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# DOES THE AFROTROPICAL ARMY ANT *DORYLUS* (*ANOMMA*) *MOLESTUS* GO EXTINCT IN FRAGMENTED FORESTS?

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## ABSTRACT

Swarm-raiding army ants are extremely polyphagous nomadic predators inhabiting tropical forests. They are considered keystone species because their raids can regulate the population dynamics of their prey and because a plethora of both invertebrate and vertebrate species are obligatorily or facultatively associated with them. Field observations and mathematical modelling suggest that deforestation and accompanying forest fragmentation cause local extinctions of the neotropical swarm-raiding army ant *Eciton burchellii* which in turn have negative effects on its associated fauna. The aim of this study was to examine whether afrotropical army ants are affected by forest fragmentation in the same way. Surveys of *Dorylus* (*Anomma*) *molestus* colonies were carried out in forest fragments of different sizes and in the matrix habitat at two sites in Eastern Kenya, along the Lower Tana River and in the Taita Hills. There was no significant relationship between the presence of *D. molestus*, forest patch size and distance to the nearest neighbouring patch at either of the sites. Colonies were often found outside the forest and can survive long enough in dry scrubland areas to reach new forest patches as far as 2 km away. We conclude that populations of this army ant species are less vulnerable to fragmentation than those of the neotropical *E. burchellii*, and that *D. molestus* can survive better in matrix habitat between forests because of several key differences in the foraging and nesting behaviour of the two species. Finally, we present a simple scenario describing the complex *D. molestus* population dynamics along the Lower Tana River and discuss the implications of our findings for conservation-oriented management of the two forest systems.

Keywords: Dorylinae, forest fragmentation, riverine forest, Tana River, Taita Hills.

## INTRODUCTION

Habitat loss is the major threat to biodiversity in tropical forests (Terborgh, 1992; Fahrig & Merriam, 1994; Laurance *et al.*, 2000). A compounding effect of this loss is the fragmentation of the once continuous forest areas (Fahrig, 2003). In forest fragments, important species interactions such as herbivory (Arnold & Asquith, 2002), seed dispersal and seedling recruitment (Cordeiro & Howe, 2003), predation (Wong *et al.*, 1998; Terborgh *et al.*, 2001) and pollination (Aizen & Feinsinger, 1994) are often altered compared to large continuous forest areas. Habitat loss inevitably results in populations of smaller size which are more susceptible to inbreeding, genetic erosion, and environmental and demographic stochasticity (Shaffer, 1981; Reed, 2005). Accordingly, some species go extinct in small forest patches, so that community composition is fundamentally affected by the size and distribution of habitat fragments (*e.g.* Beier *et al.*, 2002; Brühl *et al.*, 2003; Vasconcelos *et al.*, 2006).

Army ants are characterized by three defining traits: obligate group foraging, nomadism and highly specialised and permanently wingless queens. The aboveground foraging *Dorylus* (subgenus *Anomma*) species in tropical Africa (the “classic” African driver ants of legend and lore) and the neotropical army ants *Eciton burchellii* Westwood, 1842 and *Labidus praedator* F. Smith, 1858, have an extremely diverse food spectrum (Gotwald, 1995). Their conspicuous aboveground swarm raids can have a strong impact on prey populations (Otis *et al.*, 1986; Vieira & Höfer, 1994) and are believed to contribute to the maintenance of arthropod diversity in tropical forests by creating a mosaic of patches in different stages of recovery (Franks & Bossert, 1983). Predation by army ants in general may constitute an important factor in the evolution of nesting behaviour (Longino, 2005) and other life-history traits of leaf-litter ants (Kaspari & O’Donnell, 2003). Many invertebrate species (so-called myrmecophiles) are directly dependent on swarm-raiding army ants as their hosts (Gotwald, 1995), and some vertebrates such as kleptoparasitic birds (Willis & Oniki, 1978; Wrege *et al.*, 2005 and parasitic snakes of the genus *Typhlops* are similarly closely associated with them (Gotwald, 1995). Moreover, African army ants are an important food source for many mammals (aardvarks, chimpanzees, gorillas, honey badgers, mongooses, and pangolins; Kingdon, 1997) and may also play an important role as soil movers. For every nest built, *Dorylus* (*Anomma*) *molestus* Gerstäcker, 1859 colonies bring on average 34.4 kg of soil to the surface and this is augmented with the indigestible but presumably nutrient rich prey remains discarded by the ants over the period of their occupancy (Schöning *et al.*, 2005). Their triple importance as predators, prey and hosts for parasites and commensalists strongly suggests swarm-raiding army ants have keystone functions in tropical forest communities (Gotwald, 1995; Boswell *et al.*, 1998).

