

Reproduction-dispersal tradeoffs in ant queens

J. A. Helms IV · M. Kaspari

Received: 25 October 2014 / Revised: 30 December 2014 / Accepted: 21 February 2015
© International Union for the Study of Social Insects (IUSSI) 2015

Abstract Organisms often experience reproduction–dispersal tradeoffs mediated by body size. In ants (Hymenoptera: Formicidae) the Found or Fly (FoF) Hypothesis states that dispersing queens face an ecological tradeoff between colony founding and flight success mediated by abdominal nutrient loading. If expressed interspecifically, such a tradeoff implies biomechanical costs to more energetically demanding life history strategies. Claustally founding queens, who carry the entire resource load necessary to fuel early colony growth, may incur flight costs. We characterized the flight morphology of 21 Neotropical species representing four major subfamilies, spanning four orders of magnitude in body mass and practicing several colony founding strategies. Flight morphologies were compared in a phylogenetic context to evaluate how they varied with body size and reproductive ecology. Consistent with FoF, claustral founders had 30 % lower flight muscle ratios (FMR) and trended toward higher abdomen drag than species in which founding queens feed. The two strategies did not differ in wing loading. Instead, claustral founders evolved larger wings, counteracting the effect of heavier abdomens. Heavy nutrient loads pushed several claustral species to theoretical limits of flight by lowering FMR to levels which cause flightlessness in other insects. Selection for higher nutrient loads related to colony founding is a possible mechanism for the recurrent evolution of flightlessness in ants. The importance and conflicting

demands of nutrient storage and flight make ant queens ideal organisms for modeling reproduction–dispersal tradeoffs. By emphasizing the role of flight in ant biology, the FoF Hypothesis highlights this tradeoff and provides novel insights into ant evolution.

Keywords Colony founding · Dispersal tradeoffs · Found or Fly · Mating flight · Reproductive strategy

Introduction

Aerially dispersing plants and insects often experience reproduction–dispersal tradeoffs, in which higher nutrient loads increase reproductive or competitive ability at the expense of flight or dispersal (Harrison 1980; Guries and Nordheim 1984; Wagner and Liebherr 1992; Zera and Denno 1997; Marden 2000). Though worker castes are wingless, most of the world's more than 12,000 ant species (Bolton et al. 2006) rely on flight for dispersal and reproduction (Hölldobler and Wilson 1990; Peeters and Ito 2001). Virgin queens and males fly to disperse, find partners and mate, after which queens found new nests (Hölldobler and Wilson 1990). Flight is the deadliest phase of the life cycle because it exposes queens to predators and other hazards (Hölldobler and Wilson 1990; Nichols and Sites 1991; Peeters and Ito 2001; Fjerdingstad and Keller 2004; Frederickson 2006), and over 99 % may die during this brief window (Gordon and Kulig 1996). The role of flight in the colony life cycle and its associated biomechanical constraints (Ellington 1984; Wagner and Liebherr 1992; Dudley 2000) and high mortality combine to drive queen evolution through flight related selection (Buschinger and Heinze 1992; Wiernasz and Cole 2003; Fjerdingstad and Keller 2004; Keller et al. 2014). But the brevity of this

J. A. Helms IV (✉) · M. Kaspari
Department of Biology, University of Oklahoma, Norman,
OK 73019, USA
e-mail: jackson.a.helms-1@ou.edu

M. Kaspari
Smithsonian Tropical Research Institute, Balboa, Panama

phase—much less than 1 % of a queen's life (Hölldobler and Wilson 1990)—has resulted in comparatively little study of ant flight (but see Markin et al. 1971; Vogt et al. 2000).

Ant queens are analogous to plant seeds—nutritive propagules that disperse to found sessile colonies—and experience similar tradeoffs (Andersen 1991; Johnson 1998). Ant queens build up fat and protein reserves in their abdomens by feeding before flying from their natal nests (Peakin 1972; Boomsma and Isaaks 1985; Nielsen et al. 1985; Keller and Passera 1989; Martinez and Wheeler 1994). After arrival at a new nest site, a heavier abdomen increases a queen's reproductive output and survival until she rears enough workers to function as a colony (Mintzer 1987; Nonacs 1992; Tschinkel 1993; Balas and Adams 1996; Bernasconi and Keller 1996, 1999; Johnson 1998; Adams and Balas 1999; Wagner and Gordon 1999; Johnson 2001; Liu et al. 2001, DeHeer 2002). At the same time, heavier abdomens reduce metrics of flight ability by decreasing flight muscle ratio (FMR) and increasing wing loading and drag (Helms and Kaspari 2014). These changes likely reduce a queen's dispersal distance (Fortelius et al. 1987; Sundström 1995; Ruppell et al. 1998; Lachaud et al. 1999), ability to evade predators (Fjerdingstad and Keller 2004), and success in aerial mate choice and copulation (Davidson 1982; Fjerdingstad and Boomsma 1997; Wiernasz et al. 1995; Vogt et al. 2000; Wiernasz and Cole 2003). The Found or Fly (FoF) Hypothesis (Helms and Kaspari 2014) proposes that individual queens experience an ecological fitness tradeoff between colony founding and flight mediated by abdominal nutrient loading. It remains to be seen, however, whether such a tradeoff is expressed interspecifically.

Nutrient loads are key variables in the various reproductive strategies of ants (Keller and Passera 1989). The predominant strategy, used by a vast majority of species, is claustral founding, in which a newly mated queen seals herself in a new nest and rears workers off her body reserves (Hölldobler and Wilson 1990; Brown and Bonhoeffer 2003; Keller et al. 2014). Claustral founding requires abdominal reserves ranging from 40 % to over 60 % of queen body weight (Keller and Passera 1989). Many species, however, use an ancestral strategy in which queens leave the incipient nest to forage (Johnson 2002; Brown and Bonhoeffer 2003). Other queens may feed on symbiotic fungi (Seal 2009) or insects (LaPolla and Spearman 2007), join existing colonies or parasitize host species (Buschinger 1986, 2014; Keller and Passera 1989; Hölldobler and Wilson 1990), or are accompanied by workers from their natal nest (Cronin et al. 2013). These non-claustral strategies require lighter nutrient loads

(Keller and Passera 1989). The resulting variation in abdomen weight, by altering flight morphology, should generate flight differences among life histories, although we know of no such analyses.

The FoF Hypothesis states that the heavier abdomens of claustral founders should reduce flight ability metrics relative to non-claustral species. We predict claustral founders will have (P1) lower FMRs (P2) higher wing loading and (P3) higher abdomen drag. If the FMR drops too low a queen loses the ability to fly. Abdomen weights which lower FMR to this marginal value—from 0.12 to 0.16 in insects (Marden 2000)—represent the maximum load a queen can carry and still disperse by flight. We therefore predict (P4) claustral founders, for whom energy storage is paramount, will approach these marginal values. Evolutionary events, on the other hand, may allow species to break tradeoffs that apply to individuals. For example, insect wings can be evolutionarily labile (Mezey and Houle 2005), and increases in wing loading—the ratio of body weight to wing area—can be offset by evolving larger wings at little energetic cost. It is less clear whether tradeoff breaking is possible for FMR and drag effects, as it would require relatively expensive or complex changes in thorax investment or abdomen density.

