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Evolution and Ecology of Directed Aerial Descent in Arboreal Ants

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Synopsis Directed aerial descent (DAD) is used by a variety of arboreal animals to escape predators, to remain in the canopy, and to access resources. Here, we build upon the discovery of DAD in ants of tropical canopies by summarizing its known phylogenetic distribution among ant genera, and within both the subfamily Pseudomyrmecinae and the genus *Cephalotes*. DAD has multiple evolutionary origins in ants, occurring independently in numerous genera in the subfamilies Myrmicinae, Formicinae, and Pseudomyrmecinae. Ablation experiments and video recordings of ants in a vertical wind tunnel showed that DAD in *Cephalotes atratus* is achieved via postural changes, specifically orientation of the legs and gaster. The occurrence of DAD in Formicinae indicates that the presence of a postpetiole is not essential for the behavior. Evidence to date indicates that gliding behavior is accomplished by visual targeting mediated by the compound eyes, and is restricted to diurnally active ants that nest in trees. Occlusion of ocelli in *Pseudomyrmex gracilis* workers had no effect on their success or performance in gliding. Experimental assessment of the fate of ants that fall to the understory showed that ants landing in water are 15 times more likely to suffer lethal attacks than are ants landing in leaf litter. Variation in both the aerodynamic mechanisms and selective advantages of DAD merits further study given the broad taxonomic diversity of arboreal ants that engage in this intriguing form of flight.

Introduction

Many arboreal vertebrates use directed aerial descent (hereafter, DAD) to escape predators and to access resources (Dudley et al. 2007). Well-known examples of gliding exist among a few species of snakes (Socha 2002), some lizards (Mori and Hikida 1994; McGuire and Dudley 2005) and frogs (Emerson and Koehl 1990; McCay 2001), and a variety of mammals (Jackson 1999; Hanski et al. 2000). However, such aerial behavior had not been reported for terrestrial arthropods until it was shown for tropical ants (Yanoviak et al. 2005). This discovery raised many questions regarding the mechanisms, origins, and ecological consequences of gliding in ants and other arthropods.

To date, most studies of DAD in ants have focused on *Cephalotes atratus*, a large, black, diurnal

species common in lowland forests from Panama to Argentina (de Andrade and Baroni Urbani 1999). However, lowland tropical forests harbor hundreds of other ant species (e.g., Longino and Colwell 1997; Dejean et al. 2000; Davidson et al. 2003). A large fraction of these are arboreal or semi-arboreal (i.e., nesting in the soil or understory but foraging in vegetation), and it is not uncommon to find 30 or more ant species in a single tree crown (e.g., Wilson 1987; Schulz and Wagner 2002). Early surveys showed that DAD behavior occurs in arboreal ants apart from *C. atratus* (see Yanoviak et al. 2005; Supplementary Material), but these results were based on geographically limited observations and only partly represent the likely distribution of DAD among ant taxa. The recent completion of generic-level molecular phylogenies for ants

(Brady et al. 2006; Moreau et al. 2006) facilitates the placement of DAD in an evolutionary context, and potentially enhances our understanding of its mechanisms.

The first mechanistic approaches to understanding DAD in *C. atratus* focused on the sensory cues used by workers to locate a tree trunk during a fall. Simple occlusion of the compound eyes of ants revealed that visual cues are used in targeting (Yanoviak et al. 2005), and subsequent experimentation with the qualitative characteristics of the target (using variable colors and gray-scale columns) showed that falling *C. atratus* differentially land on relatively light-colored objects (Yanoviak and Dudley 2006). Similar experiments with other arthropods suggest that they are specifically attracted to edges of sharp contrast (i.e., a black target on a white background is also an attractor to larval stick insects under experimental conditions; Y. Zeng, unpublished data). To date, all manipulative studies of targeting in ants have focused on the compound eyes and the spectral wavelengths of light reflected from the target. The role of ocelli in DAD has not been investigated, but ocelli function as horizon detectors in some ants and other insects (Stange 1981; Fent and Wehner 1985) and thus could potentially contribute to target detection during DAD. Although *Cephalotes* lack ocelli, these organs occur in pseudomyrmecines and some arboreal formicines.

It is probable that gliding is restricted to diurnal species given the importance of visual cues in targeting. However, many arboreal ant species are either primarily nocturnal (e.g., *Camponotus atriceps*, *Cephalotes pallidus*, *Daceton boltoni*, some *Odontomachus* spp.) or active both day and night (e.g., some *Crematogaster* spp.; Hossaert-McKey et al. 2001; Azorsa and Sosa-Calvo 2008; Longino 2010; S.P. Yanoviak, personal observations). Although *C. atratus* is essentially a diurnal ant, workers often continue tending hemipteran trophobionts after sunset. It is unknown whether these workers are performing a specific nocturnal task (e.g., defending trophobionts), or if they become stranded by the onset of darkness. Regardless, such workers tend to remain in place on the apices of branches and other green stems throughout the night, thereby perhaps avoiding strong predation pressure from pseudoscorpions and other arthropods inhabiting woody crevices (Zeh and Zeh 1990; S.P. Yanoviak, personal observation). Given that many arboreal mammals are nocturnal and that physical disturbances may occur at all hours, it is likely that *C. atratus* and other ants occasionally are dislodged from tree crowns in darkness. Their ability to glide at night is unknown, although aforementioned

occlusion experiments suggest that this outcome would be unlikely.

Whether it occurs during the day or night, an arboreal ant falling from a tree crown to the ground is displaced by 3000 or more body lengths in <10 s. The equivalent distance scaled to a human adult is ~5 km. Due to the small mass and relatively low terminal velocities of most ants, the impact at the end of such a fall is unlikely to be lethal, although injury may occur. Moreover, the foreign microhabitat and ecological domain experienced upon landing are potentially fatal (Dudley et al. 2007; Yanoviak 2010), especially for ants inhabiting trees in flooded forests. Mortality rates among fallen ants are likely to be particularly high in the Amazon Basin, where a large fraction of the landscape is flooded for several months each year (Hess et al. 2003), and those flood waters support diverse assemblages of predatory fish (Saint-Paul et al. 2000). Regardless of the circumstances, the loss of worker ants represents both direct (biomass) and indirect (resources potentially obtained via foraging) costs to the colony. It is likely that such costs result in strong selective pressures leading to the evolution of DAD, especially in species with relatively expensive workers (i.e., with either small colony size or long-lived and well-defended workers). To date, information regarding the fate of falling arboreal worker ants that land in the forest understory is limited (Yanoviak 2010).

