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Intercolony Avoidance Optimizes Foraging in *Eciton burchellii* Army Ants

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Abstract

Foraging individuals optimize spatial movement to maximize resource use in heterogeneous environments. Colonies of *Eciton burchellii,* a neotropical species of army ant, forage as an army, consuming broad arrays of arthropod and social insect prey. Prey depletion in foraging paths exacerbates resource heterogeneity for *E. burchellii* and may encourage colonies to avoid contact with recently raided areas. Colonies are known to turn in opposite directions more often than random from previous days' foraging paths, which increases distances between recently raided areas. However, no evidence of colony avoidance of areas recently foraged by a conspecific colony has been presented. In this study, we analyze data collected in the Peruvian Amazon between 1998 and 2008 to examine colony spatial distribution using nearest-neighbor distance data. We found that colonies optimize movement by choosing foraging angles that deflect away from areas recently raided by conspecific colonies. In addition, we found that the observed nearest neighbor distance between *E. burchellii* colonies was more significant than expected if colonies were dispersed randomly. This dispersion pattern increases the distance between colonies and contributes to a spatial movement that optimizes foraging and decreases colony interactions at recently raided areas.

Introduction

Eciton burchellii is a carnivorous keystone Neotropical species of army ant (Franks & Bossert, 1983; Boswell et al., 1998; Boswell et al., 2000; Kaspari & O'Donnell, 2003). Its ecological importance motivated investigators to conduct field observations of *E. burchellii* movement dynamics and life cycles at locations such as Panama's Barro Colorado Island (BCI) and southeastern Peru (Franks, 1982a; Franks & Fletcher, 1983; Richards & Windsor, 2007; Willson et al., 2011). This research gave insight into the species' population dynamics (Frank & Bossert, 1983), lifecycle, and reproduction strategies (Schneirla & Brown, 1950; Rettenmeyer, 1963a). Evidence for intra-colony foraging optimization has also been presented (Franks & Fletcher, 1983; Willson et al., 2011).

Eciton burchellii army ants exist in colonies that number up to a million haplodiploid sisters, necessitating the development of a unique lifecycle that contributes to foraging optimization (Franks & Fletcher, 1983; Willson et al., 2011). Two distinct phase types complete their life cycle. During a statary phase, the colony creates a bivouac (or nest) composed of bodies of individual colony members at a protected site, such as a hollow tree. Within the bivouac, a single queen lays up to 300,000 eggs in a few days. Concurrently, a cohort of young larvae spin cocoons and begin their bodily transformation inside their pupal cases (Höldobbler & Wilson, 2009). Sporadically, during the statary phase, the colony forages during the day by choosing a direction at dawn and raiding as a fan-shaped "army" along a path across the forest floor. The colony then subdues and transports a wide variety

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of social and non-social arthropods back to the bivouac for consumption; more than 50% of its diet is social ant prey (Powell & Franks, 2006). Foraging raids return to the same bivouac site in the afternoon or evening and remain in the statary phase for an average of 21 days, based on observations at Cocha Cashu Biological Station (EBCC), Manu National Park, Peru (n = 54 bivouacs observed over a complete statary phase, SD = 1.8) (Willson et al., 2011). The statary phase thus follows the timing of egg and larval development within the nest.

A nomadic phase follows, lasting an average of 12 days at EBCC (n = 48 colonies followed over a complete nomadic phase, SD = 2.6), where the colony raids in one direction for an average of 78 m (n = 351 measured nomadic foraging raids, SD = 44) and establishes a new bivouac almost every night (Willson et al., 2011). During this phase, colony foraging increases, as a colony must feed both growing larvae and newly emerged worker cohorts. A life cycle thus takes three stages to reach adulthood: statary 1 (21 d) as eggs, nomadic 1 (~12 d) as larvae, statary 2 (21 d) as pupae, and emergence as new adults at the initiation of nomadic 2 (Schneirla, 1971).