The FoF model laid out above differs from previous analyses of queen life history evolution. For example, claustral founders have been predicted to have larger flight muscles so that muscle histolysis can help fuel colony founding (e.g., Hölldobler and Wilson 1990; Peeters and Ito 2001). Moreover, other models view the evolution of claustral founding only in terms of the costs and benefits of foraging mortality and energy provisioning (Hölldobler and Wilson 1990; Brown and Bonhoeffer 2003), and ignore the costs and benefits of dispersal. FoF provides a potentially useful alternative by considering the impacts of heavier abdomens on flight.

To contrast these approaches in the study of queen biology, we characterize the flight morphology of 21 co-occurring Neotropical species to explore the role of flight in queen evolution. The species represent four major sub-families, display a variety of reproductive strategies and span four orders of magnitude in body mass, approximating the entire range of variation among flying queens. We examine how flight morphology scales with body size in a phylogenetic context, compare reproductive strategies to evaluate predictions of FoF, and look for evidence of evolutionary compensation for heavier abdomens. By recognizing flight mechanics as a driver of ant biology we generate novel predictions and suggest a previously unrecognized life history tradeoff—the dispersal cost of claustral founding.

Materials and methods

Specimen collection

All specimens were collected in 1991–1992 in a lowland seasonally wet forest on Barro Colorado Island, Panama (9°9′19″N, 79°50′15″W). Alate queens were captured during their mating flights in black-light traps and preserved in ethanol (Kaspari et al. 2001a, 2001b). Among the species captured, we selected 21 for analysis. Species were chosen to span the entire natural range of flying queen body size, represent all four major subfamilies, and capture a variety of reproductive strategies. Although we generally chose only one species per genus, to capture intrageneric variation we analyzed multiple species for two genera, *Dolichoderus* and *Camponotus*. Some of our data for one species, *Azteca instabilis*, were previously published in a separate study (Helms and Kaspari 2014). Queens within a species vary substantially in flight morphology (Helms and Kaspari 2014), but pilot studies showed that variance of most measures stabilized after measuring three to six individuals. We thus attempted to analyze at least six individuals per

species but due to limited availability we used smaller sample sizes for some (Table 1).

Flight morphology

We characterized the flight morphology of each specimen according to the protocol outlined in Helms and Kaspari (2014). For simplification, we refer to the gaster as the “abdomen” and the mesosoma as the “thorax”. We measured head width, abdomen length and abdomen height to 0.1 mm with an ocular micrometer under a dissecting microscope. Head width is the maximum width of the head in full-face view excluding the eyes and is a standard measure of ant body size. We removed the wings, legs, abdomen and head, keeping the thorax and petiole or post-petiole intact, and dried all parts at 60–65 °C for 48 h. Unlike the other species the post-petiole of *Atta colombica* is large and broadly attached to the abdomen. In that case the petiole was left attached to the thorax, but the post-petiole was kept with the abdomen. Due to their large size *Atta* specimens were dried for 72 h. After drying we weighed the forewings, hindwings, abdomen, thorax + petiole/post-petiole, and

Table 1 Ant flight morphology

| Subfamily | Species | <i>n</i> | Mass (mg) | HW (mm) | FMR | WSpan (mm) | WArea (mm ²) | WLoad (N/m ²) | AR | WMD (mg/mm ²) | V ^{2/3} (mm ²) | Strategy |
|----------------|---------------------------------|----------|-----------|---------|------|------------|--------------------------|---------------------------|------|---------------------------|-------------------------------------|----------|
| Dolichoderinae | <i>Azteca instabilis</i> * | 73 | 21.700 | 2.4 | 0.20 | 22.30 | 79.39 | 2.67 | 6.28 | 0.0041 | 10.11 | C |
| | <i>Dolichoderus bispinosus</i> | 6 | 18.649 | 2.4 | 0.21 | 21.07 | 72.21 | 2.53 | 6.15 | 0.0042 | 9.35 | C |
| | <i>Dolichoderus debilis</i> | 6 | 1.861 | 1.1 | 0.20 | 9.54 | 15.47 | 1.18 | 5.89 | 0.0021 | 3.04 | N |
| | <i>Dolichoderus lamellosus</i> | 4 | 1.424 | 1.1 | 0.23 | 8.05 | 10.88 | 1.28 | 6.07 | 0.0015 | 1.38 | N |
| | <i>Dolichoderus laminatus</i> | 3 | 1.338 | 1.1 | 0.22 | 8.17 | 10.55 | 1.22 | 6.31 | 0.0014 | 1.84 | N |
| | <i>Dolichoderus lutosus</i> | 6 | 1.606 | 1.2 | 0.21 | 9.33 | 13.48 | 1.17 | 6.47 | 0.0018 | 1.82 | C |
| Formicinae | <i>Brachymyrmex BCILT1</i> | 6 | 0.333 | 0.8 | 0.29 | 7.77 | 9.64 | 0.35 | 6.28 | 0.0013 | 1.44 | C |
| | <i>Camponotus abdominalis</i> | 4 | 60.161 | 3.6 | 0.15 | 29.43 | 137.81 | 3.23 | 6.29 | 0.0049 | 18.01 | C |
| | <i>Camponotus mucronatus</i> | 6 | 2.799 | 1.1 | 0.14 | 12.27 | 23.15 | 1.20 | 6.43 | 0.0020 | 3.04 | C |
| | <i>Camponotus nitidior</i> | 9 | 5.950 | 1.7 | 0.25 | 15.19 | 35.58 | 1.64 | 6.50 | 0.0026 | 3.61 | C |
| | <i>Camponotus sp1</i> | 2 | 35.552 | 3.4 | 0.18 | 26.14 | 110.14 | 3.17 | 6.21 | 0.0047 | 14.18 | C |
| Myrmicinae | <i>Atta colombica</i> | 3 | 193.668 | 4.8 | 0.27 | 52.87 | 415.27 | 4.60 | 6.74 | 0.0096 | 40.75 | N |
| | <i>Cephalotes porراسi</i> | 2 | 3.978 | 1.7 | 0.22 | 12.33 | 24.96 | 1.56 | 6.09 | 0.0021 | 2.46 | C |
| | <i>Crematogaster stollii</i> | 6 | 19.335 | 2.3 | 0.13 | 21.53 | 76.40 | 2.48 | 6.07 | 0.0042 | 10.62 | C |
| | <i>Megalomyrmex symmetochus</i> | 6 | 0.590 | 0.9 | 0.30 | 7.60 | 9.17 | 0.63 | 6.31 | 0.0017 | 1.08 | N |
| | <i>Pheidole christopherseni</i> | 6 | 0.285 | 0.5 | 0.19 | 6.80 | 6.86 | 0.39 | 6.70 | 0.0011 | 0.58 | C |
| | <i>Solenopsis BCILT3</i> | 6 | 0.461 | 0.6 | 0.13 | 7.90 | 8.95 | 0.51 | 7.01 | 0.0018 | 0.90 | C |
| | <i>Xenomyrmex stollii</i> | 6 | 0.602 | 0.7 | 0.13 | 7.33 | 7.59 | 0.78 | 7.09 | 0.0016 | 1.23 | C |
| Ponerinae | <i>Hypoponera q6</i> | 6 | 0.457 | 0.8 | 0.28 | 6.70 | 6.98 | 0.64 | 6.44 | 0.0014 | 0.56 | N |
| | <i>Odontomachus bauri</i> | 6 | 9.612 | 2.4 | 0.25 | 16.04 | 40.14 | 2.34 | 6.42 | 0.0030 | 4.77 | N |
| | <i>Pachycondyla harpax</i> | 6 | 7.191 | 1.9 | 0.34 | 14.97 | 34.30 | 2.05 | 6.54 | 0.0030 | 4.24 | N |

Values are species means

Mass body dry mass, HW head width, FMR flight muscle ratio, WSpan wingspan, WArea wing area, WLoad wing loading, AR aspect ratio, WMD wing mass density, V^{2/3} abdomen drag reference area, C claustral founding, N non-claustral founding

* Some data for *Azteca instabilis* previously published in Helms & Kaspari (2014)

entire body to the nearest 0.001 mg with a Cahn microbalance. Although storage in alcohol may reduce dry mass (Porter 1992), we do not suspect the introduction of bias, as all specimens were preserved similarly. After weighing we made slides of a forewing and hindwing from each queen and photographed them with a reference ruler using a Leica dissecting microscope camera or digital camera, depending on the size of the species. We measured the lengths and areas of the forewing and hindwing using ImageJ software (Schneider et al. 2012).

