J Ethol (2001) 19:75–85

ARTICLE

**Martin Pfeiffer · Karl Eduard Linsenmair**

# Territoriality in the Malaysian giant ant *Camponotus gigas* (Hymenoptera/Formicidae)

Received: October 17, 2000 / Accepted: May 14, 2001

**Abstract** In a 5-ha area of primary lowland rain forest in Borneo, we observed four polydomous colonies of the night-active giant ant *Camponotus gigas*. The nonoverlapping, three-dimensional territories in the canopy had a ground size up to 0.8 ha. *C. gigas* showed a distinct territorial behavior: (1) specific "barrack" nests, especially containing many majors, were situated at the borders and were established during long-term territorial conflicts; (2) trunk trails were regularly patrolled by majors that attacked alien conspecifics and some other ant species violently; and (3) sentinels, often involved in long-enduring conflicts with neighboring ant colonies, defended the borders at bridgeheads. Interspecific conflicts with sympatric *Camponotus* species always led to violent, "bloody" fights of all castes. Intraspecific conflicts, however, were solved by ritual fights ("front leg boxing") of majors. *C. gigas* performed a de-escalation strategy to end short periods of true intraspecific "ant war" that we provoked experimentally. Artificially induced ritualized combats continued over weeks also in the absence of baits, indicating that borders may become established by long-term conflicts of attrition. We discuss the differences between ritual fights in desert and rainforest ants and apply Lanchester's theory of battles to our findings.

**Key words** *Camponotus gigas* · Territory · Antagonistic behavior · Ritualized fighting · Borneo · Rain forest

## Introduction

Most hitherto investigated ant species establish territories that secure access to food resources. Depending on the spatiotemporal distribution of food availability, their strategies of territorial behavior vary widely (Hölldobler and Lumsden 1980).

Territorial conflicts can be very costly for the ant colonies involved because they may lead to in wars causing massive losses of workers on both sides (Mabelis 1979; Hölldobler 1983). In this context, ritual combat behavior may have evolved as a means to solve territorial disputes in a less costly way. Especially well investigated are the ritual tournaments in *Myrmecocystus mimicus* (Hölldobler 1981). Such behavior is also known from *Iridomyrmex purpureus* (Ettershank and Ettershank 1982) and *I. pruinosum* (Hölldobler 1982), from harvester ants of the genus *Messor* (Yamaguchi 1995), and from interspecific interactions between *Polyrhachis laboriosa* and *Camponotus brutus* (Mercier and Dejean 1996; Mercier et al. 1997). The ritual combat of *Formica lugubris* and *Formica rufa* (Le Moli et al. 1982; Le Moli and Parmigiani 1982) includes a simulated acid spraying, as is also found in *Camponotus americanus* (Carlin and Hölldobler 1983). Ritual fights are known from *Lasius niger* (Czechowski 1984) and *Leptothorax acervorum* (Dobrzański 1966) as well.

The Malaysian giant forest ant *Camponotus gigas* exhibits ritual and nonritual fighting behavior. In the lowland dipterocarp rain forest of Sabah, on Borneo, we made a 24-month study (spread over 5 years) of the behavioral ecology of these mainly arboreal ants (Pfeiffer 1997). Here we present our findings on the territorial habits of this species. We especially wanted to know (1) whether majors are distributed randomly or according to a certain pattern among the nests of a polydomous colony, (2) which means are used to maintain territorial control, and (3) how territorial conflicts are solved in intra- and interspecific conflicts.

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M. Pfeiffer* (✉) · K.E. Linsenmair
Theodor-Boveri-Institute of the University of Wuerzburg,
Department for Animal Ecology and Tropical Biology (Zoology III),
Wuerzburg, Germany

*Present address:*
* University of Ulm, Department of Experimental Ecology (Bio III),
Albert-Einstein Allee 11, D-89069 Ulm, Germany
Tel. +49-731-502-2679; Fax +49-731-502-2683
e-mail: martin.pfeiffor@biologie.uni-ulm.de

## Material and methods

### Observation area and time

Our observation plot was a 5-ha area of primary mixed dipterocarp lowland forest on Borneo in Kinabalu National Park, Malaysia (for details, see Pfeiffer and Linsenmair 2000), where the ant community is the most species rich so far described for a tropical rain forest, containing 524 morphospecies from 73 genera (Brühl et al. 1998). Because *C. gigas* is predominantly night active, we usually started our observations around 1700, 0.5 h before the ants' main foraging activity, and recorded data during the nighttime using red-filtered headlamps. Observations took place during five periods totaling 2 years between July 1991 and November 1995, with 1994 as the main observation time.

### Species studied

*Camponotus* (*Dinomyrmex*) *gigas* Latreille 1802 is one of the largest ant species in the world and a dominant member of the ant communities of the Southeast Asian rain forests. Its aseasonal mating flight pattern combines phase-shifted reproductive cycles that are not synchronized within the whole population and an approximately semiannual rhythm resulting in a period of 188 ± 5 days (Pfeiffer and Linsenmair 1997). The foraging strategy of *Camponotus gigas* functions according to the predictions of the central place foraging theory and is based on its polydomous colony structure in combination with efficient communication, polyethism, and ergonomic optimization (Pfeiffer and Linsenmair 1998).

Focus colony A had a territory of 0.8 ha and about 7000 foragers; roughly 13% of them were majors. Colony B had an area of about 0.57 ha, colony C about 0.35 ha, and colony D about 0.66 ha (Pfeiffer and Linsenmair 2000). Colonies were polydomous, with 8 to 14 nests (Fig. 1).

### Determination of the proportion of minors and majors at different nests of the colony

To determine the number of foragers and the proportions of majors at different nests of the polydomous colonies, we counted the number of ants leaving the nests during the exodus period for 1.5 h after the start of nocturnal foraging activity (for details, see Pfeiffer and Linsenmair 2000). Within this time most foragers had left their nests and majors had started patrolling.

According to their activity (high, medium, low), their food input ("sink" nest or "source" nest), and their position within the colony (central, near foraging trees, at the border) (see Pfeiffer and Linsenmair 1998, 2000), we distinguished between "central" ($n = 6$), "minor" ($n = 8$), and "barrack" nests ($n = 3$). We tested for differences in majors' share of total activity among nests of these categories with an ANOVA.

