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Insectes Sociaux

International Journal for the
Study of Social Arthropods

ISSN 0020-1812

Volume 58

Number 3

Insect. Soc. (2011) 58:325-334

DOI 10.1007/

s00040-011-0171-0



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Spatial movement optimization in Amazonian *Eciton burchellii* army ants

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Received: 15 July 2010 / Revised: 15 January 2011 / Accepted: 14 May 2011 / Published online: 29 May 2011
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Abstract Foraging army ants face a problem general to many animals—how best to confront resource depletion and environmental heterogeneity. Army ants have presumably evolved a nomadic lifestyle as a way to minimize re-exploitation of previously foraged areas. However, this solution creates a challenge for an army ant colony: foraging by this colony and others creates a shifting landscape of food resources, where colonies should theoretically avoid their own previous foraging paths as well as those of other colonies. Here, we examine how colonies exploit this resource mosaic, using some of the optimality arguments first proposed and tested by Franks and Fletcher (1983), but with much larger data sets in a new location in SW Amazonia. Our data supported Franks and Fletcher's (1983) model for systematic avoidance of raided areas during the statory phase, as well as a hypothesis of distance optimi-

zation between successive statory bivouacs. We also test and find significant evidence that foraging raids turn in opposite directions from the previous day's directional angles more frequently than what would be expected if turning angles were distributed at random, which acts to move a colony away from recently exploited areas. This implies that colonies follow a straighter line path during the nomadic phase as opposed to a curved one, which acts to maximize distance between statory bivouacs. In addition to intra-colony movement optimization, we examine evidence for inter-colony avoidance from more than 330 colony emigrations and suggest that colony-specific pheromones are not necessarily repulsive to other colonies. Lastly, we compare our results with those of similar studies carried out at Barro Colorado Island (BCI), Panama. Despite a higher density of army ants in the SW Amazon region, colonies spend less time emigrating than their counterparts at BCI, which suggests a higher prey density in SW Amazonia.

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Keywords Army ants · *Eciton burchellii* ·
Tropical rainforest · Cocha Cashu · Optimal foraging

Introduction

The neotropical army ant *Eciton burchellii* is a keystone predator in the neotropical forests it inhabits (Franks and Bossert, 1983; Boswell et al., 1998; Boswell et al., 2000; Kaspari and O'Donnell 2003). Most research on *E. burchellii* has been conducted on Barro Colorado Island (BCI), Panama, and has greatly enhanced our understanding of the species' lifecycle and ecology (Schneirla and Brown, 1950; Rettenmeyer, 1963a; Schneirla, 1971; Willis, 1967; 1982b), foraging optimization (Franks and Fletcher, 1983) and colony population dynamics (Franks and Bossert, 1983). In

addition, these studies have expanded our knowledge of the important role *E. burchellii* army ants play within the arthropod community as a resource for invertebrates and vertebrates (Rettenmeyer, 1962; 1963b; Akre and Rettenmeyer, 1966; Wrege et al. 2005; Berghoff et al., 2009). While Franks and colleagues have provided rich insight into the spatial movement patterns of *E. burchellii*, including foraging activity within a colony, as well as migration (e.g., Franks 1982b; Franks and Fletcher, 1983; Franks et al., 1991; Couzin and Franks, 2003), more field data on optimization of movement patterns at the colony scale are needed from sites across the neotropics to more fully address these aspects.

Eciton burchellii army ants capture, dismember and consume a broad array of insects and various other arthropods from the forest floor as they pass over an area in a foraging ant swarm (Rettenmeyer, 1963a; Schneirla, 1971). However, these army ants disproportionately rely on a specialized resource—social arthropod nests—that take a substantial time to recover after a raiding front has passed through. Franks and Bossert (1983) determined that social arthropod (mainly ant) nests need up to 100 days to recover half of their previous abundance. In contrast, non-social arthropod prey levels recover their normal densities within a few days of a raid (Franks, 1980; Franks and Bossert, 1983). Regardless of the social structure of prey, army ants must address the intriguing issue of optimizing their feeding strategies so as to account for localized resource depletion and environmental heterogeneity.

Prey composition aside, the need for highly efficient foraging and avoidance of resource-depleted areas is compounded by the presence of larvae within the bivouac or nest. As is the case with most arthropods, *E. burchellii* larvae have voracious appetites and pose the greatest nutritional demand within the bivouac, while being unable to forage themselves. *E. burchellii*, like other army ants, has developed a specialized lifestyle, which presumably serves the dual purpose of feeding young while avoiding areas where resources have been exhausted (Schöning et al., 2005). *E. burchellii* colonies follow a cyclic pattern of nomadic and stately phases (see Fig. 1a), mediated by the duration of pupal and larval stages within a colony (Schneirla, 1971; Hölldobler and Wilson, 1990). If the nomadic lifestyle does indeed serve the purpose of solving the problem of localized resource depletion, then the foraging and movement patterns of an *E. burchellii* colony should optimize the distance between successive bivouacs and minimize re-exploitation of recently raided areas. Optimization of prey resources is complicated by other colonies moving through the landscape, and each colony is thus in reality selecting among foraging sites depressed by their own and other colonies' recent exploitation (Franks and Fletcher, 1983; Schöning et al., 2005). Colonies that forage over areas

