Title
Raiding and Foraging Behavior of Megaponera analis in the Dja Biosphere Reserve of Cameroon

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Publication Date
2017-08-11

Data Availability
The data associated with this publication are within the manuscript.

Undergraduate

Library Prize for Undergraduate Research

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What drew you to the resources you used? (Please write a minimum of 100 words)

We conducted our research at the Dja Faunal Reserve, a rainforest in Cameroon (Central Africa). There is no internet access at this location so we had to prepare all of our background research before we left UCLA. Our research focused on a species of ant (*Megaponera analis*) that is found in Sub-Saharan Africa and has not been studied very thoroughly. The pre-existing literature that covers these ants was sparse so we were hoping to gain access to of all the information available. The large reserve of research papers and access to many journals drew us to the UCLA Library and its vast online database. We could not identify any published books that studied these ants' behavior so we were drawn primarily to published research papers that we were able to access only due to UCLA Library's large collection. The organization and ease of accessibility of UCLA's online research journal database really drew us in and excited us not only about our upcoming trip but also about conducting research in and of itself.

How did you find the material? (Please write a minimum of 100 words)

We found the material primarily through JSTOR, Web of Science, and Academic Search Complete. Through these databases we located the pre-existing literature on our species and then used it to dig further. Each paper we found through the UCLA Library database led us to further studies and this cycle really bolstered our knowledge and allowed us to plan out our experiment before we left for Africa. As there are no published books on this species, we really relied on the UCLA Library's research resources. We used each of the research journal databases to compile as much information as we could about our ant species so that we could develop an experiment that would add to the pre-existing literature as well as uncover something new about these ants that had not been previously studied. We were able to study whether the ants were opportunistic when foraging, and this had not been studied before. We would not have been able to plan out a novel experiment without UCLA Library's expansive resources.

Did faculty, librarians, classmates, or others help you on your journey, and if so, who and how? (Please write a minimum of 100 words)

Our teaching assistants, Madeline Cowen and Jessica Arriens, guided us through the UCLA Library's online research databases. They are graduate students who both do research at UCLA and have become experienced at navigating through the UCLA Library resources. They were the main force that guided us in our research preparation before we left to do our field research in Africa. Also, Dr. Greg Grether and Dr. Tom Smith, our professors on this field project, helped us plan our own experiments after we reported to them what we had learned based on the many research papers that we found through the UCLA Library. The knowledge that we gathered from the UCLA Library database helped us to explain the idea behind our project to the indigenous people at the Dja who assisted us in our field studies. After we completed our experiment and returned to UCLA, we needed help identifying our species and we were able to find a published book that covered our species identifications. The book was not already in the UCLA Library's circulation, but we requested it and they were able to obtain it for us. The book was instrumental in helping us identify our species and communicate our results to known entomologists.

In creating your project, how did you determine what materials were most suitable? (Please write a minimum of 100 words)

We found that most of the research papers focused on observing and collecting behavior data on the particular species of ant. From this knowledge, we decided that we wanted to run an experiment in order to learn something new about the ants. Following this decision, we then primarily focused on finding research papers that focused on foraging behavior so we could plan an experiment. We used the key word search features of the UCLA research journal databases in order to find other research done on ants (of various species) to widen our knowledge base. All of our knowledge came from research papers that we found in journals from the UCLA Library database. Our research on this particular species of ant was the first one done in the Dja Faunal Reserve. This allowed us to collect data to compare with pre-existing literature (based on studies done in different parts of Africa) so this helped us to decide what type of research papers to focus on before we left.

What strategies did you employ as you searched collections or gathered data? (Please write a minimum of 100 words)

When we first began collecting research, we just tried to find as many studies on our specific ant species as we could. After we found these papers through the UCLA Library database, we decided to read up on more ant literature (all species). By studying papers that were about ants in general, we were able to get an idea of how to plan and carry out insect research in a feasible way. There is a vast amount of existing literature on ants, so we primarily utilized the keyword and author search features to make our searches more efficient. We utilized these strategies in order to gather and prepare as much background knowledge as we could before we left for the rainforest.

How did you winnow and refine the resources you found into a meaningful bibliography to support your work? (Please write a minimum of 100 words)

Before we left for the rainforest (to carry out our experiment), we had to prepare as much knowledge of our species as we could, since there was no internet access and we were not sure what to expect of our species. In this vein, we gathered all of the existing literature from the UCLA Library database and formulated a proposed experiment. On the field, we were lucky in that we were able to carry out our proposed experiment as well as others on our desired species. After we returned to UCLA, we began writing our paper and comparing our data to the pre-existing literature, and this helped us narrow down which studies we would refer to in our bibliography. We also utilized the general ant research papers in order to support our findings and relate our species to general ant behavior. After we completed our paper, we went through and made sure that our bibliography was built around sources that helped us to characterize our species and develop our experiments along the lines of pre-existing ant literature.

Selection Criteria

Submissions will be judged based on the following criteria:

1. The clarity and eloquence of the description of the research process.
2. Superior ability to locate, select, evaluate, and synthesize library collections in support of the research paper or project.
3. The use of UCLA Library collections, including, but not limited to, print resources, databases, primary sources, materials in all media; as well as UCLA Library services and personnel.

