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Evidence of sodium limitation in ants and termites in a Neotropical savanna

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Research Article

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Abstract

Nutritional ecology of ropical ecosystems like Neotropical savannas, which are of high conservation concern, is understudied. Sodium is essential for heterotrophs but availability often falls short relative to plant consumer requirements. Savanna plant consumers like ants and termites should be sodium-limited due to high temperatures, nutrient-poor soils, and lack of oceanic sodium deposition. We tested the hypothesis that Neotropical savanna ants and termites are sodium-limited. Termites were tested by supplementing 0.25 m^2 plots with H_2O (control), 0.1%, 0.5%, or 1.0% NaCl and measuring termite presence and artificial substrate mass loss after 1 week. Ants were tested by collecting ants that recruited to H_2O (control), 0.1%, 0.5%, and 1.0% NaCl and 1.0%, 10%, and 20% sugar baits on paired diurnal–nocturnal transects. Termites were 16 times more likely to occur on 1% NaCl than H_2O plots and wood-feeding termites were most frequent. However, the decomposition rate did not differ among treatments. Ant bait use increased with increasing NaCl concentration and 1% NaCl usage was similar to sugar bait usage. Ants were 3.7 times more active nocturnally than diurnally, but contrary to predictions bait type (water, sugar or NaCl) usage did not differ between day and night. Together, these results provide strong evidence of sodium limitation in Neotropical savannas.

Introduction

Biologically essential nutrients required for organism reproduction and survival are often patchily distributed across the landscape (Frausto da Silva and Williams 2001). Organisms differ in their nutrient requirements but must maintain some level of homeostasis around taxon-specific intake targets to optimally perform (Sterner and Elser 2002; Raubenheimer et al. 2009). Consequently, organism abundances and activity vary across nutritionally heterogenous landscapes, which can impact community structure and ecosystem processes such as productivity, nutrient cycling, and decomposition (Hooper et al. 2005; Berzaghi et al. 2018). The tropics are often oligotrophic environments in which changes in the availability of nutrients can impact ecosystem processes (Kaspari and Yanoviak 2009; Powers and Marín-Spiotta 2017; Townsend et al. 2011). Understanding nutrient limitation in tropical ecosystems is essential for conserving biodiversity and maintaining ecosystem function as anthropogenic activities alter the landscape.

Sodium is a biologically essential nutrient for heterotrophs, but not typically plants, which can have significant impacts on the activity and density of organisms, community structure, and ecosystems (Aumann and Emlen 1965; Bravo et al. 2008; Clay et al. 2014; Welti et al. 2019; Kaspari et al. 2020; Kaspari 2020; Welti et al. 2020). At the organismal level, sodium is essential for proper metabolic, osmotic, and neurological function (Schulkin 1991; Geerling and Loewy 2008). Sodium limitation occurs where sodium is in shortfall, which often includes inland environments that receive little-to-no sodium deposition through oceanic aerosols. Similarly, sodium limitation can occur where temperature and evapotranspiration rates are high because sodium is lost during metabolic water loss processes. Together, this describes most noncoastal tropical ecosystems (Peters 1986; McNaughton et al. 1997, Kaspari et al. 2008; Prather et al. 2018). Among heterotrophs, plant consumers, including both herbivores and detritivores, are the most sodium-limited because plants typically concentrate one to three orders of magnitude lower sodium in their tissues than plant consumers, creating a stoichiometric disparity between the requirements of plant consumers and their food (Kaspari 2020). The sodium ecosystem respiration hypothesis posits that sodium-limited plant consumers should increase their activity when sodium becomes available (Kaspari et al. 2009). Thus, plant consumer sodium limitation can alter nutrient cycling, shape plant communities, and mediate carbon cycling within ecosystems (McNaughton et al. 1997; Kaspari et al. 2009; Kaspari et al. 2014; Clay et al. 2015; Griffith et al. 2017).

