



# Temporal Dynamics of Scout Release-Behavior of Termitophagous Ponerine ant, *Megaponera Analis*

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**Abstract** *Megaponera analis* is an obligate termitophagous species endemic to sub-Saharan Africa. The species forages by sending out scouts to search for termites. Once termites are located, the scouts return to the nest and recruit nest mates. Scouts face unpredictable environmental conditions, including sudden flooding, temperature changes, high winds and predation by natural enemies. We observed 519 scouting trips from 18 different colonies over three years to determine how long it takes for the colony to replace a scout that has likely died while on scouting duty or is lost due to environmental perturbations. Study areas were at Maremani, Musina, Masebe and D’nyala Nature Reserves in the Limpopo Province of South Africa. We introduced definitions of scouting turnover, scouting trip, and scouting session. Scouting turnover is the time it takes a successive scout to leave the nest for a trip, whereas a scouting trip is the journey a scout takes from the nest in search of

food. Since *M. analis* shows bimodal foraging behavior, the morning observations were recorded as the first scouting session, while the subsequent session, which starts in the afternoon, was recorded as the second scouting session. The mean scouting turnover for all 519 trips was  $9.36 \pm 0.64$  (SD) minutes. When turnover was divided into sessions, the first scouting session lasted a mean of  $7.77 \pm 12.17$  (SD) minutes, while the second had  $10.34 \pm 18.32$  (SD) minutes. The minimum turnover was zero minutes, and the maximum was 124 minutes.

**Keywords** Scouting dynamics · termite predation · foraging behavior · nestmate recruitment · bimodal foraging

## Introduction

In optimal foraging, communication is central to foraging success (Pyke and Starr 2021), and nest selection is equally critical for social insects as this affects the colony’s fitness (Healey and Pratt 2008; Evison et al. 2012). Generally, organisms approach foraging in individual scouting or group searching (Dechaume-Moncharmont et al. 2005). Foraging strategies utilized by different species of ants depend on the environment and habitat where they are found (Gibb and Parr 2013), and these conditions have driven the foraging in some species to be bimodal.

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Benefits of group searching include sharing information such as food source availability (Dechaume-Moncharmont et al. 2005); however, encountering a predator or sudden change in environmental conditions can be detrimental to the colony, and this is where individual scouting has an advantage. Scouts play a pivotal role in locating and quantifying food resources and making critical decisions that affect the entire colony, such as hunting for new nest locations (Franks et al. 2002).

Both communication and nest selection are mostly the scouts' responsibility, making scouts' decisions central to the colony's survival. Biesmeijer and De Vries (2001) have differentiated between a scout and a recruit by defining a scout as an individual tasked with searching for food independently, whereas the recruit depends on the scout and nest mates for information on food sources. The scouting rate of ants is significantly influenced by nest size, with polydomous nests experiencing lower scouting rates than monodomous nests (Cao 2013). Scouts face unpredictable natural phenomena like floods and gusty winds, and how the colonies respond to these threats is unknown. Eusocial insects are characterized by a high degree of division of labor with specific tasks such as foraging, caring for the young, and nest construction and maintenance allocated to individuals (Gordon 2002). Ants are particularly sensitive to microclimatic changes, which can influence nesting behavior (Karlik et al. 2016) and foraging (Hölldobler and Wilson 1990), and scouts should communicate these changes to nest mates for collective decision-making.

Scouting in *Megaponera analis* (syn. *Megaponera foetens* and *Pachycondyla analis*) occurs bimodally, with some scouting happening from the early morning to about 11:00 am local time, while the next session starts in the late afternoon and early evenings (Longhurst et al. 1979; Longhurst and Howse 1979; Yusuf et al. 2013; Frank and Linsenmair 2017a, b; Frank et al. 2018a, b) and at night (Yusuf et al. 2013). Bimodal foraging is also practiced in non-ponerine ants, and the driving factor is likely temperature, with the foraging peaking at both sides of temperature extremes (Cerdá et al. 2009). It is currently unknown why scouting is not continuous, but this trait appears phylogenetically conserved as it is shared with *Ophthalmopone berthoudi*, which is sister genus to *M. analis* (Schmidt 2013) and also has bimodal foraging activity (Crewe and Peeters 1987). Literature, however, suggests that bimodality

could be influenced by the unavailability of the termites during hotter midday hours since termites are prone to desiccation (Hewitt et al. 1972; Longhurst et al. 1979).