Swarm-raiding army ants are likely to be vulnerable to destruction and fragmentation of forests for a number of reasons. They are sensitive to high temperatures and desiccation (Meisel, 2006), so that they avoid direct sunlight and will only forage in unshaded areas during the day under cloudy or rainy conditions. They are therefore generally dependent on forest habitats. They operate at a high trophic level and consequently occur at low densities. Individual *E. burchellii* colonies require an area of about 30 ha to survive and grow (Franks, 1982). If colonies cannot grow to the minimum size to allow fission into two, they simply perish once their queen dies. This means that colonies in forests smaller than 30 ha need to utilise neighbouring patches as well, but these may be difficult to reach, if the matrix habitat is unsuitable for foraging and the nearest patch is further away than the maximum range of single emigrations. Moreover, army ants reproduce by colony fission. This reproductive mode further limits their dispersal capacity, so that the colonisation of distant patches separated from occupied forests by water or large areas of unsuitable terrestrial habitat is highly unlikely. Finally, young queens in an isolated and small population might experience fewer mating opportunities, so that genetic diversity among workers may diminish, which may reduce colony fitness and increase the risk of extinction. A reduction of mating opportunities would be important as young queens mate with many males (Kronauer *et al.*, 2004, 2006) and honeybee studies have shown that queen mating frequencies can be considerably lower on islands where mating conditions are less favourable (Neumann *et al.*, 1999).

The sensitivity of the neotropical species *E. burchellii* to forest fragmentation predicted on the basis of its natural history has been confirmed by mathematical modelling and field observations. The models suggested that isolated *E. burchellii* populations may indeed face high chances of extinction if they are confined to areas smaller than 300 ha (Partridge *et al.*, 1996), that the random removal of 45 percent of closed canopy forest habitat leads to population extinction and that the establishment of habitat corridors between patches may not be sufficient to ensure the continued survival of a population (Boswell *et al.*, 1998). During field observations, *E. burchellii* colonies were found to abandon 1 and 10 ha forest fragments (Bierregaard & Stouffer, 1997) and only to revisit patches that were connected to continuous forest by areas with a *Cecropia* canopy (Stouffer & Bierregaard, 1995). The disappearance of *E. burchellii* from forest patches or the extinction of an entire isolated population has direct negative consequences for associated ant-following birds (Stouffer & Bierregaard, 1995) and may also result in top-down extinction cascades (Ebenman & Jonsson, 2005). More recent studies found that *E. burchellii* occurs in shade-coffee plantations up to 2—3 km away from intact forest in Panama (Roberts *et al.*, 2000) and in small forest fragments linked to other forests by corridors in Costa Rica (Meisel, 2006), confirming that *E. burchellii* is vulnerable to fragmentation, but pointing to the usefulness of corridors in maintaining its presence in isolated forest patches.

The aim of the present study was to investigate whether and how afrotropical swarm-raiding *Dorylus* army ants are affected by forest fragmentation. We conducted surveys of *Dorylus* (*Anomma*) *molestus* at two sites in eastern Kenya. The Tana River floodplain supports a large number of small to medium size forest fragments of high conservation value in an otherwise semi-arid region. The few remaining forest fragments in the Taita Hills are also rich in biodiversity, but are located at a much higher altitude, receive more rain and are surrounded by a matrix of intensively used small-holder agricultural plots and plantations, which appears to be more suitable to support army ant colonies at least temporarily. We examined the presence of colonies in forest fragments differing in size and degree of isolation as well as their presence in matrix habitats to address the following questions: 1. Are small and isolated forests devoid of army ant colonies? If so, one would expect a significant correlation between army ant presence and forest fragment size and degree of isolation. 2. What is the minimum required forest size (MRFS) to support single *D. molestus* colonies? 3. Does the MRFS differ between the two sites? Since the matrix habitat is of apparently higher quality in the Taita Hills (the weather there is wetter and cooler making the matrix habitat more accessible for the ants), we expected that the MRFS would be smaller in the Taita Hills. 4. Can *D. molestus* colonies move between neighbouring forests, and if so, how far can these be apart before exchange becomes impossible? 5. Do *D. molestus* colonies survive outside forest fragments? We compare our results with data from studies on neotropical army ants and discuss potential underlying explanations for the observed differences.

## MATERIAL & METHODS

### Study sites

*Lower Tana River*

The Tana River is the longest river in Kenya (1012 km; Saha, 1982), flowing from the south-western flanks of the central massif of Mount Kenya to the Indian Ocean north of Malindi. The lower basin includes a stretch of river of approximately 625 km, while the delta occupies an area of about 3000 km$^2$ (Beck *et al.*, 1986). There is riverine forest along the banks of the Lower Tana River from Mbalambala to the delta at Kipini (Maingi & March, 2002), which is groundwater-dependent so that its extension is limited to 0.5 – 3 km on either side of the river. The driest part of the basin is around Garissa, with an average annual rainfall of about 300 mm, rising to 600 mm downstream at Garsen and > 1000 mm at the coast (Hughes, 1990). The research station where we were based during our fieldwork receives on average 582 mm of rain per year (unpublished data, KWS Research Camp Mchelelo). There are two rainy seasons, one from November to December and the other from March to June. Mean monthly temperatures in the lower basin are 22–34 °C, lowest during May–July and highest during January–February (Hughes, 1990). The river course is often changing and floods occur seasonally, resulting in the formation of isolated inland oxbow-lakes and a dynamic system of forest fragments drying up and gradually disappearing along the old riverbed and new ones being established along recently formed river banks. These natural succession dynamics and human activities (forest clearing for farming) have created a patchy distribution of forest vegetation (see figure 1 in Wahungu *et al.*, 2005), which can be classified into five types (Hughes, 1990). The matrix between the forests consists of drought–deciduous bushland dominated by thorny *Acacia-Commiphora* scrub with scattered annual grasses (Hughes, 1990). Together the forest patches thus form an isolated island of (semi-)evergreen forest in a semiarid habitat (Hamilton, 1974) and support a high number of endemic species (Burgess *et al.*, 1998). Wahungu *et al.* (2005) estimated that the Lower Tana River forest fragments have decreased in total area by 34.5 % between 1979 and 2000.