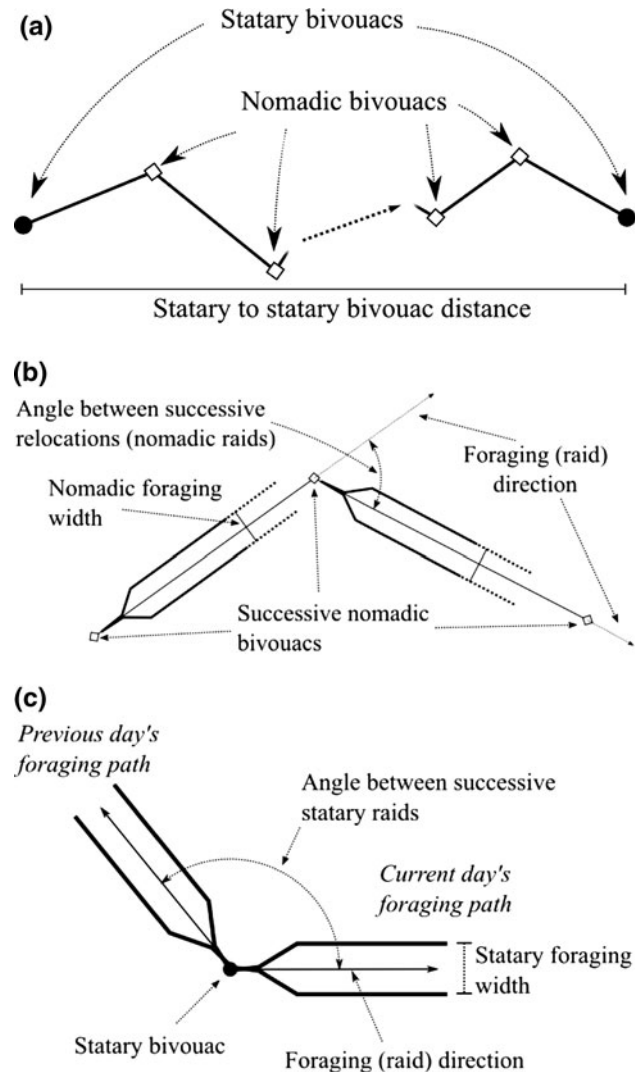


Fig. 1 Structural illustrations of **a** stately/nomadic cycle (note that there are on average 12 nomadic bivouacs, which have been removed for simplicity), **b** stately bivouac raiding patterns (*diagram* illustrates two successive days, although there is an average of 21 stately days), and **c** a successive 3-day nomadic raiding pattern

recently depleted of prey by conspecific colonies will be less productive (Franks and Fletcher, 1983). Thus, colonies must minimize re-exploitation of both areas where they and conspecific colonies have foraged previously, as is the case for *Dorylus* army ants of East Africa (Schöning et al., 2005).

Intraspecific avoidance by army ant colonies has other clear ecological advantages (Schöning et al., 2005). Colonies may lose workers in aggressive conspecific encounters. Additionally, inter-colony battles decrease the available time spent foraging. Willis (1967) observed more than 1,300 raids on BCI, yet he never observed a collision between two colonies. Swartz (1997) describes one collision from observations of 141 *E. burchellii* ant swarms in Costa Rica. Franks and Bossert (1983) performed a simulation that

measured collision rates between colonies, using data gathered on BCI, Panama, where there are approximately 3.2 colonies per 100 ha. They found that the observed collision rate was greatly below that which would occur if all *E. burchellii* colonies on the island moved independently, suggesting that colonies actively avoided each other.

Though a colony has lower nutritional needs in the starchy phase, foraging efficiency should be evident during this phase as well if there is high risk of foraging over a recently raided area. Franks and Fletcher (1983) hypothesized that foraging bouts were rotated around the bivouac in the same way that leaves spiral around a plant to minimize self-shading (noting that raids are analogous to very long thin leaves and therefore less precise positioning was expected). Justification for the leaf analogy came from Leigh (1972), who determined the optimal angle (126.4°) between leaves on a plant with 14–17 leaves. There are approximately 14–17 foraging bouts during one starchy phase. Franks and Fletcher (1983) found that the mean angle between starchy raids was 123° ($n = 41$, $SD = 40$). However, their small sample size of sequential outward movements from a starchy bivouac and the lack of support for this hypothesis at another site (Swartz, 1997) leave their findings open to speculation. We tested Franks and Fletcher's (1983) ideas with much larger data sets from a new field location.

In this paper, we address two main questions regarding optimality and spatial movement patterns in *E. burchellii* army ants: (1) Do *E. burchellii* colonies of Amazonian floodplain forest minimize re-exploitation of areas they have recently raided during the nomadic and starchy phases? Here, we examine movement angles to shed new light on how colonies move during the nomadic phase, and what foraging directions are "chosen" during the starchy phase. (2) Is there evidence from the field that *E. burchellii* colonies practice inter-colony avoidance? Here, we provide insight from observed interactions between colonies, as well as evidence that two factors—seasonal inundation of habitat, and predation attempts on a colony—may compromise movement optimization and avoidance strategies.

We present results from a multi-year study on foraging strategies of a population of *E. burchellii* army ants from the lowland rainforest of southeastern Peru. *E. burchellii* army ants have a widespread distribution, yet they have rarely been studied off BCI and variations in aspects of their ecology and spatial movement patterns have been little studied (O'Donnell et al., 2007). Predictions regarding army ant population densities and impacts on prey as a keystone predator may be misleading if assumptions are made using data gathered from a single site. Our study population from SW Amazonia may be more representative of lowland rainforest conditions in the neotropics, and we utilize published data from the well-studied *E. burchellii* population of BCI to facilitate comparisons with our results from Peru.