Scouting distance can reach 95 m, and searching can last over an hour (Longhurst and Howse 1979; Yusuf et al. 2014). Scouts use termite soil sheets as kairomones to aid them in finding food sources quickly (Longhurst and Howse 1978; Yusuf et al. 2014). When the scout locates a food source, it quantifies it and returns to the nest to recruit nestmates, laying a trail pheromone (Longhurst et al. 1978). The trail lasts up to 29 h (Hölldobler et al. 1994), thereby improving raid position fidelity until termite prey are exhausted (Bayliss and Fielding 2002), and the scout always uses the fastest way possible to the nest (Frank et al. 2018a). When the scout arrives at the nest, it recruits between 200 and 800 nestmates back to the site, where it finds termites (Frank et al. 2017; Yusuf et al. 2020). The scout will lead a group of nest mates who walk in a column formation. The scout will be ahead of the column, and behind it will be former scouts, while at the back end of the column will be major ants, and these workers maintain position fidelity (Frank and Linsenmair 2017b). Although raids in *M. analis* have been studied in detail, little is known about the dynamics of scouting and the adaptive strategies involved in successful scouting, which is essential for raids. Currently, scouting detail is limited to the journey an ant takes to go in search of termites and return to the nest for nestmate recruitment (Longhurst and Howse 1979; Yusuf et al. 2013, 2014; Frank and Linsenmair 2017a; Frank et al. 2018a, b) but there is no information on what drives the scouting behavior and how colonies drive scouting patterns. Although the scouting time range is generally known, there is no information on what drives colonies to send out scouts and what influences the stoppage of scouting. In this study, we observed scouting at various periods and in different microecological conditions over three years. We report information on *M. analis* scouting turnover and temporal aspects of scouting dynamics.

## Material and Methodology

### Study Area

This study was conducted at Maremani Nature Reserve (S22.38870, E30.23215), Musina Nature

