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Crematogaster chiarinii ants as a potential biological control agent for protecting honeybee colonies from attack by *Dorylus quadratus* driver ants in Ethiopia (Hymenoptera: Formicidae)

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Abstract

1 Driver ants of the genus *Dorylus* are well known across tropical Africa for their aggressive foraging swarms. Although these swarms have beneficial effects in clearing out invertebrate pests; they destroy thousands of honeybee colonies and, accordingly, cause significant economic losses.

2 Fear of driver ant attack leads most beekeepers in tropical Africa to hang their beehives high up on trees, making proper bee management difficult and limiting the involvement of women and the elderly.

3 In Ethiopia, forest beekeepers have recognized that beehives hung on trees containing nests of an arboreal ant *Crematogaster chiarinii* Emery 1881 remain safe from invasion by swarms of a driver ant *Dorylus quadratus* Santschi 1914. In the present study, we report investigations into the mode and efficacy of the *C. chiarinii* defence system, as well as the potential for increasing its populations and enhancing this biological protection.

Keywords Bee-keeping, biological control, *Crematogaster chiarinii*, *Dorylus quadratus*, Ethiopia, interspecies competition.

Introduction

Ants have colonized almost every place on earth and are reported to thrive in most ecosystems, amounting to 15–25% of the terrestrial animal biomass (Schultz, 2000). The significant role of ants in terrestrial ecosystems is well recognized (Holway *et al.*, 2002), including as important biological control agents for agricultural pests (Way & Khoo, 1992; Philpott & Armbrecht, 2006), in soil improvement and in nutrient cycling (Gotwald, 1986; Frouz & Jilkovà, 2008). Although some ant species are beneficial, many others cause economic losses by disrupting ecosystems; attacking beneficial insects; tending sap-sucking insects, which directly damage the host plants and may act as vectors of plant diseases; and attacking humans and domestic animals (Adams *et al.*, 1976; Robinson, 1982; Vinson, 1986; Adjare, 1990; Banks *et al.*, 1990; Vander Meer *et al.*, 1990; Buczkowski & Bennett, 2008).

In the tropics, particularly in Africa, honeybee pests are more serious and economically important than honeybee diseases. The most damaging pests are ants and many species are known to attack honeybees in various countries from the northern Maghreb through to southern Africa (Adjare, 1990; Hepburn & Radloff, 1998). Ants are reported to be the most serious and widespread natural enemies of honeybees in Sudan (El-Niweiri *et al.*, 2004) and in Uganda (Kajobe *et al.*, 2009). Additionally, persistent attack by ants has been reported as an important cause of the absconding of honeybee colonies (Hepburn & Radloff, 1998; Rachna & Kaushik, 2004; Desalegn, 2007).

As well as the general reports outlined above, Driver or Safari ants, *Dorylus* (*Anomma*) species, have been described as the greatest natural enemy of honeybees in Africa (Robinson, 1982; Adjare, 1990). In Ethiopia, numerous survey and research studies have reported that driver ants are more serious than any other honeybee enemies and pests (Desalegn, 2001; Desalegn & Amsalu, 2001; Keralem, 2005; Tesfaye & Tesfaye, 2007; Solomon, 2009; Arse *et al.*, 2010; Kinati *et al.*, 2012; Shenkute *et al.*, 2012). Desalegn (2007) estimated the annual losses of honey and bee colonies as a result of driver ant attack in the West Shewa Zone of Ethiopia to exceed $2 50 000 per year.

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Driver ants of the genus *Dorylus* are notorious for their surreptitious raids on honeybee colonies by making tunnels from their temporary nest (or bivouac) to the apiary. The ants may even nest underground within the apiary and periodically raid honeybee colonies. The ants can destroy all bee colonies in an apiary, carrying off all brood and stores in a matter of hours (Dubois & Collart, 1950; Robinson, 1982). Because hot dry conditions diminish the activities of many ant species (Adams & Tschinkel, 1995), driver ants mostly prefer to hunt at night and can destroy 20–30 bee colonies overnight in a single apiary (A. Nuru, personal observation). Honeybees may attempt to defend their nests from ant attacks by making clusters at the hive entrance, and using strong wing-fanning to push back the invaders (Rachna & Kaushik, 2004). However, when the hive entrances are large, the covers improperly fitted or the hives have cracks, the ants are able to invade from different directions, overwhelming the bee colonies. Once the ants gain entry, they kill and carry off the brood and adult bees, including the queen. In tropical Africa, apiaries commonly have to be guarded from driver ant attack day and night throughout the year, a task that is more expensive than any other cost of apiary and colony maintenance.

In those countries where driver ants are common, commercial bee farms, backyard beekeeping and the use of box hives, which involve placing hives on the ground, have all been deterred by a fear of driver ants, and beekeepers are forced to hang their traditional and even wooden box hives on the branches of trees (Fig. 1), which makes it difficult to manage the hives properly.

