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FORRAGEIO EM *Nasutitermes* aff. *coxipoensis*: COMPORTAMENTO E ESTRATÉGIAS EM RELAÇÃO À DISPONIBILIDADE DE RECURSOS

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal de Sergipe, como requisito parcial para obtenção do título de Mestre em Ecologia.

Orientadora: Dr.ª Ana Paula Albano Araújo

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por

CAMILLA SANTOS ALMEIDA

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal de Sergipe, como parte dos requisitos exigidos para a obtenção do título de Mestre em Ecologia e Conservação.

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SUMÁRIO

RESUMO

Uma gama de estratégias comportamentais e habilidades sensoriais permite aos animais minimizar os custos envolvidos na busca por alimento. Dentre os fatores envolvidos na variação dos custos de forrageio, a disponibilidade de recursos representa um papel central e é reconhecida por modular as áreas de uso dos animais. Algumas espécies de cupins exibem características que podem tornar o processo de forrageio ainda mais oneroso. Espécies do gênero *Nasutitermes*, por exemplo, apresentam gastos extras no forrageio, uma vez que além de construírem uma rede de túneis para acessar os recursos, ainda apresentam um elevado número de soldados, indivíduos troficamente dependentes. No presente estudo, avaliamos *(i)* o padrão de forrageio em *Nasutitermes* aff. c*oxipoensis* (Termitidae: Nasutitermitinae), incluindo as estratégias de busca e o papel dos soldados; e *(ii)* analisamos se colônias desta espécie respondem à variação na disponibilidade de recursos. Experimentos manipulativos foram conduzidos em campo e em laboratório a fim de analisar o padrão de forrageio de *N.* aff. *coxipoensis*. Para isso, 35 ninhos foram transplantados em áreas de dunas, em Pirambu-SE. Foram estabelecidas sete parcelas em um contínuo de aumento da densidade de recursos (iscas de cana-de-açúcar). Testes em laboratório foram realizados a fim de analisar o papel dos sinais químicos (ex. feromônio de trilha) presente na glândula esternal de operários e soldados. Durante 10 dias consecutivos foram quantificados: o número de trilhas e de túneis, o comprimento total, o número de ramificações destes e a velocidade de construção dos túneis. Os dados foram analisados utilizando-se modelos lineares generalizados e modelos mistos. *Nasutitermes* aff. *coxipoensis* apresentou forrageio principalmente noturno. Soldados foram os primeiros indivíduos a iniciarem o forrageio, no entanto, em trilhas já estabelecidas, o número de operários foi sempre maior do que o de soldados. O número de trilhas ativas permaneceu constante ao longo do período de observação, enquanto o número de túneis aumentou de forma gradativa. Em grupos compostos por soldados e operários, os operários preferiram seguir os sinais de trilha dos soldados. O número de trilhas, o comprimento total e suas ramificações reduziram com o aumento da disponibilidade de recursos. A conversão de trilhas em túneis aumentou em locais com maior densidade de recursos. Nossos resultados sugerem que os custos envolvidos na produção de soldados de *Nasutitermes* aff. *coxipoensis* parecem ser compensados pelo seu papel decisivo no forrageio. Colônias desta espécie parecem otimizar o forrageio através de uma estratégia combinada de formação de trilhas e túneis. Em locais com baixa disponibilidade de recursos os cupins forrageiam preferencialmente em trilhas, evitando a conversão destas em túneis. Tal estratégia, ainda não foi relatada na literatura. Assim, *N.* aff. *coxipoensis* apresenta estratégias para otimização do forrageio, minimizando os custos envolvidos nesse processo. Os resultados deste estudo podem contribuir para a investigação de questões sobre evolução do comportamento de forrageio de cupins, assim como para desvendar os mecanismos envolvidos nos padrões de distribuição e estruturação de comunidades desses insetos.

Palavras-chave: área de forrageio, comportamento de forrageio, densidade de recursos, glândula esternal, Isoptera.

ABSTRACT

A range of behavioral strategies and sensory abilities allow animals to minimize costs involved in the search for food. Among the factors involved in the variation of foraging costs, the availability of resources represents a central role and it is recognized for modulating the animal home range. Some species of termites can exhibit characteristics that make the foraging process even more expensive. Species belonging to the genus *Nasutitermes*, for example, have an extra cost in foraging: in addition to build a network of tunnels to access resources, they have a large number of soldiers, a caste trophically dependent. In the present study: *(i)* we evaluated the foraging pattern in *Nasutitermes* aff. *coxipoensis* (Termitidae: Nasutitermitinae), including the searching strategy and the role of soldiers; and *(ii)* we analyzed whether colonies of this species responds to variations in the availability of food resources. Manipulative experiments were conducted in the field and in the laboratory to analyze the pattern of foraging in *N.* aff. *coxipoensis*. For this, 35 nests were transplanted into areas of dunes in Pirambu-SE. Seven plots were established in a continuous increament in the density of resources (sugarcane baits). Laboratory tests were conducted to examine the role of chemical signals (eg. trail pheromone) present in the sternal gland of workers and soldiers. During 10 consecutive days it was measured: the number of trails and tunnels, their total length, number of branches and the tunneling speed (cm/day). Data were analyzed using generalized linear models and mixed linear models. *Nasutitermes* aff. *coxipoensis* showed mainly nocturnal foraging. Soldiers were the first individuals to start the foraging, however, in established trails, the number of workers were always higher than soldiers. The number of active trails remained constant over the observation period, while the number of tunnels increased. In groups of soldiers and workers, the workers chose to follow the trail signals of soldiers. The number of trails, the total length and their branches decreased with increment of resource availability. The conversion of trails in tunnels increased in areas with higher resource density. Our results suggest that the costs involved in the production of soldiers in *N.* aff. *coxipoensis* seem to be compensated by their decisive role during the foraging process. Colonies of this species seem to optimize their foraging through a combined strategy of constructing trails and tunnels. In places with low resource availability, termites forage mainly on trails, avoiding to convert trails in tunnels. This strategy has not yet been reported in the literature. Thus, *N.* aff. *coxipoensis* presents strategies in order to optimize the foraging, minimizing costs involved in this process. These results can contribute to the key question about the evolution of termite foraging behavior, as well as to understand the mechanisms involved in the distribution patterns and structuring communities of these insects.

Keywords: foraging area, foraging behavior, resource density, sternal gland, Isoptera.

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INTRODUÇÃO GERAL

Uma gama de estratégias comportamentais e habilidades sensoriais permite aos animais minimizar os custos envolvidos na busca por alimento (Alcock, 2011). Insetos sociais, por exemplo, apresentam um elaborado sistema de comunicação e divisão de trabalho que permitem uma eficiente busca por recursos e redução dos custos envolvidos nesse processo (Krebs and Davies, 1993). Cupins vivem em ninhos que abrigam um grande número de indivíduos coloniais (Costa-Leonardo, 2002) e desempenham um importante papel ecológico na ciclagem de nutrientes e estruturação dos solos em ambientes tropicais (Bignell and Eggleton, 2000; Jouquet et al., 2011; Sarcinelli et al., 2009). Ao longo da evolução do grupo, houve uma tendência em alteração do comportamento de forrageio, onde espécies mais basais utilizam o alimento como próprio ninho (espécies de sítio-único) e as mais derivadas apresentam uma separação completa entre ninho e alimento (forrageadores de sítio-central) (Traniello and Leuthold, 2000). Esta transição foi acompanhada por um aumento nos custos e riscos envolvidos no forrageio. A maioria dos forrageadores de sítio central necessita construir uma rede de túneis que liga o ninho ao recurso, o que representa um custo adicional durante o processo. No entanto, ainda é pouco compreendido se o forrageio dessas espécies é realizado de forma direcional e se estes adotam estratégias para minimização dos custos envolvidos no forrageio (Miura and Matsumoto, 1998; Traniello and Leuthold, 2000). A compreensão das respostas dos cupins às variações na disponibilidade de recurso durante o forrageio pode auxiliar no entendimento de processos ecológicos mais amplos, como estruturação de suas comunidades e funcionamento dos ecossistemas.

Variações na disponibilidade de recursos podem interferir no balanço entre custos e benefícios durante o forrageio (Alcock, 2011), modulando a distribuição dos organismos no ambiente (Aarts et al., 2013). Tal relação tem sido demonstrada para uma ampla variedade de animais [ex. insetos (Goverde et al., 2002; Grangier and Lester, 2014; Urbas et al., 2007), aves (Stratford and Stouffer, 1999; Yahnke, 2006), mamíferos (Boyle and Smith, 2010; Fortin et al., 2007; Gende et al., 2001), peixes (Menegatti and Vescovi, 2003; Santos et al., 2014) e anfíbios (Connette and Semlitsch, 2013)]. Forrageadores de sítio central - que iniciam e terminam sua busca por recurso em torno de um ninho - apresentam uma particularidade durante o forrageio, uma vez que não podem alterar totalmente suas áreas de uso em habitats de baixa qualidade (Chase, 1998; Dukas and Edelstein-Keshet, 1998; Westphal et al., 2006). Assim, tais organismos precisam lidar continuamente com as pressões locais em torno de seus ninhos, sendo esperado, portanto, que adotem estratégias a fim de otimizar seu forrageio (Araújo et al., 2011; Araújo et al., 2007; Bandeira and Vasconcellos, 2004; DeSouza et al., 2009; Jouquet et al., 2011).

