RESEARCH ARTICLE

Time-optimized path choice in the termite-hunting ant *Megaponera analis*

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ABSTRACT

Trail network systems among ants have received a lot of scientific attention because of their various applications in problem solving of networks. Recent studies have shown that ants select the fastest available path when facing different velocities on different substrates, rather than the shortest distance. The progress of decision making by these ants is determined by pheromone-based maintenance of paths, which is a collective decision. However, path optimization through individual decision making remains mostly unexplored. Here, we present the first study of time-optimized path selection via individual decision making by scout ants. *Megaponera analis* scouts search for termite-foraging sites and lead highly organized raid columns to them. The path of the scout determines the path of the column. Through installation of artificial roads around *M. analis* nests, we were able to influence the pathway choice of the raids. After road installation, 59% of all recorded raids took place completely or partly on the road, instead of the direct, i.e. distance-optimized, path through grass from the nest to the termites. The raid velocity on the road was more than double that on the grass, and the detour thus saved 34.77 ±23.01% of the travel time compared with a hypothetical direct path. The pathway choice of the ants was similar to a mathematical model of least time, allowing us to hypothesize the underlying mechanisms regulating the behavior. Our results highlight the importance of individual decision making in the foraging behavior of ants and show a new procedure of pathway optimization.

KEY WORDS: Optimal foraging, Raiding behavior, Social insect, Foraging strategy, Decision making, Orientation

INTRODUCTION

Ants deploy a large variety of foraging strategies, ranging from solitary hunting to the recruitment of bigger groups via chemical communication Hölldobler and Wilson (1990). Optimal-foraging theory tries to explain these foraging patterns and behaviors by assuming that they serve the purpose of maximizing overall energy gain. Central place foraging theory, which is derived from optimal-foraging theory, is used to understand how animals that have to return to a central place (e.g. nest), like ants and birds, should optimize their foraging behavior. These theories are, in general, able to predict foraging strategies in social insects considerably well (Bailey and Polis, 1987; Detrain et al., 2000; Loreto et al., 2013; Silva et al., 2013).

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One aspect of central place foraging in ants is the pathway choice between a food source and the nest. The shape of an ant pathway is influenced by many factors and it is expected that over time this path is the optimized, i.e. fastest, way an ant has to walk to get from the nest to the food source (Beckers et al., 1990; Loreto et al., 2013). In particular, the interconnection between ant paths and path length have been the object of recent studies (Buhl et al., 2009; Loreto et al., 2013). Many ant species have permanent paths between food sources and their nest, like leaf-cutting ants (Clark, 1994; Silva et al., 2013) and seed collectors (Detrain et al., 2000; Willott et al., 2000). They actively form these so-called trunk trails by removing objects (leaf litter) from the floor to increase the walking speed of workers (Plowes et al., 2013).

In ant species that create longer-lasting paths, the installation of the path system is based on a collective decision-making process, through simple behavioral rules on pheromone-based path laying and following. An ant that has found a food source lays a pheromone path on its way back to the nest. This pheromone decays quickly and nestmates show a preference to follow paths with high trail pheromone concentrations. Over time, the path that represents the fastest connection between a food source and the nest becomes the most used, because it has the most ants per time interval, reinforcing the path (Beckers et al., 1990; Goss et al., 1990; Oettler et al., 2013). Despite this simple working mechanism, the results are often highly complex network systems (Buhl et al., 2009; Reid et al., 2010).

Although often the fastest distance between the nest and a food source is also the shortest, there are exceptions, especially if the walking speed differs significantly between two substrates (Oettler et al., 2013). If the ants seek to optimize time spent walking between the nest and food source, they choose to walk on a faster substrate so their path can be traversed quicker, even if it is longer than a direct path. *Camponotus rufipes* tends to walk on trees and twigs rather than on the forest floor, presumably to achieve a greater velocity (Loreto et al., 2013). In *Wasmannia auropunctata*, paths adapt to the respective substrate velocity so as to minimize time (Oettler et al., 2013). Surprisingly, there has been very little research done on faster versus longer trade-offs in ant path networks and all of it has focused strictly on collective mechanisms (Loreto et al., 2013; Oettler et al., 2013).

In this study, we focused on the path choice of the termite-raiding ant *Megaponera analis* (Latreille 1802). This ponerine ant species is a mass-recruiting predator specialized on termites of the subfamily Macrotermitinae (Longhurst and Howse, 1979). The high degree of specialization of *M. analis* has resulted in a remarkable ability to optimize their raids (Frank and Linsenmair, 2017a). We present another optimization behavior that fits well into optimal foraging theory.

