

## Individual versus collective decision making: optimal foraging in the group-hunting termite specialist *Megaponera analis*



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Collective decision making is one of the main mechanisms of organization in social insects. However, individual decision making can also play an important role, depending on the type of foraging behaviour. In the termite-hunting ant species *Megaponera analis* information about foraging sites is collected by only a handful of individual scouts that have to convey this information to the colony as accurately as possible to optimize their foraging behaviour. We therefore looked at predictions made by optimal foraging theory to better understand the interplay between collective and individual decision making in this obligate group-raiding predator. We found a clear positive relation between raid size (200–500 ants) and termite abundance at the foraging site thereby confirming predictions of the maximization of energy theory. Furthermore, selectivity of the food source increased with distance, thus confirming central place prediction theory. The confirmation of these theories suggests that individual scouts must be the main driver behind raid size, choice and raiding behaviour. The marginal value theorem was also confirmed by our results: time spent at the hunting ground increased with distance and prey quantity. This raises questions on how foraging time at the food source is regulated in a group-hunting predator. Hunger decreased selectivity of scouts with respect to food sources, while average raid size increased and more scouts left the nest in search of prey, thus implying that scouts are aware of the hunger state of the colony and adapt their decision making accordingly. Remarkably, most central place foraging behaviours in *M. analis* were not achieved by collective decisions but rather by individual decisions of scout ants. Thus, 1% of the colony (10–20 scouts) decided the fate and foraging efficiency of the remaining 99%.

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By making collective decisions, group-living animals can increase the accuracy of a decision, at the cost of time (Chittka, Skorupski, & Raine, 2009). Collective decisions have been extensively studied in social insects and are considered one of the main mechanisms for regulating behavioural choices, such as nest or food choice (Hölldobler & Wilson, 2008; Mallon, Pratt, & Franks, 2001). For certain species, however, the choice of a food source cannot be taken by collective decisions. The foraging success of species that rely on independent foragers directly depends on the individual decisions they make (Pohl & Foitzik, 2011). In species in which a large portion of the colony forages independently, the mistakes made by individuals have little impact. However, in species in which the colony depends on scouts for obtaining accurate information to send large numbers of individuals to the food source, mistakes become far riskier. We therefore looked at the

foraging behaviour of the termite-hunting ant *Megaponera analis* to better understand the interplay between collective and individual decision making in their raid choice and the precision of these choices.

*Megaponera analis* is a strictly termite-eating ponerine ant species found in sub-Saharan Africa from 25°S to 12°N (Schmidt & Shattuck, 2014), specialized in raiding termites of the subfamily Macrotermitinae at their foraging sites (Lepage, 1981; Levieux, 1966). Colony size varies between 440 and 1400 adult ants (Lepage, 1981). The general foraging pattern of *M. analis* starts with scout ants searching an area of approximately 50 m radius around the nest for termite foraging sites. This searching phase can last up to 1 h and in unsuccessful cases the scout returns to the nest by a circuitous route (Longhurst & Howse, 1979). Once a scout ant has found a potential site it investigates it, while avoiding contact with the termites. After this investigation, the scout returns by a direct route to the nest to recruit nestmates for a raid (Longhurst & Howse, 1979). It recruits approximately 200–500 nestmates and leads them to the termites in a column-like march formation (Bayliss & Fielding, 2002; Longhurst & Howse, 1979). During the

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raid, division of labour occurs (Corbara & Dejean, 2000): larger ants (majors) break open the protective soil cover created by the termites while the smaller ants (minors) rush into these openings to kill and pull out the prey (Villet, 1990). After 13–20 min the hunt ends and the ants start collecting the dead termites and injured ants in need of assistance (Frank et al., 2017; Yusuf, Gordon & Pirk, 2013). Majors grasp up to seven termites between their mandibles and minors grasp up to three; the majority, however, return without termites (Yusuf et al., 2013). After collecting the termites, the column forms again and the hunting party returns to the nest together. *Megaponera analis* seems to show certain prey preferences, preferring to attack termite species that are easier to hunt and that have weaker defence capabilities (Yusuf et al., 2013).

The high variance in raid distances and raid sizes made us wonder how well the scouts used the information gathered at the prey site and how accurate these decisions were in the light of optimal foraging theory. This theory has been applied to various animals to understand their foraging patterns and behaviours (MacArthur & Pianka, 1966; Olsson, Brown, & Helf, 2008; Pearce-Duvet, Elemans, & Feener, 2011). Central place foraging theories expand upon present theories of optimal foraging to include animals that carry food back to a central place (Orians & Pearson, 1979; Schoener, 1979), as is the case for most ant species. We thus expected that increased accuracy of information conveyed by scouts would better match predictions of central place foraging theory. Additionally, although central place foraging theory has been extensively studied in honeydew-feeding ant species (Bonser, Wright, Bament, & Chukwu, 1998) and solitary foraging ants (Pearce-Duvet et al., 2011) little is known about how well it predicts the foraging patterns of group-recruiting predatory ant species, such as *M. analis*. These ants behave markedly differently to other ant species in their raiding behaviour, although certain similarities to some bee species can be observed (Abou-Shaara, 2014; Nieh, 2004), which we address in Discussion. Recruitment and foraging behaviour in ants are often regulated through pheromone trails. Food choices are passively regulated by the reinforcement of trails that lead to good food sources faster (Hölldobler & Wilson, 1990). Predatory species need to minimize the time between the prey detecting them and capture of the prey (Witte, Schliessmann, & Hashim, 2010). Widespread foraging strategies of predatory ants therefore include solitary foraging (most ponerines) and group foraging (as in driver ants) (Peeters & Crewe, 1987); in both cases no time is lost trying to recruit nestmates. In group-recruiting predatory ant species only a very small percentage of the colony leaves the nest in search of food sources before recruiting a substantial portion of the colony to go out to exploit it. If their foraging behaviour is optimized in accordance with central place foraging theory, it would imply that the scouts exert extensive control on the colony, since only they hold all the information necessary for optimizing raiding behaviour. Decision making would therefore not be regulated collectively but by individuals. *Megaponera analis* is an ideal model organism to study these questions.