The colony size in *E. burchellii* is remarkable as carnivorous army ants must continually move to new areas to forage for prey. However, large colony raids can sometimes exceed 30 m in width as the ants travel across the forest floor (Willson, 2004). Colony size and predatory feeding methods suggest that a colony needs to optimize its foraging strategies to avoid lacking prey (Franks & Fletcher, 1983; Willson et al., 2011). *Eciton burchellii* significantly depletes its primary prey, the social ants, in raided areas. After a foraging raid, social insect populations were suggested to need up to 100 days to recover just half of their pre-raid densities (Franks & Bossert, 1983). Thus, colonies should avoid recently foraged areas to optimize resource use. Kaspari et al. (2011) suggest that *E. burchellii* specialize in foraging patches of high prey biomass, which may be a strategy to maximize resources. A more difficult question is how a colony orients its movement to consistently reach areas of high prey biomass and avoid recently raided areas. One known strategy is that *E. burchellii* colonies separate statary bivouacs more than would be expected if movement during the nomadic phase was random. At both EBCC, Peru, and BCI, Panama, nomadic phase colonies diverged in the opposite direction of the previous day's raid path more often than random, which significantly increased the distance between statary bivouacs (Franks & Fletcher, 1983; Willson et al., 2011).

This study explored another strategy *E. burchellii* colonies may use to avoid areas recently raided by nearby conspecific colonies. Willson et al. (2011) provide anecdotal details of three observed collisions between colonies from more than 18 months of daily observations of multiple colonies and 601 bivouac emigrations, emphasizing the rarity of a collision event. Here, we hypothesized that nomadic phase colonies detect recently laid pheromones from conspecific colonies and choose foraging angles that diverge from the corresponding trail, thus avoiding an area with potentially less prey. We used our extensive dataset to computationally examine this question, which was only previously modeled via computer simulation with hypothetical data (Franks & Bossert, 1983).

Materials and methods

Field data collection

Data presented here were gathered over seven field seasons in mature floodplain forest at EBCC in the southeastern Peruvian Amazon (11°54' S and 71°22' W, elevation ~ 400 m) from September 1998 to July 2008, totaling 18.5 months of field time. Fieldwork was concentrated on a core study plot area of 100 ha, although some *E. burchellii* colonies were found and followed beyond that core area through a 270-ha trail network at the study site. Colonies were followed daily for up to 5 months until they were lost in herbaceous secondary growth or swamp, moved too far from the core study site, or the field season ended. Field methods follow those described in Willson et al. (2011).

Statistical calculations

We isolated situations where a nomadic foraging colony emigrated two days in a row, with three successive, different bivouacs on three consecutive nights: bivouac *a*, *b*, and *c*, respectively. We then calculated the closest distance from bivouac *b* to all linear foraging paths less than 31 days old from a conspecific colony in its nomadic phase. If this distance was less than 50 m, we calculated the angle deviation of the foraging path between bivouacs *b* and *c* from the path between *a* and *b*. We hypothesized that nomadic colony bivouacs, when close to a recent (< 31 days old) foraging path made by a conspecific colony, would choose an angle that would "deflect" away from the conspecific's path. We quantified this hypothesis by determining an expectation on whether the nomadic colony bivouac, *b* (within 50 m of a recent conspecific foraging path) would pick a foraging path at an angle that diverged clockwise or counterclockwise (right or left) from the previous day's path. If the colony's foraging angle from bivouac *a* to *b* was less than the angle perpendicular to the old foraging path of the conspecific, we expected it to turn right. Conversely, if it was greater, we expected a turn left. We forced the day-over-day foraging angle diversion, Θ, positive when in the expected direction, and negative when in the unexpected direction.