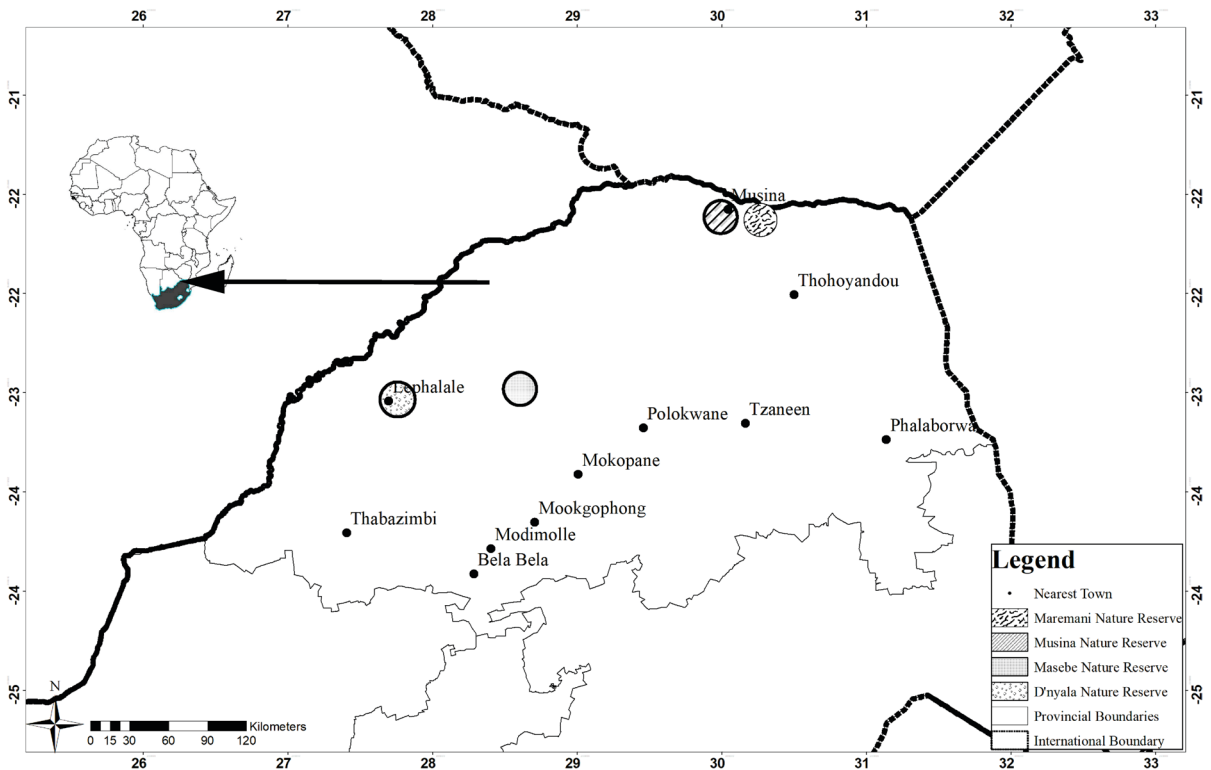
Reserve (S22.39052, E 30.02015), Masebe Nature Reserve (S23.64234, E28.57558) and D’nyala Nature Reserve (S23.74902, E27.82533) in Limpopo Province of South Africa (Fig. 1). Maremani and Musina are 40 km apart, whereas Masebe and D’nyala are 80 km apart. There is a distance of about 250 km between Maremani-Musina and Masebe-D’nyala Nature Reserves. The climate in Maremani and Musina Nature Reserves is hot and arid, whereas that of Masebe and D’nyala Nature Reserves is a semi-arid steppe. Scouting turnover observations were carried out between 04:00–12:00 and 16:00–02:00 from nine (9) colonies at Masebe, four (4) colonies at D’nyala, three (3) colonies at Maremani and two (2) colonies at Musina Nature Reserves making a total of 18 colonies over a period of three years.

*Scouting Release Observations*

Whenever the scout left the nest, time was recorded, and the scout was picked and placed in a container

to prevent scouts from continuing with their scouting journey. To avoid picking ants that were nest entrance lingerers, scouting ants were allowed to walk a minimum of 40 cm before being picked. Additionally, this was done to prevent the alarm pheromone from reaching the nest and disrupting the colony. Observations were carried out from October to January, which are summer months (Rankoana 2022), and observation efforts were the same across sites. If no new scouts were seen after two hours, the observations were stopped, and the session was recorded to be complete, and the collected scouts were returned back to their nests. Observations were alternated among colonies to avoid starving the colonies. For all observations, temperature and humidity were recorded at five-minute intervals using DS1923-F5# iButton (iButton-Link, USA).

This study introduced new definitions: scouting turnover, scouting trip and scouting session. We defined scouting turnover as the time it takes for a subsequent scout to leave the nest for a scouting trip



**Fig. 1** Map of study area showing nature reserves across the Limpopo Province of South Africa. The Y-axis shows latitudes, and the X-axis shows longitudes. The insert shows the position of the study area on the African continent

after the first scout, while a scouting trip is defined as the journey a scout takes from the nest in search of food sources. The scouting session is when the first scout leaves the nest for scouting trips until no other scouting trips are undertaken from the observed colony. Since *M. analis* shows bimodal foraging behavior, the morning observations were recorded as the first scouting session, while the subsequent session, which starts in the afternoon, was recorded as the second scouting session. Observation periods were categorized as follows: Morning: 06:00–11:59; Afternoon: 12:00–17:59; Evening: 18:00–21:59; night: 22:00–05:59.

