Temporal and spatial patterns in the emigrations of the army ant *Dorylus (Anomma) molestus* in the montane forest of Mt Kenya

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Abstract. 1. The emigration behaviour of the army ant *Dorylus (Anomma) molestus* was studied in the montane forest of Mt Kenya. This species forages by massive swarm raids (mean width 10.3 m ± 4.6 m SD), which are assumed to have a strong negative impact on the densities of prey populations.

2. For non-reproductive colonies the stay duration in a nest is highly variable (median 17, range 3–111 days). This suggests that the frequency of emigrations is not dictated by a brood cycle as an underlying endogenous pattern generator.

3. Colony density is high (mean nearest neighbour’s distance 82.1 m ± 29.4 m SD) and mean foraging range is 75.0 m, so encounters with neighbouring colonies occur frequently.

4. The straight line emigration distance is on average 92.7 m (± 29.7 SD). The emigration direction is random with respect to absolute bearing and also relative to the direction of the previous emigration. However, the emigration direction is influenced by the location of the nearest neighbour. Colonies typically emigrate directly away from their nearest neighbour.

5. Local food depletion is likely to be the ultimate cause for emigrations in this species, because emigration distance is larger than foraging range and colonies move away from their nearest neighbour. A small percentage of emigrations may be triggered by pangolin attacks on nests.

6. Contrary to the prediction of a recently developed mathematical model for epigaeic swarm-raiding *Dorylus (Anomma)* species, *D. (A.) molestus* colonies do not engage in intraspecific battles. Possible reasons for the absence of fights between colonies despite apparently fierce intraspecific competition are discussed.

Key words. Competition, encounters, nest relocation, nomadism, swarm raiding.

Introduction

Nest relocations (i.e. movements of the whole colony to a new nest site, hereafter emigrations) are a common phenomenon in ants. They can be caused by various factors such as nest disturbance, changes in microclimate, predation, competition from neighbouring colonies, and local food depletion (reviewed in Hölldobler & Wilson, 1990).

Nomadism (i.e. ‘relatively frequent migrations . . . accomplished in such an orderly fashion’; Wilson, 1958) is one of the key defining characteristics of army ants (Wilson, 1958; Gotwald, 1982; Brady, 2003), although the actual emigration frequency of the numerous species with subterranean lifestyles is still unknown (see, e.g. Berghoff et al., 2002a). For army ants local depletion of food resources is thought to be the ultimate cause for emigrating (Wilson, 1958) and,
indeed, overfeeding reduces the emigration frequency of the army ant Neivamyrmex nigrescens (Topoff & Mirenda, 1980) and of Leptogenys distinguenda (Witte & Maschwitz, 2000), a ponerine ant from south-east Asia that displays swarm-raiding behaviour as well as frequent emigrations.

In order to maintain a high rate of food intake and therefore colony growth, army ant colonies should move at a frequency and in directions that will minimise re-exploitation of recently raided areas (Franks & Fletcher, 1983), unless food resources are either not exhausted by raids (as is apparently the case in D. (Dichthadia) laevigatus; Berghoff et al., 2002b) or recover very quickly to former density levels. Colonies of the neotropical army ant Eciton burchelli (formerly E. burchellii; Bolton, 1995) send out successive raids from the same nest site during the statary phase in directions that will allow more efficient use of the surrounding area than would be achieved by raiding into random directions. Moreover during the intervening nomadic phases they raid and later emigrate along roughly the same compass bearing as on the previous day so that the successive bouts of statary phase foraging are separated further than they would be if colonies performed a random walk (Franks & Fletcher, 1983). However, as in other ants the spatial foraging and emigration patterns of army ants are likely to be influenced by competing conspecific colonies and perhaps also to a lesser extent by colonies of other army ant species with a similar diet. Franks and Fletcher (1983) hypothesised that E. burchelli colonies avoid areas recently raided by other colonies by altering the course of or even terminating their raids when encountering older foreign foraging or emigration trails. The trail pheromone of E. burchelli is highly persistent for up to 31 days (Blum & Portocarrero, 1964; Billen & Gobin, 1996) and may give foreign colonies a cue for detecting and avoiding areas where prey populations have not yet recovered to levels that allow efficient foraging. To date, there have been only two observations of such a direct avoidance upon encountering a foreign trail in this species (Willis, 1967, p. 7; Swartz, 1997, p. 17). On the other hand, there are several observations of colonies that crossed foraging or emigration trails of foreign colonies within 21 days after those had passed (Swartz, 1997, p. 17; Willson, 2003, pp. 32–33). Only during direct encounters of foraging workers do E. burchelli colonies show unambiguous avoidance: raids are ended abruptly and workers retreat to the nest and start a new raid in another direction (Swartz, 1997, pp. 18–19; Willson, 2003, pp. 31–32).

