

The role of visual cues in directed aerial descent of *Cephalotes atratus* workers (Hymenoptera: Formicidae)

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Summary

Animals often depend on properties of reflected light (e.g. color, brightness) to locate resources. We compared reflectance properties of tree trunks with surrounding vegetation, and examined how differences in reflectance profiles of surrogate tree trunks (red, yellow, green, blue, black, gray, dark gray and white sheets) affected the directed aerial descent of worker *Cephalotes atratus* (L.) ants. Across the visual spectrum, tree trunk reflectance was 2–10 times higher than the surrounding foliage and differed among trees. In two separate experiments, one with colored sheets and one with black, white and gray sheets, nearly half (42% and 47%, respectively) of falling ants directed their descent to a bright white sheet when

given a choice of target colors or shades of gray. When colored and gray sheets were presented individually, landing frequencies were lower than expected for all except white sheets. Glide performance was highly variable, but there was a tendency for higher glide indices to be associated with the white sheet relative to the green sheet. We conclude that visually mediated aerial behavior in falling canopy ants is strongly influenced by reflectance properties of the target object, specifically brightness, and correlates with preferred natural targets of tree trunks.

Key words: ant, *Cephalotes atratus*, behavior, color, gliding, orientation, tropical forest.

Introduction

Insects use a variety of visual stimuli to locate resources, and the quality of visual information thus obtained is strongly influenced by the characteristics of reflected light, especially its brightness and hue. Color is especially important, providing feedback about resource quality (e.g. fruit ripeness, flower condition) as well as location (e.g. von Frisch, 1967; Prokopy et al., 1983; Casper and La Pine, 1984; Kelber et al., 2002). Brightness and color of a reflective surface are also functions of the characteristics of incident light, which vary vertically within forests (Endler, 1993). In concert, these features determine the degree of contrast between an object and its background, thus influencing signal quality, crypsis and resource detection (Endler, 1993; Altshuler, 2003).

Incident light is greatly modified within forests, becoming scattered and diffused by the complex matrix of leaf surfaces, but also by trunks and other woody components (Endler, 1993; Shashar et al., 1998). Tree trunks are a conspicuous part of the visual landscape in even the most dense tropical forests, and the light reflected from tree bark is described as having moderate brightness along with moderate to high wavelengths, i.e. they appear as brown (Endler, 1993). However, when viewed by

humans from midstory and canopy heights, many tree trunks in lowland forest are light-colored columns that sharply contrast against a dark green background of foliage (Fig. 1). This phenomenon characterizes many tree species in the lowland tropics regardless of intrinsic bark color because light-colored epiphytic lichens are ubiquitous in highly exposed areas such as forest edges and canopies (Frahm, 2003).

Tree trunks and branches compose the fundamental habitat template for arboreal ants (e.g. Yanoviak and Kaspari, 2000). Most ants navigate and defend this reticulate setting using pheromones for communication (e.g. Hölldobler and Wilson, 1990), but some taxa (e.g. the Pseudomyrmecinae) also have large eyes and ocelli. In such ants, vision may supplement or supersede the use of chemical signals for local navigation, and may be essential in preventing the loss of workers that fall or jump from tree branches.

Workers of *Cephalotes atratus* (L.) (Formicidae: Myrmicinae) and several other arboreal ant species direct their aerial trajectories during a fall (Yanoviak et al., 2005). This behavior is visually mediated and targeted toward tree trunks, lianas and climbing ropes, all of which generally appear lighter in color than the surrounding vegetation (Fig. 1). The attraction

