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Distinct isotopic signatures reveal effect of ecoregion on small mammals of Ghana

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Species reside in dynamic environments, simultaneously experiencing variations in climatic conditions, habitat availability and quality, interspecific interactions, and anthropogenic pressures. We investigated variation in foraging ecology of the small mammal community between land-use classifications (i.e., protected national parks and unprotected lands abutting them) in Mole National Park (MNP) and Digya National Park (DNP), representing distinct ecoregions of Ghana. In 5,064 trap nights, we sampled 153 individuals of 23 species within the 2 national parks and adjacent lands outside protected boundaries to describe variation in community composition. We also used δ^{13} C and δ^{15} N isotopic ratios from fresh feces to determine main effects and interactions between land use and ecoregion on trophic structure in species and communities of small mammals. Small mammals exhibited distinct community assemblages between ecoregions (i.e., national parks): *Gerbilliscus guineae*, *Hybomys trivirgatus*, *Malacomys edwardsi*, *Lemniscomys bellieri*, *L. zebra*, and *Taterillus gracilis* were only captured in the dry savanna ecoregion of MNP. Additionally, isotopic signatures for nitrogen were significantly lower in MNP (2.83 ± 0.17‰) compared to DNP (4.97 ± 0.33‰), indicating that small mammals occupied different trophic levels between ecoregions. The most common species, *Praomys daltoni* exhibited variation in isotopic signatures between ecoregions and land use, with higher δ^{15} N found within MNP boundaries. We found no distinction in δ^{13} C at the community or species level within or across protected areas. Ultimately, understanding shifts in the ecology of species can inform predictions about community structure and ecosystem function under future environmental and anthropogenic scenarios.

Key words: community, climate, diet, *Praomys*, protected areas, West Africa

Geography and ecology interact in a complex and sometimes unpredictable manner. Individuals must cope with variation in environmental conditions as well as in habitat availability and quality throughout their geographic distributions (Gaston 2009; Khaliq et al. 2014). Concurrently, a suite of biotic factors govern species ranges, patterns of behavioral activity, and movement of individuals within their home ranges (Sexton et al. 2009; Bozick and Real 2015; Lesmeister et al. 2015; Monterroso et al. 2016). Changes in spatial patterns of community assembly also influence access to resources through mutualisms and competitive interactions (HilleRisLambers et al. 2012; Araujo and Rozenfeld 2014). Further, anthropogenic pressures that accelerate rates of climate change and land degradation can limit the capacity of species to fill their ecological roles of predation, seed dispersal, etc. (Ellis 2015). Because species will respond differently and asynchronously to these perturbations, community composition also shifts with anthropogenic pressures such that changes in the behavior, diet, phenology, or physiology of a single species can have ecosystem-level ramifications (Bolnick et al. 2011). Species that occur in regions of the world experiencing rapid change with ineffective protected areas warrant particular attention as their persistence and ecological function may be compromised in the future.

West Africa is expected to experience high levels of species turnover for mammals from changing climates (Baker et al. 2015). Such predicted variation in species composition can alter spatial patterns of biodiversity as well as numerous ecological interactions in the future. Even more dramatic are expected shifts in biomes that could result from extreme changes in climate. In Ghana, deciduous and evergreen forests may expand in

coverage, whereas contractions in savanna biomes may occur according to projections for West Africa (Heubes et al. 2011). Such changes modify wildlife habitat and site occupancy particularly for habitat specialists. Further, immediate pressures from agriculture, urban expansion, and extractive resources to support growing human populations and economies throughout the continent degrade landscapes and increase vulnerabilities to extinction (Seto et al. 2012; Edwards et al. 2014; Laurance et al. 2014). Therefore, investigating current patterns of species distributions, community structure, and functional traits over extant gradients of land use and environmental conditions are necessary to anticipate impacts under future global change scenarios.

