

Temporal and spatial patterns in the migrating behaviour of the army ant *Dorylus (Anomma) molestus* in the montane forests of Mt Kenya



Fig. 1 A *Dorylus (Anomma) molestus* colony migrates on a stick over a stream.

Abstract

The migration behaviour of the army ant *Dorylus molestus* was studied in the montane forest of Mt Kenya. This species forages by massive swarm raids (mean width 10.3 m) which are assumed to have a strong negative impact on the densities of prey populations. For non-reproductive colonies the stay duration in a nest is highly variable (median 17, range 3-111 days) so that brood cycle as an underlying endogenous pattern generator can be ruled out. The straight line migration distance is on average 94 m (range 42.1-174 m). The migration direction is random with respect to absolute bearing and also relative to the direction of the previous migration. Colonies migrate away from their nearest neighbours and thus increase the distance to them. However, they do not end up further away from any other colony after migration. Colony density is high (mean nearest neighbour's distance 80 m) and mean foraging range is about 70 m so that encounters of neighbouring colonies occur frequently. Contrary to the prediction of a recently developed mathematical model for epigaeic swarm raiding *Dorylus* species, *D. molestus* colonies do not engage in intraspecific battles. Local food depletion is likely to be the ultimate cause for migrations in this species, because migration distance is larger than foraging range and colonies move away from their nearest neighbours. A small percentage of migrations is triggered by pangolin attacks of nests. Possible reasons for the absence of fights between colonies despite apparently fierce intraspecific competition are discussed.

Introduction

Nest relocations (i.e. movements of the whole colony to a new nest site, hereafter migrations) 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 and 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 migration of the numerous species with subterranean life-styles 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 migrating (Wilson 1958). And indeed, overfeeding reduces the migration frequency of the army ant *Neivamyrmex nigrescens* (Topoff and Mirenda 1980) and of *Leptogenys distinguenda* (Witte and Maschwitz 2000), a ponerine ant from south-east Asia which displays swarm-raiding behaviour as well as frequent migrations. In order to ascertain

large food intake and therefore colony growth army ant colonies should move at a frequency and in directions that will minimize re-exploitation of recently raided areas (Franks and Fletcher 1983), unless food resources are not exhausted by raids (as is apparently the case in *D. laevigatus*, Berghoff et al. 2002b) or recover very quickly to former density levels. Colonies of the neotropical army ant *Eciton burchellii* (formerly *E. burchelli*, Bolton 1995) send out successive raids during the starchy phase into 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 migrate along roughly the same compass bearing as on the previous day so that the successive bouts of central place foraging are separated further than they would be if colonies performed a random walk (Franks and Fletcher 1983). However, as in other ants the spatial foraging and migration 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 & Fletcher (1983) hypothesized that *E. burchellii* colonies avoid areas recently raided by other colonies by altering the course of or even terminating their raids and / or migrations when encountering older foreign foraging trails. The trail pheromone of *E. burchellii* is highly persistent for up to 31 days (Blum & Portocarero 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, p. 17). On the other hand there are several observations of colonies which crossed foraging or migration 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. burchellii* colonies show unambiguous avoidance: raids are ended abruptly and workers retreat to the nest and start a new raid into 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 & Cunningham-van Someren (1990) observed five direct collisions between foraging colonies. In these instances sporadic agonistic behaviour was observed twice, but the colonies more or less ricocheted off one another (Gotwald, pers.comm.) without engaging in a battle. 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 migrating. 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 we provide a detailed description of the temporal and spatial migration patterns of *D. molestus* in a closed canopy forest habitat. We analyse the migration patterns on the population level (i.e. in relation to the location of neighbouring colonies) to clarify the influence of intraspecific competition on migration patterns.