According to Willson et al. (2011), *E. burchellii* colonies in the nomadic phase diverged from one day's foraging path to the next by a mean of 62° (n = 68, SD = 46.2). We used a bootstrapping approach to compute a distribution of 1000 angles with this mean and standard deviation while randomly multiplying the angles by 1 or -1 to account for colonies turning right or left. We then compared the observed angle deviations of bivouacs close to conspecific nomadic foraging paths from < 31 days to the distribution of 1000 angles determined from expected deviations using a 2-sample t-test to determine if the groups of angles were significantly different.

Furthermore, using methods proposed by Sinclair (1985), we determined whether colonies in the study site were dispersed so that the distance to a colony's nearest neighbor was greater than if the colonies were dispersed randomly. We calculated the mean nearest neighbor distance (NND) for all colonies with observed neighbors at EBCC. Then, we compared it to the expected mean nearest neighbor distance of randomly dispersed colonies in an area of similar size to the study site at EBCC (250 ha) and colony density (4.9 colonies/100 ha) (Willson, 2004). Calculations of angle deviations and spatial distances were completed using programming in Python, and statistical analysis was completed using Statkey 3.0.3 (Lock et al., 2021) software.

Results

Interspecific Colony Deflection Analysis

From the 48 complete nomadic *E. burchellii* colony movements we mapped in the field, we found 17 cases where bivouac *b* (of three successive bivouacs *a*, *b*, and *c*) was within 50 m of a nomadic foraging path of a conspecific colony. The mean distance between bivouac *b* and the path of another conspecific colony was 27.1 m (n = 17, SD = 11.8). The angle deviations, considered positive when turning in the expected direction and negative in the unexpected direction, had a mean of 52.6° (n = 17, SD = 51.6). This is significantly different from the angle divergence expected of colonies, disregarding whether close to a recent conspecific colony foraging path or not, in their nomadic phase as determined by Willson et al. (2011) (t = 4.03, df = 17, p = 0.001). These results suggest that an *E. burchellii* colony optimizes its movement to forage in prey-rich areas, choosing foraging angles that deflect away from areas recently raided by a neighboring conspecific colony.

Spatial Distribution Analysis

We calculated the mean nearest neighbor distance for *E. burchellii* colonies at EBCC at 457.7 m (n = 1627, SD = 321.9). We found that the expected mean nearest neighbor distance if the colonies were randomly dispersed was 282.6 m (Sinclair, 1985). Hence, the observed nearest neighbor distance for *E. burchellii* colonies was significantly greater than the expected nearest neighbor distance if the colonies were dispersed randomly (t = 13.62, df > 1000, p < 0.05). This suggests that colonies are regularly dispersed, with increased distance and fewer interactions between colonies at recently raided areas.