Various cultural practices and mechanical ant-barrier methods have been used to minimize the driver ant invasions to honeybees. However, none of these methods are perfect in protecting the honeybee colonies, and it is generally considered virtually impossible to identify a foolproof way of protecting bees from ants (BfD, 2012). Driver ants are capable of crossing many physical barriers; for example, they can cross narrow water bodies by clinging each other and making bridges to allow their fellows to pass over them. Similarly, if the hives are suspended, the ants attempt to climb nearby objects and gain access to the hives by dropping from above.

Thus, it is very important to seek alternative methods for controlling or minimizing the attacks of ants on honey bees. Biological control methods are among the possible options for combating ant attack. A number of ant species are well documented as important agents in the biological control of undesirable pests (Philpott & Armbrecht, 2006). Way and Khoo (1992) listed several such species from seven genera (*Oecophylla*, *Dolichoderus*, *Anoplolepis*, *Wasmannia*, *Azteca*, *Solenopsis* and *Formica*). *Oecophylla smaragdina* (F.) has been widely used in biological control of citrus fruit insect pests in China ever since ancient times (Huang & Yang, 1987). It also has been observed as an effective pest controlling agent on Mango orchards in Australia (Peng & Christian, 2005), citrus plantations in South East Asia (Offenberg *et al.*, 2013) and palm oil trees in Malaysia (Pierre & Idris, 2013). Similarly, in the Neotropics, *Azteca delpini* Emery has been used as a potential biological control against citrus pests (Jaffe *et al.*, 1990) and coffee pests (Vandermeer *et al.*, 2002).

Ant interspecific aggression also is well known; for example, between *Linepithema humile* (Mayr) and *Tapinoma sessile* (Say) (Buczkowski & Bennett, 2008); between *L. humile* and *Pogonomyrmex subnitidus* (Zee & Holway, 2006); and between *Azteca* ant species and leaf-cutter ants (Overall & Posey, 1984). Generally, the defence of foraging territories and intra- and interspecific disputes among different ants is well documented (Adams, 1990, 1998; Tschinkel *et al.*, 1995). Fighting over territory and resources is also well recognized (Hölldobler & Wilson, 1977; Hölldobler & Lumsden, 1980; Hölldobler, 1983; Hölldobler & Wilson, 1990; Franks & Partridge, 1993, Sakata & Katayama, 2001; Tanner, 2006) and such behaviour can be used for the biological control of undesirable ants.

In Cameroon, dominant arboreal *Crematogaster* ants are well known for their rapid hunting workers that collectively forage and capture small to large prey by spread-eagling and depositing venom on the prey body (Richard *et al.*, 2001). The genus is also known for its rapid nest mate recruitment, as well as its aggressive and territorial behaviours (Longino, 2003), which are attributes that can be utilized well as potential biological control agents against undesirable pests.

Figure 1 Bee colonies hung on branches of trees to prevent driver ant attack.

Figure 2 Carton nests of *Crematogaster chiarinii* on trees approximately 5 m above the ground.

The Sheka community of South West Ethiopia, particularly the forest beekeepers, use the arboreal *Crematogaster chiarinii* to protect honeybee colonies from *Dorylus quadratus* attacks by hanging their bee hives selectively on forest trees where these ant nests are found (Fig. 2). Before the present study, however, how and why honeybee colonies near *C. chiarinii* nests remain safe and the potential of *C. chiarinii* as a biological control agent against *D. quadratus* had not been studied. Nothing was known of the level of aggressive interaction between the two ants, nor how *C. chiarinii* defends its territory. Thus, we investigated the nature of conflict between the species; the form of the aggressive reactions; how wide an area of apiary or how many hives can be protected by a single *C. chiarinii* colony; and possible ways of artificial propagation of *C. chiarinii* colonies.

Materials and methods

Study sites

The experiment was conducted at two locations in South West Ethiopia between 2010 and 2012. These were Sheka Zone at Masha (7°43′24.79′′N, 35°29′03.64′′E), at an altitude of 1971 m, and Kaffa Zone at Bonga (7°16′48.82′′N, 36°14′25.7′′E), at an altitude of 1860 m. Both comprise areas of mixed arable farming and woodland, including much relict primary tropical forest, and both receive a relatively high (2000 mm) annual rainfall (Chernet, 2008).

Ant identities

The two species of ant in the present study, *Dorylus* (*Anomma*) *quadratus* Santschi 1914, type location Tanzania, and *Crematogaster* (*Crematogaster*) *chiarinii* Emery 1881, type location Ethiopia, were identified by one of us (Brian Taylor; BT). The generic determination was straightforward using keys developed by Bolton (1995) and enhanced by Taylor (2014). Neither *Dorylus*, nor *Crematogaster* have fully researched modern keys but BT has examined all the available literature. The *Dorylus* is a very close match, if not identical, to the original Santschi description. Our specimens (Fig. 4) match the type worker of *C. chiarinii* (http://www.antweb.org/specimen.do?name=casent0904518). Full taxonomic information is available on the Taylor website (Taylor, 2014). The specimens will be deposited with the Oxford University Museum of Natural History.