During a long-term study of the army ant Dorylus (Anomma) molestus in Kenya, Gotwald and Cunningham-van Someren (1990) observed five direct collisions between foraging colonies. In these instances sporadic agonistic behaviour was observed twice (Gotwald & Cunningham-van Someren, 1990), but the colonies more or less ricocheted off one another without engaging in a battle (W. H. Gotwald, pers. comm.). Moreover, the authors found that foraging ranges of neighbouring colonies as well as of successive nests of the same colony often overlapped. These findings indicate that competition for food between colonies may be intense but at the same time question the importance of food depletion as the central ultimate cause for emigrating. Because the study was conducted in a highly modified habitat (diverse farmland; Gotwald, 1995, Fig. 4.14), it is possible that colony movements were constrained by characteristics of the heterogeneous habitat. In the present paper a detailed description of the temporal and spatial emigration patterns of D. (A.) molestus in a closed canopy forest habitat is provided. The emigration patterns are analysed at the population level (i.e. in relation to the location of neighbouring colonies) to clarify the influence of intraspecific competition on them.

Materials and methods

Study site and study species

The observations on Dorylus (A.) molestus Gerstäcker (species status; Gotwald, 1974) reported here were made in the forest reserve at the eastern slope of Mt. Kenya, Chogoria, central Kenya (0°14′S, 37°34′E) at an altitude of 1850 m a.s.l. The vegetation on the study site is montane Ocotea usambarenensis forest, although the density of this tree is quite low due to selective timber harvesting in the past. As the site is located on a mountain slope it consists of moderately, sometimes steeply rising and falling ridges and valleys with streams. The area receives a total of about 2250 mm of rainfall, mostly in the two rainy seasons from March to May and from October to December (Bussmann, 1994, map 1). During swarm raids D. molestus searches intensely in the top soil layers, in the leaf litter, on the ground surface, and up in the vegetation. Prey includes (in order of decreasing biomass proportion) earthworms, insects, slugs, and myriapods (C. Schönig, unpubl. data). Other coexisting army ant species in this habitat are D. (Dorylus) affinis, D. (Dorylus) sp., and D. (Rhogmus) laevipodex, all of which hunt in the soil.

Mapping of colony movements

Between October 2001 and March 2002 and between January and April 2003 the relative positions of colonies and their movements were mapped using a compass and metre tape in the same general contiguous area. Colonies were located either by following foraging trails or by finding nests directly. Nest locations were marked with red and white tape at eye level. After detection, colonies were monitored every day by carefully searching for trails extending from the nest. When an emigration trail was found, it was followed to the new nest and the straight-line distance and the compass bearing from the old nest were measured. Whenever possible, the trail length was also determined by laying a metre tape parallel to, and at a distance of 20 cm from, the active trail. Moreover the bearing and straight-line distance from the new to neighbouring nests.
were measured. This was carried out only occasionally in 2001/2002, but regularly in 2003. If no trail was found, the presence of ants in the nest was checked by disturbing the nest by beating it with a stick or a cutlass. Numerous large workers immediately run out of the entrances of active nests upon such disturbance. In 2001–2002 up to 25 colonies were monitored in this way. Individual colonies were followed over the course of between 2 weeks and 6 months. In 2003 up to 20 colonies were monitored over observation periods of between 2 and 9 weeks. It is unknown whether the colonies monitored in 2003 were the same or different from the ones observed in 2001/2002.