After measurements we calculated flight morphology metrics for each specimen. Flight muscle ratio is the ratio of flight muscle mass to body mass and may be the most important predictor of insect flight ability (Marden 1987, 2000; Dudley 2000). FMR is proportional to acceleration and load lifting ability, and a higher FMR increases maneuverability, flight endurance and the range of temperatures at which an insect can fly. We calculated FMR by dividing the thorax + petiole/post-petiole mass by total body mass. The thorax is mostly flight muscle and thorax mass is a standard surrogate for flight muscle in insects, including ants (Fjerdingstad and Boomsma 1997; Van Dyck and Matthysen 1999; Norberg and Leimar 2002; Dillon and Dudley 2004; Darveau et al. 2005; Merckx and Van Dyck 2006). The petiole and post-petiole—narrow segments connecting the thorax and abdomen—were left attached for practical reasons. Although the petiole and post-petiole are small and unlikely to affect our results, it is worth noting that including them in the thorax mass slightly overestimates FMR. To calculate wing loading—the ratio of body weight to wing area—we divided body weight by the total area of all four wings (N m^{-2}). Wing loading is negatively related to maneuverability, flight endurance and maximum flight speed, and positively related to minimum power and speed requirements for flight (Norberg and Rayner 1987; Rayner 1988; Hedenström 1992; Dudley 2000; Vogt et al. 2000; Darveau et al. 2005). Drag decreases overall flight performance (Dudley 2000) and is proportional to a cross sectional reference area. We are primarily interested in abdomen drag and used a volumetric reference area, abdomen volume^{2/3} (mm^2), which intuitively links mass and shape (Alexander 1990; Vogel 1994). To calculate volume we treated the abdomen as a prolate spheroid with abdomen length and height as the major and minor axes. Wingspan is the combined length of both forewings, and wing area is the combined area of all four wings. Aspect ratio is a measure of wing narrowness and is calculated as $(4 \times \text{forewing length}^2)/\text{total wing area}$. Higher aspect ratios—narrower wings—increase aerodynamic efficiency (Norberg and Rayner 1987; Rayner 1988; Dudley 2000). To calculate wing mass density—a measure of wing stiffness and durability—we divided total wing mass by total wing area (mg/mm^2).

Reproductive strategy

We assigned each species a reproductive strategy based on literature and information on AntWeb (AntWeb 2013). We use the term *claustral founding* to refer to strategies in which the queen does not feed during colony founding and fuels early colony growth entirely off her body reserves. We use the term *non-claustral founding* to refer to all strategies in which the queen is likely to feed during the founding process, either through foraging or symbioses. Our definitions differ slightly from accepted usage, in which *claustral founding* refers to queens that are isolated in the incipient nest, regardless of whether they feed. We emphasize, however, the energetic demands of reproduction and therefore classify colony founding as subsidized or not by an outside source. The difference affects one species (*Atta colombica*, see below), and our overall results were unaffected by its classification. Members of the subfamily Ponerinae (*Hypoponera*, *Odontomachus*, *Pachycondyla*) lack adult storage proteins, which allow queens to store the amino acids necessary for producing workers, and must forage during the founding period, making them non-claustral (Peeters and Ito 2001; Brown and Bonhoeffer 2003). Among the Formicoid clade (in this study, subfamilies Dolichoderinae, Formicinae and Myrmicinae) claustral founding is the predominant reproductive strategy (Hölldobler and Wilson 1990; Brown and Bonhoeffer 2003; Keller et al. 2014). Members of these subfamilies were conservatively assumed to be claustral unless known otherwise (Dolichoderinae—*Azteca*, *Dolichoderus bispinosus*, *D. lutosus*; Formicinae—*Brachymyrmex*, *Camponotus*; Myrmicinae—*Cephalotes*, *Crematogaster*, *Pheidole*, *Solenopsis*, *Xenomyrmex*), a method that is likely to overlook cases of non-claustral founding as reproductive strategy is unknown for many species. Species known or suspected to found colonies in nests of other social insects (*Dolichoderus debilis*, *D. lamellosus*, *D. laminatus*, AntWeb 2013; *Megalomyrmex*, Adams et al. 2013) were assumed to have access to food during the founding period and designated non-claustral founders. Leaf-cutters (*Atta*) found colonies alone but feed on symbiotic fungi during the founding period (Mintzer 1987; Seal 2009; Augustin et al. 2011) and are here designated non-claustral.

Scaling relationships

To characterize how flight morphology varies with body size across the ants, we examined the scaling relationships of flight morphology against body mass using species means (Table 1). We calculated scaling exponents as the slopes of log–log regressions of flight characters against body mass and checked for deviations from isometry by comparing the observed scaling exponents with those predicted by

isometric growth. In effect, this examines whether large ants are the same shape as small ants. To account for evolutionary history we repeated the process using phylogenetically independent contrasts of genus averages. One log-transformed variable—wingspan—deviated slightly from normality. The drag–mass relationship showed heteroscedasticity, decreasing in variance with increasing body size, probably as a result of measurement error of small abdomens.

Flight characterization

We characterized the overall flight morphology of species by plotting each species average on a two dimensional “flight ability space”. The axes of the flight ability space represent variation in the two characters most important for predicting insect flight ability—FMR and wing loading. Variation in these traits corresponds predictably to variation in several basic flight parameters—maneuverability, maximum flight time and minimum speed required for flight. FMR values are shown as standard normal values. Wing loading measures are the residuals of a log–log regression of wing loading on body mass. The plot therefore captures variation in wing loading after accounting for effects of body size variation. FMR was independent of body size, so we tested the prediction that claustral founders have lower FMRs than non-claustral founders with a *t* test. We compared other traits with ANCOVAs on ln-transformed characters with ln head width as a covariate.

After analysis, two presumed claustral founders—*Camponotus nitidior* and *Brachymyrmex BCILT1*—clustered with non-claustral founders in flight ability space, suggesting non-claustral founding. The colony founding strategies of these species are unknown and they were conservatively presumed claustral. To further test whether they are actually non-claustral, we estimated the fat content of these species by calculating the abdomen mass ratio. Fat content is an indicator of reproductive strategy in ants, with fat in claustral founders making up over 40 % of body mass (Keller and Passera 1989). Abdomen mass ratio is an overestimate of fat content and therefore a conservative measure in this case.

