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Original investigation

Isotopic niche structure of a mammalian herbivore assemblage from a West African savanna: Body mass and seasonality effect

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ABSTRACT

Understanding the mechanisms of species coexistence within local assemblages can play a crucial role in conservation of a species. There is little understanding of how large mammalian bovid species from West Africa partition diet resources, and to what extent they may vary their diet and habitat selection seasonally in order to coexist. Here we studied an assemblage of eleven bovid species in Pendjari Biosphere Reserve, West Africa and used faecal stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to test the impact of body mass diet partitioning at a seasonal scale. We found a significant positive relationship between isotopic niche similarity and body size similarity both in dry ($p < 0.001$) and wet ($p < 0.001$) season. Partitioning of carbon isotope niches is at least partly due to interactions amongst species rather than historical effects. Our findings also show numerous patterns in resource partitioning amongst the 11 bovid species studied, suggesting that different species used dietary resources in contrasting ways. In practice, actual resource competition between bovid species is difficult to demonstrate, but there exists much overlap in diet along the stable carbon isotope axis for most of the studied species. However we conclude that in our study area, especially in the wet season, niche breadth and diet overlap remain large. Abundant resources and low herbivore densities mean there is no need for herbivores to specialize, because they do not have to compete over scarce resources.

Introduction

How so many African savanna herbivore species are able to coexist despite their common reliance on a single resource (plants) is the subject of numerous discussions in community ecology (Ritchie and Olff, 1999). Of all dimensions of an animal's niche, resource use (diet) and body size are the factors most commonly considered in studies of community structure (Prins and Olff, 1998; Henley and Ward, 2006).

This is especially the case for assemblages of large-bodied mammalian herbivores, for which feeding style (browser, grazer, or intermediate) and body size are expected to drive niche partitioning and evolutionary diversification. Despite some debate on the topic, most authors now agree that evolutionary convergence and niche partitioning occurs along the browser/grazer continuum (Hofmann, 1989; Gagnon and Chew, 2000; Cerling et al., 2003). Much attention has also been paid to the fact that resource partitioning through size differences between closely related animal species that co-occur in the same habitat may often shape the niche structure of a community (Prins and Olff, 1998; Ritchie and Olff, 1999).

The effect of body mass on community structure is less certain. Predicted patterns such as a positive relationship between body mass and percent grass in a species' natural diet are not universal (Sponheimer et al., 2003; Codron et al., 2007). The widely-cited expectation that larger-bodied species can tolerate diets of lower quality due to longer retention times in the gastrointestinal tract (and hence more efficient fermentation/digestion). This breaks down at very large body size when retaining partially-digested food in the gastrointestinal tract becomes less efficient than replacing it with new ingesta (Clauss et al., 2007a, 2007b).

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Moreover, lower diet qualities of larger herbivores in fact appears to be a function of higher absolute intake requirements (Muller et al., 2013) than any digestive process per se (Bell, 1971; Jarman, 1974; Demment and Van Soest, 1985), casting doubt on the role of body size in niche partitioning.

Several methods have been applied in understanding herbivore diet partitioning, such as direct observations, investigations of rumen content, and micro-histological faecal analysis (Bowen and Siniff, 1999). Stable isotope analysis provides an alternative approach to investigating dietary niches that, while lacking fine-scale detail of traditional approaches, offers rapid insights into diet at multiple taxonomic and temporal scales. This method has proved useful for assessing resources used by a large range of organisms in varied environments (Newsome et al., 2007; Crawford et al., 2008). Because stable isotopes are differentially distributed in source-sink type systems, they trace nutrient flow through food webs and can be used to estimate the contribution of isotopically distinct food items in a consumer's diet, provided that there are significant differences in the isotopic compositions of the dietary sources (Fry, 2006). In wildlife ecology, stable isotope ratios of carbon (expressed as $\delta^{13}C$ values) and nitrogen ($\delta^{15}N$) in animal body tissues and excreta have been widely utilized to examine species' diets, reflecting differential intake of C_3 versus C_4 resources (e.g. browse and grass in African savannas), and differences in trophic position, respectively (Layman et al., 2012). Consequently, dietary niche segregation patterns for whole assemblages are readily documented using this approach (Stewart et al., 2003; Codron et al., 2009).