Brood samples

In some army ants the temporal emigration patterns are tightly linked to a cycle in egg production by the queen (reviewed in Gotwald, 1995). For D. (A.) wilverthi, Raignier and van Boven (1955) found three modes in the size–frequency distribution of stay durations. They also reported that the majority of brood carried during emigrations are pupae. They interpreted these findings as evidence that such a cycle also explains the timing of emigrations in D. wilverthi. To study the brood composition during emigrations, all workers and the brood they carried were collected from 20-cm sections of emigration trails with an aspirator. For four emigrations, such samples were taken repeatedly from different sections within 1 h. For one emigration, these samples were taken repeatedly from different sections throughout the entire 2-day-long emigration process. In addition, brood was collected from one nest, which was partly dug up when the colony had stayed there for 33 days and was not emigrating.

Foraging parameters

Three foraging parameters relevant to the understanding of emigration behaviour were measured: (1) Swarm raid width as the distance between the furthest two ants on either side of the swarm front. (2) Swarm raid velocity by placing sticks at the points marking the maximum swarm width every 10 min, n times, and determining the distance between successive points on each side. The means of the distances on the two sides were calculated and in turn averaged. The sample size varied between one and three between observations. In the statistical analysis the sample unit was then one swarm raid. Swarm raid measurements were taken at relative humidities above 85% and at temperatures between 17 and 20 °C. In areas of closed canopy forest maximum temperatures on the ground hardly ever exceed 21 °C during the day; during the night temperatures may drop down to 8 °C, especially during the dry season. (3) Whenever a diminishing swarm raid was encountered, the maximum length of the foraging trail was measured as described for emigration trails when the swarm made no further progress.

Data analysis

In the examination of temporal emigration patterns stay duration was defined as the period from the first day of an emigration into a new nest to the last day before the emigration to the next new nest. To determine whether colonies showed a preferred absolute emigration direction, the Rayleigh test was used (Fisher, 1993). As the declination values for 2001/2002 and 2003 were unknown, both data sets were treated separately in this test. To examine whether colonies showed a preferred emigration direction relative to the previous, the turn (0–360°) between successive emigrations was calculated and then the Rayleigh test was again used. To test whether the directions taken by colonies were related to the location of their nearest neighbour, the Rayleigh test was used after directions were standardised by setting as 0° the direction between the colony and its nearest neighbour prior to relocation (Brown, 1999). A paired r-test was employed to determine whether emigrations resulted in colonies being more distant from the colony that had been their nearest neighbour prior to the emigration. Brown (1999) found that colonies of the seed-harvesting ant Messor andrei were on average more distant from their new nearest neighbour after a nest relocation than they had been before from their old nearest neighbour, although it is hard to understand how this is possible at the population level, unless the population was declining in numbers per unit area either because it was occupying a larger area or colonies were dying. Using similar methods as Brown (1999) it was determined whether D. molestus colonies ended up further from other colonies after an emigration by using a paired r-test. In contrast to the analysis of temporal emigration patterns, a nest was considered occupied in the analysis of spatial emigration patterns even when an emigration was already in progress because colonies can organise raids from both the new and old nest while emigrating (see Results) and may therefore compete with all colonies neighbouring both the old and new nest. For all analyses requiring the identification of the nearest neighbour, only those emigrations were taken into account for which the distances to the nearest neighbours had actually been measured. Distances and bearings were not taken from a map because the pronounced heterogeneity of the landscape made accurate mapping of the area very difficult.