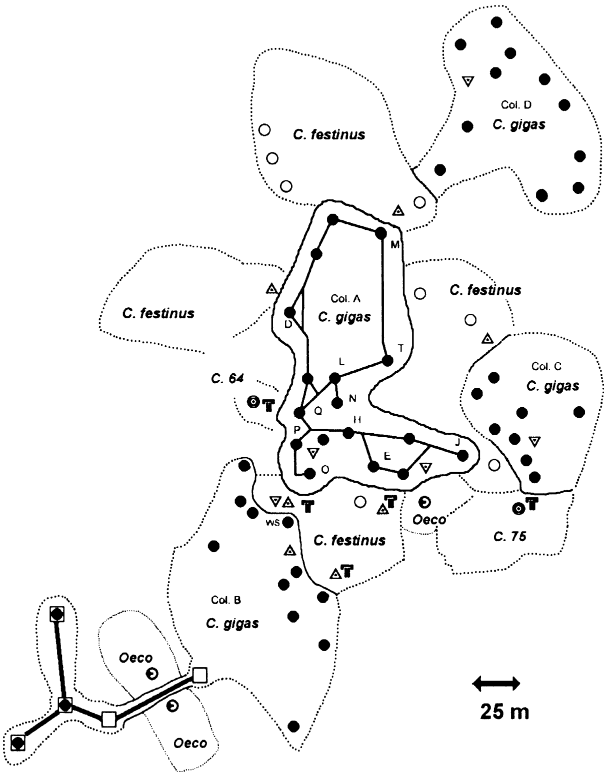

**Fig. 1.** Territorial distribution of four colonies of *Camponotus gigas* and colonies of other large, night-active, and competing ant species in our research area in June 1994. The territorial borders of the *C. gigas* colony A (*bold solid lines*) have been proven by experiments (see Pfeiffer and Linsenmair 2000). The borders of other *C. gigas* territories were roughly determined by various observations (*solid lines*), all other territorial borders are only guessed at (*dotted lines*). The nests of *C. gigas* are symbolized by *black dots* (●). In the center is colony A, with the *black lines* indicating the bamboo runway system between the nests and *letters* marking some nests that we mention in this article. In colony B, *black lines* and *squares* represent the bridges and towers of the Canopy Walk Way that served for ants as a trunk trail. This colony of *C. gigas* consisted of two parts that had been divided by a colony of *Oecophylla*. *White dots* (○) represent nests of *Camponotus* c.f. *festinus*; (◉), nests of two other *Camponotus* species (*C.* 64 and *C.* 75); ⊙, nests of *Oecophylla smaragdina* (*Oeco*), **T**, places of tournaments that had been elicited by our experiments; ▽, permanent sentries of *C. gigas* at the base of trees; △, permanent sentries of both *C. gigas* and *C.* c.f. *festinus*

### Analysis of major worker patrolling

We marked 90 major workers at three neighboring nests of colony A (at Q, 54 ants; at H, 30 ants; at E, 6 ants; see Fig. 1) to analyze their patrolling behavior. For this purpose we elicited alarm by attacking the guards at the nest entrance with tweezers and caught all majors that left the nests for defense. These ants were marked individually with small plastic tags and were observed during the following 10 nights for 2 × 5 h and 2 × 3 h at three nests simultaneously by three observers, and for 6 × 1 h by one observer walking along the trails between the nests.

### Analysis of antagonistic behavior

We studied the fighting behavior of ants of two hostile *C. gigas* colonies at a natural tournament place at ground level during 1 week in April 1993. For a further experimental analysis of intraspecific aggression behavior, we chose colonies A and B in our field site. At their common border in each of the territories, we built a table that was isolated from the ground by use of "Tangle Foot" insect glue and connected by laths of bamboo to the trail systems of the concerned colonies. On these tables we fed ants at petri dishes filled with sugar water for 1 week, until ants accepted these dishes as part of their territories. Then, both tables were connected with bamboo laths (through a small stripe of territory of *C. festinus*; see Fig. 1), and ants of both colonies were fed jointly at one petri dish. Within 30 min, an "ant war" broke out in the contact zone. Using this assay we started long-term experiments on May 1, 1994, May 8, 1994, and October 20, 1995.

We observed the behavior of the fighting colonies over time intervals of 2 weeks to 1.5 months. On each of 10 days we recorded about 30 min of fights on a video recorder (Panasonic NV-MS95E, 12 V red video lamp; Germany); these records were later analyzed to obtain the temporal parameters of the behavioral sequences.

The influence of colony-specific trail marking on the dominance behavior of ants was studied in 85 confrontation experiments, by placing two ants of the same caste of antagonistic colonies on a 1-m-long section of trail and observing their interactions. Trail sections were renewed after each confrontation and were taken from the colonies' artificial trails that had been in use for at least 1 week. We checked for two behaviors: dominance in the fight and jumping off the trail. In 20 similar experiments we tested with fresh bamboo laths (without chemical trails). We analyzed interspecific aggression behavior in long-term experiments with *C. gigas* colonies A and B and one adjacent colony of *Camponotus* (*Tanaemyrmex*) *festinus* F.R. Smith (specimens are deposited with the collection of the University of Würzburg, *Camponotus* no. 11).

Colonies were connected by bamboo trails. To simulate an efficient trophobiont, we used infusion systems filled with sugar water (10% solution) that was continuously dripping (2–5 drops/min). These baits, which were refilled every day, were installed inside the territory of *C. festinus*, but very close to the borders of the two *C. gigas* territories. In eight similar assays we provided petri dishes with human urine (supplied as a nitrogen source; see Pfeiffer and Linsenmair 2000) or sugar water at bamboo trails between colonies of *C. gigas* and adjacent colonies of other *Camponotus* species. Interspecific competition behavior at ground level was examined at 300 petri dishes filled with urine that were placed in twenty 100-m transects throughout our plot. Recruitment behavior inside the territory and at the borders several days after fighting was studied at petri dishes filled with urine. We recorded the number of minors and majors that appeared at the baits and the time of arrival of the first majors.

## Results

### Majors activity pattern within the focus colony

The distribution of majors among the worker force of the different nests of colony A was compared by analyzing the total numbers of majors and minors we had counted at each nest during several observations of the evening exodus of the ants. Differences at the 17 nests of the colony were highly significant (chi-square test; df = 33, $\chi^2 = 2723.8$, $P < 0.001$). When we tested differences between nest categories (see Methods), majors' share of total activity differed significantly between the barrack nests [mean share of majors (MSM), 24.9%] that lay near the colony's borders and were the starting points of majors for patrols to the frontier, and both other groups: central nests (MSM, 2.8%) and minor nests (MSM, 0.4%; ANOVA: $F(2,14) = 32.3$, $P < 0.001$; Scheffé post hoc test: $P < 0.001$ for both groups; see Table 1).

