

# Serial monodomy in ants: an antipredator strategy?

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**Abstract.** 1. The term serial monodomy is used to describe a life-history phenomenon in social insects. Serially monodomous colonies maintain multiple nests for their exclusive use, but only occupy one nest at a time.

2. The hypothesis that colony odours mediate nest relocation decisions was tested in the serially monodomous species *Aphaenogaster araneoides* from Central America. Odour extracts of colony members were created using a non-polar solvent.

3. Colonies strongly avoided reoccupying nests treated with colony odour extracts, while control colonies often returned to nests subjected to solvent-only control. Behavioural observations indicated that *A. araneoides* colonies are capable of detecting army ant (*Eciton burchellii*) raids up to 1.4 m from the raiding front, with several seconds to evacuate nests.

4. It is proposed that the function of serial monodomy in *A. araneoides* is the reduction of nest odour to enhance detection of predaceous army ants. Serial monodomy may be a widespread but undocumented mode of nesting where army ants occur in tropical and subtropical climates.

**Key words.** Army ant, emigration, gypsy ant, humidity, life history, nest relocation, odour, predator avoidance.

## Introduction

The movements of ant colonies are widespread but largely overlooked. It is estimated that the majority of species relocate their nests as a regular part of their life history (McGlynn *et al.*, 2004). Nevertheless, little is known about how ants use their nests (Tschinkel, 2004), much less how they move from one nest to another. While research on the organisation of nest movements has been conducted in the laboratory (Sendova-Franks & Franks, 1995; Theraulaz *et al.*, 1999; Pratt *et al.*, 2002; Franks *et al.*, 2003), we have little insight into the selective forces that may favour a semi-nomadic lifestyle.

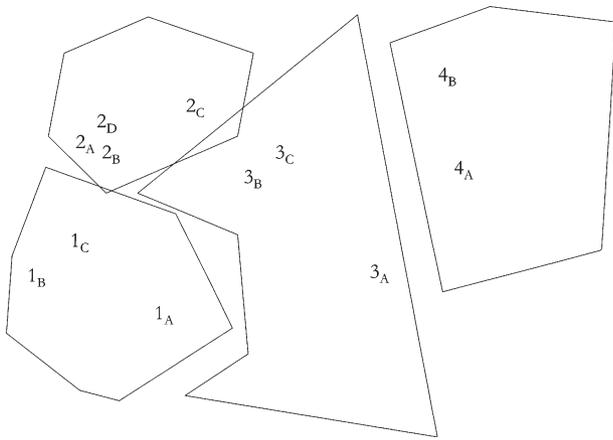
Knowledge of nest relocation in field populations is diffuse. The broad, but sporadic, pattern of research (reviewed in McGlynn *et al.*, 2004) suggests that investigators principally study nest relocation when unexpectedly encountered during an unrelated experiment. Although colonies can emigrate as a response to trauma or infestation, nest relocation events often occur in the absence of overt stimuli (Smallwood, 1982a; Byrne, 1994). Where documented, the environmental and demographic

correlates of relocation behaviour show no pattern across taxa or environmental conditions.

To clarify one mode of nest relocation, a specific spatial pattern of nest relocation is identified as *serial monodomy*. This phrase describes the behaviour in which colonies maintain multiple nests for their exclusive use, occupying one nest at a time and relocating among nests on a regular basis. Serial monodomy has been demonstrated in five species: the southwestern North American *Pheidole desertorum* Wheeler (Droual, 1981, 1983; Droual & Topoff, 1981); *Stenamma expositum* Smith and *Stenamma alas* Longino (Longino, 2005); temperate Japanese *Pristomyrmex pungens* Mayr (Tsuji, 1988); and the gypsy ant *Aphaenogaster araneoides* Emery (McGlynn *et al.*, 2004). Other nest-relocating species are clearly not serially monodomous and move among nests adventitiously, such as *Aphaenogaster rudis* Enzmann (Smallwood, 1982b), *Rhytidoponera metallica* (Smith) (Thomas, 2002), *Polyrachis ammon* (Fabricius) (Gibb & Hochuli, 2003) and *Pogonomyrmex badius* (Latreille) (Tschinkel, 2004).