The pathway choice of *M. analis* is, in contrast to most trunk trails among ants, not based on a collective decision but decided by individual scouts: *M. analis* has scout ants that make solitary searches for termite-foraging sites (henceforth referred to as

'raiding sites') and then recruit and lead a worker column, consisting of several hundred individuals, to the prey location (Longhurst and Howse, 1979; Frank and Linsenmair, 2017a). The path is therefore determined solely by the scout ant, and is not the result of pheromone-based reinforcement of existing paths. These raids occur 3–5 times a day but the location of the raids changes constantly, meaning that the determined path has to be chosen individually for each raiding site. The savanna habitat of *M. analis* in our study area represents a heterogeneous environment with scattered open areas, which are surrounded by savanna grasses of varying density. The quickest path between the nest and a raiding site is therefore not always the direct path, but rather a detour on less-dense terrain. We therefore hypothesized that *M. analis* would detour on easier terrain to minimize travel time.

To test whether the ants are capable of adapting their raiding paths, we installed artificial roads around the ants' nests. We recorded the raids of several colonies before and after road installation and present a theoretical model for pathway optimization based on a minimization of travel time. We found a remarkable pathway choice ability in scouts of *M. analis*, which is surprisingly similar to that of collective pathway choices in other ant species.

MATERIALS AND METHODS
Study site
The research was conducted from August to November 2015 at the ecological research station of the Comoé National Park in Côte d'Ivoire. The park is located in the north-east of the country and covers an area of about 11,500 km^2. The vegetation ranges from the more humid Guinean savanna zone to the dryer Sudanian savanna zone. The station is situated in the south of the national park, and all of the colonies that were studied were located in a typical grassland savanna with some low shrubs and a few scattered trees. The region typically has a rainy season from April to October (during which the field study was conducted) and a dry season from November to March (Konaté and Kampmann, 2010).

Study design
For this study, eight colonies were selected from the savanna around the ecological research station. Only those colonies that had no larger obstacles (e.g. houses, streets) nearby were chosen for the experiments. No live *Macrotermes bellicosus* mounds were found in a 20 m radius around each nest. The nests of *Pseudocanthotermes*, the main prey of *M. analis*, were fully underground and often decentralized, so it was not possible to map or control for proximity to prey nesting or feeding sites (Bignell et al., 2011). For each colony, the grass within a 20 m radius around the nest was cut to create a homogeneous environment (Fig. 1); where necessary, open areas were covered by a scattering of cut grass. The nests were observed during the day from 08:00 h until 11:00 h and subsequently from 16:00 h to 18:00 h, as these were the times during which the ants were most active (Frank et al., 2017). Every raid occurring during these time periods was recorded.

The experiment had three phases. First, we recorded the distance and duration of ant raids 3 days after creating the homogenized environment. Second, we installed artificial roads around each colony and immediately started recording at least five raids per colony. Third, to determine whether the ants needed time to adapt to the roads, we waited for at least 14 days and then again recorded at least five raids per colony.

Removing grass created the artificial roads for phase 2 and 3 and consequently created an earth surface that was trampled flat. Four
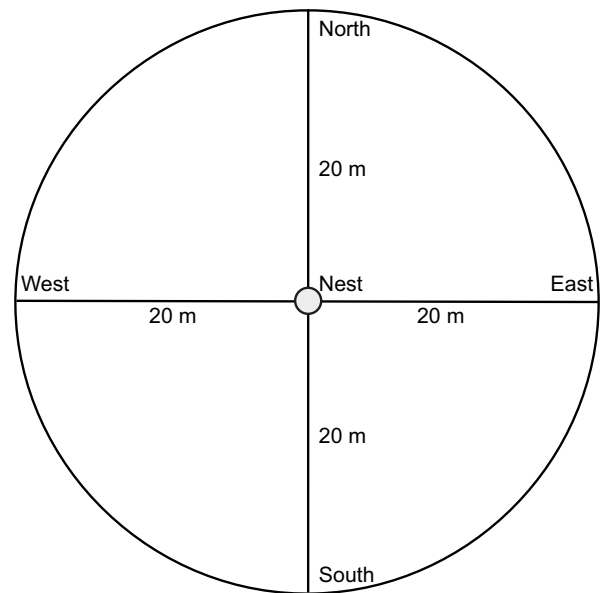

Fig. 1. Field study design. Sketch of the installed roads around the *Megaponera analis* nests.

such roads were installed per colony (one in each cardinal direction), each with a length of 20 m and a width of approximately 30 cm (Fig. 1).