All statistical analyses were performed with the computer programs Statistica (StatSoft Inc., 1999) and Oriana (Kovach Computing Services, 2004).

Results

General description of emigrations

Colonies of D. molestus find their new nest sites during raids. The cues that workers use for selecting a new nest
site are unknown. When a new nest site is chosen, intense bi-directional traffic continues even when the swarm raid in the area of the new nest site has ceased. Workers start to excavate the new nest, while the foraging trail linking the old and new nest is usually gradually turned into a tunnel through the building activities of smaller workers that remove soil particles from the ground of the foraging trail and use them to build over it an arcade ceiling (see Gotwald, 1995, plates 5A,B). In areas where the soil is hard-packed and digging is therefore impeded the trails are usually covered by a thick wall of workers (see Gotwald, 1995, plate 14A). By using logs or twigs, colonies can pass over streams and rivers. The nest-building activities can start up to 5 days before brood is actually transported to the new nest. During the emigrations, which last up to 3 days, workers usually carry just one brood item, but occasionally up to three when transporting small larvae. Brood items are carried in the same way as food items, i.e. slung longitudinally underneath the body. Brood items are not carried by groups of cooperating workers. Up to three raids can be conducted simultaneously from the old and new nest sites whilst the colony is moving to the new nest site. Nests are usually conspicuous structures indicated by characteristic craters of excavated soil that spread out over areas with a maximum extension of on average 3.02 m (± 1.04 m SD, n = 28). The amount of soil brought up during the entire nest stay was on average 34.4 kg (natural water content in dry season, ± 9.7 kg SD, n = 5). Nests are often located at the base of trees, but can also lie directly in open ground. They have been found in areas with a closed canopy, in tree-fall gaps, as well as in open grassland at the road side. Sometimes colonies nest in abandoned mammal burrows and are then more difficult to detect. Reoccupation of older nests is a common phenomenon. Ten out of 32 nests of colonies monitored in 2003 had been occupied before. When marks from old nests of the 2001/2002 observation period were taken down at the end of observations in 2003, nine out of 27 nests showed signs of recent reoccupation.

**Emigration parameters**

The median stay duration for non-reproducing colonies was 17 days (n = 87, range 3–111 days, calculated on the basis of all data from 2001 to 2003, dry as well as wet season combined; Fig. 1). In the course of fission events the mother colony left the nest after 28, 30, and 31 days (n = 3). Afterwards males first emerged in the remaining daughter colony 41, 42, and 56 days after the original parental colony had moved in. The daughter colonies left 58, 53, and 70 days after the original parental colony had moved in, i.e. 17, 11, 14, 20, 15, and 26 days after males first emerged (n = 6), or 30, 23, 39, 20, 29, and 38 days after the mother colony left. All colonies that produced males subsequently split into two new functional colonies. In the small number of observed fission events, mother and daughter colonies did not emigrate directly away from each other. The angles between fission and emigration directions were 204°, 75°, 314°, 90°, 21°, and 225°. The distribution of these angles is uniform (Rayleigh test, Z = 0.05, P = 0.95). There were no significant differences between the straight-line distances of normal, fission, and first emigrations (ANOVA: F2,134 = 0.56, P = 0.57) and so emigrations of all three categories were pooled. The straight-line emigration distance was on average 92.7 m (± 29.68 SD, range 42.1–174 m, n = 135). The ratio between straight-line distance and trail length was on average 0.84 (± 0.12 SD, range 0.38–0.97). Emigrating colonies did not show a preference for an absolute direction (Rayleigh test, 2001–2002: n = 101, Z = 2.393, P = 0.09; 2003: n = 33, Z = 0.14, P = 0.87). They also did not show a preferred direction relative to their previous emigration. The distribution of angles relative to previous emigration was uniform (n = 90, Rayleigh test, Z = 0.05, P = 0.95).