Methods

Data collection

Data presented here were gathered over seven field seasons in mature floodplain forest at the Cocha Cashu Biological Station in the southeastern Peruvian Amazon ($11^\circ54' S$ and $71^\circ22' W$, elevation ~ 400 m) from September 1998 to July 2008, totaling 18.5 months of field time. Most data were gathered during the rainy season; 3 months of data from 2007 to 2008 were from the dry season. During the first 1–3 weeks of each field season, three to five researchers walked trails throughout the study plot each day and located *E. burchellii* colonies within this area, with our focus on a core area of 100 ha. Established trails within the study plot were spaced at intervals of approximately 250 m. We searched trails for columns of *E. burchellii* army ants in the afternoon when foraging fronts are generally farthest from the bivouac and therefore crossing more trails. Trails were monitored daily throughout each field season, and new colonies were found as they entered the study plot. Plot size varied from 162 ha to approximately 270 ha. During nomadic phases, we monitored and followed each colony daily from bivouac to bivouac until it left the study plot, was lost by us or the field season ended. Loss of a colony was generally due to the colony's movement into very thick *Heliconia* spp.-dominated herbaceous swamps, where tracking was difficult.

Nomadic colonies were best tracked by following late-afternoon colony emigrations from that day's bivouac to the next day's bivouac before dark. The term "emigration" as used here refers to the movement of an entire *E. burchellii* colony's bivouac from one location to a new location. This technique proved much more reliable than searching along a nomadic colony's foraging route from the previous day, since that sometimes led to loss of the colony when multiple foraging routes were used (see Swartz, 1997 for implementation of that alternative method). Ant colonies almost always emigrated from their old bivouac by 17:00 hour, allowing us to find the next day's bivouac before dark.

When colonies entered the starchy phase, we nonetheless checked every afternoon so as to be prepared for a sudden emigration. If a newfound colony did not move for 3 days, we considered it to be in the starchy phase. The total duration of the starchy phase was recorded for each colony.

We checked *E. burchellii* colonies in the morning for foraging activity, regardless of the phase they were in, and observed each ant swarm for approximately 1 h if ants were foraging. We almost always observed nomadic colonies before noon because colonies tended to decrease in foraging cohesiveness in the mid-afternoon, when trail raiding (foraging in advancing trails) often replaced swarm raiding (foraging as a wide, cohesive moving "carpet" of ants

covering the ground). This decrease in foraging activity has been termed the “siesta effect” by Schneirla (1971). At the end of an observation, we calculated swarm width with a metric tape measure by spanning the leading edge of the active swarm, with an observer standing on either side of the ant swarm. We estimated straight-angle foraging direction from the bivouac using two observers, one standing at the bivouac and the other at the ant swarm front. Observers took compass readings on each other via visual and voice signals and estimates were averaged. Distances from the bivouac to the nearest Cocha Cashu trail marker (trails were marked every 25 m) were estimated using a combination of pacing and visual distance marking, or measured directly with a metric tape measure. All observers regularly tested visual distance marking and pacing against known distances of 25-m intervals to minimize observer error. Additionally, we measured speed (m/h) of the advancing ant swarm by flagging the ant swarm front and the distance the swarm advanced over a given time period (generally 1 h). Bivouac locations and the Cocha Cashu trail map were plotted in Microsoft Excel to calculate distances between successive bivouac relocations.

Data and statistical analyses

We calculated army ant colony density for each season for a 100-ha core area of the study plot. We made weekly colony counts based on which bivouacs were located in the study plot and determined a mean colony density from the weekly counts over each field season. We calculated a core density rather than the density of the entire plot, because plot size varied per year and sampling was less thorough on the edges of the study plot. Because of intensive daily monitoring, we were aware of all *E. burchellii* colonies in the core area, and mean densities from each season were based on actual counts of colony bivouacs rather than extrapolations or estimates. To account for the time needed to find all army ant colonies over the sampled area, we omitted the first 3 weeks of each field season’s *E. burchellii* colony counts.

Statistical calculations

Using known bivouac locations, we calculated the mean distance a colony moved its bivouac on a given night during the nomadic phase and mean distance from stately to a consecutive stately bivouac. We determined directional angles (-180° to $+180^\circ$) between successive nomadic emigrations by calculating the difference of the emigrational bearing of the current day’s nomadic phase with the previous day’s emigrational bearing. For example, if two successive daily emigrational bearings were measured as 120° and 250° , the directional angle associated with that measurement is 130° ($250^\circ - 120^\circ$). This can be thought of as

the colony making a clockwise turn from the previous day’s foraging angle. We illustrate these angles in Fig. 1b. We averaged the directional angles across our entire data set for a calculation of the mean “straightness” of *E. burchellii* colony paths over the nomadic phase (Franks and Fletcher, 1983). Using the same data, we also calculated the absolute value of the average divergence from one night’s path to the next, which is a measure of the mean directional angle as a colony moves its bivouac from night to night. Figure 2 illustrates the relationship between the mean directional angle and divergence. Mean directional angle is the average signed magnitude of the amount of clockwise or counterclockwise turn that a colony makes each day during the nomadic phase. Divergence is the absolute magnitude of those directional angles and is representative of the magnitude of turn a colony makes.