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Raiding and Foraging Behavior of *Megaponera analis* in the Dja Biosphere Reserve of Cameroon

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Abstract

The Dja Biosphere Reserve in Cameroon is one of several regions in sub-saharan Africa home to the termitophagous ant *Megaponera analis*. This species has been studied in various regions of Africa but not in Congolese lowland rainforests. We are the first to conduct research on *M. analis* in this type of habitat. We collected quantitative data and conducted three field experiments in an effort to add information to the current pool of knowledge on these ants. We collected descriptive data to quantify *M. analis* raiding behavior, which included a mean velocity going out to forage of 2.96 cm/s and a mean velocity returning to nest of 3.40 cm/s. The average distance the ants travelled from ant nest to termite nest was an average of 22.43 m and the total number of ants in a raid averaged 237.2 ants. We then compared these mean values with past studies of *Megaponera* at forest and savannah ecosystems and found many similarities. Our field experiments were broken down into three hypotheses: (1) *M. analis* is opportunistic when foraging, (2) the buzzing noise made by the ants when agitated is used as a warning signal, and (3) ants in a raiding column are able to recognize their nestmates from other ants. In the first field experiment to test if *M. analis* is an opportunistic forager, we performed termite manipulations. We found that the ants took all termites they encountered during a raid excursion but they are species-specific. In the second field experiment, we performed playback experiments on both *M. analis* and their potential predator, the skink (*Trachylepis*). Neither the ants or lizards showed significant response to the playbacks so it remains unclear what purpose

the buzzing noise serves. In the third field experiment, we tested for nest mate recognition by introducing ants from different colonies to each other. We observed that *M. analis* was aggressive towards members of foreign colonies. This indicates that they can distinguish between nestmates and non-nestmates.

La réserve de Biosphère du Dja est l'une des nombreuses régions en Afrique subsaharienne où se trouve la fourmi termitophage, *Megaponera analis.* Cette espèce a été étudiée dans diverses régions d'Afrique mais pas dans la forêt de basse altitude du Bassin du Congo. Nous sommes les premiers à mener une telle étude sur *M. analis* dans ce milieu. Nous avons recueilli des données quantitatives et avons conduit trois expériences sur le terrain afin d'améliorer les connaissances déjà disponibles sur ces fourmis. Nous avons recueilli les données descriptives pour décrire le comportement *M. analis* pendant les raids, la vitesse moyenne lors de la sortie du nid était de 2,96 cm/s contre 3,40 cm/s lorsque les fourmis revenaient au nid. La distance moyenne parcourue par les fourmis entre la fourmilière et la termitière était de 22,43 m et le nombre total de fourmis dans un raid était en moyenne égal à 237.2 fourmis. Nous avons ensuite comparé ces valeurs moyennes avec celles des études antérieures sur *Megaponera* dans des écosystèmes forestiers et savanicoles et avons trouvé de nombreuses similitudes. Nos expériences sur le terrain ont été réparties en trois hypothèses : (1) *M. analis* est opportuniste pendant le fourragement, (2) le bourdonnement émis par les fourmis lorsqu'elles sont pertubées est un signal d'avertissement, et (3) les fourmis peuvent différencier leurs compagnons de nids des autres fourmis. Dans la première expérience, nous avons, pendant le raid, proposé des termites aux fourmis et avons noté que les fourmis les ont saisies toutes, mais elles sont spécialistes d'une seule espèce. Dans la deuxième expérience, nous avons rejoué le bruit des fourmis à elles-mêmes d'une part et à leur potentiel prédateur, le scinque (*Trachylepsis*) d'autre part. Aucun des deux groupes n'a montré une réaction significative ; il reste donc à déterminer à quoi sert ce bourdonnement. Dans la troisième expérience, nous avons testé l'agressivité des fourmis en mettant les fourmis venant de colonies étrangères les unes avec les autres. Nous avons observé que *M. analis* était agressive envers les membres des colonies étrangères. Cela indique qu'elles peuvent faire la distinction entre leurs compagnons de nid et les autres fourmis.

Introduction

Megaponera analis, (previously known as *Pachycondyla analis* and *Megaponera foetens*), is a sub-Saharan ant species that forages on termite nests. This species has been studied in a Tanzanian coastal dry forest (Bayliss and Fielding, 2002), a Nigerian primary savannah woodland (Longhurst and Howse, 1979), an Ivory Coast savannah (Levieux, 1966), southern Africa (Fletcher, 1973), and a Kenyan savannah (Yusuf et al., 2014). They have been thoroughly studied in these different habitats as models of social communication and foraging systems. No research, however, has been done in a Congolese lowland rainforest until now. We studied *M. analis* in the Dja Biosphere reserve in Cameroon, Africa. The Dja Biosphere reserve is a 526,000-ha dense tropical rainforest. Our study of this species in the lowland rain forest of Cameroon allows us to compare its biology with studies conducted in other regions and habitats of Africa.