Driver ants of the subgenus *Anomma* are well known for their enormous colonies of two or more million individuals. All *Dorylus* species have polymorphic workers, with sizes ranging from the large majors around 11–12 mm in length to the smallest minors at 4 mm (Fig. 3). The colonies move from temporary nests or bivouacs, thoroughly scouring a broad territory before moving on after consuming all the local food prey (Raignier & van Boven, 1955). *Crematogaster* is the fourth most diverse ant genus, with more than 400 species, distributed all over the world (Bolton, 1995). Most species of the genus *Crematogaster* are tropical and form principal arboreal fauna (Longino, 2003), usually foraging out across a number of adjacent trees and shrubs, with some foraging on the ground (Taylor, 1977). The establishment and dominance of the genus in tropical forest probably stems from the utilization of hemipteran honeydew excretions by ants as a major component of their diet. The extraordinary abundance of arboreal ants in tropical forests has been associated with the high productivity of the tropical canopy foliage, and the adaptation of the ants to extract their carbohydrate and nitrogen requirement from the plant and insect (Hemiptera) excretions (Davidson & Patrell-Kim, 1996; Davidson, 1997; Davidson *et al.*, 2003).

Crematogaster chiarinii is indigenous to moist to humid southwest parts of Ethiopia, where its distribution is restricted to intact natural and partially disturbed forests and agro-forestry farmlands. The species occurs within the altitude range of 1200–2600 m, and in areas with an annual rainfall exceeding 1000 mm. In common with several other Afrotropical and Neotropical members of the genus, the monodomic (with a single nest per colony) *C. chiarinii* constructs a large nest of triturated (chewed) wood, also known as carton (Fig. 2). The nest is hard with a distinctive architecture and probably comprises more than one million individuals per colony. Such nests are usually built on the trunks of large live trees from 5 m up to 15–20 m above the ground snd positioned underneath branches. Nests were observed on a wide range of species of trees, such as acacia, *Cordia africana*, *Albizia* spp. *Grevillea robusta*, *Croton mcrostachys* and many others, usually those with rough bark.

Dorylus *(Anomma)* *quadratus* Santschi B Taylor det.	Ethiopia Nuru Adgaba	2011 Bonga 07°23'N 36°14'E	Hand collected, surface foraging 1650 m

Figure 3 Polymorphism of *Dorylus quadratus* workers (major worker, top, head only shown).

Figure 4 Worker of *Crematogaster chiarinii*.

Determination of aggressive behaviour

To describe and quantify the aggressive behaviour in interspecific encounters between *C. chiarinii* and *D. quadratus*, we used three different bioassays: dyadic encounters, interaction between groups of workers and interactions between colonies. Because both species are common in the same general habitat, it was easy to locate sufficient nests and foraging workers.

Dyadic encounters

Dyadic (or one-to-one) encounters were used to determine the fighting ability of individual ants. Single workers from each species (median morphs of *D. quadratus*) were randomly picked and then placed simultaneously in a round plastic container (diameter 5 cm, height 7 cm) with a perforated cover that allowed air circulation. A total of 40 fighting reactions (20 at Bonga and 20 at Masha) were conducted. Fight initiators, type of interaction (physical fighting), the winner and the time required to win were observed and recorded. In addition to physical fighting, the incidence of a strong abdominal gaster flexation as an indicator of chemical defence was observed for *C. chiarinii*.

Group interaction

The test using interaction between groups of workers sought to assess the fighting abilities of both species in such encounters and to determine the level of worker cooperation. Thirty-two workers from each species were selected and kept in separate aerated plastic containers. For *D. quadratus*, equal proportions of the major, median and minor morphs were used. Both sets of workers were tipped gently into a single aerated plastic container (30 × 20 × 8 cm) with a transparent cover. The workers of each species were placed in opposite sides of the box separated by piece of wooden board before the start of observation. Combat durations of 1, 5, 10, 20, 30, 40, 50 and 60 min were tested, using fresh ants each time. Each duration was repeated five times at each location. The mean number of ants that died were recorded. In addition to physical combat, gaster flexation by *C. chiarinii* was observed.

Colony interaction

For the test of interaction between colonies, large numbers of individuals of both ant species were used in accordance with the procedures described by Human and Gordon (1996, 1999) and Zee and Holway (2006), with some modifications. The luring of driver ants into domestic buildings by providing them with raw meat is common in rural areas of Africa to eradicate pests, such as cockroaches, house bugs, spiders and others (A. Nuru, personal observation). In our first set of experiments, *D. quadratus* workers were attracted by providing them with honeybee comb containing different stages of brood. Initially, the comb was placed close to the *D. quadratus* bivouac until the worker swarm moved on to it. After approximately 30 min, the comb was gradually dragged along the ground, with an additional brood dropped to motivate foraging along the way, until it was very close to the base of a tree with a *C. chiarinii* nest. In this way, we were able easily to induce large numbers of *D. quadratus* workers into the *C. chiarinii* territory and bring the species into contact.

