strong selective environment that shapes ant biology at all levels. Physical demands of flight are reflected in ant physiology and morphology, flight-related selection drives life history evolution, and ants interact with other species and mediate ecosystem processes high above the earth's surface. By some measures, ants even outperform other flying animals. Queens often carry loads impossibly heavy for other insects, and some species can travel over 30 kilometers in search of new nest sites. Flying ants are ideal model systems for a diverse array of questions ranging from nutrient allocation tradeoffs to potential mechanisms of sympatric speciation. Many applied conservation issues may also be informed by studies of ant flight, including the dynamics of species invasions, range shifts in response to climate change, and the movement of contaminants through food webs. But despite its importance, flight remains one of the biggest gaps in our understanding of ant biology. We have learned much by studying what ant colonies do on the ground but have only begun to ask what they do in the air.

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