High numbers of majors were also found at the central nests of the colony. Some of them were sentries at the nest entrances. When we elicited alarm by attacking sentries with tweezers, dozens of majors (up to 50 at central nest Q) rapidly left the nest and spread out to patrol the surrounding areas (about 1.50 m around the nest) for about 5–10 min.

### Patrolling of majors

The trail system and the areas around the nest entrances were regularly patrolled by majors that attacked alien conspecifics or ants of some of the other species that were occasionally met on the trunk trails. These ants were either forced to leave the trail by jumping to the ground or they were captured and carried to the nest. Patrolling started shortly after exodus and stopped at dawn when the main activity period ceased. At ground, ants left the nest for short round trips within an area of 1–3 $m^2$; on trails, they moved for about 5–10 m to the track's next turnoff, then they came back and scouted out the other direction before they returned to their nest. Extended patrols could reach the next nests at the trails. Then, majors entered these nests in most cases and stayed there for a few minutes before they returned to their starting point.

Of 90 majors that we had marked individually, we observed 50 again during the following 10 nights; 32 of these that had been tagged at the central nest Q were reobserved 7.25 (mean) times; only 70.6% of these observations were made at nest Q, and the rest at neighboring nests or on the trunk roads between them. At nest H, 18 marked majors were reobserved on average 5.94 times; 79.4% of these observations occurred at nest H. Patrolling behavior of the 8 most active majors is shown in Table 2. Patrols of single ants were staggered. The trails between the nests were run from both sides, so patrols of neighboring nests led to complete guarding of the trails.

**Table 1.** The number of ants and the portion of majors leaving and entering at "central" (Q, D, T, F, Z, B), "minor" (E, H, N, R, L, W, M, V), and "barrack" (O, J, P) nests of colony A during peak activity time at sunset

| Nest | Observation-periods each 15 min | Mean number of ants/period | Mean number of majors/period | Percent of major workers |
|---|---|---|---|---|
| Q | 155 | 149.3 | 3.7 | 2.5 |
| D | 18 | 141.1 | 2.1 | 1.5 |
| T | 30 | 195.7 | 6.9 | 3.5 |
| F | 88 | 53.3 | 1.6 | 3.0 |
| Z | 35 | 35.8 | 0.8 | 2.1 |
| B | 12 | 45.5 | 2 | 5.0 |
| E | 148 | 130.4 | 0.2 | 0.1 |
| H | 107 | 103.1 | 1.0 | 1.0 |
| N | 39 | 50.5 | 0.2 | 0.4 |
| R | 27 | 43.1 | 0.3 | 0.7 |
| L | 23 | 40.0 | 0.0 | 0.0 |
| W | 21 | 20.1 | 0.0 | 0.0 |
| M | 15 | 150.7 | 1.0 | 0.7 |
| V | 9 | 39.2 | 0.1 | 0.3 |
| O | 9 | 30.2 | 3.7 | 12.1 |
| J | 7 | 32.4 | 11.7 | 36.2 |
| P | 7 | 10.8 | 2.9 | 26.4 |

Activity was measured at the nest entrances in periods of 15 min; the share of majors at barrack nests differed significantly from those of both other categories

**Table 2.** Activity pattern of eight major workers most active in patrolling during our examination

| No. of *Camponotus gigas* individuals | Observation nights | Number of patrols | | | |
|---|---|---|---|---|---|
| | | Nest Q | Nest H | Nest E | *n* |
| S 139 | 5 | 16 | 1 | 0 | 17 |
| S 200 | 3 | 4 | 10 | 2 | 16 |
| S 208 | 5 | 2 | 9 | 3 | 14 |
| S 247 | 3 | 12 | 2 | 0 | 14 |
| S 249 | 7 | 20 | 3 | 1 | 24 |
| S 267 | 5 | 2 | 25 | 0 | 27 |
| S 277 | 3 | 2 | 11 | 0 | 13 |
| Mean | 3.88 | 7.25 | 7.62 | 0.75 | 15.6 |

Listed are ant numbers, the number of nights we noticed the ant, the number of patrols at the different nests, and total *n*

## Sentries at the colony borders

At strategically most important points (e.g., at the base of foraging trees and at the end points of the bamboo trails), *C. gigas* established steady sentinels. Every night small groups of major workers (mostly two to four ants) went out to stand sentry at these well-defined places; at dawn they retreated to their nests. Inside our observation area we detected 12 of these sentries (see triangles in Fig. 1), all near ground level. When we carried out spot checks we found that ants guarded these posts over long periods of time (mean, 77 days; $n = 6$; range, 30–139; SD, 40.7). When we marked majors of three colonies of *C. gigas* individually at their posts, we recorded that single individuals were present at one spot for a mean of 8.7 consecutive nights ($n = 41$; range, 2–20; SD, 5.04), thus performing a special form of *ortstreue* (site fidelity).

In many cases these sentinels were involved in long-term conflicts with rivaling *C. gigas* colonies or colonies of other sympatric *Camponotus* species. Small groups of their opponents were found in their immediate neighborhood. From time to time single majors of both sides stalked to the antagonistic sentries, and often these "scout patrols" resulted in combats (see following).

## Results of the fighting experiments: starting an "ant war"

We provoked three long-term conflicts between adjacent colonies to obtain more information about the conflict strategies of *C. gigas*. In our first experiment about 50 minors of both sides gathered at one bait, and fighting among them broke out within 20 min. Ants threatened each other with opened mandibles and body jerking; some gripped each other at the mandibles and pulled in different directions. Colony A recruited about 90 majors from central nest Q that first gathered in a large column on their part of the bamboo trail and investigated their withdrawing foragers by intensive antennation. Suddenly, all majors of A attacked simultaneously and occupied the tabletop, killing or badly injuring several minors of B that mostly fled and gathered at their trail.

Majors of A advanced on the footbridges of colony B, and threatened the minors continuously with widely opened mandibles, but attacked only occasionally. The intimidated minors of B let the majors pass toward their nest. However, freshly recruited majors from far-distant nests of B arrived at the front and fought with majors of A in a series of ritual one-to-one combats along the bamboo trail to prevent them from entering their nest. As the trail was only 2 cm wide, a fighting major could block it. Hostile majors fought each other ritually; they "boxed" with their front legs and pulled each other at the mandibles (for details, see following). If the attacking ant won, it could pass and went on further to the enemy nest. Defenders that were already fighting had to let other majors pass also. Most of the minors retreated to their nest.