## PREDICTIONS

We made the following predictions about the foraging behaviour of *M. analis* in the light of central place foraging theory.

(1) Animals should forage to maximize their net energy intake per unit feeding time, by minimizing the energy invested and selective food choice (Schoener, 1971). We expected *M. analis* to select food sources with a high amount of energy gained per unit time (i.e. hunting as many termites as possible per ant in as little time as possible). Furthermore, to minimize energy investment, raid size should vary according to the size of the patch and the density of foraging termites (to optimize the ratio of termites per ant).

(2) As distance from the central place increases, selectivity should increase (Orians & Pearson, 1979). Since food sources further away take more time and energy to reach, they should be richer in termites to compensate for the longer travel time. *Megaponera analis* should therefore only conduct raids to distant termite sources if they are of high quality.

(3) The optimal time a predator should spend at a food source before moving on to another site depends on the distance between feeding sites, if food intake rate at a hunting site decreases over time (Charnov, 1976). Applied to the central place foraging theory this implies that the longer the travel time the longer one should exploit the food source before returning to the nest. *Megaponera analis* should therefore spend more time at feeding sites further away from the nest.

(4) Food selectivity depends on the consumer's hunger state, with increased food intake leading to increased diet selectivity and specialization (MacArthur & Pianka, 1966; Schoener, 1971). We expected *M. analis* to start conducting raids on less favourable termite sources if no successful raids occurred for a while and the hunger state of the colony was high. Furthermore, foraging behaviour was expected to become more risk prone (Cartar & Dill, 1990).

A combination of laboratory and field experiments allowed us to test these predictions and shed light on the mechanisms regulating the foraging behaviour of group-recruiting predators. Do the individual scouts or collective decisions by the colony regulate it?

## METHODS

### Study Area and Organism

The study area is a humid savannah woodland in the Comoé National Park, northern Côte d'Ivoire (Ivory Coast), at the Comoé National Park Research Station (8°46'N, 3°47'W). The annual rainfall is 1500–2200 mm, mostly falling from May to September (Konaté & Kampmann, 2010). Colonies of *M. analis* were located in a radius of approximately 2000 m from the research station. The distances between the colonies varied between 10 and 200 m. Nests were most commonly located by following a raiding column or scout ant returning to the colony. In total 450 raids of 54 different colonies were observed. In these raids, the main termite species hunted was *Pseudocanthotermes* sp. but raids on *Macrotermes bellicosus* were also observed. Of these 450 field raids, data on the raiding parameters for this study were collected in 144 raids (134 for undisturbed colonies and 10 for hungry colonies). Colony size for 12 excavated colonies was between 900 and 2300 ants, a result comparable to previous studies in other regions (Villet, 1990; Yusuf, Crewe, & Pirk, 2013).

### Data Collection

Observations in April 2013 established that raiding activity was highest in the morning and afternoon hours between 0600 and 1100 hours and between 1500 and 1900 hours local time, which corresponds to previous observations (Bayliss & Fielding, 2002; Longhurst & Howse, 1979; Yusuf, Gordon, Crewe, & Pirk, 2014). Night raiding was also observed, but was not included in this study. Experiments and observations in the field were therefore carried out from 0700 to 1100 hours and from 1500 to 1800 hours from April to September 2013, August to October 2014, January to March and July to September 2015 as well as March to May 2016. Even though *M. analis* is known to show monophasic allometry within its worker sizes (Crewe, Peeters, & Villet, 1984; Villet, 1990), for statistical analysis and illustration the workers were divided into majors (head width > than 2.40 mm), minors (head width

<1.99 mm) and intermediates (head width 2.40–1.99 mm) as proposed by Villet (1990).

### Laboratory Colonies

Four excavated colonies were placed in artificial nests in the field stations' laboratory. The nests (20 × 20 cm and 10 cm high), made of PVC plastic, were connected to a 1 × 1 m arena. To enable raids, this arena was connected to a second arena (1 × 1 m) by a corridor either 10 or 30 m long. The ground was covered with soil from the natural habitat around the field station. The experiments were conducted after giving the ants 7 days to habituate to the artificial nests. Between experiments each ant colony was fed twice a day in the first arena, with a total of 300 termites per day, to ensure constant conditions. For the experiments *M. bellicosus* termites were placed in the second arena. These termites were found by scouts and triggered raiding behaviour on which we performed the experiments. Termites were placed in the second arena either at 0800 or 1600 hours and observed until a raid occurred or until 3 h elapsed. All laboratory experiments were carried out three times per colony (for a total  $N = 12$  per experiment). Owing to time constraints, the hunger experiments for large and small hunting grounds could only be done five times each with three colonies. All colonies were released into the wild at the end of the study (to their original nest location). For further details on laboratory keeping see Yusuf et al. (2013).

Although our results showed that field raids were predominantly conducted on *Pseudocanthotermes militaris*, we also observed raids on *M. bellicosus* in the field. We can thus safely assume that the species predated in the laboratory, *M. bellicosus*, is not an unnatural prey choice. We chose *M. bellicosus* as the prey species because of its ease of collection (collected from the surrounding area by attracting them with pots filled with dry grass overnight). Both species, *M. bellicosus* and *P. militaris*, forage principally on wood, grass or litter on the surface and cover their food with a thin layer of soil. The main difference between these species is the larger worker and soldier size of *M. bellicosus*. This might have affected the injury rate of *M. analis* during a raid, although this was not analysed in this study, but see Frank et al. (2017) for details on injured ants.

### Experiments

Data on raid size (number of ants participating in a raid) and termite-carriers (number of ants carrying termites on the return journey) were collected by counting the individuals of the raiding column on the outward and return journeys. The durations of the different raid phases (outward journey, time at the hunting ground and return journey) were also timed. Hunting time was defined as the time between the arrival of the ants at the food source and the start of the departure of the return column.

In the field, distance to the termite-feeding site was measured by using a 40 m long measuring tape. In the laboratory, distance to the food source was either 10 or 30 m.