Early speculation about the kinematic mechanisms used by ants to control their aerial descent focused on the presence of a postpetiole—the second segment of the narrow abdominal “waist” of some ants (Yanoviak et al. 2005). The observation that species lacking a postpetiole (e.g., in the subfamily Formicinae) also glide indicates that this structure is not essential for DAD. Subsequent field experiments with *C. atratus* employed video analysis and experimental ablations to reveal the functional roles of the legs and gaster (the bulbous terminal segments of the ant abdomen; Yanoviak et al. 2010). Specifically, presence of the hindlegs affects both the success rate (frequency of landing on tree trunks) and performance (the ratio of vertical to horizontal distance travelled) of falling *C. atratus*. Here, we similarly employ experimental leg ablations to test the hypothesis that asymmetrical leg loss further destabilizes falling ants.

Documenting the behaviors of ants while in flight remains one of the most challenging aspects of research on DAD. The small body size and rapid descent of ants, combined with the relatively large vertical distance over which DAD occurs (Yanoviak et al. 2005),

make accurate measurement of their kinematics and aerodynamics extremely difficult under field conditions. However, recent advances in video recording and image-analysis technology are facilitating the measurement of three-dimensional glide trajectories of ants *in situ*. Similarly, the combination of a vertical wind tunnel with portable high-resolution video equipment is revealing those postural adjustments used by ants to effect aerodynamic control and maneuvers (our unpublished data).

Here, we provide further results regarding five pending questions about aerial gliding behavior in ants: (1) Apart from *C. atratus*, which ant taxa exhibit DAD, and what is the phylogenetic distribution of DAD among ants? (2) Do ocelli play a role in DAD behavior? (3) Is DAD exhibited either by nocturnal ants or by diurnal ants active at night? (4) What is the fate of ants that fall to the forest floor? and (5) What are the aerodynamic mechanisms used by ants that effect directionality during a fall?

Methods

Field work was conducted at eight sites in the New World and Africa (Table 1). We used the single-rope technique (Perry 1978), canopy walkways (Lowman and Bouricius 1995), and towers to access the crowns of at least nine focal trees at each site. Some experimental observations were also obtained by dropping ants from the laboratory balcony at Site 4 (Table 1). Additional methodological details and site descriptions are provided elsewhere (Table 1).

DAD surveys and phylogenetic mapping

We surveyed the ants in each focal tree by placing tuna baits on the principal branches and then hand-collecting in readily accessible sections of the crown

for at least 1 h. Workers of each common species (i.e., those represented by two or more individuals) were dropped from the crown >15 m above the ground, and their capacity for DAD was observed and noted. Each ant was either marked with white paint or dusted with orange fluorescent powder to improve visual contrast and to prevent duplicate trials with the same individuals. Ants were placed individually in a flouon-coated vial that was then held a measured distance from the tree trunk and inverted, releasing the ant into free fall. When possible, the vertical distance between the point of release and the ant's contact with the tree trunk was estimated using either a string marked with flags every 0.5 m or a laser distance meter.

We used the survey data gathered above to map the current known taxonomic distribution of DAD onto a generic-level phylogeny based on the combined information from Moreau et al. (2006), Brady et al. (2006), LaPolla et al. (2010), and P.S. Ward, unpublished data (University of California, Davis). We similarly plotted the occurrence of DAD onto recent phylogenies of the genus *Cephalotes* (de Andrade and Baroni Urbani 1999) and the subfamily Pseudomyrmecinae (Ward and Downie 2005).

Occlusion of ocelli

To test the relevance of ocelli to DAD in ants, we conducted occlusion experiments similar to prior manipulations of the compound eyes of *C. atratus* workers (Yanoviak et al. 2005). In this case, we applied white enamel paint (Testors, Inc.; Rockford, IL, USA) to the head of each of 25 *Pseudomyrmex gracilis* workers collected from the forest canopy. Experimental ants ($n=12$) received a small spot of paint that completely occluded all three ocelli (see

Table 1 Sites used for field-based investigations of DAD in ants and other arthropods.

Site	Location	Latitude	Longitude	Date	References
1	Arkansas, USA	34.7226 N	92.3582 W	2009–2010	Warren and Rouse 1969; Moore 1999
2	La Selva, Costa Rica	10.4308 N	84.0066 W	2006–2009	McDade et al. 1994
3	El Remanso, Costa Rica	08.3778 N	83.2973 W	2006	Allen 1956; Quesada et al. 1997
4	BCI, Panama	09.1570 N	79.8475 W	2006–2010	Leigh et al. 1996; Yanoviak and Kaspari 2000; Yanoviak et al. 2005, 2010; Yanoviak and Dudley 2006
5	ACTS, Peru	03.2492 S	72.9090 W	2006–2010	Madigosky and Vatnick 2000; Yanoviak and Dudley 2006; Yanoviak et al. 2010
6	Iquitos–Nauta, Peru	04.1466 S	73.4819 W	2004–2007	Mäki et al. 2001; Yanoviak et al. 2005
7	CICRA, Peru	12.5692 S	70.1000 W	2007	Wilson and Sandoval 1997
8	Gamba, Gabon	02.7168 S	10.0000 E	2006	Yanoviak et al. 2007, 2008a

Supplementary Material), whereas control ants ($n=13$) received a similar spot of paint on the head just anterior to the ocelli. Ants were stored at 5°C for 2 h prior to the manipulation, and paint was applied under $\times 10$ – 20 magnification with the ant resting on a makeshift cold stage (i.e., ice in a Petri dish). The mass of each ant was measured to the nearest 0.1 mg on an electronic balance before paint was applied.