M. analis shows a characteristic behavior of raiding termite nests (Fisher and Bolton, 2016). Raids tend to occur right after dawn and right before dusk. It is hypothesized that the activity of the ants is influenced by temperature (Bayliss and Fielding, 2002). Once scout ants have located a potential food source, they return to their colony and recruit a column of workers to begin a raid. On average, 300 workers join the foraging party. The party follows the pheromone trail previously laid by the scout to the termite nest (Jackson et al., 2007). Upon arrival, the major workers break through the termite tunnels and minor workers dig further in. Termites are then captured, stung, and placed near the tunnel entrance. Both major and minor workers then haul the prey back to their colony (Crewe et al., 2014). *Megaponera* foraging behavior has been studied and each successive study has found similar patterns in this behavior (Hölldobler et al., 1994).

The primary purpose of this study was to compare the raiding behavior of *M. analis* in Cameroon to that of the same species in other regions and environments in Africa. We also carried out a series of field experiments to further characterize the behavioral repertoire and social structure of this species. The goal of the first experiment was to determine whether the workers are able to opportunistically predate termites that they encounter while following a raiding trail and, if so, whether their response depends on the species of termite. We hypothesized that *M. analis* does forage optimally. The goal of the second experiment was to investigate the function of a buzzing noise that the ants make when a raiding column is disturbed; specifically, whether the buzzing noise is used as a signal to their nestmates that there is danger or is it used to warn a predator. We hypothesized that the buzzing noise is used as a warning signal to potential predators but we also tested for effects on the behavior of the ants themselves. The third experiment addressed nest mate recognition; specifically, does *M. analis* differentiate between members of their own colony and members of a foreign colony? We hypothesized that *M. analis* can distinguish between nestmates and foreigners. To investigate these behavioral traits, we carried out termite manipulations, playback experiments, and intercolony aggression experiments.

Methods

Study Site

This study took place in the Dja Biosphere Reserve in Cameroon, Africa (02°40' to 03°23'N; 12°25' to 13°35'E, elevation 400 to 800 m) during the dry season from January 30, 2017 to February 13, 2017. The Reserve is a dense tropical rainforest surrounded by the Dja River and covering approximately 526,000 ha. Rainfall averages 1600 mm annually. Research was conducted near the center of the reserve at the 25 km^2 study area surrounding the Bouamir Research Station (3°11′N, 12°48′E) (Holbrook and Smith, 2000).

Sample Size

Data was collected on 28 colonies found near the field station and along foot trails (Figure 1). We gathered descriptive data and conducted experimental trials on 21 colonies. Experimental trials were carried out on an additional seven colonies.

Descriptive Data Collection

Before conducting field experiments, we collected quantitative descriptive data for each colony during a raid, including: velocity of the raiding column, number of ants in total and ants carrying termites, distance traveled, temperature, humidity, and type of habitat. This data was collected to compare to previous studies (at other sites). The velocity was recorded by timing how long it took an ant to travel 50 cm from their home nest to the designated termite nest (Yusuf et al., 2014). This was done by laying a measuring tape parallel to the pheromone trail and timing how long it took an individual ant to travel the 50 cm, both to and from the raid. On the way back from the raid, a velocity estimate was taken of an ant carrying a termite. Ants were counted as they exited their nest during a raid, and as they returned after a raid. The number of ants carrying termites was also tabulated to estimate the foraging success of each raid. The length of the pheromone trail was measured as the distance from the ant nest to the termite nest along the trail. The temperature and relative humidity of the air was recorded using Kestrel 3000 Pocket Weather Meter (MPN #0830) and the surface temperature of the entrance of the ant nest was recorded using an infrared thermometer. The nest type was recorded and the nest height was measured using a measuring tape. Time of day was recorded when the raid party was first seen by observers and when the last ant entered the ant nest after the raid. GPS coordinates were recorded and logged in a handheld GPSMap 60CSX (Unit ID: 3570101364).

Termite Manipulation

Termite manipulations were done on a total of 21 raiding parties to test if *M. analis* is opportunistic when foraging. Two species of termites were collected to present to the raid party on their way to raid a termite nest and on their way back after a raid. The first species was of the genus *Cubitermes*. The second species was *Macrotermes ivorensis*. We tested only one species of termites per trial to control for any potential termite preferences by the ants. Multiple termites were experimentally placed along the pheromone trail of the ants and the ants' reaction was observed and recorded. The behavior was recorded as either taking the termite or rejecting it.

Ant Playbacks

To test whether the buzzing noise *M. analis* makes might be used in either intra- or inter-colony communication, we recorded the respective buzzing noise of the ants at each colony we collected our quantitative descriptive data from earlier. This was done using an iPhone 6S. At each colony, we played back a recording from the same colony as well as another recording from a different colony. We controlled for the iPhone by holding it to the colony for ten seconds and watching for any reaction. This confirmed there would be no reaction to the presence of the iPhone itself (before noise stimulus was presented from it). We also recorded several ambient forest noises (without the ant buzzing) to use as a control. These were also played to the colony for ten seconds. We recorded ant response by observing if there were any changes in behavior, including change in movement, speed, or buzzing noises made in response.