Por um lado, sabe-se que cupins são seletivos em relação ao recurso consumido, preferindo itens maiores (DeSouza et al., 2009; Evans and Gleeson, 2006), de melhor qualidade nutricional (Higashi et al., 1992) e que conferem baixo risco de predação (DeSouza et al., 2009; Korb and Linsenmair, 2002). No entanto, a capacidade desses insetos em modular a construção de túneis em resposta à disponibilidade de recursos só foi investigada (até o momento) em condições de laboratório. Tais trabalhos mostraram que colônias de cupins reduziram a velocidade de construção (Araújo et al., 2011; Traniello and Leuthold, 2000), o número e tamanho de túneis em situações de maior oferta de recursos (Arab and Costa-Leonardo, 2005; Araújo et al., 2011; Hedlund and Henderson, 1999).

Nasutitermes consiste no gênero mais diversificado e derivado filogeneticamente, incluindo espécies com hábitos alimentares variados, e que são reconhecidos por apresentarem uma elevada proporção de soldados em relação aos demais grupos de cupins (Haverty, 1977). Tais espécies são forrageadores de sítio central, que forrageiam por trilhas expostas na superfície (*"open air"*; Bordereau & Pasteels, 2011) ou pela construção de uma rede de túneis e galerias (acima ou abaixo do solo), interconectando o ninho à fonte alimentar (Grace & Campora, 2005).

O objetivo desta dissertação foi analisar o comportamento de forrageio de *Nasutitermes* aff. *coxipoensis* (Blattodea: Termitoidea: Termitidae) e se estes animais utilizam estratégias para minimizar os custos envolvidos no forrageamento através da modulação do tamanho de suas áreas de uso frente à variação na disponibilidade de recursos. A dissertação foi dividida em dois capítulos. O capítulo 1 consiste no artigo "Combined foraging strategies and soldier behaviour in *Nasutitermes* aff. *coxipoensis* (Blattodea: Termitoidea: Termitidae)", que analisa o comportamento de forrageio, incluindo a combinação conjunta de formação de trilhas e túneis e o papel dos soldados nesse processo. Já o capítulo 2 apresenta o artigo "Resource density regulation of termite foraging range: A field test of optimization strategies", no qual mostramos as estratégias de *N.* aff. *coxipoensis* em resposta à variação na densidade de recursos no ambiente.

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CAPÍTULO 1

Combined foraging strategies and soldier behaviour in *Nasutitermes* aff. *coxipoensis* (Blattodea: Termitoidea: Termitidae)

Camilla S. Almeida, Paulo F. Cristaldo, Daniela F. Florencio, Nayara G. Cruz, Abraão A. Santos, Alexandre P. Oliveira, Alisson S. Santana, Efrem J. M. Ribeiro, Ana P. S. Lima, Leandro Bacci & Ana P. A. Araújo

Em revisão na Behavioural Process

ABSTRACT. A range of behavioural strategies and sensory abilities allow animals to minimize costs involved in the search for food. By build a network of tunnels and presenting a large number of soldiers (*i.e.*, trophically dependent individuals), *Nasutitermes* spp. termites feature behaviours that imply additional costs during this process. Here, we evaluated *N.* aff. *coxipoensis* foraging strategies focusing in the role of soldiers during foraging. Field experiments were carried out via nests transplantation to dune areas, and laboratory experiments evaluated termite responses to sternal gland chemical signals from workers and soldiers. *Nasutitermes* aff. *coxipoensis* presented primarily nocturnal foraging. Soldiers typically initiated foraging, however in established trails, the number of workers was always higher than that of soldiers. The number of trails remained constant over time, while the number of tunnels increased linearly over time. A higher proportion of tunnels originated in surrounding areas than directly from the nests. At observation points with tunnels, there were more stationary than walking soldiers; the opposite was true in observation points without tunnels. In mixed groups, the workers chose to follow soldier chemical signals, and in these groups, soldiers were the first to follow trails. Our results allowed us to identify a not common foraging strategy in termite species; which included the establishment of trails followed by construction of tunnels. Such foraging strategies occurs predominantly at night and soldiers play a key role on the foraging process. This foraging strategy reported here seems to be employed to optimize the energetic gain.

Keywords. Foraging decision; foraging trail; sternal gland; tunnelling.

INTRODUCTION

Increased effort toward search for and manipulation of resources may be accompanied by greater exposure to negative interactions (*e.g.*, competition and predation risk; Lima and Dill, 1990). Such costs involved in acquiring energy are known to influence evolutionary responses related to foraging strategies, life history characteristics, and social behaviour of animals (Wilson, 1985). Defensive (or territorial behaviour) and inter-individual cooperation are strategies that are widely distributed among animals (Tian and Zhou, 2014). In some cases, group cooperation is so high that certain individuals have behavioural or morphological adaptations for defence (Oster and Wilson, 1978). Such adaptations arose independently in a diverse array of groups, including mole rats (O'Riain and Jarvis, 1997), shrimp (Duffy and Macdonald, 2010), benthic cnidarians (Mcshea and Venit, 2002), insects (aphids: Braendle and Foster, 2004; thrips: Perry et al., 2004) and even in trematode worms (Hechinger et al., 2011).

Eusocial insects (*i.e.*, bees, ants, wasps and termites) represent the most extreme examples of collective foraging (Smith and Szathmáry, 1995; Wilson, 1985). Eusocial colonies can house a large number of individuals that perform complex tasks through simple individual behaviour, without having a central control (Greene and Gordon, 2007; Traniello and Leuthold, 2000). Various behavioural strategies and sensory abilities allow these animals to minimize costs involved in foraging (Grangier and Lester, 2014; Lanan and Bronstein, 2013; Richter, 2000; Westphal et al., 2006). However, in Isoptera (Blattodea: Termitoidea), some behavioural and evolutionary aspects of foraging are still poorly understood (Miura and Matsumoto, 1998; Traniello and Leuthold, 2000).

Termites have different nesting and foraging habits (*sensu* Abe, 1987), including: “one-piece” species, in which the nest itself serves as a food source; “intermediate foragers”, in which the nest and food are not clearly distinct; and “central-place foraging” species, in which nest and food are fully independent. In the latter, species can foraging by exposed trails on surface ("open air"; Bordereau and Pasteels, 2011) or by construction of a tunnel network and galleries (either above or below ground) by workers, thereby interconnecting the nest and the food source (Grace and Campora, 2005). Such behaviour can increase protection against predation and desiccation, but may also increase the costs associated with searching for resources.

Chemical signals are a primary sensorial channel used by termites during processes of collective foraging (Reinhard and Kaib, 2001; Traniello and Leuthold, 2000), and these signals facilitate the localization, recruitment and exploitation of resources (Lima and Costa-Leonardo, 2012). Trail pheromone is one such substance, produced by the sternal gland (Lima and Costa-Leonardo, 2012). Although this structure is present in both worker and termite soldiers (Costa-Leonardo and Haifig, 2010), the pheromone seems to be deposited only by workers during the recruitment phase (Costa-Leonardo et al., 2009; Lima and Costa-Leonardo, 2012). The precise role of emission of this substance, and responses to these signals by the soldiers are poorly explored (but see Traniello and Busher, 1985). Termite soldiers are known to have limited behavioural repertoires (Noirot, 1990), with colony defence as their primary function (Prestwich, 1984). The morphological specialization of this caste is so pronounced that they are unable to feed themselves, being completely dependent on trophallaxis by workers (Noirot and Noirot-Thimothee, 1969; Noirot, 1990). Thus, maintenance of this caste becomes energetically costly, requiring greater foraging effort from workers.

Species in Nasutitermitinae subfamily have a higher proportion of soldiers (see Haverty, 1977) which may represent an additional energetic cost to colonies. Here, we evaluate in a natural (field) environment the food searching of the central-place forager *Nasutitermes* aff. *coxipoensis* - a common species in tropical regions, often found in association with grasses and in sandy soil. According to a brief report by Mathews (1977), this species may forage in "open-air" (e.g. both at night and in mornings after rain) and also construct tunnels during foraging. Experiments were done to test wether *N.* aff. *coxipoensis* employ strategies involved in *(i)* realize nocturnal foraging; *(ii)* optimize their foraging through an initial exploration of trails and directional tunnels construction; and *(iii)* optimizing of the role of soldiers during foraging process.

MATERIALS AND METHODS

Ethics statement

Permission for termite collection was issued by ICMBio, IBAMA (47652-1). No specific permits were required for the laboratory experiments described herein, which were conducting using a species that is neither endangered, nor protected.

Study area and field nest manipulation

The experiment was conducted at the Santa Isabel Biological Reserve (10°43'56" S, 36°50'36" W), in the Pirambu municipality, Sergipe state, northeastern Brazil. Regional vegetation consists of grasslands (grasses and sedges), post-beach, restinga, coconut palms, wetlands, and marshes. The climate in region is tropical wet and dry (Aw) according to Köppen climate classification systems (Pidwirny, 2011). The experiment was conducted in March 2015 ('dry season'), in dune areas intermixed with restinga.

Experimental manipulation included transplanting *N.* aff. *coxipoensis* nests (*N=35)* in dune areas previously cleared of all vegetation. Entire nests were removed from their original locations and immediately placed in central 5 x 5 m quadrants, with minimum distance of 0.5 m between quadrants. Excavations (30 cm depth) were made prior to transplantation, in which the nests were inserted and the bases coated with local substrate. Only visibly active nests, that have immature individuals were used and all transplanted nests were similar in size ($P = 0.15$). Pilot tests showed that transplantation of nest did not affect the behaviour of termites. *Nasutitermes* aff. *coxipoensis* specimens were collected and their identification confirmed by comparison with material from the Termitology Laboratory at UnB, where voucher specimens (# UnB-10616, 10617, 10618, 10619, 10620, 10621) are stored.