Majors that were continuously fighting for more than about 20 min (mostly with several enemies, one after the other) showed signs of fatigue and were easily passed: they could no longer open their mandibles wide and long enough to threaten their opponents. Many of them were quivering with their whole body, and their muscular system seemed out of control. Majors in the fighting column of colony A exchanged places in the active fight, and completely exhausted fighters went back to their nests. At the climax of the battle, we counted a total of 132 majors of both parties and 21 minors of B that were involved in the combat. Fighting diminished at dawn and stopped in the morning when all fighters withdrew at the end of their nocturnal activity period.

To repeat the experiment later, we removed the connecting bars and replaced the baiting stations. Within the following week, foraging activity along this part of the border was extremely reduced and the ratio of majors to minors during a recruitment was shifted toward the majors (Fig. 2). At our second experiment, which took place 1 week later at the same place, fighting did not escalate as before: both colonies recruited fewer than ten majors that each fought only in a ritual manner, and minors withdrew completely from the tournament place. This time we did not break down the connecting trail in the morning, so both colonies kept in contact. Ritual fighting continued over 30 days and guards were observed for at least 45 days. As the earlier individual markings showed, these were the same individuals during the whole time.

Patrols of both sides searched the ground below the combat zone over 1 month, sometimes being involved in ritual fights with ground patrols of their opponents. However, fighting was restricted to the small frontier area and deescalated gradually. Figure 3 shows the distribution of major sentries during the course of deescalation. One month after the combats had started, a "no-ant zone" had been established.

In 1995, we repeated the whole experiment a third time with findings similar to that of the second period. All results can be summarized as follows:

A. Within 1 week after the first confrontation, the majors' numbers in the central area of combat decreased quickly. It differed significantly at the second (mean, 33; SD, 26.2) and the sixth day (mean, 7; SD, 1) of the experiments (chi-square test; df = 2, $\chi^2 = 10.64$, $P < 0.01$).

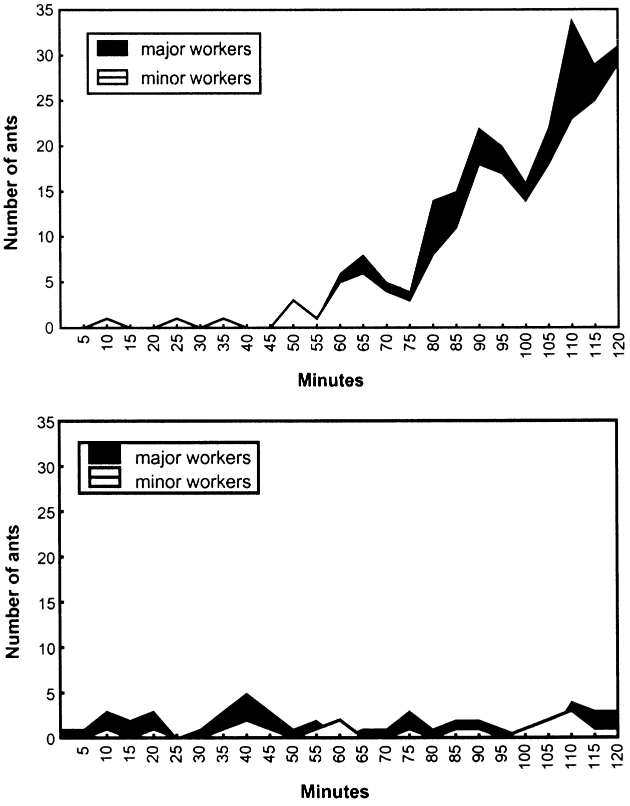

**Fig. 2.** Differences in the recruitment behavior of *C. gigas* in different zones of danger. *Upper*: typical recruitment at a petri dish with urine inside the territory on May 13, 1993, near nest Q. Major workers appeared not earlier than 1 h after the start of recruitment and made up only a small part of all foragers. *Lower*: recruitment pattern in an experiment directly at the border after two nights of territorial fighting between two *C. gigas* colonies on May 3, 1994. Only a few minors appeared at the bait; the relation of majors to minors at the bait was much higher than in the experiment shown previously

B. The frequency of the tournaments diminished in the course of time; 4–8 days after the first combat the intervals between the fights had lengthened significantly (Table 3; Mann–Whitney *U* test: $U = 114$, $Z = -4.1$, $P < 0.001$).

C. Compared to the recruitment toward "safe" locations, we observed during recruitments to the border area several days after a combat (1) significantly fewer ants (Mann–Whitney *U* test; $U = 1.0$, $Z = -3.125$, $P < 0.01$, $n = 15$); (2) a much higher percentage of majors (*U* test; $U = 0.0$, $Z = -3.24$, $P < 0.01$, $n = 15$); and (3) an earlier arrival of the first major workers (*U* test; $U = 0.0$, $Z = -3.24$, $P < 0.01$, $n = 15$) that were the first to arrive at baits at the frontier (Table 4). In five experiments that were not included in this calculation we observed no recruitment at all, although ants were forced to the baits with tweezers, a method that usually worked well in eliciting intake of food and a subsequent recruitment of nestmates.