Small mammals include species of conservation concern that exhibit varying sensitivities to changes in environmental and land-use patterns (Schipper et al. 2008; Terry and Rowe 2015). Small mammals play key roles in nutrient cycling, distribution of vegetation, and disease transmission (Hillyer and Silman 2010; Davidson et al. 2012; Prugh and Brashares 2012). We investigated variation in small mammal communities focusing on variation in trophic niches between land use (i.e., protected and unprotected areas) in 2 distinct ecoregions of Ghana. Specifically, we sampled within 2 national parks and adjacent unprotected lands to describe variation in community composition of small mammals. We employed δ^{13} C and δ^{15} N isotopic ratios to determine effects of land use and ecoregion on trophic structure in small mammals within individual species and across the whole community. Community assembly theory simultaneously recognizes a convergence of functional traits (e.g., diet, habitat use, etc.) under similar environmental conditions and the resultant intra- and interspecific competition that may emerge from employing similar adaptive strategies (HilleRisLambers et al. 2012; Violle et al. 2012). Therefore, we expect: 1) greater similarity in community composition within an ecoregion than between ecoregions; 2) narrower diet breadth (i.e., smaller range in δ^{13} C) but more trophic structure (i.e., higher δ^{15} N) in diverse communities; and 3) land use to have a greater influence than ecoregion on species richness and diet selection.

Materials and Methods

Study area.—We worked in a single protected area in 2 dominant ecoregions of Ghana: West Sudanian savanna and Guinean forest-savanna mosaic (Fig. 1). Mole National Park (MNP; 09°11′-10°06′ N and 01°22′-02°16′ W) is the largest protected area in the country spanning 4,840 km^2. MNP exhibits extreme arid conditions with high temperatures averaging 36.5°C in the warmest month, and with relatively low rainfall 1,055 ± 5.07 mm/year. The centrally located Digya National Park (DNP; 07°06′-07°44′ N and 0°06′-0°42′ W) spans 3,478 km^2 with a maximum average temperature in the warmest month of 35.5°C and receives 1,326 ± 14.52 mm/year of rainfall. We extracted park area from the World Database of