To minimize observer bias, blind methods were used when all the behavioural data were analyzed, except when the study involved focal animals in the field.

Nasutitermes *aff.* coxipoensis *foraging pattern*

To observe the foraging pattern of *N.* aff. *coxipoensis* colonies, behavioural observations in natural conditions were conducted in the transplanted nests.

Daily foraging activity was monitored at nests randomly selected ($N=9$) beginning at 6 p.m., with observations at 2h intervals for 24 hours total. An observer entered carefully in the quadrants stepping only in the parts not used by termites and has measured the number of trails established, and the activity of soldiers and workers on all trails. The activity of individuals on each trail, was estimated in a focal point which was established closer to the nest. Observation at each focal point included quantification of the total number of workers and soldiers in transit at both trail direction during one minute.

Trail formation and tunnel construction in *N.* aff. *coxipoensis* in nests ($N=10$) was monitored for ten consecutive days after 24 hours of nest transplantation. The number of primary trails was always quantified in the morning (6 a.m. - 10 a.m.) by observing traces left on the soil surface. The number of primary tunnels constructed on the surface was measured via direct observation. Plastic straws were inserted besides the final construction each day and mappings were made to follow and identify each tunnel along time. After the initial appearance of a tunnel, we noted whether construction began at the nest, or at another point within the quadrant area surrounding the nests.

In each nest observed were selected all trails contained points with constructed tunnels and the same number of trails without constructed tunnels. In all cases it was only observed one point/ trail. At each point, we observed an area of 3 cm surrounding the trails in which the number of soldiers standing or walking was quantified. The analyzed area, in points with tunnel construction, included 1,5 cm of the length of the tunnel. Points without constructed tunnels were selected randomly along the trails.

Role of soldiers in N. *aff.* coxipoensis *foraging*

In order to inspect the role of soldiers in *N.* aff. *coxipoensis*, we arbitrarily selected transplanted nests (*N=12*) for evaluation of the initial foraging pattern that occurs prior to trail establishment. Observations began at 4 p.m. and continued for three consecutive nights in all the points of each nest that have activity.

We recorded the caste of individuals making the first exit and return events at each nest, and subsequently recruited individuals.

Nasutitermes aff. *coxipoensis* nests (not transplanted; *N=3*) were chosen to evaluate the perception of signal paths between workers and soldiers. Nests were removed and taken to the laboratory for bioassays. Worker (SGW) and soldier (SGS) sternal glands extracts were prepared from 4th and 5th sternites dissected from 100 cold-immobilized individuals per caste in each colony. Individual sternites were immediately submerged into hexane solvent (10 µl/gland), extracted for 6 h at 4° C, then combined for a second hexane wash (100 µl at room temperature). Final extracts (both SGW and SGS) were stored at -18 °C prior to use in trail-following bioassays.

Trail-following bioassays were conducted to test the preferences of *N.* aff. *coxipoensis* groups to sternal glands extracts. The extract choice tests were conducted using three distinct groups *per* colony: *(i)* ten workers, *(ii)* ten soldiers and *(iii)* mixed group (composed by five workers and five soldiers), totalizing nine tested groups. Y-shape open-field trail-following bioassays (10 cm with a 120° angle between branches [stem with 3 cm and each branch with 7 cm]) were performed in ambient temperature conditions under dimmed light using paper disc olfactometer (see more details in Cristaldo et al., 2014; Sillam-dussès et al., 2005). Hamilton syringes (10 µL) were used to lay down the SGW and SGS trails in each arm of the Y drawn on filter paper. For each bioassay, a group of 10 individuals were placed inside a plastic Petri dish (⌀ 3 cm) that was modified to allow termite exit without disturbance. Extract choice was evaluated only for the first individual to leave the Petri dish, however in the mixed group the identity of second caste to leave was also recorded. For each group tested, a new trail was laid down on fresh filter paper. Bioassays were performed independently for each group using extracts made from the respective colony; and performed using 0.01 glands/µl, an extract concentration shown in preliminary trials to induce significant trail following activity in *N.* aff. *coxipoensis* workers and soldiers (see Table 1).

Statistical analyses

All analyses were carried out in R software (R Development Core Team, 2015) using Generalized Linear Models (GLM) followed by residual analysis to check the suitability of the error distribution and model fitting.

We used linear regression with normal error distribution to analyse the average number of trails made throughout the day. Linear Mixed models (*nlme* package) were used to determine variation in the average number of workers and soldiers on the trails per nest (*y*-vars) throughout the day (*x*-vars), and to test the variation of the average number of trails and tunnels (*y*-vars) over time after transplantation of nests (*x*-vars). 'Nest' was considered as a fixed factor.

The relationship between the proportion of tunnels per nest (*y*-var) that are built beginning at the nest or another point in the surrounding area (*x*-var) was tested by deviance analysis (ANODEV). Similar analysis was done to investigate the relationship of the average number of soldiers (walking or standing) (*y*-var) on points with or without tunnelling (*x*-var). In all cases mixed model (*nlme* package) was used, with 'nest' as a fixed factor. Variation in the number of workers and soldiers present during initiation of foraging were evaluated using a *t* test. Data from trail-following bioassays were analysed trough *glm* with binomial error distribution.

RESULTS

Nasutitermes *aff.* coxipoensis *foraging pattern*

Nasutitermes aff. *coxipoensis* showed primarily nocturnal foraging, in which activity taking place between 6 p.m. and 6 a.m. with trails establishment and tunnel construction. During the night *N.* aff. *coxipoensis* constructed trails that departed directly from nests ($P<0.001$; Table 2; Fig. 1A). Workers and soldiers both actively foraged on established trails, but the average number of workers was significantly higher than that of soldiers ($P<0.001$; Table 3; Fig. 1B).

Trails formed at night left traces on the surface that could be visualized and quantified during the day. The number of trails formed by *N.* aff. *coxipoensis* on each day remained constant over the ten days of observation, however, the number of active tunnels increased linearly over time ($P<0.001$; Table 3; Fig. 2A). Tunnels were always built along the trails formed, indicating that some of the trails are converted into tunnels. Tunnels were usually constructed when meet potential resource, such as leaves or small twigs brought by the wind. Surprisingly, most of the tunnels built did not originate directly from the nest, but instead from points around the nest inside of the quadrant area ($P<0.001$; Table 3; Fig. 2B). At observation points with constructed tunnels, there were a significantly greater number of soldiers standing near tunnel edges than walking (*P*<0.001; Table 3; Fig. 3). Soldiers were positioned along the entire length of the tunnel margins, always with heads facing the external side. At observation points without tunnelling, most of the soldiers were walking instead of remaining stationary (*P*<0.001; Table 3; Fig. 3).

Role of soldiers in foraging

During early foraging, soldiers were the first caste to leave the nest (88.8% of observations, *N*=33). After exploration of the external area and initial return to the nest, recruitment of other soldiers was common (78.8%, *N*=33). During this initial phase, which occurs before trail establishment, the number of soldiers scattered around the nest is greater than the number of workers (*P*<0.001).

In the lab bioassays, *N.* aff. *coxipoensis* groups showed distinct preference to SGW *vs.* SGS trails (Fig. 4); workers significantly prefer SGW trails over SGS trails (*P*=0.03) (Fig. 4A). However, soldiers and mixed groups (*i.e.*, both soldiers and workers) significantly preferred SGS trails (soldier groups: *P*=0.02; mixed groups: *P* <0.001) (Fig. 4A). Bioassays with mixed group showed that the soldier caste was significantly more likely to initiate following of artificial trails (*P*=0.001; Fig. 4B). In contrast, no significant differences were observed in second caste with regard to Petri dish exit, *i.e.,* both worker and soldier castes had the same probability of leaving the arena after the initial soldiers left to follow trails (*P*=0.120; Fig. 4B). Regardless of which caste left the Petri dish after the soldier, these individuals mostly chose the same trail as the soldier (*P*<0.001).

Table 1. Distance followed by workers and soldiers in sternal glands extracts made from workers (SGW) and soldiers (SGS) in different concentrations. *P*=0.05.

Caste tested	**Extract**	**Concentration**	**Distance followed (cm)**	***P***
Workers	SGW	1 Eq/cm	9.4±0.18 **a**	**< 0.001**
		10^{-1}Eq/cm	9.7±0.14 **a**	
		10^{-3}Eq/cm	6.23±0.14 b	
	SGS	1 Eq/cm	9.6±0.10 **a**	**< 0.001**
		10^{-1}Eq/cm	10±0.082 **a**	
		10^{-3}Eq/cm	7.2±0.12 b	
Soldiers	SGW	1 Eq/cm	8.7±0.13 **a**	**< 0.001**
		10^{-1}Eq/cm	9.2±0.17 **a**	
		10^{-3}Eq/cm	6.2±0.10 b	
	SGS	1 Eq/cm	8.2±0.14 a	**< 0.001**
		10^{-1}Eq/cm	9.4±0.30 b	
		10^{-3}Eq/cm	5.2±0.14 c	

Table 2. Summary of Generalized Linear Model inspecting the relationship between average number of trails formed by soldiers and workers during 24 hours total. *P*=0.05.

Term	**DF**	**Deviance**	***F***	***P***
Number of trails				
Model	1	53.664	97.487	<0.001
Time of day	1	22.849	120.958	<0.001
Time of day (^2)	1	2.477	74.017	<0.001
Error	9			

Table 3. Summary of Linear Mixed Models inspecting the relationship between *(i)* average number of trails and tunnels, *(ii)* initial position of tunnels construction and *(iii)* soldier behavior during tunnels construction. In all models, nests were included as a fixed factor. *P*=0.05.