The natural history of serial monodomy is best described in *A. araneoides* (McGlynn *et al.*, 2002, 2003, 2004; Fig. 1). In this species, diet consists an array of litter-dwelling arthropods; seeds are occasionally collected. Colonies typically contain fewer than 200 workers and a single ergatoid queen. Colonies nest in a soil substrate, with the majority of nests positioned at the base of an understorey plant, with the remainder found

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**Fig. 1.** Schematic indicating the relationships among nests and home ranges in serially monodomous ants. Each colony, designated by number, occupies a home range within a polygon. Nests, designated by letter, are maintained and occupied exclusively by a single colony, which occupies one nest at a time.

positioned against the buttresses of canopy trees or in open soil. Nests are shallow and wide; entrances are markedly large, with a diameter exceeding 15 mm. Home ranges range up to several square metres for large colonies, and the average distance between nests utilised by a single colony is less than a metre. Nest relocation frequency ranges from a few days to a few weeks, and is strongly determined by colony size, with larger colonies moving more frequently. The number of unoccupied nests per colony varies from two to six, with faster growing colonies maintaining more nests in reserve. The timing of relocation events is linked to weather: nest relocations are most likely to occur when temperature is high and humidity is low. McGlynn *et al.*, (2004) argued that these environmental and demographic correlates support an *attraction hypothesis*, in which the build-up of odours within nests attracts predators passing across their nest entrances.

Army ants have been implicated as the selective force for serial monodomy in four of the five known serially monodomous species, *P. desertorum*, *S. explitum*, *S. alas*, and *A. araneoides*. In the case of the former, Droual (1983) proposed that pre-existing nests facilitate an efficient and safe escape from underground attacks from *Neviamyrmex* army ants. Both *Stenammina* species have been observed to blockade nest entrances with a *nest pebble* when heterospecific ants are introduced to the colony (Longino, 2005). In *A. araneoides*, McGlynn *et al.* (2004) demonstrated that relocation timing was robustly predicted by the environmental volatility of aromatic compounds, suggesting that colonies preferentially occupy nests with reduced colony odours.

The purpose of the present study was to evaluate the prediction that colony odours mediate nest relocation decisions in *A. araneoides*, to gain insight into the functional role of serial monodomy. To achieve this goal, interactions between army ants and *A. araneoides* colonies were observed, and the odours within the nests of *A. araneoides* colonies were manipulated in the field.

## Methods

### Site and colony selection

Experiments were conducted during May and June 2005 in a lowland tropical rainforest in northeastern Costa Rica. Six field sites were selected within old growth at La Selva Biological Station ([www.ots.ac.cr/en/laselva](http://www.ots.ac.cr/en/laselva)). These sites were located at least 100 m apart spanning a distance over 2 km, located along the Camino Circular Lejano and Camino Experimental Sur adjacent to sites used for earlier research on *A. araneoides* (McGlynn *et al.*, 2002, 2003). These sites were chosen for their relatively flat ground that would not erode from the combined effect of daily visits and rainfall.

Colonies of *Aphaenogaster araneoides* were located using two methods. In the first method, direct search for the nests occupied by *A. araneoides* was performed. The second method involved a scan for foragers, who were fed a tiny morsel of food (drained oil-packed tuna, white cheese, or the filling of Cremas<sup>®</sup> sandwich cookies manufactured by Riviana Pozuelo San Jose, Costa Rica), and followed back to their nests. Colonies were assigned unique colony identification numbers at each site, and the nest occupied by the colony at the time of discovery was assigned an identification letter coupled with the colony number. The movements of colonies among nests were tracked until the conclusion of the study (as described in McGlynn *et al.*, 2003). In summary, every nest was checked in 24-h intervals, and when a colony was found to emigrate into a previously undocumented nest, the nest was assigned an identification letter. Note that like all serially monodomous ants, nests belonging to a colony are positioned within their home range and nests are not shared among colonies.