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Organisms in inland tropical rainforests are often sodium-limited (Rothman et al. 2006; Kaspari et al. 2009; Brightsmith 2008; Bravo et al. 2010; Clay et al. 2014), but tropical seasonally dry and semiarid or arid (hereafter referred to as '(semi)arid') environments like savannas are understudied, particularly in the Neotropics. The high sand content and low cation-exchange capacity of soils in many (semi)arid and seasonally dry environments increase the likelihood of sodium loss and thus shortfall for plant consumers (Kaspari 2020). In African savannas, herbivore sodium limitation is evident from population-level processes to the structure of vegetation (McNaugton et al. 1997; Grant and Scholes 2006; Griffith et al. 2017). Plant consumers within Neotropical savannas likely are similarly sodium-limited but have received little attention (but see Vieira and Vasconcelos 2015).

Tropical savannas are characterized by the inability of tree communities to form closed canopies and low aboveground biomass (De Castro and Kauffman 1998; Hoffmann et al. 2012). The Brazilian savanna (Cerrado) consists of grasslands, savannas, and shrublands and comprises about 1.8 million km^2 in central Brazil, which is roughly 25% of Brazil and 4% of the global tropical land area (Coutinho 1978; Ab'Saber 1983). Tropical savanna plant consumers should be just as sodium-limited, if not more, than those in lowland tropical rainforests. Specifically, high temperatures increase water loss, and thus sodium loss and lower precipitation results in adaptations for desiccation resistance such as concentrating Na^+, which necessitates continued ion intake (Peters 1986; Addo-Bediako et al. 2001; Kaspari et al. 2008). Additionally, sodium should be environmentally rare because nutrients in tropical savanna soils are often more depauperate than soils of tropical forests (Pellegrini 2016 and sources therein), and the low effective cation-exchange capacity creates a high leaching potential for cations (Lopes and Guilherme 2016). Lastly, lack of oceanic aerosol inputs in inland tropical savannas should result in little-to-no wet sodium ion deposition. Thus, plant consumers and the ecosystem processes they impact are likely sodium-limited.

Termites and ants dominate many ecosystems, including Neotropical savannas (Tuma et al. 2020). The Brazilian Cerrado has over 140 species of termites with ~50% of these endemic (Constantino 2005) and over 130 species of ants (Lopes and Vasconcelos 2008). There is limited research on ant communities and their ecology, but biodiversity studies indicate that Brazilian savanna and grasslands have high and similar species richness to adjacent forests (Silvestre & Brandão 2000, da Silva et al. 2004, Marques & Del-Claro 2006; Lopes and Vasconcelos 2008; Klunk et al. 2018). Termites consume massive amounts of organic debris in tropical savannas. Organic debris, particularly wood, tends to be more nutrient-poor than living plant material. Concentrations of nitrogen, sulfur, and phosphorous decrease, while cations like Ca^{2+}, Na^+, and Mg^{2+} as well as heavy metals stored in leaf vacuoles increase with leaf age (Montes and Medina 1977; Medina et al. 1978; Medeiros and Haridasan 1985; Tolsma et al. 1987). Moreover, wood tends to have less sodium than leaves (Seastedt and Crossley 1981). The digestion of recalcitrant cellulose, hemicellulose, and lignin also often requires sodium (e.g., NaOH; Mafa et al. 2020). Sodium is concentrated in the guts of wood-feeding termites where their microbial symbionts are concentrated and drive digestion (Yoshimura et al. 2002). Studies from tropical rainforests demonstrate wood-feeding termites are sodium-limited and in Africa, termite mounds are often found in sodic soils (Grant and Scholes 2006; Kaspari et al. 2014; Clay et al. 2015). Thus, termites and their rates of decomposition in inland savannas should be sodium-limited (e.g., the sodium ecosystem respiration hypothesis; Kaspari et al. 2009).

Ants are ecosystem engineers and often have significant impacts on community structure and ecosystem function through species interactions and movement of nutrients (Hölldobler and Wilson 1990; Tuma et al. 2020). Because many ants are omnivores, savanna ants that consume more plant-derived than animal material should be sodium-limited whereas strict carnivores or those that consume proportionally more animal tissue should not be sodium-limited (Kaspari et al. 2008; Vieira and Vasconcelos 2015; Clay et al. 2017). Additionally, ants partition their foraging across the day and night in tropical savannas (Marques & Del-Claro 2006). In seasonally dry and (semi)arid environments, animal activity is often most concentrated during night hours because of lower temperatures and higher humidity (Marques and Del Claro 2006; Vonshak et al. 2009; Hölker et al. 2010). Therefore, ants in Neotropical savannas should be more active at night. Similarly, because daytime foraging ants experience higher temperatures and lower humidity, which should result in increased metabolic activity, water loss, and consequently sodium loss (Peters 1986; Gillooly et al. 2001; Brown et al. 2004; Prather et al. 2018), diurnal ants should be more sodium-limited than nocturnal ants. However, the nutritional ecology of nocturnal versus diurnal species is largely an unexplored field (Gaston 2019).