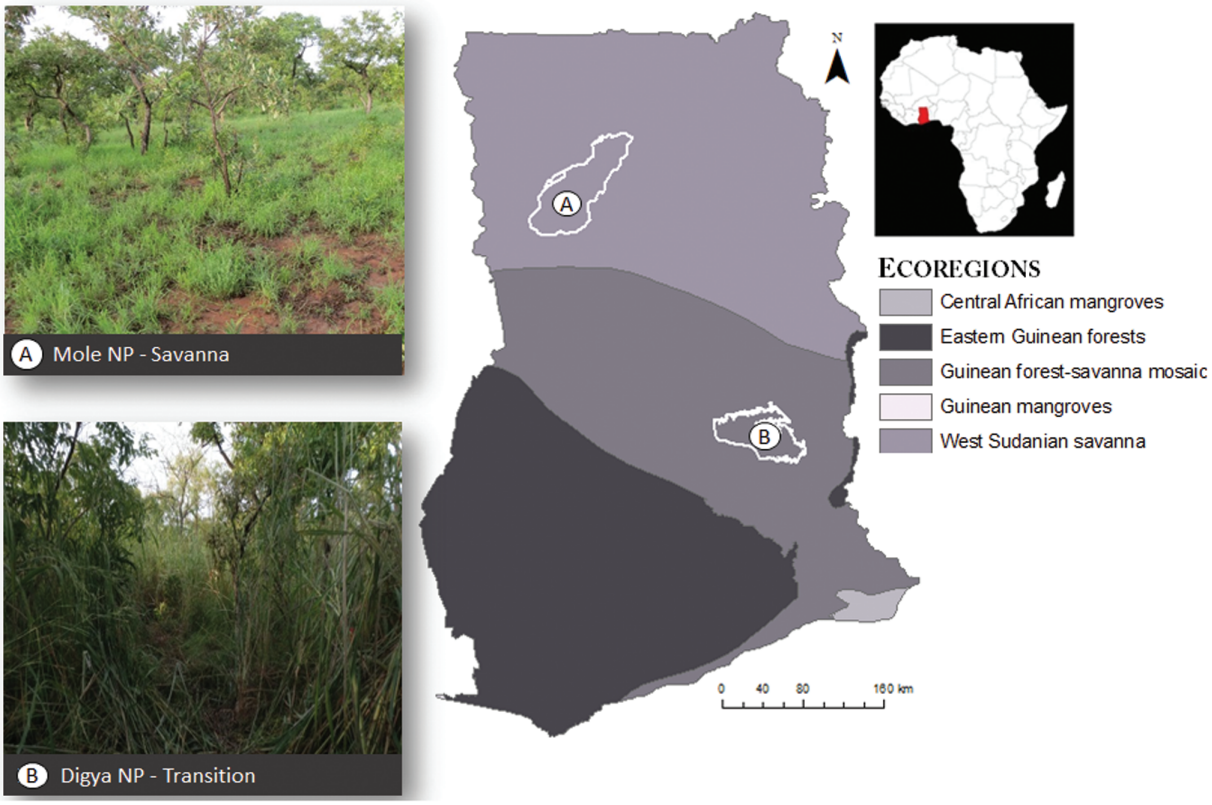

Fig. 1.—Map of ecoregions in Ghana, West Africa, with study areas outlined in white. (A) Mole National Park has high temperatures and receives the least amount of rain, (B) Digya National Park located in the transition zone between savanna and forests has moderate temperatures and levels of rainfall.

Protected Areas (protectedplanet.org) and all climate data come from the WorldClim database (Hijmans et al. 2005).

Study design and animal capture.—We constructed paired grids of 70 m × 140 m inside and outside at each national park that were separated by an average of 5 km to avoid edge effects influencing the assemblages of small mammals. We implemented 7 and 5 paired grids within and around MNP and DNP, respectively. Each grid consisted of 49 Sherman traps (7.6 × 9.5 × 30.5 cm; H. B. Sherman Co., Tallahassee, Florida) spaced 20 m apart in a checkerboard pattern with 10 m misalignment between columns. Traps were baited with groundnut paste, cassava, or powdered fish with palm oil to attract multiple types of consumers. We also placed 9 Tomahawk traps (50.8 × 17.8 × 17.8 cm, model number 204; Tomahawk Live Trap Co., Hazelhurst, Wisconsin) spaced 60 m apart in the center and perimeter columns of grids at DNP. The inclusion of Tomahawk traps led to the addition of only 1 species (*Cricetomys gambianus*) that was captured both inside and outside DNP boundaries; we removed this species from cross-park comparisons. All traps were checked twice daily (0600–0800 and 1600–1800 h) and we trapped grids for 4 consecutive nights. Land use activities immediately outside protected area boundaries consisted of human settlements, charcoal production, aquaculture, livestock husbandry, and various farming activities (e.g., cocoa, rice). We sampled MNP in May to June 2012 and DNP in November to December 2012 to reduce heterogeneity in precipitation and thus, the effects of seasonality when making cross-park comparisons. This work was conducted under Animal Care and Use Committee #R304 at the University of California Berkeley and adheres to American Society of Mammalogists (ASM) guidelines (Sikes et al. 2016).

During processing, all newly caught animals were individually marked with a permanent marker or metal ear-tag (1005-1; National Band and Tag Co., Newport, Kentucky). We collected ear-notches from each individual and stored them in RNA*later* or 95% ethanol. Though some small mammals in the region are distinguishable using physical characteristics, we used molecular techniques to ensure species identifications and enhance representation of sequence data from the region. As such, we extracted DNA from tissue samples following guidelines of QIAamp DNA Micro Kits (QIAGEN, Germantown, Maryland) and then amplified and sequenced DNA using primers on ~815 base pairs of the mitochondrial cytochrome b gene (L14723: ACCAATGACATGAAAAATCATCGTT and H14896: TAGTTGTCGGGGTCTCCTA; Ducroz et al. 2001). The resulting sequences were manually edited, aligned, and checked against accessioned sequences in Genbank as well as with study-confirmed sequences using the Geneious Pro software v. 5.1.7 (Kearse et al. 2012).