Material and Methods

Study site and study species

The observations on *Dorylus (Anomma) 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 1850m asl. The vegetation on the study site is montane *Ocotea usambarensis* forest, although the density of this tree is quite low due to selective timber harvest in the past. As the site is located at a mountain slope it consists of moderately undulating, sometimes steep 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). *Dorylus molestus* colonies have a density of about one colony per 2 ha at this site. During swarm raids colonies of this species search the vegetation, on the surface and intensely in the leaf-litter and top soil layers. Prey includes (in order of decreasing biomass proportion) earthworms, insects, slugs and myriapods (Chapter II). 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 we mapped the relative positions of colonies and their movements using a compass and metre tape in the same general contiguous area. We located colonies 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 a migration trail was found, we followed it to the new nest and measured straight line distance, compass bearing from the old nest and whenever possible trail length. Moreover the bearing and straight line distance from the new to neighbouring nests were measured. This was done only occasionally in 2001/2002, but regularly in 2003. If no trail

was found we checked for the presence of ants in the nest by disturbing it through beating with a stick or cutlass. In active nests numerous large workers immediately come running out of the entrances upon disturbance. In 2001-2002 we monitored up to 25 colonies in this way. Individual colonies were followed over the course of between two weeks and 6 months. In 2003 we monitored up to 20 colonies over observation periods of between two 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 migration patterns are tightly linked to a cycle in egg production by the queen (reviewed in Gotwald 1995). For *D. wilverthi* Raignier and van Boven (1955) found three modes in the size-frequency distribution of stay durations and that mostly pupae are being carried during migrations. They interpreted these findings as evidence that such a cycle does also explain the timing of migrations in *D. wilverthi*. To study the brood composition during migrations we collected samples by removing all workers and brood from migration trail stretches of 20 cm with an aspirator. For four migrations such samples were taken repeatedly from different stretches within one hour. For one migration these samples were taken repeatedly from different stretches throughout the entire two day long migration process. Moreover brood was collected from one nest which was partly dug up when the colony had stayed there for 33 days and was not migrating.

Foraging characteristics

Additionally three foraging parameters relevant for the understanding of migration behaviour were measured: (1) Swarm raid width as the maximum width of the swarm front perpendicular to advance direction. (2) Swarm raid velocity by placing sticks at the points marking the maximum swarm width every ten minutes 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 n 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 when no further progress was made.

Data analysis

For the examination of temporal migration patterns stay duration for a nest was defined as starting from the first day of the migration into that nest to the last day before the migration leading to the new nest. To determine whether colonies showed a preferred absolute migration direction we used the Rayleigh test (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 migration direction relative to the previous, we calculated the turn (0° - 360°) between successive migrations and then again used the Rayleigh test. To test whether the directions that colonies moved in was related to the location of their nearest neighbours 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). The paired *t*-test was employed to determine whether migrations resulted in colonies being more distant from the colony that had been their nearest neighbour prior to the migration. The paired *t*-test was also used to determine whether colonies were more distant from their new nearest neighbour than they had been before from their old nearest neighbour. In contrast to the analysis of temporal migration patterns a nest is considered occupied in the analysis of spatial migration patterns even when a migration is already in progress because colonies can organize raids from both the new and old nest while migrating (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 migrations 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 surface made accurate mapping of the area very difficult.

All statistical analyses were performed with the computer programmes STATISTICA ('99 Edition, StatSoft, Inc.) and ORIANA (Version 2.01, Kovach Computing Services).

Results

General description of migrations

The colonies 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 which 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 therefore impeded the trails are usually covered by a thick wall of workers (see Gotwald 1995, plate 14A). By using logs or (sometimes even feeble) twigs colonies can pass over streams and rivers (see fig.1). The nest building activities can start up to five days before brood is actually being transported to the new nest. During the migration which last up to three days workers carry usually just one brood item, but occasionally up to three when transporting small larvae. Brood items are being 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. While the colony is moving to the new nest site, up to three raids can be conducted simultaneously from both the old and new nest site. Nests are usually conspicuous structures indicated by characteristic craters of excavated soil which 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. We have found them in areas with closed canopy as well as 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 we took down marks from old nests of the 2001/2002 observation period at the end of observations in 2003, 9 out of 27 nests showed signs of recent reoccupation.