*Taita Hills*

The Taita Hills of south-eastern Kenya (including Sagala) cover an area of ca 250 km$^2$, rise to 2209 m, and are isolated from other highlands by ≥ 80 km of semi-arid plains in any direction (Lovett, 1985). Forest clearing for farming has left less than 400 ha of original indigenous cloud forest in three larger fragments and nine tiny remnants (see figure 1 in Galbusera *et al.*, 2004) embedded in a mosaic of human settlements, smallholder cultivation plots and plantations of exotic trees (Brooks *et al.*, 1998). As the northern-most extension of the Eastern Arc Mountains, the Taita Hills forest fragments harbour a highly diverse flora and fauna, including three endemic bird species (*e.g.* Brooks *et al.*, 1998). The annual rainfall in Wundanyi Town (at 1200 m) is 1329 mm and that in the hilltop forests probably exceeds 1500 mm, with monthly maxima in April and November (Beentje, 1987). Conditions are rather humid throughout the year due to the high elevation and cloud cover. The Taita Hills are divided into three distinct isolates (Bytebier, 2001): 1. The main hill complex is Dabida with the highest peak Vuria at 2209 m; 2. Mbololo, separated from Dabida by a narrow valley with scrubland vegetation at 900 m and rising to 1800 m, which supports the largest and most undisturbed forest fragment of the Taita Hills complex (178.8 ha); 3. Sagala, separated from Mbololo by the Voi River and *ca.* 15 km of dry plains (about 700 m), which rises up to an altitude of 1520 m and has a few scattered patches of indigenous forest within large plantation areas. Even further isolated (some 35 km to the south of Sagala) is

Mount Kasigau (1641 m altitude) with some 202 ha of indigenous forest.

### Study species

Originally described as a separate species by Gerstäcker in 1859, *D. (Anomma) molestus* currently has the status of a subspecies of *D. nigricans* Illiger, 1802 (Bolton, 1995). However, as will be shown in a forthcoming study (Schöning *et al.*, Revision of the African driver ants, in prep.), *D. molestus* is a species distinct from *D. nigricans* and will thus be treated here as such. It has a wide distribution in eastern Africa from Mozambique to Ethiopia (Schöning *et al.*, Revision of the African driver ants, in prep.). Gotwald (1974), Gotwald & Cunningham-van Someren (1990) and Schöning *et al.* (2005) provide further information on the emigration and foraging behaviour of this army ant species. Voucher specimens from both study sites have been deposited in the collection of the Zoological Museum of the University of Copenhagen.

### Surveys

Field work was conducted along the Lower Tana River in November 2005 and in the Taita Hills in December 2005. Eighteen (Tana River) and 15 (Taita Hills) natural and plantation forests were selected and systematically searched for the presence of *D. molestus* colonies. A team consisting of a researcher and two or three assistants walked slowly throughout each fragment, leaving no areas larger than 50 by 50 m unvisited, and carefully observed the ground for army ant trails, swarm raids and nests. Once a trail or swarm raid was found, we followed it to locate the nest site. At the nest, we took a worker sample for later identification and future reference. The surveys were carried out in the rainy season when foraging is generally more conspicuous with swarm raids also taking place in open unshaded areas. More prominent and persistent trail structures are constructed under rainy conditions, and these can be found up to several days after the ants used them, thus increasing our detection of colonies. Search effort was approximately proportional to area size, but since the aim of the survey was to establish presence or absence of colonies, more intense effort was focussed on patches where initial searches did not yield any colonies. In addition, we searched for *D. molestus* colonies in the habitats between forests, either opportunistically when walking or driving to the selected forest patches or purposely to determine army ant presence between forest fragments. As the activities of aboveground foraging army ant colonies are conspicuous and sometimes bothersome to humans, we also asked local residents for information on the location of colonies and we did in fact discover some colonies based on their responses. All nest locations were marked with a GPS receiver. In only two cases out of 80 did we not succeed in discovering the nest site after finding a trail. For all forest nests, we determined whether they were within 50 m of the forest edge. For this purpose, forest was defined as a wooded area composed mainly of trees taller than 10 m and with a canopy cover exceeding 50 % (Mbora & Meikle, 2004).