Data analysis

All statistics were done in R (R Core Team 2012). Variables were checked for normality with the Shapiro–Wilk test. Allometric scaling regressions of species data were standardized major axis regressions using the “lmodel2” package (Legendre 2011) to account for measurement error of independent variables (McArdle 1988). Regressions for calculating residuals used OLS regressions which are more

appropriate for prediction (Sokal and Rohlf 1995). Regressions were tested for heteroscedasticity using the “car” package (Fox and Weisberg 2011). For paired comparisons we checked for homogeneity of variance using Bartlett’s test.

For phylogenetically independent comparisons we constructed a genus level tree with the “ape” package (Paradis et al. 2004), using data for tree topology and branch lengths from Moreau et al. (2006). Phylogenetically independent contrasts were done with the “geiger” package (Harmon et al. 2008). Phylogenetically independent scaling regressions of genus averages used OLS regression.

Results

We characterized the flight morphology of 178 queens from 21 species in all four major subfamilies (Table 1). The species spanned four orders of magnitude in body mass with commensurate variation in flight morphology, capturing nearly the entire natural range of variation among flying queens. The largest queens (*Atta colombica*) were nearly 700 times heavier than the smallest (*Pheidole christophersenii*), at 195 and 0.29 mg dry weight. FMR ranged from 0.13 (*Crematogaster stollii*, *Solenopsis BCILT3*, *Xenomyrmex stollii*) to 0.34 (*Pachycondyla harpax*), wing loading from 0.35 N m⁻² (*Brachymyrmex BCILT1*) to 4.60 N m⁻² (*Atta colombica*), and abdomen drag areas from 0.56 mm² (*Hypoponera q6*) to 40.75 mm² (*Atta colombica*). Wing shape, in contrast, was relatively invariant with aspect ratios ranging from 5.89 (*Dolichoderus debilis*) to 7.09 (*Xenomyrmex stollii*).

Dimensionless flight morphology metrics—FMR and aspect ratio—were unrelated to body mass. All other characters increased with size, with body mass accounting for most of the variation (Table 2). Wing loading was the only character to deviate from isometry using unadjusted species averages. After accounting for phylogeny and using genus averages, however, all dimensional flight morphology metrics except drag were allometric. With the exception of wing mass density—a measure of wing durability not clearly linked to flight—all deviations from isometry are consistent with decreased relative flight ability in larger ants. Larger species have higher wing loading and shorter and smaller wings than expected from isometric scaling with body mass.

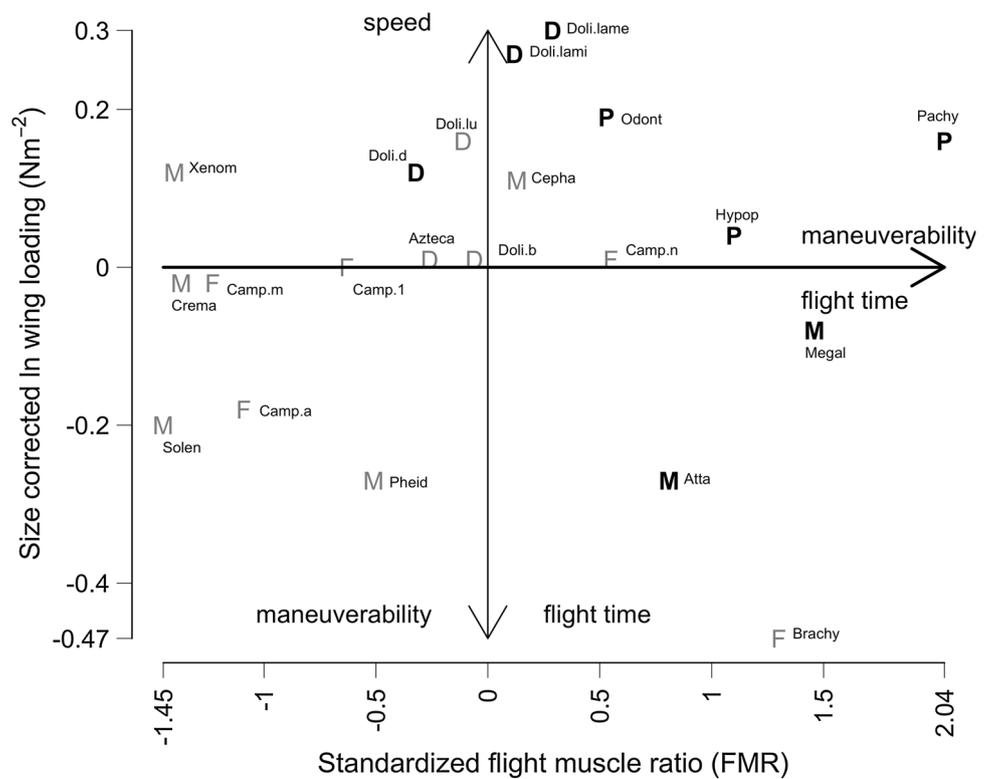
The plot of size-corrected wing loading against FMR suggests a phylogenetic component to flight morphology, although sample sizes do not permit high power comparisons between subfamilies (Fig. 1). Myrmicines, the most taxonomically diverse subfamily, likewise display the most flight morphological diversity and are widely scattered

Table 2 Allometric scaling of ant flight morphology with body mass

| Character | Predicted exponent | Observed exponent | r^2 | PIC exp | r^2 | Flight |
|--------------|--------------------|-------------------|-------|--------------|-------|--------|
| FMR | 0 | 0 | 0.003 | 0 | 0.01 | – |
| Wing loading | 0.333 | 0.390 | 0.93 | 0.404 | 0.97 | Worse |
| Drag | 0.666 | 0.629 | 0.96 | 0.614 | 0.97 | Better |
| Aspect ratio | 0 | 0 | 0.044 | 0 | 0.1 | – |
| WMD | 0.333 | 0.302 | 0.95 | 0.288 | 0.96 | ? |
| Wingspan | 0.333 | 0.309 | 0.97 | 0.289 | 0.96 | Worse |
| Wing area | 0.666 | 0.621 | 0.97 | 0.588 | 0.98 | Worse |

Scaling exponents are calculated according to the formula $\ln(\text{character}) = \text{constant} + \text{exponent} \times \ln(\text{body mass})$, by using SMA regressions. Predicted exponents are those predicted by isometric growth. PIC exponents are calculated using phylogenetically independent contrasts with OLS regressions on genus averages. Exponents in bold deviate from isometry at $P < 0.05$. “Flight” shows whether deviations act in a direction to increase or decrease relative flight ability

Fig. 1 Ant species in flight ability space. Y-axis values are residuals of a log–log regression of wing loading versus body mass. Letters (*D*, *F*, *M*, *P*) denote subfamilies. *Plain text letters* represent claustral species and *bolded letters* those that feed while founding. *Arrows* and *text* show how flight performance is predicted to vary, and *arrow thickness* represents relative importance of each axis. Maneuverability and flight time increase with flight muscle ratio and decrease with wing loading, and minimum flight speed increases with wing loading



across the space. Dolichoderines cluster around average FMR and high wing loading, suggesting short duration, high speed, low maneuverability flight relative to other ants. Ponerines are concentrated in the top right quadrant, displaying both high wing loading and high FMR, suggesting moderate to long duration, high speed, moderately to highly maneuverable flight. With the exception of *Brachymyrmex*, Formicines appear to vary primarily in FMR, hovering around average wing loading.