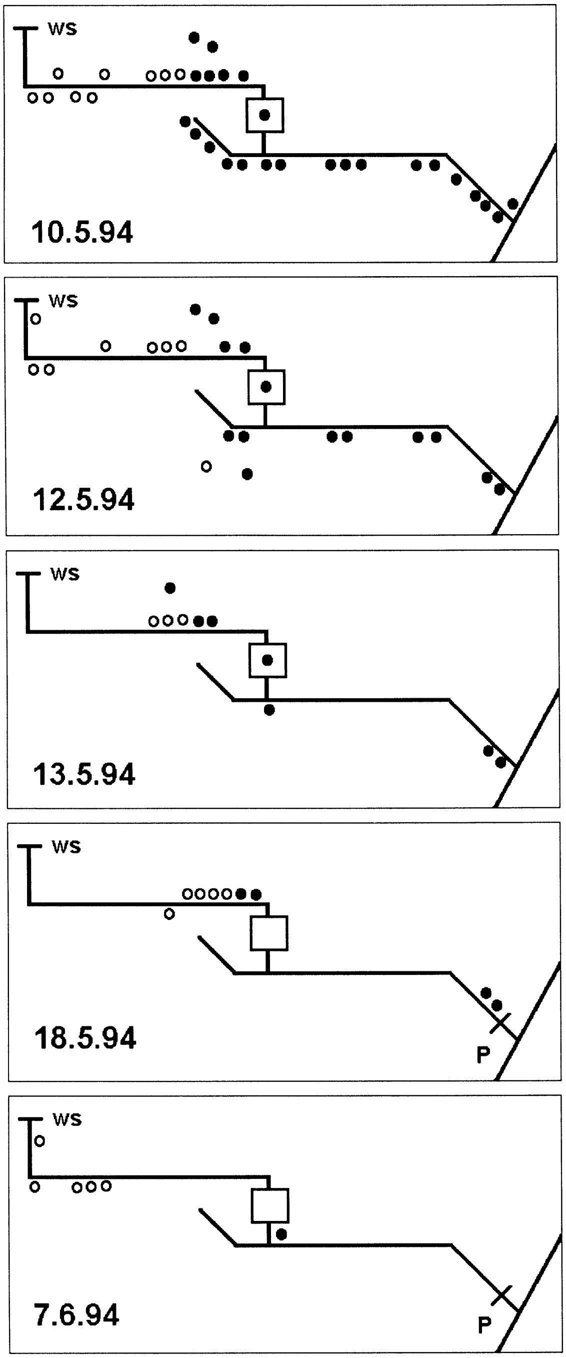

**Fig. 3.** Course of ritual fighting at the border of two rival colonies of *Camponotus gigas*, starting 2 days after an "ant war" experiment. The scheme shows a series of dated maps with the location of sentries of major workers of both colonies. These permanent sentries kept their place during the whole night. The *black line* represents the bamboo bridges, which were connected by a feeding table. Each *point* represents a major either involved in the fighting, guarding on the bridge (points near to the line), or patrolling the ground. ●, major of colony A (nest Q, etc.); ○, major of colony B; *WS*, a nest of colony B (the next nest of colony A was about 10 m away from the upper margin). During the fights, a new "barrack" nest was founded by colony A (*P*). The distance between the left and the right margin of the map is approximately 50 m (During this experiment minors were recorded on the bridge very rarely and only for short time intervals. They were ignored during mapping). Feeding had stopped on May 8, 1994. In the course of time the number of guarding majors decreased; they concentrated at strategic points, and in the end the ants were separated by a neutral zone

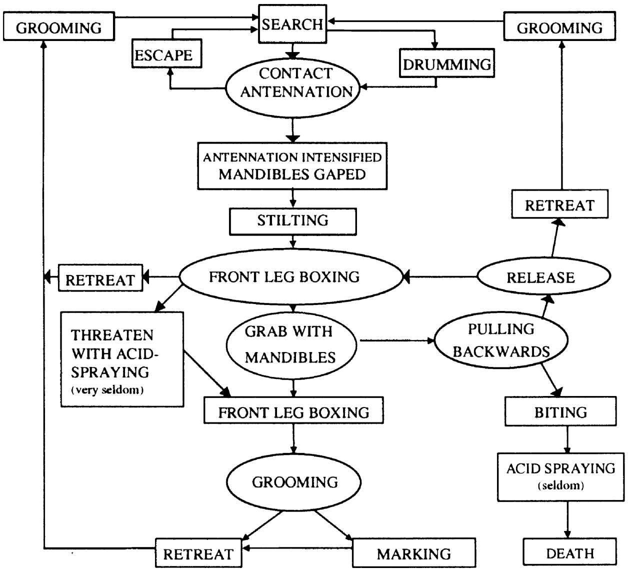

**Fig. 4.** Flowchart of an antagonistic encounter of two *C. gigas* major workers from different colonies, showing all possible outcomes

## Ritual combat

We observed ritual tournaments during territorial conflicts at eight colonies of *Camponotus gigas* and took quantified data ($n = 180$ fights) from four colonies. Generally, ritual tournaments were restricted to majors that fought each other only in a ritual manner. Figure 4 illustrates all possible (partly overlapping) phases of the behavioral repertoire that arose during a confrontation between two major ants of antagonistic colonies.

The fighting occurred as follows: the assailant went to the border of the opposing colony, where the alien major was standing sentry. Occasionally the aggressor drummed at the ground with its gaster, producing audible sound. It opened its mandibles and reared the first pair of legs. When it touched the defender, the fight began. At night there is hardly any light on the forest floor, so the ants had to orientate by chemotaxis and mechanosensory information. Their antennation was intensified during the fighting and reached a rate of 3–4 Hz. Ant gasters were vibrating up and down. Both ants threatened with open mandibles and raised their body in a "stiltlike" posture, depressing the femora and flexing the tarsi (Fig. 5). They stood up on their hind legs and swept their front legs alternatively up and down, producing a "paddling" motion directed at their opponent ("front leg boxing"; sensu Ettershank and Ettershank 1982), at a rate of 4–6 Hz. Each major tried to grasp its antagonist at its mandibles. Then, with a quick jerk, the inferior ant was deprived of its balance and was pulled over the ground in a retrograde movement. After a short distance, the ant was released and both parties retreated. Mostly, the decision was made while "boxing." The "round" was won by the ant that was able to hold up its front legs longer; its opponent retreated immediately.

Such a victory did not stop the combat. It was only interrupted by a short period of self-grooming of antennae and

**Table 3.** Duration of ritual fights and the intervals between them, measured in different periods after three “ant wars”

| Period | Fight [s] | SD | *n* | Interval [s] | SD | *n* |
|---|---|---|---|---|---|---|
| After 1–2 days | 66.0 | 44.4 | 32 | 64.9*** | 97.2 | 22 |
| After 4–8 days | 108.2 | 101.8 | 30 | 527.5*** | 801.8 | 31 |
| Mean/total | 86.4 | 79.9 | 62 | 335.5 | 653.9 | 53 |

In the first 2 days after the war, ritual tournaments between single majors of each colony were carried out in short intervals; 4–8 days later, the intervals between the fights had lengthened significantly (marked as ***); the length of the fights, however, did not differ significantly

