

Directed Aerial Descent Behavior in African Canopy Ants (Hymenoptera: Formicidae)

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Abstract Several species of neotropical ants direct their aerial descent toward tree trunks during a fall from the forest canopy. The primary goal of this study was to determine if afrotropical arboreal ants exhibit similar gliding behavior. Ants were collected from nine tree crowns in late secondary forest at a hydrocarbon extraction site near Gamba, Gabon. Of the 32 species tested, the behavior was observed in five *Cataulacus* spp. and three *Camponotus* spp., making this the first report of gliding in African ants. Aerial glide performance (horizontal distance traveled per unit vertical drop distance) decreased with increasing body size among species and among individuals of *Cataulacus erinaceus*. Characteristics of directed descent behavior in *C. erinaceus* were very similar to those of the neotropical ant *Cephalotes atratus*.

Keywords Body size · canopy · Gabon · gliding · tropical forest

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Introduction

Falling from the canopy to the understory 30 m below is a significant hazard for wingless arboreal animals such as ants. Yet canopy-dwelling ants frequently jump or fall from branches and leaves (Weber 1957; Yanoviak and Dudley 2006), resulting in a substantial but typically overlooked “ant rain” (Haemig 1997; Longino and Colwell 1997). Although the force of impact after a fall from the canopy is unlikely to kill or seriously injure small, hard-bodied animals such as arthropods, the forest understory (especially when flooded) is physically unfamiliar and biologically hazardous territory for arboreal ants (SPY unpublished data). In the neotropics, several species of arboreal ants use visual cues to direct their aerial descent toward tree trunks during a fall, apparently to avoid the costs associated with landing in the understory (Yanoviak et al. 2005; Yanoviak and Dudley 2006). To date, this behavior has not been documented in afrotropical ants.

Cephalotes are common arboreal ants in the neotropics (de Andrade and Baroni Urbani 1999). Prior research on directed aerial descent behavior in this genus showed a relationship between ant body size and glide performance within and among species (Yanoviak et al. 2005; Yanoviak and Dudley 2006). Specifically, smaller individual ants and smaller species of *Cephalotes* generally are better gliders (i.e., they fall shorter vertical drop distances before landing on tree trunks). This pattern is fairly consistent among neotropical gliding ant genera (SPY, personal observation) and can be attributed to basic aerodynamics: smaller ants have enhanced lift/drag ratios (Yanoviak et al. 2005) and during free fall reach a minimum viable glide velocity (U_{\min} ; Kingsolver and Koehl 1994) more rapidly than larger individuals. However, field observations suggest that variation in glide performance also is influenced by ant behavior during the early stages of the fall (Yanoviak and Dudley 2006). To date, such body size-performance relationships have been documented only for *Cephalotes* spp.

This study was undertaken as part of an arboreal ant survey (Yanoviak et al. 2007) conducted through a collaboration between the Smithsonian Institution and Shell Gabon to document the effects of large-scale hydrocarbon extraction on biodiversity and forest ecology (Alonso et al. 2006). The primary objective of this project was to determine if afrotropical arboreal ants exhibit directed aerial descent behavior like their neotropical counterparts (Yanoviak et al. 2005). Our goals were to: (1) document the taxonomic distribution of the behavior among common arboreal ants, (2) quantify variation in glide performance among species and among body sizes within a species, and (3) compare aspects of the behavior between neotropical and African ants.

Materials and Methods

Fieldwork was conducted at the Shell Gabon concession in Gamba, Gabon (2°43' S, 10°00' E). The concession primarily consists of forest-savanna mosaic on sandy soils, and lies within the Gamba Complex of protected areas (Thibault et al. 2004). The region receives ca. 2,100 mm of rainfall per year with a dry season from June to

September. Data were collected during the seasonal transition in April 2006. Additional details about the site are provided elsewhere (Fisher 2004; Alonso et al. 2006; Laurance et al. 2006; Yanoviak et al. 2007).