Additionally, to test the randomness of clockwise and counterclockwise directional turns during nomadic and stately phases, we applied a bootstrapped modification to the Runs test (Bradley, 1968). For this test, a “run” was a consecutive sequence of directional angles of the same sign (either clockwise or counterclockwise) from the previous day’s directional angle. As such, we need only consider the turn direction over time without consideration of compass bearing or distance traveled. Specifically, we observe runs of similar turning directions over time. The total number of runs observed from all bivouacs was compared to what would be expected if directional angles were distributed at random. A large number of runs indicates that colonies change direction more often (i.e., zig-zag), while a small

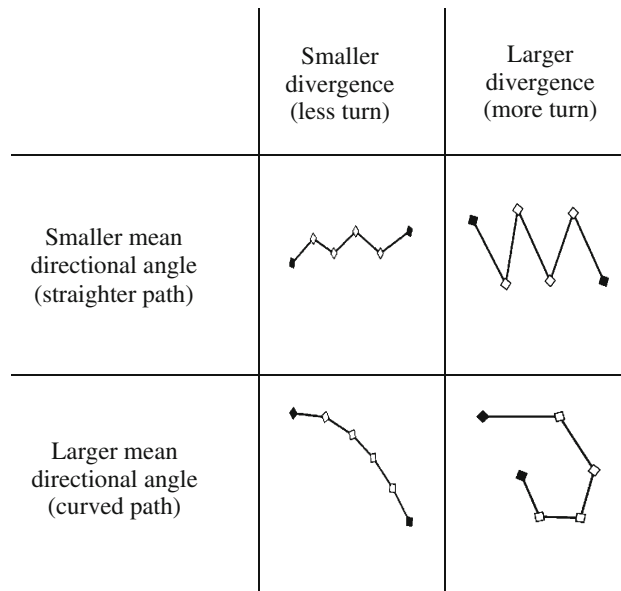


Fig. 2 Comparison of mean directional angle and divergence angle values given different path types. This figure illustrates that mean directional angle is a measure of path center, while divergence is a measure of turn

number of runs would indicate a spiraling type of pattern. Note that when a nomadic bivouac path exited and then reentered the study plot over a course of more than 1 day, we considered this the beginning of a new contiguous path since the angle incorporating the position outside of the study plot cannot be calculated. Similarly, the turning direction could not be calculated when an ant colony in the nomadic phase stayed in the same position. As a result, many of the contiguous paths comprised fewer days than the period of the nomadic phase.

Finally, we used Welch's two-sample t tests (when applicable) to make comparisons with data from BCI, Panama and one sample t tests when testing the significance of mean angles between successive stary raids, mean distance between stary bivouacs, mean directional angle during nomadic movements and mean distance between stary bivouacs. Each of these results is presented in the next section. Statistical analyses were performed using the statistical package R (R Development Core Team, 2009), while data processing was done with scripts written in the Python programming language.

Results

Basic ecological parameters

We measured *E. burchellii* colony density for Cocha Cashu at 4.9 colonies per 100 ha. Mean nomadic foraging width was 12.1 m ($n = 259$, $SD = 7.2$), while mean stary foraging width was 9.14 m ($n = 222$, $SD = 6.2$). Mean foraging speed was 14.3 m/h ($n = 179$, $SD = 3.8$) (Table 1). In gen-

eral, the observed army ant colonies at Cocha Cashu were more abundant than on BCI, had a shorter nomadic phase length, moved a shorter distance between stary bivouacs and emigrated less often during the nomadic phase than BCI army ants. The observed nomadic swarm widths were twice as large compared to those on BCI (Table 1). The summarized BCI data for these measurements did not include a standard deviation; thus, statistical comparisons at the population level (such as the t test) are not available.

Question 1. Do E. burchellii colonies of Amazonian floodplain forest minimize re-exploitation of areas they have recently raided?

Evidence based on analyses of distance traveled between nomadic bivouacs, colony foraging angles and the direction chosen during nomadic emigrations suggests that *E. burchellii* behavior minimizes re-exploitation of areas that were recently raided. We discuss the details of these observations in turn.

Distance between bivouacs

An army ant colony can avoid recently foraged areas by separating its stary bivouacs more than would be expected by a random walk (Franks and Fletcher, 1983). The mean distance between a given colony's nomadic bivouacs at Cocha Cashu was 78.0 m ($n = 351$, $SD = 44.0$ m), while the mean distance between successive stary bivouacs was 489.5 m ($n = 29$, $SD = 231.5$ m). Neither of these values is significantly different from BCI values ($t = -0.96$, $df = 740$, $P = 0.337$ and $t = -0.65$, $df = 63$, $P = 0.52$, respectively). If a colony moved randomly from one bivouac to the next for the duration of the nomadic phase, the expected distance between a colony's successive stary

Table 1 Comparative data for *E. burchellii* ant swarms at two neotropical sites: Cocha Cashu biological station, Peru and Barro Colorado Island (BCI), Panama

	Cocha Cashu	n	SD	BCI	n	SD
Colony density (per 100 ha)	4.9	–	–	3.2	–	–
Nomadic phase length (days)	12	48	2.6	15 ^a	42	–
Stary phase length (days)	21	54	1.8	20 ^a	51	–
Dist. betw. stat bivs. (m)	489.5	29	231.5	529 ^b	38	267
Dist. betw. nom. bivs. (m)	78.0	351	44.0	80.9 ^c	512	43
Mean angle betw. succ. Relocations	3.46	68	88.2	8.29 ^d	56	52.11
Mean divergence	62.0	263	46.2	–	–	–
Mean angle betw. succ. stat raids	129.3	480	60.1	123 ^d	41	40
Nomadic swarm width (m)	12.1	259	7.2	6 ^c	–	–
Stary swarm width (m)	9.14	222	6.2	6 ^c	–	–
Foraging speed (m/h)	14.3	179	3.8	14.8 ^c	113	–
% nom. days w/out emigration	30.7	736	–	14.1 ^a	860	–

Mean angle between successive relocations is the mean change in direction of emigration between two successive nights. Mean divergence is the mean absolute value of divergence from one night's emigration to the next. BCI data taken from: ^aWillis (1967), reanalyzed by Schneirla (1971), ^b(Willis (1967), reanalyzed by Franks (1980), ^cWillis (1967) and ^dFranks and Fletcher (1983)

bivouacs would be a mean of 270.4 m (equation from Pearson, 1906; in Franks and Fletcher, 1983). The mean distance between stately bivouacs was thus significantly greater than that expected from a random walk ($t = 5.1$, $df = 28$, $P < 0.001$).