Migration 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 2001-2003, dry as well as wet season combined, fig. 2). In the course of fission events the mother colony left the nest after 28, 30 and 31 days (n=3). Afterwards males first emerged after altogether 41, 42 and 56 days. The daughter colonies left after a total stay in the nest of 58, 53 and 70 days, or 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 migrate away from each other. The angles between fission and migration directions were 204°, 75°, 314°, 90°, 21° and 225°. The distribution of these angle is uniform (Rayleigh test, $Z=0.05$, $p=0.95$). There were no significant differences between the straight line distances of normal,

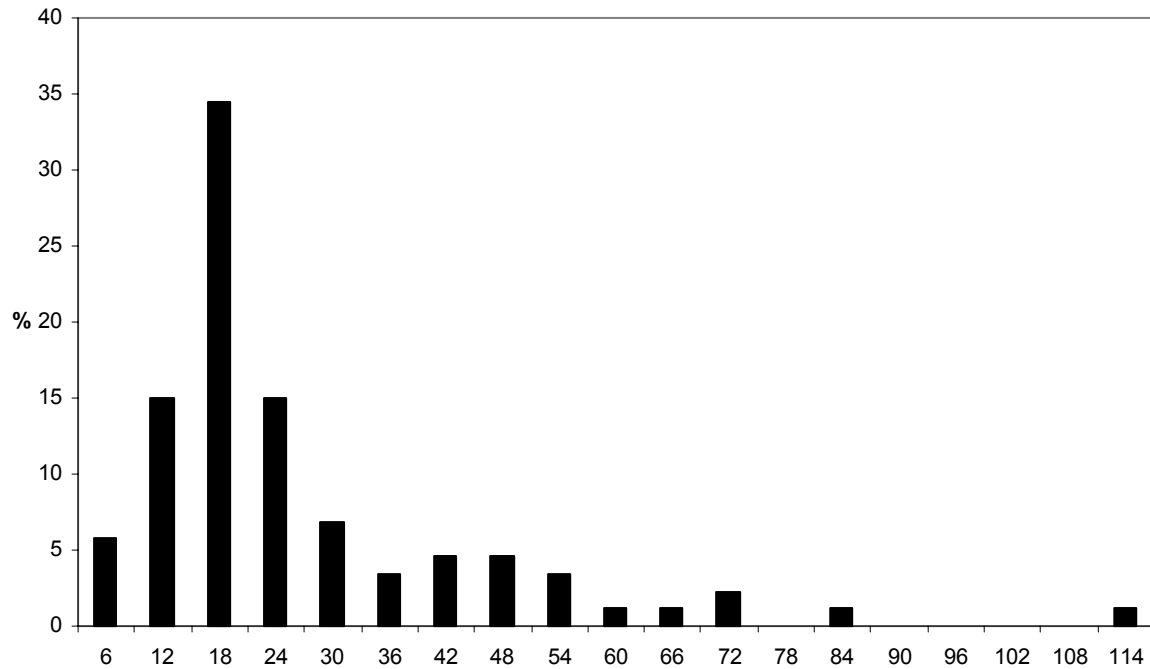


Fig. 2 Frequency distribution of stay durations (in days) of non-reproductive colonies (n=87). Numbers on the x-axis indicate the upper limit of the respective range, with the limit being included.

fission and first migrations (ANOVA $df=2$, $F=0.56$, $p=0.57$) and so migrations of all three categories were pooled. The straight line migration distance was on average 93.6 m (± 30.58 SD, range 42.1-174 m, $n=120$). The relationship between migration trail length and straight line migration distance is best described by the model Trail Length (m) = 19.2 m + 1.00 · Straight line distance (m) ($r^2 = 0.74$, $t=11.47$, $p<0.0001$, $n=48$). The ratio between straight line distance and trail length was on average 0.84 (range 0.38 – 0.97). When migrating colonies did not show a preference for an absolute direction (Rayleigh test, 2001-2002: $n=101$, $Z=2.393$, $p=0.09$; 2003: $n=33$, $Z=0.14$, $p=0.87$). Neither did they show a preferred direction relative to their previous migration. The distribution of angles relative to previous migration is uniform ($n=90$, Rayleigh test, $Z=0.05$, $p=0.95$).