Lizard Playbacks

To test whether the buzzing noise made by *M. analis* is as a warning signal to potential predators, we conducted ant playbacks to skinks. Lizards are known to eat ants and are therefore believed to be a potential predator of *M. analis* (Meyers and Herrel, 2005). All of the skinks we tested were of the *Trachylepis* genus, potential species including: *affinis, albilabris, makolowodei*, and *polytropis*. More research is necessary to confirm they include *M. analis* in their diet. We obtained a 1.80-meter stick and zip-tied an iPhone 6S to one end. During the hours 09:00 to 12:00, we waited for skinks to bask and perch in accessible areas where we would then play the recordings to them. We flipped a coin to randomly choose which recording to use on our first sample, then alternated between ant and ambient noise. For each trial, the iPhone was placed within a half-meter of each individual skink and played a noise for ten seconds. Trials were aborted if the lizard moved away prior to our presentation of the stimulus.

Thirty recordings of both ambient and ant noise were used to ensure multiple exemplars of each respective type of noise. We completed 20 trials overall, with most skinks being tested for both ambient and ant noise. A trial was classified as having no reaction when the skink remained still and did not move away within ten seconds. It was classified as having a response to the playback noise when the skink would scurry a few paces, pause, turn its head, and then flee the area. Recordings of behavior were only taken during each playback duration.

Nest Mate Recognition

To determine whether *M. analis* can distinguish between members of its own colony and those of a foreign colony, we first collected major and minor workers from different colonies encountered along trails. Each of the samples were separated by colony number and placed into separate plastic bags. The ants were then marked on the abdomen with Decocolor paint markers (Uchida of America Corp., Torrance, CA, U.S.A.). We designated these ants as the foreign colony and took the samples with us when surveying surrounding trails. When we encountered a new column of *M. analis,* we designated it as the home colony. Major and minor workers from the home colony were taken, placed in a plastic bag, and marked with a different color. Next, we simultaneously introduced the foreign and home colony ants from the plastic bags to the column. A pair of majors ants, one from each colony, were introduced simultaneously. Once the response to the majors was recorded, the pair of minors were then introduced. We used a scale from 1 to 5 to describe behavioral response to foreign and home ants where 1 indicated no response, 2 was for interactions lasting for less than three seconds, 3 for contact lasting greater than three seconds, 4 for aggressive interactions such as fighting and stinging, and 5 was for interactions resulting in the death of the introduced ant. We continued to follow the ants until both the home column entered the nest and the foreign ant travelled a distance far away enough for us to lose sight of it. This process was applied to 12 different home colonies for a total of 12 sampling units.

Results

Descriptive Data

In the Dja Biosphere Reserve, *M. analis* colonies were primarily above-ground, inactive termite nests, though we observed some colony nests that were located directly underground, as was found in a previous study (Villet 1990). The average nest height was 25.76 cm (sd = 19.26). The surface temperature of each ant nest was always a few degrees Celsius cooler than air temperature. On average, surface temperature was 22.61 °C (sd = 1.25 °C, n = 20) and air temperature was 25.40 °C (sd= 1.77 °C, n = 20) (Table 1).

The air temperature at which *M. analis* conducted raids in the Dja was very similar to the air temperature at which raids were conducted in a Tanzanian coastal dry forest (Bayliss and Fielding, 2002) (Two-sample t-test, p=0.330) (Table 3). However, raids in the Kenyan Savannah at Mpala occurred at a lower average air temperature of 23.10 °C (Two-sample test, p<0.001).

In the Dja, the mean velocity of ants going to forage (mean=2.96 cm/s) was slower than ants without termites coming back from a forage (mean=3.40 cm/s). Both of these values were again similar to the velocities of ants travelling in the Tanzanian coastal dry forest. A study conducted in a Nigerian Guinea Savannah (Longhurst, Baker, and Howse, 1979) found going and returning velocities to be mean=3.80 cm/s and mean=4.60 cm/s, respectively. However, ants at this location were on average faster going to raid than at the Dja (Two-sample t-test, p=0.0027). *M. analis* tended to travel much faster in the Kenyan Savannah than in the Dja as well (mean going out=6.70 cm/s and mean coming back=13.03) (Two-sample t-test, p<0.001).

M. analis raiding parties travelled distances of up to 53.34 m from their colony to a termite nest. The mean distance travelled at the Dja (mean=22.43 m, sd=12.07, n=20) was almost 10 m further than the mean distance travelled at the Tanzanian coastal dry forest (mean=13.03 m, sd=8.22 m, n=97). Colonies that traveled more than 15 meters had a greater percentage of ants successfully return with termites (mean=24.08%, sd=22.08, n=14) than colonies that traveled less than 15 meters to raid (mean=9.26%, sd=16.57, n=6) (Table 1).

Interestingly, the average number of total ants in a raiding party at the Dja (mean=237.2, sd=206.4, n=20) was similar to what other studies found in the Tanzanian coastal dry forest (Two-sample t-test, p=0.551), Kenyan savannah (p=0.646), and Nigerian guinea savannah (0.473). In the Dja, the average number of successful ants returning from a raid was 75.80. Again, the studies in Tanzania and Nigeria had similar means (p=0.757 and 0.791, respectively). The Nigerian guinea savannah did not have information regarding the number of successful ants.