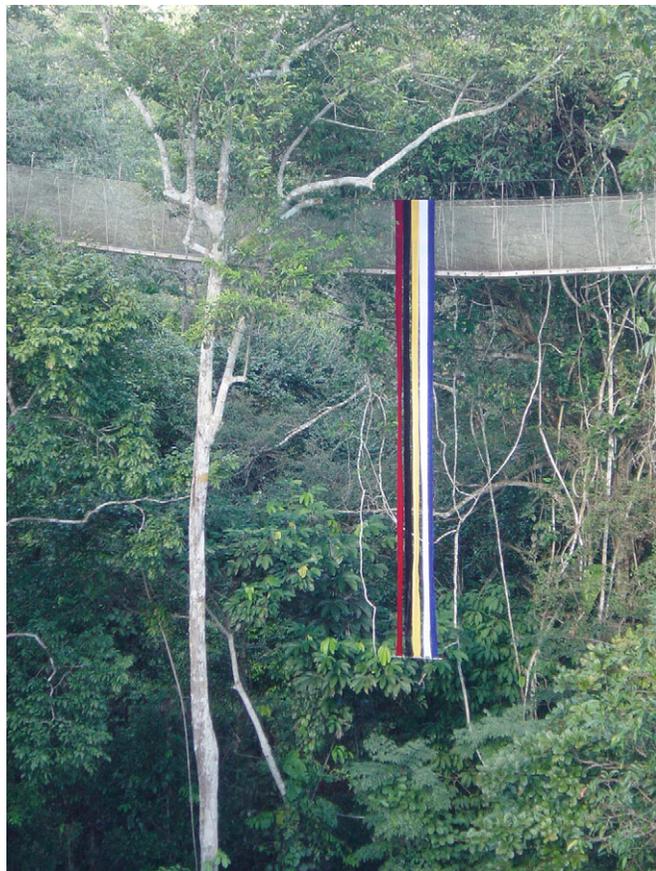


Fig. 1. Experimental configuration of colored sheets used to evaluate preference in falling ants. The sheets were suspended from a more sheltered location (platform 5-B) for experiments. The arrangement shown here corresponds to run #7 (Table 1).

of falling *C. atratus* to light-colored columns is sufficiently strong that a long, narrow piece of suspended white cloth can be an effective surrogate tree trunk for observations of directed descent (Yanoviak et al., 2005). However, this apparent preference for targets with high reflectance is based solely on qualitative observations. We have examined experimentally how the reflectance properties of such simulated tree trunks influence the ability of arboreal ants to direct their aerial trajectories during a fall.

Our principal objective was to test the hypothesis that falling ants orient their trajectories towards brighter, light-colored columns. We predicted that falling *C. atratus* workers would direct their descent to lighter colors and shades (white and yellow) with higher frequency, rather than to darker colors and shades (red, blue, green, gray, dark gray and black) when offered a choice of colored or gray columns. We further expected that attraction to the lighter targets would be independent of the spatial order of the juxtaposed columns. Finally, we predicted that falling ants would demonstrate significantly better glide performance (i.e. a shorter drop distance to a successful landing) when presented with lighter targets relative to darker shades and colors.

Materials and methods

Most field work was conducted in March and May 2005, and January 2006 at the Amazon Center for Tropical Studies (ACTS) canopy walkway near Iquitos, Peru (3.25°S, 72.90°W). Data were also obtained from forests located 48 and 60 km SSW of Iquitos along the Iquitos-Nauta highway (Mäki et al., 2001) in May and July 2005. Both the ACTS and highway sites are classified as humid tropical lowland forest (Holdridge et al., 1971), are associated with clay soils, and receive ~3000 mm of rainfall annually. Detailed climate and floristic information for the region are provided elsewhere (Madigosky and Vatnick, 2000; Vásquez, 1997).

We used a GretagMacbeth™ Eye-One spectroradiometer to quantify reflectance of potential natural targets for falling ants, focusing on tree trunks and associated surrounding vegetation at the ACTS walkway and highway sites. We recorded 40–100 reflectance measurements (ranging from 380 to 730 nm at 10 nm intervals) on the vertical trunk surface at or below the lower crown branches of each of 21 trees. Measured trees included two *Inga* spp. (Fabaceae) and two *Brosimum lactescens* (Moraceae); the remaining 17 trees were of different genera. Individual measurements were each separated by ~10 cm along and around the trunk. The total number of measurements obtained for a given tree depended on variation in reflectance properties such that fewer measurements were taken on more homogeneous trunks. We similarly quantified the reflectance of surrounding vegetation near the focal trees by measuring the upper surface of 15 leaves on each of 51 neighboring lower canopy and midstory trees. The point of measurement on each leaf avoided the midvein but otherwise was selected haphazardly. When possible, we included measurements of the leaves of the focal tree and nearby epiphytes. We compared the reflectance properties of the trunks and vegetation by plotting the average ($\pm 95\%$ C.I.) median reflectance values at each wavelength for the 21 trunks and 51 plants. We also compared average total reflectance (i.e. the sum of reflectance values across all wavelengths for a given measurement) among trees with a one-way ANOVA (SAS Institute, 2002).