Here, we test the hypothesis that Neotropical savanna termites and ants are sodium-limited. For termites, we predicted that (a) termite presence would increase on plots receiving supplemental sodium and (b) wood-feeding termites would recruit more to plots with supplemental sodium than litter- or soil-feeding termites. Consequently, we also predicted that (c) decomposition rate would be higher on supplemental sodium plots than control plots not receiving additional sodium and (d) decomposition rates would be highest on plots receiving the highest concentrations of supplemental sodium. For ants, we predicted that (a) ants would be most active at night and (b) would generally prefer the highest concentration of supplemental sodium, and (c) use of the highest concentrations of supplemental sodium would be most intense in the daytime due to high temperatures increasing metabolism and leading to higher sodium loss (e.g., Prather et al. 2018). We tested termite sodium limitation by establishing ten blocks of four treatment plots that received either water as a control or water with one of three different concentrations of NaCl, and measuring termite recruitment and decomposition after 1 week. We tested ant sodium limitation by placing baits along 20 transects that consisted of 10 paired day and night transects (pairs are transects run at the same location but either during the day or night) with three different concentrations of NaCl, a water control, and an additional three concentrations of sugar to determine ant activity.

Methods

Study site

The study occurred in the Serra Vermelha region close to Redenção do Gurguéia municipality around a district called 'São José' just outside the Serra das Confusões National Park in Piauí State, Brazil (−9.463°S, −44.204°W) from 20 November to 6 December 2019. Serra das Confusões National Park is an ecotonal area between Caatinga and Cerrado environments and is characterized as tropical semiarid climate (Machado et al. 2004). This study was conducted in the Cerrado habitats of the area, but with elements of Caatinga in plant physiognomy including intermixed deciduous and thorny plants. This area is characterized by frequent fires that result in nutrient-poor soils consisting of latosols (oxisols) and podzolic soils like alfisols and ultisols where trees grow and lithosols (lithic dystropepts) in upland grassland Cerrado (Eiten 1972; Haridasan 1990; Castro et al. 2009). Soils are acidic (pH typically 4.8-5.1) with low N, P, K, Ca, Mg, Zn, B, and Cu, low effective cation-exchange capacity (median 1.1 $\mathrm{cmol_c\ dm^{-3}}$, range 0.35–8.10 $\mathrm{cmol_c\ dm^{-3}}$) and high Al (Lopes and Guilherme 2016). There are distinct wet and dry seasons, with May–October being the dry season and November–April having the highest rainfall intensity (Nimer 1989). Annual precipitation is ~940 mm concentrated mainly in the wet season, and average annual temperature is 26°C (range 19.1°C to 36°C).

Experimental design: Termites

We haphazardly established 10 blocks of 4 treatments to test whether termites are sodium-limited. Blocks were not specifically associated with termite colonies; their placement was every 30 m along a transect. Blocks were 4 × 4 m and each of the treatment plots within blocks was 0.5 × 0.5 m. Treatment plots were established in the outside corners of blocks to maximize the distance between them (3 m between plots), and treatment was randomly assigned to plots. Blocks were separated by 30 m to minimize the likelihood of sampling termites recruiting to plots from the same termite colony. Treatments were H_2O (control), 0.1% NaCl, 0.5% NaCl, or 1.0% NaCl that was NaCl added to water by weight. These concentrations are similar to those of other studies (Kaspari et al. 2008, Jia et al. 2015, Risch et al. 2016). A single preweighed 100% cellulose sponge (~1.5g) was placed in the middle of each plot and staked down at the initiation of the experiment. We then evenly added 150 ml of their respective treatment to each plot at initiation, 2 days, and 4 days. The additional sodium supplementation on days 2 and 4 followed significant rain events. One week after initiation, we harvested plots and surveyed plots for termites, and termite presence/absence was recorded. We collected the decomposition substrate (cellulose sponges), which were then dried and reweighed for mass loss. Additionally, we measured litter depth at each of the four corners of plots by inserting a thin metal rod through the litter layer until it hit topsoil and measuring to the top of the litter layer. When termites were present, they were identified as species, and we assigned termites to a feeding group (soil, litter, wood) using Ernesto et al. (2018) and Mikaelyan et al. (2015) (Table 1). All termite specimens collected were stored in labeled glass vials containing 80% alcohol and were subsequently deposited in the Isopteran collection of the Federal University of Paraíba.