Termite Manipulations

To determine whether *M. analis* is opportunistic, we used Fisher's exact test to see if the ants were more likely to forage on either species (*Macrotermes ivorensis* vs. *Cubitermes*) if offered termites (p = 3.402 x 10^-5). Out of ten trials, *M. analis* took no termites of the first species. The ants encountered the termites and touched them with their antennae, sometimes even grasping the termites with their mandibles, but then left the termites behind and continued to move in their column. For the second species of termites, all but one of 11 raiding parties took them. The ants stung, grabbed, and carried the termites just like they would during a normal raid. The one party that did not take these termites behaved the same way as the ten parties did with the first species of termites.

Ant and Lizard Playbacks

Playbacks of ant and ambient noises were done on both ants and lizards. Of 20 raiding parties, *M. analis* did not react once to the playbacks of their own buzzing noise or to ambient noise. The column continued to move forward without any change in behaviour. In the lizard playback experiments, five of 17 lizards reacted to the ant noise while one of 17 lizards reacted to the ambient noise. Lizard reactions to the *M. analis* recordings were found not to be significantly different from reactions to ambient noise (Fisher's exact test, $p = 0.17$)

Nest Mate Recognition

M. analis reacted aggressively towards the foreign ants from the experimental group but they remained neutral towards their nestmates from the control group (Fig. 3). The main party recognized their nestmates and did not attack them once in any of the 12 trials. However, foreign ants were grabbed, bitten, and stung 9 times out of 12 trials. Interactions between the main party and the experimental group were often ranked as a 4 (mean=3.33, n=12). Interactions between the main party and the control group were often ranked as a 2 (mean=1.83, n=12). The average rankings of the two groups was statistically different; colonies responded more aggressively to foreign ants than the painted nestmates (Wilcoxon paired-sample rank test, p-<0.003). The number of attacks on nestmates was also significantly different from the number of attacks on foreign ants (Fisher's exact test, p<-0.001).

Discussion

Our descriptive quantitative data helps to characterize *Megaponera analis* among the other existing data. The temperature of the ant nests was consistently cooler than the temperature of the air. The velocity of the ants returning to their nest was higher in comparison to the ants leaving their nest, and this trend was found in Kenyan savannah (Yusuf et al., 2014) and

Nigerian primary savannah woodland (Longhurst et al., 1978). The reverse was found in Tanzanian coastal dry forest (Bayliss and Fielding, 2002), so a wider study of this species of ant would allow further analysis of the relationship between velocity and location. The distance that the ants traveled varied in our observations, but we found that colonies that traveled more than 15 meters had a greater percentage of ants return with termites (successfully) than those that traveled less than 15 meters. Figure 2 offers a plot of percent success of a raiding colony as a function of the distance traveled. This figure suggests that with more data samples, a stronger correlation/trend between distance traveled and success rate could be found. We did not find any big trend relating to direction of raids. The number of ants in a column, as well as the number of ants that were successful in foraging, was consistent throughout our study and it was similar between the other studies as well.

The results suggest that *Megaponera analis* is opportunistic for genus *Macrotermes,* but not for *Cubitermes* supports our hypothesis that ants forage opportunistically, but the genus/species of termites they prefer to forage matters. *M. analis* never took *Cubitermes* but took *Macrotermes ivorensis* 90% of the time. We observed that in addition to inspecting *Cubitermes* with their antennae, ants would sometimes even grab *Cubitermes* termites with their mandibles and then quickly drop them. *Cubitermes* were always rejected, regardless of whether or not they were picked up. A future experiment to test the preferential behavior of ants would be done by presenting multiple termite species at the same time. With this experiment, one could observe the behavior of the ant and how it is able to distinguish between the species of termites.

Further experimentation must be conducted to understand the preferential behavior of the ants. Based on our observations, the differing habitats of the different termite species may play into why the ants prefer one. The *Macrotermes ivorensis* live in the ground while the *Cubitermes* live in free-standing soil mounds that are raised off the ground. We never observed *Megaponera* leaving the ground whilst on a raid. It is possible that the ants we observed do not recognize *Cubitermes* (when we offered it) because they do not raid in that type of habitat. While the raiding parties were opportunistic, they never abandoned their party or quit their raiding activities. The ants rejected *Cubitermes* sensed the species by touching them with their antennae and mandibles.

Ant and Lizard Playbacks

Ants did not respond once to playbacks of their own buzzing noise, and there appears to be no correlation between the ants' buzzing noises and skink reactions. It is possible that these ants cannot hear airborne-presented noises as has been found in a different species of ant (Hickling and Brown, 2000). For skinks, we did playbacks only on the *Trachylepis* genus (potential species including: *affinis, albilabris, makolowodei*, and *polytropis*). Five lizards reacted to the buzzing noise of the ants but this correlation was not statistically significant. Our experiment is inconclusive because it is unknown which skinks, if any, prey on *M. analis*. More research is needed to determine whether skinks are predators of *M. analis.* In addition, future experiments could study the relationship between the ants' buzzing noise and other potential predators. The true purpose of this buzzing noise remains unknown, but further research could help elucidate this.

