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Bulk feeder or selective grazer: African buffalo space use patterns based on fine-scale remotely sensed data on forage quality and quantity

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ABSTRACT

The distribution and behaviour of African large grazers are regulated primarily from the bottom up, with some species showing clear preferences for certain vegetation types. While the African buffalo (*Syncerus caffer*) is sometimes considered a bulk grazer, other studies indicate that they can be selective and show seasonal variations in their home ranges. We used very high resolution satellite imagery to evaluate how the quality and quantity of the vegetation influence space use by buffalo herds in Kruger National Park, testing the bulk-selective hypotheses. Using telemetry data from six buffalo, we analyzed seasonal differences in home ranges and core areas. We investigated resource selection and preference at various spatial scales for a subset of three buffalo, comparing habitat use against vegetation biomass and nitrogen content, derived from a high resolution RapidEye image of the wet season. Overall buffalo preferred open vegetation types, with sparse trees and fertile soils, and had home ranges that partially overlapped between dry and wet seasons (average overlap 50%). Buffalo formed home ranges non-randomly within the study area, choosing vegetation of higher quality and quantity. Within home ranges, however, they selected for higher quality forage, and not for higher quantity. Our results showed that the dichotomy between unselective bulk grazers or selective feeders can be scale dependent, as buffalo behaved more like bulk feeders at the scale of home ranges but were more selective within their home range, preferring quality over quantity.

1. Introduction

Understanding African buffalo (*Syncerus caffer*) space use patterns is important for sustainable management of South Africa's protected areas, as buffalo herds can shape plant communities in savannahs by affecting primary production (McNaughton, 1985), as well as nutrient distribution and cycles (McNaughton et al., 1997). However, in turn, the distribution and behaviour of buffalo and other African large grazers are regulated primarily from the bottom up, with quality and/or quantity of fodder being the main drivers (Prins, 1996; Sinclair, 1977; Sinclair et al., 2003). The influence of predation on population dynamics and space use plays a limited role in comparison with that of rainfall conditions and food sufficiency (Sinclair, 1977; Prins, 1996; Sinclair et al., 2003; Radloff and Du Toit, 2004; but see Ogutu and Owen-Smith, 2005; Owen-Smith and Mills, 2008).

A crucial question in bottom-up regulation is whether the ranging behaviour of African buffalo reflects an attraction for high quality foraging grounds, or whether animals choose places with sufficient quantity of food. While some studies describe buffalo as "supreme bulk grazers" (Owen-Smith and Cumming, 1993) others indicate a more selective behaviour towards certain grass species, and even certain parts of grasses, to fulfil their dietary requirements (Sinclair, 1977; Macandza et al., 2004). Resource selection will also depend on the spatial scale at which habitat use is considered (Bailey et al., 1996; Senft et al., 2014), yet published studies of buffalo space use patterns do not examine scale dependency (e.g. Ryan et al., 2006; Winnie et al., 2008; Matawa et al., 2012).

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Understanding the foraging behaviour of buffalo might require fine resolution data that reflect vegetation quality and quantity at the level of home ranges, a major methodological challenge in the heterogeneous savannah environment. In order to surmount this limitation we analyzed patterns of space use by three female buffalo fitted with radio collars in Kruger National Park (South Africa) with respect to fine-scale data derived from RapidEye sensor, depicting vegetation quality as nitrogen (N) content and vegetation quantity as above-ground biomass (Grant and Scholes, 2006; Ramoelo et al., 2014). In savannah ecosystems, both nitrogen content and biomass depend on rainfall and soil fertility (Grant and Scholes, 2006; Ramoelo et al., 2012), and nitrogen concentration positively correlates with protein content (Clifton et al., 1994; Wang et al., 2004), a major nutritional need for herbivores (Prins and Beekman, 1989; Prins and Van Langevelde, 2008). Relationships between nitrogen, biomass and animal distribution have been typically studied using faeces and vegetation surveys (Leite and Stuth, 1990; Leslie and Starkey, 1985; Ryan et al., 2006; Wofford et al., 1985). However, with new technologies such as RapidEye satellite sensor, which provides, e.g., useful in vegetation studies red-edge spectral band, it is now possible to estimate and map N content and biomass at a very high resolution (Cho et al., 2012; Ramoelo et al., 2014, 2012). According to our knowledge, no study has yet linked fine-scale patterns of nitrogen content and biomass derived from satellite images, with buffalo location data from Global Positioning System (GPS) collars.