Ants were tested for DAD at Sites 2, 4, and 5 (Table 1) as described above. Drops were initiated an average horizontal distance from the tree trunk of 1.1 m (range = 0.4–2.0 m) and >20 m above the forest floor. The vertical distance between the drop point and the landing point was estimated for each trial as described above. This information was used to quantify aerial performance as a glide index (the horizontal distance traveled per unit vertical drop distance) for each successful trunk landing.

Nocturnal behavior

Cephalotes atratus workers were dropped from trees at night under either overcast or moonless conditions at Sites 4 and 5 (Table 1; $n=10$ workers at each site). Drop tests were conducted as described above, with the exception that each ant was marked with two coats of luminescent paint (Glow, Inc.; Severn, MD, USA) on its head and gaster >2 h beforehand. We additionally drop-tested four primarily nocturnal species (*D. boltoni*, *C. pallidus*, *C. atriceps*, and *Camponotus* sp. indet.) during daylight hours at Site 5.

Loss in the understory

The fate of ants (mainly *C. atratus*) landing in either water or dry understory leaf litter was tested at Sites 4 and 5. Ant workers were individually tossed into the water of Lake Gatun within 3 m of the shoreline (Site 4), or into streams and backwaters of tributaries of the Napo and Amazon Rivers (Site 5). The activities of each ant, and its interactions with fish or other animals, were monitored continuously for up to 30 min. Ant size (maximum head width excluding eyes and spines), air temperature, channel width and approximate central depth, presence of overhanging or emergent vegetation, and general weather conditions were recorded for each trial. In addition, the behaviors of individual *C. atratus* workers dropped into the center of a circular pan (30 cm diameter) filled with river water to 2 cm depth were observed for 60 min.

Dry understory trials also were conducted at Sites 4 and 5. For each trial, one *C. atratus* worker was dropped from a height of ~ 2 m onto the understory leaf litter and its activities were monitored for up to 30 min. In Peru (Site 5), we additionally measured understory stem density and connectance in three height classes (<0.5 , 0.5–2.0, and >2.0 m). Specifically, we counted the number of stems located within a haphazardly selected circular patch of forest floor 3 m in diameter and adjacent to (but not including) the base of a canopy tree (>25 m tall). We recorded the number of stems in each height class that either were physically isolated from or in contact with other stems leading to the canopy. One *C. atratus* worker was dropped onto the litter in the center of the circle and was observed for 30 min or until it climbed a stem leading to the canopy. This experimental setup was replicated at 10 locations in primary rainforest, each ~ 5 m from the nearest trail.

Aerodynamics and kinematics

We tested the prediction that both success and performance in gliding in *C. atratus* following asymmetrical ablations of legs would be lower than those for either unmanipulated controls or for ants with symmetrical ablations. Methodological details are provided elsewhere (Yanoviak et al. 2010); briefly, we removed up to two legs (middle leg = ML, hind leg = HL) and the gaster (G) from ants collected from multiple colonies at Sites 4 and 5. Experimental treatments included single HL ablation (-1HL), symmetrical ablation (-2HL or -2ML), symmetrical ablation plus gaster ablation (-G-2HL or -G-2ML), and asymmetrical ablations (-RHL-LML or -LHL-RML). Ants were drop-tested as described above. We analyzed success rates among treatments with exact binomial tests (Sokal and Rohlf 1995) using the observed control rate as the expected frequency for each treatment. We assessed differences in performance among treatments by comparing average glide indices with ANOVA.

We conducted parallel observations using a vertical wind tunnel to determine how different appendages of ants are used as aerodynamic control surfaces. Workers of *C. atratus* and other arboreal ants were released into a working section (i.e., a transparent chamber, $30 \times 15 \times 15$ cm) containing a vertical updraft with flow velocity comparable to the expected terminal velocity of each ant. Compact digital cameras (Casio Exlim) recorded events within this working section at 60 frames/s from three different axes, producing simultaneous orthogonal views of

the postures associated with various maneuvers during gliding.

Analyses

Quantitative analyses were conducted with SAS 9.2 (SAS Institute Inc 2002). All proportional data were angular-transformed to improve normality (Sokal and Rohlf 1995). Other data were log-transformed when necessary to correct heterogeneity of variance. We used *t*-tests assuming unequal variance and non-parametric tests when transformations were ineffective. Head width (HW) was used as a measure of body size for *C. atratus* and was either compared among treatments or included as a covariate whenever body size potentially influenced treatment effects. HW is highly correlated to mass and other morphometrics in *C. atratus* (Yanoviak et al. 2005, 2008b). All means are given ± 1 SE unless otherwise noted. Means were compared with Tukey's *post hoc* tests when ANOVAs revealed significant differences.

Results

As in previous studies of DAD, this behavior was remarkably consistent and easily observed in most taxa in which it occurred. In addition to drop tests of worker ants, we tested four workers of the wasp *Polybia* sp. after experimental ablation of the wings and five dealate queens of unidentified *Cephalotes* spp. None of these individuals showed evidence of DAD.

Phylogenetic distribution

DAD evolved multiple times independently within the Formicidae, and currently is known to occur in three subfamilies: Myrmicinae, Formicinae, and Pseudomyrmecinae (Figs. 1 and 2). Species within all *Cephalotes* clades tested to date exhibit DAD (Fig. 3). However, there was considerable qualitative variation in gliding ability among different *Cephalotes* species. Noteworthy among these are the relatively poor gliding abilities of *C. pallidus*, *C. setulifer*, and *C. texanus*, all of which had success rates $< 50\%$. Glide indices were not measured in every trial for logistical reasons, but never exceeded ~ 0.20 for these species. As with *Cephalotes*, virtually all pseudomyrmecines tested to date exhibited DAD (Fig. 2). The two exceptions, *Pseudomyrmex boopis* and *P. tenuis*, are understory species rarely found on vegetation > 3 m above the ground.

Although the generalities of DAD are relatively consistent among species, we observed three noteworthy deviations from the patterns described elsewhere (Yanoviak et al. 2005; Yanoviak and Dudley 2006).