Migration in relation to the nearest neighbour

Colonies moved away from their nearest neighbours ($n=47$, mean vector $\mu=186.3^\circ$, Rayleigh test, $Z=13.3$, $p<0.00001$, fig. 3) and thus increased their separation (mean distance before 82.13m, mean distance after 152.07 m, paired t-test $t=-11.5$, $df=47$, $p<0.00001$). However, at

the new nest site the new nearest neighbour was not further away than the previous one had been before the migration (distance before mean 79.61m, distance to new nearest neighbour mean 79.10m, paired t-test $t=0.07$, $df=28$, $p=0.94$). The migration distance is not correlated with the nearest neighbour's distance prior to the migration ($r^2=0.03$, $t=1.25$, $p=0.22$, $N=48$).

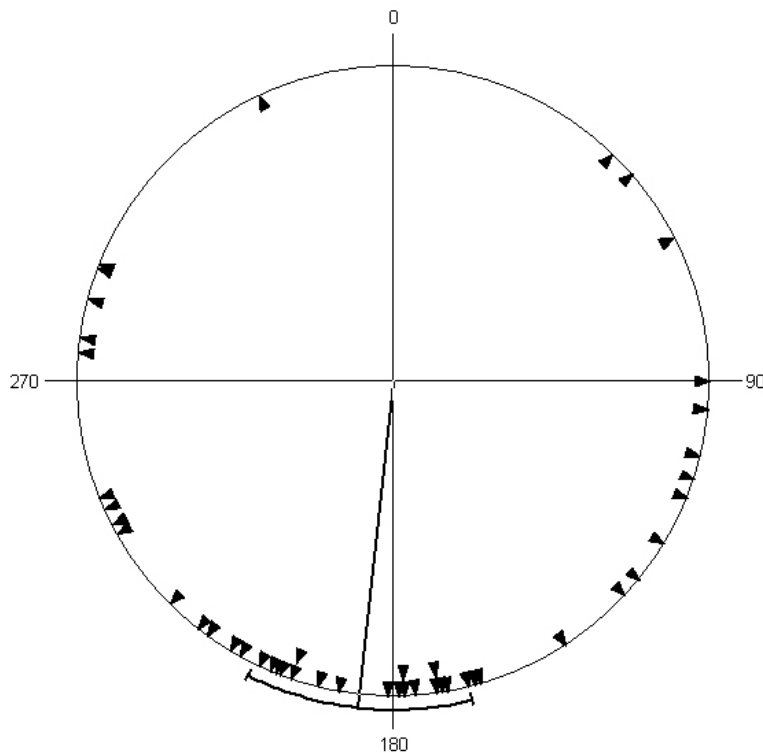


Fig. 3 Raw data plot of migration directions relative to nearest neighbour (n=47).

Brood samples

The brood composition of five migrating 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. Colonies essentially forage all the time day and night. When all the workers return on one trail, others are already starting a new raid to another direction. Colonies usually foraged along one trail but occasionally on two or three trails simultaneously. Swarm raid width was on average 10.3m (n=42, range 3.2-23.7m,

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

Colony	A'	E'	I'	H'	L'	C
Date	11.03.2003	14.02.2003	19.03.2003	30.03.2003	11.02.2003	11.02.2002
Migration after _ days	5	6	10	14	unknown	nest
N Brood items	1041	1080	416	298	1490	2054
% Brood category						
Pupae	87.6	89.3	92.8	98.3	52.3	58.9
Larvae	12.1	10.7	7.2	1.7	30.9	20.8
Eggs	0.3	0	0	0	16.8	20.3

median 8.7m). Swarm raids proceeded at a speed of 1.20 m per 10 min (± 0.28 SD, range 0.77 – 1.79 m/ 10 min, n=12) or 7.2 m per hour. Foraging trail length was on average 89.3 m (± 32.2 m, range 30.2-198.0 m, n=64). Applying the above model describing the relationship between straight line distance and trail length for migrations one obtains 70.1 m as the average foraging range. This is adequate because all migrations followed along previous foraging trails and thus the relationship between trail length and straight line distance should be identical for raids and migrations.

Behaviour during encounters

Direct encounters between foreign 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 spread-eagled by workers of the foreign colony in all these instances. No raids were ended as a result of the encounter but their courses diverted so as to allow both colonies to continue in their hunting or migration efforts. In 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 then retreated to their nest.