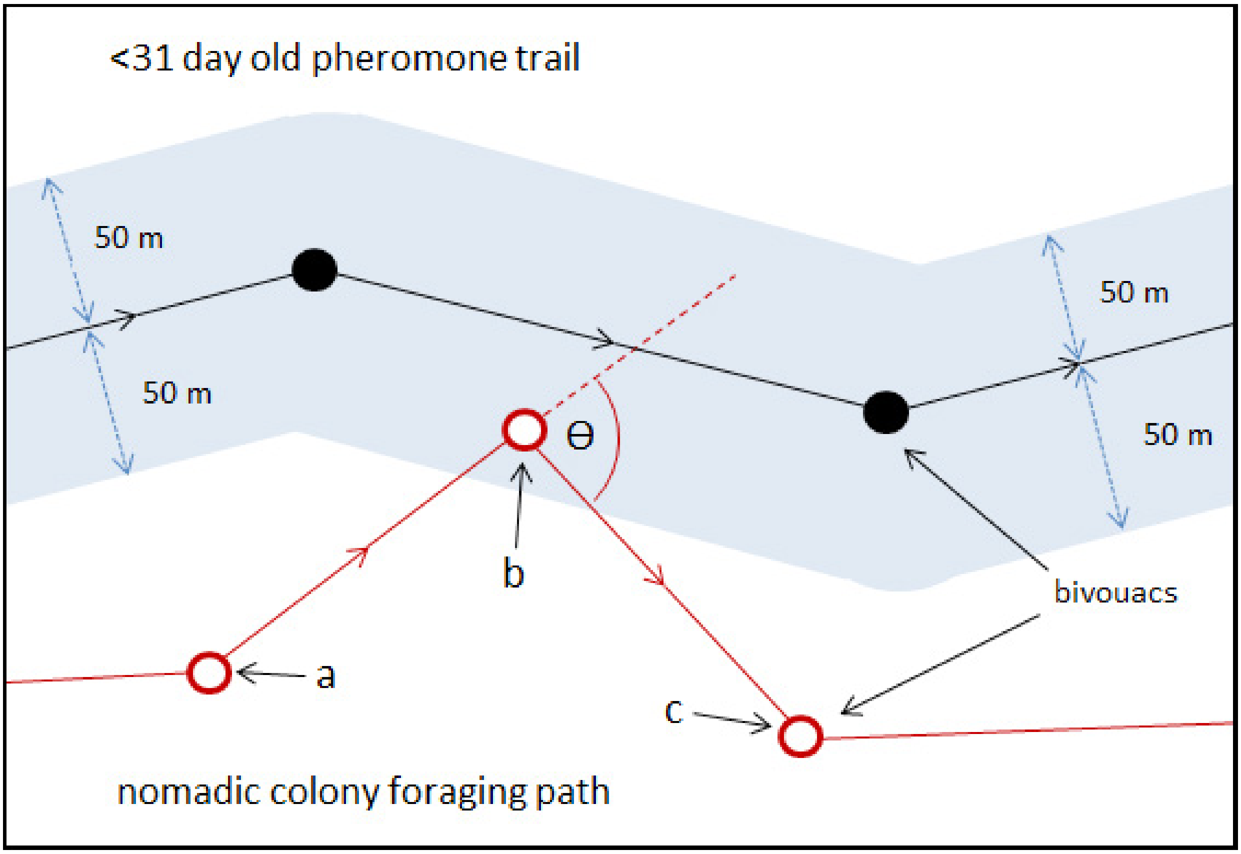

Fig 1. Three successive nomadic bivouacs within 50 m of a conspecific path and angle deviation, Θ, for an *Eciton burchellii* colony.