First, whereas it appears that all *Cephalotes* spp. glide toward targets gaster-first, *Nesomyrmex anduzei* and most *Camponotus* spp. clearly glide to trunks head-first. Second, the formicines generally showed the greatest variation within and among species in ability to glide. Specifically, workers of *Gigantiops destructor* and larger workers of *Camponotus sericeiventris* were able to orient to tree trunks when falling, but were unable to effect a horizontal trajectory. Early in a fall, these species exhibited an aerial righting reflex (i.e., they rolled to a dorsal-side up position) and then rotated about the central vertical axis such that they faced the tree trunk. This position was maintained throughout the entire descent, and the ants ultimately landed in the understory even though the tree trunk dominated their field of view and was only a few body lengths away. This behavior was corroborated by observations of *G. destructor* workers in the vertical wind tunnel; they adopted a stable parachuting posture but showed no tendency for lateral movement. Finally, several species of *Dolichoderus* and *Pachycondyla* autorotate when falling. Video recordings suggest that this is achieved through extension of the legs and lateral (i.e., asymmetric) displacement of the gaster during descent.

Occlusion of ocelli

Covering the ocelli of *P. gracilis* with paint (Supplementary Material) did not affect their rate of success in DAD relative to controls; all ants in both groups landed on the target tree trunk. Likewise, the average glide index did not differ between experimental (0.249 ± 0.014) and control ants (0.246 ± 0.014 ; $t = 0.15$, $df = 23$, $P = 0.88$). Average body size (mass) was similar between groups ($t = 1.07$, $df = 23$, $P = 0.30$).

Nocturnal behavior

The *C. atratus* workers marked with luminescent paint and dropped at night exhibited a righting reflex, but none showed a horizontal trajectory suggestive of DAD. Likewise, nocturnal *Camponotus* spp. and *D. boltoni* dropped in the daytime fell dorsal-side up, but showed no ability to glide (Azorsa and Sosa-Calvo 2008). Although not quantified, success and performance in gliding in *C. atratus* appear to be significantly diminished under conditions of low light (i.e., dusk and dawn).

Landing in the understory

Worker *C. atratus* dropped onto understory leaf litter ($n = 36$) had much lower mortality rates

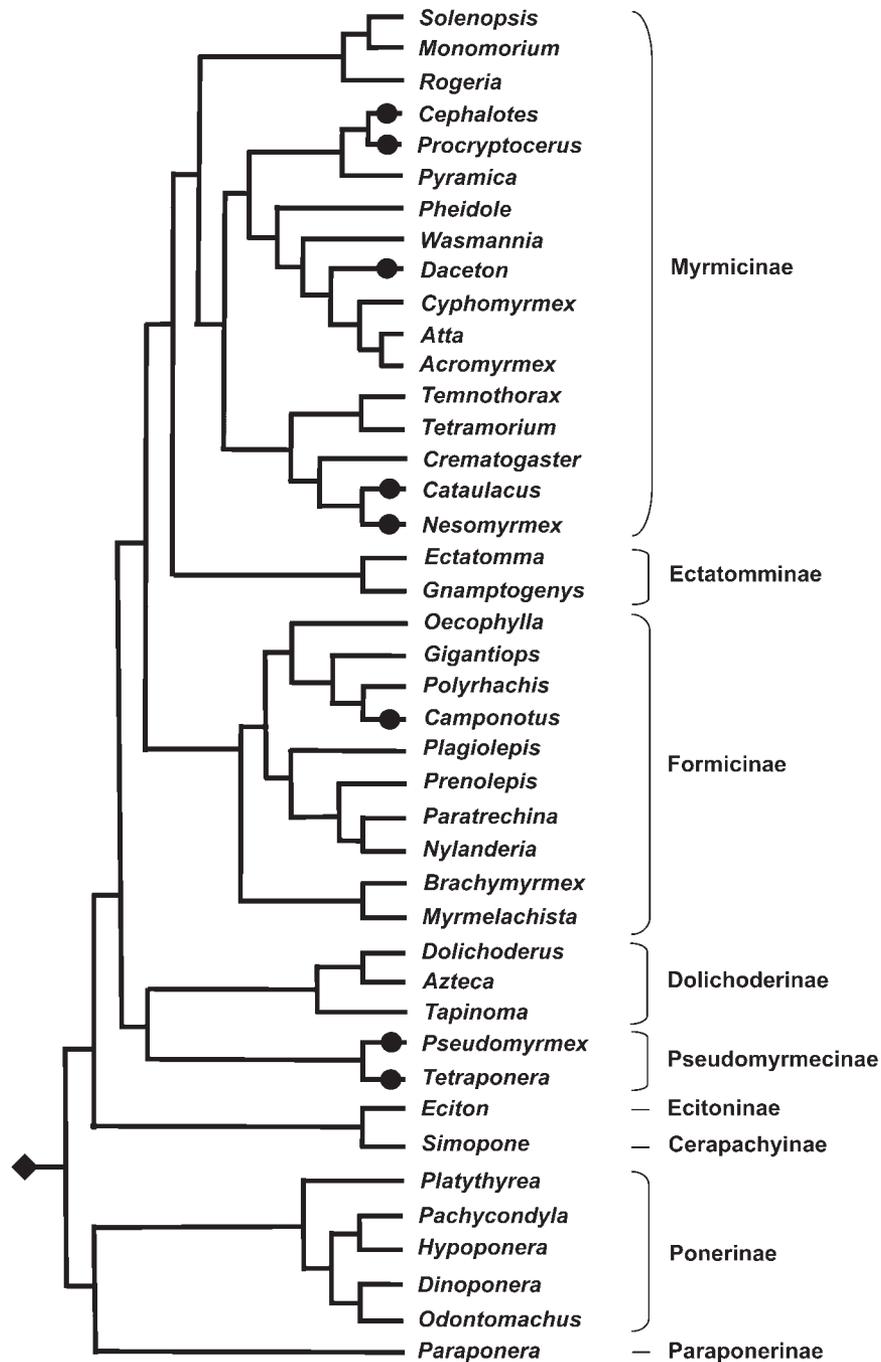


Fig. 1 Cladogram illustrating the current known distribution of DAD among arboreal and semi-arboreal ant genera based on drop tests conducted at various sites (Table 1). Only genera that have been drop tested are shown. Filled circles indicate genera with at least one species exhibiting DAD. The phylogeny is redrawn from Brady et al. (2006), Moreau et al. (2006), LaPolla et al. (2010), and P.S. Ward unpublished data; no branch length information is included and some clades have stronger support than others.