We tested the null hypothesis that termites had an equal likelihood of being present on control plots as any of the three NaCl treatment plots using logistic regression. Termite presence or absence was the dependent variable. We tested the null hypothesis that decomposition rate (sponge mass loss) was equal among treatments using a Kruskal–Wallis test. We tested the null hypothesis that termite-feeding groups (i.e., soil, litter, wood, wood/litter) recruited equally to sodium-supplemented plots using a Chi-square Goodness-of-Fit test. All analyses were conducted in SPSS v.26 (IBM 2019).

Experimental design: Ants

Diurnal and nocturnal ant sodium limitation was tested by laying baits along transects with paired diurnal and nocturnal trials. Paired trials consisted of a transect placed during the day and subsequently a transect placed in the exact same location at night during a single 24 h period. Each transect trial (day or night) consisted of 100- 1.5 ml vials (plastic microcentrifuge tubes) that contained ~0.5 ml of cotton soaked in one of seven treatments: H_2O only ($n = 10$), 0.1% NaCl ($n = 15$), 0.5% NaCl ($n = 15$), 1.0% NaCl ($n = 15$), 1.0% sugar ($n = 15$), 5.0% sugar ($n = 15$), and 10% sugar ($n = 15$). Water was used as a control to separate ant recruitment to baits due to water limitation versus nutrient limitation, and sugar was used as a general measure of carbohydrate limitation and activity (Kaspari et al. 2008, Clay et al. 2017). We placed baits along transects during the day between 1000 h and 1700 h and during the night between 2000 h and 2200 h at least 2 h after sunset which occurred ~1800 h, both day and night pairs were run in a single 24 h period. A day and a night paired trial was run ($n = 10$ pairs) to test if sodium limitation and general activity differed between day and night. Ten day-night transect trial pairs ($n = 20$ trials total) were run over 3 days in three Cerrado habitats. Transects run concurrently within a habitat were separated by ≥30 m. Temperature and humidity were measured at the initiation of baiting transects using a Kestrel 3000 pocket weather station ($n = 3$ day and $n = 3$ night measurements). We placed a random bait every 1 m along a transect by laying an open vial on the ground for 100 m. After 1 h, we collected ants by snapping shut the vial with the ants inside. The number of ants and ant species per vial were then measured, and ants were identified to genus and morphospecies using Bolton (1994). All ant specimens were preserved in 70% ethanol and were deposited in the Entomological collection of the Federal University of Paraíba.

We tested the null hypothesis that ants would recruit equally to baits between daytime and nighttime (time), and among control, NaCl concentrations, and sugar concentrations (treatment), and that there was no interaction between time and treatment on ant recruitment to baits in paired transects using repeated-measures ANOVA. Following methods of previous studies, we used presence or absence of ants in bait vials as our dependent variable because the number of ants in vials was highly impacted by the size of the ant and species differences in foraging strategies (e.g., *Dinoponera* vs. *Brachymyrmex*) (Kaspari et al. 2008, Clay et al. 2017). Ant vial usage was $\log_{10}(x+1)$ transformed to meet assumptions of normality prior to analysis. Bait type use ($n = 7$ bait types) per transect in either day ($n = 10$) or night ($n = 10$) was the unit of replication, not vials, which avoids potential pseudoreplication of treating each vial as the unit of replication, and paired day and night transects were the repeated measures. Differences among treatments were tested using Tukey HSD post hoc analysis. We tested the null hypothesis of no differences in day and night temperature and percent humidity using paired *t*-tests. All statistics were performed in SPSS v.26 (IBM 2019) with $\alpha = 0.05$.