The termite abundance in the laboratory experiments was manipulated by offering either 50 termites in an area of 50 cm<sup>2</sup> (small hunting ground) or 250 termites in an area of 1260 cm<sup>2</sup> (large hunting ground). The areas where the termites were released were closed off with plastic barriers, thus preventing them from leaving the designated hunting area. Furthermore, the area where the termites were released was kept moist and had dry grass on it (in contrast to the surrounding area, which consisted of dry soil) so that the termites could build galleries. The termites were given 1–2 h to build their galleries before the ants gained access to the arena. Scout numbers were quantified by

counting the ants outside the nest before each experiment. This number was only a conservative estimate as individual scouts entered and left the nest frequently, making it impossible to count them accurately (i.e. we could not tell whether a new scout left the nest or whether it was one we had previously seen entering the nest).

The hunger state of the colonies was manipulated by preventing raids for 48 h. In the field, this was done by placing 30 cm high PVC walls around the nest, which were dug 10 cm into the ground (to include all nest entrances within the enclosure). Observations throughout the starvation period confirmed that the scouts were unable to leave the enclosure (they were observed to search for exits during the activity period). In the laboratory, colonies were simply not fed for 48 h.

### Statistical Analysis

For statistical analysis and graphical illustration, we used the statistical software R v3.1.2 (R Core Team, 2013) with the user interface RStudio v0.98.501 and the R package ggplot2 v2.1.0 (Wickham, 2009). We tested for deviations from the normal distribution with the Shapiro–Wilks test ( $P > 0.05$ ). A Bartlett test was used to verify homoscedasticity ( $P > 0.05$ ). If data were normally distributed and homoscedastic an ANOVA was used to compare the significance of the results. If this was not the case a Kruskal–Wallis rank sum test was used, followed by a Dunn's test with Holm–Bonferroni correction for post hoc analysis. For comparisons between two nonparametric groups a Wilcoxon rank sum test was used. Linear correlations were calculated with a Pearson correlation test. Median values in the text are followed by a median absolute deviation.

## RESULTS

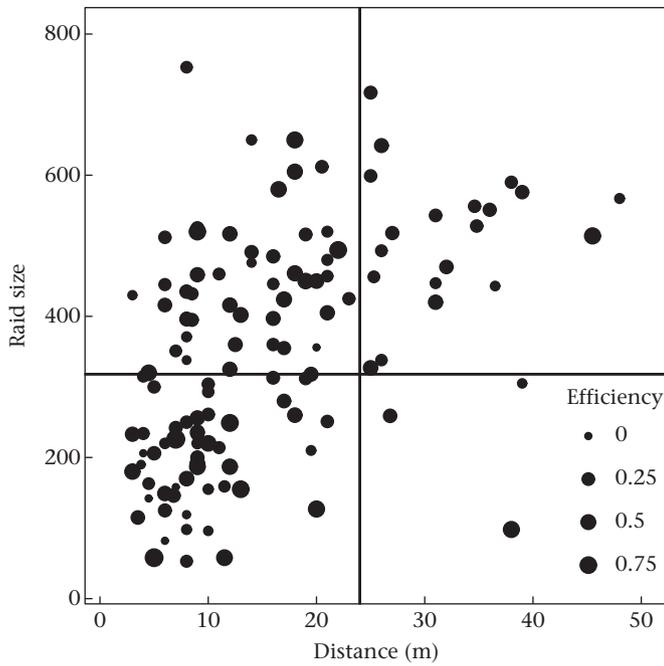
### Raiding Behaviour

In the field, raids of *M. analis* occurred two to five times a day per colony. Raiding activity was highest in the morning and afternoon but also seemed to be strongly influenced by temperature, rainfall and humidity. During the dry season (January–March) raiding activity was more pronounced during the night. The main termite species hunted in our study site was *P. militaris*, making up 95% of the analysed raids ( $N = 134$  raids).

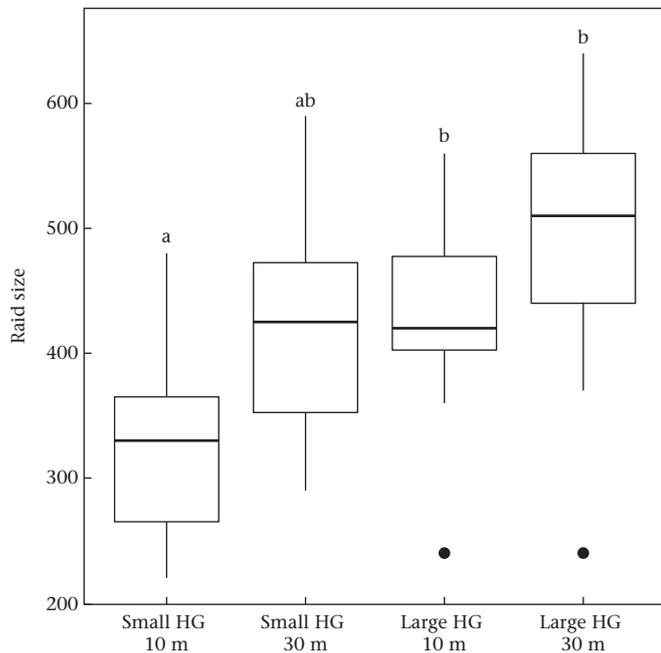
### Maximization of Energy and Central Place Prediction

In the field, raids of *M. analis* varied in size between 50 and 800 ants conducting raids up to 48 m from the nest (Fig. 1). The median percentage of ants carrying termites back to the nest after a raid was  $29 \pm 19\%$  (efficiency), of which each individual carried a median of  $3 \pm 2$  termites ( $N = 50$  termite-carriers). The percentage of termite-carriers was not significantly influenced by either distance or raid size (ANOVA:  $F_{2,116} = 0.18$ ,  $P = 0.84$ ). Small raids (less than the median raid size of 318) conducted to distant locations (further than half the maximum raid distance, i.e. >24 m) made up only 2.2% of the raids (three of 134 raids; Fig. 1, lower right quadrant).