### Data analysis

To test whether colonies tend to be absent in smaller and more isolated forests at the two sites, we used logistic regression as implemented in the software package Statistica 6.0 with absence (0) / presence (1) as the dependent variable and forest size ($\log_{10}$-transformed) and distance to nearest forest patch with *D. molestus* present ($\log_{10}$-transformed) as predictor variables. The area sizes of Tana River forest fragments were obtained from Wahungu *et al.* (2005), who determined forest sizes in 2000. More recent data were not available for the forest patches under consideration. Distances to the nearest patch harbouring *D. molestus* were estimated from the map in Wahungu *et al.* (2005), but only between patches on the same side of the river, as water is an insurmountable barrier for colony movements. For colonies found outside forest areas, the distance of the nest to the river and to the nearest forest fragment was either measured directly with a metre tape or conservatively estimated after importing GPS data in Google Earth. Data on forest areas in the Taita Hills were obtained from a recently developed GIS model (F. Andriaensen, pers. comm.).

## RESULTS

All colonies found at both sites belonged to the species *D. molestus*. Altogether, 42 colonies were found along the Tana River, 24 in forests and 18 in matrix habitats. Fourteen colonies were found on the eastern side of the river, the remaining 28 on the western side. In addition, we discovered five very recently abandoned nest sites. Fourteen of the 18 examined forest patches harboured *D. molestus* (table 1). The relationship between *D. molestus* presence, forest fragment size and isolation was not significant (Overall logistic regression model, $X^2 = 4.15$, df = 2, p = 0.13; forest fragment 26 was excluded from the analysis because the nearest forest patch with *D. molestus* could not be established). The colonies in matrix habitats were on average 753 m away from the nearest forest (± 596 m SD, range 80 – 2000 m) and 1323 m away from the river (± 1195 m SD, range 60 – 3250 m).

*Table 1.* Dorylus molestus *occurrence in forests along the Lower Tana River. Forest patch names and data on patch size were obtained from Wahungu* et al. *(2005).*

| Forest patch | Search effort (man x hours) | Size (ha) | *D. molestus* colonies found | Nests within 50m of forest edge | Nearest patch with *D. molestus* on same river side (distance in m) |
|---|---|---|---|---|---|
| 2a, 2b, 2c | 21 | 534 | 4 | 2 / 4 | 5 (750) |
| 3a | 6 | 37.4 | 0 | - | 4a (900) |
| 3b | 4.5 | 14.8 | 0 | - | 4a (300) |
| 4a | 4.5 | 30.9 | 2 | 2 / 2 | 4b (300) |
| 4b | 3 | 4.1 | 1 | 1 / 1 | 4a (300) |
| 5a, 5b | 12 | 54.3 | 3 | 3 / 3 | 2a, 2b, 2c (600) |
| 6 | 3 | 68.2 | 2 | 2 / 2 | 4b (300) |
| 7 | 6 | 48.4 | 0 | - | 5a, 5b (300) |
| 8 | 6 | 19.2 | 1 | 1 / 1 | 9 (300) |
| 9 | 6 | 17.1 | 0* | 1 / 1 | 8 (300) |
| 10a | 9 | 6.9 | 2 | 2 / 2 | 10b (300) |
| 10b | 13.5 | 90.7 | 2 | 2 / 2 | 11, 17 (50) |
| 11, 17 | 18 | 207.8 | 0* | 1 / 1 | 10b (50) |
| 12 | 6 | 11.2 | 1 | 1 / 1 | 16 (50) |
| 15 | 3 | 12.3 | 1 | 1 / 1 | 11, 17 (145) |
| 16 | 9 | 262.8 | 3 | 0 / 3 | 12 (50) |
| 26 | 6 | 60.3 | 2 | 2 / 2 | ? |
| 27 | 7.5 | 27.7 | 0 | - | 26 (510) |
| TOTAL | 144 | 1508.1 | 24 | 19 / 24 | - |

* no colonies found, but very recently abandoned nests indicated *D. molestus* presence.

At one of the colonies in the matrix habitat we saw signs of a recent attack on the nest by the subterranean army ant *D. (Typhlopone)* sp. Numerous dead workers of the two species had been discarded on the refuse pile in lethal embrace (voucher specimens also deposited in the collection of the Zoological Museum, University of Copenhagen). We found no signs of ongoing fighting but the colony was emigrating, perhaps in response to the attack. Such attacks by *D.* (*Typhlopone*) species on *D.* (*Anomma*) colonies can result in the death of the attacked colony and had previously only been seen in West Africa (Leroux, 1982). As *D.* (*Typhlopone*) are known mostly from savannah habitats (*e.g.* Bodot, 1967; Darlington, 1985), we subsequently tested the hypothesis that *D. molestus* colonies suffer higher predation levels in matrix habitat. For all the *D. molestus* nests that we found after this observation as well as some previously located nests that were easy to reach, we carefully examined the refuse pile for dead *D.* (*Typhlopone*) workers. We found that the occurrence of *D.* (*Typhlopone*) workers in refuse piles did not differ between colonies nesting in forest and those nesting in matrix habitat (Fisher's Exact Test, one-tailed, 2/12 in matrix nests vs. 0/5 in forest nests, $p = 0.49$).