(2.8%) than did those dropped into water (42%; $n = 48$). Likewise, the rate at which ants dropped onto the litter were attacked by resident arthropod species was lower (0.2 ± 0.05 attacks/min) than the attack rate by fish in water (6.9 ± 2.22 attacks/min; $t = 4.20$, $df = 50$, $P < 0.001$). The principal attackers in the litter were ants (mainly *Ectatomma* spp. and

Odontomachus spp.), rove beetles (Coleoptera: Staphylinidae), and spiders. Whereas *C. atratus* successfully escaped attacks by most predators, they were typically pursued in the litter and killed by diurnal *Odontomachus*.

Most (72%) ants landing on litter climbed the nearest stem within 5 min. Ants generally spent

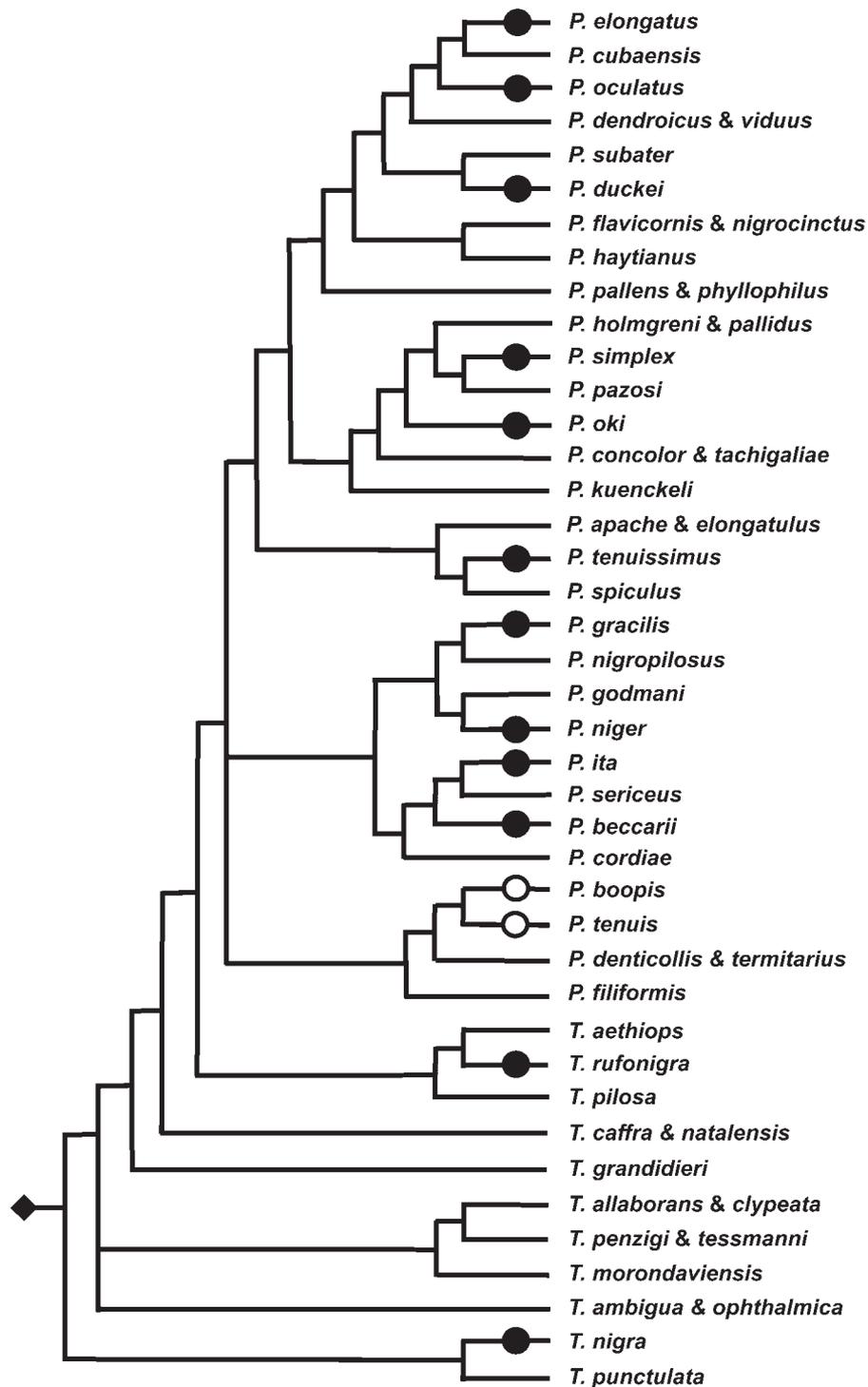


Fig. 2 Cladogram illustrating the current known distribution of DAD among taxa within the ant subfamily Pseudomyrmecinae. Filled circles indicate species exhibiting DAD. Open circles indicate species that were tested but do not glide. The phylogeny is redrawn from the DNA-based tree of Ward and Downie (2005) and P.S. Ward, unpublished data. No branch length information is included.

most of their time climbing and descending stems (62%) versus wandering in the litter (38%), where they appeared to move more tentatively. The 10 observation plots at Site 5 contained an average of 63.3 stems (range=39–147), 80% of which were

<50 cm tall (Table 2). The proportion of stems connected to the canopy increased with stem height (Table 2). Half (56%) of the ants dropped onto litter eventually climbed a stem leading to the canopy during the observation period. The average