### Nest odour manipulation experiment

A nest odour manipulation experiment was conducted by adding colony odours into unoccupied nests and comparing the relocation behaviour of 27 treatment and 30 control colonies, distributed among the six field sites. If the initial nest eroded within the minimum observation period, or the territory of the colony was severely disturbed, the colony was removed from the study, accounting for different sample sizes for control and treatment categories. Ten workers were removed from each colony by direct subtraction from the nest entrance. The 10 workers from treatment colonies were placed in 10 ml of analytical grade hexane for 3 h in new glass vials. Equivalent control hexane vials were created for control colonies. Once each colony relocated from their initial nest (henceforth, the focal nest), the application of hexane extracts to the focal nest of treatment colonies and control hexane to the focal nest of control colonies was initiated. Each day, an aliquot of 250 µl of hexane was micropipetted 1 cm deep into the entrance of the focal nest between 08.00 and 12.00 hours, using separate pipette tips for each colony. All colonies received solvent-only control or extract treatment aliquots to the focal nest for at least 10 days, 6 days greater than the mean relocation frequency of *A. araneoides* in the present study.

Behaviours associated with movement among nests were evaluated with relocation frequency and nest infidelity, variables

used by McGlynn *et al.* (2004). Relocation frequency for each colony is the number of movement events divided by the number of days the colony was under observation. One can estimate the total number of nests used by a colony by measuring relative chance that a colony will relocate to a nest not previously observed as occupied. This variable, *nest infidelity*, is the residual of the linear regression of the number of nests dependent on the number of relocation events. McGlynn *et al.* (2004) found relocation frequency was strongly positively correlated with colony size, nest infidelity was strongly associated with colony growth rates, and that the two variables are independent of one another. The maximum vapour pressure deficit (VPD) of air was calculated as a measure of the volatility of aromatic compounds, based on data-logged half-hourly temperature and humidity records (available from the La Selva Biological Station website, <http://www.ots.ac.cr>). For each colony, relocation rate (the proportion of colonies relocated on each day) was compared with the maximum VPD in past 24 h.

#### Army ant attraction experiments

To evaluate the potential role of odour in the attraction of army ants, a set of observations and manipulations of interactions between above-ground foraging army ants [*Eciton burchellii* (Westwood) and *E. lucanoides conquistador* Weber] and *A. araneoides* was conducted. These experiments were conducted in the same time period as the nest odour manipulation. First, interactions were recorded when army ants raided through experimental plots containing marked colonies of *A. araneoides*, and personal communications were received from a researcher (Johel Chaves, Purdue University) following *E. burchellii* colonies in an unrelated study. Second, artificial nests of *A. araneoides* were presented to field colonies of *E. lucanoides conquistador* and *E. burchellii*. For each of five replicates, approximately 25 workers and 15 brood were collected from the field and placed within a 3 × 20 cm PVC tube containing soil from the excavated nest. The tube was capped on one end and covered with cloth mesh secured by duct tape on the opposite end.

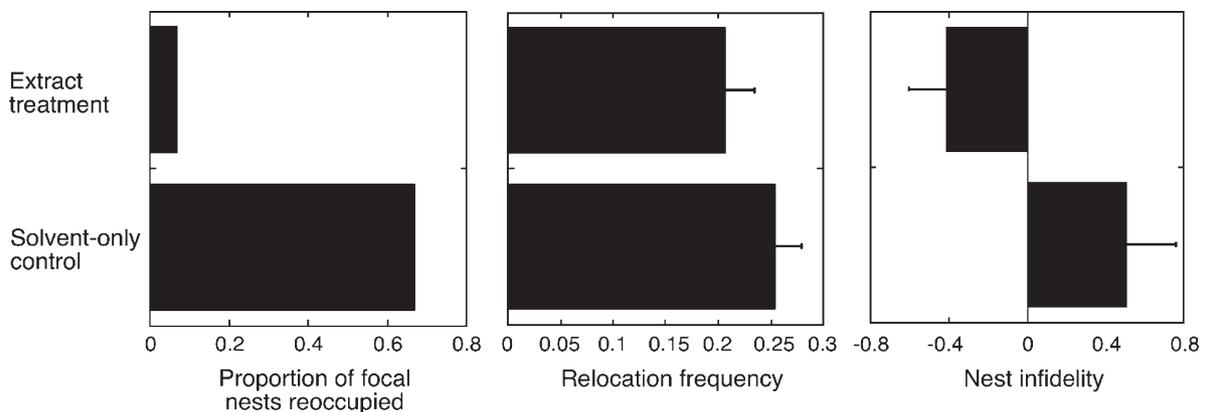
Control tubes were created using haphazardly selected soil from the same site. After 24 h, control and treatment tubes were placed on arbitrarily selected opposite sides of army ant foraging trails. Placement started at 10 cm from the edge of the trail for a duration of 30 s, then at 5 cm for 30 s, and finally at 1 cm for 30 s. Two sets of tubes were applied to *E. burchellii*, and three to *E. lucanoides conquistador*; tubes were not reused once contacted by army ants, which occurred in each replication. Last, eight tubes of 50 *E. burchellii* workers were created, represented by a diversity of caste members, and each of these tubes were presented to five nests of *A. araneoides* to observe the frequency and timing of an evacuation response, for a total of 40 colonies.