In the second set of experiments, a portion of *C. chiarinii* nest with brood and adults was removed from a tree and placed on the ground close to a *D. quadratus* bivouac from where the latter were marching on honeybee brood combs. To assess how territorial defence would affect the levels of combat, the experiment was repeated four times in *C. chiarinii* territory and four times in *D. quadratus* territory.

In these experiments, the general reactions of the two species, the length of time taken to complete fighting, the winner and loser, and the number of individuals that died or were physically injured on both sides were counted and recorded. Besides visual observations, each was video recorded and the interactions were studied by repeated watching and zooming of the videos. This enabled us to detect any otherwise missed aggression behaviours. A combined video film with clips of all aspects of activity, interactions and the studies described below is provided in the Supporting information (Video S1).

To evaluate the possible use of chemical repellent by *C. chiarinii*, approximately 200–300 workers were caged with a clean cloth. The cage was placed on the middle of a mass of *D. quadratus* with no other *C. chiarinii* present and the reactions of the *D. quadratus* were recorded. Separately, the corpses of freshly crushed *C. chiarinii* were also placed in the middle of a mass of *D. quadratus* and the reactions observed. Each test was repeated three times.

Other studies of C. chiarinii

To assess the possibility of rapid multiplication and large-scale utilization of the beneficial *C. chiarinii*, we investigated the feasibility of using an artificial method of nest propagation. Polygyny (multiple functional queens) and the occurrences of natural reproduction by budding are known for other ant species, such as *O. smaragdina* (Peng *et al.*, 1998; Dejean *et al.*, 2007) and *Formica truncorum* Fabricius (Elias *et al.*, 2005). Artificial propagation of polygynous colonies via the introduction of nests to new sites has been reported for *Formica* spp. in Europe (Greathead, 1976) and *Dolichoderus thoracicus* in Asia (Way & Khoo, 1992). Thus, the presence of several functional queens per colony of *C. chiarinii* led us to test the possibilities of artificial propagation by simple splitting of a nest. Each of four nests was symmetrically split into two to four smaller units, containing brood as well as adults. From four mother colonies, a total of 12 new colonies (splits) were produced and fixed on tree branches at a mean distance of 500 m away from the original nests. The successful establishment of the split colonies was assessed by observing activities such as food collection, as well as maintenance and guarding of nests, for a period of 1 year, from September 2011 to August 2012.

To assess the effective foraging area of a single colony, observations were made on four apiaries with one *C. chiarinii* nest each. Accordingly, the branch of a tree with an ant nest was carefully removed intact and placed upright in the centre of each apiary (Fig. 5). Although primarily arboreal, a number of *Crematogaster* species are known to forage on the ground (Taylor, 1977). In this test, the transplanted *C. chiarinii* colonies continued to forage on the ground as if emerging from their natural nest.

Additionally, the foraging *C. chiarinii* workers were induced to travel from the nest along ropes stretched in different directions across the apiary. Although artificial, the use of ropes effectively mimicked the natural foraging routes of these arboreal ants. Such columns of workers streaming along vines was reported for *Crematogaster erecta* Mayr 1866, by Longino (2003). The radius of the rope was gradually increased by 5-m increments from 5 m to 30 m. For every 5-m radius, the numbers of workers that reached the perimeter was counted and compared. The counting was conducted by placing an inverted transparent plastic container (10 × 10 cm) over foragers on the ground and immobilizing them by spraying for easy counting. The total area covered by foragers from a single nest was used

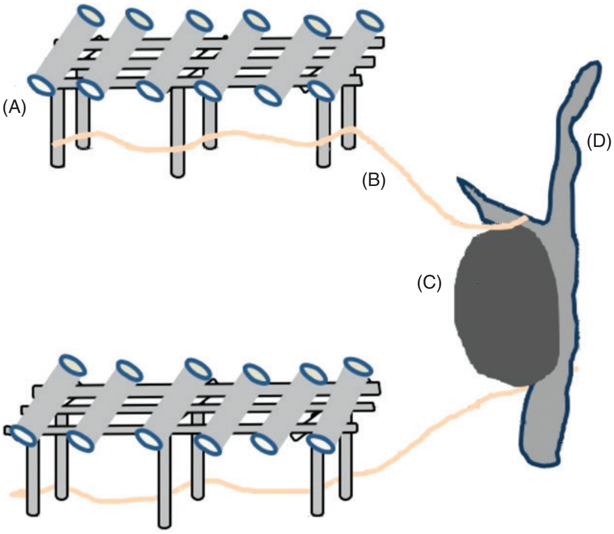

Figure 5 Schematic representation of an experimental apiary with an artificially introduced *Crematogaster chiarinii* nest (A = traditional hives on stand; B = rope extended from *C. chiarinii nest* to each leg of hive stand; C = *C. chiarinii* nest; D = branches of trees with the nest erected near to the apiary).

to estimate the size of the apiary and the optimum number of hives that could be protected against *D. quadratus* predation.