Orientation to target color and brightness

Experimental data for the color and brightness choice experiments were obtained at the ACTS canopy walkway platform 5-B, which receives minimal tourist traffic and provides an unobstructed 22 m fall from the lower crown of the platform tree to the understory. In March 2005, we suspended five colored velvet sheets (red, black, blue, yellow and white) side-by-side from the platform railing. Each sheet was 10 m long and 16 cm wide; their juxtaposition produced a multicolored column 80 cm in total width (Figs 1 and 2). The column was hung approximately centered in front of the platform tree trunk and was 1.6 m horizontally distant from the trunk. Plastic pipes were passed through loops at both ends of the sheets to improve stability of the assembly (Fig. 1). We followed the same protocol in May 2005, but replaced the blue sheet with a green felt sheet of equal

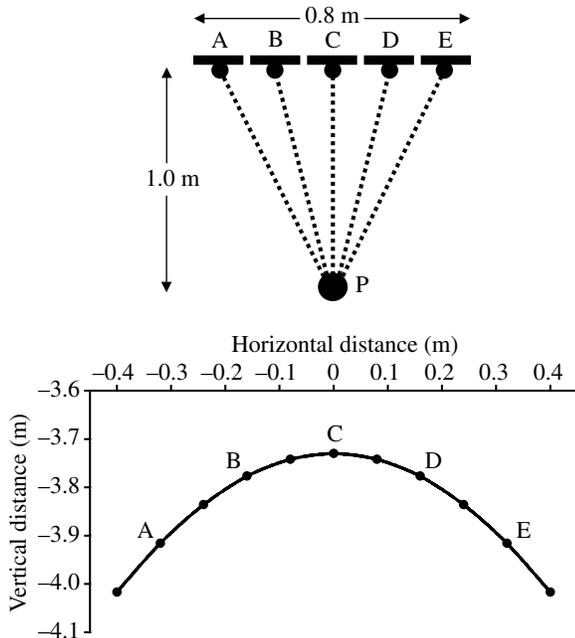


Fig. 2. Diagram of experimental arrangement as viewed from above (top) and potential landing points as viewed laterally and perpendicularly to the array of sheets (bottom). The null frequency of contact with a sheet is a function of distance from the drop point (P) to its landing position (A–E). Relative to the most direct path (i.e. from P to C), the distance from P to A or to E is 5.1% greater, and from P to B or to D is 1.3% greater. Thus, the proportions used to calculate null frequencies for *G*-tests were: 0.195 (landing points A and E), 0.203 (landing points B and D) and 0.205 (landing point C).

dimensions. The experiment was not run with blue and green sheets together (i.e. resulting in a total of six sheets in the column) because of time and logistical limitations. We measured each sheet at five different points spaced ~ 1 m apart with the spectroradiometer to quantify their reflectance properties (Fig. 3).

Foraging *Cephalotes atratus* (L.) workers were collected from four trees (representing at least two distinct colonies) at horizontal distances ranging from 50–150 m from platform 5-B. We dropped 27–38 *C. atratus* workers in each of 14 trials (trials 1–7 in March 2005 and 8–14 in May 2005), and rearranged the color order in the column between trials (Table 1). Logistical constraints prevented us from testing every possible combination and placement of the five different sheets. However, we arranged the color order such that all paired color combinations were presented at least twice (e.g., white was next to black in two trials, and next to non-black colors in the remaining five trials; Table 1). All experimental trials were conducted under fair weather conditions between 08:00 and 16:00.