Foraging angle during stately phase

The angle between a colony's successive foraging bouts during the stately phase affects the amount of overlap between new foraging areas and recently foraged areas surrounding the stately bivouac. Army ants at Cocha Cashu had a mean angle of 129.3° between successive stately raids ($n = 480$, $SD = 60.1$). Systematic foraging around a bivouac during the stately phase would be considered random if the mean angle between successive foraging bouts was 90° (Franks and Fletcher, 1983). The estimate for Cocha Cashu was significantly different from random movements ($t = 14.33$, $df = 479$, $P \approx 0$). Further, there was no statistically significant evidence that the mean angle of the army ants at Cocha Cashu differed from the optimal angle for separating raids of 126.4° ($t = 1.057$, $df = 479$, $P = 0.291$) described by Franks and Fletcher (1983).

Directional angles between emigrations

Army ant colonies at Cocha Cashu had a mean directional angle for movement between nomadic bivouacs of 3.46° with $SD = 88.2$ ($n = 68$), which is not statistically significantly different from zero degrees ($t = 0.323$, $df = 67$, $P = 0.747$). Using the same data, we calculated the mean divergence from one night's emigration path to the next. On average, with 95% confidence, *E. burchellii* colonies at Cocha Cashu turned between 56.4° and 67.6° ($n = 68$, $SD = 46.2$) from the previous night's emigration path.

We observed a total of 87 runs of consecutive directional angles out of a total of 182 measured directional angles during the nomadic phases. The bootstrap distribution of runs is approximately normal with a mean of approximately 66 runs ($SD = 5.8$) and results in a bootstrapped P value of 0.0001. This P value, along with the higher than expected number of runs, implies that there is significant evidence that colonies turn in opposite directions from the previous day's directional angles more frequently than would be expected if turning angles were distributed at random. Generally, this implies that colonies follow a straighter line path during the nomadic phase as opposed to a curved one and attempt to maximize the distance between their stately bivouacs. During the stately phases we observed 121 runs of directional angles out of a total of 320 measured directional foraging angles. The bootstrap distribution mean was approximately 130 with a P value of 0.123, showing that the

number of runs was not statistically different from random directions.

Question 2. What is the field evidence that E. burchellii colonies practice inter-colony avoidance?

Franks and Bossert (1983) used a simulation model to determine that colonies were actively avoiding each other on BCI, but actual observances of inter-colony avoidance are rare and limited to one study (Swartz, 1997). We observed three head-on collisions between colonies during 18.5 months of daily colony observation and 601 bivouac emigrations. In each case, both colonies involved were in the stately phase and unusually close to each other (bivouacs were a mean of 65.3 m apart). We report here on the details of those collisions to supplement what little is known about colony behavior during inter-colony encounters.

In the first instance, Colony A utilized a hollow tree as a bivouac site for 3 days during the end of its nomadic phase. It emigrated from this site and chose a stately bivouac 26 m away, in a large hollow tree. Four days later, Colony B moved into the tree Colony A had previously occupied and assembled its stately bivouac in the exact same area of the tree Colony A had been using. The two colonies remained situated 26 m apart for 23 days, the duration of Colony A's stately phase. The colonies collided while foraging from their stately bivouacs at least once. This collision resulted in Colony A's full retreat to its bivouac and the initiation of a new foraging angle, and Colony B's deflection from its initial path (at the site of contact) by approximately 90° . The second collision we observed occurred between two stately colonies that, for 15 days, utilized hollow trees 45 m apart. Colony C's foraging path took them directly to the bivouac site of Colony D, which was also foraging. Colony C stopped foraging, retreated to its bivouac and began a new foraging direction. In the third instance, colonies E and F met between their two stately bivouacs, as each colony was foraging in the direction of the other's bivouac. Both colonies had dispersed fronts that were interconnected over a width of more than 30 m, and ants retreated back to separate bivouacs for the day after the interaction.

Same-season bivouac site re-use by separate colonies was very rare. Of 712 unique bivouac locations (from a total of 2,101 monitored bivouacs), there were three instances of bivouac site re-use by another colony within the same field season. The first is described above; in the others, a nomadic colony utilized the bivouac site of a stately colony that had left 20 days earlier, and a stately colony re-used the exact stately site of a colony that had emigrated 3 days earlier.

In addition to colony collisions, we calculated seven events where one colony emigrated across the emigration path of a different colony <21 days after the first had passed ($n = 331$ known emigrations). Six of the seven observed trail crossings occurred 11–19 days after the first colony had

passed, while the seventh occurred just 2 days after the first colony had passed. No deflection behavior was evident in any of these crossings.

Discussion

Intracolony optimization

Movement patterns of successive statory raids at Cocha Cashu were not, on average, significantly different than the optimal angle described by Franks and Fletcher (1983) for BCI. Our larger sample size ($n = 480$ vs. 41 for BCI) adds weight to their finding that army ants do seem to optimize foraging angles around the bivouac to minimize re-exploitation of recently raided areas in the statory phase. These results differ from the conclusion reached by Swartz (1997) for army ants in Costa Rica. Our bootstrap analysis of statory foraging directional angles shows that although the mean day-to-day directional foraging angle is near optimal, the “selection” of the exact angle is not necessarily a continuous corkscrewing foraging pattern around a bivouac site. Instead, the day-to-day directional angle seems to be randomly selected either from a clockwise or counterclockwise direction from the previous day's foraging angle.