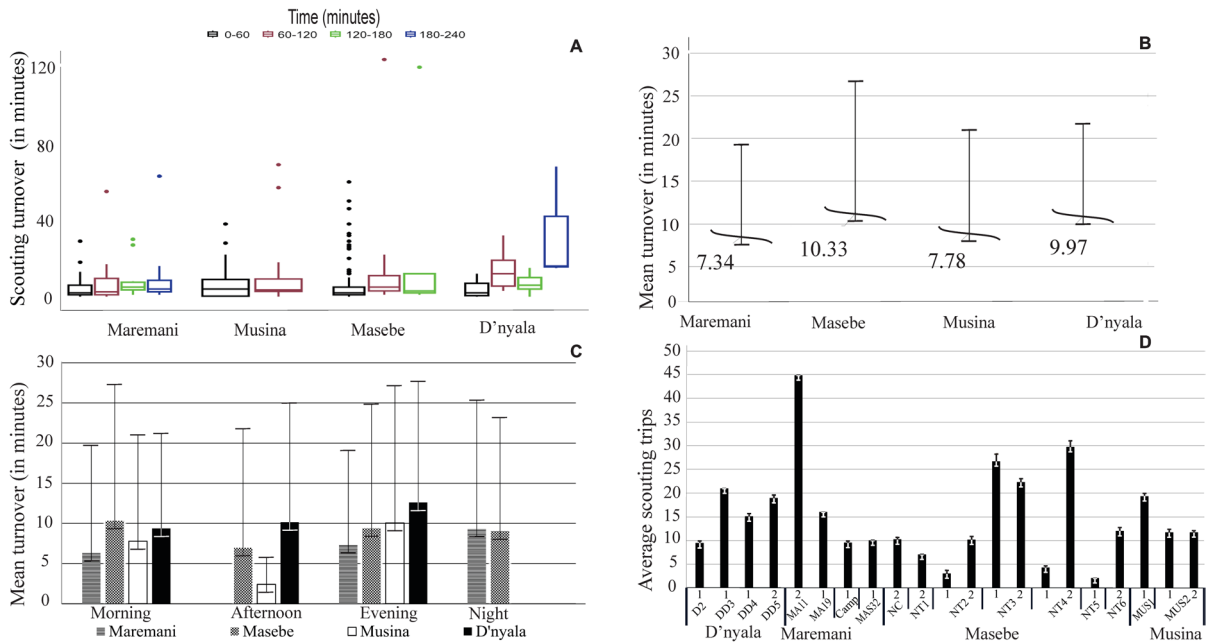
### Statistical Analyses

The data were tested for normality, and non-parametric statistics were used when they were not normally distributed. The chi-squared test was used to correlate scouting turnover and temperature range, time of observation, and humidity. Where a significant difference was found, such a variable's effect was tested using the epsilon square (Cohen 1988), and multiple comparisons were made using the Dunn Test (Dinno and Dinno 2017). Box and scatter plots displayed the relationship between observation times and scouting turnover. All the statistical analyses and scatter plots used R (R CoreTeam 2013), whereas Microsoft Excel© was used to plot the bar of the graphs.

### Results

We observed 519 scouting trips from 18 colonies across the study area (See Tables S1, S2). On average, it took over all colonies  $9.36 \pm 0.64$  (SD) minutes for a scouting turnover. The mean of the first session of scouting was  $8.66 \pm 14.67$  (SD) minutes with a median of 3, while the second session mean was  $8.75 \pm 15.04$  (SD) minutes with a median of 3. The minimum turnover was zero minutes, while the maximum was 124 min. To test whether scouting turnover was linear, box plots were made for all four nature reserves, with each data point representing a scouting trip. The median was within 0–60 min of observation in all four reserves, thereby showing increased scouting turnover at the beginning of the session. The boxplots showed that the turnover time was faster at the beginning of scouting trips