For every raid, we recorded several parameters. To calculate raid velocity, travel path (distance) and time were recorded for the outward and return journey. If the ants used the road, we measured the time and distance on the road separate to that in the grass. The velocity of the raiding column was then calculated by dividing the distance by the travel time for the road and grass separately.

The site of the raid is expressed as (x, y) coordinates relative to the focal ant nest, with Y as the direct distance from the raid site to the nearest road and X as the distance from that point to the origin (i.e. ant nest) (Fig. 2). The location of the raiding sites was acquired through trigonometric calculation using the direct distance to the ants' nest (D) and the distance of the ants on the road (R) and grass (G; Fig. 2); for formulas, see 'Model of least time', below. When the ants used the road, the distance they walked in the grass from the point of deviation from the road to the raiding site (G; Fig. 2) was measured twice: once as the distance actually walked by the ants and once as the direct distance. As there was no significant difference
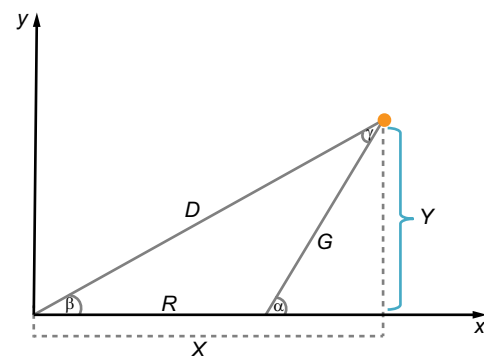

Fig. 2. Sketch of the geometrical parameters collected/calculated for the pathway of a raid. D, direct distance; R, road distance; X, x-coordinate; Y, y-coordinate; G, grass distance; α, deviation angle from road to raiding site; β, direct distance angle from nest to raiding site in relation to road; orange dot, raiding site; γ, deviation angle from the direct route towards the road.

between the two (n=73, Mann–Whitney U-test: W=2775.5, P=0.67), we used the direct distance for our model. For calculating the time required to follow a theoretical direct pathway through the grass, we used overall median grass velocities of all raids and applied them to the distance. For raids that did not use the roads, we used the median road speed (of all raids) to calculate the optimal path, i.e. if velocity data were missing, the median values were used for calculation purposes. In addition, each raid was documented with a pencil sketch of the approximate direction and pathway (Figs S1 and S2).

Because some colonies migrated or did not start any raids during the observation time, a full data set is only available for five colonies (Fig. S1). Three of the observed colonies were mostly active during the night; their nests were closed off during the night using plastic walls, which were removed during the day, thus forcing them to perform their raids during the daytime.

Model of least time

For each raid, the theoretical quickest route was calculated. Using the distances R and G, the time t that the ants would take to walk to the food source was calculated:

$$t = \frac{|R|}{v_{\text{road}}} + \frac{|G|}{v_{\text{grass}}}, \tag{1}$$

where R_0 is the time-minimized distance on the road and G_0 is the time-minimized distance on the grass. Requiring dt/dR=0 (for $R{\geq}0$) results in:

$$R_0 = X - \frac{e}{\sqrt{1-e^2}} \cdot Y. \tag{2}$$

G_0 can now be calculated through trigonometry:

$$G_0 = \sqrt{(X - R_0)^2 + Y^2}, \tag{3}$$

where X is the horizontal distance (=x-axis value) and Y is the vertical distance (y-axis value) to the food source with respect to the ants' nest and e is the relationship between the grass and road velocities:

$$e = \frac{v_{\text{grass}}}{v_{\text{road}}}. \tag{4}$$

For the raids that used the road, X and Y values were not measured but were calculated by trigonometry and the measured road (R), grass (G) and direct (D) distances:

$$X = \frac{D^2 - G^2 + R^2}{2R}, \tag{5a}$$

$$Y = \sqrt{D^2 - X^2}. \tag{5b}$$

As $R{\geq}0$, negative results for R in Eqn 2 imply that the direct path is the fastest path (see Eqn 1), this was the case in one trial, which thus had to be removed from the analysis of the optimal deviation angle.