Discussion

Why do *Dorylus molestus* colonies migrate? Leroux (1982) observed several occasions on which *D. nigricans* colonies migrated in response to attacks by subterranean *D. (Typhlopone)* spp. Species of this subgenus have never been found at our site. 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. Elephants sometimes pass over *D. molestus* nests and may thereby damage their structure. However, we did not observe any colony which migrated soon after elephants had passed over its nest (n=3). Nests were sometimes attacked at night presumably by pangolins which dug holes into the nests from the side. On the next morning when we monitored the respective nests, these holes were filled with masses of large workers. In three cases did colonies migrate directly after the attack. As the colony whose nest we dug up to collect a brood sample also started to move away in the following night, we conclude that colonies do sometimes migrate away when their nests have been substantially damaged so that they would be very vulnerable to another attack. The fact that large numbers of large workers come regularly out of the nest at night and cover it in defensive posture as deterrence indicates that colonies may even especially prepare themselves in expectation of possible attacks. However, since we have observed only six cases of pangolin attacks throughout the entire study period, there must be another more significant reason for *D. molestus* to migrate.

Generally colonies send out at least one swarm raid every day with an average width of about 10 m. If raids are systematically arranged around the nest, then the whole area within a distance of 27 m and 62.5 % of the area within a distance of 70 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 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 70 m around the nest alone without interference from neighbouring colonies. Migration distances are about 34 % larger than normal foraging range. Colonies will thereby manage to reach areas that they had not exploited before even though the theoretical (circles with a 70 m radius centred on the nest) as well as the real foraging areas (determined by Gotwald and Cunnigham – van Someren 1990) will still overlap. Food

depletion is thus likely to be the ultimate cause for migrations in this species. This is further supported by the fact that colonies migrate away from their nearest neighbour, i.e. away from areas which will probably have been exploited most thoroughly recently. Colonies could achieve this by two mechanisms. It has been shown 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). If homebound workers retrieving food items lay an odour trail which will be used by outbound workers joining the swarm raid depending on pheromone concentration, then more workers will join the side of the swarm with a higher food density and thus cause a greater progress on that side. If colonies of *D. molestus* can in a similar way track gradients in food density, they will on the one hand explore and on the other hand finally migrate into areas of higher food density. The area between two colonies is likely to be exploited more thoroughly than others and would therefore be chosen as a new nest site relatively rarely or not at all. Alternatively it is conceivable that encounters with other colonies can somehow be used to as a cue to avoid certain directions when migrating. Encounters signal the presence of another colony and as other colonies exploit areas around them in the same way an encounter will directly indicate areas of low food density. Whether colonies use either of these mechanisms could be tested experimentally by manipulating the food density of areas and thus providing a stimulus for migrating. There is also the possibility that migrations can be caused by unfavourable nest conditions due to parasites. This idea is currently also debated as a possible reason for migrations of the leaf-cutting ant *Atta colombica* on Barro Colorado Island, Panama (Hubert Herz, Scott Powell, pers. comm..) and deserves further investigation.

If colonies avoid food depleted areas, one has to wonder why they end up with a new nearest neighbour that is just as close to them as their previous one has been. The most simple explanation would be that the habitat is so tightly packed with colonies that they cannot find any other less crowded areas. Moreover colonies are constrained in their migration decisions by a lack of information. In contrast to e.g. 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), 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' migrated away from its nearest neighbour G' but its new nest site K'3 is located just 34m away from the nest of colony I' which had migrated into that area just a day before and perhaps had not foraged in the area where K' decided to migrate into. Both colonies stayed so close to each

other for ten days before both migrated again away from each other on the same day (colony I' actually went back to its previous nest site).

If food depletion is the ultimate cause for migrating, when should colonies migrate? Certainly not every time they find an area rich in food resources, because then they will at times migrate unnecessarily often. The costs of migrations are difficult to estimate. Nest excavation is presumably an energetically costly undertaking and although colonies can continue to forage while migrating, fewer workers will be available for foraging and thus food intake will be reduced. But the greatest cost of migrating is probably the threat to the queen when she makes her way to the new nest and so high migration frequency should be disadvantageous. It has been suggested that the temporal migration pattern of *D. 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 migrating *D. molestus* colonies also indicate a link between brood composition a nest stay duration at first sight. However, the trend of increasing pupae proportion with nest stay duration is probably rather reflects inadequate sampling procedures. Larvae pupate after 26 days (*D. nigricans*, Leroux 1982) and so it is hard to understand why e.g. 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 one hour can easily produce confounded results. And indeed, for the colony whose brood was collected throughout the entire course of the migration we found brood of all stages in more equal proportions. While these data do not allow definite conclusions as to whether queens produce discrete broods or lay eggs continuously, it is however important to note that worker brood of all developmental stages can be transported at any time. That renders colonies mobile and enables them in general to move to a favourable area quickly after it is discovered.