Ants were dropped from a point 1 m in front of the center sheet in the series (Fig. 2). Each ant was placed in a small plastic vial coated internally with fluon. The vial was inverted at the drop point during periods of still air (as determined by

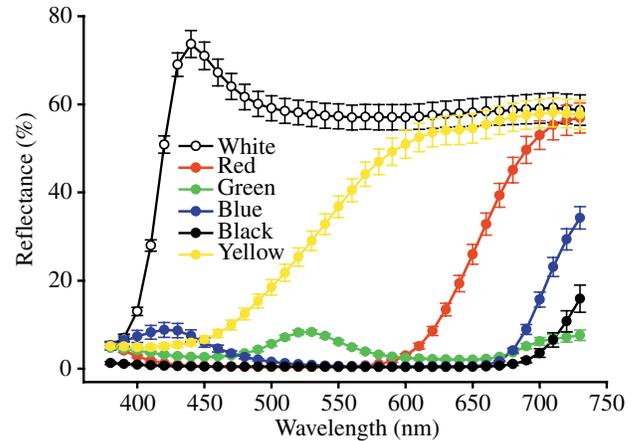


Fig. 3. Reflectance profiles for each of the six colored sheets. Each point represents the mean ($\pm 95\%$ C.I.) of five separate measurements.

lack of motion in the sheets) and the trajectory of the ant visually monitored until the end of its fall. The landing point of the ant was recorded as red, blue, black, white, yellow, green, or as a ‘miss’ or ‘lost’. Ants in the ‘miss’ group directed their aerial descent, but did not land on any of the sheets (i.e. they fell more than 10 m before ultimately gliding to the platform’s tree trunk). ‘Lost’ ants either fell to the ground or glided to a different tree. Each ant was used only once in the experiment.

We repeated the above setup in January 2006 using four cotton/polyester sheets representing a brightness gradient (white, gray, dark gray and black; Table 2). Reflectance was

Table 1. Arrangement of colored sheets in the fourteen experimental runs conducted in March and May, 2005

Run	Position				
	A	B	C	D	E
1	Bk	Yl	Bu	Wh	Rd
2	Yl	Bk	Bu	Rd	Wh
3	Bu	Bk	Wh	Yl	Rd
4	Bu	Wh	Bk	Rd	Yl
5	Wh	Yl	Bu	Rd	Bk
6	Wh	Yl	Rd	Bu	Bk
7	Rd	Bk	Yl	Wh	Bu
8	Bk	Yl	Gr	Wh	Rd
9	Yl	Bk	Gr	Rd	Wh
10	Gr	Bk	Wh	Yl	Rd
11	Gr	Wh	Bk	Rd	Yl
12	Wh	Yl	Gr	Rd	Bk
13	Wh	Yl	Rd	Gr	Bk
14	Rd	Bk	Yl	Wh	Gr

Green was substituted for blue in runs 8–14. The five positions A–E correspond to the color order from left to right, as observed by a falling ant (Fig. 1).

Rd, red; Bk, black; Wh, white; Bu, blue; Yl, yellow; Gr, green.

Table 2. Arrangement of gray sheets in the seven experimental runs conducted in January 2006

Run	Position			
	A/B	B/C	C/D	D/E
15	Bk	Dk	Gy	Wh
16	Wh	Bk	Dk	Gy
17	Gy	Wh	Bk	Dk
18	Dk	Gy	Wh	Bk
19	Dk	Wh	Gy	Bk
20	Wh	Dk	Gy	Bk
21	Bk	Wh	Dk	Gy

Because only four sheets were used, their relative positions fall between the labeled points on Fig. 1 (e.g. A/B=the leftmost sheet, viewed from the perspective of a falling ant).

Bk, black; Wh, white; Gy, gray; Dk, dark gray.

measured at five different points on each sheet using the aforementioned spectroradiometer (Fig. 4). The sheets were hung from platform 5-B and data were recorded as described above.

To test for any confounding effects of handling and initial conditions, ants used in the gray shade experiment were dropped using one of three methods: (1) with forceps, (2) with a fluon-coated vial as described above, and (3) by inducing a natural jump or fall. Thirty ants were dropped using each of the three techniques. All remaining ants used in the gray shade experiment were dropped using the fluon-coated vial because this was the easiest and most efficient method.