As predicted by FoF (P1), non-claustral founders—located on the right of the flight ability space (Fig. 1)—have 40 % higher FMRs than claustral founders (0.187 ± 0.05

vs. 0.261 ± 0.05 , t test, $P = 0.003$, Fig. 2). Also as predicted (P3), claustral founders trended toward larger abdomens with higher abdomen drag (ANCOVA $F(1, 18) = 3.860$, $P = 0.065$; Tables 3, 4; Fig. 3). Contrary to predictions based only on the role of flight muscle histolysis in colony growth (e.g., Hölldobler and Wilson 1990; Peeters and Ito 2001), we found no difference between claustral and non-claustral founders in size-corrected thorax mass [ANCOVA $F(1, 18) = 0.0987$, $P = 0.76$; (Tables 3, 4; Fig. 3)].

Contrary to prediction (P2), species appeared to break the wing loading tradeoff through evolutionary events. Despite

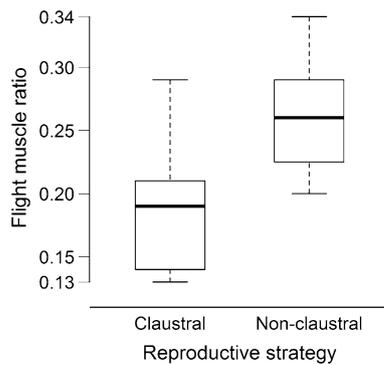


Fig. 2 Claustral queens have lower flight muscle ratios than non-claustral species. *Boxplots* show medians and quartiles of species averages

Table 3 ANCOVA results testing for flight morphology differences between claustral and non-claustral queens

| Trait | Factor | df | F | P |
|--------------|-------------|----|--------|--------|
| Wing loading | Head width | 1 | 185.33 | <0.001 |
| | Strategy | 1 | 0.100 | 0.76 |
| | Error | 18 | | |
| Wing area | Head width | 1 | 338.42 | <0.001 |
| | Strategy | 1 | 6.94 | 0.017 |
| | HW*Strategy | 1 | 6.38 | 0.022 |
| | Error | 17 | | |
| Drag | Head width | 1 | 216.90 | <0.001 |
| | Strategy | 1 | 3.86 | 0.065 |
| | Error | 18 | | |
| Thorax mass | Head width | 1 | 887.37 | <0.001 |
| | Strategy | 1 | 0.099 | 0.76 |
| | Error | 18 | | |

All variables are ln transformed

Table 4 Regressions of flight morphology on head width

| Character | Strategy | Slope | Intercept | r ² |
|--------------|----------|-------------|-------------|----------------|
| Wing loading | C | 1.13 | -0.13 | 0.90 |
| | N | 1.05 | -0.66 | 0.93 |
| Wing area | C | 1.60 | 2.79 | 0.95 |
| | N | 2.11 | 2.27 | 0.96 |
| Drag | C | 1.67 | 0.66* | 0.94 |
| | N | 2.01 | 0.23* | 0.91 |
| Thorax mass | C | 2.82 | -1.35 | 0.98 |
| | N | 3.19 | -1.45 | 0.99 |

All variables are ln transformed

Pairs in bold differ at $P < 0.05$

* Marginally significant difference at $P = 0.065$

higher nutrient loads in claustral founders, the two groups did not differ in size-corrected wing loading (ANCOVA $F(1, 18) = 0.0998$, $P = 0.76$; Tables 3, 4). Instead,

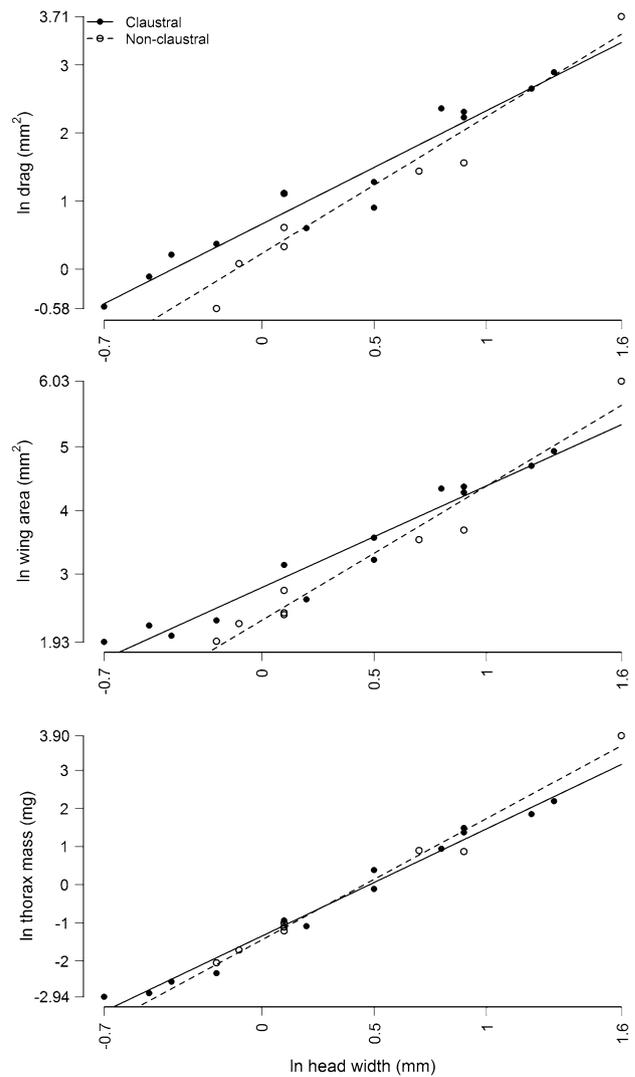


Fig. 3 Abdomen drag, wing area and thorax mass versus body size in claustral and non-claustral queens. Claustral queens trend toward higher drag as a result of larger abdomens. They also have larger wings which offset potential wing loading increases from heavier abdomens. Claustral queens do not have heavier thoraces

claustral founders had larger wings than non-claustral founders [ANCOVA $F(1, 17) = 6.938$, $P = 0.017$; (Tables 3, 4; Fig. 3)], compensating for wing loading effects of heavier abdomens.

Although we conservatively treated them as claustral in all our analyses (see Methods), the high FMRs of *Camponotus nitidior* (0.25 ± 0.02) and *Brachymyrmex BCILTI* (0.29 ± 0.04) were similar to non-claustral species. Their abdomen mass ratios (*C. nitidior*, 0.25 ± 0.05 ; *B. BCILTI*, 0.32 ± 0.07) also suggested non-claustral founding. All other presumed claustral founders in this study were over 40 % abdomen mass.

FMRs of five species—all claustral founders (P4)—were in the marginal range where insects lose the ability to fly—

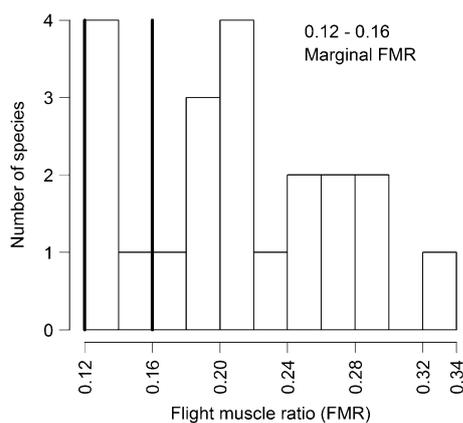


Fig. 4 Ant flight muscle ratios. *Dark lines* denote marginal FMRs which mark the threshold of flightlessness in other insects. All five species within this range are claustral founders

0.12 to 0.16 (Table 1; Fig. 4). Four species—*Camponotus mucronatus*, *Crematogaster stollii*, *Solenopsis BCILT3*, and *Xenomyrmex stollii*—had queens at 0.12 or below, with a low of 0.11 in two individuals of *S. BCILT3*. Moreover, all our queens were captured in flight and we overestimated FMR (see Methods), so the marginal FMR for these species is probably less than 0.13 and for some is likely below 0.11. These queens therefore had among the lowest FMRs of any flying insect.