**Emigration in relation to the nearest neighbour**

Colonies moved away from their nearest neighbours (n = 48, mean vector μ = 184.8°, circular standard
deviation 63.9°, Rayleigh test, $Z = 13.8, P < 0.00001$, the mean vector is insignificantly different from 180°, $t$-test, $t_{47} = 0.07, P = 0.95$, Fig. 2) and thus increased their separation (mean ± SD distance before 82.13 ± 29.46 m, mean ± SD distance after 152.07 ± 50.15 m, paired $t$-test $t_{47} = -11.5, P < 0.00001$). At the new nest site the new nearest neighbour was on average no further away than the previous one had been before the emigration (initial distance to old nearest neighbour: mean ± SD 79.61 ± 28.37 m, resulting distance to new nearest neighbour: mean ± SD 79.10 ± 24.69 m, paired $t$-test, $t_{28} = 0.07, P = 0.94$).

Brood samples

The brood composition of five emigrating colonies and one whose nest was dug up is shown in Table 1.

Foraging parameters

As no significant differences were detected between dry and wet season data, all foraging data of 2001–2003 are combined in the following analyses. Colonies essentially foraged all the time, day and night. When all the workers returned on one trail, others were already starting a new raid in another direction. Colonies usually foraged along one trail but occasionally on two or three trails simultaneously. Swarm raid width was on average 10.3 m ($n = 42, ± 4.60$ m SD, range 3.2–23.7 m). Swarm raids proceeded at a speed of 1.20 m per 10 min (± 0.28 SD, range 0.77–1.79 m per 10 min, $n = 12$) or 7.2 m per hour. Foraging trail length was on average 89.3 m (± 32.2 m SD, range 30.2–198.0 m, $n = 64$). In order to allow meaningful comparisons between foraging distances and distances between nests, the foraging range, i.e. the maximum distance the swarm raid reaches from the nest, needs to be calculated. By multiplying foraging trail lengths with the ratio between straight-line distance and trail length for emigrations, 75.0 m was obtained as the average foraging range. This is appropriate because all emigrations followed along previous foraging trails and thus the relationship between trail length and straight-line distance should be identical for raids and emigrations.

Behaviour during encounters

Direct encounters between conspecific colonies were observed on five occasions. In no case did the encounter result in a battle. Rather, only a single worker was observed to be spreadeagled by workers of the foreign colony in all these instances. No raids ended as a result of the encounter but their courses were diverted so as to allow both colonies...
to continue in their hunting or emigration efforts. On one occasion a colony foraged towards and eventually exactly onto the nest area of another whose foraging trail extended in the opposite direction. The swarm raid had lost impetus by the time it reached the nest, which was hidden underneath a thick leaf litter layer, so it was impossible to ascertain whether direct contact between workers occurred. The swarm-raiding workers all gradually retreated to their nest. It is unknown whether this was a direct reaction to encountering another nest. The colony in the nest did not show any response to the approach of the other colony.

**Discussion**

Why do *D. molestus* colonies emigrate? Leroux (1982) observed several occasions on which *D. (Anomma) nigricans* colonies emigrated in response to attacks by subterranean *D. (Typhlopone)* spp. Colonies of this subgenus have never been found at the field site of the work reported here. Attacks of the occurring subterranean species on *D. molestus* were never observed. In one case *D. (Rhogmus) laevipodex* workers actually hunted termites (*Apicotermitinae*) on a *D. molestus* nest without any apparent interaction between the ants of the two species.