Term	**DF**	***F***	***P***	**StDev**	**Residuals**
Activity in trails over time					
Intercept	1	25.342	<0.001		
Time	1	14.436	<0.001		
Time^2	1	11.079	0.012		
Caste (worker/soldier)	1	8.230	0.021		
Random effects					
Nests				2.686	
Caste (worker/soldier)				4.757	8.248
Average number of trails and tunnels					
Intercept	1	50.0528	<0.001		
Day	1	226.837	<0.001		
Type (trail/ tunnel)	1	42.850	<0.001		
Random effects					
Nests				3.997	
Type (trail/tunnel)				7.244	7.622
Tunnels construction origin					
Intercept	1	416.603	<0.001		
Position (from the nest or around the nest)	1	67.936	<0.001		
Random effects					
Nests				2.92e-06	
Position				0.201	0.0004
Soldier behavior x tunnel construction					
Intercept	1	169.026	<0.001		
Tunnels construction (with or without)	1	20.014	<0.001		
Behavior (stopped or walking)	1	0.615	0.453		
Tunnel construction: Behavior	1	36.485	0.001		
Random effects					
Nests				0.0002	
Behaviour				0.869	2.529

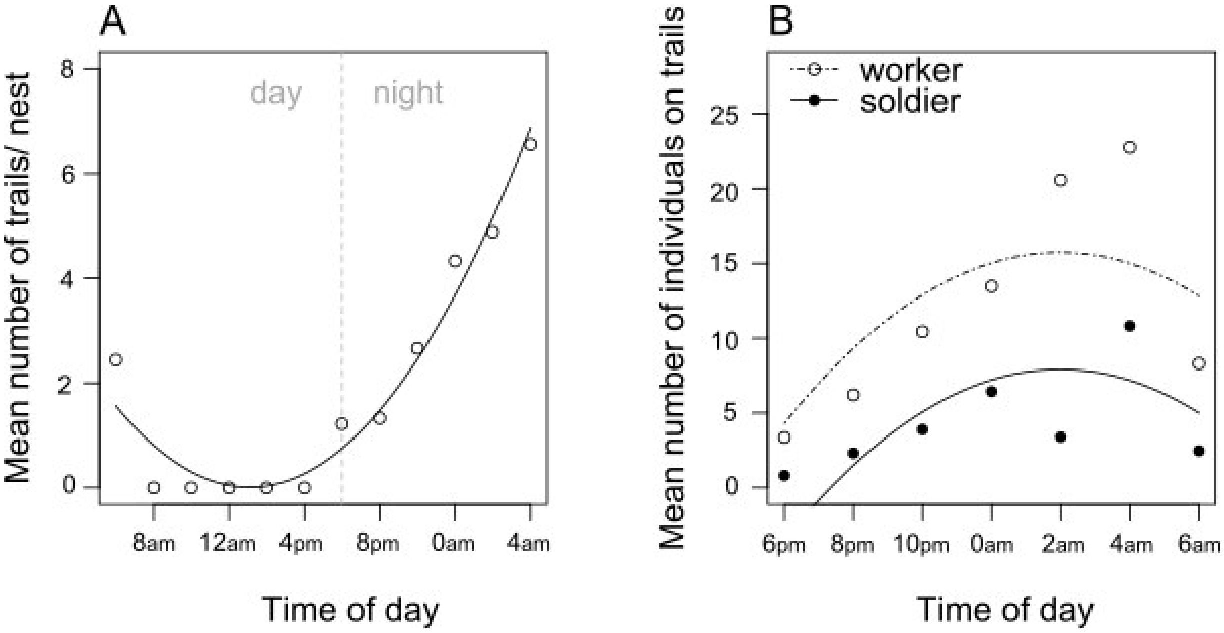

Fig 1. Trail activity during night foraging in *Nasutitermes* aff. c*oxipoensis.* (A) Average number of trails/nest formed by soldiers and workers during 24 hours total **(B)** Average number of individuals (workers and soldiers) in transit on trails/min during night (focal point: 3 cm; more details on Material and Methods section). March 2015. Pirambu, SE, Brazil.

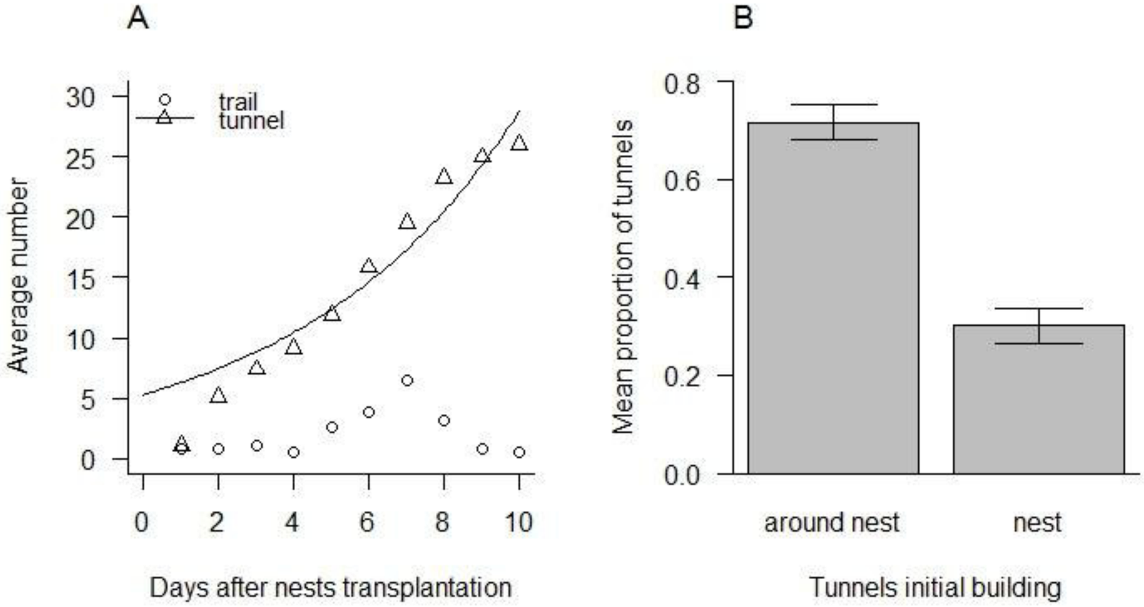

Fig 2. Trails formation and tunnel construction pattern in *Nasutitermes* aff. *coxipoensis* over ten consecutive days after nests transplantation. **(A)** Total number of trails formation and active tunnels constructed over days after nest transplantation. Each point represents the number of trails and tunnels that were active along the days. **(B)** Average proportion of tunnels constructed originating directly from the nests or at another point within the quadrant area surrounding the nests. March 2015. Pirambu, SE, Brazil.

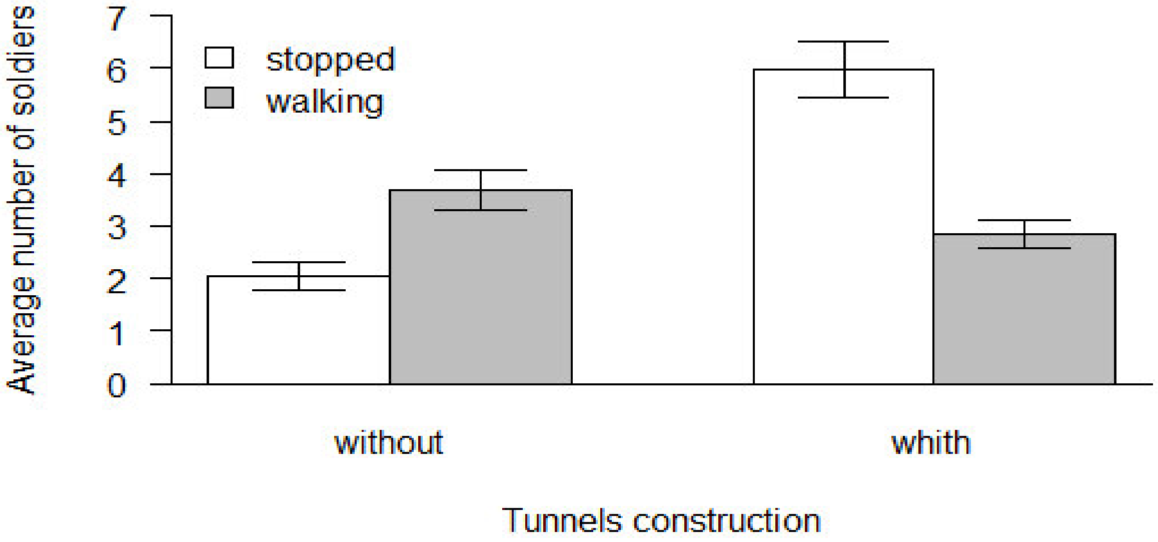

Fig 3. Average number of *Nasutitermes* aff. *coxipoensis* soldiers stopped and walking on foraging trails with or without constructed tunnels. See Material and Methods. March 2015. Pirambu, SE, Brazil.