Results

Termites

After 1 week, termites were present on 45% of plots, and we found eight species of termites from six genera across all plots (Table 1). Termites were found more often on sodium-supplemented plots than control plots ($\chi^2 = 8.115$, d.f. = 3, $p = 0.044$). Treatment accounted for 24.6% of the variation in termite presence (Nagelkerke R^2), and the variance in termite presence was classified correctly in 70% of cases. Termites were 16 times more likely to be on 1.0% NaCl addition plots than control plots ($p = 0.013$) and although not statistically significant, termites were 2.67 times more likely to be on 0.1% and 0.5% NaCl addition plots than control

Table 1. Termites collected on plots after 1 week of NaCl treatment by subfamily and feeding classification

Termite Subfamilies	Genus species	Feeding Classification
Nasutitermitinae	*Nasutitermes coxipoensis*	Wood
Nasutitermitinae	*Nasutitermes kemneri*	Wood
Nasutitermitinae	*Nasutitermes* sp.	Wood
Nasutitermitinae	*Velocitermes* sp.	Litter
Rhinotermitinae	*Heterotermes sulcatus*	Wood
Syntermitinae	*Cornitermes silvestrii*	Litter
Syntermitinae	*Rhynchotermes piauy*	Litter
Termitinae	*Amitermes amifer*	Wood

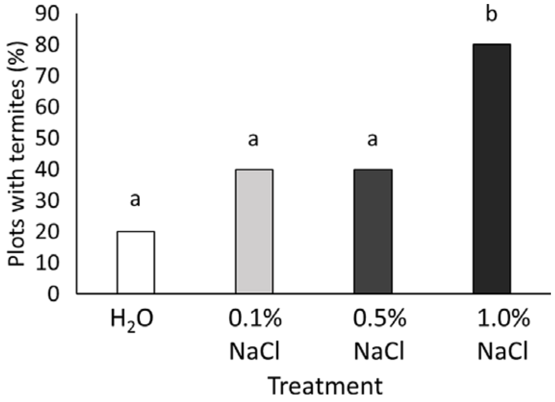

Figure 1. Percent of plots with termites (presence/absence) for each treatment after 1 week on their respective treatment plots: H_2O (controls), 0.1% NaCl, 0.5% NaCl, and 1.0% NaCl. Letters indicate significant differences ($\alpha = 0.05$).

plots ($p = 0.337$; Fig. 1). Termites found on sodium-supplemented plots were either litter (3 species) or wood feeders (5 species) (Table 1), but wood-feeding termites occurred 3 times more frequently (presence/absence) than litter-feeding termites on sodium-supplemented plots ($\chi^2 = 4.000$, d.f. = 1, $p = 0.046$).

After 1 week, eight of the artificial substrates were missing from plots. Some were found off plots likely moved by mammals, and others were never found leaving a total of 32. Artificial substrates lost a median of 13% of their mass in 1 week but the mass loss was highly variable (interquartile range [IQR]: 49.9%). Median decomposition rate was highest on 0.1% NaCl addition plots (60.1%, IQR: 64.9%), which was 4.8 times faster than the median decomposition rate on control plots (12.4%, IQR: 48.4%), but the decomposition rate did not significantly differ among treatments ($\chi^2 = 4.620$, d.f. = 3, $p = 0.202$). Litter depth was highly variable with a median of 3.1 cm (IQR: 4.3cm), and after 1 week did not differ among treatments ($\chi^2 = 1.336$, d.f. = 3, $p = 0.721$).

Ants

Overall, 18.4% of vials had ants with a total of 1,292 ants collected representing 23 species from 11 genera (Table 2). During the day, average temperature (± standard deviation) was 34.6°C ± 2.2°C and humidity was 48% ± 8.6%, which were 1.2 times higher and 1.4 times lower than nighttime temperature (28.7°C ± 0.7°C; $t = 5.176$, d.f. = 2, $p = 0.035$) and humidity (65.7% ± 8.3%; $t = -2.640$, d.f. = 2, $p = 0.119$), respectively.