The real deviation angle from the road (α) taken by the ants was calculated by:

$$\tan\alpha = \frac{Y}{X - R}. \tag{6}$$

The deviation angle of our model (α_0) of least time was

calculated by:

$$\tan\alpha_0 = \frac{\sqrt{(1-e^2)}}{e}. \tag{7}$$

In one case, we had a positive e-value (grass velocity was 0.006 cm s^{-1} faster than road velocity). This was probably due to external influences on the experimental setup, which led to the areas we classified as 'dense' (i.e. grass) actually being clear enough for the ants to walk unhindered (the areas we covered with grass could be partly cleared by animals, wind or rain). While we tried to prevent such external disturbances, it was not always possible. This trial was therefore discarded from our model analysis, as our experimental setup did not fulfill our primary criteria in this case.

The percentage of saved travel time (T_s) of the optimal route travel time (T_o) in comparison to the direct route travel time (T_d) was calculated by:

$$T_s = \frac{T_d - T_o}{T_d} \times 100. \tag{8}$$

Statistical analysis and visualization

The statistical software R v3.1.2 with the user interface RStudio v0.98.501 was used for statistical analysis and illustration. To test whether the data had a normal distribution, a Shapiro–Wilk test was performed, and for checking the variance homogeneity, a Bartlett test was used. As the data were never normally distributed and did not show variance homogeneity, all analyses were conducted with a fixed linear mixed-effects model (LMM) with colony as a random factor. To test for a correlation between the deviation angle (α) and the e-value, a Pearson's product-moment correlation test was used, between α and α_0, with the calculated optimal deviation angle as reference. To test whether a disproportionate number of raids occurred on the road, a Fisher's exact test for count data was used (tested against the probability of raids occurring on the road if a random distribution of raiding sites is assumed). The pencil sketches of the real path choices were digitalized using the program GeoGebra v.5.0.207.0. All values mentioned in the text are medians and are followed by a median absolute deviation.

RESULTS

Raid pattern before road installation

Before installing the roads, there were a total of 21 raids, recorded from seven different colonies (Figs S1 and S2). With a few exceptions, the path used by the ants was not significantly longer than the direct path to the raiding site [3.95±5.85% longer; n=21, LMM: t=6.92, d.f.=34, P=0.54; random effect (colony): s.d.=302; residual: s.d.=452].

The travel time for the outward (median: 420±220 s, n=76) and return journey (median: 456±263 s, n=84) for all raids was recorded. The path was always the same for the two journeys and travel time did not differ significantly [data for outward journey missing for eight raids; n=76, LMM: t=6.9, d.f.=151, P=0.82; random effect (colony): s.d.=187; residual: s.d.=248]; thus, for all analyses we used the travel time of the return journey.

Raid pattern after road installation

The velocity of the column was measured on two different substrates: the earth substrate (artificial road) and the grass. The road velocity (3.4±0.8 cm s^{-1}, n=37) was nearly twice as fast as
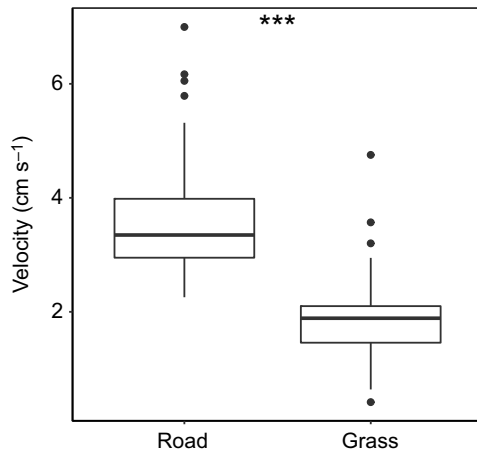
Fig. 3. Relationship between raid speed and substrate. Raid column velocity on the road ($n=37$) compared with that on grass ($n=73$) for all raids. Box-and-whisker plots show: median (horizontal line), interquartile range (box), distance from upper and lower quartiles of 1.5 times the interquartile range (whiskers) and outliers (>1.5 times the upper or lower quartile; circles). ***LMM: $P<0.001$.

the grass velocity (1.9 ± 0.6 cm s^{-1}, $n=73$; includes raids from both before and after road installation), irrespective of the colony [LMM: $t=-11.68$ d.f.=101, $P<0.001$; random effect (colony): s.d.=0.34; residual: s.d.=0.81; Fig. 3]. The relationship of the two velocities was characterized by $e=v_{grass}/v_{road}$, which was 0.41 ± 0.15 ($n=26$).