Nestmate Recognition

Our results support our hypothesis that ants can differentiate between their nestmates and ants from other colonies. In our observations, we noticed several common behaviors between home colony ants and foreign-introduced ants. Each time we introduced an ant, whether home or foreign, it was first inspected by the home column. This behavior involved the ants using their antennae to stop and brush the newly introduced ant. This redundant inspection-behavior offers further insights into how the ants assess their surroundings.

When a foreign ant was presented, the level of aggression was recorded as a level 4 (a reaction of biting and stinging by home colony ants) in a majority of the trials. The foreign ant always dispersed after being attacked (we never observed a foreign ant enter a nest). On a few occasions, we watched a foreign ant initially follow a home colony pheromone trail only to quickly disperse after coming into contact with the native ant column. Previous studies have detailed that ants instinctively follow a pheromone trail, and perhaps *Megaponera* cannot differentiate between pheromones of different colonies (Luke and Panait, 2004). Pheromone trails are able to be relocated, so it is also possible ants may sometimes accidently follow the wrong trail, which could result in a fight (Robinson et al., 2008). No fight resulted in death (level 5), but the longest fight we recorded lasted about 4.5 minutes. When an ant from the home colony was reintroduced to the native column, there appeared to be a disturbance and the ants would inspect the reintroduced individual, but rarely followed this up with an aggressive behavior. Only in one trial did we observe a level 3 reaction to a home colony ant, while the 11 other trials were primarily level 2. We can visualize this comparison in Figure 3. To further characterize and categorize this behavior, ant specimens should be collected outside the Bouamir reserve area to better test if distance correlates with aggression between ant colonies.

Acknowledgements

We would like to thank Professors Greg Grether and Thomas Smith, as well teaching assistants, Madeline Cowen and Jessica Arriens, for their guidance throughout this whole process and all the time and energy invested in making this research possible. We would like to thank Kevin Njabo for helping with logistics as well. A big thank you to the Baka guides and Eco-guards for guiding us through the forest. Thank you to the staff at Bouamir Camp as well. We would like to thank Vincent Deblauwe for help with mapping our ant colonies. Thank you to Brian Fisher and Paul Eggleton for ant and termite identifications. A special thanks to the Congo Basin Institute for accommodating us at Bouamir Camp and providing supplies. We would like to extend a thank you to the Institute of the Environment and Sustainability and the Center for Tropical Research. This study was carried out through the UCLA Field Biology Quarter program, with financial support from the Department of Ecology and Evolutionary Biology at UCLA and the PIRE Grant.

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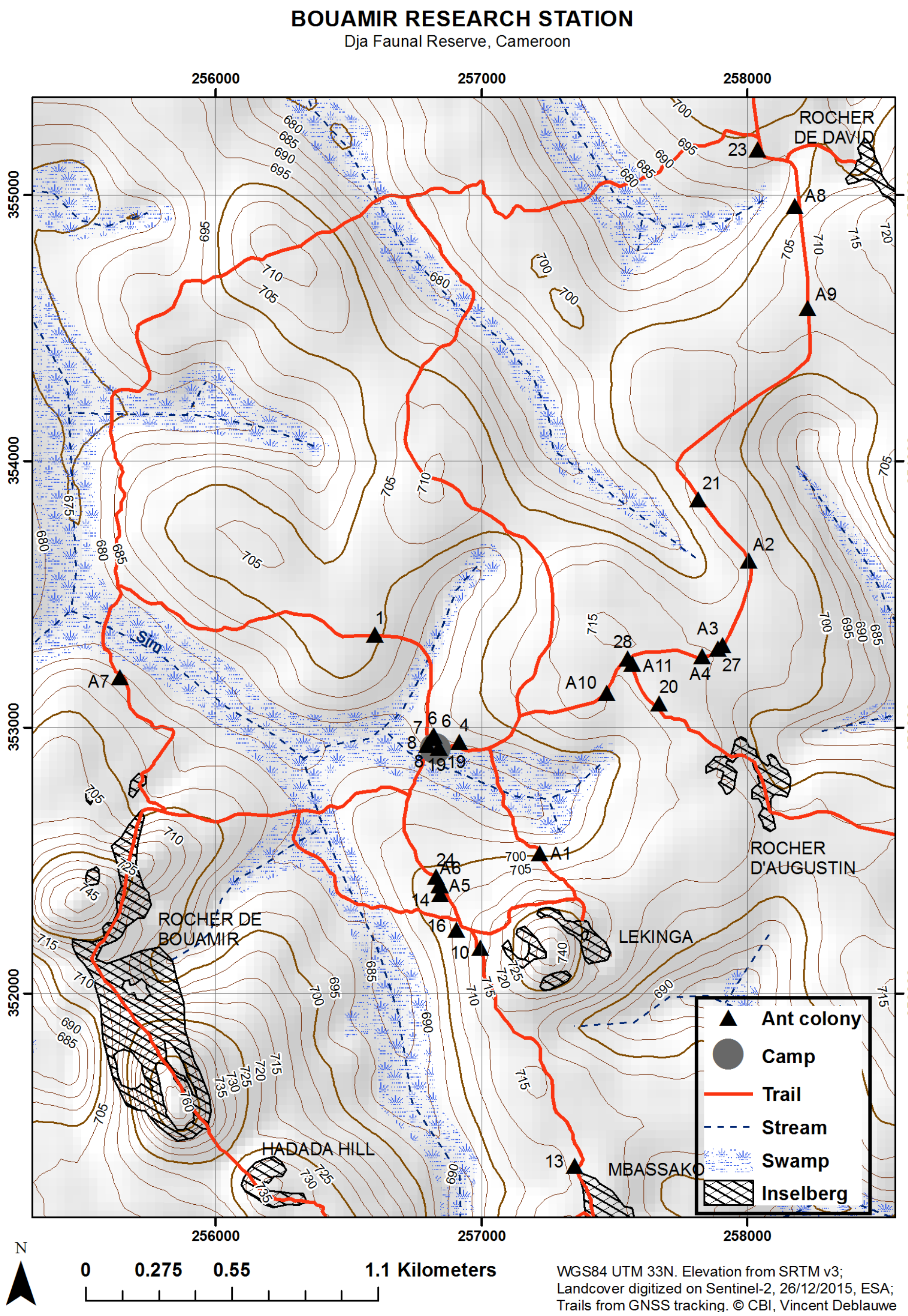