Statistical analysis

In the dyadic encounters experiment, chi-square tests of proportions, based on the numbers of workers in each species that died at both locations, were used to test the fighting ability of individual ant in each species ($n = 40$). In the group interaction experiment, a repeated measures analysis of variance (ANOVA) with the number of deaths at eight time periods as the dependent variables and species and location as factors was used to determine the species effect with respect to the number of deaths in group fighting over time ($n = 8$ periods × 2 species × 2 locations × 5 repeats = 160). The data passed tests of homogeneity of the variances (Levene: $P > 0.17$ for time periods 1–50 min and $P = 0.031$ at 60 min) and normality (Kolmogorov–Smirnov: $p > 0.15$). In the Colony interaction experiment, an ANOVA was used with the number of deaths as the dependent variable and species and territory as factors ($n = 16$). The data passed tests of homogeneity of the variances (Levene: $P = 0.1592$) and normality (Kolmogorov–Smirnov: $P > 0.20$).

Results

Dyadic encounters

In all 40 tests, the *C. chiarinii* initiated the fighting and, in all cases, the first response of the *D. quadratus* was avoidance. Because the ants were kept in confined containers, however, physical fighting or prolonged aggression took place in every test and either or both combatants were killed. Physical combat predominated with the *C. chiarinii* mainly attacking the *D. quadratus* from behind by biting and stretching the legs, although they were observed also to bite the constrictions between the alitrunk and the coxae. Once a *C. chiarinii* had achieved a grip, the *D. quadratus* was unable to bend either to remove or to attack its foe. After only a few minutes of struggling, the driver ants were observed to die or become immobilized. The *D. quadratus* were only observed to start fighting as a defence when bitten as part of attempts to free themselves and could attack effectively only in response to a frontal assault (i.e. when it was possible to use their mandibles). Generally, fighting was relatively brief, from 10 to 30 min (mean of 25 min). If a *D. quadratus* was able to get its foe between the mandibles, killing was instantaneous. Of the 40 one-on-one fighting instances, 18 (45%) (10 from Bonga and eight from Masha) resulted in death of the *D. quadratus*, whereas, in 12 (30%) cases (five from Bonga and seven from Masha), the *C. chiarinii* died. In the remaining 10 trials (25%) (five from Bonga and five from Mash), both ants died. The distributions of number of workers that died from *D. quadratus* were higher than *C. chiarinii* at both locations, although the results were not significant (chi-square: $\chi^2 = 0.556$, d.f. = 2, $P = 0.7575$). However, the distributions of the number of *C. chiarinii* workers that initiated the fighting at Bonga and Masha were significantly higher than those of *D. quadratus* workers [chi-square (Yates correction): $\chi^2 = 48.7$, d.f. = 1, $P < 0.0001$]. In addition to the physical fighting, strong abdominal curling of *C. chiarinii* was observed in every case.

Interaction between groups of workers

In group fighting, the *C. chiarinii* initiated combat, whereas the *D. quadratus* sought to escape. The *C. chiarinii* commonly helped each other, with at least two or three attacking a single *D. quadratus* (Fig. 6). The mean ratio of *D. quadratus* to *C. chiarinii* involved in fighting was only 0.52, showing that each *D. quadratus* was attacked by a mean of 1.9 *C. chiarinii*. The latter pulled the legs of their opponents in different directions until they became spread-eagled and motionless. In *D. quadratus*, the assistance of a fellow worker was rare and of short duration.

The body size of the *D. quadratus* did not affect the outcome because the *C. chiarinii* are very small and fast and the ‘major’ *D. quadratus* morph could not effectively grasp the *C. chiarinii*, which sometimes were seen to escape without harm through the closed mandibles of a major.

Except in the 1- and 5-min combat tests, in all longer durations, significantly higher numbers of dead workers were recorded for *D. quadratus* than *C. chiarinii* (Fig. 7). As the duration of fighting increased, the numbers of dead workers were observed to increase gradually in both species.

In the 60-min duration group fighting, from the total of 320 individuals in 10 rounds of repeated combat (32 individuals per test), 230 of them or a mean of 23 ± 3.56 (72%) ($n = 20$) *D. quadratus* died. From the 320 *C. chiarinii*, a total of 150 or a mean of 15 ± 1.94 (47%) ($n = 32$) died.

Figure 6 Co-operation between *Crematogaster chiarinii* workers in group fighting the larger *Dorylus* (media morph).