In the laboratory, raid size clearly correlated with termite abundance at the feeding site rather than distance (Fig. 2, Table A1), with rich termite sites generally being exploited by large raids. Ant colony size also positively affected raid size (Fig. A1a; Pearson correlation:  $r_{66} = 0.58$ ,  $P < 0.001$ ). The percentage of the colony participating in a raid decreased with colony size. Small colonies conducted raids consisting of up to 75% of the colony, while larger colonies only allocated 35% of the colony to a raid (Fig. A1b; Pearson correlation:  $r_{65} = -0.65$ ,  $P < 0.001$ ).



**Figure 1.** Correlation between raid size and distance. Efficiency is the proportion of ants carrying termites after the raid; dot size corresponds to the proportion of efficiency. Raid size is the number of ants participating in the raid.  $N = 134$  raids. Horizontal line: median raid size (318 ants). Vertical line: half of the maximum raid distance (24 m).



**Figure 2.** Raid size for differing distance and food quantity in the laboratory ( $N = 12$  per experiment). Small HG: small hunting ground (50 termites in an area of  $50 \text{ cm}^2$ ); large HG: Large Hunting ground (250 termites in an area of  $1260 \text{ cm}^2$ ). 10 m and 30 m: distance from the nest to the feeding site. Box plots show median (horizontal line), interquartile range (box), distance from upper and lower quartiles times 1.5 interquartile range (whiskers), outliers ( $>1.5 \times$  upper or lower quartile) and significant differences (different letters;  $P < 0.05$ ).

#### Marginal Value Theorem

In the field, hunting time at the foraging site increased significantly with distance from the nest (Fig. 3a; Pearson correlation:  $r_{124} = 0.38$ ,  $P < 0.001$ ). Hunting time was defined as the time

between the arrival of the ants at the food source and the start of the departure of the return column. The number of termites killed per minute during the hunting period decreased with longer stays at the foraging site (Fig. 3b; Pearson correlation:  $r_{112} = -0.16$ ,  $P = 0.026$ ). In the laboratory, hunting time also increased with food abundance and distance (Fig. 4, Table A2).

#### Hunger State Prediction

In the field, starved colonies tended to conduct raids to significantly shorter distances (median  $1.9 \pm 0.9 \text{ m}$ ;  $N = 10$  raids) than control colonies (median  $12 \pm 8.9 \text{ m}$ ;  $N = 134$  raids; Wilcoxon test:  $W = 1320$ ,  $P < 0.001$ ). Raid size also varied strongly, with very small raids (50 ants) being conducted to very short distances (1 m; Fig. A2). The number of scouts leaving the nest in search of food also clearly increased with increasing hunger, with two to three times as many scouts leaving the nest in starved colonies (30–50 scouts per colony versus 10–20 scouts in control colonies, although these numbers are only approximations, since the exact number could not be determined).

In the laboratory, our experiments showed that raid size for starved colonies was significantly larger than for normal raids (Fig. 5, Table A3), both for small and large termite abundances at the hunting ground, although a larger sample size would be necessary to state this with certainty (Wilcoxon test:  $W = 7$ ,  $P = 1$ , effect size = 0.19; power = 0.057). The time between the discovery of the food site by the scout and the start of the raid was also significantly shorter in starved colonies ( $425 \pm 145 \text{ s}$ ) than satiated colonies ( $1040 \pm 889 \text{ s}$ ; Wilcoxon test:  $W = 0.81$ ,  $P < 0.001$ ).

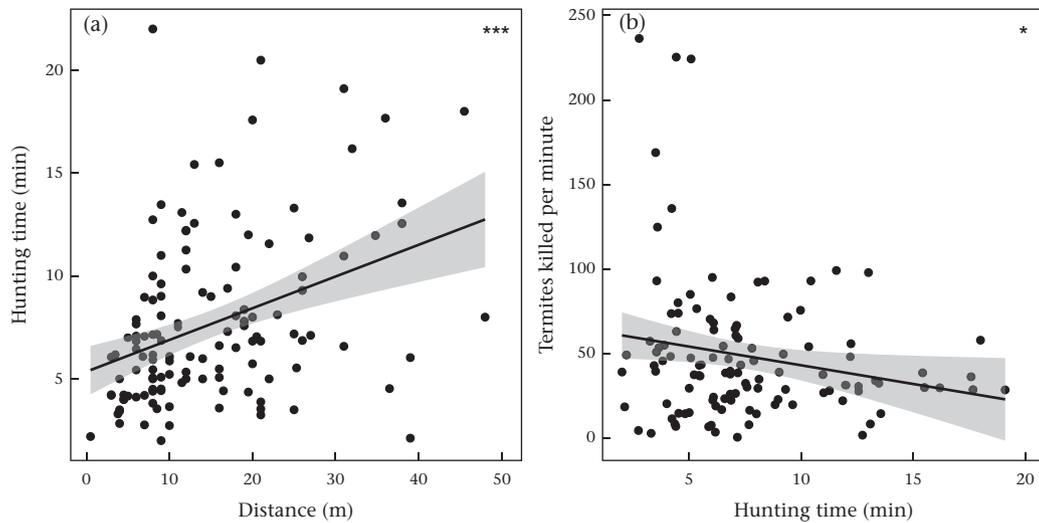
#### DISCUSSION

We confirmed various central place foraging theory predictions for *M. analis*. The scouts not only collected qualitative information about the food source, but also conveyed this information accurately to the colony. This gave us new insights into the importance of different factors for their raiding behaviour, such as termite quantity and distance. Remarkably, most of the decisions that optimized their raiding behaviour were regulated not collectively, but by individual scout ants.