Fig. 1 Map of Bouamir Research station and surrounding trails. The black triangles represent the *M. analis* colonies (n=28) observed in this study.

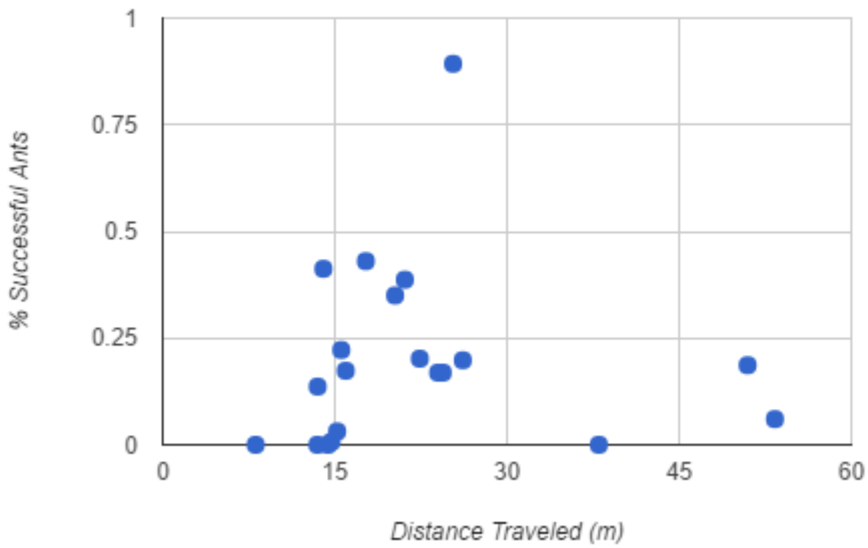
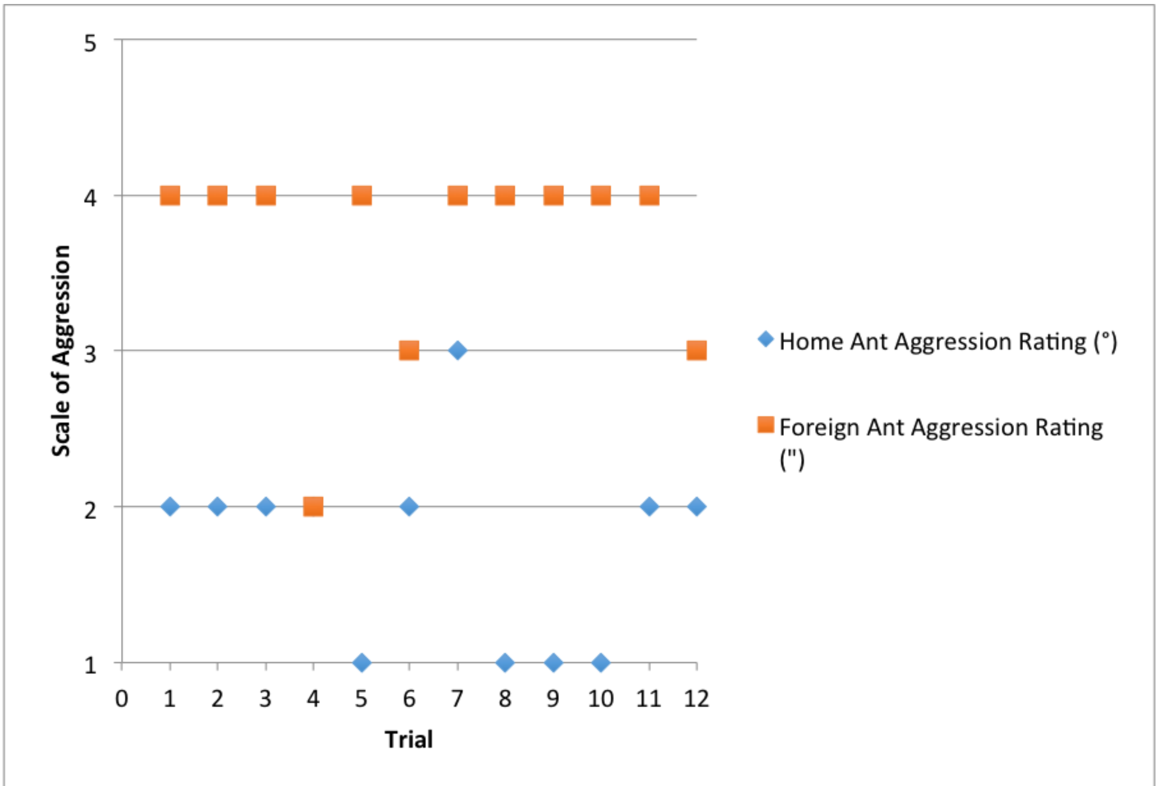