#### Analysis

All ants were identified using the Ants of Costa Rica, available at [www.evergreen.edu/ants/AntsofCostaRica.html](http://www.evergreen.edu/ants/AntsofCostaRica.html). Statistical analyses are consistent with the recommendations of Dytham's (2003) dichotomous key. Fisher's Exact test was used to compare the frequency of nest reoccupation between control and treatment colonies. After checking that the data met the criteria for parametric tests, two-way analyses of variance were employed to compare the relocation behaviour variables with respect to the two treatment and six site categories, and a *t*-test was used to compare the mean relocation distances of control and treatment colonies. Variation around the mean is expressed as ± 1 SD.

#### Results

Of the 27 control colonies, 18 (67%) returned to the solvent-only nests, whereas only two (7%) of the 30 extract-treated colonies returned to the extract-treated nests (Fig. 2; Fisher's Exact test,  $P < 0.0001$ ). Means for relocation behaviour variables are presented in Fig. 2. Relocation frequency did not respond to treatment ( $F_{1,56} = 1.62$ ,  $P = 0.26$ ), but significantly varied among the six sites ( $F_{5,51} = 3.11$ ,  $P = 0.02$ ) with no interaction

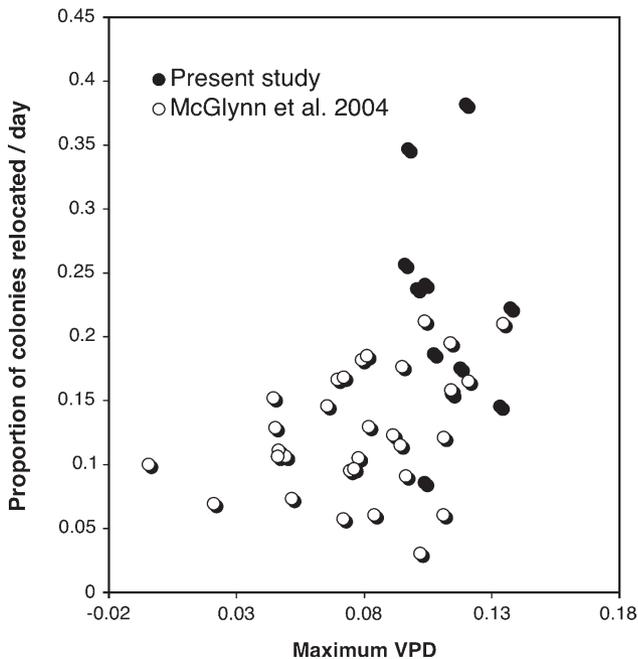


**Fig. 2.** Relocation behaviour of treatment and control colonies.  $n_{\text{treatment}} = 30$ ,  $n_{\text{control}} = 27$ . Error bars represent 1 SE, see text for statistics. Relocation frequency is the mean number of moves per day per colony, and nest infidelity is an estimate of the total number of nests utilised by a colony.

effect ( $F_{5,51} = 0.45$ ,  $P = 0.81$ ). Nest infidelity, an estimate of the number of nests used by a colony, was greater in the solvent control ( $F_{1,55} = 4.60$ ,  $P = 0.04$ ) and varied significantly among sites ( $F_{5,51} = 3.60$ ,  $P = 0.008$ ), but with no interaction effect ( $F_{5,51} = 0.36$ ,  $P = 0.87$ ). The mean relocation distances among treatment and control colonies, for those with complete information, were not significantly different ( $t_{28} = -0.12$ ,  $P = 0.91$ ). Solvent control colonies moved less than 1 m ( $0.87 \pm 0.24$  m,  $n = 14$ ), similar to extract-treated colonies ( $0.91 \pm 0.20$  m,  $n = 16$ ).