Deviations from the direct distance enabled faster travel times because of the higher velocity on artificial roads. Altogether, 63 raids were recorded after the installation of the roads in five different colonies (Table S1); 59% ($n=37$) of these raids used the artificial road (Fig. S1). This detour allowed the ants to be $34.77\pm23.01\%$ ($n=25$; one case was excluded because $e>1$) faster

than if they had walked the calculated direct distance through the grass, while the distance covered was only $4.86\pm5.00\%$ longer ($n=26$).

We had two phases of recording per colony (after road installation), the first starting directly after road installation and the second at least 2 weeks later. In the first phase, only 37.8% of raids used the road, while 88.4% of raids used the road 14–24 days after road installation (Fig. S1).

Time-optimized model
We determined the fastest route with our model and compared it with the actual raids that used both road and grass ($n=26$, Fig. 4). In 24 out of 26 cases, the ants deviated before the optimal deviation point from the road (Fig. 4). In our model, the time versus distance relationship is not linear. The time saving gets smaller the closer the ants are to the optimal deviation point from the road (Fig. 5A) and time loss increases faster if the ants overshoot the optimal point, i.e. deviations after the optimal point lead to larger time losses than earlier deviations (Fig. 5A). Furthermore, we tested whether there exists a dependency of the deviation angle α of the raids from the road on e (Fig. 5B). According to our model, smaller e-values should lead to higher α-values, i.e. longer travel time on the road. This dependency was not significant ($n=25$; Fig. 5B, Pearson test: $t=1.65$; d.f.=24, $P=0.11$). The angle with which the scout ants deviated from the direct route towards the road (angle γ) at the raiding site did not show normal distribution, i.e. there was no fidelity to a certain fixed deviation angle ($\gamma=27\pm25$ deg; Shapiro–Wilk test: $n=25$; $W=0.84$; $P=0.0015$).

Some raids did not use the roads but instead walked the direct path. In these cases, the theoretical time saving of using the optimal path was significantly lower ($8.99\pm10.15\%$, $n=25$) compared with that for raids that made a detour, irrespective of the colony ($37.26\pm19.84\%$, $n=25$; Fig. 6) [LMM: $t=3.95$, d.f.=44, $P<0.001$; random effect (colony): s.d.=4.1; residual: s.d.=18.2]. The model further
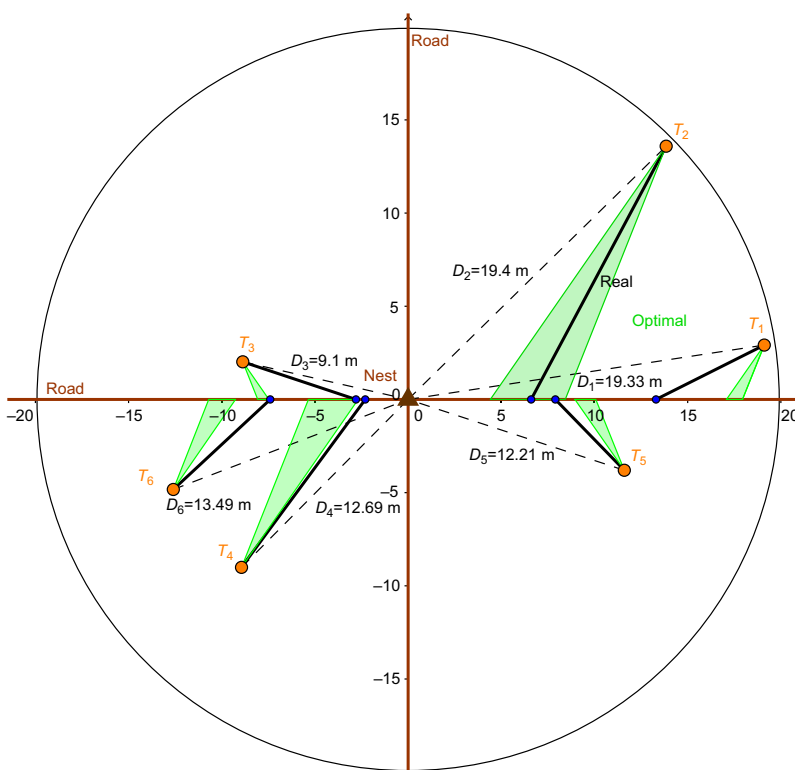