Discussion

Flight is central to ant life histories. FoF emphasizes the link between flight and reproduction to predict how flight shapes queen evolution. Consistent with FoF, our results suggest the evolution of claustral founding reduces dispersal ability by (P1) lowering FMR and (P3) increasing abdomen drag. Claustral founders are expected to be less maneuverable and fly at narrower temperature ranges and for shorter periods than non-claustral queens of similar size, reducing their ability to evade predators, find suitable nest sites and disperse long distances. On the other hand, wing loading (P2) was invariant with strategy because of evolutionary changes in wing area. Several claustral species had FMRs on the verge of flightlessness (P4) and crossing this threshold is a possible mechanism for recurrent loss of flight in ant lineages. These relationships support the view that a queen's morphology reflects the conflicting demands of flight and post-dispersal survival. This is reminiscent of tradeoffs in plants and other insects (Harrison 1980; Guries and Nordheim 1984; Wagner and Liebherr 1992; Zera and Denno 1997; Marden 2000), suggesting that ants model a general reproduction–dispersal tradeoff.

We focus on females because queens—incipient colonies—are the relevant dispersal units for populations. Gene

flow, however, is mediated by both sexes and studies of male flight are necessary to fully explore genetic consequences of dispersal differences (Peeters 2012). Males likely experience dispersal tradeoffs related to sperm load and mating behavior (Davidson 1982; Fjerdingstad & Boomsma 1997; Shik et al. 2013), and their morphology may covary with that of queens. Comparing population structures of claustral and non-claustral founders, while controlling for effects of varying queen number (Seppä et al. 1995; Liautard & Keller 2001; Hannonen et al. 2004), would further test FoF and illuminate the gene flow role of males.

Emphasis on the metabolic role of flight muscles in fueling colony growth, as opposed to their primary flight function, has led to the prediction that claustral founders have larger flight muscles than non-claustral founders (e.g., Hölldobler and Wilson 1990; Peeters and Ito 2001). Flight muscle, however, plays a secondary role in fueling colony growth and abdominal reserves are the primary source of energy and amino acids in founding queens (Wheeler and Buck 1995, 1996; Wheeler and Martinez 1995; Brown and Bonhoeffer 2003). We find flight muscles in claustral founders are actually smaller relative to body mass, as predicted by FoF, and find no difference in absolute thorax mass (Keller and Ross 1993). If claustral founders do evolve larger flight muscles, it would likely be in response to the increased abdominal weight to be carried (Peeters and Ito 2001) rather than as an energy source.

Several claustral species flew at FMRs impossible for other insects, suggesting unknown adaptations for load-bearing flight. We captured queens flying with FMRs of 0.11, carrying what may be the heaviest body load documented in flying insects (Marden 1987, 2000). The closest relatives of ants—bees and wasps—lose the ability to fly at FMRs below 0.18 (Marden 1987). We speculate that this superior load-bearing ability is a response to the selective demands of nutrient loading for claustral founding (Keller and Passera 1989). Further, by capturing queens ranging from high FMR to these marginal values we begin to address the evolution of flightless queens. Researchers view flightlessness in ants as the result of a qualitative tradeoff between nutrient loading and dispersal (e.g., Sundström 1995; Heinze and Keller 2000). By recognizing quantitative variation within flying queens rather than lumping ants as flying or flightless, we extend the tradeoff to all ants and illustrate a potential mechanism for the evolution of flightlessness. Because extreme nutrient loads would cause queens to drop below marginal FMR, flightlessness may evolve automatically in response to selection for greater nutrient loads in founders, provided they have an alternate dispersal method. Further changes associated with flightlessness, such as shortening or loss of wings (Heinze and Keller 2000) or reductions in flight muscle (Peeters

et al. 2012), may follow. This simple mechanism may explain the ubiquity of flightlessness, which occurs in over 50 genera from all major subfamilies of ants (Peeters 2012).

Finally, flight morphology may predict life history (Keller et al. 2014). Two presumed claustral founders—*Camponotus nitidior* and *Brachymyrmex BCILTI*—had flight muscle and abdomen mass ratios similar to non-claustral species. Claustral founding is the rule in cavity-dwelling *Camponotus*. *Camponotus nitidior*, however, founds colonies on leaf surfaces (AntWeb 2013), making queen foraging possible. In support of this idea, *C. nitidior* queens also appear to have well developed worker-like neck muscles, an indicator of queen foraging (Keller et al. 2014). Almost nothing is known about colony founding in *Brachymyrmex*, but many species are mutualists of plant-feeding hemipterans (AntWeb 2013). Queens may found colonies among symbionts and thereby obtain food. Although pure speculation, either situation—queen foraging or symbiosis—would mean the species are actually non-claustral as suggested by flight morphology.

Flight links the primary functions of ant queens—dispersal and reproduction—and thereby plays a fundamental role in their ecology. We illustrate several examples in which flight shapes queen biology. Likewise, examination of flight should grant insight into dispersal polymorphisms (Bourke and Franks 1991; Keller and Ross 1993; Sundström 1995) and invasions (Markin et al. 1971; Yamauchi and Ogata 1995; Ruppell and Heinze 1999). By recognizing the coupling of reproduction and flight, and highlighting reproduction–dispersal tradeoffs, FoF provides a useful starting point for addressing these issues and others. Ants are flyers and to understand them we must expand our focus from what they do on the ground to ask what they do in the air.

Acknowledgments We thank the Republic of Panama, Barro Colorado Nature Monument and the Smithsonian Tropical Research Institute for allowing us to work on Barro Colorado Island. This project could not have succeeded without Rosemary Knapp who allowed us to use her lab. Adam Kay provided valuable advice. Jon Shik and two anonymous reviewers provided helpful comments that improved the manuscript. This work was supported by National Science Foundation grant EF-1065844 to MK. JAH is funded by a National Science Foundation Graduate Research Fellowship and a University of Oklahoma Alumni Fellowship.