Foraging ecology.—Stable isotopes are proving to be insightful tools for investigating trophic ecology across taxa and ecosystems with increasing application to small mammal systems (Post 2002; Newsome et al. 2007; Boecklen et al. 2011; Ben-David and Flaherty 2012). We used carbon and nitrogen isotopic ratios to determine differences in resource use and trophic structure in assemblages of small mammals between ecoregions and land uses. C3 plants have a ratio of $^{13}C/^{12}C$ between −33‰ and −24‰ in contrast to C4 plants that show lower preference for the lighter isotope with ratios between −14‰ and −11‰ (Ben-David and Flaherty 2012). Nitrogen ratios in the tissue of consumers are generally 2–5‰ higher than those of their diets (Bearhop et al. 2004; Newsome et al. 2007). Therefore, carbon ratios provide insights about consumption patterns while nitrogen ratios elucidate trophic position within the community. We processed oven-dried scat samples collected from small mammals trapped within and around MNP (n = 37; 59% inside) and DNP (n = 44; 43% inside). Carbon (^{13}C) and nitrogen (^{15}N) in finely homogenized scat samples were analyzed by continuous flow dual isotope analysis using a CHNOS Elemental Analyzer interfaced to an IsoPrime100 mass spectrometer at the Center for Stable Isotope Biogeochemistry at University of California, Berkeley. Long-term external precision for C and N isotope analyses is 0.10‰ and 0.15‰, respectively. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ are expressed in standard delta notation (δ) in per mil units (‰) and calibrated against international references (atmospheric N and V-PDB). Repeated measures of scat samples (70% were run twice) resulted in a sample precision of ± 0.1‰ for $\delta^{13}C$ and $\delta^{15}N$.

Analyses.—We compared community dissimilarity of small mammals captured inside and outside grids as well as between protected areas using ordination methods. Permutational multivariate analysis of variance (PERMANOVA) was performed on Bray-Curtis distance matrices (999 permutations for R statistics) to determine the significance of differences between land use and ecoregions. If environmental conditions (i.e., ecoregion) exert a greater influence on small mammal communities than land use (i.e., protected versus unprotected area), we expect greater similarity in species richness and composition between sampling locations in close proximity that are experiencing similar environmental conditions. In contrast, if land use exerts greater influence than ecoregion, then dissimilarity will be highest when comparing assemblages inside versus outside national park boundaries regardless of the ecoregion sampled. All analyses were completed in "vegan" package of R version 3.1.2 (R Development Core Team).

We used nonparametric tests to evaluate attributes of trophic structure in small mammals. Specifically, we made inferences about diet breadth and trophic level at the community level using $\delta^{13}C$ and $\delta^{15}N$, respectively. Within species, we expected a greater degree of specificity inside the boundaries of the protected areas (i.e., smaller range of $\delta^{13}C$ values). We also expected a greater degree of community structure reflected in wider $\delta^{15}N$ values inside park borders as a function of species richness.

Results

Animal capture.—Our sampling effort comprised 5,064 trap nights, yielding the capture of 153 individuals of 23 species in 12 genera of small mammals in the 2 study areas. Species richness was highest at MNP with 18 species in total compared to 11 species at DNP. Only 5 species were shared between

the 2 ecoregions, indicating distinct small mammal communities between parks. *Gerbilliscus guineae*, *Hybomys trivirgatus*, *Malacomys edwardsi*, *Lemniscomys bellieri*, *L. zebra*, *Steatomys* sp., and *Taterillus gracilis* were only captured in the dry savanna ecoregion of MNP. In addition to park-level differences, only one-third of the number of individuals were captured outside MNP boundaries compared to inside the park, with slightly lower species richness. In contrast, species richness and capture rates were comparable between grids inside and outside of DNP, though slightly higher outside. Based on Bray-Curtis dissimilarity distances, the greatest dissimilarities were between the inside–outside grid locations in DNP, which degraded through space with higher similarities in the north (Dissimilarities - DNP: 0.47; MNP: 0.36).