Fig. 4. Examples of raids compared with the time-optimized model. Green shaded area, area in which the model predicts ants to deviate from the road (with standard deviation of e); solid black line, actual raid path; dashed line, direct distance; brown line (x- and y-axis), roads; D_{1-6}, direct distance in meters; T_{1-6} (orange dot), raiding site. Note that the raids were from different colonies and the cardinal direction is not correctly illustrated in this graph. For actual sketches of each colony, see Fig. S1.
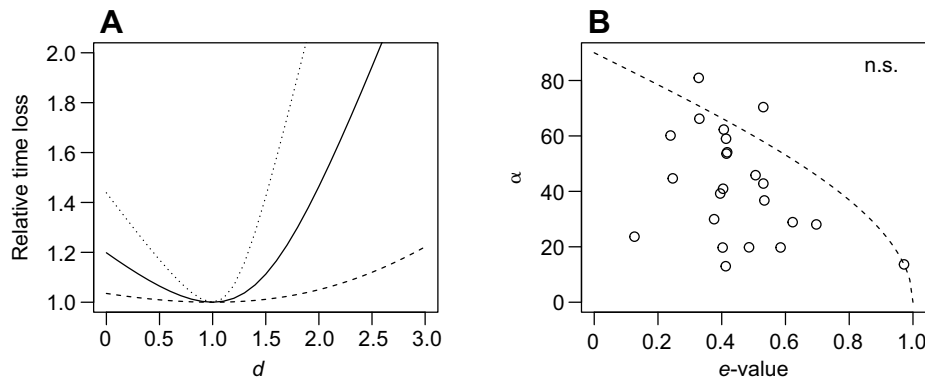
Fig. 5. Effects of differing deviation points from the road on travel time. (A) Effect of varying deviation point from the road (d) on relative time loss, with varying $Y{:}X$ ratio (i.e. relative distance of the feeding site from the road). The optimal deviation point from the road to minimize travel time is $d=1$. The lines represent different $Y{:}X$ ratios: solid line, 0.5; dashed line, 1 (i.e. further away from the road); dotted line, 0.25 (i.e. closer to the road). The y-axis represents the percentage time loss through a sub-optimal deviation point from the road, i.e. a value of 1 is the minimal travel time. (B) Real deviation angle α compared with e-value (grass velocity/road velocity). Dashed line, calculated optimal deviation angle (α_o) according to our model of least time in relation to e.

shows that the time-saving potential of the optimal path is greater the nearer the raiding site is to the road.

Hunting ground distribution

The spatial distribution of the raided locations changed after the installation of roads. Given that our studied area was a circle with a radius of 20 m around each nest, the total surface area was 1256 m² per nest. The four installed roads had an approximate width of 30 cm and a length of 20 m, which makes a total surface of 24 m², which is 2% of the total surface area. However, of all raids recorded after road installation ($n=63$), a greater number than expected walked solely on the road (17%; $n=11$ out of 63; Fisher's exact test: $P<0.001$, $n=63$), i.e. the raiding sites were directly on the artificial road.

The installation of the roads had no effect on the direct distance from the location of the raiding sites to the nest. Before

Fig. 6. Possible time saving through detours on the road. Detour not used: potential time that could have been saved if a detour on the road had been used optimally (model) for raids in which ants walked the direct distance through the grass ($n=25$). Detour used: potential time saved assuming the detour on the road had been used optimally (model) compared with the direct distance travel time for raids that used the detour (road, $n=25$). Box-and-whisker plots are as for Fig. 3. ***LMM: $P<0.001$.

road installation, the direct distance to the raiding site was 1030±519 cm ($n=21$); after road installation, it was 920±578 cm ($n=63$; LMM: $t=-0.33$, d.f.$=75$, $P=0.74$; random effect: s.d.$=211$; residual: s.d.$=499$).

DISCUSSION
Time-minimized path choice

The artificial creation of roads influenced raid patterns of *M. analis*, allowing them to minimize travel time through deviations on the roads. Studies specifically focusing on ant pathway formation, dependent on further-for-faster trade-offs, are rare and such trade-offs have solely been investigated as collective processes (Loreto et al., 2013; Oettler et al., 2013). In *M. analis*, however, while the outcome of a time-optimized route is rather similar, the pathway choice represents the decision of a single scout ant. The pathway choice by this ant resembles in this regard the intuitive choice made, for example, by humans (Kretz, 2009) and is probably not based on other foragers.