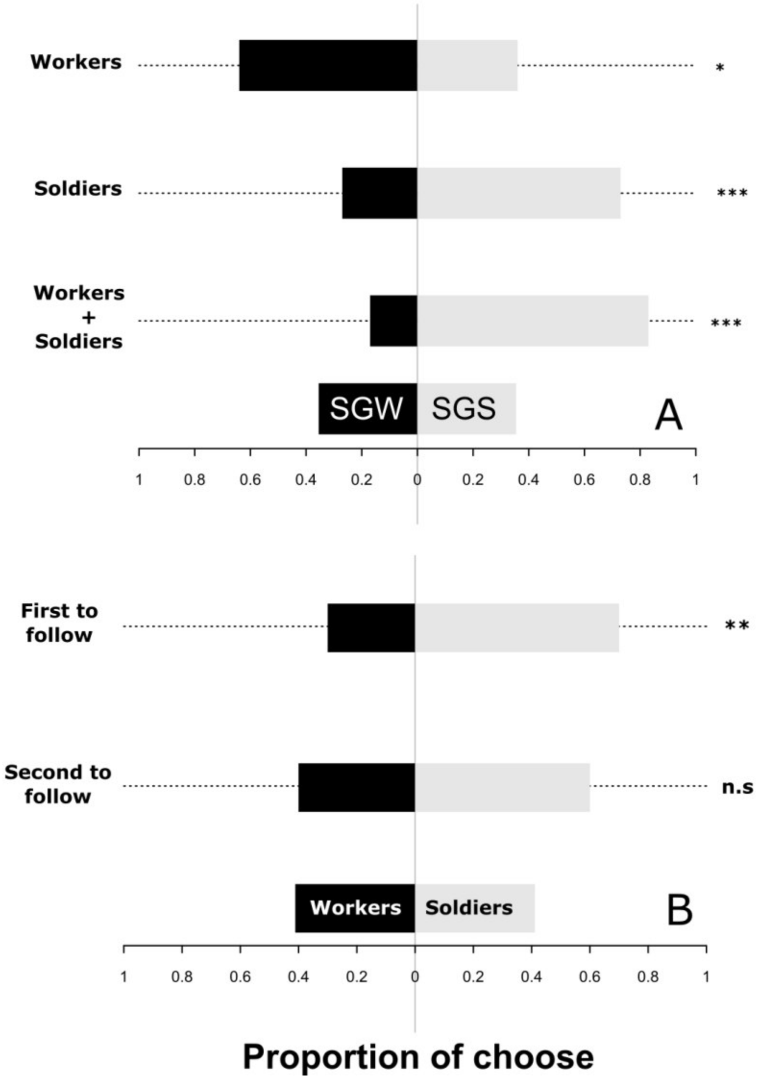

Fig 4. Choice preference and behaviour of *Nasutitermes* aff. *coxipoensis* groups towards sternal gland extracts from workers (SGW) and soldiers (SGS). In the panel A, horizontal *axis* depicts the average proportion of the number of individuals choosing for a given arm of the Y-shape olfatometer. In B, horizontal *axis* depicts the average proportion of workers and soldiers that left the Petri dish in the base of Y at first and second and follow the artificial trail in the mixed group (see more details in Results).

DISCUSSION

Along the diversification of Isoptera clade, there was a trend toward separation between nest and food resource, which boosted the emergence of a true worker caste (see Legendre et al., 2008). However, emergence from the nest presents limitations once termites are softbodied organisms with little sclerotization. Among the central-place foraging termites, species capable of searching for food at the soil surface do so at night, while others build a network of tunnels either underground or below the surface of the soil (Traniello and Leuthold, 2000). Our results show that *N.* aff. *coxipoensis* exhibit two of these strategies, *i.e.*, in addition to forming exposed trails, they also build a network of surface tunnels. Foraging strategy present here is, in the best of our knowledge, not explicitly related for termite species. It may function to optimize tunnelling behaviour in *N.* aff. *coxipoensis*.

In termites, tunnel construction tends to increase foraging costs because it requires labour from numerous workers, their displacement from other activities, and greater exposure to predators. Although tunnels are technically an extension of the nest (*e.g.*, the primary physical barrier for protection of colonies) they do not represent a perennial investment. In addition to the costs of construction, the feasibility of the tunnel also depends on spatial and temporal resource availability; previous studies have demonstrated tunnel abandonment in some colonies (Tschinkel, 2010), which is likely occurs either when tunnels do not improve resource acquisition (Evans and Gleeson, 2006), or when risk of predation is high (DeSouza et al., 2009; Korb and Linsenmair, 2002). A portion of the costs involved in *N.* aff. *coxipoensis* tunnelling seems to have been circumvented by a number of strategies. First, nocturnal foraging (Fig. 1A) minimizes the risk of desiccation, allowing foragers (both workers and soldiers) to explore areas on the surface prior to tunnel construction (Fig. 1B). This exploration by means of trails is fixed over time (Fig. 2A), suggesting that colonies must explore food resources simultaneously (APA Araújo, *pers. obs.*). On the other hand, the linear increase in the number of tunnels over time suggests that trails are converted into tunnels only when food sources are perceived. Interestingly, most of the tunnels did not originate directly from nests (Fig. 2B). In addition to contributing to cost reduction, this strategy may serve to provide refuge along the trails. In fact, previous studies have demonstrated that some termites species build satellite nests around the home range, which appears to increase both the foraging area and food stock for colonies (Holt and Easey, 1985), and may protect the colony from natural disasters (e.g., fire; Desouza et al., 2003).

The trend of increased exposure on the soil surface (*e.g.*, Nasutitermitinae; Mathews, 1977), on the other hand, may also increased foraging risks (Korb et al., 2012). Indeed, central-place foraging species (*e.g.* in Nasutitermitinae subfamily [see Haverty, 1977]) have a higher proportion of soldiers and more efficient or sophisticated defence mechanisms (e.g., chemical defence [Prestwich, 1984] and signal alarm complexity [Cristaldo et al., 2015]). The increase in soldier investment, however, may represent an additional cost to colonies due to greater trophic dependence. In fact, previous studies indicate that soldiers can perform additional tasks beyond defence, including initial exploration of foraging areas (Casarin et al., 2008; Traniello, 1982; Traniello and Busher, 1985) and control of colony microorganisms (Rosengaus et al., 2000). Here we show that *N.* aff. *coxipoensis* soldiers also exhibit behavioural flexibility. Soldiers begin exploration of areas surrounding the nest environment, with continued participation in trail construction (Fig. 2B) and performance of escorting services during tunnel construction (Fig. 3). Although the role of soldiers as initiators of foraging is not common to all termites (Arab et al., 2012; Reinhard and Kaib, 2001), it has been reported in some groups (Casarin et al., 2008; Moura et al., 2006; Olugbemi, 2011), including genus *Nasutitermes* (Miura and Matsumoto, 1998; Traniello, 1982; Traniello and Busher, 1985). This behaviour may therefore be common among the Nasutitermitinae species.

Interestingly, beyond participation, soldiers initiate and appear to lead foraging efforts. Our results from trail-following bioassays initially seemed to indicate that trail following behaviour caste is specific in this species (Fig. 4A). However, when mixed groups were tested termites preferred to follow sternal gland extracts made from soldiers, which likely indicates quantitative or qualitative differences in soldier and worker trail pheromones. Preference to

SGS over SGW was previously observed in *N. corniger* and *N. ephratae* (see Arab et al., 2005). Further, *N. costalis* trails laid by soldiers were observed to recruit only soldiers, but trails laid by workers recruited both workers and soldiers (Traniello, 1982). Interestingly, only when tested in mixed groups individuals were more prone to follow the decisions of soldiers (Fig. 4B), the first caste to follow the artificial trails (Fig. 4B) and initiate foraging in the field. The results of our trail-following assays seem to indicate that soldiers play a key role in colony foraging decisions, as has been suggested for *Longipeditermes longiceps* (open-air forager) (Miura and Matsumoto, 1998; Traniello and Busher, 1985). In the Nasutitermitinae, different pressures may have driven greater diversification of the tasks performed by the soldiers, thereby offsetting colony costs.

In conclusion, here we show that *N.* aff. *coxipoensis* optimizes their foraging through initial exploration of trails at night and directional tunnel construction, with active participation of soldiers throughout the process via leading group decisions and initiating the foraging process. These results contribute to discussion of the evolution of foraging habits within Isoptera clade.

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CAPÍTULO 2

Resource density regulation of termite foraging range: A field test of optimization strategies

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Submetido a Animal Behaviour

SUMMARY

Resource availability can regulate the area that animals use. Construction of tunnels and galleries by termites during foraging incurs high costs. Thus, it is expected that mechanisms exist to minimize these costs. In this study, we used a manipulative field experiment to test the hypothesis that termite colonies reduce foraging effort in areas with high resource density compared to areas with less abundant food. The experiment was conducted in dune areas in Pirambu, Sergipe, Brazil. Seven experimental plots were established with a continuous increase in resource density (sugarcane baits). Five *Nasutitermes* aff. *coxipoensis* colonies were transplanted from their original sites to each experimental plot, totalling 35 nests. Trails and tunnels built on the soil surface were evaluated for 10 days after transplantation. The number and total length of tunnels and trails, and the number of branches of each were quantified. Data were analysed using linear regression analysis. Results show that the number of trails, the total length, and the number of branches decreased with increasing resource availability. The number of branches constructed in tunnels, and construction speed (cm/day) peaked at intermediate resource levels. These results suggest that *Nasutitermes* aff. *coxipoensis* increases the search effort by forming trails on the soil surface at low density of local resources, and that few of these trails are converted into tunnels; at high resource density more trials are converted into tunnels. These results suggest optimization of foraging effort depending on resource density, a mechanism that may help to elucidate termite distribution patterns.