During the night, ants were collected in baits 3.7 times more frequently than during the day (Time: $F_{1,63} = 52.478$, $p<0.001$). Only 9 species from 7 genera were collected on baits during the day versus 19 species from 10 genera during the night; 5 species from 5 genera were collected both during day and night (Table 2). Ant activity on bait type (water, sugar, or NaCl) did not differ between day and night (Time × Treatment: $F_{6,63} = 52.478$, $p = 0.170$; Fig. 2). Of all baits with ants, NaCl usage represented 32.3% while sugar usage represented 66.0%, and water represented 1.6%. Ants differed in water, sugar, and NaCl bait usage (Treatment: $F_{6,63} = 10.768$, $p<0.001$) and showed evidence of both sodium and sugar limitation, but not water limitation. Specifically, ants used all sugar and NaCl baits significantly more than water controls (all $p \leq 0.023$) with the exception of 0.1% NaCl, which was only marginally different from water ($p = 0.067$). Ants were found in the lowest sugar concentration (1%) baits at a similar frequency to all three NaCl treatments (all $p \geq 0.05$), and ants were found in the highest NaCl concentration (1%) at a similar frequency to all three sugar baits (all $p \geq 0.05$; Fig. 3).

Discussion

Tropical savannas are hotspots of biodiversity, and the Brazilian Cerrado is globally one of the largest, most species-rich, and most threatened (Silva & Bates 2002, Myers et al. 2000, Klink & Machado 2005). However, despite its importance, the nutritional ecology of Neotropical savannas is understudied. Sodium is emerging as a nutritional focus because its availability can impact populations, communities, and ecosystems by driving changes in organismal behavior and limiting densities and distributions (Schulkin 1991; Dudley et al. 2012; Kaspari 2020). Here, we tested whether ants and termites, which are dominant taxa, ecosystem engineers, and used as bioindicators (Jouquet et al. 2011; Bignell & Eggleton 2000; Hölldobler & Wilson 1990; Viana-Junior et al. 2014), are sodium-limited. Ants that used NaCl baits similar to sugar baits and termites were 16 times more likley to occur on 1% NaCl supplemented plots than control plots. Both these results indicate Cerrado ants and termites are highly sodium-limited. Thus, the landscape of sodium availability in Neotropical savanna likely impacts species interactions and ecosystem function.

Because higher temperatures increase sodium limitation due to increased metabolic activity and water loss (Peters 1986; Prather et al. 2018), we predicted that diurnal ants would be more sodium-limited than nocturnal ants. However, we found no difference in bait type usage between day and night (e.g., no Time × Treatment interaction). Although metabolic activity exponentially increases with temperature (Gillooly et al. 2001; Brown et al. 2004), a temperature threshold is reached where activity and metabolism start to decline (Kingsolver and Huey 2008; Angilletta 2009; Prather et al. 2018). Daytime temperatures may have been at or near this critical threshold. An alternative explanation is that daytime-adapted foraging species may have similar or lower rates of water loss than nighttime-adapted foraging species, resulting in little-to-no difference in sodium limitation. If arid-adapted organisms have lower rates of water loss per unit body mass and metabolic rates than mesic-adapted organisms (Addo-Bediako et al. 2001), and if nighttime foragers, which in many cases are strictly nocturnal (Marques and Del Claro 2006), resemble mesic- rather than xeric-adapted insects, then this would result in similar sodium demands. However, this remains to be tested. The latter

Table 2. Ant species identified from baits. Numbers represent the percent of each species found in vials during the day vs. the night (Day and Night, respectively), and the percent of ants collected in both the day and night vials for water controls (H_2O), for all NaCl treatments (NaCl) and for all sugar treatments (Sugar). Last is the percentage of vials that contained each species out of the total vials with ants (Total Vials)

Genus	Species	Day	Night	H_2O	NaCl	Sugar	Total Vials
Acromyrmex	sp1	0	100	0	0	100	0.27
Brachymyrmex	sp1	0	100	0	0	100	0.54
Camponotus	sp1	93	7	0	54	46	7.61
Camponotus	sp2	0	100	0	0	100	0.54
Camponotus	sp3	0	100	0	100	0	0.27
Crematogaster	sp1	57	43	0	57	43	1.90
Crematogaster	sp2	0	100	0	100	0	0.27
Crematogaster	sp3	0	100	6	35	59	4.62
Dinoponera	sp1	0	100	0	0	100	0.54
Dorymyrmex	sp1	31	69	0	23	77	3.53
Dorymyrmex	sp2	100	0	0	0	100	0.27
Ectatomma	sp1	0	100	2	27	72	48.64
Pheidole	sp1	100	0	0	0	100	0.27
Pheidole	sp2	17	83	8	25	67	3.26
Pheidole	sp3	0	100	0	100	0	0.82
Pheidole	sp4	0	100	8	25	46	3.53
Pheidole	sp5	0	100	0	100	0	0.27
Pseudomyrmex	sp1	100	0	0	0	100	0.27
Solenopsis	sp1	100	0	0	25	75	4.35
Solenopsis	sp2	0	100	0	20	80	1.36
Solenopsis	sp3	0	100	0	50	50	4.89
Solenopsis	sp4	0	100	0	47	53	5.16
Tapinoma	sp1	96	4	4	12	84	6.79