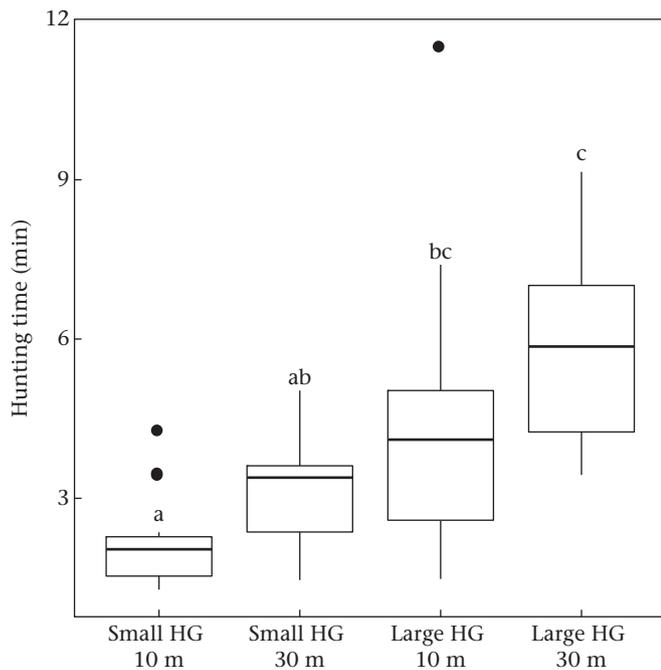
#### Maximization of Energy

In the laboratory, there was a clear positive relation between raid size and termite abundance at the foraging site thereby confirming predictions of the maximization of energy theory. These results support our hypothesis that scouts have to be able to assess the richness of a food source while examining it.

In the field, the median percentage of termite-carriers in a raid was 29% regardless of distance or raid size. Termites were very rarely observed to be left behind at the hunting ground (in any obvious quantity); we assume that the ants try to adjust their raid size to the richness of the food source, leading to only 30% of the ants having to transport back termites. The other ants have other essential roles in the hunting process, such as killing the termites and potentially also protecting the termite-carriers on the return journey. This was supported by experiments in the laboratory, with smaller raids only going for smaller hunting grounds (Fig. 2). We believe that the laboratory results can be extrapolated to the field since the information about patch quality, for regulation of raid size, was collected by scouts in the field and in the laboratory under similar conditions (the termites in the laboratory had 1–2 h to create foraging galleries prior to investigation by the scouts). Of course, once the actual hunt started these raids were markedly different; thus information on



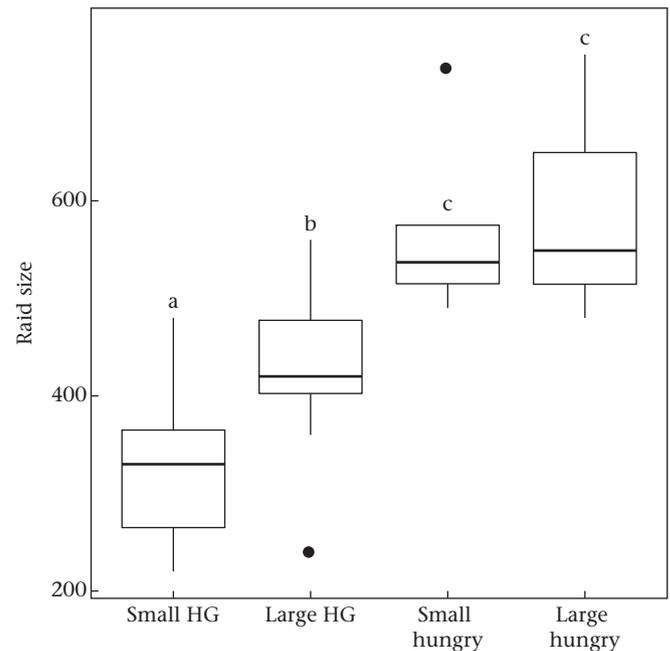
**Figure 3.** Relation of hunting time to distance and killing rate. A scatterplot is shown with linear regression line and 95% confidence interval (shaded area) for (a) time spent at the hunting ground in relation to distance from the nest and (b) the number of termites killed per minute during the hunting period in relation to the time spent at the hunting ground. \* $P < 0.05$ ; \*\*\* $P < 0.001$ .



**Figure 4.** Hunting time for differing distance and food quantity in the laboratory ( $N = 12$  raids per experiment). Hunting time: time spent at the foraging site; small HG: small hunting ground (50 termites in an area of  $50 \text{ cm}^2$ ); large HG: large hunting ground (250 termites in an area of  $1260 \text{ cm}^2$ ). Box plots show median (horizontal line), interquartile range (box), distance from upper and lower quartiles times 1.5 interquartile range (whiskers), outliers ( $>1.5 \times$  upper or lower quartile) and significant differences (different letters;  $P < 0.05$ ).

hunting time and percentage of termite-carriers should be compared with care.

Our field observations are in line with previous observations (Lepage, 1981; Levieux, 1966; Longhurst & Howse, 1979). Other studies in Tanzania and Kenya seem to imply that colony size is the main factor in raid size variation (Bayliss & Fielding, 2002; Yusuf et al., 2014). While this factor also played a role in our observations (Fig. A1a), the variation in raid size within the colonies can probably best be explained by adaptation of the raid



**Figure 5.** Raid size for hungry and satiated colonies in the laboratory. Small HG: small hunting ground ( $N = 12$  raids; 50 termites in an area of  $50 \text{ cm}^2$ ); large HG: large hunting ground ( $N = 12$  raids; 250 termites in an area of  $1260 \text{ cm}^2$ ); small hungry: colony starved for 48 h for small HG ( $N = 5$  raids); large hungry: colony starved for 48 h for large HG ( $N = 5$  raids). Box plots show median (horizontal line), interquartile range (box), distance from upper and lower quartiles times 1.5 interquartile range (whiskers), outliers ( $>1.5 \times$  upper or lower quartile) and significant differences (different letters;  $P < 0.05$ ).

size to the termite foraging site. Intercolonial differences in raid size were also not proportionate to colony size. Large colonies seemed to conduct raids barely larger than those of small colonies (Fig. A1b), suggesting that raid size is limited by other factors. Some possible limitations could be the recruitment capacity of the scout, raid organization or lack of richer/larger hunting grounds. Larger colonies seem to also have the advantage of conducting two raids simultaneously (personal observation).

Individual learning by the scouts might have influenced our results in the laboratory with the scouts learning the position of the food sources. Although this should not have influenced our main results, in the field the same site can also be exploited multiple times. The number of termites at the feeding site changes constantly, depending on humidity, time of day and activity of the termites; it is therefore still always necessary for the scout to properly assess the feeding site to adapt the raid size accordingly, which is also what we observed in the laboratory.