Key-words: Food searching, foraging area, Isoptera, *Nasutitermes*, resource density.

INTRODUCTION

Foraging behaviour can be influenced by intrinsic biological characteristics and individual capabilities, as well as internal and external environmental factors such as starvation and resource density, respectively (Bell, 1990). Balancing the costs and benefits of foraging (Pyke, Pulliam, & Charnov, 1977) can result in changes in the extent of home range, with consequences for ecological processes (Börger, Dalziel, & Fryxell, 2008). One hypotheses of home range regulation suggests that if animals accumulate enough resources to satisfy their minimum biological threshold, they will use the smallest area possible to provide the necessary energy for survival and reproduction ("area minimization strategy"; Mitchell & Powell 2004). Empirical evidence has supported this idea, indicating a negative relationship between foraging area and resource density (Ford, 1983), in both vertebrates [e.g., mammals (Jorge & Peres, 2005; McLoughlin, Ferguson, & Messier, 2000; Mitchell & Powell, 2007; Saitoh, 1991), birds (Carpenter & MacMillen, 1976; Hixon, Carpenter, & Paton, 1983; Powers & Mckee, 1994)], and invertebrates [e.g., ants (Urbas, Araújo Jr., Leal, & Wirth, 2007)]. However, starvation serves as a stimulus for animals to actively forage (Bell, 1990), and in times of low resource density extensive foraging may promote conflict in terms of the balance between costs and benefits. In this situation animals apparently cannot realize an optimal foraging, except whether they have abilities to minimize these costs, as we show to species study here.

Foraging costs could be even more pronounced in so-called central place foragers, animals with foraging systems constrained around nests (e.g. as in eusocial insects) (Brown & Gordon, 2000; Kotler, Brown, & Knight, 1999). Unlike animals that feed at the resource location, central place foragers must return to the nest with food item(s). To handle this task, they have developed complex signalling mechanisms that are used to share information during foraging, such as warning of predation risk and recruitment to the food source

(Beekman & Lew, 2008).

In termite species, central-place foraging strategy can include open-air (above ground) foraging, or may include construction of a network of tunnels that link the nest and food sources (Grace & Campora, 2005). In the latter, termites build a matrix composed of main tunnels with secondary branches that can span hundreds of meters. The initial food search phase is thus extremely costly in terms of energy. Building tunnels at random until food is discovered is likely not an optimal foraging strategy. Further, because resource suitability (i.e. quantity and quality) and foraging risk varies in time and space, tunnels are an ephemeral investment that adds extra constraints to already costly building processes (Campora & Grace, 2001). In resource-deprived sites, these costs can be unbearable because under threat of starvation, food-searching stimuli are enhanced but energy to search is limited (Bell, 1990). This elevated cost of food searching means that tunnelling colonies should adjust their foraging in response to resource density, using the smallest area possible to provide the required energy (area minimization strategy) (Mitchell & Powell, 2004). Most studies of termite foraging behaviour have evaluated subterranean species in artificial laboratory systems. To our knowledge, no direct experimental approaches have been used to evaluate termite foraging area regulation in response to resource density in natural environments.

Nasutitermes aff. *coxipoensis* occurs in Northeastern Brazil, in sandbank areas with grasses interspersed by open dunes. *N.* aff. *coxipoensis* exhibits a previously unknown foraging strategy: foraging begins in the early evening by formation of trails on the soil surface, and the labour is carried out by members of both worker and soldier castes. This process extends throughout the night, and tunnels are usually built when a food resource is found on the trails. Trails built by *N.* aff. *coxipoensis* are clearly observed during the first hours of the day (*Chapter 1*). Here, we assess whether an alternative strategy exists in which termites may reduce the costs of searching for food while maintaining efficiency in food discovery. We observed tunnelling decisions made by *N.* aff. *coxipoensis* termite colonies after transplantation to sandbank sites with controlled quantities of food resource. We show that termites employ a strategy to minimize tunnel construction in resource-deprived sites, and use a more economic strategy for trail foraging. The high costs of producing foraging structures are thus circumvented, which we interpret as optimization of foraging efforts.

MATERIALS AND METHODS

Ethics statement and species identification

Permits for termite collection were issued by ICMBio, IBAMA (47652-1). No specific permits were required for the laboratory experiments described herein, which were conducting using a species that is neither endangered nor protected. *N.* aff. *coxipoensis* were individually identified and the voucher specimens (#UnB-10616, 10617, 10618, 10619, 10620, 10621) are deposited in the collection of the Termitology Laboratory at the University of Brasilia.

Study area

The experiment was conducted in March 2015 ('dry season') at the Santa Isabel Biological Reserve (10^{o}43’56’’S, 36^{o}50’36’’W) in Pirambu, Sergipe, Northeastern Brazil. The climate in this region is characterized as megathermic humid and sub-humid, with annual precipitation between 1,500 a 1,800 mm and a mean annual temperature of 26° C. The climate in region is tropical wet and dry (Aw) according to Köppen climate classification systems (Pidwirny, 2011).

Experimental design

N. aff. *coxipoensis* colony foraging area was evaluated by manipulating food resource density in open-dune areas without vegetation. Seven plots (16 x 16 m) were established with different resource densities, forming 5 x 5 m quadrants, with a central quadrant surrounded by four peripheral quadrants separated by a distance of 0.5 m (Fig. 1A). One *N.* aff. *coxipoensis* colony was transplanted to the centre of each quadrant (see item 3.2 below), for a total of five nests per plot. The minimum distance between plots was 3m. Transplanted nests had similar volumes ($P = 0.15$).

Resource manipulation

The number of food items that one individual finds is proportional to the number of items available in time and space (Bell, 1990); thereby, reduction of resource density could promote higher costs due to increased time and energy spent during searching behaviour (Chase, 1998). For central-site foragers, searching for food amounts to considerable energetic costs because of the need to return to the nest after resource location. The costs for tunnel construction may be even greater, especially when foraging is non-directional. For manipulation of resources density, we delimited six concentric circumferences 0.5m apart in each nest. We determined circumference at eight points (e.g., the cardinal and side directions), where resources were distributed (sugarcane baits on 15 x 4 x 2 cm billets) (Fig. 1B). Within each plot, all sides contained identical resource distribution and quantity. The total amount of resources per quadrant (25 m^2) ranged from 0-48 baits (N = 840 baits), which represented a resource density gradient from 0 to 1.92 baits/m^2 across plots. This resource density gradient was used to represent differences in the relative difficulty (i.e., in terms of energy expenditure) of finding and using food resources, where more abundant resources equates to lower energetic costs for termites.

Any potential resource fragments that fell into the grid (e.g., small fragments of branches and leaves) were removed each morning.

N. *aff.* coxipoensis *nest transplants*

Only active nests with similar size (*P* = 0.15) were used (N = 35). Entire nests were removed and deposited on trays using shovels and picks. Immediately after removal, nests were transplanted at a minimum distance of 30m from the original location. Holes (30 cm deep) were dug in the centre of each quadrant where nests were then inserted, and nest bases were covered with local soil. Preliminary tests indicated that transplantation does not affect colony viability.

Evaluation of foraging area

We evaluated colony foraging area by direct observation daily for 10 consecutive days after nest transplantation. In each nest we quantified length (cm), the total number of trails and tunnels as well as the number of primary and secondary routes, and tunnel construction speed (cm/day).

DATA ANALYSIS

All analyses were carried out in R software (R Development Core Team, 2015) using Generalized Linear Models (GLM) followed by residual analysis to confirm suitability of error distribution and model fitting. Mean values (N = 5 nests/plot) of trail and tunnel measurements (y-vars) were calculated within each level of resource density. The difference in means of total number, number of principal structures (trails and tunnels), number of primary branches, and length (cm) of trails and tunnels (y-vars) were analysed as a function of resource density (x-var). Tests for each y variable were done separately using linear regression analyses with Poisson error distribution corrected for overdispersion. For the tunnelling speed (cm/day) we used negative binomial error distribution.

RESULTS

On average, there was a greater total number of trails and number of main trails in places with low resource availability (Fig. 2A-B). However, no significant differences were detected for the same parameters in tunnels (Fig. 2A-B; Table 1). Moreover, both the number of branching paths and tunnels show significant variation with resources density ($P < 0.05$) (Fig. 2C). The average number of branching paths reduced linearly with resource level and the number of tunnel branches peaked at intermediate levels of resource density (Fig. 2C; Table 1). The average total length of trails significantly reduced with increased resources ($P < 0.001$), while the total length of tunnels showed no correlation with resource level ($P > 0.05$) (Fig. 2D; Table 1).

Tunnel construction speed (cm/day) also peaked at intermediate levels of resource density ($F_{2,5} = 3375$, $P < 0.001$) (Fig. 3). The results show that termites convert a greater extent of trails into tunnels (length of tunnels/length of trails) in sites with higher resource density ($F_{2,5} = 2551$, $P = 0.001$) (Fig. 4).

Table 1. Summary of generalized linear models inspecting the variations of trails and tunnels constructed by *Nasutitermes* aff. *coxipoensis* in a resource density gradient (sugarcane baits/m^2). Pirambu, Sergipe, Brazil. 2015. *$P = 0.05$.