(Fig. 2A). The average scouting turnover across reserves was longer for the Masebe Nature Reserve ( $10.33 \pm 16.96$  (SD) minutes), followed by the D'nyala Nature Reserve ( $9.97 \pm 11.82$  (SD) minutes), Musina was third and Maremanni was the shortest ( $7.78 \text{ min} \pm 13.22$  (SD) and  $7.34 \pm 11.75$  (SD) respectively) (Fig. 2B). However, the differences are below 1 min for reserves close to each other, with Masebe and D'nyala having a difference of 0.36 min while Maremani and Musina had a difference of 0.44. When observations were categorized according to the observation time per reserve, the mean turnover per observation time across reserves was faster in the afternoons in all reserves. At the same time, evening and night interchanged across the reserves (Fig. 2C). When scouting trips were assessed across all reserves for both sessions, the colonies sent either 20 or less scouts on average per session, with the exception of five colonies sending 20 or more scouts on average per session across colonies (Fig. 2D, A). The observation period significantly affected the scouting turnover, but the effect was not statistically significant,  $\epsilon^2 = 0.07$ , ( $\chi^2(3, n = 519) = 37.761, p < 0.001$ ). A pairwise post-hoc Dunn test with Bonferroni adjustments indicated that the differences were at Afternoon – Evening ( $p < 0.01$ ), Afternoon – Morning ( $p < 0.001$ ), Evening – Morning ( $p < 0.001$ ) and Afternoon – Night ( $p < 0.001$ ) while Evening – Night as well as Morning – Night showed no significant difference. The temperature had a significantly strong effect on scouting turnover,  $\epsilon^2 = 0.39$ , ( $\chi^2(2, n = 519) = 141, p < 0.002$  (Fig. 3A). An increase in temperature resulted in less scouts being sent out by colonies. When the temperatures were observed across the observation categories, the mean temperatures were higher in the afternoon, followed by the evening and night, while the morning had the lowest (Fig. 3B). Humidity had a positive correlation with the scouting turnover (Fig. 3C). When mean humidity was analyzed across all observation categories, morning had higher mean humidity, followed by night, while afternoon had the lowest (Fig. 3D). A correlation between temperature and humidity found an inverse relationship (see Figure S2B). Average temperature and humidity across reserves were plotted, and Maremani had the highest temperature (Figure S2). Overall, results showed that *M. analis* is a bimodal



**Fig. 2** Boxplot of scouting turnover across reserves (A) drawn using individual scouting trips at various time range (in minutes) showing a median of the first 60 min being lowest. Mean scouting turnover across the reserves (B) with standard deviations: D'nyala=11.82, Maremani=11.75, Masebe=16.96, and Musina=13.22. Mean scouting turnover per reserve per observation period (C). Reserve standard deviations: [(D'nyala: Morning=11.81, Afternoon=14.86,

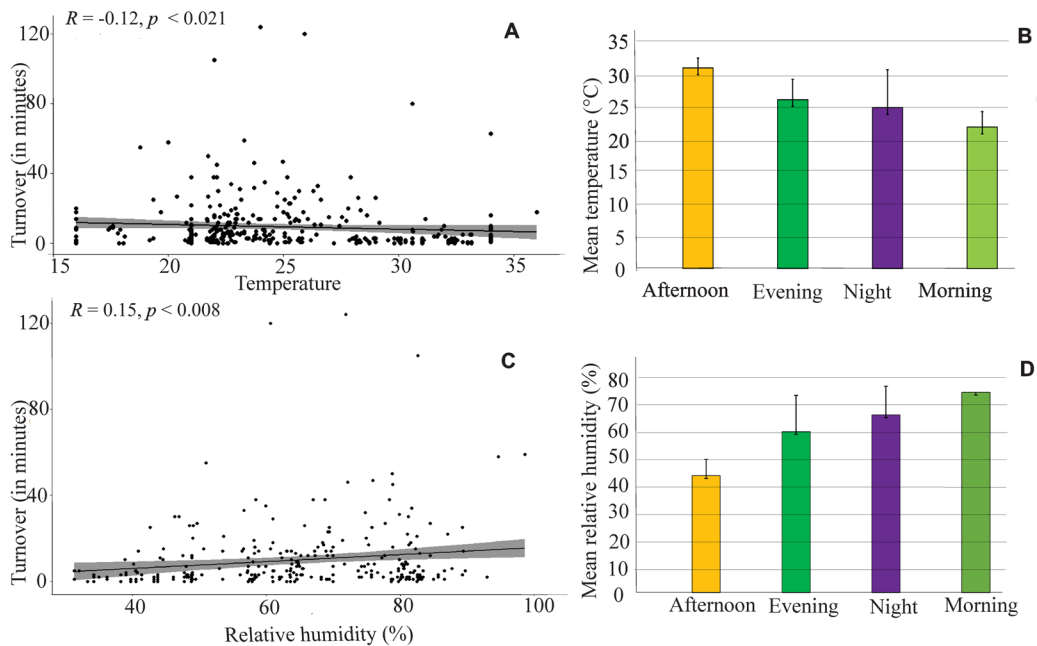
Evening=15.05; Maremani: Morning=13.33, Evening=7.34, Night=9.29; Masebe: Morning=10.33, Afternoon=14.83, Evening=15.47, Night=14.14; Musina: Morning=7.78, Afternoon=3.36 and Evening=17.1. Average scouting trips per colony (D) across the four reserves. Scouting sessions 1 and 2 are so labeled. Observation periods were categorized as follows: Morning: 06:00–11:59; Afternoon: 12:00–17:59; Evening: 18:00–21:59; night: 22:00–05:59