In ants, individuals can assess the quality/quantity of a food source to decide whether to recruit other ants or exploit the food source individually, thereby optimizing energy investment according to the food source (Hölldobler & Wilson, 1990; Witte et al., 2010). In *M. analis* individual exploitation of a food source is not an option. Conducting large raids to small hunting grounds would lead to a waste of energy, unnecessarily occupying a portion of the colony. The ability of *M. analis* to adjust their raid size to the hunting ground allows a more flexible allocation of limited resources (ants) in the foraging process and relies on individual decisions made by scouts, which collect the necessary information.

#### Central Place Prediction

At short distances the full spectrum of raid sizes was observed. With increasing distance from the nest, the minimal raid size started to increase, thereby reducing the variance until 98% of the raids were large at the furthest distances (Fig. 1). In the previous section, we showed that raid size correlated positively with termite abundance at the foraging site. We therefore conclude that food selectivity increases with distance. Furthermore, our laboratory experiments showed that raid size depended on termite abundance at the foraging site and not on its distance (Fig. 2), thereby confirming central place foraging theory.

The efficiency of a single ant seemed to be independent of raid size or distance (Fig. 1). At the same distance a large raid to a large food source is as efficient as a small raid to a small food source, from an energetic point of view. Why then do the ants not conduct small raids to far distances? We may explain this pattern by looking at the foraging process from the perspective of the individual scout rather than the raid. Scouts are exposed to considerably larger risks when searching for food sources alone. Those that move further from the nest spend more time travelling and are therefore exposed to predation risks for longer. This increased risk can potentially only be outweighed if it leads to conducting raids to rich foraging sites.

Distance also seemed to affect raid size, although the significant differences were clearer when looking at the termite abundance at the food source. An outlier is the result for large raids conducted at far distances for poor termite sites in the laboratory (Fig. 2). It is worth keeping in mind, however, that the experimental set-up removed the possibility of choice, forcing the ants to exploit the presented food source. If no other choices are present it makes sense for the ants to exploit an, under natural circumstances, unfavourable food source.

In conclusion, these experiments allowed us to identify food source quality rather than distance as the main factor affecting raid size. However, we still do not fully understand the raiding behaviour in the light of present theories due to the lack of observations of small raids to far locations.

#### Marginal Value Theorem

The hunting time at a food source in *M. analis* seemed to be in line with what the marginal value theorem predicts. Hunting time

increased with distance (Fig. 3a) but killing/collecting speed decreased over time (Fig. 3b), while richer food sources were exploited longer than poorer food sources (Fig. 4).

The diminishing returns over time at a raiding site are likely to be more pronounced in termites than more passive food sources. Termites start to actively retreat into their galleries as soon as the ants arrive, with the soldiers staying behind to protect the retreating workers (Corbara & Dejean, 2000). Nevertheless, a clear positive relation was observed between hunting time, distance and termite abundance, both in the laboratory and in the field. Since in the laboratory termites were unable to retreat, this may lead to less natural behaviour by the termites when attacked. Something to consider is also the handling time after the fight (i.e. collecting the dead termites); this phase is included in our definition of hunting time and could depend on the number of termites killed at the food patch. We believe that the handling time remained relatively constant since the raid size depended on the termite numbers (i.e. more ants were available to handle more termites). Furthermore, results for hunting grounds with the same termite numbers showed an increase in hunting time at greater distances (Fig. 4). We therefore believe that it is safe to assume that the hunting behaviour is in line with what the marginal value theorem predicts.

The marginal value theorem has been extensively studied in solitary foraging animals and ants (Olsson et al., 2008; Pearce-Duvet et al., 2011). Studies on ants mostly focus on single-prey loaders (Pearce-Duvet et al., 2011), in which the marginal value theorem does not apply (Charnov, 1976). There are some studies on honeydew-feeding ants (such as *Lasius niger*, *Lasius fuliginosus*, *Myrmica ruginodis*), which have observed foraging strategies in line with the marginal value theorem (Bonser et al., 1998). Our study is the first, though, to show these patterns in a group-hunting predatory ant species such as *M. analis*. The processes that regulate this for group-foraging ants remain unclear. *Megaponera analis* has various reasons, such as predation risk, to return to the nest together and they take great care to do so (Bayliss & Fielding, 2002; Longhurst & Howse, 1979). We propose a quorum decision-making process as the regulating mechanism for the hunting time. The ants could have a certain termite encounter threshold, which at a certain point leads the ants to switch from hunting termites to collecting dead termites. Further experiments are necessary, though, to determine a clear regulatory mechanism for the hunting time.

#### Hunger State Prediction

We observed that with increased hunger prey selectivity decreased and average raid size increased. We also observed more scouts searching for prey, in some cases doubling the number of scouts compared with satiated colonies.

Field experiments showed that raids were conducted to much shorter distances ( $1.9 \pm 0.9$  m versus  $12 \pm 8.9$  m), some of them even being conducted to locations so near (ca. 1 m) that a trail to the termites was formed rather than a normal raid, with very few ants participating. Additionally, our laboratory experiments showed that hungry colonies always tended to conduct overly large raids (Fig. 5), with shorter investigation of the hunting ground by the scouts beforehand ( $425 \pm 145$  s versus  $1040 \pm 889$  s for satiated colonies).

We hypothesize that a reduction in distance suggests that scouts become less selective in their prey choice, conducting a raid to the first termite location they find. This would imply that under normal circumstances scouts encounter termite foraging sites much more frequently but decide against exploiting them if they are too small. The reduced investigation time in hungry colonies

probably make it harder for the ants to adapt their raid size to the feeding site (due to a lack of accurate information) and may explain the lack of raid size variation in hungry colonies. An alternative hypothesis could be that hungry ants in the colony are easier to recruit, thus always leading to larger raids for the same recruitment effort (Fig. 5).