**Table 4.** Recruitments of majors versus minors to baits inside the territory and at the borders, several days after fighting Group T (upper): recruitments of *C. gigas* to baits inside its territory; group B (lower): recruitments at the borders, several days after fighting

| Date | Duration of experiment (min) | *n* | Group | Arrival of first major (min) | Mean number of majors | SD | Mean number of minors | SD | Mean of ants | Percent of majors |
|---|---|---|---|---|---|---|---|---|---|---|
| 13.05.93 | 120 | 24 | T | 55 | 1.88 | 2.64 | 7.83 | 9.18 | 9.71 | 19 |
| 17.05.93 | 160 | 83 | T | 54 | 2.87 | 2.50 | 15.93 | 11.27 | 18.80 | 15 |
| 20.05.93 | 110 | 85 | T | 42 | 3.84 | 2.95 | 13.89 | 9.74 | 17.73 | 22 |
| 17.02.94 | 180 | 17 | T | 135 | 0.29 | 0.59 | 4.53 | 6.23 | 4.82 | 6 |
| 18.02.94 | 90 | 16 | T | 73 | 0.56 | 0.81 | 9.75 | 10.01 | 10.31 | 5 |
| 31.03.94 | 180 | 123 | T | 15 | 0.13 | 0.34 | 6.69 | 3.62 | 6.82 | 2 |
| 01.07.94 | 60 | 59 | T | 50 | 0.14 | 0.43 | 16.31 | 7.17 | 16.44 | 1 |
| 03.05.94 | 120 | 24 | B | 0 | 1.04 | 1.23 | 0.83 | 0.82 | 1.88 | 56 |
| 04.05.94 | 90 | 11 | B | 0 | 3.64 | 1.57 | 2.27 | 0.90 | 5.91 | 62 |
| 06.05.94 | 60 | 14 | B | 0 | 1.07 | 0.83 | 1.50 | 1.22 | 2.57 | 42 |
| 09.05.94 | 120 | 12 | B | 0 | 0.86 | 0.38 | 0 | 0.00 | 0.86 | 100 |
| 09.05.94 | 110 | 7 | B | 0 | 0.67 | 0.52 | 0 | 0.00 | 0.67 | 100 |
| 30.10.95 | 390 | 13 | B | 0 | 0.25 | 0.46 | 0 | 0.00 | 0.25 | 100 |
| 30.10.95 | 390 | 13 | B | 0 | 0.75 | 1.39 | 0 | 0.00 | 0.75 | 100 |
| 31.10.95 | 60 | 6 | B | 0 | 1.00 | 1.00 | 1 | 1.00 | 2.00 | 50 |

Given are date, the length of the experiment, the number of observations, the arrival of the first major after recruitment had started (0 min means that a major was the first at the bait), the mean numbers of majors and minors and their SDs, the total number of ants, and the percentage of the majors. The small number of observations in group B is due to the low activity at the border. During these observations there were hardly any changes in the number of ants visiting the baits

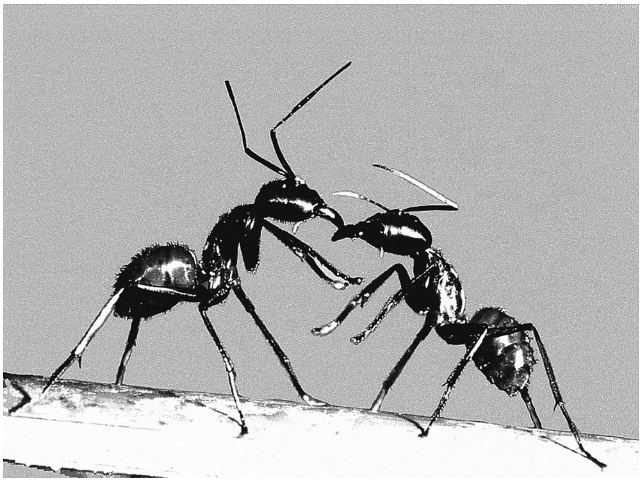

**Fig. 5.** Two major workers of *Camponotus gigas* in a ritual fight

front legs. In these breaks, ants often retreated to their territories, where two or three of their major nestmates were still on guard. Sometimes ($n > 18$ of 180) the fighters started boxing again when they met their nestmates, but they did it in a weakened form. The sequence of the movements was much slower in comparison to real fights. The mandibles were opened only half way, and the tarsi were not raised as high and never touched the nestmate.

When an assailant retreated, its opponent marked its track, pulling its gaster close over the ground. We observed drops coming out from the acidoporus, so a marking substance may have come from the hindgut or poison gland. However, as the gaster was dragged along the ground with its full length, additional glands may be involved in this marking. After a few minutes’ break, ants returned to the tournament site: if they were tired, they were relieved by their nestmates. Usually fighting lasted the whole night. Only very seldom, and just for a short time, did one group retreat as a whole.

On average, a single bout including antennation, stilting, front leg boxing, and grasping with the mandibles lasted 86.43 s ($n = 62$; SD = 79.86), and the interval between the fights 335 s ($n = 63$; SD = 600.89). However, length of the different parts was quite flexible. Mostly, just one or two pairs of majors were fighting, while the other majors were involved in the combat only rarely. We rarely observed two or three majors attacking one opponent on the ground, but, if so, this never happened other than in a ritual way. Yet, we noted some majors carrying on their bodies the cutoff heads of dead majors that had taken firm hold with their mandibles; these were clear signs of nonritual fights among *C.*

*gigas*. In only 2 of 180 fights that we observed did aggression become so intense that neither fighter released their mandible grip; instead, they sprayed acid on each other and died within minutes.

### Trail marking and dominance

We tried to establish by confrontation experiments whether territorial marking of trails affected the dominance of minors from different colonies toward each other or the chance of majors to win in ritual tournaments. We compared behavior on own and alien trails (Table 5). Minors were more dominant on their own trails than on alien trails [a; $G$ test (df = 1), $G = 5.01$, $n = 98$; Bonferroni corrected, $P < 0.05$] and jumped more often from alien trails [b; $G$ test (df = 1), $G = 5.39$, $n = 98$; Bonferroni corrected, $P < 0.05$]. Majors showed a similar tendency; however, we found no significant influence of trail marking on their behavior. (This finding was probably because the experimental setting was too artificial and put both parties under stress.)

When tested on a neutral trail both castes showed significant behavioral differences: 8 of 18 minors (44.4%) withdrew and tried to hide below the trail, whereas only 1 of 22 majors (4.5%) did so (Fisher test; $n = 18$, Bonferroni corrected, $P < 0.05$). Taken together, all workers jumped less often from their own trails (14 of 84) than from neutral trails [16 of 40; $G$ test (df = 1), $G = 7.52$, $n = 124$; Bonferroni corrected, $P < 0.05$].

### Interspecific competition

Some ant species establish absolute territories by excluding nearly all other ants (Hölldobler and Wilson 1990). However, this was not the case in the large territories of *C. gigas* that interacted in various ways with sympatric ant species[1] (for a complete list of species, see Pfeiffer 1997).