Natural jumps were induced by allowing an ant to walk on a stick secured to the 5-B platform railing immediately above and perpendicular to the hanging sheets. Movement of the ant along the stick back toward the railing was restricted with a barrier of toothpaste. The ant was then exposed to conspecific alarm pheromones by placing ~10 *C. atratus* workers inside a plastic 500 ml bottle, which was then shaken, uncapped, and gently

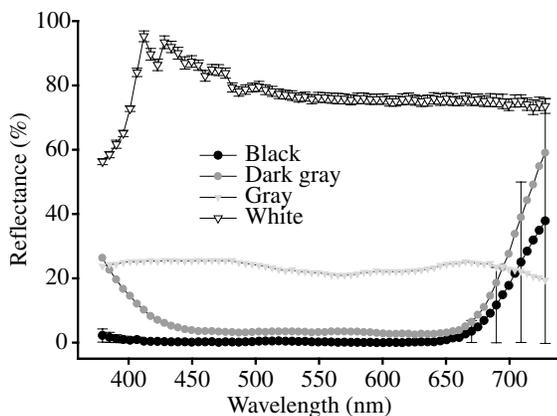


Fig. 4. Reflectance profiles for the four sheets used to assess the ants' attraction to targets of different brightness. Each point represents the mean (± 1 s.d.) of five measurements. Some points and error bars were omitted for clarity.

squeezed while positioned ~10 cm lateral to (and directed toward) the ant on the stick. All *C. atratus* workers exposed to alarm pheromones in this manner responded by dropping or jumping off the stick. They also jumped when exposed to alarm pheromones of other species in the tribe Cephalotini (i.e. *Cephalotes* spp. and *Procryptocerus* spp.). The only limitation of this methodology was that the ants in the bottle had to be replaced or allowed to rest after several successive trials, presumably because they became accustomed to the disturbance and/or their supplies of pheromone were exhausted.

We used *G*-tests with Williams' correction (Sokal and Rohlf, 1995) to compare landing frequencies of ants on the colored columns to null frequencies for each of the 14 trials. The null frequency for each of the five sheets used in the color experiment was calculated as its relative distance from the drop point, which itself was a function of the position of the sheet in a given trial (Fig. 2). Following the trajectory pattern and glide angle described (Yanoviak et al., 2005), the null landing pattern approximated a hyperbolic conic section for a cone with apex ~3 m below the drop point and with a slope of 15°. Thus, an ant landing in position A or E (Fig. 2) traveled 5.1% farther than an ant landing at C, and an ant landing at B or D traveled 1.3% farther. A similar correction for expected null frequencies was applied to the four sheets used in the gray shade experiment.

We compared the mean proportion of ants landing on each color and shade with a one-way analysis of variance (ANOVA) and a Tukey multiple comparison test. Proportional data were arcsine square-root transformed before analysis and statistical significance of the ANOVA results was determined with Bonferroni-adjusted α of 0.025.

Effects of target color and brightness on glide performance

To measure gliding performance, we dropped 340 *C. atratus* workers (eight trials of 36–52 ants each) as described above, but presented them with only one of the colored or gray sheets in each trial. We hung a weighted string marked with flagging at 1 m intervals next to the sheet, and measured glide performance as the vertical drop distance to the point of contact (to the nearest 0.5 m) (Yanoviak et al., 2005). Ants not landing on the sheet were scored as miss or lost as described above, and each ant was used only once. We analyzed the landing frequency on each of the colored sheets with a *G*-test using a null expected success rate of 85% (Yanoviak et al., 2005), and a one-way ANOVA to compare glide performance (in terms of glide indices) among the different colored sheets.

Glide performance is influenced by body size such that smaller ants tend to fall shorter vertical distances before landing on the sheets (Yanoviak et al., 2005). To avoid this potentially confounding variable in performance tests, we estimated the mass of each dropped ant from head widths measured with calipers in the field (see Yanoviak et al., 2005). We used a nested ANOVA to determine if the average log-transformed mass of ants differed among target colors or shades, and if the success of landing on a sheet of any particular color varied with body size. Finally, because the white and black sheets used in

performance tests in January 2006 were of different material (cotton/polyester) from those used in 2005 (velvet), we compared glide indices between the fabric types using *t*-tests.