We collected ants from the crowns of nine different mature canopy or emergent trees in the concession. Tree crowns were accessed using the single-rope technique (Perry 1978). Ants were collected by hand and with tuna baits from the trunk (above 5 m) and crown branches of each tree (see Yanoviak et al. 2007). We tried to include the full range of body sizes for the polymorphic species used in the experiments described below. However, ants generally were collected haphazardly, and samples of most species closely reflected the caste and size composition of active individuals encountered in each tree.

We tested ants for gliding behavior by placing individuals in a small plastic vial coated internally with a non-stick substance (flulon). The vial was held beside a branch in the tree crown 1–3 m from the trunk, and slowly inverted with the vial opening oriented away from the trunk until the ant slid out. The behavior of the falling ant was recorded as described elsewhere (Yanoviak et al. 2005), and ants not landing on the focal tree trunks were scored as “miss” or “lost” depending on whether or not the landing point was visible to the observer. The use of a flulon-coated vial was the most efficient technique for dropping ants; it provided consistent initial drop conditions while requiring minimal handling and disturbance to the animal (vs forceps or naturally-induced falls; Yanoviak and Dudley 2006). Very small ants were dusted with fluorescent orange powder before being dropped to make them more visible. Trials with gliding and non-gliding ant species in the neotropics showed that the powder has no measurable effect on their gliding behavior (SPY unpublished data).

Glide performance was quantified for four locally common species of ants in terms of success rate (percent of ants landing on the focal tree trunk) and glide indices (glide index=horizontal distance from trunk/vertical drop distance traveled before landing on the trunk; see Yanoviak et al. 2005). We compared average glide indices among species with a one-way ANOVA to provide an overview of differences among taxa; however, too few species were measured to statistically separate the independent effects of phylogeny and body size.

We quantified intraspecific variation in glide performance by calculating glide indices for different size workers of *Cataulacus erinaceus*. We chose this species because it is the largest of the four taxa for which we obtained performance data, and it showed the greatest intraspecific variation in body size. Body mass (M) for *C. erinaceus* was estimated from head width (HW) measured with digital calipers in the field. The scaling relationship for these estimates, $M=HW(0.026)-0.0504$, was determined from the fresh weight of 13 *C. erinaceus* workers measured to the nearest 0.0001 g on an electronic balance in the lab. Unlike the power function observed for the neotropical ant *Cephalotes atratus* (L.) (Yanoviak et al. 2005), a linear model gave the best fit to the *C. erinaceus* data (regression: $F_{1,11}=24.02$, $P<0.001$, $R^2=0.69$). Workers of both species are continuously polymorphic in terms of body size, and the difference in model fit is probably due to smaller sample size and narrower overall body size range among individuals of *C. erinaceus*.

The glide performance of *C. erinaceus* was compared with that of similar-sized *C. atratus* workers by analyzing differences in their average glide indices with a t -test.

We also tested for differences between the slopes of their glide index vs. mass relationships with regression (SAS Institute 2002). For these and all other statistical analyses, normality was determined with Kolmogorov–Smirnov tests, data were log-transformed when necessary to correct variance heterogeneity, and Bonferroni-adjusted α values were used to account for multiplicity (SAS Institute 2002; Sokal and Rohlf 1995).

Ants were identified using published keys and information compiled by Taylor (2006). Voucher specimens were deposited at the California Academy of Sciences (San Francisco), the Smithsonian laboratory in Gamba, the Museo de Historia Natural Javier Prado (Lima, Peru), and the US National Museum (Washington, DC, USA).

Results

Thirty-two of the 36 ant species collected in the forest canopy of the Shell concession (Yanoviak et al. 2007) were tested for the presence of directed aerial descent behavior (Table 1). The remaining four species were not tested because too few individuals were encountered. We observed directed aerial descent behavior in three *Camponotus* species and all five *Cataulacus* species collected (Table 1). Breezy conditions and low sample sizes prevented accurate assessment of the behavior in *Tetraponera* spp. Some gliding species can correct their trajectories to compensate for wind effects (SPY, personal observation); however, we did not see evidence of breeze compensation or orientation to the trunk in falling *Tetraponera*, suggesting that these ants are not gliders.