Community-level comparisons.—We used stable isotopes from fecal samples to examine resource use and trophic levels by comparing communities between 2 parks, for which we pooled grid data and aggregated species (Fig. 2). Though species assemblages were different, we found almost complete dietary overlap among species occurring within MNP and DNP based on $\delta^{13}C$ values: −23.17 ± 0.23‰ at MNP and −23.88 ± 0.45‰ at DNP (Mann–Whitney *U*-test: $P = 0.929$). In contrast, significant differentiation in $\delta^{15}N$ values indicated more community structure and higher trophic levels for species in the small mammal community occurring in DNP (4.97 ± 0.33‰) compared to MNP (2.83 ± 0.17‰). Next, we investigated how land use may alter patterns of consumption and trophic levels at each park by comparing grids inside and outside of the parks. At DNP, consumption patterns (mean difference in $\delta^{13}C = -1.31$) as well as community structure (mean difference in $\delta^{15}N = 0.33$) were comparable between grids inside and outside of the park, although both indicators were higher outside park boundaries. We found similar results for MNP, with little difference in what small mammals consumed inside versus outside park boundaries (mean difference in $\delta^{13}C = -0.23$) or in their community structure (mean difference $\delta^{15}N = 0.63$), although trophic level indicators from $\delta^{15}N$ values were higher inside park boundaries.

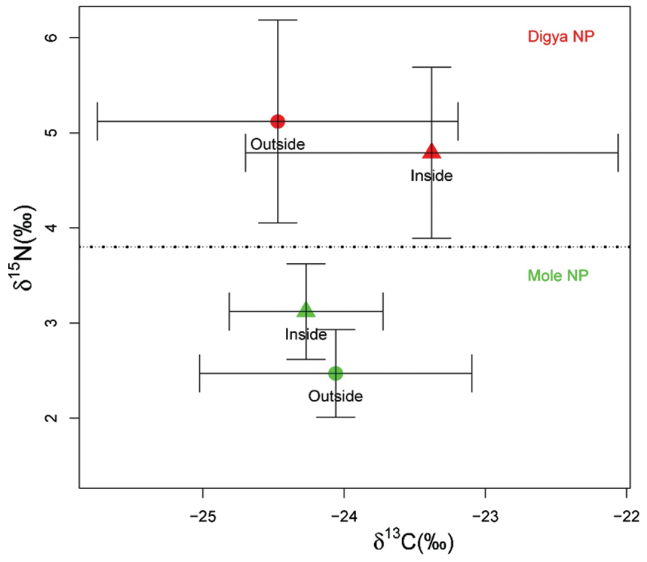

Fig. 2.—Spatial variation in $\delta^{13}C$ and $\delta^{15}N$ values of the small mammal communities sampled in Ghana, West Africa. Data represent means and *SE* from 153 individuals across 23 species captured inside and outside Mole National Park and Digya National Park.

Species-level comparisons.—We explored spatial variation in diet between parks and grid locations for the most dominant species (Table 1). *Praomys daltoni* represented 36% and 31% of all individuals captured at MNP and DNP, respectively. We found that *P. daltoni* occupied different trophic levels within the small mammal communities with significantly higher $\delta^{15}N$ values observed in DNP (Fig. 3, Mann–Whitney *U*-test: $P < 0.001$). We did not detect any difference in consumption patterns via $\delta^{13}C$ across parks. At DNP, *P. daltoni* appeared to occupy the same trophic level in the small mammal community regardless of grid location (Mann–Whitney *U*-test: $P = 0.69$) and exhibited similar consumption patterns (Mann–Whitney *U*-test: $P = 0.37$). However, *P. daltoni* did occupy a higher trophic level inside MNP boundaries compared to outside (Mann–Whitney *U*-test: $P = 0.04$), although no differences in consumption were detected (Mann–Whitney *U*-test: $P = 0.37$).