Raids where the ants took a detour were considerably faster compared with a simulated direct distance. The variance in time saved (34.77±23.01%) can be explained through the location of the foraging site: the closer the raiding sites are to the road, the greater the benefit of using the detour, according to our model. This could explain cases in which *M. analis* did not detour on the road: the possible gain through detouring here was significantly smaller than in those cases where the ants actually detoured (Fig. 6).

Deviations from the model

The raid path often deviated from the road earlier than predicted by our model. One explanation could be a trade-off between distance and time saving. Our model only considers time saving; however, there could be a higher predation risk dependent solely on distance traveled on the road and not on travel time (for example, through ambush by predatory spiders), which could then favor to some extent a distance-minimized model. As the time saving gets smaller the closer the ants are to the optimal deviation point from the road and increases quickly afterwards (Fig. 5A), a slightly shorter distance walked on the road would have no large impact on time saving. Therefore, scouts might choose an approximate angle more towards the nest location (when leaving the raiding site). This would result in a slightly longer travel time but would provide more security against inaccuracies; further experiments are required to support this.
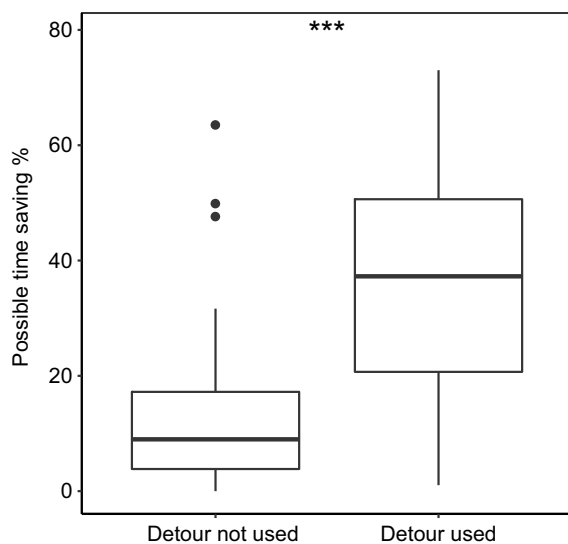
Error-compensating mechanisms have been observed in other ants as well. Desert ants (*Cataglyphis*) are able to estimate the error they make in their orientation (Wehner and Rössler, 2013). They take into account how far they have traveled, as longer distances are associated with an accumulation of errors of the path integrator. The higher the possible error, the further their nest search area widens (Merkle et al., 2006; Merkle and Wehner, 2010).

For the optimal model, the relationship between grass and road velocity (*e*) directly determines the angle α and thus the deviation point from the road. Our results suggest that *M. analis* is unable to adapt the deviation angle depending on differing *e*-values (Fig. 5B). However, it is important to note that the *e*-values were highly variable (range from 0.13 to 0.97) and substrate velocities can depend on various different variables (temperature, density of grass), making definitive conclusions at this point premature. Further controlled experiments are necessary.

Pathway choice mechanism

The individual ability of scouts to calculate a deviation from the direct distance to minimize time was remarkable and the underlying mechanisms with which they were able to do so remain unclear. We propose a simple mechanism with which this could be achieved. We observe in total two decisions the scout ant has to make. (1) Does it use the roads (deviation) or does it walk the direct distance back to the nest? Our results seem to suggest that the ants were able to make this decision depending on the time saved through the deviation (Fig. 6). This only depends on the angle β between the nest and food source in relation to the road (Fig. 2). (2) What is the best angle to deviate from the road (angle α) to minimize time? This second angle only depends on the relationship of surface speeds (*e*-value) and not on distance. The ants could have a fixed deviation angle from the direct route (angle γ) based on a simple distinction between easy versus difficult terrain. This angle could be used for their pathway choice as an approximation of the optimal model. However, our results do not support this hypothesis, showing no clear fidelity to a particular angle γ. Other factors therefore might play a role in this decision and the chosen angle.