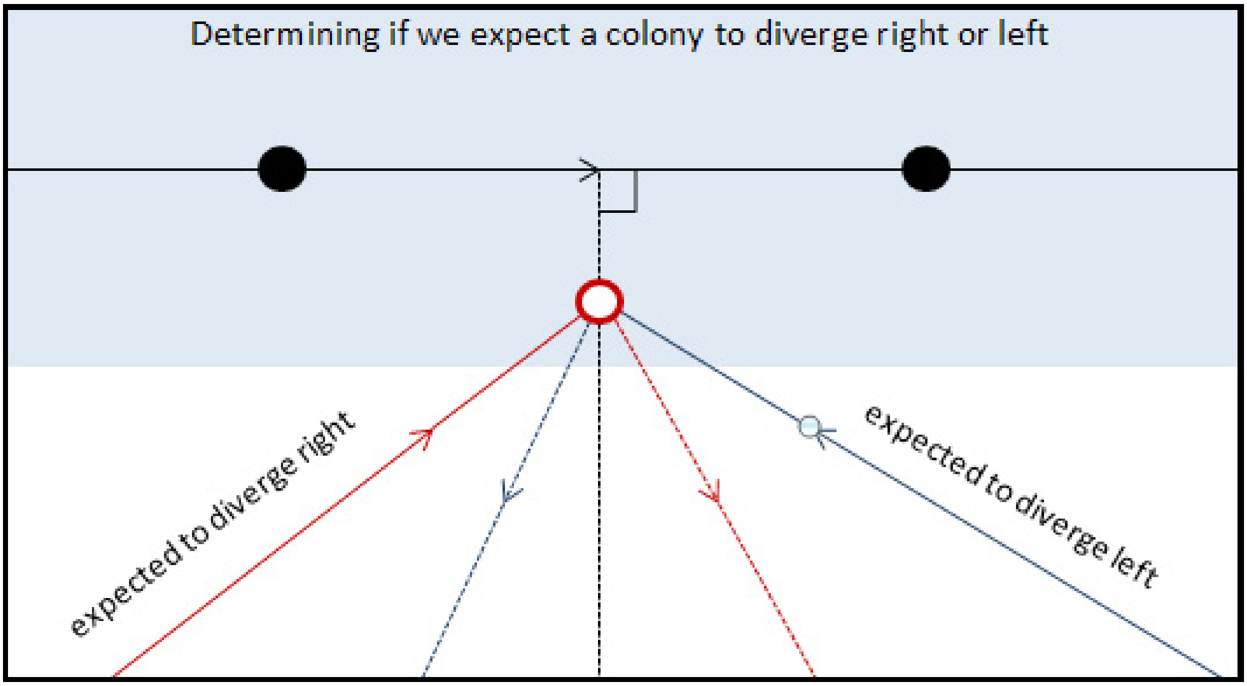

Fig 2. Perpendicular line of the conspecific path and expected divergence. In this example, the perpendicular line is 270°, and as the red and blue paths are less and greater angles than 270°, they are expected to diverge right and left, respectively.

Discussion

Avoidance of recently raided areas through deflection

By examining *Eciton burchellii* colonies that emigrate and establish a bivouac < 50 m away from a conspecific emigration path < 31 days old, we observed apparent deflection behavior in emigrating colonies. These results support our hypothesis that an *E. burchellii* colony may alter a planned nomadic route based on detecting recent pheromones from a nearby conspecific colony. Pheromone trails of a closely related species to *E. burchellii* are insoluble in water and impervious to light and heat for at least 31 days (Shneirla & Brown, 1950; Blum & Portocarrero, 1964). These pheromone trails may provide information to conspecific colonies where an area has been recently foraged. Franks and Fletcher, (1983) predicted that other colonies could detect these chemical trails and initiate deflection from recently foraged areas. Our results are the first to support this hypothesis with quantitative field data.

Army ants are keystone predators in neotropical forests, and improved knowledge of their ecological characteristics could aid in predicting population abundances and effects of environmental heterogeneity. Additionally, *E. burchellii* indicates overall environmental health and is sensitive to negative anthropogenic disturbances, such as habitat fragmentation (Harper, 1989). Observations of population disturbances might aid in motivating forest conservation efforts, as a disturbance to this species has a ripple effect on the numerous insect and vertebrate species that depend on *E. burchellii* colonies for their survival (Pérez-Espona, 2021).

Conclusions

Our results present new information on a strategy that *Eciton burchellii* army ants use to optimize spatial movement. First, due to our large sample size of colony movements and long-term fieldwork, we present the first reported evidence that nomadic army ant colonies deflect away from areas recently raided by conspecifics. We also determined that separate colonies were more regularly dispersed than would be expected if colonies were randomly placed throughout the study site. This suggests that *E. burchellii* colonies avoid recently raided areas and cause conspecific colonies to be spaced far apart, leading to higher prey density. These findings support the hypothesis that *E. burchellii* colonies actively optimize their foraging via intra-colony movement and avoid conspecific colonies and their recently foraged areas.

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Authors' Contribution

T.K.: was involved in the conceptualization, methodology, data curation, formal analysis, visualization, and writing of this manuscript.
S.W.: was involved in the conceptualization, methodology, investigation, data curation, formal analysis, writing, and funding acquisition of this manuscript.

Data availability statement

Data used in the analyses presented here are uploaded as supplemental material.

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