Results

Reflectance profiles showed dramatic brightness and color differences between tree trunks and the surrounding foliage at canopy and mid-canopy heights. The reflectance intensity (i.e. brightness) of tree trunks was 2–10 times greater than the leaves of nearby vegetation at wavelengths <720 nm (Fig. 5). Moreover, trunks showed high reflectance over the entire visual spectrum (i.e. predominantly white coloration, compare Figs 1, 3–5), whereas leaves exhibited a comparatively small peak in the 525–575 nm range, corresponding to green and greenish-yellow (Fig. 5). Also, the average total reflectance differed significantly among individual trees ($F_{20,1368}=12.51$, $P<0.0001$).

Orientation to target color and brightness

We dropped a total of 659 *C. atratus* workers in the color and gray shade choice experiments. Most (90.6%) landed on one of the sheets. Forty four ants (6.7%) missed the sheets and landed on the trunk of the tree supporting the platform. Eighteen ants (2.7%) were lost in the experiment, but no more than two ants were lost in any given trial. Successful glides to the target were not influenced by the different methods of dropping ants. In the test of drop methods, all 30 pheromone-induced falls ended in glides to the sheet or trunk, as did 29 of 30 ants dropped with forceps and 29 of 30 dropped with the fluon-coated vial. Overall results were similar among the different months of the study.

Landing frequency of ants on the colored and gray sheets differed significantly from that expected by chance in 19 of 21 trials (colors: $G_{adj}>12.73$, $d.f.=4$, $P<0.025$; gray shades: $G_{adj}>9.34$, $d.f.=3$, $P\leq 0.025$), and ants were strongly attracted to the white sheet regardless of its position in the series. The

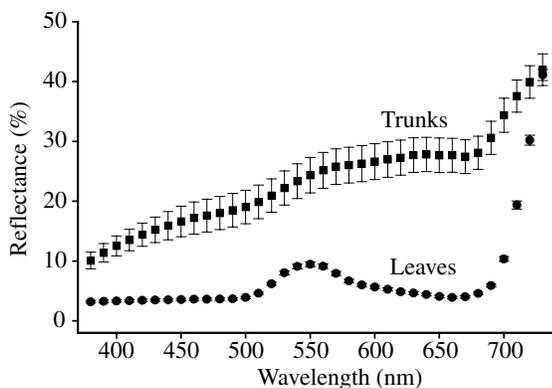


Fig. 5. Reflectance profiles for tree trunks (squares, $N=21$) and surrounding vegetation (circles, $N=51$ plants). Each point represents the average ($\pm 95\%$ C.I.) of the median reflectance values obtained from 40–100 measurements per tree trunk, and from 15 leaf measurements per plant.

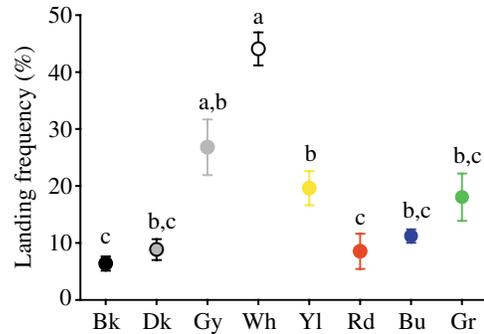


Fig. 6. Proportion of dropped ants landing on each of the colored sheets. Values are means \pm s.e.m.; $N=7$ trials for dark gray, gray, green and blue, $N=21$ for white and black and $N=14$ for all others; 27–38 ants dropped per trial. Bk, black; Dk, dark gray; Gy, gray; Wh, white; Yl, yellow; Rd, red; Bu, blue; Gr, green. Similar letters indicate lack of difference between means.

two replicates for which ants showed no significant association with color or shade had white and yellow (run #9) or white and gray (#16) sheets at opposite ends of the experimental configuration (Tables 1 and 2). The majority of ants dropped in run #9 (57%) still landed on either the yellow or white sheets, and 70% landed on either white or gray in run #16.