**Table 5.** Influence of trail marking on the dominance of *C. gigas* in intraspecific confrontations of similar castes

| | Minors ($n = 98$) | | Majors ($n = 68$) | |
|---|---|---|---|---|
| | Own trail | Alien trail | Own trail | Alien trail |
| Number of ants | 50 | 48 | 34 | 34 |
| Dominant | 34.0%[a] | 14.6%[a] | 20.6% | 17.6% |
| Not dominant | 66.0%[a] | 85.4%[a] | 79.4% | 82.4% |
| Jump off the trail | 12.0%[b] | 31.3%[b] | 23.5% | 44.1% |
| No jump | 88.0%[b] | 68.8%[b] | 76.5% | 55.9% |

We noted whether the ants were dominant in the fights and whether they jumped off the trail during combat

Frequencies of behavior shown on own and alien trails were compared in $G$ tests with Bonferroni correction; significant differences are marked with letters

[a] $G$ test (df = 1), $G = 5.01$, $n = 98$; Bonferroni corrected, $P < 0.05$

[b] $G$ test (df = 1), $G = 5.39$, $n = 98$; Bonferroni corrected, $P < 0.05$

A series of smaller, night-active, nondominant species (including two species of *Camponotus* and one of *Crematogaster*) were more or less tolerated on *Camponotus gigas* trails and even at (arboreal) baits. Another group (mostly Dolichoderinae and several species of *Polyrhachis*, especially *P. ypsilon*) used these trails only during daytime and replaced *C. gigas* inside its arboreal territory. A third group of ants, including large Ponerinae, interacted with *C. gigas* on the ground mostly by scramble competition; only some species of tiny Myrmicinae monopolized resources. A last group of (night-active) sympatric Formicinae (mostly *Camponotus* species), however, had arboreal territories that were defended against *C. gigas*, and vice versa.

One of these Camponotini, *Camponotus festinus*, was very abundant in our field site, established several colonies there (see Fig. 1), and even settled at deserted nest sites of *C. gigas* ($n = 2$). Interactions with *C. gigas* differed in distinct strata of the forest. At 10 of 300 ground-level baits we observed both species feeding simultaneously, thus displaying scramble competition. However, when we presented similar baits ($n = 9$) on bamboo trails 1.50 m in height between neighboring territories, both species changed to "interference competition." Following mass recruitments of both sides, the ants fought violently at the baits, causing several deaths. During these interspecific combats we never observed ritual fighting behavior; in most cases the ants (of all castes) attacked each other with their mandibles but also used their poison gland and sprayed acid.

In several long-term experiments, we provoked fights of *C. gigas* with neighboring colonies of *C. festinus*. By baiting with infusion systems that dispensed only small drops of sugar water, we avoided mass recruitments and therefore large battles between the ants. Usually several *C. gigas* majors occupied the bait, but workers of *C. festinus* were sitting below the bamboo trail or in the vegetation above it and attacked the larger *C. gigas* from there. Most of the few major workers of *C. gigas* that guarded the baits lost parts of their antennae and legs within a few nights. This situation continued over days: *C. gigas* dominated at the bait; however, *C. festinus* controlled the trail to it, thus preventing *C. gigas* from larger exploitation. The "pin-prick" strategy of *C. festinus* succeeded in the end, and *C. gigas* had to retreat from all baits. However, even after the baits were removed, sentries of both sides were found at the borders for a mean of 31.4 days ($n = 12$, SD = 36.1); this result showed that not only the baits, but also the territory border, were guarded by them. Similar results were also obtained with two other sympatric *Camponotus* species (see Fig. 1).

## Discussion

Lumsden and Hölldobler (1983) claimed, for a detailed analysis of the territorial strategy of ants, the examination of (1) the distribution of resources within the territory, (2) the territorial "architecture," (3) the social organization of its defense, and (4) its spatiotemporal structure.

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[1] It must be mentioned that majors of all these species are smaller than most minors of *C. gigas*

Resources used by *C. gigas* are randomly distributed: invertebrates, bird droppings, and cadavers, on which *C. gigas* feeds occasionally, are widely dispersed within the rain forest, as well as groups of trophobiotic Homoptera (Pfeiffer 1997). Territories of *C. gigas* colonies had clear-cut borders that were defended even in absence of a bait against intra- and interspecific enemies. However, this defense was restricted to the arboreal parts of the territory and took place at "bottlenecks" that gave the opportunity to guard them with a few majors, e.g., the base of the trees. On the ground, *C. gigas* guarded only the immediate surrounding of their nest entrances, and resources were used in scramble competition. Similar findings were reported by Jackson (1984) from Cameroon, who found exclusive territories only in tree-dwelling ant species; ground-dwelling ants had overlapping territories because of the lack of "bridgeheads" that could be easily protected. Partly, this finding may also reflect problems with territorial marking, which is much easier on arboreal trails than on large ground areas. Our data show that in *C. gigas* territorial marking supported the dominance of territory owners.

In Kinabalu Park, several abundant species defended their mutually exclusive, arboreal territories during the night: *Camponotus gigas*, *C. festinus*, *Camponotus* 64, *Camponotus* 75, and *Oecophylla smaragdina*. However, at least *C. gigas* tolerated several nondominant species even on its trunk trails. The three-dimensional territories of the giant ants extended over wide areas and are among the largest we know (Hölldobler and Wilson 1990). The polydomic nesting structure of *C. gigas* intensified territorial control. Majors were concentrated in specialized "barrack nests" at the endangered territorial borders and in the central nests of the colony to protect the queen, brood, and food supplies. Majors in central nests may have a second function as food storage as is shown, e.g., from majors of *Colobopsis nipponicus* (Hasegawa 1993). In "minor" nests that lay within the territory near foraging trees (Pfeiffer and Linsenmair 2000) the percentage of majors was low. During territorial conflicts, high numbers of majors could easily be mobilized by long-range recruitment from central nests to the borders (as we have already shown by computer counts for minors during foraging; see Pfeiffer and Linsenmair 1998). Compared with a random arrangement of majors at all nests, this strategy allowed colonies to keep a lesser investment for producing major workers. Border defense as a primary task of the majors is also known from other ant species, e.g., *Pheidole dentata*, *Pheidole titanis*, or *Azteca trigona* (Wilson 1976; Feener 1988; Adams 1994).

*C. gigas* showed two different strategies to defend its territory: (1) ritual combat during intraspecific competition and (2) "true," violent fights in interaction with other ant species. Ritualization seems to have evolved in many ant species because the lack of a fixed territory can lead to frequent confrontations of workers from neighboring colonies. These species have overlapping territories, foragers of different colonies that meet in the field perform short displays of ritual aggression behavior; this is the case in *M. mimicus* (Hölldobler 1976), in the Australian *Iridomyrmex purpureus* (Ettershank and Ettershank 1982), in *Messor aciculatus* (Yamaguchi 1995), or in the interspecific competition of *Polyrhachis laboriosa* and *Camponotus brutus* (Mercier and Dejean 1996). In *I. purpureus* and *M. aciculatus*, minors perform front leg boxing; the behavioral patterns resembled those of *C. gigas*, but periods of fighting are only 12 s or up to 1 min, respectively.