forager, with mornings being the preferred time followed by the evenings, while afternoon and night had the lowest number of trips (Fig. 4).

### Discussion

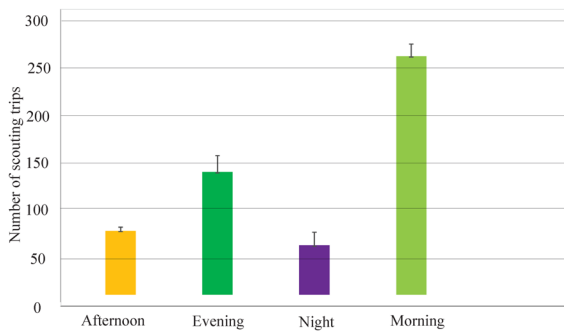
The effect of temperature on scouting turnover in this study aligns with the prior studies that found temperature to influence ants foraging behavior (Crist and Williams 1999; Ruano et al. 2000; Van Oudenhove et al. 2011; Bishop et al. 2014). Frank and Linsenmair (2017b) confirmed this with *M. analis*. Since *M. analis* rely on trail pheromone, which decays rapidly with a rising temperature (Bayliss and Fielding 2002; Yusuf et al. 2014), the temperature is arguably among the driving factors of *M. analis* foraging. Apart from trail decomposition, in general ants are susceptible to desiccation due to their high surface-to-volume ratio (Kumar and O'Donnell 2009). *Megaponera analis*

is relatively large (Villet 1990) and is characterized by its melanism in its exoskeleton (Clusella Trullas et al. 2007) and, therefore, prone to overheating by radiation (Kaspari et al. 2015) due to quicker insolation of solar radiation (Law et al. 2020). On average, *M. analis* has been reported to prefer a temperature of between 23.10 and 25.40 °C when observed in Kenya, Cameroon and Tanzania (Patel et al. 2018). In Limpopo Province, where this study took place, sunrise is as early as 05:00, and temperatures can reach 25 °C within a few hours from sunrise and set at 19:00 during summertime (Mulaudzi et al. 2015). Several termite species forage during cloudy days or in the late afternoon when the temperature is cool (Hewitt et al. 1972). The preferred temperature of *M. analis* seems to be congruent with the foraging conditions of most termites. It is suggested that bimodal scouting in this species has evolved as a response to the avoidance of high, mid-day temperatures by its prey (Hewitt et al. 1972). This is not the first ant