Term	DF	Deviance	*F*	*P*
Total number				
Trails				
Density	1	68.945	97.501	0.004*
Density (^2)	1	26.538	37.528	0.003*
Error	5	95.483	67.515	
Tunnels				
Density	1	13.691	3.552	0.132
Density (^2)	1	10.168	2.638	0.179
Error	5	23.859	3.095	
Number of primary trails/tunnels				
Trails				
Density	1	59.114	62.088	0.001*
Density (^2)	1	28.972	30.414	0.005*
Error	5	88.116	46.251	
Tunnels				
Density	1	11.285	2.196	0.212
Density (^2)	1	7.205	1.402	0.302
Error	5	18.491	1.799	
Number of primary branches				
Trails				
Density	1	12.841	54.275	0.001*
Density (^2)	1	0.132	0.559	0.495
Error	5	12.974	27.418	
Tunnels				
Density	1	2.693	6.849	0.058
Density (^2)	1	3.216	8.179	0.045*
Error	5	12.245	15.571	
Total length				
Trails				
Density	1	100.676	109.846	< 0.001*
Density (^2)	1	17.663	19.272	0.012*
Error	5	118.340	64.559	
Tunnels				
Density	1	0.069	0.051	0.832
Density (^2)	1	8.002	5.940	0.071
Error	5	8.071	74.017	

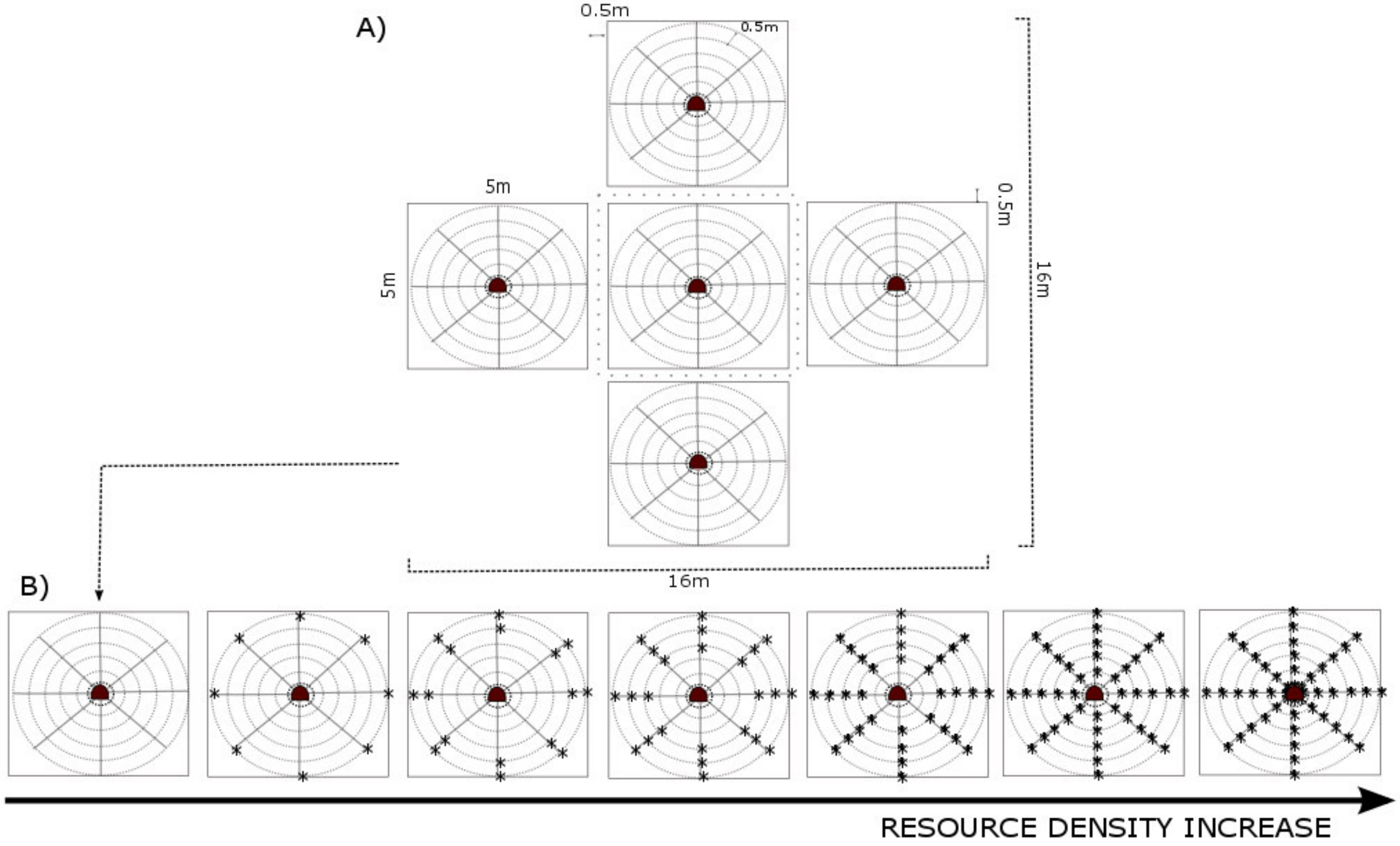

Fig. 1. Schematic representation of the experimental design for transplantation of *N.* aff. *coxipoensis* nests and manipulation of food resources. A) A 16 x 16m plot representing a resource density gradient consisting of five quadrants (5 x 5 m) placed 0.5 m from each other; B) Representation of a quadrant of each plot, showing increasing variation in resource density (between 0-48 sugarcane baits per plot) and variation in distance from the bait to the nests. Resource density in each plot ranged from 0 to 1.92 baits/m^2. * Represents sugarcane bait (15 x 3.5 x 2cm). ■ Represents one *N.* aff. *coxipoensis* nest transplanted to the center of a quadrant.

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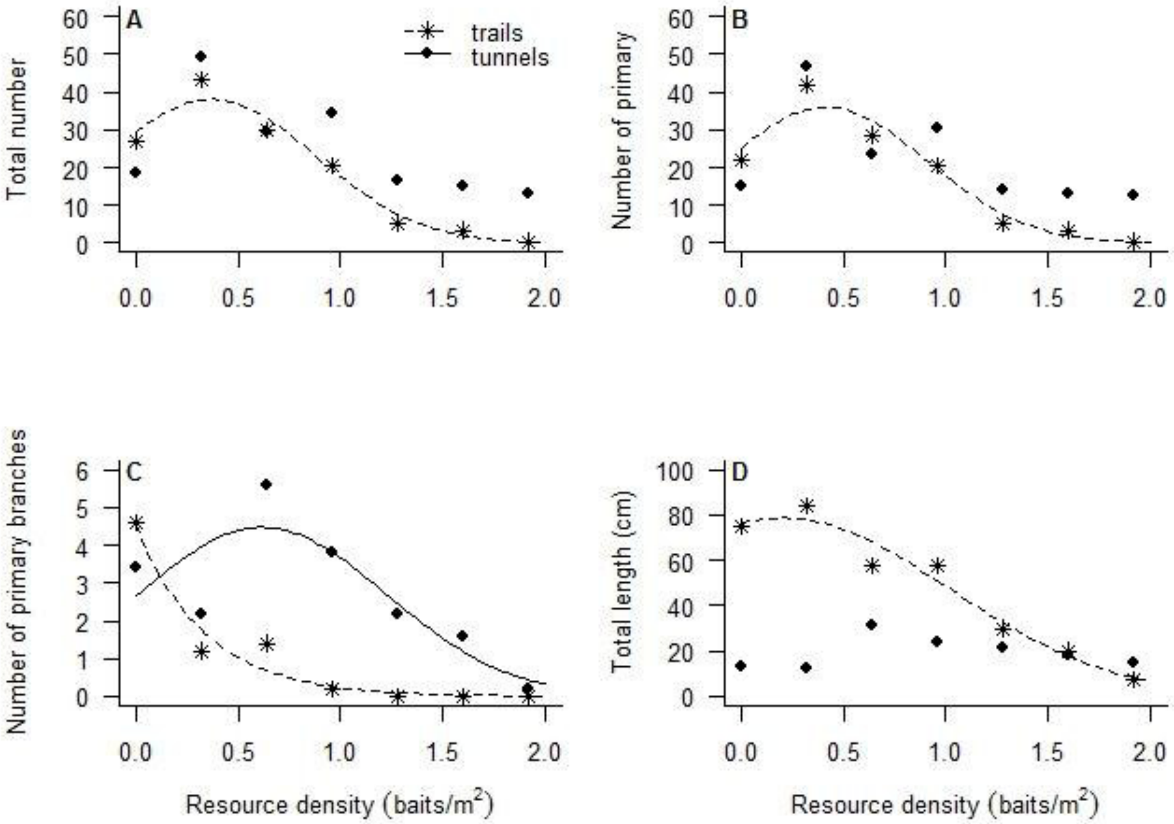

Fig. 2. Trail formation and tunneling behavior of *Nasutitermes* aff. *coxipoensis* in plots with resource densities. Effects of resource density (baits/m^2) on mean values of **A)** total number of trails and tunnels; **B)** number of primary trails and tunnels; **C)** number of primary branches; **D)** total length of trails and tunnels. Each point represents the mean activity of the five nests over ten days post-transplantation in quadrants with different resource densities.