Based on the proportional distribution of landings in each run (both color and gray shade experiments combined), most falling *C. atratus* workers directed their descent to the white sheet (Fig. 6; $F_{7,90}=20.8$, $P<0.0001$). Intermediate proportions of ants landed on the yellow and gray sheets, whereas black and red were least attractive (Fig. 6).

Effects of target color on glide performance

The number of successful glides in the performance tests was significantly lower than expected for all colors except white ($G_{adj}>9.57$, $d.f.=1$, $P<0.005$; see sample sizes in Fig. 7),

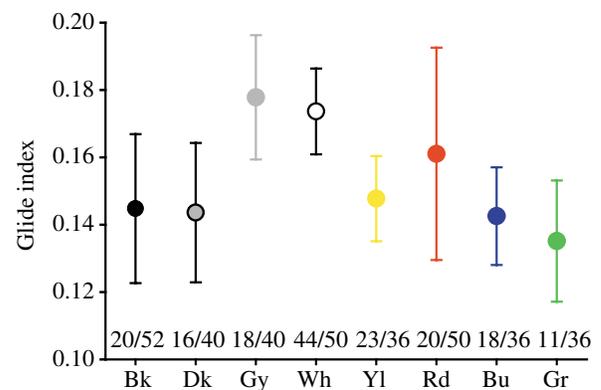


Fig. 7. Glide index (horizontal distance/vertical distance) for ants landing on each colored sheet presented individually. Bk, black; Dk, dark gray; Gy, gray; Wh, white; Yl, yellow; Rd, red; Bu, blue; Gr, green. Values are means $\pm 95\%$ C.I.; number pairs indicate the number landing on each sheet out of the total number dropped (i.e. the first in each pair is the sample size for the plotted mean).

whereas the frequency of ants landing on the white sheet (88%) was statistically similar to the 85% success rate observed in prior studies of gliding in *C. atratus* ($G_{adj}=0.37$, d.f.=1, $P>0.50$) (Yanoviak et al., 2005). We observed that ants were more likely to orient to more distant alternative targets when the contrast between the experimental target and the surrounding vegetation was low (e.g. with target sheets of green, black, and red).

Variance heterogeneity in the performance data was high and could not be corrected by standard data transformations. This was specifically due to the greater variance associated with the red sheet (Fig. 7). Thus we used a nonparametric Kruskal–Wallis test in place of ANOVA to assess differences in glide indices (i.e. performance) among colors. This test yielded a significant result ($\chi^2=24.78$, d.f.=7, $P=0.0008$). When the red sheet data were removed from the analysis, ANOVA and Tukey comparisons showed significantly better glide performance to the white vs. the green sheet ($F_{6,143}=4.29$, $P=0.0005$, $\alpha=0.025$). This statistical difference reflects a physical difference in vertical drop distance of only 1.6 m (drop distance, mean \pm 1 s.d.: green=7.7 \pm 1.59 m, white=6.1 \pm 1.37 m). Minor differences in behavior among individual ants during the non-equilibrium portion of the descent had large effects on overall gliding performance and contributed to the high variance in glide indices (S.Y., personal observation).

There was no effect on glide performance (i.e. glide indices) of the different fabric types (cotton/polyester *versus* velvet) used for the black and white sheets (black: $t=0.73$, d.f.=18, $P=0.48$; white: $t=0.83$, d.f.=42, $P=0.41$). Also, the average mass of dropped ants did not differ among the color treatments, and an ant's successful glide to a sheet did not vary with body size within a given target color (Table 3).

Although the experiments reported here were always conducted in fair weather, we found that the strongest and most consistent attraction to the white sheet occurred under overcast conditions. Any patches of direct sunlight landing on the colored sheets (and even the black sheet) appeared to override color differences, causing some ants to modify their trajectories several times during the fall. This was most apparent when the ants were presented with single sheets in the performance experiment. Specifically, sunflecks on the sheet occasionally caused ants to follow a spiral trajectory, ultimately gliding to the platform tree trunk after passing the free end of the sheet.