References

- Adams E.S. and Balas M.T. 1999. Worker discrimination among queens in newly founded colonies of the fire ant *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* **45**:330–338.
- Adams R.M.M., Liberti J., Illum A.A., Jones T.H., Nash D.R. and Boomsma J.J. 2013. Chemically armed mercenary ants protect fungus-farming societies. *Proc. Natl. Acad. Sci. USA* **110**:15752–15757.
- Alexander D.E. 1990. Drag Coefficients of Swimming Animals: Effects of Using Different Reference Areas. *Biol. Bull.* **179**:186–190.
- Andersen A.N. 1991. Parallels between ants and plants: implications for community ecology. In: Huxley C.R. and Cutler D.F. (eds) *Ant-plant Interactions*. Oxford University Press, Oxford, pp 539–558.
- AntWeb 2013. <http://www.antweb.org>. Accessed 7 October 2013
- Augustin J.O., Santos J.F.L., Elliot S.L. 2011. A behavioral repertoire of *Atta sexdens* (Hymenoptera, Formicidae) queens during the claustral founding and ergonomic stages. *Insectes Sociaux* **58**:197–206.
- Balas M.T. and Adams E.S. 1996. The dissolution of cooperative groups: mechanisms of queen mortality in incipient fire ant colonies. *Behav Ecol Sociobiol* **38**:391–399.
- Bernasconi G. and Keller L. 1996. Reproductive conflicts in cooperative associations of fire ant queens (*Solenopsis invicta*). *Proc. Roy. Soc. B.* **263**:509–513.
- Bernasconi G. and Keller L. 1999. Effect of queen phenotype and social environment on early queen mortality in incipient colonies of the fire ant, *Solenopsis invicta*. *Anim. Behav.* **57**:371–377.
- Bolton B., Alpert G., Ward P.S. and Naskrecki P. 2006. *Bolton's Catalogue of Ants of the World*. Harvard University Press, Cambridge, MA, CD-ROM
- Boomsma J.J. and Isaaks J.A. 1985. Energy investment and respiration in queens and males of *Lasius niger* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **18**:19–27.
- Bourke A.F.G. and Franks N.R. 1991. Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. *Biol. J. Linn. Soc.* **43**:157–178.
- Brown M.J.F., Bonhoeffer S. 2003. On the evolution of claustral colony founding in ants. *Evol. Ecol. Res.* **5**:305–313.
- Buschinger A. 1986. Evolution of social parasitism in ants. *Trends Ecol. Evol.* **1**:155–160.
- Buschinger A. 2014. Social parasitism among ants: a review (Hymenoptera: Formicidae). *Myrmecol. News* **12**:219–235.
- Buschinger A. and Heinze J. 1992. Polymorphism of female reproductives in ants. In: Billen J. (ed) *Biology and Evolution of Social Insects*. Leuven University Press, Leuven, pp 11–23.
- Cronin A.L., Molet M., Doums C., Monnin T. and Peeters C. 2013. Recurrent Evolution of Dependent Colony Foundation Across Eusocial Insects. *Annu. Rev. Entomol.* **58**:37–55.
- Darveau C.A., Hochachka P.W., Welch K.C. Jr, Roubik D.W. and Suarez R.K. 2005. Allometric scaling of flight energetics in Panamanian orchid bees: a comparative phylogenetic approach. *J. Exp. Biol.* **208**:3581–3591.
- Davidson D.W. 1982. Sexual Selection in Harvester Ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behav. Ecol. Sociobiol.* **10**:245–250.
- DeHeer C.J. 2002. A comparison of the colony-founding potential of queens from single- and multiple-queen colonies of the fire ant *Solenopsis invicta*. *Anim. Behav.* **64**:655–661.
- Dillon M.E. and Dudley R. 2004. Allometry of maximum vertical force production during hovering flight of neotropical orchid bees (Apidae: Euglossini). *J. Exp. Biol.* **207**:417–425.
- Dudley R. 2000. *The Biomechanics of Insect Flight: Form, Function, Evolution*. Princeton University Press, Princeton.
- Ellington C.P. 1984. The aerodynamics of hovering insect flight. II. Morphological parameters. *Philos. Trans. Roy. Soc. B.* **305**:17–40.
- Fjerdingstad E.J. and Boomsma J.J. 1997. Variation in size and sperm content of sexuals in the leafcutter ant *Atta colombica*. *Insectes Sociaux* **44**:209–218.
- Fjerdingstad E.J. and Keller L. 2004. Relationships between phenotype, mating behavior, and fitness of queens in the ant *Lasius niger*. *Evolution* **58**:1056–1063.

- Fortelius W., Pamilo P., Rosengren R. and Sundström L. 1987. Male size dimorphism and alternative reproductive tactics in *Formica exsecta* ants (Hymenoptera, Formicidae). *Ann. Zool. Fenn.* **24**:45–54.
- Fox J. and Weisberg S. 2011. An {R} Companion to Applied Regression, 2nd ed. Thousand Oaks CA: Sage. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>. Accessed 18 May 2014.
- Frederickson M.E. 2006. The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites. *Oecologia* **149**:418–427.
- Gordon D.M. and Kulig A.W. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology* **77**:2393–2409.
- Guries R.P. and Nordheim E.V. 1984. Flight characteristics and dispersal potential of maple samaras. *Forest Sci.* **30**:434–440.
- Hannonen M., Helanterä H. and Sundström L. 2004. Habitat age, breeding system and kinship in the ant *Formica fusca*. *Mol. Ecol.* **13**:1579–1588.
- Harmon L.J., Weir J.T., Brock C.D., Glor R.E. and Challenger W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**:129–131.
- Harrison R.G. 1980. Dispersal polymorphisms in insects. *Ann. Rev. Ecol. Syst.* **11**:95–118.
- Hedenström A. 1992. Flight performance in relation to fuel load in birds. *J. Theor. Biol.* **158**:535–537.
- Heinze J. and Keller L. 2000. Alternative reproductive strategies: a queen perspective in ants. *Trends Ecol. Evol.* **15**:508–512.
- Helms J.A. and Kaspari M. 2014. Found or Fly: nutrient loading of dispersing ant queens decreases metrics of flight ability (Hymenoptera: Formicidae). *Myrmecol. News* **19**:85–91.
- Hölldobler B. and Wilson E.O. 1990. *The Ants*. Belknap Press of Harvard University Press, Cambridge, MA.
- Johnson R.A. 1998. Foundress survival and brood production in the desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* (Hymenoptera, Formicidae). *Insectes Sociaux* **45**:255–266.
- Johnson R.A. 2001. Biogeography and Community Structure of North American Seed-Harvester Ants. *Ann. Rev. Entomol.* **46**:1–29.
- Johnson R.A. 2002. Semi-claustral colony founding in the seed-harvester ant *Pogonomyrmex californicus*: a comparative analysis of colony founding strategies. *Oecologia* **13**:60–67.
- Kaspari M., Pickering J. and Windsor D. 2001a. The reproductive flight phenology of a neotropical ant assemblage. *Ecol. Entomol.* **26**:245–257.
- Kaspari M., Longino J., Pickering J. and Windsor D. 2001b. The phenology of a Neotropical ant assemblage: evidence for continuing and overlapping reproduction. *Behav. Ecol. Sociobiol.* **50**:382–390.
- Keller L. and Passera L. 1989. Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera; Formicidae). *Oecologia* **80**:236–240.
- Keller L. and Ross K.G. 1993. Phenotypic Basis of Reproductive Success in a Social Insect: Genetic and Social Determinants. *Science* **260**:1107–1110.
- Keller R.A., Peeters C. and Beldade P. 2014. Evolution of thorax architecture in ant castes highlights trade-off between flight and ground behaviors. *eLife* **3**:e01539.
- Lachaud J., Cadena A., Schatz B., Perez-Lachaud G. and Ibarra-Nunez G. 1999. Queen dimorphism and reproductive capacity in the ponerine ant, *Ectatomma ruidum* Roger. *Oecologia* **120**:515–523.
- LaPolla J.S. and Spearman L.A. 2007. Characterization of an *Acropyga arnoldi* mating swarm and early stage colony founding behavior. *Trans. Amer. Entomol. Soc.* **133**:449–452.
- Legendre P. 2011. lmodel2: Model II Regression. R package version 1.7-0. <http://CRAN.R-project.org/package=lmodel2>. Accessed 18 May 2014.
- Liautard C. and Keller L. 2001. Restricted effective queen dispersal at a microgeographic scale in polygynous populations of the ant *Formica exsecta*. *Evolution* **55**:2484–2492.
- Liu Z., Yamane S., Kojima J., Wang Q. and Tanaka S. 2001. Flexibility of first brood production in a claustral ant, *Camponotus japonicus* (Hymenoptera: Formicidae). *J. Ethol.* **19**:87–91.
- Marden J.H. 1987. Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* **130**:235–258.
- Marden J.H. 2000. Variability in the Size, Composition, and Function of Insect Flight Muscles. *Ann. Rev. Entomol.* **62**:157–178.
- Markin G.P., Dillier J.H., Hill S.O., Blum M.S. and Hermann H.R. 1971. Nuptial flight and flight ranges of the imported fire ant, *Solenopsis saevissima richteri* (Hymenoptera: Formicidae). *J. Georgia Entomol. Soc.* **6**:145–156.
- Martinez T. and Wheeler D.E. 1994. Storage Proteins in Adult Ants (*Camponotus festinatus*): Roles in Colony Founding by Queens and in Larval Rearing by Workers. *J. Insect Physiol.* **40**:723–729.
- McArdle B.H. 1988. The structural relationship: regression in biology. *Can. J. Zool.* **66**:2329–2339.
- Merckx T. and Van Dyck H. 2006. Landscape structure and phenotypic plasticity in flight morphology in the butterfly *Pararge aegeria*. *Oikos* **113**:226–232.
- Mezey J.G. and Houle D. 2005. The dimensionality of genetic variation for wing shape in *Drosophila melanogaster*. *Evolution* **59**:1027–1038.
- Mintzer A.C. 1987. Primary polygyny in the ant *Atta texana*: number and weight of females and colony foundation success in the laboratory. *Insectes Sociaux* **34**:108–117.
- Moreau C.S., Bell C.D., Vila R, Archibald S.B. and Pierce N.E. 2006. Phylogeny of the ants: diversification in the age of angiosperms. *Science* **312**:101–104.
- Nichols B.J. and Sites R.W. 1991. Ant Predators of Founder Queens of *Solenopsis invicta* (Hymenoptera: Formicidae) in Central Texas. *Environ. Entomol.* **20**:1024–1029.
- Nielsen M.G., Skyberg N. and Peakin G. 1985. Respiration in the sexuals of the ant *Lasius flavus*. *Physiol. Entomol.* **10**:199–204.
- Nonacs P. 1992. Queen condition and alate density affect pleometrosis in the ant *Lasius pallitarsis*. *Insectes Sociaux* **39**:3–13.
- Norberg U. and Leimar O. 2002. Spatial and temporal variation in flight morphology in the butterfly *Melitaea cinxia* (Lepidoptera: Nymphalidae). *Biol. J. Linn. Soc.* **77**:445–453.
- Norberg U.M. and Rayner J.M.V. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. Roy. Soc. B* **316**:335–427.
- Paradis E., Claude J. and Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**:289–290.
- Peakin G.J. 1972. Aspects of productivity in *Tetramorium caespitum* L. *Ecol. Pol.* **20**:55–63.
- Peeters C. 2012. Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens (Hymenoptera: Formicidae). *Myrmecol. News* **16**:75–91.
- Peeters C. and Ito F. 2001. Colony Dispersal and the Evolution of Queen Morphology in Social Hymenoptera. *Ann. Rev. Entomol.* **46**:601–630.
- Peeters C., Keller R.A. and Johnson R.A. 2012. Selection against aerial dispersal in ants: two non-flying queen phenotypes in *Pogonomyrmex laticeps*. *PLoS ONE*:e47727.
- Porter S.D. 1992. Frequency and distribution of polygynous fire ants (Hymenoptera: Formicidae) in Florida. *Florida Entomol.* **75**:248–257.
- R Core Team 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>. Accessed 18 May 2014.