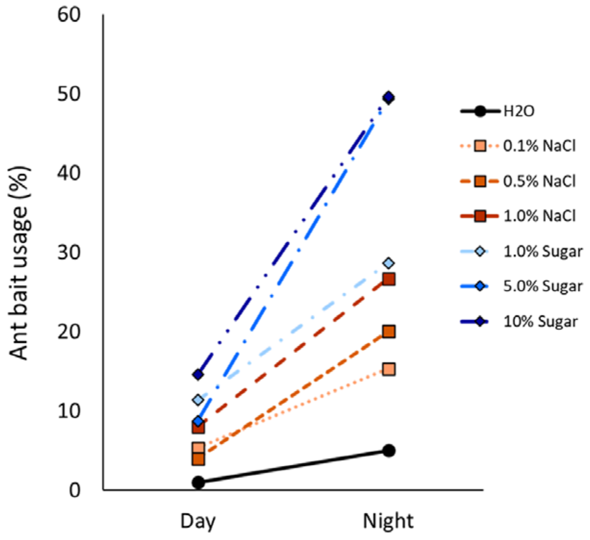

Figure 2. Percent ant bait usage of each treatment during day and night.

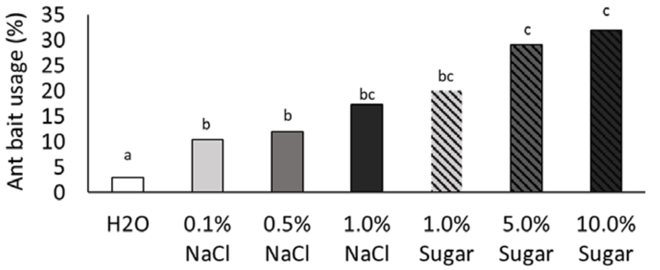

Figure 3. Percent ant bait usage of each treatment overall (day and night combined). Different letters above bars indicate significant differences among ant bait use among treatments.

highlights the additional osmotic challenges for species in xeric environments; as such, it was surprising that ants did not recruit to more H_2O baits. One possibility is that this study took place at the beginning of the rainy season when water limitation may be reduced. Alternatively, the use of water baits alone may have been lower than the use of sodium baits because both sodium and water are required for osmoregulation (Geerling and Loewy 2008). Indeed, desert water-loss strategies for insects include increasing extracellular sodium concentrations (Addo-Bediako et al. 2001). Lastly, there is some evidence that nocturnal ectotherms have higher metabolic rates and lower thermal tolerances (Hare et al. 2010; Garcia-Robledo et al. 2018), which may increase sodium demand during the night. The interplay between sodium, temperature, and water for xeric-adapted species likely underpins much of the ecology of seasonally dry and (semi)arid environments.

Surprisingly, ant use of sodium baits, particularly 1% NaCl solution, did not differ from their use of sugar baits. In most studies on ants, recruitment to sugar and salt has been measured in mesic forests and ants typically recruited more strongly to sugar than salt (Kaspari et al. 2008; Kaspari et al. 2010; Clay et al. 2017). However, roughly equivalent or higher salt:sugar recruitment appears to be common in hot, inland, xeric grasslands and savannas (Kaspari et al. 2008; Resasco et al. 2014; Prather et al. 2018; Vieira and Vasconcelos 2015; Peters et al. 2014, but see Kaspari et al. 2020). Together, this suggests sodium limitation not only increases with temperature and distance from coastlines, but may also vary with precipitation. Given the Cerrado is becoming hotter and drier and nocturnal taxa are at particular risk under future climate change predictions (Hofmann et al. 2021), understanding the nutritional, metabolic, and foraging ecology of nocturnal species in biodiversity hotspots like Neotropical savanna is increasingly important for future conservation efforts.