Nests were sometimes attacked at night, presumably by pangolins, which dug holes into the nests from the side. On the next morning when the respective nests were monitored, these holes were filled with masses of large workers. In three cases colonies emigrated directly after the attack. As the colony whose nest was dug up to collect a brood sample also started to move away in the following night, it is concluded that colonies sometimes emigrate when their nests have been substantially damaged so that they would be very vulnerable to another attack. A similar response to an attack by a predator has also been observed in another *D. (Anomma)* species. At Taï (Ivory Coast) colonies of *D. (A.) nigricans* emigrate within a day after their nest has been attacked by chimpanzees (Boesch & Boesch, 1990; C. Boesch, pers. comm.). At our Mt Kenya study site substantial numbers of large workers regularly come out of *D. molestus* nests at night. Such workers adopt stereotyped defensive postures and may serve as deterrence. This behaviour also suggests that colonies may even prepare themselves prior to possible attacks. However, as only six cases of pangolin attacks were observed throughout the entire study period, there must be another more important reason for emigrations by *D. molestus* colonies.

Elephants sometimes pass over *D. molestus* nests and may thereby damage their structure. However, no colonies were observed emigrating soon after elephants had passed over their nests (*n* = 3).

It is also conceivable that colonies emigrate due to parasite infestations. Emigrations have been implicated in the reduction of parasite prevalence in reindeer, baboons, and butterflies (Hausfater & Meade, 1982; Folstad *et al.*, 1991; Altizer *et al.*, 2000) and it has been suggested that infection of the fungus garden with the virulent pathogenic fungus, *Escovopsis*, can stimulate emigrations of colonies of the leaf-cutting ant *Atta colombica* (Hart, 2002). Myrmecophilous arthropods, parasitic blind snakes (*Typhlops lineolata*) as well as fungi or bacteria could make living conditions in *D. molestus* nests unfavourable. However, when moving to new nest sites, the workers are accompanied by the myrmecophilous arthropods as well as the blind snakes (C. Schönig, pers. obs.). If emigrations were a countermeasure against high parasite prevalence, shorter emigration distances might be expected. Moreover, colonies often re-use nests previously utilised by themselves or conspecific colonies (see also Leroux, 1982, pp. 31–34 for *D. nigricans*) and will then probably encounter the spores of any potentially parasitic fungi or bacteria. Thus, emigrations are unlikely to be an effective mechanism to control parasite infestation levels and should therefore have a different adaptive significance.

Generally colonies send out at least one swarm raid every day with an average width of about 10.3 m. If raids are systematically arranged around the nest with the maximum angles between neighbouring raids, then the whole area within a distance of 27.9 m and 51% of the area within a distance of 75 m (the mean foraging range) from the nest will have been raided at least once within 17 days (the median stay duration) (calculated as in Franks & Fletcher, 1983). *Dorylus molestus* has a generalist diet. Although the populations of its prey animals may recover more quickly to pre-raid levels than those of social insects, it is hard to imagine that the area around the nest could be used in a sustainable manner. This is even harder to

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**Table 1.** Brood composition of emigrating colonies. Please note that the sampling procedures were different for colony L. Brood composition of colony C, whose nest was dug up after 33 days, is shown for comparison.