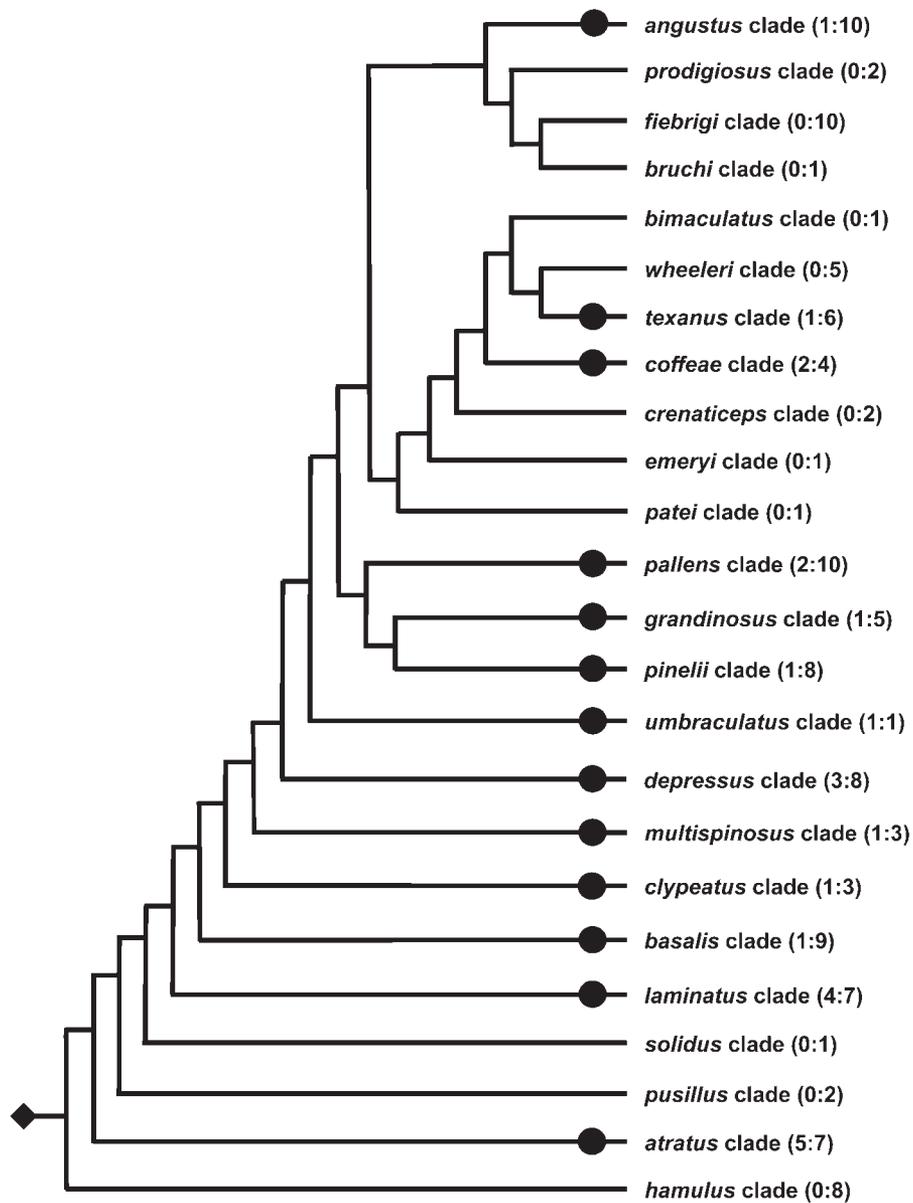


Fig. 3 Cladogram illustrating the current known distribution of DAD among extant *Cephalotes* clades. Filled circles indicate clades with at least one species exhibiting DAD. Numbers indicate the quantity of species tested within each clade and the total number of extant species in that clade. All *Cephalotes* species tested to date exhibit DAD. The tree is based on de Andrade and Baroni Urbani (1999). No branch length information is included.

time elapsing before encountering a stem leading to the canopy was 10.5 ± 1.39 min and did not differ between the sites ($t = 0.09$, $df = 18$, $P = 0.93$). None of the ant behaviors in litter varied with HW (linear regressions; $F < 0.44$, $P > 0.51$).

The fate of *C. atratus* dropped into water was most strongly influenced by the characteristics of the water body. Ants dropped into Lake Gatun in Panama and medium-sized streams (i.e., >10 m channel width) in Peru were attacked by fish at a lower average rate (2.2 ± 1.87 attacks/min, $n = 32$ ants) than were ants dropped into standing

backwaters or small streams (16.4 ± 4.78 attacks/min; $n = 16$ ants; $t = 5.50$, $df = 21$, $P < 0.001$). Consequently, *C. atratus* workers had lower mortality (12.5%) and survived longer (15.6 ± 1.10 min) in both Lake Gatun and medium-sized streams than in backwaters and small streams (100% mortality; 0.3 ± 1.58 min; Wilcoxon $Z = 5.70$, $P < 0.001$). Ant size had no effect on attack rate or longevity ($F_{1,46} < 1.90$, $P > 0.45$). Fish in medium-sized streams frequently rejected *C. atratus* workers after an attack. In most cases of rejection, the ants floated back to the surface and continued repeated grasping motions

Table 2 Average (± 1 SE) number of stems (Abundance) and percent of stems connected to the canopy (Connectance) in each of three stem-height classes.

	Height class			F
	<0.5 m	0.5–2.0 m	>2.0 m	
Abundance	52.6 (10.02) ^a	5.2 (0.42) ^b	5.5 (0.40) ^b	150.7*
Connectance	10.5 (1.50) ^a	42.6 (6.71) ^b	84.8 (7.05) ^c	34.7*

Within rows, equivalent superscript letters indicate means that do not differ.

* $P < 0.0001$.

with their legs. Some fish in these streams visually examined the ants for >10 s before either attacking or avoiding them. In contrast, fish in Amazonian backwaters appeared to attack indiscriminately all small objects landing on the water surface.