We found that *Cataulacus* spp. direct their falls in a manner remarkably similar to species in the neotropical tribe Cephalotini (*Procryptocerus* spp. and *Cephalotes* spp.), including gliding to tree trunks abdomen-first (Yanoviak et al. 2005). We also observed that workers of *Camponotus* spp., *Cataulacus* spp. and *Crematogaster africana* will occasionally jump or drop voluntarily from tree branches in response to an approaching object or alarm pheromones, as do some neotropical arboreal ants (e.g. *C. atratus*; Weber 1957; Yanoviak and Dudley 2006). However, both in this study and in the neotropics, dislodged *Crematogaster* spp. did not subsequently control the direction of their falls.

Gliding success rates (i.e. the proportion of dropped ants landing on a tree trunk) varied widely among tested species, and ranged from >90% in *C. erinaceus* to <45% in *Camponotus* sp. 1 (Fig. 1). Gliding success was partly related to worker size and caste in *Camponotus* sp. 1. Almost all individuals assumed the same posture and aligned their longitudinal body axis perpendicular to the trunk during a fall, but only mid- to small-sized workers subsequently were able to direct their motion horizontally through the air. Soldiers and large workers fell straight to the ground (often facing the trunk during most of the descent), even when dropped from horizontal distances <50 cm from the trunk. Mechanisms for this size-related difference were not obvious in the field. The 50% glide success of *Cataulacus* nr. *satrap* (Fig. 1) was much lower than we expected based on observations of morphologically similar cephalotines in the neotropics (SPY, unpublished data).

Table 1 Ant Species Tested for Gliding Behavior

| Taxon ^a | n ^b | Glide |
|---|----------------|-------|
| Cerapachyinae | | |
| <i>Simopone conciliatrix</i> Brown | 5 | No |
| Dolichoderinae | | |
| <i>Plagiolepis alluaudi</i> Emery | >20 | No |
| <i>Tapinoma luridum longiceps</i> (Wheeler) | >20 | No |
| Formicinae | | |
| <i>Camponotus</i> sp. 1 | 15 | Yes |
| <i>Camponotus</i> sp. 2 | 5 | Yes |
| <i>Camponotus</i> sp. 3 | 8 | Yes |
| <i>Camponotus</i> sp. 5 | 5 | No |
| <i>Camponotus</i> sp. 7 | 10 | No |
| <i>Oecophylla longinoda</i> (Latreille) | 10 | No |
| <i>Paratrechina grisoni</i> (Forel) | 7 | No |
| <i>Polyrhachis decedentata</i> André | 5 | No |
| <i>Polyrhachis lanuginosa</i> Santschi | 5 | No |
| <i>Polyrhachis latispina</i> Emery | 15 | No |
| Myrmicinae | | |
| <i>Cataulacus erinaceus</i> Stitz | >20 | Yes |
| <i>Cataulacus guineensis</i> F. Smith | >20 | Yes |
| <i>Cataulacus mocquersyi</i> André | 2 | Yes |
| <i>Cataulacus</i> nr. <i>satrap</i> Bolton | 15 | Yes |
| <i>Cataulacus tardus</i> Santschi | 5 | Yes |
| <i>Crematogaster (Sphaerocrema)</i> sp. 1 | >20 | No |
| <i>Crematogaster africana</i> Mayr | >20 | No |
| <i>Crematogaster ambigua</i> Santschi | >20 | No |
| <i>Crematogaster buchneri</i> Forel | >20 | No |
| <i>Crematogaster depressa</i> (Latreille) | >20 | No |
| <i>Monomorium</i> sp. 1 (nr. <i>leopoldinum</i>) | 10 | No |
| <i>Monomorium</i> sp. 2 (nr. <i>floricola</i>) | 15 | No |
| <i>Pyramica maynei</i> (Forel) | 13 | No |
| <i>Tetramorium ictidum</i> Bolton | >20 | No |
| <i>Tetramorium occidentale</i> (Santschi) | 5 | No |
| Ponerinae | | |
| <i>Platythyrea conradti</i> Emery | 10 | No |
| <i>Platythyrea modesta</i> Emery | 8 | No |
| Pseudomyrmecinae | | |
| <i>Tetraponera mocquersyi</i> (André) | 1 | ? |
| <i>Tetraponera ophthalmica</i> (Emery) | 3 | ? |