Fig. 2 Scatter plot of colonies' success rate as a function of distance traveled. Each plot point is a separate colony.



Intercolony Aggression Scale	
1	No Interaction
2	Interaction<3s
3	Interaction>3s
4	Fighting
5	Death

Fig. 3: Scale of Aggression in *M. analis*. Level of intercolony aggression between nestmate ants and foreign ants based on 12 trials conducted in the Dja.

Table 1: Average and standard deviations of quantitative behavioral data collected on raiding columns from 20 different colonies. The percentage of successful ants was separated into colonies that traveled less than 15 meters to raid and colonies that traveled more than 15 meters to raid (as well as calculated overall).

M. analis Raid Data		
	Means	Standard Deviation
Ant Nest Temp. (°C)	22.61	1.251
Air Temp. (°C)	25.39	1.774
%RH	82.00	4.430
Velocity Out (cm/s)	2.960	1.083
Velocity In W/o Termites (cm/s)	3.394	1.174
Velocity In W/ Termites (cm/s)	2.647	0.3998
Distance (m)	22.43	12.08
Duration of Raid (min)	15.33	9.708
#Raid Ants	237.2	206.4
#Successful Ants	75.80	186.0
%Ants with Termites Overall	20.14	21.62
%Ants with Termites (Raid Distance < 15m)	9.26	16.57
%Ants with Termites (Raid Distance > 15m)	24.80	22.08

Table 2: Mean, standard deviation, and sample size comparison of quantitative raid data between the Dja, a Tanzanian coastal dry forest (Bayliss and Fielding, 2002), a Nigerian primary savannah woodland (Longhurst and Howse, 1979), and a Kenyan savannah (Yusuf et al., 2014).

	The Dja	Tanzanian Coastal Dry Forest	Kenyan Savannah	Nigerian Primary Savannah Woodland
Temperature (°C)	25.40 (1.77) n=21	24.87 (3.35) n=79	23.10 (0.21) n=330	N/A
Velocity Out (cm/s)	2.60 (1.08) n=12	3.2 (0.77) n=18	6.70 (2.30) n=330	3.80 (N/A) n=220
Velocity In (cm/s)	3.10 (1.17) n=17	2.98 (0.72) n=21	13.03 (6.40) n=330	4.60 (N/A) n=220
Distance (m)	22.43 (12.07) n=20	13.03 (8.22) n=97	N/A	N/A
# Ants in Raiding Party	237.2 (206.4) n=20	266.6 (159.6) n=113	259.0 (138.3) n=330	203.0 (116) n=67
#Ants Carrying Termites	75.80 (186.0) n=20	88.98 (65.54) n=113	64.62 (22.03) n=330	N/A

Table 3: Two-sample t-test comparison between the Dja and a Tanzanian coastal dry forest (Bayliss and Fielding, 2002), a Nigerian primary savannah woodland (Longhurst and Howse, 1979), and a Kenyan savannah (Yusuf et al., 2014) (*Two-Sample T-test, 2017)*.

Two-Sample T-Test: P-Value	The Dja vs. Tanzanian Coastal Dry Forest	The Dja vs. Kenyan Savannah	The Dja vs. Nigerian Guinea Savannah
Temperature (°C)	0.330	<0.001	N/A
Velocity Out (cm/s)	0.113	<0.001	See Table 3
Velocity In (cm/s)	0.714	<0.001	See Table 3
Distance (m)	0.003	N/A	N/A
# Ants in Raiding Party	0.551	0.646	0.473
# Ants Carrying Termites	0.757	0.791	N/A

Table 4: One-sample t-test comparison between the Dja and a Tanzanian coastal dry forest (Bayliss and Fielding, 2002), a Nigerian primary savannah woodland (Longhurst and Howse, 1979), and a Kenyan savannah (Yusuf et al., 2014) (Keller, 2011).

One-Sample T-Test: Value	The Dja vs. Nigerian Guinea Savannah
Temperature (°C)	N/A
Velocity Out (cm/s)	0.0027
Velocity In (cm/s)	0.539
Distance (m)	N/A
# Ants in Raiding Party	N/A
#Ants Carrying Termites	N/A