Despite their paddle-like tarsi (see Supplementary Figure 1 in Yanoviak et al. 2010), *C. atratus* workers were unable to make consistent forward progress in water. In contrast, *Pachycondyla villosa* and *P. foetida* swam on the surface toward emergent objects with average velocity 4.66 cm/s (± 0.603 ; $n = 5$). Whereas all *C. atratus* dropped in the same general location were consumed in <50 s, only two of seven *Pachycondyla* were eaten by fish. In similar trials conducted in a small stream, all of five *Dolichoderus bidens* and seven of 13 *D. attelaboides* were eaten by fish in <60 s. The surviving *D. attelaboides* escaped by either swimming or drifting to emergent vegetation.

Aerodynamics and kinematics

The rate of successful glides (i.e., frequency of landing on the tree trunk) were lower relative to controls for ants lacking their gaster and both ML, or their gaster and both HL, and for ants with asymmetrical leg ablations (Fig. 4). Performance (i.e., the average glide index) was lower in all treatments relative to controls (ANCOVA: $F_{4,122} = 12.9$, $P < 0.0001$; Fig. 4); body size (HW) was similar among treatments ($F_{1,122} = 3.25$, $P = 0.074$). Ants lacking their ML and gaster were stable during descent, but their ability to effect a glide trajectory was significantly reduced. In contrast, ants whose legs had been asymmetrically ablated were relatively unstable when airborne; most appeared to wobble from side-to-side during descent when observed from above. Ants missing both hindlegs and the gaster were able to direct their descent to tree trunks with similar frequency and performance as observed in prior studies (Yanoviak et al. 2010).

High-resolution recordings of ants in the vertical wind tunnel revealed the basic postures associated

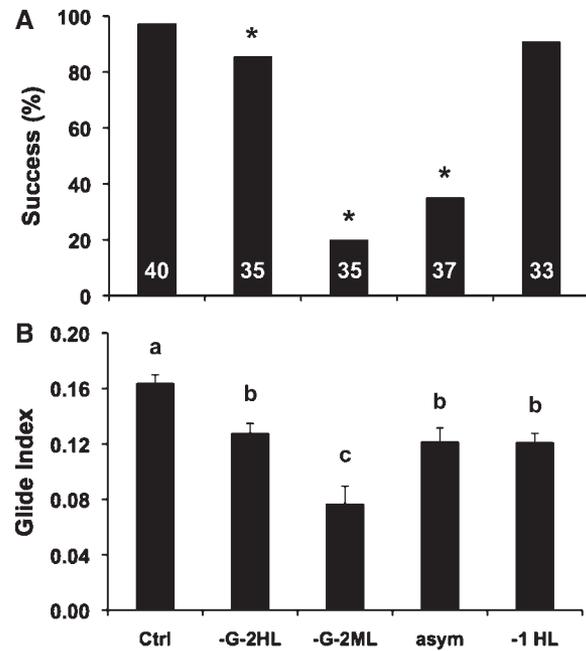


Fig. 4 Glide success (A) and performance (average \pm SE glide index) of *C. atratus* workers used in ablation experiments. Ctrl = no ablation, -G-2HL = gaster and both hindlegs removed, -G-2ML = gaster and both midlegs removed, asym = removal of one hind leg and one middle leg from opposite side of the body, and -1HL = removal of one hind leg. Asterisks indicate frequency of landing on trunks differs from that of the controls based on the exact binomial test. Numbers superimposed on bars in the upper panel are the total number of ants dropped in each treatment. Letters above bars in the (B) indicate means that do not differ.

with gliding in ants. For example, *C. atratus* workers consistently hold all legs elevated above the main body axis and outstretched, while the gaster is flexed slightly below the main body axis (Fig. 5). This configuration maintains the parts of the body with a lower surface area:mass ratio (i.e., the head, trunk and gaster) below the legs, which have a comparatively higher surface area:mass ratio. Consequently, the center of mass is maintained below the center of aerodynamic pressure. This arrangement is aerodynamically stable, facilitating effective control over the trajectory. This stable configuration also maintains the head and thorax at an angle to the vertical (typically $\sim 30^\circ$), essentially creating a bluff body held at an angle to an incident flow, which is expected to generate transverse forces pushing the ant backwards (Flower 1964; Ellington 1991). Indeed, most gliding ants introduced into the working section of the wind tunnel quickly moved to and attempted to land upon the walls of the working section, whereas nongliding ants typically stayed in the center and ultimately either fell to the bottom or were lifted out by the updraft.



Fig. 5 Still image captured from a video recording of a *C. atratus* worker floating on a column of air in a vertical wind tunnel; side and front views. Note that *C. atratus* is a backwards-gliding ant, and so lateral motion occurs in this posture with the abdomen leading.

Further analysis showed that *C. atratus* workers vary the fore-aft position of the middle legs and hind legs, as well as the angle of flexion of the gaster, to tilt the body's angle of attack relative to the incident flow. These changes result in correlated changes in transverse movement speed. Asymmetric postures of legs also were observed to be correlated with turning maneuvers. For example, more detailed kinematic analyses (in progress) indicate that moving the middle legs and hind legs forward on the left side and rearward on the right side results in a turn to the left (see also Yanoviak et al. 2010).

Discussion

Although most arboreal ant species remain to be tested for DAD, the phylogenetic distribution of taxa in which gliding is known to occur reveals three general patterns. First, DAD evolved independently in multiple lineages within ants, thus providing an excellent example of parallel evolution. The alternative possibility—that gliding is a basal character that was secondarily lost in nonarboreal taxa—seems unlikely given the absence of DAD in arboreal ponerimorphs. Second, DAD is linked to arboreal nesting. This outcome is most evident within *Pseudomyrmex* and the Formicinae, for which only the understory species (of those tested to date) do not glide. Moreover, ground-nesting species that forage in the canopy, such as *Paraponera clavata*, *Atta cephalotes*, *G. destructor*, and *Ectatomma tuberculatum*, do not glide. Finally, unlike gliding frogs, for which DAD also has multiple independent origins (Emerson and Koehl 1990), ant species in which gliding occurs do not show obvious external morphological differences from their nongliding congeners. The dorsoventrally flattened and flanged body of many *Cephalotes* spp. may improve their lift:drag ratio; however, such traits clearly also function in defense and may be secondarily related to aerial performance.