<table>
<thead>
<tr>
<th>Colony</th>
<th>A'</th>
<th>E'</th>
<th>L'</th>
<th>H'</th>
<th>L'</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emigration after n days</td>
<td>5</td>
<td>6</td>
<td>10</td>
<td>14</td>
<td>unknown</td>
<td>nest</td>
</tr>
<tr>
<td>Brood items n</td>
<td>1041</td>
<td>1080</td>
<td>416</td>
<td>298</td>
<td>1490</td>
<td>2054</td>
</tr>
<tr>
<td>% Brood category</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pupae</td>
<td>87.6</td>
<td>89.3</td>
<td>92.8</td>
<td>98.3</td>
<td>52.3</td>
<td>58.9</td>
</tr>
<tr>
<td>Larvae</td>
<td>12.1</td>
<td>10.7</td>
<td>7.2</td>
<td>1.7</td>
<td>30.9</td>
<td>20.8</td>
</tr>
<tr>
<td>Eggs</td>
<td>0.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>16.8</td>
<td>20.3</td>
</tr>
</tbody>
</table>
Imagine when one compares the average nearest-neighbour distance to the average foraging range. There are probably very few instances when a colony can actually ever exploit the area up to 75 m around the nest alone without interference from neighbouring colonies. Emigration distances are about 24% larger than the normal foraging range. Colonies will thereby manage to reach areas that they had not fully exploited before even though the theoretical (circles with a 75 m radius centred on the nest) as well as the real foraging areas (determined by Gotwald & Cunningham-van Someren, 1990) before and after an emigration will still overlap. By contrast, Longhurst and Howse (1979) found that emigration distances of the termite-hunting ponerine ant *Pachycondyla analis* (formerly *Megaponera foetens*; Bolton, 1995) are smaller than its foraging range and concluded that emigrations are not triggered by local food depletion but other factors such as nest site flooding and perhaps also attacks by subterranean army ants. Conversely, it is concluded here that food depletion is likely to be the ultimate cause for emigrations in *D. molestus*. By emigrating, colonies gain access to areas that they have not exploited previously. Moreover, colonies tend to emigrate directly away from their nearest neighbour, i.e. away from areas that have probably been exploited both most thoroughly and in the most recent past. At the time of the emigration the new foraging area is likely to hold more food than the old foraging area because it has been exploited only in part or even not at all during the time the colony remained in its previous nest. Thus, colonies do not gain a larger foraging area but probably a newer one by emigrating.

How do colonies determine in which direction to emigrate? Colonies might achieve the observed movement away from nearest neighbours by two mechanisms. It has been shown for other army ants that swarm raids can to some extent trace areas of high food density and adjust their direction accordingly (Franks *et al.*, 1991; Witte & Maschwitz, 2000). Homebound workers retrieving food items lay odour trails that direct outbound foragers to areas where food has been found. This can cause swarms to make most rapid progress into food-rich habitat patches. If colonies of *D. molestus* can in a similar way track gradients in food density, they will explore preferentially and finally emigrate into areas of higher food density. The area between two colonies is likely to be exploited more thoroughly than other areas and would therefore be very rarely chosen as a new nest site. If colonies employ such a mechanism, it can be predicted that prey retrieval rates during raids towards new nest sites are substantially larger than during previous raids. Alternatively, it is conceivable that encounters with other colonies can somehow be used as a cue to avoid certain directions when emigrating. Encounters signal the presence of another colony and as other colonies exploit areas around them in the same way, encounters should directly indicate areas of low food density. Whether colonies use either of these mechanisms should be tested experimentally by manipulating the food density of areas and thus providing a stimulus for emigrating.

If food depletion is the ultimate cause for emigrating, when should colonies emigrate? Certainly not every time they find an area rich in food resources, because then they would emigrate unnecessarily often. The costs of emigrations are difficult to estimate. Nest excavation is presumably an energetically costly undertaking and although colonies can continue to forage while emigrating, fewer workers will be available for foraging and thus food intake will be reduced. However, the greatest cost of emigrating is probably the risk of death for the queen when she makes her way to the new nest. For these reasons, high emigration frequencies should be disadvantageous. It has been suggested that the temporal emigration pattern of *D. (A.) wilverthi* is related to a cycle in egg-laying activity and brood development, even if not as strictly as in some neotropical army ant species (Raignier & van Boven, 1955). The brood composition data for emigrating *D. molestus* colonies also indicate, at first sight, a link between brood composition and the duration of stay at a nest site. However, the trend of increasing pupae proportion with nest stay duration probably reflects inadequate sampling procedures. Larvae pupate after 26 days (*D. nigricans*; Leroux, 1982) and so it is hard to understand why, for example, 87.6% of all brood items can be pupae after a nest stay of 5 days if the queen is producing eggs either cyclically or continuously. If different brood types are not transported simultaneously, then sampling over a period of only 1 h can easily produce biased results; and, indeed, for the colony whose brood was collected throughout the entire course of the emigration, brood of all stages were found in more equal proportions. At this point we would also like to report some important additional observations that were made at a higher altitude at Mt Kenya later in October 2004 when filming *D. molestus* colonies with a BBC film crew. When completely digging up a conveniently located nest to film the nest interior, brood of all stages were found as well as newly eclosed callow workers. The queen was physogastric, laying eggs and hardly able to move. It is not known how long the colony had stayed in the nest, but the simultaneous presence of brood in all developmental stages and of newly eclosed workers indicates a non-phasic brood production (Berghoff *et al.*, 2002a). Our tentative conclusion would therefore be that *D. molestus* queens lay eggs continuously (perhaps interrupted by short intervals during which they move to the new nest during emigrations). It is finally important to note that worker brood of all developmental stages can be transported at any time. This renders colonies mobile and enables them in general to move to a favourable area quickly after it is discovered.