These results suggest that foraging behaviour becomes more risk-prone under hunger, supporting hunger state prediction theory and observations in bumblebees, *Bombus terrestris* (Cartar & Dill, 1990). Furthermore, bumblebees also became more sensitive to recruitment pheromones in hungry colonies (Molet, Chittka, Stelzer, Streit, & Raine, 2008). We hypothesize that by conducting large raids to feeding sites that, in principle, would not need it the colony invests a larger portion of its resources (ants) for the small chance of gaining more termites. The reduced food site selectivity and investigation time by the scouts suggest that they prefer to conduct a raid to a potentially unfavourable feeding site, thereby reducing the risk of being discovered at the cost of information. This implies an interesting interplay between collective and individual selectivity of prey choice. The colony would need to convey their hunger state to the scouts so that they can adapt their individual prey selectivity accordingly.

#### Individual Decision Making

Most of our results suggest a high degree of control by individual scouts on the foraging behaviour of the entire colony. Individual scout ants regulated most optimal foraging behaviours observed in this study. Scouts have to be acutely aware of the hunger state of the colony to know how selective they can be with their prey choice. They need to collect sufficient information about a termite foraging site to decide whether to conduct a large or small raid, while keeping distance from the nest in mind. This information must then be passed on to the colony so that the appropriate raid can be conducted. Unlike honeybees, *Apis mellifera*, it is not necessary for the scouts to pass on detailed information about the location of the feeding site to the others, since the scout leads the column of ants to the termites. Thus, the only information that is vital during recruitment is the termite abundance at the food source, thereby varying the number of raiding ants. Scouts do not always succeed with recruitment after finding a foraging site (personal observation), suggesting that some control by the colony in the collective decision to conduct a raid is present. The number of scouts searching for food also seems to depend on the hunger state of the colony and is therefore probably regulated collectively, potentially through thresholds regarding hunger. Although it is possible that the hunting time at the foraging site is also regulated by scouts (by giving a signal when to stop), we believe that a collective decision by the raiding ants (quorum decision making) is more likely.

#### Scouts in Social Insects

The foraging behaviour of *M. analis* can to some extent be compared with that of slave-making ants (Pohl & Foitzik, 2011). In the slave-making ant *Protomognathus americanus* the colony also depends on the accuracy of the decisions made by individual scouts for their raiding efficiency. Individual scouts can assess the size of a potential host colony and make their decision accordingly, with larger colonies having more pupae to be stolen (Pohl & Foitzik, 2011). One big difference to *M. analis* is that these colonies only include a handful of ants (three to six slave-maker ants) versus over 1000 in *M. analis* colonies. Furthermore, just because prey can be hunted in a group does not imply that it will be. *Ophthalmopone berthoudi*, for example, is a solitary hunting termite specialist in the sister genus of *Megaponera* (Peeters &

Crewe, 1987). There are various strictly termitophagous ant species that hunt solitarily or in groups. It is unclear, though, how exactly these different strategies for the same food source evolved and there are likely to be various factors influencing it (Peeters & Crewe, 1987).

Honeybees and some stingless bee species (Nieh, 2004) also have a certain proportion of workers scouting for food while the rest wait in the nest to be recruited (Abou-Shaara, 2014). Both *A. mellifera* and *M. analis* hunt a stationary but temporally variable food source: termite foraging sites do not normally change position if left undisturbed but are only active at certain times of day, similar to nectar and pollen in flowers. This is an important prerequisite since the time taken by a scout to return to the nest and recruit nestmates would be problematic when hunting mobile prey, although there are exceptions where scouts are present as in the ponerine ant *Leptogenys diminuta* (Witte et al., 2010). The necessity for scouts in group-hunting species can also be bypassed by directly foraging in groups, as in *Leptogenys* sp. in Cambodia (Peeters & De Greef, 2015). These ants hunt large millipedes in groups of several dozen workers; subduing their prey would otherwise be difficult. Thus, the millipede can be overwhelmed immediately without first recruiting nestmates, which would increase the risk of losing such mobile prey (Witte et al., 2010).

One very clear difference between honeybees and *M. analis* is the ratio of scouts to recruits. In honeybees 5–25% of the workers act as scouts, foraging individually and recruiting if need be (Seeley, 1983), while in *M. analis* scouts comprise roughly 1%. This stark difference could be due to the number of foraging trips. While *M. analis* will only exploit three to five food sources over a day, honeybees exploit dozens of different sources in the same time window (Abou-Shaara, 2014) and more importantly are able to do so alone. Since *M. analis* requires only a few hunting trips per day, a much smaller number of scouts could suffice to find enough adequate food sources. This could be comparable to certain kleptoparasitic stingless bee species, such as the genus *Lestrimelitta*, which invade other bee nests for food (Gruter, von Zuben, Segers, & Cunningham, 2016). Bumblebees offer an interesting example of a eusocial species foraging on stationary food sources without clear recruitment (Dornhaus & Chittka, 2004a). The current scientific reasoning for this is that the benefits of recruitment decrease with increasing patchiness of food sources (Dornhaus & Chittka, 2004b). Bumblebees forage mostly in open meadows in a very heterogeneous environment with many food sources (Dornhaus & Chittka, 2004a), so while activation of nestmates can be observed, there is no need for direct recruitment to a specific location. Ultimately the foraging behaviour of *M. analis* can be compared with that of many other social insects (stingless bees, slave-making ants); further studies are necessary, though, to determine the factors that truly regulate scout numbers and group/solitary foraging in a cross-family comparison.

#### Conclusion

In conclusion, we were able to show that most central place foraging predictions are fulfilled by the raiding behaviour of *M. analis*. Remarkably, this is not only achieved by collective decisions but also by an interplay between individual decisions by scout ants and collective responses by the colony, thereby having 1% of the colony (10–20 scouts) potentially deciding the fate and foraging efficiency of the other 99%.

#### AUTHOR CONTRIBUTIONS

E.T.F. and K.E.L. designed the study. E.T.F. collected and analysed the data and wrote the paper. Both authors discussed the results and commented on the manuscript.

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## Appendix

**Table A1**

Statistical differences in raid size depending on distance and food quality as shown in Fig. 2

Caste 1	Caste 2	Z	P
Small HG 10m	Small HG 30m	–1.90	0.11
Small HG 10m	Large HG 10m	2.33	0.049
Small HG 10m	Large HG 30m	3.90	<0.001
Small HG 30m	Large HG 10m	0.15	0.44
Small HG 30m	Large HG 30m	1.44	0.15
Large HG 10m	Large HG 30m	–1.44	0.22

Kruskal–Wallis rank sum test ( $X^2_3 = 15.7$ ,  $P < 0.001$ ) followed by Dunn's test; small hunting ground (HG) 10 m:  $N = 15$  raids; small HG 30 m:  $N = 8$  raids; large HG 10 m:  $N = 12$  raids; large HG 30 m:  $N = 13$  raids. See Fig. 2 for further explanation.