The majority of invertebrate (and vertebrate) activity occurs at night in seasonally dry and (semi)arid ecosystems, yet few studies examine nocturnal invertebrate ecology (Vonshak et al. 2009; Hölker et al. 2010; Gaston 2019; but see Zeh 1990 on scorpion biology). Similar to our study, Marques and Del Claro (2006) found that ants divided the temporal niche with nearly one-third of species strictly diurnal, one-third strictly nocturnal, and another third active in both day and night. Resource limitation in deserts often drives intense competitive interactions for shared resources (Brown and Davidson 1977; Vonshak et al. 2009), and species can reduce competition by partitioning time of foraging (Albrecht and Gotelli 2001; Spotti et al. 2014). Ant species diversity is high within Neotropical savannas like Cerrado (Lopes and Vasconcelos 2008) creating opportunity for interspecific competition for limited resources. As a community, ants in our study used sodium and sugar similarly in the day and night, although individual species varied in their resource preference (Table 2). For example, all five species found only on NaCl baits were also only found at night, whereas no strictly diurnal-foraging ant species were found only on NaCl baits, but rather they were mainly found on sugar baits. However, in other systems sodium limitation may strongly differ between nocturnal and diurnal foragers and this may change food web structure. For example, if there is more opportunity for carnivory at night due to more prey (Vonshak et al. 2009), then ants may obtain their sodium by consuming sodium-rich prey (Clay et al. 2017). Alternatively, if there are more species active at night, competition for limited sodium may reduce population abundances and select alternate strategies for maintaining sodium balance. The landscape of nocturnal nutritional ecology is largely unexplored, but is likely to yield distinct patterns from diurnal nutritional ecology.

The sodium ecosystem respiration hypothesis posits that rates of decomposition should increase when supplemental sodium is provided to otherwise sodium-limited detritivores (Kaspari et al. 2009; Kaspari et al. 2014). Termites in our study responded rapidly to sodium supplementation (within 1 week). This is similar to what Clay et al. (2014, 2015) and Kaspari et al. (2009) found in highly sodium-limited Amazonian rainforests. Yet despite evidence that Neotropical savanna termites are sodium-limited, we found no difference in decomposition rate with sodium-supplementation compared to controls. Decomposition rate was highly variable in part driven by termites moving mud and soil onto the decomposition substrates, resulting in some substrates gaining mass. However, no difference in decomposition rate could also result from the limited temporal scale of this study (1 week) (Kaspari et al. 2014; but see Kaspari et al. 2009). Additionally, wood-feeding termites were the most frequently encountered termites on sodium-supplemented plots, and the cellulose sponge substrates may not have been attractive to these termites. Increased termite recruitment to areas of sodium deposition is likely to stimulate decomposition and thus nutrient cycling over longer time scales.

Conclusion

Neotropical savannas such as Brazilian Cerrado are experiencing heavy anthropogenic disturbance largely due to conversion to agriculture for soybeans and livestock (Sano et al. 2010; Alencar et al. 2020). Burning and the mechanical conversion of savanna to agricultural land typically results in lower carbon stocks and increased sodium through the rapid decrease in plant biomass that is deposited as ash (Kellman et al. 1985; Fearnside 2000). Moreover, irrigation practices, fertilizer, and livestock excretion and feces can all increase sodium after the land is converted (de Sousa et al. 2018). As such, increased termite activity in response to sodium pulses in the short term, and potentially over longer time scales, may further exacerbate carbon loss, but this has yet to be tested. Similarly, ants, many of which consume both plant- and animal-derived tissue, may alter their level of carnivory (e.g., Clay et al. 2017) or experience changes in competitive interactions in response to sodium pulses and pressures associated with land use change that would ultimately alter the structure of food webs. As Neotropical savannas continue to get hotter and drier, this is likely to most strongly impact nocturnal species (Hofmann et al. 2021). Therefore, understanding the geography and temporal dynamics of sodium limitation and its impacts on tropical savanna food webs is essential for their conservation and the development of mitigation strategies.

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