- Rayner JMV 1988. Form and function in avian flight. *Curr. Ornithol.* **5**:1–66.
- Rüppell O. and Heinze J. 1999. Alternative reproductive tactics in females: the case of size polymorphism in winged ant queens. *Insectes Sociaux* **46**:6–17.
- Rüppell O., Heinze J. and Hölldobler B. 1998. Size-dimorphism in the queens of the North American ant *Leptothorax rugatulus* (Emery). *Insectes Sociaux* **45**:67–77.
- Schneider C.A., Rasband W.S. and Eliceiri K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**:671–675.
- Seal, J.N. 2009. Scaling of body weight and fat content in fungus-gardening ant queens: does this explain why leaf-cutting ants found claustrally? *Insectes Sociaux* **56**:135–141.
- Seppä P., Sundström L. and Punttila P. 1995. Facultative polygyny and habitat succession in boreal ants. *Biol. J. Linn. Soc.* **56**:533–551.
- Shik J.Z., Donoso D.A. and Kaspari M. 2013. The life history continuum hypothesis links traits of male ants with life outside the nest. *Entomol. Exp. et Appl.* **149**:99–109.
- Sokal R.R. and Rohlf F.J. 1995. *Biometry: the principles and practice of statistics in biological research, 3rd ed.* W.H. Freeman and Company, New York.
- Sundström L. 1995. Dispersal polymorphism and physiological condition of males and females in the ant, *Formica truncorum*. *Behav. Ecol.* **6**:132–139.
- Tschinkel W.R. 1993. Resource allocation, brood production and cannibalism during colony founding in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* **33**:209–223.
- Van Dyck H. and Matthysen E. 1999. Habitat fragmentation and insect flight: a changing ‘design’ in a changing landscape? *Trends Ecol. Evol.* **14**:172–174.
- Vogel S. 1994. *Life in Moving Fluids: The Physical Biology of Flow.* Second edition. Princeton University Press, Princeton.
- Vogt J.T., Appel A.G. and West MS. 2000. Flight energetics and dispersal capability of the fire ant, *Solenopsis invicta* Buren. *J. Insect Physiol.* **46**:697–707.
- Wagner D. and Gordon D.M. 1999. Colony age, neighborhood density and reproductive potential in harvester ants. *Oecologia* **119**:175–182.
- Wagner D.L. and Liebherr J.K. 1992. Flightlessness in insects. *Trends Ecol. Evol.* **7**:216–220.
- Wheeler D.E. and Buck N.A. 1995. Storage proteins in ants during development and colony founding. *J. Insect Physiol.* **41**:885–894.
- Wheeler D.E. and Buck N.A. 1996. Depletion of reserves in ant queens during claustral founding. *Insectes Sociaux* **43**:297–302.
- Wheeler D.E. and Martinez T. 1995. Storage proteins in ants (Hymenoptera:Formicidae). *Comp. Biochem. Physiol.* **112B**:15–19.
- Wiernasz D.C. and Cole B.J. 2003. Queen size mediates queen survival and colony fitness in harvester ants. *Evolution* **57**:2179–2183.
- Wiernasz D.C., Yencharis J. and Cole B.J. 1995. Size and mating success in males of the western harvester ant, *Pogonomyrmex occidentalis* Hymenoptera: Formicidae). *J. Insect Behav.* **8**:523–531.
- Yamauchi K. and Ogata K. 1995. Social Structure and reproductive systems of tramp versus endemic ants (Hymenoptera: Formicidae. of the Ryukyu Islands. *Pac. Sci.* **49**:55–68.
- Zera A.J. and Denno R.F. 1997. Physiology and ecology of dispersal polymorphism in insects. *Ann. Rev. Entomol.* **42**:207–230.