In contrast to all other species, in *C. gigas* ritual fights were carried out merely by major workers that met regularly at fixed bridge points to defend the borders of nonoverlapping territories. These majors performed an extreme form of site fidelity. Up to now, *ortstreue* has only be reported in connection with foraging areas (Hölldobler and Wilson 1990); for *C. gigas*, however, we use this term to describe the fidelity of majors to their posts and tournament places.

In the tournaments of *M. mimicus*, Lumsden and Hölldobler (1983) distinguished between two models that would allow the opposing colonies to assess each other's strength: head counting and cast-polling (Hölldobler 1984). Head counting could be measured most easily in the arboreal fights of *C. gigas*, as fighting majors formed pairs along the trails during combat. Additional majors could pass these fighters and reach the nest of their opponents, thus taking advantage of their local majority. Cast-polling was also easy: smaller majors had less strength and were tired within a shorter time; they had to be replaced more frequently. As most of the combats were carried out by only a few majors (especially when the "hot phase" was over), it seems that cast-polling was enough to determine the strength of a colony. This hypothesis is supported by the fact that minors had a strong tendency to withdraw from prolonged agonistic encounters. One strong ant could stop a number of opponents when it blocked the narrow arboreal trails. It is likely that, for energetic reasons, the strongest majors could be produced by large colonies only.

All combats that we observed were solved by a strategy of de-escalation. Although in *Myrmecocystus mimicus* (Hölldobler 1976) or *I. purpureus* (Ettershank and Ettershank 1982) hundreds of ants are involved in gradually growing ritual tournaments, in *C. gigas* the number of fighters was reduced to a handful of majors within a couple of days, while breaks between the single fights were prolonged. Not only was the method of the combat ritualized, in the end the fight itself involved representatives, possibly because its arboreal territory could be protected most effectively by a few strong majors. In the rain forest, it seems to be more appropriate to guard certain bridgeheads of a fixed territory over a long time, whereas in a desert environment a ritual fighting strategy needs more participants.

Davidson (1997) stressed the importance of carbohydrate-rich diets (e.g., honeydew) for ant protection of (absolute) territories. From our point of view, high dietary ratios of CHO : protein seem to be especially important for the development of a ritual competition pattern that results in purely energetic costs. The ritualization of aggressive behavior in *C. gigas* may be based on a cost–benefit calculation. When energy is at low cost, nitrogen (as an essential factor in the production of a large worker force) is a minimum factor. Considering the enormous territories of *C. gigas* and its relatively small colony size, the costs for defending the territory in nonritual fights may be too high. The very large majors are especially valuable and are, according to our observations, in many situations timid rather than aggressive.

Our study points to a series of long-term ritual conflicts of attrition between small groups of majors with which a colony of *C. gigas* is faced at many border sections of its territory. Only if the ownership of the territory was unclear, as at the start of our first experiment, did territorial conflicts result in major warfare. In contrast to our observations, Tho (1981), D. Jones, and C. Brühl (personal communication), reported intraspecific warfare in which majors killed each other in higher numbers. Why fighting was nonritual in these cases we can only guess: perhaps the strength of the colonies differed greatly and the territories were not only to be maintained but enlarged. In our study area, at least on one occasion, a founding colony of *C. gigas* seemed to have been eliminated by the old owners of the territory, but we did not observe this directly.

Interspecific conflicts, however, resulted in nonritual combats, which shows that ritual fights are only possible if both sides have same risks. The huge majors of *C. gigas* were tough fighters, but not very quick; even much smaller species were able to hurt them seriously by attacking their legs or antennae. Although at first dominant in most of the conflicts, in the course of time they could be overcome by pinprick strategies. For smaller ants (e.g., other *Camponotus* species, or minors of *C. gigas*), the risk of being injured in a ritual fight was high, and the chance to win it was negligible. Thus, minors withdrew from most intraspecific fights. On the other hand, the potential loss of biomass in a violent fight is lower in smaller ant species, compared to the risk of *C. gigas*, especially when smaller ants apply a guerilla tactic. This relationship may explain why interspecies combats were nonritual.

Another access to this problem is given by Lanchester's (1916) theory of combat (see Franks and Partridge 1993, for details) that concisely presented two models relevant also in combats of ants: the linear law and the square law. Initially used to calculate losses in nonritual combats, they are also suited to discuss the differences of intra- and interspecific conflicts in *C. gigas*. The linear law will apply if the battle is a series of one-to-one conflicts with excess individuals waiting for a free opponent, and it predicts that a few good fighters are better than many poor ones. This is the case in the intraspecific ritual duels of *C. gigas* in which some individuals with massive individual fighting value can decide the battle. If, however, all individuals are equally vulnerable to attacks from every individual on the opposing side, losses are proportional to the number of the opposing side and many poor fighters should succeed over a small number of good ones. This scenario happened in interspecific fights when several majors of smaller *Camponotus* species attacked one *C. gigas* in a violent "freestyle" manner, thus enlarging their chance to win. The same was true when numerous minors of *C. gigas* attacked alien ants on their trails.

Despite the differences in tactics between ritual and nonritual fighting, the result was the same in both cases. The territorial interactions were so intensive that they resulted in a no-ants zone between the rivaling colonies. Thus, both mechanisms seem to be equally effective within their ecological context by providing clear territorial borders.

**Acknowledgments** We are grateful to Sabah Parks for assistance and help that allowed this study to be conducted. We especially thank Datuk Dr. Lamri Ali, Mr. Eric Wong, Dr. Jamili Nais, and Mr. Kasitah Karim for various kinds of support. We thank Antonia Uecker, Sabine Hussmann, and Matthias Dolek for help in the field work, Dr. Carsten Brühl for the determination of *C. festinus*, Dr. Andreas Floren, Prof. Dr. A. Buschinger, and three anonymous referees for helpful comments on the manuscript, and Prof. Dr. Herbert Vogt for help with the statistics. This study was funded by the DAAD (Deutscher Akademischer Austauschdienst). We also thank the "Deutsche Forschungsgemeinschaft" (DFG) for granting the infrastructure for our activities within the framework of the "DFG Schwerpunktprogramm Mechanismen der Aufrechterhaltung tropischer Diversität."

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