We suggest that subsequent field research and phylogenetic analyses concerning DAD should focus on the Formicinae, especially *Camponotus* spp., because the behaviors of these taxa appear to be transitional to dedicated gliding. Workers of *G. destructor* can orient (but not glide) toward a target while falling, and different sizes of workers within *Camponotus* spp. exhibit variable capacities for DAD. Study of such intermediates will permit identification of the functionality of transitional stages, as well as of the origins of diversity in aerial behaviors that evidently characterize arboreal ants more generally.

Autorotation in falling *Dolichoderus* spp. and *Pachycondyla* spp. may exemplify such transitional behavior. Autorotation appears functionally to slow descent, as in samaras and other seeds that spin while airborne (Burrows 1975; Green 1980). The lower terminal velocity provided by spinning allows greater opportunities for horizontal movement via wind currents (Norberg 1973), thereby increasing the potential for contact with vegetation before reaching the forest floor. Landing at considerable distances from the home tree following a spinning fall was not problematic for workers of arboreal *Pachycondyla* spp., which showed remarkable ability to return to their arboreal nests after significant horizontal and vertical displacement. Although the mechanisms of homing used by most species are unknown, other *Pachycondyla* and their relatives use visual landmarks and possibly geomagnetism as navigational cues (Hölldobler 1980; Acosta-Avalos et al. 1999).

DAD apparently is restricted to diurnal ants falling in daylight. The inability of nocturnal ants (or of diurnal ants falling at night) to glide to targets is not surprising given the importance of visual cues to DAD (Yanoviak and Dudley 2006). However, the apparent absence of gliding in arboreal ants that are nocturnal raises two questions for further study: (1) is the probability of these ants inadvertently

falling lower at night? and (2) do nocturnal ants use alternative mechanisms to regain their tree trunk in the event of a fall?

The irrelevance of ocelli to gliding by *P. gracilis* suggests that information potentially provided to falling ants by these organs (e.g., horizon detection) is either unnecessary or is superseded by that from the compound eyes. Apart from extension of ocellar occlusion experiments to other species, one appropriate continuation of this study would be to determine those cues used by falling ants to effect the aerial righting response. In the complex mosaic of light in tropical forests (e.g., Canham et al. 1990; Clark et al. 2008), sensation of air-flow directionality and of gravity may be more important for dorsoventral orientation than is detection of the horizon.

Cephalotes atratus workers falling onto the understory leaf litter are often attacked and sometimes killed by other organisms (Yanoviak 2010; this study), but mortality rates clearly are highest when ants land in waters occupied by fish. When fish are absent or selective, floating ants can survive for extended periods (>60 min), allowing ample time to escape either by swimming (*Pachycondyla* and *D. attelaboides*) or drifting (*C. atratus*) to emergent objects. The difference in mortality rates observed here between types of bodies of water is also partly attributed to the corresponding fish fauna. Lake Gatun in Panama is an artificial impoundment dominated by non-native peacock bass (*Cichla monoculus*). Although these fish will take surface prey, they showed little interest in floating *C. atratus*. Frequent visual inspection and rejection of ants by fish in medium-sized Amazonian streams suggests that these fish are more selective and may be deterred by the ants' spines or possibly chemical defenses. Collecting and identifying the resident fish in each of these habitats was beyond the scope of this study, but would enhance the conclusions of future research on this topic.

Although *C. atratus* workers were frequently attacked while wandering through the leaf litter, mortality rates were much lower in this study than reported earlier (Yanoviak 2010). This result is attributed to the patchy distribution of predatory *Odontomachus* spp.; when present in the experimental area, they generally killed *C. atratus*. It is likely that mortality in the litter is higher than observed in the present study because potential vertebrate predators may have fled the study area or were otherwise wary of investigators. Regardless, given the high leaf area indices typical of tropical forests (e.g., Clark et al. 2008), most ants falling from the canopy

presumably will land on vegetation several meters above the leaf litter. Understory stem counts and connectance data indicate that an ant landing on a stem >2 m tall is very likely to find a direct pathway to the canopy. Thus, mortality associated with falling into a non-flooded understory is probably low in most cases.

Ablation experiments conducted with ants in the field and in the vertical wind tunnel clarified the mechanistic roles of thoracic appendages in DAD. Elsewhere we showed that the hind legs are important determinants of success and performance in gliding (Yanoviak et al. 2010). Here, we show that such success and performance both are reduced to an even greater extent in *C. atratus* workers that lack middle legs and the gaster, or that are subject to asymmetrical ablations of legs. In both cases, the control surfaces are displaced relative to the ant's center of mass. Although this displacement clearly disrupted normal DAD, a small percentage of ants in each treatment were still able to control their descent, albeit feebly. This result suggests considerable resilience of the sensorimotor system in compensating for large-scale anatomical deficits.

Observations of ants in the wind tunnel additionally revealed details of leg and gaster position during stable gliding, as well as how changes in overall posture are correlated with changes in trajectory. Stability in falling ants clearly is maintained by holding the legs elevated above the rest of the body, thereby keeping the center of aerodynamic pressure above the center of mass. Likewise, it is evident that gliding ants effect significant changes in body trajectory via coordinated postural changes, specifically the fore-aft positioning of the legs and the angle of flexion of the gaster.

In summary, experimental and observational studies of DAD in ants are improving our understanding of the selective pressures and kinematics associated with the behavior. Further investigation of the diversity of aerodynamic mechanisms used by gliding ants, and particularly by representatives of the Formicinae, may elucidate the origins of DAD and the functional utility of transitional morphologies and behaviors. Likewise, many ecological aspects of DAD, such as its relevance to "ant rain" in forests (Haemig 1997) remain to be investigated. Extension of these studies to a broader range of wingless arboreal taxa, especially basal hexapods, may yield insight into the origins of winged flight in arthropods (e.g., Yanoviak et al. 2009).

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Supplementary Data

Supplemental Data are available at *ICB* online.

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