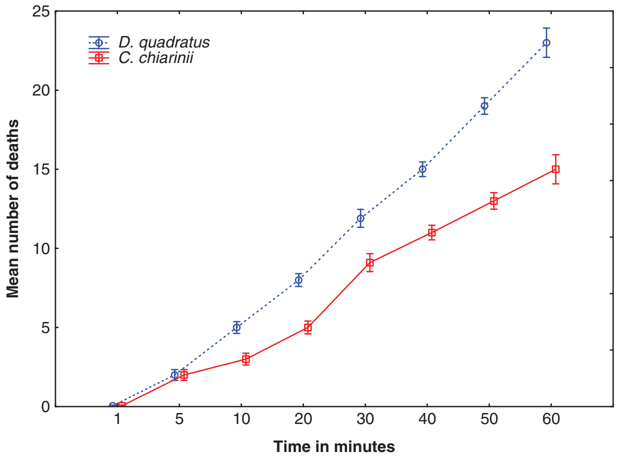

Figure 7 Mean number of deaths of the two ant species in group fighting over time intervals (with SE bars).

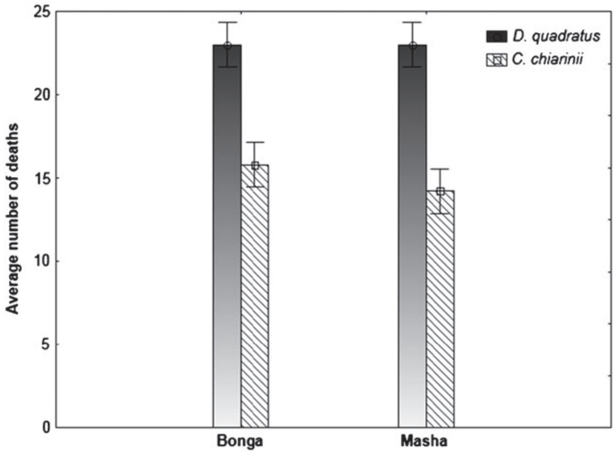

Figure 8 Mean number of dead workers of the two ant species in 60 min of group fighting in both locations (with SE bars).

The numbers of dead *D. quadratus* were significantly higher than *C. chiarinii* ($F = 93.18$, d.f. = 1,17, $P < 0.0001$) and a significant species and time interaction effect also was obtained ($F = 16.42$, d.f. = 7119, $P < 0.0001$). In 60-min group fighting, the mean number of *D. quadratus* that died in both locations was 23, whereas the mean numbers of *C. chiarinii* died in Bonga and Masha locations were 15.8 and 14.2, respectively (Fig. 8). No significant location effect on the number of deaths was observed ($F = 0.51$, d.f. = 1,17, $P = 0.4868$) and there was no significant location and time interaction effect ($F = 0.27$, d.f. = 7119, $P = 0.9648$). A multiple regression analysis with the number of deaths as the dependent variable and duration and a species dummy as the independent variable was used to determine the mean death rates of the two species. The mean death rate for *D. quadratus* was 0.37 deaths per minute (3.7 per 10-min duration) and, for *C. chiarinii*, the mean death rate was 0.25 deaths per minute (2.5 per 10-min duration). The mean difference in the number of deaths over all time periods for *D. quadratus* is 3.2-fold higher than that for *C. chiarinii* ($t = 10.0$, d.f. = 157, $P < 0.0001$).

In all group fighting, most of the *C. chiarinii* were observed fighting and moving with strong abdominal curling, suggesting the use of some sort of chemical repellent. In addition to deaths, during each confrontation, a mean of 5% or 12% of *D. quadratus* was physically injured, losing one or two of their legs or else having their legs stretched or immobilized.

Interaction between colonies

Because this test was conducted in an open arena, the experiments simulated the natural situation. Fierce interaction between the two ant species was readily observed. When they came into contact, the entire *D. quadratus* swarm immediately started to run away. In six out of the eight confrontations, *D. quadratus* lost the battle and immediately retreated (see Supporting information, Video S1). Only in two cases were the *C. chiarinii* defeated and so the *D. quadratus* were able to enter the *C. chiarinii* nest and carry away the brood and queens. *Crematogaster chiarinii* won three times in its home territory and also three times when placed in the *D. quadratus* foraging area, whereas *D. quadratus* overcame the *C. chiarinii* once in its own area and once in the *C. chiarinii* territory.

The primary interactions were physical fighting. In most cases, the battle between the colonies lasted for a mean of only 8 min (range 5–15 minutes). Retreat of *D. quadratus* workers was seen within 3–5 min. It is likely that this was a result of alarm pheromone communication because all of the *D. quadratus* workers fled simultaneously. Those individuals unable to escape kept fighting until they were killed. In each fight, a mean of 217.5 ± 74.2 (range 125–320) *D. quadratus* were observed to die or be physically injured, whereas a mean of only 36.8 ± 15.9 (range 15–61) *C. chiarinii* were recorded as dead or injured. The numbers of *D. quadratus* deaths were significantly higher ($n = 16$, $F = 39.17$, d.f. = 1,12, $P < 0.0001$). However, no significant territory effect on the number of deaths was observed ($n = 16$, $F = 0.043$, d.f. = 1,12, $P = 0.8389$) and there was no significant interaction effect ($n = 16$, $F = 0.024$, d.f. = 1,12, $P = 0.8788$), in that the *C. chiarinii* were the winners even in the *D. quadratus* area. Unlike the physical contact situation, neither the freshly crushed *C. chiariniii* corpses, nor the caged workers appeared to effect retreat by *D. quadratus*.