In the Taita Hills we found 36 *D. molestus* colonies, 17 in forest areas and 19 in the matrix habitats, as well as three recently used nests (table 2). All of the examined forests contained *D. molestus*, except for two that had burnt recently (Mwambirwa in September 2005, Choke in October 2005). Colonies were also not found in any other of the forest areas that had burnt recently (*e.g.* part of the Kinyeshamvua plantation forest), suggesting that colonies die in fires. Since there was no variation in the dependent presence/absence variable, there was no indication that fragmentation or patch isolation had any effect. Dedicated searches in the dry savannah area in the Paranga valley between Dabida Massif and the Mbololo Massif yielded two colonies (at 998 and 1089 m). One other colony was found at the base of the Dabida massif close to the dam in Mwatate (846 m asl). One more colony and a recently abandoned nest were further discovered in forest areas when climbing Mount Kasigau.

*Table 2.* Dorylus molestus *occurrence in natural forests and plantations in the Taita Hills and Kasigau. Data on forest patch size were provided by Frank Adriaensen (Animal Ecology Research group, University of Antwerp, Belgium).*

| Forest patch | Hill | Search effort (men x hours) | Size (ha) | Colonies found | Nests within 50m of forest edge |
|---|---|---|---|---|---|
| Natural forests | | | | | |
| Chawia | Dabida | 6 | 93.6 | 1 | 1 / 1 |
| Choke [B] | Dabida | 10 | 73.5* | 0 | - |
| Fururu | Dabida | 6 | 8.4 | 2 | 0 / 2 |
| Kasigau | Kasigau | 8 | 202.3* | 1 | 0 / 1 |
| Macha | Dabida | 4.5 | 1.7 | 1 | 1 / 1 |
| Mbololo | Mbololo | 8 | 178.8 | 2 | 2 / 2 |
| Mwachora | Dabida | 4.5 | 2.1 | 1 | 1 / 1 |
| Ngangao | Dabida | 26 | 135.9 | 1 | 0 / 1 |
| Ndiwenyi | Dabida | 3 | 4.2 | 1 | 1 / 1 |
| Iyale | Dabida | 7.5 | 22.3 | 2 | 0 / 2 |
| Plantation forests | | | | | |
| Kinyeshamvua | Dabida | 12 | 54.1 | 1 | 0 / 1 |
| Wesu Rock | Dabida | 3 | 19.3 | 1 | 1 / 1 |
| Mwambirwa [B] | Mbololo | 3 | 148.0 | 0 | - |
| Sagala | Sagala | 6 | 70* | 2 | 0 / 2 |
| Vuria | Dabida | 12 | 105.2 | 1 | 0 / 1 |
| TOTAL | | 119.5 | 1119.4 | 17 | 7 / 17 |

[B] Forest was recently burnt. * Another data source: Forest Department, Wundanyi.

The *D.* (*Typhlopone*) species attacking *D. molestus* colonies along the Tana River also occurs in the Taita Hills area. We found foraging workers in the drier bushland areas on the lower slopes, but there were no signs of recent attacks by these subterranean army ants at any of the discovered *D. molestus* nests.

Along the Tana River, only colonies in forest areas foraged during the day when the weather was dry. Colonies in matrix habitats were then restricted to nocturnal foraging and were often found retreating to the nest in the morning hours (before 09:00 h; see figure 1). Under rainy or cloudy conditions we also saw colonies foraging in the matrix habitat during the day. In the Taita Hills, the situation was essentially the same but since the matrix habitat is much more complex in terms of vegetation structure, temperatures are lower, and cloud cover was more frequent, a larger proportion of colonies in matrix habitat foraged during the day under dry conditions.

Figure 1. *A foraging trail of* Dorylus (Anomma) molestus *in the dry scrubland along the Lower Tana River. This picture was taken early in the morning when the ants were all returning to the nest (see arrow for ant trail).*

## DISCUSSION

### Persistence of *Dorylus molestus* in forest fragments and matrix habitat

The surveys showed that the swarm-raiding army ant *D. molestus* is not strictly dependent on forest habitat at either of the two study sites. This finding has important implications for the viability of populations in heterogeneous landscapes with fragmented forests. As expected for a species not restricted to forests, the occurrence of *D. molestus* across forest fragments was not related to forest patch size and isolation and the minimum required forest patch size was effectively zero at both sites.