Discussion

Land use and environmental conditions can synergistically or independently alter the ecology of species through various antagonistic and mutualistic pathways. Here, we evaluated the influence of ecoregion versus protected area status on community attributes and foraging ecology of small mammals using isotopic ratios from fecal samples. We found distinct differences in the small mammal species richness and composition between parks. With higher temperatures and less rainfall in MNP, the small mammal community was comprised of dry savanna species. Community composition results were largely consistent with broad-scale range maps, though few empirical studies exist for comparison. Our study provides many new records where species occurrence data are lacking—see Amori and Luiselli (2011) for a meta-analysis of small mammal communities from West Africa.

Species are expected to benefit from residing inside protected areas that are effectively managed due mostly to reduced anthropogenic disturbances (Geldmann et al. 2013; Pimm et al. 2014; Watson et al. 2014). Small mammals are no exception, as evident with positive associations between habitat quality and species richness (Parsons et al. 2013; Dambros et al. 2015). However, greater heterogeneity in vegetation cover and other habitat characteristics outside protected area boundaries could result in unexpectedly high levels of species richness and similarities in composition across land uses (Seiferling et al. 2012; Wegmann et al. 2014). For example, Caro (2001) found higher species diversity and abundances of small mammals outside protected areas in Tanzania. Many other studies have examined the effect of land-use by comparing species composition, richness, and habitat characteristics inside and outside protected areas (Bruner et al. 2001; Naughton-Treves et al. 2005). Subsequently, it is essential to understand how protected areas alter ecological functions and processes for individual species as well as entire communities (Gaston et al. 2008).

Table 1.—Mean $\delta^{13}C$ and $\delta^{15}N$ values with associated variation (*SD*) for individual species of small mammal captured in Digya and Mole National Parks, Ghana, West Africa in 2012. Only species with more than 2 incidences are reported.

Species	*n*	Park	Mean $\delta^{13}C$ (*SD*)	Mean $\delta^{15}N$ (*SD*)
Cricetomys gambianus	7	Digya	−27.2 (0.6)	3.1 (1.2)
Gerbilliscus guineae	13	Mole	−23.2 (1.7)	2.5 (0.9)
Gerbilliscus kempi	1	Digya	−20.1 (NA)	1.4 (NA)
	3	Mole	−24.7 (1.2)	2.6 (0.7)
Gerbilliscus sp.	6	Digya	−22.5 (1.9)	2.9 (1.1)
	2	Mole	−24.8 (1.2)	2.0 (1.4)
Mastomys erythroleucus	9	Digya	−23.4 (3.1)	5.9 (1.7)
	6	Mole	−24.2 (1.7)	3.4 (1.7)
Mastomys natalensis	3	Digya	−25.7 (1.4)	7.3 (3.3)
Praomys daltoni	13	Digya	−23.7 (2.7)	5.9 (1.8)
	22	Mole	−24.7 (1.2)	2.9 (1.4)
Taterillus gracilis	4	Mole	−25.3 (1.2)	2.7 (0.6)

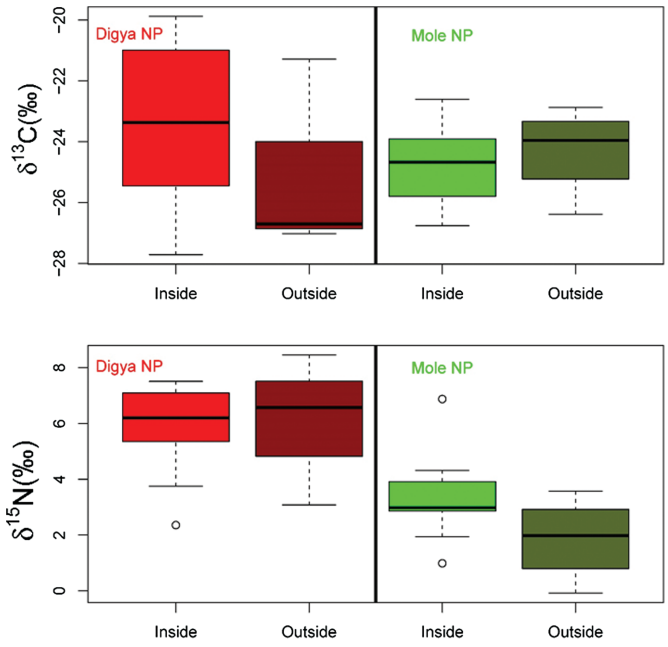

Fig. 3.—Comparison of $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios of *Praomys daltoni* to evaluate variation in consumption patterns (via carbon ratios) and trophic level (via nitrogen ratios) by park and grid locations.