**Fig. 3** Spearman's correlation (A) scatter plot between temperature across all sites and scouting turnover. Mean temperature recordings (B) across different observation periods with standard deviations: Afternoon=1.57, Evening 3.18, Morning 2.41 and Night=5.92. Spearman's correlation (C) between

scouting turnover and humidity (p-value=0.008,  $R=0.15$ ). Mean humidity availability across different observation periods. Standard deviations: afternoon=5.89, evening 13.30, morning=10.43 and night=10.57. Recordings were done from 04:00 until 02:00 the next day (D)



**Fig. 4** Overall scouting trips per observation period. Standard deviations: afternoon=0.56, evening 1.08, morning=0.81 and night=8.17

found to have a bimodal activity rhythm. Workers of *Myrmecia croslandi* changed their foraging pattern from continuous to bimodal when there were temperature changes (Jayatilaka et al. 2011). Another relative of *M. analis*, *Dinoponera gigantea*, also has a bimodal foraging pattern, preferring mornings and late afternoons into the night (Oliveira et al. 2002). *Ophthalmopone berthoudi*, which shares a clade with

*M. analis* (Schmidt 2013), also has bimodal foraging activity (Crewe and Peeters 1987). However, *Dinoponera gigantea* is found in the Brazilian rainforest (Oliveira et al. 2002), and the temperature regime at the base of the forest is known to be substantially cooler and stable compared to areas without canopy, which are characterized by mercurial temperatures (Kosheleff and Anderson 2009).

Despite the stable forest ground temperature, *D. gigantea* workers limit foraging during the mid-day hours to mornings and late afternoons (Oliveira et al. 2002). Given the temperature stability on the forest ground, if the temperature alone influenced foraging, epigeal ants found in tropical forests like *D. gigantea* would not have bimodal foraging. The mean temperatures in this study showed that the evening had higher temperatures than the night (Fig. 3B), but despite this, the evening had more scouting trips than night (Fig. 4). This suggests that temperature alone is not the key factor of scouting turnover. Humidity was found to have a direct proportional relationship with the scouting turnover (Fig. 3C), and the highest scouting trips recorded in the morning were

accompanied by the highest mean humidity in the mornings (Fig. 3D), thereby strengthening our conclusion that the increase in humidity favors the turnover. These results could partly explain why this species has not dispersed to the desert areas since these are characterized by high temperatures and low humidity. We suggest that mornings have higher scouting trips because *M. analis* uses its large eyes for navigation, which cannot be done effectively in the dark since their eyes are not night-adapted. The large eyes play a role in locating as many visual cues as the scout can remember. In Tanzanian populations of *M. analis*, a study found rainfall and humidity to be the driving factor in *M. analis* foraging (Bayliss and Fielding 2002). These results support our result that humidity also plays a role in influencing scouting turnover. Given the aforementioned discussion about temperature and scouting turnover, we suggest that humidity and temperature work in concert to influence scouting turnover. Humidity is important as it helps both the ants and termites avoid desiccation, but termites benefit more by not having to provide the entire moisture for gallery construction from their gut (Shanbhag and Sundararaj 2012). On the other hand, it is also beneficial energy-wise for *M. analis* to find freshly built galleries as this will save them the energy needed to cut the galleries open. Despite humidity having a positive correlation with scouting trips and temperature having a negative correlation, the evening had both the higher mean temperature and lower mean humidity compared to the night (Fig. 3B and D), but still had the highest scouting trips as compared to the night, suggesting that the night is not the favorable for scouting.

We found rapid scouting turnover at the beginning of the sessions (Fig. 2A, S1A), and when the scouting time increased, scouting turnover was delayed. We suggest that this delayed turnover is used as a tradeoff in case all scouts experience mass predation. Indeed, food searching does not always produce the desired result, which is why there are sporadic scouting trips during the night and afternoon. The results of scouting turnover per reserve across various scouting periods support the latter argument by having afternoon observations with the quickest scouting turnover in all reserves, with the exception of Maremane where temperatures are harshly high (Fig. 2C, S2). Since bimodal behavior is also practiced by *Ophthalmopone berthoudi* (Crewe and Peeters 1987), which is the

only species sharing a monophyletic clade with *M. analis* (Schmidt 2013), we can safely say this behavior is inherited behavior from the common ancestor and further suggests that the trait has probably evolved to match the adaptation and foraging strategy of some termites, which are sensitive to heat (Hewitt et al. 1972).