Floodplain habitat at Cocha Cashu leads to some areas that are seasonally unsuitable for *E. burchellii* due to water cover (S. Willson, personal observation). During particularly rainy months, depressions in the landscape become swamps, which may remain inundated for months at a time. In other areas, the landscape either becomes a mosaic of habitat “islands” amidst inundated forest, or remains sufficiently dry that army ants can forage unimpeded throughout the rainy season. During at least some parts of the rainy season at Cocha Cashu, *E. burchellii* army ants frequently cannot proceed in straight paths while foraging, due to depressions and wet areas. Although this could decrease the distance army ants move between successive statory bivouacs, the mean distance estimate at Cocha Cashu was not significantly different from that of BCI ($t = 0.96$, $df = 741$, $P = 0.337$). Franks and Fletcher (1983) found that BCI colonies maximize the distance between successive statory bivouacs by following roughly the same compass bearing as that taken on the previous day. Our analysis of nomadic movement suggests that colonies flip day-to-day directional angles clockwise and counterclockwise more often than would be expected from random. This adds additional support that colonies attempt to maximize the distance between successive statory bivouacs by traveling in a straighter path than a random walk (see Britton et al. (1996) for mathematical modeling on the question of longer vs. shorter emigrations).

Predation attempts on a colony may compromise movement optimization

An interesting aspect of foraging optimization and bivouac site selection that warrants further investigation is the impact of predation events on army ant colonies. Predation may reduce observed patterns of optimization as it puts outside pressures on a colony to shift their “optimal” movement patterns in response to a perceived or real threat to the integrity of the bivouac, larvae and/or single queen. Predation by mammals is suggested to play a role in migration patterns of the African driver ants *Dorylus (Anomma) molestus* (Schöning et al., 2005); we observed two events indicating that predation affects *E. burchellii* emigration patterns as well. Neotropical army ants seemingly have considerably fewer mammalian predators than their African counterparts (Schöning et al., 2005). One of those predators is the giant anteater (*Myrmecophaga tri-dactyla*). Giant anteaters are rare in rainforests, and feed from multiple ant colonies (of multiple species) each day, taking a number of ants from each colony (Emmons, 1990). We observed two interactions between a giant anteater and an *E. burchellii* colony at Cocha Cashu. One encounter is notable because it completely disrupted the normal foraging and emigration behavior of that colony. We found the anteater at 14:45 hour standing amidst trails of army ants <15 m from a terrestrial, exposed *E. burchellii* bivouac. The army ants had halted all foraging and were in the process of a full emigration of their bivouac along a circuitous chemical trail to a new site <10 m away, on the limb of a tree 4 m above the ground. The colony was on the third day of their nomadic phase. For the next 2 days, the colony remained in their arboreal bivouac and did not forage. On the sixth day of their nomadic phase foraging resumed, and the colony moved their bivouac out of the tree that night. We did not see the anteater again. This was the only time we observed a nomadic colony halting its daily foraging activity or emigrating to a new bivouac in mid-afternoon. We view this anecdote as clear evidence that other environmental factors, from standing water to predator avoidance, may force army ants to choose “less optimal” movement patterns on a given day.

Inter-colony avoidance

Although simulations of multiple interacting colonies by Franks and Bossert (1983) suggest there are mechanisms for colony avoidance, our observations are the first to test movement patterns of *E. burchellii* colonies in the field for evidence of intraspecific avoidance. Pheromone trails of the army ant *E. hamatum* are insoluble in water and impervious to light and heat for at least 31 days (Schneirla and Brown, 1950; Blum and Portocarrero, 1964). Franks and Fletcher

(1983) suggest that pheromone trails may provide information to other conspecific colonies that an area has been recently foraged, and they predict that a colony should detect chemical trails and deflect from recently foraged areas. Our data from real colony interactions do not fully support this prediction.

Higher density of colonies at Cocha Cashu should translate into increased interactions between colonies compared to those on BCI (4.9 vs. 3.2 colonies/100 ha). Army ants at Cocha Cashu displayed a low collision rate, although they did not always avoid the pheromone trails of other colonies laid down within the previous 3 weeks. In fact, two colonies re-used the exact stately bivouac site within 3 days of a previous stately colony's departure, indicating that colony-specific pheromones are not necessarily repulsive to other colonies. Since bivouacs divide through fission during the dry season, it is possible that these instances of bivouac re-use were between sister colonies, months after the fission had taken place.

Comparisons from Cocha Cashu and BCI: what can we learn?

Army ant density at Cocha Cashu is more than 50% higher than on BCI. Additionally, army ants have a shorter nomadic phase length and separate distances between stately bivouacs by an average of 40 m shorter than BCI colonies. They also emigrate less often during the nomadic phase than BCI army ants. We suggest that the floodplain habitat of Cocha Cashu provides a higher prey base for *E. burchellii* colonies and affects optimization by allowing ants to stay in one foraging area for a longer duration of time. It is well known that habitat quality affects insect abundance, and the dry hilltop environment of BCI is quite different ecologically from the tropical moist forest of southwestern Amazonia (Levings and Windsor, 1982; Levings and Windsor, 1984; Richards and Windsor, 2007).