In addition, food selectivity can also translate into seasonal patterns of habitat use if animals shift their territory in search for optimal resources. Although buffalo herds are not necessarily territorial (Ryan et al., 2006), they are often confined to home ranges that can be used continuously for years (Mloszewski, 1983). Some studies have described larger home ranges during dry periods, when food and water become scarcer (Funston et al., 1994; Ryan et al., 2006), but these were based on limited sample sizes.

Our objective in this paper is to test the level of selectivity and the spatial scale at which selection is expressed in a large savannah herbivore, the African buffalo. We argue that high resolution data on vegetation quality or quantity are necessary to reveal whether buffalo are bulk grazers and choose forage quantity (higher biomass), or selective feeders attracted by food quality (high nitrogen content). In addition, selectivity should be evaluated at multiple scales, such as at the level of home ranges and within home ranges (third and fourth orders of selection after Johnson and Prairie, 1980). Furthermore, in this study we also investigated whether buffalo ranging varies with season. We hypothesize that buffalo change their ranging only partially when the area dries out and resources are less available. This hypothesis was tested by investigating a seasonal overlap of home ranges and core areas, based on GPS data of six individuals, during several months associated with the wet and dry seasons.

2. Materials and methods

2.1. Study area

The study area is located in the central-southern region of Kruger National Park (KNP) in South Africa (Fig. 1). This low-lying landscape, known as “Lowveld”, is part of the savannah biome, characterized by the coexistence of trees and C4 grasses (Huntley, 1982; Venter et al., 2003), and shaped by geological substrate and climate. The long-term average annual rainfall measured at the locality of Lower Sabie is 603 mm (South African National Parks, www.sanparks.org/parks/kruger/tourism/climate.php). Rains occur from October to April, considered the summer (wet) season. Winters are dry and mild with frequent bush fires (Venter et al., 2003). The dominant geology consists of gneiss and granite with local intrusions of gabbro, basalt and shale (Venter et al., 2003). The area is mostly flat in the basalt sites, and undulating in the granitic areas. Average elevation is 450 m.

The main vegetation types are: (a) “Delagoa lowveld” with soils rich in sodium, and dominated by dense thickets; (b) “granite lowveld”, with nutrient-poor sandy or clayey soils and dominated

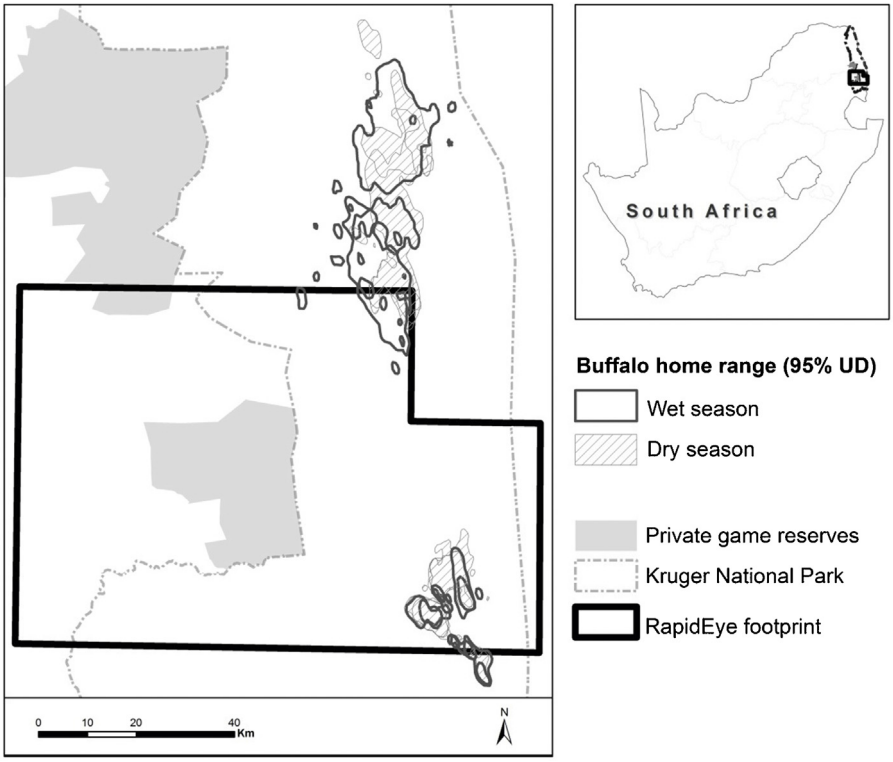

Fig. 1. Map of the study area showing the wet and dry season home ranges of buffalo (95% kernel estimations) and the area covered by the RapidEye image.