Within the examined forests, *D. molestus* army ants often built nests in edge areas, but it is unclear whether this is the result of active preference or an epiphenomenon, because a large proportion of small forest patches is automatically within 50 m of the edge when typical habitats are narrow strips along river beds. For example, in a 5 ha forest patch of circular shape the proportion of edge habitat would be 64 % (48, 23 and 8 % in circular patches of 10, 50 and 500 ha, respectively). However, most forest patches along the Lower Tana River have an elongated or irregular shape, because the extension of forest along the river is constrained by the ground water table and substantial forest clearing has further fragmented these forest strips. The real edge area proportions may thus be much higher than the ones calculated for circular patches. The frequent observations of colonies in edge areas do show, however, that *D. molestus* does not avoid the drier and warmer conditions of edge areas. More importantly, the species has now been documented to occur in the entire highly diverse spectrum of matrix habitats, ranging from dry scrubland close to the coast to smallholder agricultural and agroforestry plots with mixed crops in high altitude regions. This ecological flexibility of *D. molestus* was also borne out in a study on emigration behaviour by Gotwald & Cunningham–van Someren (1990). The movements of one colony were followed over a period of 432 days, in which it nested frequently in grassland and agricultural plots but only rarely in the close-by forest areas (see *Figure*. 4.14 in Gotwald, 1995). Other *D.* (*Anomma*) species are also known to use non-forest habitats. Raignier & van Boven (1955) found *D. wilverthi* Emery, 1899, in primary and secondary forest as well as in coffee and cacao plantations. Leroux (1982) reported the presence of *D. nigricans* in savannah habitat at Lamto (Ivory Coast) and Schöning *et al.* (in press) also found *D. rufescens* Santschi, 1915, in savannah habitat, but both sites receive at least twice as much rainfall annually as the Tana River area [1300 mm at Lamto (Menaut & Cesar, 1979) and 1826 mm at Gashaka (Sommer *et al.*, 2004) *vs*. 582 mm along the Tana River]. There is a drawing in Hölldobler & Wilson (1994, p. 109) that indicates the presence of *D.* (*Anomma*) in very dry East African savannah habitat, but this illustration was not based on actual observations (B. Hölldobler, pers. comm.). Thus, the observations made along the Lower Tana River are remarkable in that they extend the range of habitats known to support swarm-raiding afrotropical army ants. The presence of *D. molestus* in dry scrubland was highly surprising, since the elaborate mobilisation of hundreds of thousands or millions of swarm-raiding workers can only be efficient when prey densities are high. We found *D. molestus* colonies nesting in areas with almost bare ground and little shade where densities of available arthropod prey were presumably low and species adapted to foraging in hot and dry conditions like *Ocymyrmex nitidulus* Emery, 1892 were regular elements of the ant community.

Our discovery of *D. molestus* nests in several non-forest habitats in this study raises several interesting questions. Were those colonies restricted to nocturnal foraging in areas with low prey densities simply “dwindling into oblivion” after leaving the forest fragments? Along the Tana River, colonies can occur as far as 2 km away from the next forest patch. Unlike birds or large mammals, army ants would appear to be unable to direct their movements towards distant forest areas and to rely on finding these by chance. However, the large average distance of matrix-habitat colonies from the nearest forest (larger than the length of eight emigrations in a continuous forest population at Mount Kenya; Schöning *et al.*, 2005) attests to the ability of colonies to disperse and survive in matrix habitat long enough to reach neighbouring forest fragments (which are usually less than 1 km away).

Furthermore, nest size, swarm raid width and trail length did not indicate that colonies nesting in the matrix were particularly small (C. Schöning, pers. obs.). Due to the lower temperatures, higher humidity and generally more suitable matrix habitat (more shade and more complex vegetation structure) in the Taita Hills, colonies at that site can probably survive and disperse even better outside the forest than those along the Tana River. Are the populations at both sites actually declining slowly and has the equilibrium state simply not yet been reached (compare Brooks *et al.*, 1999)? This scenario cannot be ruled out (especially along the Tana River), but seems unlikely, as forests have been cleared and fragmented for a long time: an estimated 56 % of the Tana River forest area was lost between 1960 and 1985 (Decker, 1994) and extensive indigenous forest areas in the Taita Hills were transformed into agricultural plots already before the 1940's (Brooks *et al.*, 1998). The fact that this long history of ongoing forest fragmentation has not resulted in significant extinctions of local *D. molestus* populations suggests that the present metapopulations are still viable; however, further work should evaluate whether overall densities may have declined and if genetic erosion may have taken place, especially in the Tana River area.

Results of more limited surveys in other areas of Kenya show that *D. molestus* is not entirely independent of forest habitat and that populations can probably only persist in a region as long as the proportion of forest or highly favourable matrix habitat with closed canopy exceeds a certain threshold. Careful extensive searches at Kajiado (a savannah site between Nairobi and the Tanzanian border) did not yield any colonies (C. Schöning, pers. obs.). Another area devoid of *D.* (*Anomma*) is the large Marsabit forest (152 km$^2$; Gachanja *et al.*, 2001), which covers a young volcanic mountain in northern Kenya isolated from other forests by more than 80 km in all directions (C. Schöning, pers. obs.). The area around the mountain appears too dry to be inhabitable for *D. molestus*, so that this forest was probably never successfully colonised from neighbouring populations.