Furthermore, individual learning by the scouts about the position of the road could be involved, as road use increased over time. This could be explained through replacement of old scouts (death) by new ones that are only confronted with the already manipulated environment. In desert ants, individual foragers can use and remember several spontaneously formed routes during their foraging walks (Mangan and Webb, 2012). As previous studies have shown, naive individuals perform intense orientation walks and thus gain knowledge about landmarks and other orientation-facilitating information, which are stored in their long-term memory (Fleischmann et al., 2016; Sommer et al., 2008). The navigational toolkit of ants reaches from simple homing to complex navigation with utilization of route memory (Cheng et al., 2009; for a review on ant orientation, see Wehner and Rössler, 2013). It should be noted that most studies on ant navigation focus on desert ants of the genera *Cataglyphis* and *Melophorus*, and no such studies have been done on *M. analis*. However, under the presumption that the path integrator and route memory are present in *M. analis*, our observations are well within the explanatory scope of current ant navigation knowledge. The most important part of our observations, the detouring behavior, does not necessarily imply the use of an internal map; instead we hypothesize that the ants' 'navigational toolkit' is probably sufficient to explain this orientation capability, as has been shown before (Cruse and Wehner, 2011). Ultimately, we need to know more about the general searching and foraging patterns of scouts in *M. analis* to better understand the underlying mechanisms regulating this behavior.

Raid site distribution

The raiding sites were located directly on the road itself significantly more often than expected by a random termite distribution; 17% of all observed raids after road installation were located on the road, suggesting preferred walking/searching by the scout ants on the road compared with the overall grass area around the nest. Although there were no specific measurements made, it is safe to assume that the artificial roads did not attract more termites; because of litter removal, the opposite would be expected.

Evolution

The high grade of nutritional specialization on termites of the subfamily Macrotermitinae is likely to be the main evolutionary driver for the remarkable capabilities of *M. analis* regarding their optimal foraging behaviors (Frank and Linsenmair, 2017a; Frank and Linsenmair, 2017b). Most termite predators are either single foragers or have a kleptoparasitic lifestyle like *Centromyrmex* (Schmidt and Shattuck, 2014), in which deviations from a direct path are likely to be less beneficial. True group hunting with closed columns of workers is rare in other ants, e.g. *Neoponera laevigata* species group (Leal and Oliveira, 1995) and some *Leptogenys* species (Maschwitz and Schönegge, 1983). They also resemble raids of some dulotic ant species, especially those of *Polyergus* genus, in which a scout also leads a raiding column (Topoff et al., 1987; Tanaka and Kojima, 2001; Trager, 2013). However, a pathway choice behavior as in *M. analis* has not yet been shown in any other species.

Although our roads were artificial and would not occur naturally in the environment of *M. analis*, there are similar natural occurrences – for instance, small open areas with no grass coverage. The African savanna is also a quickly changing environment with annual bushfires that can open new natural pathways for the scout ants to walk. *Megaponera analis* is a fairly big ant species, and thick grass areas can be obstacles, which the ants need to circumvent (Kaspari and Weiser, 1999).

Although the deviations lead to a longer travel distance, it is safe to assume that walking in obstructive vegetation over a longer time period would be more costly in terms of energy. For many ants that use permanent paths (e.g. trunk trails) for transportation, this is one of the main factors (Plowes et al., 2013; Silva et al., 2013). However, because termite-foraging sites change constantly, it would not be beneficial for *M. analis* to install permanent trunk trail systems.

Ultimately, a precondition for developing a time-minimized pathway choice mechanism is a heterogeneous environment (leading to substrate-dependent velocities). Another factor that could play a role is group foraging (the more ants use a given path, the greater the benefit of improving it). These two conditions apply to many ant species; in *M. analis* a collective decision on path choice cannot be made because of the constantly changing position of food sources, which are searched for by individual scouts. We would expect to find similar path choice behaviors in other group-hunting foragers; further comparative studies are necessary to better understand the evolutionary drivers of this behavior.

Conclusions

We observed that *M. analis* is able to minimize travel time through detours on artificial roads, with values close to the minimum time predicted by our model, and propose a new mechanism for its

regulation. As road usage increased over time, we hypothesize that scouts possibly learn the position of roads and can thus integrate this information into their pathway choice. Previous studies have shown pathway optimization in other ant species as well (Loreto et al., 2013; Oettler et al., 2013); however, this is the first reported case where this decision is not regulated collectively, but comes solely from an individual scout ant.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: E.T.F.; Methodology: E.T.F.; Validation: P.O.H.; Formal analysis: E.T.F., P.O.H.; Investigation: E.T.F., P.O.H.; Data curation: E.T.F., P.O.H.; Writing - original draft: P.O.H.; Writing - review & editing: E.T.F., P.O.H.; Supervision: E.T.F., K.E.L.; Project administration: K.E.L.; Funding acquisition: E.T.F., K.E.L.

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