Because the timing of relocation events is known to be associated with VPD, the present study sought to explore how treatment colonies responded differentially to environmental changes in VPD. No relationship was found with maximum VPD and the proportion of colonies relocating on a given day ( $R^2 = 0.01$ ). However, the results were consistent with the previously documented fact that VPD predicts relocation rates, as rates of relocation and VPD were exceptionally high with low variance (Fig. 3). The irregular VPD during the experiment was associated with a prolonged dry spell atypical of the season.

The results of the application of the *A. araneoides* artificial nests to field army ant colonies yielded absolutely identical results among treatments and controls for both army ant species. None of the 10 or 5 cm applications resulted in contact with army ants in the treatments or controls, and all of the 1 cm application



**Fig. 3.** Vapour pressure deficit (VPD) and relocation rates (the proportion of ant colonies that relocated on a given day). Days when aromatic compounds are more volatile result in a greater fraction of colony relocations. The present study was conducted during an atypically hot and dry period, resulting in higher rates of relocation relative to an earlier study during more typical weather.

for both treatments and controls were contacted by army ants. The abundance of army ants was not scored at the 1 cm distance, but in all cases contact was apparently incidental.

Observations of *A. araneoides* colonies under attack from *E. lucanoides conquistador* and *E. burchellii* colonies indicate that all individuals can evacuate from a nest within 5 s, even in large colonies. In four unambiguous observations, colonies of *A. araneoides* rapidly evacuated a nest several seconds prior to the arrival of army ants, in cases where not a single army ant was present at the nest entrance when evacuation commenced. Nevertheless, the tubes of *E. burchellii* did not elicit any evacuation response by *A. araneoides*, even when the tubes were placed at nest entrances and the odours of the tube were obvious to the investigator.

## Discussion

Nest relocation by *A. araneoides* colonies is clearly mediated by colony odours. This finding is consistent with the *attraction hypothesis*, but the combined evidence suggests an alternative explanation. An odour-masking hypothesis is proposed, in which endogenous colony odours inhibit the ability of *A. araneoides* to detect incoming raids by army ants. Evidence and parsimony support the odour-masking hypothesis over the attractant hypothesis. Colonies of *A. araneoides* may flee their nest prior to attack, and the mechanism of an early warning is most likely olfactory, considering that even non-prey species such as humans can smell army ants at a distance of several metres. Odour is a far more likely cue than sound, as the army ant raids are distant and inaudible at the front of the raiding columns when *A. araneoides* colonies are attacked. The life-dinner principle (Dawkins & Krebs, 1979) supports the notion that strong selection upon *A. araneoides* will result in an escape mechanism, rather than a detection mechanism (for the generalised army ants, which eat at least dozens (for *E. lucanoides conquistador*) if not thousands (for *E. burchellii*) of prey species).

While *A. araneoides* moves its nests in response to its olfactory environment, there remains no evidence that army ants smell their prey. The prevailing view among army ant biologists is that prey are detected principally by olfaction, even though there remains no published history of experimentation on how army ants locate prey (Gotwald, 1995). Given the volume of behavioural research on army ants and the consensus supporting olfactory prey detection, it is likely that others have attempted to document how army ants smell prey. The negative results, that army ants do not detect prey, and prey do not evacuate in response to the presentation of army ants, would typically remain unpublished and without much interest. However, the findings are curious when it appears that odours play a significant role in the relocation behaviour of a common prey species in an attempt to avoid predation. These results, in the author's view, constitute a charge for future investigation, as commonly held opinions should not be rejected handily. Entire army ant colonies are difficult to manipulate, and the artefacts of manipulating prey and predator are great. Prey selection decisions of raiding columns are an emergent phenomenon resulting from

complex social interactions, and future investigations will require creatively designed experiments on predators and prey *in situ*.