Table 3. Results of a nested ANOVA comparing average body size of ants used in the performance experiment among colors and shades, and comparing ants that either hit or missed the sheet within colors or shades

Effect	d.f.	Type III SS	F	P
Color/shade	7	0.889	1.29	0.26
Hit–miss (color/shade)	8	0.972	1.23	0.28
Error	324	31.98		

Body size = log-transformed mass.

Discussion

Our results strongly support the prediction that *Cephalotes atratus* ants orient toward bright vertical columns during a fall, and that the high contrast between tree trunks and the darker surrounding foliage provides the preferred visual target for falling ants. Reflectance profiles obtained for trunks and leaves in this study are superficially similar to those described elsewhere (Endler, 1993), which showed that total radiance from tree bark was greater than for leaves in shade. However, that study (Endler, 1993) did not find high reflectance from trunks at lower wavelengths (<550 nm) as observed in this study. We attribute this to differences in the height above the ground that the trunks were measured in each study [\sim 5 m (Endler, 1993) and >10 m here] and the great abundance of white crustose lichens on tree trunks at canopy heights in the Amazon. Such lichens often yield high reflectance at low wavelengths, resulting in remarkably flat reflectance profiles down to 300 nm (J. A. Endler, personal communication).

Although we did not test all possible colors, shades and combinations in the choice experiment, ants clearly were most responsive to white and gray, and moderately responsive to colors reflecting strongly in the 440–450 nm range. This was the only region for which the black and red sheets had considerably lower reflectance than the blue and yellow sheets, which may explain the intermediate attractiveness of the latter two colors. The similarly low relative abundance of ants landing on red and black sheets suggests that *C. atratus*, like most insects (Chapman, 1998), cannot see red.

We attribute the lack of marked difference in gliding performance among colors and gray shades to intrinsic properties of the aerial trajectory. Most of the variation in the total vertical distance traveled during directed descent appears to be linked to the accelerating and parachuting phase of the drop sequence, during which the ant makes the transition from undirected parachuting to visually acquiring and orientating to a landing target (see Yanoviak et al., 2005). The relatively high frequency of landings on the white sheet shows that differences in target quality affect the number of successful landings, but not necessarily the vertical distance traveled. Glide indices in *C. atratus* appear to be more strongly influenced by other factors, especially differences in individual ant behavior in the first 2–3 m of the fall. Although we detected a significant difference in glide performance between the white and green sheets, this difference does not represent a sufficiently large vertical drop to be biologically relevant, except possibly for *C. atratus* living in trees <10 m tall, or for falls between branches within the canopy.

Our results support the hypothesis that differences in reflectance properties among potential targets influence successful directional orientation and aerial targeting in falling ants. However, the moderate number of ants that landed on the green, black, dark gray and red sheets suggests that other characteristics of light reflected from targets are also relevant to this behavior. For example, various flying insects and wingless workers of some ant species use polarized light as an orientation cue, particularly as a horizon detector (e.g. von

Frisch, 1967; Fent and Wehner, 1985). Celestially polarized light penetrates far beneath the forest canopy and may become highly linearly polarized under dense foliage (Shashar et al., 1998). Moreover, light reflected from tree trunks tends to be vertically polarized whereas light from leaves generally is polarized in the horizontal plane, and these patterns tend to persist even under heavily shaded conditions (Shashar et al., 1998). Thus, multiple orientation cues are available in terms of direction of polarization of incident and reflected light, and we speculate that falling ants may be using such cues, in addition to brightness and contrast as shown here, to locate tree trunks and other targets during aerial descent.

Finally, horizon detection and use of polarized light in orientation (e.g. *via* a celestial compass) may be improved by, if not be dependent upon, the presence of ocelli (e.g. Fent and Wehner, 1985). Whereas *C. atratus* workers lack ocelli, other arboreal ant taxa, including some that exhibit directed aerial descent (e.g. *Pseudomyrmex* spp.) (Yanoviak et al., 2005), do have ocelli and would be appropriate subjects for further experiments on visual orientation within tropical forests.

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