Artificial propagation test

From the 12 colonies that were obtained by artificial splitting of four mother *C. chiarinii* colonies, nine (75%) adapted and became established as an independent and successful colony in the new location. The others failed and were gradually abandoned. This preliminary trial demonstrated the possibility of artificial multiplication of several colonies from a single *C. chiarinii* nest.

Assessment of the maximum foraging area of a C. chiarinii *colony*

Foragers from *C. chiarinii* colonies were observed to reach a mean distance of a 28-m (range 22–34 m) radius from the nest. Because there were probably more than a million individuals in one nest, the densities of ants that reached approximately 28 m was very high, with an overall mean of 25 individuals per 10 cm^2. From the mean distances fully covered (28 m^2 radius) and the density of foragers per unit area, we estimated that one *C. chiarinii* colony could protect honeybee hives within a mean area of 2462 m^2 ($\pi r^2 = 3.14 \times 28^2$), which could accommodate 100–200 beehives/apiary, depending on the distance between the hives.

Discussion

Despite the large differences in body size between the two ant species, in all types of fighting, the small *C. chiarinii* were the fight initiators, which is an important aggression interaction to defeat its enemy and defend its territory. *Crematogaster chiarinii* gained the upper hand in all fighting except in one-to-one fighting cases. The most obvious reasons for the success of *C. chiarinii* are their speed of attack and the strength of their cooperation in nest-mate support and group combat, although the role of individuals is still very important to win the group fighting. Rapid hunting, collectively capturing small to large prey by spread-eagling and depositing venom on prey body (Richard *et al.*, 2001), and rapid nest mate recruitment and aggression were reported as common among *Crematogaster* (Longino, 2003). Strong nest-mate cooperation and its role in territorial defence, pursuit, attack, capture and killing potential competitors has been reported for other ant species such as *Oecophylla longinoda* (L.) in Africa, *O. smaragdina* in Australia (Hölldobler & Wilson, 1977; Hölldobler, 1983) and the Argentine ant (*Linepithema humile*) (Buczkowski & Bennett, 2008).

Dorylus quadratus workers are proficient at attacking relatively big insects or other animals. The main attack and defence morphs of *D. quadratus* have elongated and relatively slender mandibles (Fig. 3), making it easy for the small *C. chiarinii* to escape even when caught, often unharmed. The overall combat strategy of *C. chiarinii* combining group attack, as well as spread-eagling the opponents, and their small body size appears to be very effective against larger ants.

In dyadic encounters, although more of the *D. quadratus* workers died, the absence of significant differences in number of deaths could be the lack of an option (as a result of confinement) for the loser to escape and thus combat continues until both die. The death of one or both combatants as a result of prolonged fighting between two ant species has been reported elsewhere (Marlier *et al.*, 2004). Although individual fighting ability is important, group and colony interactions are more useful in an assessment of the ability of a colony because both represent natural conditions. The absence of significant variations in fighting results between locations in both dyadic and group encounters may indicate that the populations of the two locations are the same.

The almost immediate disintegration of the *D. quadratus* swarm during confrontation, and the retreat of the whole mass within 3–5 min, leaving behind large numbers of dead, weak and motionless workers, may indicate the occurrence of chemical release by *C. chiarinii*. The release of volatile chemicals causing the retreat or even paralysis of opponents was reported for another genus member *Crematogaster striatula* Emery 1892 (Rifflet *et al.*, 2011). Moreover, during confrontations, *C. chiarinii* were observed to show strong gaster flexation, which is the norm for *Crematogaster* when releasing compounds as defensive or offensive weapons and directing their venom at their enemies (Buren, 1958, Longino, 2003; Marlier *et al.*, 2004; Buczkowski & Bennett, 2008). The direct application of abdominal secretion topically on their foe, including other ant species, was reported for *Crematogaster scutellaris* (Daloze *et al.*, 1991; Marlier *et al.*, 2004). The more and immediate repellent properties of *Crematogaster* venom against termites and ants have been reported previously (Heredia *et al.*, 2005).

Although it was not possible in the present study to directly record and prove the use of chemicals, the general behaviours observed suggest that *C. chiarinii* may have complemented the physical fighting ability by releasing chemicals with repellent and/or toxic properties. The apparent lack of effect of the crushed *C. chiarinii* parts or of caged workers on *D. quadratus* possibly was a result of the absence of optimum conditions triggering the release of chemicals in the procedures that we followed or, instead, direct topical application of the chemicals is necessary. This aspect remains to be clarified in further studies.