The mean nomadic ant swarm width at Cocha Cashu is double that found on BCI and may be due to differences in mean colony size across sites. These differences, coupled with colony density differences, may affect the impact that *E. burchellii* has on each area's leaf-litter prey base, particularly social ant prey. In a simulation model, Franks and Bossert (1983) found that, at any given time, the prey ant community in half of their study area was undergoing the process of succession. Army ants acted as keystone predators by depressing populations of the dominant ant competitor in the leaf litter, which provides competitive space for other, less dominant ant species to move in (Kaspari and O'Donnell, 2003). In this way, army ants increase ant species diversity and alter abundance regimes of multiple social insect species. Differences in population and ecological parameters for this keystone predator across the neotropics

may help explain the latitudinal biodiversity gradient of social insects within the tropics.

Alternatively, are these differences an artifact of BCI's status as a dry hilltop island amidst the lowland neotropics, with perhaps abnormally low insect prey abundance? Or does Cocha Cashu have a relatively high abundance of insect prey due to its location in seasonally inundated alluvial floodplain forest? Leaf-litter insect samples from BCI (Willis, 1976; Levings and Windsor, 1982) indicate high seasonality in insect abundances. Drying of the forest on BCI through the effects of wind and isolation may cause an overall decrease in leaf-litter arthropod abundance over time due to desiccation (see Levings and Windsor, 1982 for a discussion of the effects of a severe dry season). Standardized leaf-litter arthropod measurements are needed for Cocha Cashu, as differences in sampling techniques affect density estimates (Levings and Windsor, 1982). At present, relative leaf-litter arthropod densities between the two sites remain unknown.

Conclusion

The parameters presented here for army ants at Cocha Cashu provide a contrasting study to those at BCI, Panama. Specifically, we find that at the Cocha Cashu research site, colony density is higher, emigrations occur less often and colonies follow a slightly different foraging pattern than those at BCI. This may not be surprising considering that the environment on BCI has experienced the effects of isolation, drying and loss of top predators, and may not be representative of most lowland neotropical rainforest (Willis, 1974; Glanz, 1982, 1990; Robinson, 1999, 2001; Condit et al., 1996; Condit, 1998). Basic natural history data for army ants from multiple sites are important, so that researchers may gain an understanding of how populations of this keystone species differ over geographic areas and the consequences of these differences on both the army ant's prey base and on obligate army ant following birds (Willson, 2004). As forest fragmentation in the neotropics becomes more pervasive, managers and conservation planners will look to species like army ants, which are intolerant to fragmentation, as indicator species of rainforest health (Harper, 1989).

Acknowledgments S. Willson would like to thank her field assistants, who are too numerous to name, for their dedication and exuberant effort in helping to gather these data over a span of 11 years. Special thanks goes to John Terborgh and the staff at Cocha Cashu for making the station a wonderful place to live and work. Rex Cocroft, Aaron Savit and Brad Baldwin provided helpful comments and suggestions to earlier drafts of the manuscript. We thank Nigel Franks and an anonymous reviewer for their insightful comments to a later draft. This study was supported by a Teagle Foundation Scholarship, two Trans World Airlines (TWA) Scholarships, a Graduate Assistance in

Areas of National Need (GAANN) Fellowship, an Organization for American States (OAS) Fellowship, a Ford-Knight Fellowship through Earlham College and a Center for International and Intercultural Studies (CIIS) Fellowship through St. Lawrence University (all to S. Willson).