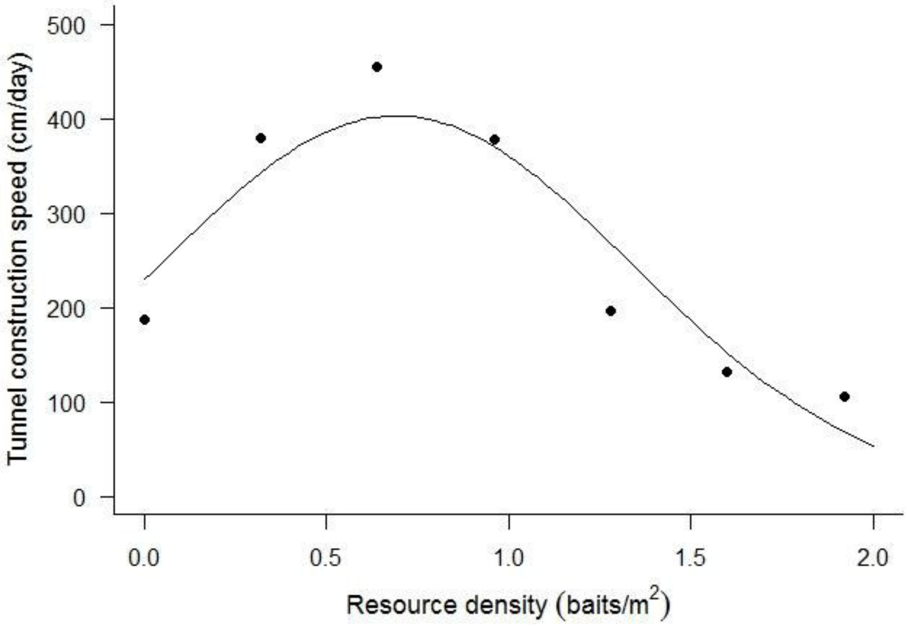

Fig. 3. Tunnel construction speed by *Nasutitermes* aff. *coxipoensis* in plots with different resource densities. Tunnel construction speed (cm/day) is highest at intermediate resource density. Each point represents the mean activity of the five nests over ten days post-transplantation in quadrants with different resource densities.

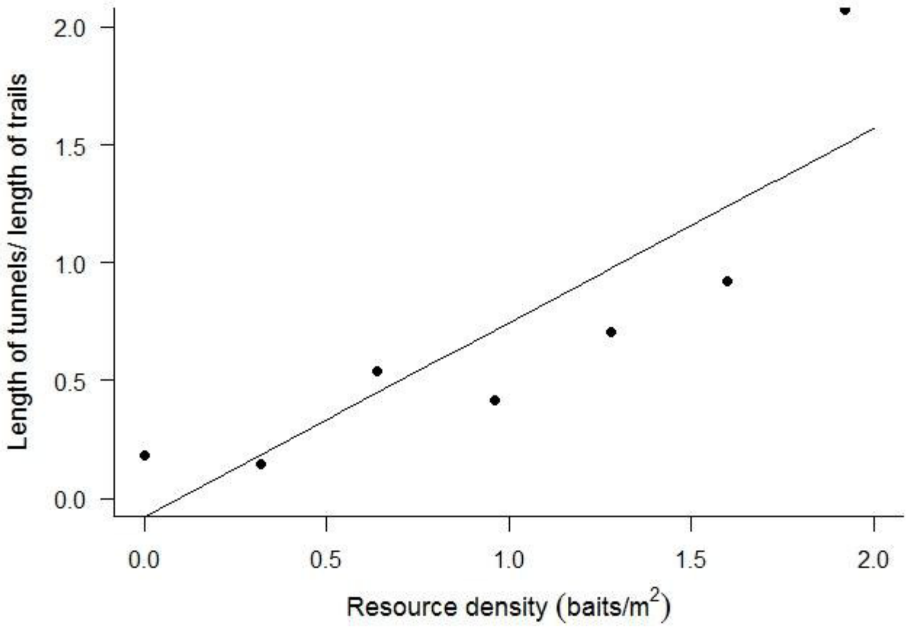

Fig. 4. Proportion of trail lengths converted into tunnels in plots with different resource densities, calculated by (length of tunnels/length of trails). The conversion of trails into tunnels increases with higher resource density. Each point represents the mean activity of the five nests over ten days post-transplantation in quadrants with different resource densities.

DISCUSSION

Our results indicate that extent of foraging area in *N.* aff. co*xipoensis* colonies is regulated by resource availability, and that foraging area significantly decreases with increasing resource density. The increase in foraging area in low-resource density areas occurs through establishment of more and longer trails (Fig. 2A-D). At low resource density, the proportion of established trails converted into tunnels was less than in colonies with high resource density (Fig. 4). These results indicate that termite colonies with low resource density increase their foraging areas, as expected when the chance of resource encounter is low. However, high foraging effort seems to be minimized by initial establishment of trails that are then converted into tunnels, which occurs more frequently in places with profitable resources (e.g. intermediate to high resource density).

The average number of tunnel branches is highest at intermediate resource density (Fig. 2C). Tunnel branches have been reported to be responsible for increasing exploitation of the foraging area by connecting distinct food sources that are used simultaneously (see Arab & Costa-Leonardo, 2005). Tunnel construction speed was faster only at intermediate resource levels (Fig. 3), indicating that *N.* aff. *coxipoensis* colonies optimize food searching effort by minimizing costs. When resources are limited or absent, no stimulus occurs for colonies invest in tunnel construction. At higher resource density, the greater proximity of resources to the nest eliminates the necessity to increase foraging range. When resources are present but not in abundance (i.e., intermediate density) termite hunger can serve as a stimulus to increase tunnel construction speed. The observed foraging patterns mentioned above suggest that *N.* aff. *coxipoensis* use an area minimization strategy (proposed by Mitchell & Powell, 2004).

For species that forage underground, a similar foraging pattern has been reported in laboratory arenas. At low resource availability, subterranean termite species built longer tunnels faster and in higher numbers compared to arenas with high resource availability (Arab & Costa-Leonardo, 2005; Araújo et al., 2011; Gallagher & Jones, 2005; Hedlund & Henderson, 1999). However, the literature shows that in contrast with the species in this study, subterranean termites only construct tunnels that incur higher costs in places with scarce resource availability (i.e., to the best of our knowledge other mechanisms have not been reported). In general, there is no consensus as to whether subterranean termite species foraging is directional or not. Hedlund & Henderson (1999) suggest that food size affects tunnel volume and length, however other studies concluded that the presence of food did not affect tunnel distribution (Campora & Grace, 2001; Su & Puche, 2003).

Taken together, our results show that *N.* aff. *coxipoensis* colonies perform directional foraging, and thus optimize energetic expenditure. The combined foraging strategy (e.g. open air foraging and tunnelling) seems to promote optimization through reduction of the conversion rate of established trails into tunnels at unprofitable sites, as initially suggested by Almeida *et al.* (*Chapter 1*) (Fig. 4). This strategy can promote a more efficient cost/benefit balance compared to species that only forage underground.

At a broad scale, variation of foraging area extension according to resource density can elucidate some conflicting patterns observed in termites. For example, previous studies have proposed that regulation of foraging area by termite colonies maybe the mechanism promoting inverse relationships between termite abundance/richness and resource availability (Araújo et al., 2007) and overlapping of foraging areas of different termite species in extreme resource gradients (very low or very high) (Araújo et al., 2009). In the first study, the regulation of foraging areas according to resource level can permit termite colonies to retract their foraging range in higher quality habitats, which potentially impairs sampling detection and consequently produces false low abundance/diversity records (e.g. Araújo et al., 2007). On the other hand, at low resource levels foraging area expansion may increase termite detection. In the second study, Araújo et al. (2009) show that the regulation of foraging area by resource availability can also result in overlapping of foraging areas of distinct termite species in both low and high resource availability. This pattern maybe explained by the following hypotheses: *(i)* in resource-poor sites, termites increase food searching which in turn expands foraging areas, and *(ii)* in resource-rich sites, the decrease in foraging area may be accompanied by an increase in termite colonization, and expulsion of neighbour colonies carries no benefits. Therefore, foraging area regulation by resource availability may also influence termite species spatial overlapping and species coexistence at a local scale.

The inverse relationship between resource density and foraging area has also been shown in ants (Brown & Gordon, 2000; Leal & Oliveira, 2000; Urbas et al., 2007) and other eusocial insects (see Richter, 2000; Westphal, Steffan-Dewenter & Tscharntke, 2006). Leaf-cutting ants reduced trail length and foraging area in forest edges, which have an increased proportion of more palatable resource (*i.e.* pioneer plants); foraging areas were increased in the forest interior where resource suitability is low (i.e. greater abundance of defensive plants) (Urbas et al., 2007). Similarly, ants prefer to use food items closer to the nest when resources are abundant (Brown & Gordon, 2000). However, to the best of our knowledge the current study is the first to show reduction of foraging area with increased resource density for termite colonies in field conditions.

The present study shows that resource density directly influences the home range used by *N.* aff. *coxipoensis* colonies. These results suggest that this species evaluates the environment and is able to respond to local conditions by adjusting cost-benefit relationships during foraging processes. This mechanism may be important in regulation of termite community structure, and may also intensify interspecific interactions among termite species, as well as between termites and other taxa.

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CONSIDERAÇÕES FINAIS

- *N.* aff. *coxipoensis* otimiza seu forrageio através da exploração inicial de trilhas e construção direcional de túneis, com participação ativa de soldados em todo processo pela tomada de decisão do grupo e iniciação do processo de forrageio.
- A densidade de recursos influencia diretamente a área de uso utilizada pelas colônias de *N.* aff. *coxipoensis*.
- Estes resultados sugerem que essa espécie avalia o ambiente e é capaz de responder às condições locais, ajustando a relação custo-benefício durante o processo de forrageio.
- Tal mecanismo pode ser importante na regulação da estrutura de comunidades de cupins.
- Os resultados contribuem para a discussão da evolução dos hábitos de forrageio dentro do clado Isoptera.