Our results support the general contention that different taxa may respond to forest fragmentation in different ways depending on their ability to traverse or live in matrix habitats between forest fragments (Marshall *et al.*, 2006). For example, in the Taita Hills Galbusera *et al.* (2004) found that the genetic diversity of the bird *Pogonocichla stellata* Vieillot, 1818, which disperses easily between forests and can use the matrix habitat to some extent (V. Lehouck & T. Spanhove, pers. comm.), is higher than the genetic diversity of the Taita thrush *Turdus helleri* Mearns, 1913 whose dispersal capacity is much more limited. Whether other afrotropical army ants respond to forest fragmentation in other ways than *D. molestus,* remains to be investigated.

### Comparing the vulnerability of *Eciton burchellii* and *Dorylus molestus* to forest fragmentation

Essentially all swarm-raiding army ants appear to be sensitive to high temperatures, low humidity and direct exposure to strong sunlight (Roberts *et al.*, 2000; Meisel, 2006; S. Powell, pers. comm.; C. Schöning, pers. obs.), so that open areas outside forests might always be less accessible for their diurnal raids. Swarm-raiding army ants must hunt daily to feed themselves and their brood, because they cannot store food (Schöning & Moffett, in press). This precludes holding out in the nest over prolonged periods of time when conditions are unsuitable for foraging. Like all other army ants, swarm-raiding species reproduce through colony fission and new nest sites are found during raids, so that dispersal of all swarm-raiding army ants can be expected to be constrained by the same factors and in very similar ways. However, the results presented here suggest that *D. molestus* is less negatively affected by habitat fragmentation than the neotropical *E. burchellii*. First, *E. burchellii* has not been reported to nest in areas without a closed canopy (*i.e.* natural or plantation forests or shade-coffee plantations). Second, *E. burchellii* does not reach forest patches that are not connected to other forest areas by corridors or that are separated by unsuitable habitat for distances exceeding a single emigration distance. In contrast, the African *D. molestus* can apparently survive in and disperse through matrix habitats due to a number of special characteristics of its foraging and nesting behaviour (table 3). This species nests up to 1.20 m deep in the soil (Schöning *et al.*, 2005; C. Schöning, pers. obs.), which appears to be an efficient protection against drying out in the extreme heat and low humidity of the dry season in the matrix habitat at the Lower Tana River. While the bivouac-forming *E. burchellii* has not been reported from altitudes above 1800 m (Roberts *et al.*, 2000), *D. molestus* colonies at Mount Kenya occur up to an altitude of 2950 m (Schöning & Kinuthia, in review) where night temperatures can drop below 0 °C in the dry season, suggesting that subterranean nesting also protects *D. molestus* colonies against these kinds of environmental extremes. Moreover, *E. burchellii* requires logs to form bivouacs and might thus simply be nest-site limited in open matrix habitats (Roberts *et al.*, 2000). Since *E. burchellii* is constrained to hunt during the day and to emigrate at night at least during the nomadic phase, it can generally not use dry and open habitats where foraging is often only possible during the night. Finally, the minimum area required by a single colony of *D. molestus* is lower than for *E. burchellii*, because prey populations recover more quickly to initial densities after a raid (Franks, 2001). Hence, *D. molestus* colonies might persist in small forest fragments (< 5 ha) for long periods of time without being forced to leave under unfavourable conditions. This suite of characteristics appears to make *D. molestus* populations more robust against adverse effects of moderate deforestation and fragmentation.

*Table 3. Differences between* E. burchellii *and* D. molestus *thought to be relevant for their ability to survive in fragmented forest landscape (based on information in Franks, 1980, 1982; Gotwald, 1995; Leroux, 1982; Roberts* et al.*, 2000; Schöning* et al.*, 2005).*

| Trait | *Eciton burchellii* | *Dorylus molestus* |
|---|---|---|
| Nest | bivouac (exposed or hidden in log / tree cavity) | subterranean |
| Foraging time | day | anytime, continuous when conditions are favourable |
| Emigration time | night | anytime, continuous when conditions are favourable |
| Emigration pattern | stereotypic reproductive cycle consisting of a 16 day nomadic phase and a 20 day statary phase | irregular |
| Food spectrum | Diverse, but social Hymenoptera make up 50 % of food items | Diverse, social insects play a minor role |
| Area requirement | large: maximum only 3.2 colonies/km$^2$ | small: 30.1 colonies/km$^2$ have been observed for similar *D.* (*Anomma*) species |