In all these considerations it must be pointed out that the parameters prey density and prey population recovery time, colony density, colony size, foraging range, migration distances, and migration frequencies are tightly linked. Prey density and prey population recovery time are decisive factors in so far as they will ultimately determine the overall biomass density of army ant colonies. Colony density should be inversely proportional to colony size. The foraging pattern, i.e. the use of the area around the nest, dictates a certain migration pattern. If colonies forage with narrower swarm raids, this will increase their foraging range as swarm raid width and velocity are inversely proportional (Franks 1980, Leroux 1982). A colony

could thus stay in the nest longer as successive raids can be spaced with larger distances to each other. However, the colony would eventually also have to migrate further. On the other hand wider swarms reduce the foraging distance and will necessitate an earlier migration. So narrower swarm raids and consequently longer foraging distances should be favoured, if migrations are very costly, but then the (central place) foraging costs will be high. These theoretical considerations are supported by a comparison of the migration patterns of *D. nigricans* in Ivory Coast and *D. molestus* at Mt Kenya. Differences in foraging and migration parameters are probably due to habitat characteristics such as prey density, prey recovery time and costs associated with migrations. *Dorylus nigricans* colonies have larger swarm raid widths (mean 12 m, n=12, calculated from data given in table XI, p. 66, Leroux 1982) and comparatively shorter foraging distances (foraging trail length 59 m, Leroux 1982). *D. nigricans* colonies should thus exhaust the prey in their foraging range more quickly and then be forced to migrate earlier than *D. molestus*. On average *D. nigricans* colonies migrate every 8 days, while *D. molestus* colonies migrate on average only every 23 days. Furthermore, *D. nigricans* colonies migrate along trails of an average length of 112 m and so about exactly twice as far as they forage on average, while in the *D. molestus* population at Mt Kenya the ratio is much smaller than 2 (112.8 m vs. 89.3 m).

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 we assume that intraspecific competition is fierce. This seems even more likely if our interpretation is correct that the habitat is so tightly packed with colonies that they cannot find any other less crowded areas when migrating. 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 evolutionary stable strategy (Boswell et al. 2001). Neither *D. molestus* (Gotwald pers. communication, this study), nor *D. nigricans* (Leroux 1982) nor *D. wilverthi* (Ragnier & van Boven 1955) colonies do not fight each other under regular circumstances. Ragnier & 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. This behaviour was the exception rather than the rule (Leroux 1982) and so one has to conclude that epigaeic swarm raiding *Dorylus* species do in general not fight against conspecific colonies. The best strategy of colonies in a situation of extreme

competition for area and therefore food might be to locate areas of higher food density and exploit these before other colonies achieve this. Although they always reach areas with a new fierce competitor close by, the time factor may be decisive. So when colonies are forced to migrate, they must find good new patches and may then either luck out (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) with their decision. Because of their foraging mode which requires huge numbers of workers army ant colonies cannot maintain a territory. The only way they can secure exclusive access to close by food resources is to exploit them quickly themselves. Another possible explanation would be that colonies refrain from fighting because they have no way of knowing whether high their chances of success or alternatively peril are. Finally, the two colonies resulting from fission events do not appear to migrate away from each other and will therefore incidentally either move away from each other or meet again. If neighbouring colonies are closely related to each other, then engaging in a battle may mean to attack one's own offspring. *Formica pratensis* workers behave less aggressively to workers of more closely related colonies than to those of less related colonies (Beye et al. 1998). If the two colonies resulting from fission events stay in the same area battles between *D. molestus* colonies may be avoided because workers can recognize closely related workers in a similar way as *F. pratensis* workers.