This is the first documentation of nest evacuation in advance of army ant raids to the knowledge of the author. This evacuation response may be a potent way to reduce the costs of predation, but is not a great or novel sensory capability. The ant *Cataglyphis fortis* can smell crumbs of dry cookies more than 3 m away (Wolf & Wehner, 2000), and other species of ants can detect trace odours in the environment (Littleddyke & Cherrett, 1978; Roces, 1990, 1994). Why have other prey ant species not been observed to evacuate nests in advance of army ant raids? If nest relocation by *A. araneoides* is prerequisite to detecting army ants, then the costs of relocation may not outweigh the benefits of avoiding attacks. The cost–benefit relationship between relocation and predator avoidance is affected by species-specific attributes, and other species lack the nest architecture and rapid mobility of *A. araneoides* to benefit from mere seconds of warning. The relocation distances are short, on average less than a metre; the benefit of moving is not necessarily to move far away from the attracting cues, but simply to get the colony members outside of the odour-bearing nest. Because army ants are thought to cross each square metre of the forest every day or two (Kaspari & O'Donnell, 2003), mechanisms to avoid army ant predation must occur on the scale of centimetres rather than metres.

The architecture of *A. araneoides* nests is amenable to, if not selected by, the early detection and flight response to army ants. Nests are shallow with large openings and do not contain refuse, permitting the flow of ambient odours and simultaneous egress by several ants carrying brood. This strategy contrasts with aggressive defences mounted against army ants by other species using small nest entrances to constrict the entry of army ants (McDonald & Topoff, 1986). Nest architecture is the product and determinant of several colony-level behaviours (Wilson, 1971; Sendova-Franks & Franks, 1995; Theraulaz *et al.*, 1999), potentially including the escape from army ants. Continued research is not likely to yield success in the laboratory, because experimental interactions will fail to approximate *in situ* odour and other environmental cues prompting relocation. In particular, laboratory colonies function differently than field colonies with respect to air flow, as task performance rates are dependent upon underground CO<sub>2</sub> gradients that do not occur in traditional lab nests (Tschinkel, 2004).

Relatively little is known of the mechanisms of social insect prey to reduce the cost of army ant attacks, which is surprising given the ecological dominance of army ants in tropical and subtropical climates. The density of army ants is higher than suggested by casual observation, as single colony of *A. araneoides* chances an encounter a several times per week (Kaspari & O'Donnell, 2003). While visits by the above-ground foraging *E. burchellii* may only occur once per month, underground foragers such as *Labidus* and *Neviamyrmex* are quite common (Berghoff *et al.*, 2002). It is unknown if the fissures navigated by subterranean army ants create odour signatures similar to those of above-ground foraging army ants, and difficult to test whether prey can receive advance warning of underground army ant raids. Given that the subterranean army ants are more abun-

dant than surface-level army ants, it is quite likely that the phenomena documented in the present research are spurious outcomes of the evolutionary struggle that happens underground beyond our knowledge.

Many litter-nesting ant species in tropical rainforests may be serially monodomous. These minute ants, like the soil-nesting *A. araneoides*, move their nests frequently (Byrne, 1994) and are susceptible to army ant raids. If serial monodomy were widespread in tropical forests, a curious puzzle for tropical ant ecologists would be resolved. The dilemma is that the number of available nests apparently limits the number of colonies, even though many nests are unoccupied; this suggests that the empty nests have some value (McGlynn, 2006). In both leaf litter (Kaspari, 1996) and arboreal (Philpott, 2005) environments, supplementation of artificial nests was found to significantly increase the density of occupied nests, even though most artificial nests were unoccupied. If these ants were serially monodomous, one would predict that empty nests had been occupied recently and retain colony odours, and that colonies have claimed possession of nests and defend them *in absentia*. This is consistent with anecdotal observations when collecting litter nests at this field site, many of which are structurally sound but retain the distinctively pungent odour of litter-nesting colonies. Information about the taxonomic breadth of serial monodomy is currently only limited by our knowledge of the natural history of ants, which is scant for most species coexisting with army ants.

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