

Emigrating on the Fly: a Novel Method of Army Ant Colony Movement Observed in *Eciton mexicanum*

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Revised: 5 August 2017 / Accepted: 7 August 2017
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Abstract We describe an emigration of the Neotropical army ant *Eciton mexicanum* where the head of the emigration column was separated in time from previous raid column activity, and the emigration was not connected to the new bivouac site by a column of workers. Over 12 h elapsed between raid activity and the onset of emigration, suggesting the emigration followed a long-lasting pheromone trail. We suggest the bivouac site had been selected the night before the emigration by foraging workers.

Keywords Chemical communication · Costa Rica · Dorylinae · La Selva

Introduction

Periodic colony movements are a characteristic behavior of many ant species (McGlynn 2012). Army ant colonies (Dorylinae), particularly those in the above-ground active genus *Eciton*, are well-known for their regular colony emigrations (Schneirla 1971; O'Donnell et al. 2009). Above-ground army ant emigrations can traverse linear distances over 100 m (Rettenmeyer 1963). Emigrations frequently travel under cover of darkness, but army ant species differ in the diel timing of their emigrations (O'Donnell et al. 2009). Emigrations typically follow the route of the day's principal foraging raid, involving a reversal of worker traffic direction along the raid route (Rettenmeyer 1963; Schneirla 1971). The emigration column of workers is generally continuous between the new and the old bivouac sites.

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Here we present an observation of an emigration of the Neotropiocal army ant *Eciton mexicanum* in lowland wet forest on the Atlantic slope of Costa Rica. To our knowledge, this is the first published observation of a discontinuous army ant emigration column, i.e., an emigration front not connected to the new bivouac site by an unbroken stream of workers. The initiation of emigration during daylight hours is also of interest, as *E. mexicanum* raid activity is largely nocturnal at La Selva (J.T. Longino, <http://ants.biology.utah.edu/~longino/AntsofCostaRica.html>, accessed 3 May 2017).

Observations of Emigration Behavior

Observations were made at the La Selva Biological station (N10°25.844', W84°0.177', 50 m asl) north of the Sarapiquí river near the administration buildings. We identified the army ant species as *E. mexicanum* based on worker color, propodeal spines, petiolar morphology, and morphology of the major worker (soldier) mandibles. Nocturnal *E. mexicanum* raids passed through the observation area, consistently in the same location, for at least three consecutive nights prior to the observed emigration. We cannot say for certain the same colony was observed on each night, but this is a parsimonious assumption because the raids originated from the same direction and apparent location. Prey-bearing army ant foragers are typically returning to the bivouac, and based on their direction of travel the raids originated from a lightly wooded area adjacent to the Puerto Viejo River. On each day the raid columns crossed a 1 m-wide raised cement walkway and entered an area of open lawns, ornamental plantings, and patches of trees.

On 16 March 2017, at approximately 1715 h local time, we observed a relatively dense *E. mexicanum* column, two workers wide, crossing the walkway. Ant traffic was unidirectional and many workers in the column were carrying prey items; we did not observe army ant brood being carried at this time. Emigrating army ant bivouacs generally break down from the outside-in, and prey are often carried in the emigration early in its development; army ant brood are carried later in the emigration process (Rettenmeyer 1963). Travel direction of the laden workers was opposite the direction taken on the previous days, away from the inferred source bivouac location. We followed the column of ants approximately 10 m from the walkway to an open area of mainly bare soil, where it terminated in an advancing cluster of several dozen unladen workers. The cluster of workers resembled a small raid front, approximately 25 cm wide and 40 cm deep, progressing steadily over the ground and along exposed tree roots at an estimated rate of 15–20 m/h. The unidirectional traffic and prey carriage away from the presumed previous bivouac site suggested this was an early stage of a colony emigration to a new bivouac site. We searched ahead of the advancing worker cluster to a distance of 15 m and saw no other *E. mexicanum* columns or individual workers. We had passed the site traveled by the advancing column several times earlier in the day between approximately 0530 h and 1300 h, and we did not observe army ant workers in the area. An *E. mexicanum* raid column had passed through the area the previous night.

When we returned to the site after dark, at approximately 1930 h, a stronger unidirectional emigration column 3–4 workers wide was following the same path the advancing front had followed earlier, moving in the same direction. By this time, no

prey carriage was observed and most workers were carrying army ant larvae, indicating the colony was in the nomadic phase of development (Schneirla 1971). The large size of the larvae, equivalent to worker body length, suggested the colony was in the late-nomadic phase of development (Schneirla 1957). Numerous soldiers flanked the emigration column. *Eciton mexicanum* soldiers are rarely seen along raid columns, based on extensive personal observations over several years (S.O'D.). We tracked the column to dense a pile of garden debris under a cluster of several banana (*Musa* sp.) plants, where the ants entered the debris pile and were no longer visible. We walked a complete circle around the debris pile and saw no ants entering or exiting from other directions, and we assume this was the location of the new bivouac site.

Interpretation and Implications

While army ant colonies can dynamically adjust emigration behavior environmental conditions (Topoff and Mirenda 1980), many aspects of emigration behavior are thought to consistently follow well-characterized stereotyped group-level behaviors. One such behavior is the development and maintenance of a continuous column of ants while moving from one bivouac to another bivouac during the nomadic phase (Rettenmeyer 1963). Our observation indicates this pattern is not as rigid as previously assumed, which may alter our understanding of the mechanisms and collective organization of army ant colony emigrations.

The apparent discontinuity of the emigration front from an ant column reaching the bivouac site could have been caused by a disturbance that disrupted column traffic, with the advancing cluster in the process of re-establishing the emigration trail. This explanation is unlikely because no alarmed workers were observed within 15 m of the advancing cluster, and no alarm behavior or soldiers were evident in the advancing cluster or along the column of workers. The emigration was not interrupted by rain: a weak rain shower (approximately 1 mm accumulation) fell between 0700 and 0730 h on 16 March when no army ants were present in the observation area; no other rain fell during the observation period nor the previous night (La Selva weather station data, accessed 2 May 2017: <http://www.ots.ac.cr/meteoro/default.php?pestacion=2>). Because the colony had raided in a direction toward the new bivouac site on previous nights, the emigration was not a back-tracking return move to an old bivouac site in response to a lost queen (Rettenmeyer 1963). Because we did not observe the initiation of the emigration at the original bivouac site, it is not known whether the emigration represented a typical colony movement, or if it was an absconding event induced by a predator attack (Willson et al. 2011) or other major disturbance at the original bivouac site.

We conclude there was a temporal and physical break between the end of raiding column traffic and the onset of emigration. We could not establish whether the advancing cluster was searching for a bivouac site. We suspect the ants were following a previously established pheromone trail given the heavy raid traffic in the area on previous nights, and the relative rapidity and directness of travel of the cluster. This would indicate the bivouac site had been previously selected by foraging workers. The absence of *E. mexicanum* workers in the area during the day suggests at least 12 h elapsed from establishing the trail to the new site and the emigration. *Eciton* species

trail pheromones are notable for their durability in tropical field conditions: workers can follow trails after several days have elapsed (Torgerson and Akre 1970). Whether some workers were present in or near the sheltered bivouac site, and whether the site was chemically marked in some way, is not known. Our observations indicate bivouac site selection can occur decoupled from emigration behavior in some army ants.

Acknowledgements Data were collected during the 2017 Organization for Tropical Studies graduate course on Neotropical Social Insects. Observations were conducted under a course research permit from the Costa Rican government (SINAC/MINAET). Support was provided by the Organization for Tropical Studies.

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