^a Identifications and taxonomic authorities are from Taylor (2006)

^b Total number of individuals of each species observed in glide tests

Average glide indices (vertical drop distance traveled per unit horizontal distance) differed significantly among the four species ($F_{3,46}=16.9$, $P<0.0001$; Fig. 1), and showed a linear decline with increasing body size in *C. erinaceus* ($F_{1,15}=8.75$, $R^2=0.37$, $P<0.01$; Fig. 2). In addition to gliding backwards, quantitative aspects of directed descent behavior in *C. erinaceus* were comparable to those of the neotropical species *C. atratus* (Yanoviak et al. 2005). Both land on tree trunks with >90% success, and the slopes of their glide index vs. mass regressions were similar over the same range of body sizes ($t=0.46$, $df=1$, $P=0.65$; Fig. 2). However, *C. erinaceus* had a lower average (\pm SE) glide index (0.15 ± 0.009) than *C. atratus* (0.31 ± 0.016 ; $t=9.65$, $df=39$, $P<0.0001$; Fig. 2).

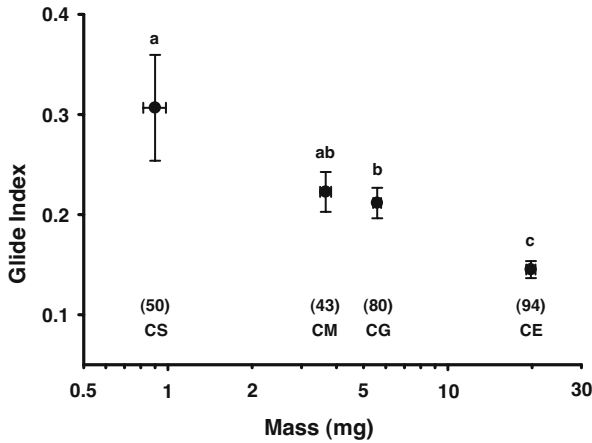


Fig. 1 Average (\pm SE) mass and glide performance of workers of four common ant species. Numbers in parentheses are success rates (percentage of dropped ants landing on the tree trunk). Similar lower case letters (*a-c*) indicate glide index means that do not differ. CS=*Cataulacus* nr. *satrap* ($n=5$ successful glides), CM=*Camponotus* sp. 1 ($n=12$), CG=*Cataulacus guineensis* ($n=16$), and CE=*Cataulacus erinaceus* ($n=17$). Glide index=horizontal distance from tree trunk/vertical drop distance.

Discussion

Yanoviak et al. (2005) documented directed aerial descent behavior in several genera and many species of neotropical canopy ants. Here we extend those findings to include several species in two genera of arboreal ants that are abundant and broadly distributed in tropical African forests. However, our survey of arboreal ants in Gabon was not complete, and many central African taxa remain to be tested for gliding behavior. In particular, definitive results for the genus *Tetraponera* (Pseudomyrmecinae)