Because land use can influence habitat quality, individuals residing within particular conditions will have varied access to resources and therefore may exploit different food items (Araújo et al. 2011; Fischer et al. 2012). Previous research highlighted the importance of environmental conditions and land use in structuring small mammal communities (Amori and Luiselli 2011; Hurst et al. 2013; Kelt et al. 2013; Smiley et al. 2016). Rautenbach et al. (2014) found that rodent and shrew communities varied seasonally and across vegetative types in South Africa. We explored how the foraging ecology of small mammals varied based on ecoregion (i.e., park) and land use (i.e., grids inside or outside the parks). We found an extremely narrow distribution of $\delta^{13}C$ values that indicated the exclusive use of C3 plants by small mammals in the communities sampled in our study. A similarly narrow dietary breadth has been reported in small mammals of Canada (Baltensperger et al. 2015), while opposite results were found for rodents of South America (Galetti et al. 2016). We found the greatest differences between parks in $\delta^{15}N$ values, with values being significantly higher in DNP compared to MNP. However, we must view this result cautiously given that environmental conditions also can influence enrichment values of nitrogen in the tissue of consumers (Newsome et al. 2007). We intentionally sampled in different seasons to reduce heterogeneity in precipitation patterns across parks. DNP is located within a transition zone comprised of a mosaic of savanna and forest plant species and surrounded by water on 3 sides. We suspect that such variation promoted the observed differences in community attributes. Interestingly, greater divergence was found for consumption patterns based on $\delta^{13}C$ values in DNP between grids inside and outside the park, whereas MNP exhibited more differentiation in community structure via $\delta^{15}N$ values. We attribute this distinction between grids in DNP (though not significantly different) to increased access to anthropogenic food sources as well as the presence of domestic animals and agricultural plants.

We observed a narrower dietary breadth in the small mammal community where species richness was highest in MNP. As a result, we also found some evidence of resource partitioning, with *P. daltoni* occupying a higher trophic level where species richness was highest at the northern site. These results are consistent with the findings of Jiang et al. (2015), who demonstrated the importance of intraspecific interactions and environmental variables in explaining spatial-temporal communities in small mammals from arid grasslands in China. Additionally, Codron et al. (2015) reported species occupying similar isotopic niches exhibited spatial separation for small mammals in South Africa. For small mammals in Illinois, there was also an interaction between small mammal species and geographic location in isotopic values (Van der Merwe and Hellgren 2016).

We documented dramatic differences in community composition of small mammals across ecoregions, which raises concerns if future climates shift the distribution of biomes as predicted for West Africa (Heubes et al. 2011). Specifically, contraction in savannas such as those at MNP could lead to the loss of several species we found only present at this site. Furthermore, alterations to the small mammal community highlight public health concerns in and around protected areas,

given several species such as *C. gambianus* and *Mastomys erythroleucus* detected in this study have implications for disease transmission (Friggens and Beier 2010; Han et al. 2015). Such conditions may further exacerbate community dissimilarities across space and promote construction of novel communities (Lurgi et al. 2012). The response of species to environmental perturbations also has consequences for community assembly and structure (Rowe et al. 2014; Terry and Rowe 2015). We documented variation in ecological function (e.g., trophic level) for individual species and communities based on geography. Species capable of adapting their behaviors, demography, or physiology may promote their future viability at the cost of increasing competition. Alternatively, species that succumb and are extirpated release available resources for other species to expand niches and may cause affiliated species to suffer the same fate—all of which are circumstances that alter spatial patterns of diversity, ecosystem functioning, and possibly human health risks.

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