Neighbouring army ant colonies can restrict each others’ foraging activities and thereby compete (Mirenda & Topoff, 1980; Leroux, 1982). Because the average nearest neighbour’s distance is small compared to the normal foraging range, it is assumed that intraspecific competition in *D. molestus* is fierce. A recent study predicted that colonies of swarm-raiding army ants with a generalist diet such as *D. molestus* should engage foreign colonies in battles as an evolutionarily stable strategy (Boswell *et al.*, 2001). Neither
D. molestus (W. H. Gotwald, pers. comm.), nor D. nigricans (Leroux, 1982) nor D. wilverthi (Ragnier & van Boven, 1955) colonies fight each other under regular circumstances. Ragnier and van Boven (1955) and Leroux (1982) saw many instances where the trail of one colony even crossed over that of another. In 4 years of field research Leroux (1982) observed two battles between D. nigricans colonies, one of which apparently resulted in the death of the inferior colony's queen. However, such behaviour was very rare (Leroux, 1982) and so it has to be concluded that epigaeic swarm-raiding Dorylus species in general do not fight against conspecific colonies in spite of frequent encounters. The best strategy for colonies in a situation of extreme competition for food might be to find areas of higher food density and exploit these before other colonies can do so. Although on average they reach areas with a new competitor close by, the time factor will also be decisive. When colonies choose to emigrate, they must find good new patches and may then either be fortunate (the new nearest neighbour is not so close by, has arrived very recently too or has not yet extracted food in the area) or not (the new nearest neighbour is very close by, has stayed for a long time and has exploited large parts of the colony's theoretical foraging ground). There will always be an element of chance in such emigration decisions because colonies are constrained by a lack of information. In contrast to nomadic mammal groups, which can indicate their own position or locate the position of other groups through long-distance acoustic communication (e.g. black and white colobus monkeys, Colobus guereza, Davies & Oates, 1994), army ant colonies can only assess the quality of areas and avoid competition with other colonies by direct exploration through foraging, but they cannot sense ahead of them. For example, in 2003 colony K' emigrated away from its nearest neighbour G' but its new nest site K'3 was located just 34 m (the second shortest nearest neighbour’s distance recorded in this study) away from the nest of colony I', which had emigrated into that area just a day before and perhaps had not foraged in the area into which K' had decided to emigrate. The two colonies stayed just 34 m from each other for 10 days before both emigrated again away from each other on the same day (colony I' actually went back to its previous nest site). Because of their foraging mode, which requires huge numbers of workers, swarm-raiding army ant colonies cannot maintain an absolute territory. The only way they can secure exclusive access to close-by food resources is to exploit them quickly themselves. Another possible explanation for the absence of intraspecific fights would be that colonies have no way of estimating a priori their chances of success or failure.

In conclusion, our demonstration that D. molestus colonies emigrate into areas beyond their normal foraging range and move directly away from their nearest neighbours strongly suggests that frequent emigrations in this species occur to favour their foraging success. This finding supports earlier suggestions concerning the adaptive value of emigrations in these extraordinary social insects. This study also provides new insights into how the exploitation of foraging areas and competition between army ant colonies differ from those in other more sessile ant colonies.

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