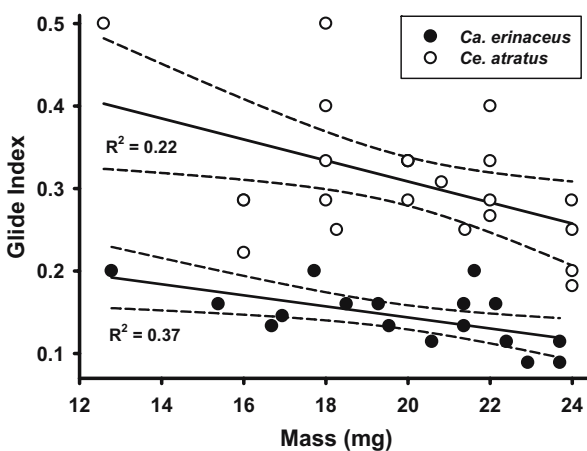


Fig. 2 Glide performance vs body size for the ant *Cataulacus erinaceus* ($n=17$) and for *Cephalotes atratus* over the same size range ($n=24$; from Yanoviak et al. 2005). Dashed lines indicate 95% confidence limits. Glide index=horizontal distance from tree trunk/vertical drop distance. Regression slopes differ from zero ($P \leq 0.02$) but not from each other (see text).

would be helpful given that this is the only paleotropical representative of the family (Ward and Downie 2005), and that several species in the neotropical genus *Pseudomyrmex* are gliders (Yanoviak et al. 2005).

The general pattern of decreasing glide index with increasing body size within *C. erinaceus* and among species in this study is similar to that observed for neotropical *Cephalotes* spp. (Yanoviak et al. 2005). This pattern is largely explained by basic aerodynamics and the shape of the ants' trajectory (Kingsolver and Koehl 1994; Yanoviak et al. 2005). Most of the variation in vertical distance to a successful landing occurs in the initial uncontrolled parachuting phase of the fall (Yanoviak and Dudley 2006), which is shorter for smaller ants because they attain the minimum velocity required to gain control sooner. However, as shown by the difference in average glide index between similar-sized workers of *C. erinaceus* and *C. atratus*, other factors beyond body size also play important roles in determining glide performance. In this case, high similarity in the qualitative aspects of gliding in the two species suggests that the difference in glide indices is a function of morphology (e.g., differences in lift/drag ratios). Finer-scale investigations of these two species, as well as comparisons between *Cataulacus* spp. and *Procryptocerus* spp., are needed to identify the relative contributions of morphology, behavior, and other factors on glide performance.

Differences in trunk landing success rates among species are less easily explained and provide interesting avenues for further research. The low success rate for *Camponotus* sp. 1 in this study is consistent with observations of neotropical *Camponotus* spp. (SPY unpublished data), and is somewhat related to caste and body size as described in "Results" above. However, several other anatomical (e.g., visual acuity, appendage morphology) and behavioral factors also appear to influence landing success. In particular, the behavioral context of the fall (e.g. whether the ant was walking, feeding, or defending at the time of disturbance) may determine whether an ant glides to the trunk or plummets to the ground. Our field observations suggest that such context-dependency contributed to the low success rate of *Cataulacus* nr. *satrap*.

The similarity between *Cataulacus erinaceus* and the neotropical *Cephalotes atratus* in qualitative aspects of their directed descent behavior, especially the backwards glide to the tree trunk, is striking. Both species also possess similar morphologies, gaits, and nesting and foraging habits. For these reasons, the counterintuitive glide orientation of *C. erinaceus* suggests close common ancestry with the tribe Cephalotini. However, molecular phylogenies show that the two taxa are not closely related within the subfamily Myrmicinae (Brady et al. 2006; Moreau et al. 2006), suggesting *Cataulacus* spp. and the Cephalotini evolved traits supporting arboreal lifestyles in parallel.

In sum, we provide the first documentation of directed aerial descent behavior in African ants. Our results add a seventh genus (*Cataulacus*) to the six previously known to include gliding species (*Camponotus*, *Cephalotes*, *Daceton*, *Nesomyrmex*, *Procryptocerus*, and *Pseudomyrmex*), and more than 20 species to the list of ants that do not exhibit the behavior (Yanoviak et al. 2005; SPY unpublished data). We expect that this information, in combination with results from ongoing field surveys and phylogenetic analyses, eventually will provide a basis for understanding the evolutionary origins and potential ecological correlates of directed descent behavior

in ants. In Africa and other regions, more detailed comparative studies (e.g. under controlled laboratory conditions) are needed to explain the effects of morphology and behavior on glide performance.

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