Overall, the present study revealed what appeared to be strong conflict between the two ant species. The underlying reasons, however, did not appear to be the obvious factors of competition for food resources or nest sites because they have totally different nesting sites and feeding habits. What is more likely is the observation of a great capacity for defence by *C. chiarinii*. The *Dorylus* have no territories as such but move from bivouac (not a fixed nest) to bivouac. They then swarm out from a bivouac, clearing an entire area before a lack of food compels the carnivorous colony to move. One of us (BT) recently received samples from pitfall traps set at 10-m intervals in lines of twenty traps (i.e. over 190 m). In one line, workers of another African *Dorylus* were trapped in large numbers in consecutive traps 1–13 and none were found in traps 14–20. The numbers in 1–3 were relatively low and this suggested that the swarm area had a diameter of approximately 100 m. By contrast, *C. chiarinii* is a sedentary species, which rears its brood in a confined and permanent nest. It therefore has to protect its young brood, food reserve, nest and territory from any intruders. Raiding, defence of foraging territories and intra- and interspecific disputes among various ant species have been well documented (Adams, 1990, 1998; Tschinkel *et al.*, 1995; Zee & Holway, 2006). Moreover, the presence of fighting over territory and resources between different ant species is well recognized (Hölldobler & Lumsden, 1980; Hölldobler & Wilson, 1990; Franks & Partridge, 1993; Sakata & Katayama, 2001; Tanner, 2006).

The demonstrations of the defence capacity underlines the potential for use of *C. chiarinii* as a biological control against *D. quadratus* swarms that otherwise attack honeybee apiaries with desirable low level hives. Elsewhere, other ant species have been used as important biological control against many crop pests, including competing ants (Overall & Posey, 1984; Huang & Yang, 1987; Jaffe *et al.*, 1990; Way & Khoo, 1992; Vandermeer *et al.*, 2002; Peng & Christian, 2005; Philpott & Armbrecht, 2006).

The ready propagation of artificially split colonies to form independent colonies is a result of the fact that *C. chiarinii* colony nests normally have several reserve functional queens. Polygyny (multiple functional queens) and the occurrence of natural reproduction by budding were documented for *O. smaragdina* (Peng *et al.*, 1998; Dejean *et al.*, 2007) and in *Formica truncorum* Fabricius (Elias *et al.*, 2005). Such artificial propagation of polygynous ant colonies through the introduction of a nest to a new site has been reported for *Formica* spp. in Europe (Greathead, 1976) and *D. thoracicus* in Asia (Way & Khoo, 1992). Natural colony fragmentation (polydomy) in the vicinity of abundant exudate resources also is well known in tropical arboreal ants (Davidson, 1997). The introduction of *O. smaragdina* nests onto one orchard tree, then promoting colony expansion (colonization) to the whole orchard by connecting adjacent trees with bamboo strips, has been reported as common practice since ancient times in China (Huang & Yang, 1987).

Although there are no reports of artificial splitting and propagation of a monodomic ant nest into many splits, the findings of the present study indicated that symmetrical splitting of a *C. chiarinii* nest has the potential for artificial propagation and utilization. The factors leading to the failure of a few splits to establish may include an inadequate distribution of resources among the splits or the exposure of the brood to unsuitable external factors. In this regard, further detailed studies on nest architecture, reproductive biology and social organization of *C. chiarinii* are important. The potential of a *C. chiarinii* colony to protect an apiary size up to 2500 m^2 from *D. quadratus* swarms is based on the high density (25 per cm^2) of *C. chiarinii* foragers at a distance as far as a 28-m radius from the nest.

Conclusions

The observed ability of *C. chiarinii* to defeat *D. quadratus* with apparent ease, or at least to cause a mass retreat, suggests significant potential use of this ant as a biological control agent against the latter. Moreover, the populous nature of *C. chiarinii* colonies coupled with their aggressive and territorial behaviour supports that recommendation. Very importantly, unlike many other ant species, *C. chiarinii* has no tendency to enter honeybee nests and predate the brood, which favours its use to guard apiaries.

Besides minimizing manual guarding expenses, the use of *C. chiarinii* to protect an apiary from *D. quadratus* attack will reduce fears of keeping hives at ground level, hopefully encouraging commercial bee farm and backyard beekeeping in many tropical African countries.

Because *C. chiarinii* is not found in areas of intensive cultivation, nor in areas devoid of tree cover, its distribution is expected to decline with deforestation. Such a decline in ant biodiversity has been reported as a potential threat with drastic consequences for ecosystem services (Philpott & Armbrecht, 2006). Further detailed studies on the social, biological, behavioural and ecological aspects of *C. chiarinii* are desirable for a better understanding and utilization of the species as a biological control against the notorious *D. quadratus* in particular and other undesirable pests in general.

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Supporting information

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Video S1. Adgaba *et al.* ant interactions.

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