**Table A2**

Statistical differences in hunting time depending on distance and food quality as shown in Fig. 4

Caste 1	Caste 2	Z	P
Small HG 10m	Small HG 30m	1.43	0.077
Small HG 10m	Large HG 10m	–3.06	0.001
Small HG 10m	Large HG 30m	4.80	<0.001
Small HG 30m	Large HG 10m	–1.23	0.11
Small HG 30m	Large HG 30m	–2.66	0.004
Large HG 10m	Large HG 30m	1.58	0.057

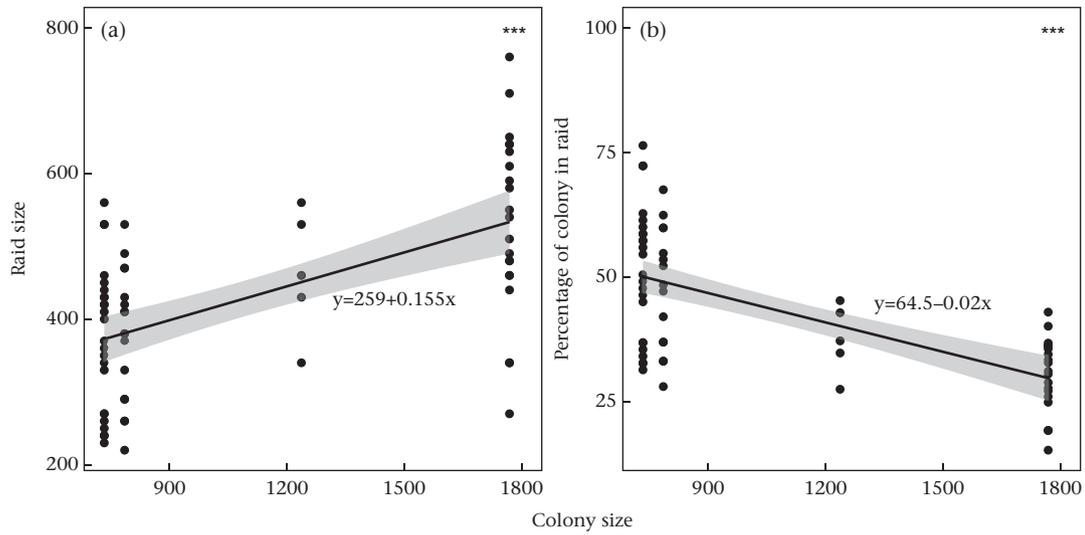
Kruskal–Wallis rank sum test ( $X^2_3 = 24.7$ ,  $P < 0.001$ ) followed by Dunn's test; small hunting ground (HG) 10 m:  $N = 15$  raids; large HG 10 m:  $N = 12$  raids; small HG 30 m:  $N = 8$  raids; large HG 30 m:  $N = 13$  raids. See Fig. 4 for further explanation.

**Table A3**

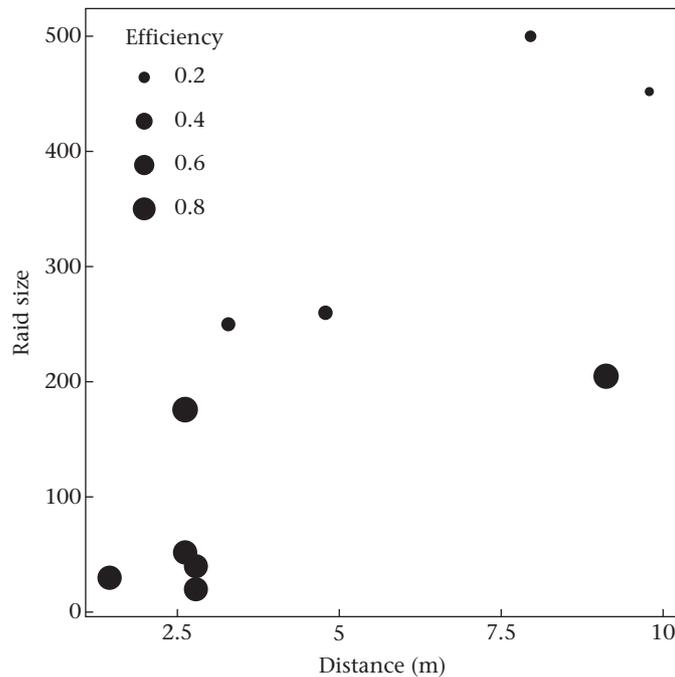
Statistical differences in raid size depending on hunger state and hunting ground as shown in Fig. 5

Caste 1	Caste 2	Z	P
Small HG 10m	Large HG 10m	-2.29	0.011
Small HG 10m	Small hungry	-2.99	0.001
Small HG 10m	Large hungry	-3.66	<0.001
Large HG 10m	Small hungry	-1.56	0.05
Large HG 10m	Large hungry	-1.88	0.03
Small hungry	Large hungry	-0.004	0.5

Kruskal–Wallis rank sum test ( $X^2_3 = 19.0, P < 0.001$ ) followed by Dunn's test; small hunting ground (HG) 10 m:  $N = 15$  raids; large HG 10 m:  $N = 12$  raids; small hungry:  $N = 5$  raids; large hungry:  $N = 5$  raids. See Fig. 5 for further explanation.



**Figure A1.** (a) Raid size in relation to colony size and (b) percentage of colony participating in the raid in relation to total colony size in the laboratory. Black line: linear regression line; shaded area: 95% confidence interval. \*\*\* $P < 0.001$ ;  $N = 69$  raids.



**Figure A2.** Correlation between raid size and distance for starved colonies. Efficiency is the proportion of ants carrying termites after the hunt. Raid size is the number of ants participating in the raid.  $N = 10$  raids.