Generally, termites are sensitive to high temperatures like most insects, but in the study of four termite species from different genera, including the genera *Odontotermes*, which is among the preferred prey by *M. analis* (Longhurst et al. 1978), exposure to sunlight increased mortality of termites (Hewitt et al. 1972). This implies that termites will directly avoid too much sun exposure, and this behavior was likely reciprocated by *M. analis* as part of the adaptive strategy in order to optimize foraging. Scouting peaked between 06:00 and 10:00 and between 14:00 and 20:00 in another termite specialist *Neoponera commutata* (Mill 1984). The number of raids substantially decreased as the night progressed. These results agree with our results that scouting trips were highest in the morning, evening and afternoon, respectively, with the night experiencing the lowest activity (Fig. 4). Both Yusuf et al. (2014) and Mill (1984) found that nighttime had the lowest termite catches and that foraging should not continue at night, as such, foraging would not be optimal (Pyke 1984). Moving scouting activity to the morning was more likely an adaptive foraging strategy to optimize foraging and collect more termites with minimal energy. Another possibility of the morning having higher scouting numbers could be due to the availability of light, which makes scouting easier than at night. Concerning the costs of raiding, literature had already established that it is energy costly for the colony to send one column out (Duncan 1995). Mill (1984) suggests that the reason why scouting peaks during morning and evening is that the termite soldiers are preparing for withdrawal back to the nest or were preparing to go out of the nest due to the nocturnality of the species from the *Syntermes* genera. Incongruent with our results, Yusuf et al. (2014) reported that more raids (56%) were recorded in the morning as compared to the evening raids, which were 42%, whereas nocturnal raids were 7% (7%).

The reserves in the more arid part of the study area, viz. Maremani and Musina Nature Reserves had the quickest turnover compared to the reserves in the

Waterberg region (Fig. 2C). Maremani and Musina Nature Reserves are characterized by poor basal covers (Curl Lewis et al. 2018) compared to the Masebe and D'nyala Nature Reserves, which have rich grass, forbs and herbs diversity (Mundalamo 2019). Basal cover influences the microclimatic aspects of the foraging area by creating shade, leaf litter, and suppressing wind erosion. Basal cover helps maintain soil temperature, moisture, and relative humidity, while its absence is associated with harsh microclimatic fluctuation including winds and rise in temperatures (Ewers and Banks-Leite 2013). A study on the foraging behavior of leaf-cutting ants found that changes in microclimatic conditions changed the foraging behavior of *Atta cephalotes* (Bustamante et al. 2020). The quick turnover at these reserves could be an adaptive strategy to avoid desiccation since barren land is hot and dry and Musina and Maremani had generally higher average temperatures (Fig. S2).

## Conclusion

We investigated the scouting dynamics of *M. analis* and the environmental factors that influence this behavior. We were able to report on the scouting turnover rate at the population and reserve levels. We documented the ecological variables that play a crucial role in creating microclimatic conditions that are favorable to scouting by *M. analis*. We showed which times of the day *M. analis* is likely to be out hunting termites and established the bimodal timing of its foraging. We conclude that microclimatic conditions are central to the scouting behavior of *M. analis* and that the bimodal lifestyle of *M. analis* is most likely an inherited trait that probably evolved due to its prey's bimodal nature. We attempted to provide an answer for how colonies respond when their scouts are not returning from foraging. However, it is still unclear why this species is only found in certain parts of South Africa. We were able to present data proving that *M. analis* is a bimodal forager, preferring the mornings compared to other times of the day or night.

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**Author Contributions** All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Rifilwe Modiba. The first draft of the manuscript was written by Rifilwe Modiba while Yusuf Abdullahi and Christian Pirk commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data Availability** The data used to arrive at the conclusion of this manuscript are available as part of the supplementary material.

## Declarations

**Competing Interests** The authors declare no competing interests.

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