References

- Akre R.D. and Rettenmeyer C.W. 1966. Behavior of Staphylinidae associated with army ants (Formicidae: Ecitonini). *J. Kans. Entomol. Soc.* **39**: 745-782
- Berghoff S.M., Wurst E., Ebermann E., Sendova-Franks A.B., Rettenmeyer C.W. and Franks N.R. 2009. Symbionts of societies that fission: mites as guests or parasites of army ants. *Ecol. Entomol.* **34**: 684-695
- Blum M.S. and Portocarrero C.A. 1964. Chemical releasers of social behavior. IV. The hindgut as the source of the odor trail pheromone in the neotropical army ant genus *Eciton*. *Ann. Entomol. Soc. Am.* **57**: 793-794
- Boswell G.P., Britton N.F. and Franks N.R. 1998. Habitat fragmentation, percolation theory and the conservation of a keystone species. *Proc. R. Soc. Lond. B Biol. Sci.* **26**: 1921-1925
- Boswell G.P., Franks N.R. and Britton N.F. 2000. Habitat fragmentation and swarm raiding army ants. In: *Behavior and Conservation* (Gosling L.M. and Sutherland W.J., Eds). Cambridge University Press, Cambridge. pp 141-158
- Bradley J.V. 1968. *Distribution-free Statistical Tests*. Prentice-Hall, Englewood Cliffs, NJ. 450 pp
- Britton N.F., Partridge L.W. and Franks N.R. 1996. A mathematical model for the population dynamics of army ants. *Bull. Math. Biol.* **58**: 471-492
- Condit R. 1998. Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. *Climatic Change* **39**: 413-427
- Condit R., Hubbell S.P. and Foster R.B. 1996. Changes in tree species abundance in a neotropical forest: Impact of climate change. *J. Trop. Ecol.* **12**: 231-256
- Couzín I.D. and Franks N.R. 2003. Self-organized lane formation and optimised traffic flow in army ants. *Proc. R. Soc. Lond. B Biol. Sci.* **270**: 139-146
- Emmons L.H. and Feer F. 1990. *Neotropical Rainforest Mammals: A Field Guide*. University of Chicago Press, Chicago. 281 pp
- Franks N.R. 1982a. A new method for censusing animal populations: The number of *Eciton burchellii* army ant colonies on Barro Colorado Island, Panama. *Oecologia* **52**: 266-268
- Franks N.R. 1982b. Ecology and population regulation in the army ant *Eciton burchellii*. In: *The Ecology of a Tropical Forest* (Leigh Jr. E.G., Rand A.S. and Windsor D.M., Eds), Smithsonian Institution Press, Washington. pp 389-395
- Franks N.R. and Bossert W.H. 1983. The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In: *Tropical Rain Forest: Ecology and Management* (Sutton S.L., Whitmore T.C. and Chadwick A.C., Eds). Blackwell, Oxford. pp 151-163
- Franks N.R. and Fletcher C.R. 1983. Spatial patterns in army ant foraging and migration: *Eciton burchellii* on Barro Colorado Island, Panama. *Behav. Ecol. Sociobiol.* **12**: 261-270
- Franks N.R., Gomez N., Goss S. and Deneubourg J.L. 1991. The blind leading the blind in army ant raid patterns: testing a model of self-organization. *J. Insect Behav.* **4**: 583-607
- Glanz W.E. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. In: *The Ecology of a Tropical Forest* (Leigh Jr. E.G., Rand A.S. and Windsor D.M., Eds). Smithsonian Inst. Press, Washington. pp 455-468
- Glanz W.E. 1990. Neotropical mammal densities: How unusual is the community on Barro Colorado Island, Panama? In: *Four Neotropical Forests* (Gentry A.H., Ed). Yale University Press, New Haven. pp 287-313
- Harper L.H. 1989. The persistence of ant-following birds in small Amazonian forest fragments. *Acta Amazonica* **19**: 249-263
- Hölldobler B. and Wilson E.O. 1990. *The Ants*. Harvard University Press, Cambridge. 731 pp
- Hooge P.N. and Eichenlaub B. 1997. Animal movement extension to Arcview. Vers. 1.1. Alaska Science Center: Biological Science Office, U.S. Geological Survey, Anchorage, AK, U.S.A
- Kaspari M. and O'Donnell S. 2003. High rates of army ant raids in the Neotropics and implications for ant colony and community structure. *Evol. Ecol. Res.* **5**: 933-939
- Leigh E.G. 1972. The golden section and spiral leaf arrangement. *Conn. Acad. Sci. Trans.* **44**: 163-176
- Levings S.C. and Windsor D.M. 1982. Seasonal and annual variation in litter arthropod populations. In: *The Ecology of a Tropical Forest* (Leigh Jr. E.G., Rand A.S. and Windsor D.M., Eds). Smithsonian Inst. Press, Washington. pp 355-387
- Levings S.C. and Windsor D.M. 1984. Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica* **16**: 125-131
- O'Donnell S., Lattke J., Powell S. and Kaspari M. 2007. Army ants in four forests: geographic variation in raid rates and species composition. *J. Anim. Ecol.* **76**: 580-589
- Pearson K. and Blakeman J. 1906. Mathematical contributions to the theory of evolution. XV. A mathematical theory of random migration. *Drapers' Company Research Memoirs: Biometric Series III*. Cambridge University Press, London
- R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rettenmeyer C.W. 1962. The behavior of millipedes found with neotropical army ants. *J. Kans. Entomol. Soc.* **35**: 377-384
- Rettenmeyer C.W. 1963a. Behavioral studies of army ants. *Univ. Kans. Sci. Bull.* **44**: 281-465
- Rettenmeyer C.W. 1963b. The behavior of Thysanura found with army ants. *Ann. Entomol. Soc. Am.* **56**: 170-174
- Richards L.A. and Windsor D.M. 2007. Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *J. Trop. Ecol.* **23**: 169-176
- Robinson W.D. 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. *Conserv. Biol.* **13**: 85-97
- Robinson W.D. 2001. Changes in abundance of birds in a Neotropical forest fragment over 25 years: A review. *Anim. Biodiv. Conserv.* **24**: 51-65
- Schöning C., Washington M.N. and Franks N.R. 2005. Temporal and spatial patterns in the emigrations of the army ant *Dorylus (Anomma) molestus* in the montane forest of Mt. Kenya. *Ecol. Entomol.* **30**: 532-540
- Schneirla T.C. 1971. *Army Ants: A Study in Social Organization*. (Topoff H.R., Ed). W.H. Freeman and Co., San Francisco. 349 pp
- Schneirla T.C. and Brown R.Z. 1950. Army-ant life and behavior under dry season conditions, 4: Further investigation of cyclic processes in behavioral and reproductive functions. *Bull. Am. Mus. Nat. Hist.* **95**: 263-353
- Swartz M.B. 1997. Behavioral and population ecology of the army ant *Eciton burchellii* and ant-following birds. Ph.D. thesis, Univ. Texas, Austin
- Willis E.O. 1967. The behavior of bicolored antbirds. *Univ. Calif. Publ. Zool.* **79**: 1-132
- Willis E.O. 1976. Seasonal changes in the invertebrate litter fauna on Barro Colorado Island, Panama. *Rev. Bras. Biol.* **36**: 643-657

- Willis E.O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* **44**: 153-169
- Willson S.K. 2004. Obligate army-ant-following birds: A study of ecology, spatial movement patterns, and behavior in Amazonian Peru. *Ornithol. Monogr.* **55**. 67 pp
- Wrege P.H., Wikelski M., Mandel J.T., Rassweiler T. and Couzin I.D. 2005. Antbirds parasitize foraging army ants. *Ecology* **86**: 555-559