### Army ant population dynamics along the Lower Tana River

The matrix habitat along the Lower Tana River is the driest habitat known to support epigaeic afrotropical army ants. We propose that the following key factors determine the population dynamics at this site, and given our limited data set to permit analyses to address these ideas, we suggest that these be avenues for further research. First, the river represents an insurmountable barrier to colony movements. The large males can probably disperse over long distances (many kilometers) and easily fly across the river and mate with queens on the opposite side. Female gene flow, by contrast, is in the form of whole colony dispersal by walking, and is therefore much more restricted. Within their life-time, colonies will probably move over distances that are much shorter than male flying distances. Moreover, whole colonies cannot cross the river except for the very rare chance event of a colony finding itself on the opposite side of the river after the river has changed its course. Second, recurrent floods probably cause local extinctions of army ant colonies close to the river. The construction of five upstream dams has reduced the frequency of high floods since 1988 (Maingi & Marsh, 2002) but they still occur and water levels may rise 3 m above ground level in forest close to the river (A. Gafo, pers. comm.). Due to their nesting behaviour, *D. molestus* colonies are unlikely to survive such floods by rafting. Third, matrix habitat is mostly unsuitable for diurnal foraging under dry conditions and prey densities are presumably much lower than those in forest areas. Both factors combined probably lead to lower colony densities and lower prey intake rates by colonies in matrix habitat. Reduced prey intake rates are in turn likely to result in lower growth rates and ultimately in reduced fitness of colonies confined to matrix habitat. Fourth, the growth rates of matrix colonies are likely to be further reduced and their mortality rates increased if predation on colonies by *D.* (*Typhlopone*) would be more frequent in matrix areas. We did not detect a significant trend in this regard, but our sample size was very small. Fifth, reproduction rates are generally low in army ants. Leroux (1982) estimated that *D. nigricans* colonies may fission only approximately once every two years.

Assuming that these key factors can predict basic patterns in the population dynamics, we expect that local colony birth rates may exceed death rates in forest fragments with the surplus dispersing into matrix habitat where death rates might exceed birth rates. Matrix habitat would thus act as a net "sink" (Pulliam, 1988). In the dry season or in years with very dry conditions throughout, the difference between birth and death rates might be larger than in the rainy season or in years with more favourable weather. Recurrent periods of exceptionally severe weather might then ultimately limit the distribution of this army ant species, because only colonies in forest or forest fragments might be able to survive in years with extremely adverse weather conditions. This would explain why the species is limited to landscapes with a yet undetermined critical threshold proportion of forest habitat as suggested by the observations at other sites in Kenya.

If floods result in the death of colonies in forest habitat close to the Tana River, this habitat devoid of colonies might be recolonised by matrix colonies, thus reversing the normal source-sink dynamics. Alternatively, these "empty" forest patches devoid of army ant colonies might be recolonised by colonies from neighbouring forest patches. Assuming that colonies cannot detect high quality habitat until they reach it during foraging, recolonisation can only take place by "diffusion" and is likely to be slow, especially if the flooded area was large. This implies that it might take several years until a vacant forest is occupied by the maximum number of colonies that it can support, which would explain why some large forests were not occupied (table 1). It would be interesting to investigate, however, whether the assumption of random migration in matrix habitat is indeed valid, because any adaptation to detect forest fragments over larger distances for example via an ability to detect air-humidity gradients would allow much more predictable and efficient migrations across unfavourable habitat. Regardless of whether forests cleared by flooding are colonised by matrix colonies or colonies from neighbouring forests, flooding may cause recurrent bottlenecks in the genetic population structure. The genetic diversity of the Tana River *D. molestus* population might therefore be expected to be rather low.

### Management implications

The ecological flexibility of *D. molestus* makes this army ant apparently resilient to the adverse effects of forest fragmentation. It is still widely distributed in forests and non-forest habitats at the Tana River as well as in the Taita Hills. However, further clearing of forests and burning of forests and matrix areas may reduce population sizes below critical values, especially along the Tana River. We therefore suggest measures to control further forest destruction at both sites.

*Dorylus molestus* is known to support a rich myrmecophile fauna (*e.g.* Kistner, 1982) and several East African bird species have been observed to attend its swarm raids (*Neocossyphus rufus* Fischer & Reichenow, 1884, *Alethe fuelleborni* Reichenow, 1900, *A. poliocephala* Bonaparte, 1850, *Sheppardia lowei* Grant & Mackworth-Praed, 1941, *S. aurantiithorax* Beresford, Fjeldså, & Kiure, 2004, and *S. montana* Reichenow, 1907; see Keith *et al.*, 1992; J. Fieldså, pers. comm.; C. Schöning, pers. obs.). Furthermore, predation by *D. molestus* might help maintain arthropod diversity by the same mechanism that has been suggested for the neotropical *E. burchellii* (Franks & Bossert, 1983). Thus, for management purposes, obtaining quantitative data on the relationships between *D. molestus* and other organisms in East African forest ecosystems should be considered a priority. This is because if species are greatly dependent on *D. molestus* (such as many myrmecophiles; Kistner 1982), then a potential local extinction of *D. molestus* might result in the demise of the local populations of associated species.

Finally, the observed ecological flexibility makes *D. molestus* also an ideal candidate species to be targeted for conservation in certain types of agroecosystems. As long as some canopy shade is available and the vegetation structure is sufficiently complex to provide enough prey and favourable microclimatic conditions, *D. molestus* colonies can apparently survive in agricultural plots. However, from the perspective of resident farmers it would be desirable to know whether army ant colonies provide economic advantages rather than merely supporting a rich associated myrmceophile fauna. In particular, it would be important to find out whether swarm-raiding army ants are useful biocontrol agents and how negative effects of their foraging activities such as attacks on humans and livestock (*e.g.* cattle, chickens and honeybees) can be avoided.

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