Diet, niche partitioning, and community structure of African mammal herbivore assemblages has been studied extensively in East and southern African savannas, but less attention has been paid to West African assemblages (Schuette et al., 1998) despite the rich diversity of ungulates and inherent environmental (climate, vegetation) uniqueness of this region (Kassa et al., 2007; Assédé et al., 2012). Recently we showed, using stable carbon isotope analysis of faeces, that the diets of several West African herbivore taxa differ fundamentally in terms of browse/grass composition in comparison with the same (or closely-related) species elsewhere on the continent (Djagoun et al., 2013a). Therefore, the role of body size in structuring these assemblages is even less well-known than it is in East and southern African environments. In that context, resolving patterns of niche partitioning within West African ungulate assemblages has much to contribute to our understanding of ungulate communities in general.

The aim of this study is to determine whether species-specific stable isotope niches within a West African savannah herbivore assemblage do reflect differences in body size across taxa. Based on competition theory, we expect that species of similar body size would have more similar dietary (and hence isotopic) niches compared with differently-sized syntopic taxa. Using the carbon ($\delta^{13}C$) data published in Djagoun et al. (2013a), we test the hypothesis that isotopic niche segregation amongst sympatric species is non-random, reflecting differential use of dietary niches between browsers and grazers, as well as within these guilds. We then present previously unpublished faecal stable nitrogen isotope data, to further resolve the niche breadths of each taxon, and ultimately to compare patterns of isotopic similarity with body size similarity across taxa.

Material and methods

Study area

This study was carried out in the Pendjari Biosphere Reserve (PBR), located in the north-west part of Benin in the District of Atacora (10°40′–11°28′N and 0°57′–2°10′E) (Fig. 1.). This Biosphere Reserve consists of the Pendjari National Park (2660 km^2) surrounded by two hunting zones: the Pendjari hunting zone (1750 km^2), and Konkombri hunting zone (251 km^2). The dominant vegetation type is savanna interspersed by patches of dry forests with deciduous trees (Assédé et al., 2012).The park is located in the Sudanian Zone with a single wet season from April/May to October and one dry season from November until March. Average annual precipitation is 1000 mm, with 60% falling between July and September (Sinsin et al., 2002). During the wet season large parts of the park are flooded.

Materials and isotope analysis

Of the various tissues that can be used for isotopic diet reconstructions of living animals, faeces are usually the most readily available, since they can be obtained entirely non-invasively. The faecal samples in this study are the same as those for which the carbon isotope values were reported in Djagoun et al. (2013a). The sample comprises 11 bovid species inhabiting the PBR, collected monthly from December 2011 to May 2012. Each month, five samples representing different individuals of each species were collected, for a total of 30 samples per species, from a range of habitats within the reserve (Fig. 1). Sample numbers are slightly smaller forred-flanked duiker (*Cephalophus rifulatus, n* = 24), common duiker (*Sylvicapra grimmia, n* = 28), oribi (*Ourebia ourebi, n* = 28) and topi (*Damaliscus lunatus korrigum, n* = 26) due to difficulty in locating and observing animals. Only fresh samples were collected, in order to ensure that the samples had not been contaminated by fungi, microorganisms or invertebrates. Species affiliation and freshness of each sample were determined by an experienced ranger of the PBR. Any chance of misidentification was further reduced by a post hoc protocol: dung samples were compared with fresh samples that were identified with certainty, based on the size, shape and indentation of the pellets. In addition, samples were then double-checked (blind test) by experienced local trackers and finally checked again using a field manual (Stuart and Stuart, 1997). In some cases, collections were made by locating animals and then following on foot.

Dried, homogenized samples were analyzed for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios by stable light isotope ratio mass spectrometry (details in Djagoun et al., 2013a; Codron and Codron, 2008), and results expressed in the delta (δ) notation in parts per mil (‰) relative to the Vienna Pee Dee Belemnite (VPDB), and atmospheric N_2 standards, respectively according to the equation:

$\delta X = \left[\left(\frac{R_{sample}}{R_{s\tan dard}}\right) 1\right] \times 10^3$,(1)where X is ^{13}C or ^{15}N and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of internal laboratory standards (Merck Gel, Valine, and homogenized *Acacia* leaves) indicated that measurement precision was <0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Data analysis

Carbon isotope evidence from faeces of PBR bovids reflect significant differences in diet between dry and wet seasons (Djagoun et al., 2013a). Therefore, the sample for each season was analyzed separately throughout this study. We checked for differences in stable isotope niches of species initially using nonparametric Kruskal-Wallis tests, with species as the independent variable, and $\delta^{13}C$ and $\delta^{15}N$ values as dependent variables, respectively, because assumptions of normality were violated. A more rigorous test for niche segregation within the bovid community was done by calculating the average degree of carbon isotope niche overlap in the data, and comparing this with the overlap expected based on chance alone using null models. For this test, faecal