



Utility of a forage-productivity model for predicting herbivore abundance in the eastern Karroo, South Africa, varies among habitats



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ABSTRACT

The question of how many herbivores an area can support for long-term persistence is fundamental to managing wildlife in increasingly fragmented landscapes. Species-specific spatial requirement information is scarce, so many studies have used models to predict carrying capacities for indigenous herbivores based on forage productivity estimates and metabolic requirements of the herbivores. Testing such models against empirically derived observations is, however, rare in the peer-reviewed literature. We modeled predicted relative abundances of the medium- to large-sized herbivore community of a reserve in the semi-arid eastern Karroo, South Africa, following Boshoff et al. (2001, 2002a). We also addressed the overestimation abundance of small species by incorporating an adjustment factor based on the relationship between body size and population metabolic rate. We tested both model's outputs against empirically derived game count data for the same herbivore community which revealed significant differences in species relative abundances predicted by the two models. Habitat-specific regression analyses revealed that incorporating a population metabolism adjustment factor into the model resulted in a generally better fit than the original model. Furthermore, the model performed best for apparently structurally simple habitats. These results support the use of forage-based productivity models to estimate potential abundances of indigenous herbivores.

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1. Introduction

How many animals can an ecosystem support? This fundamental question troubles many a wildlife manager and ecologist alike (McLeod, 1997). In particular, wildlife management initiatives require information on habitat-specific species' space requirements to manage for the long-term persistence of populations and/or the sustainable use of biodiversity (Boshoff et al., 2001, 2002a; McNeely et al., 1990). Moreover, with escalating fragmentation and isolation of wildlife areas (through fencing or by creating other barriers to dispersal; Hayward et al., 2009) and the consequent need for information on how to manage such systems, this question is becoming increasingly significant (Fynn and Bonyongo, 2011; Ortega-Huerta and Peterson, 2004).

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Because ground-surveys are both expensive and time consuming, comprehensive, empirically derived abundance information is not available for many species or areas (Boshoff et al., 2001). Thus, a commonly-used approach (with much variety in techniques and definition; MacNab, 1985) is to predict potential herbivore abundances for areas using the species' metabolic requirements and estimates of food availability and quality – the so-called carrying capacity (Boshoff et al., 2001, 2002a; Bothma et al., 2004; Dekker, 1997; Hobbs and Swift, 1985; Hobbs et al., 1982; Mentis and Duke, 1976; Muya et al., 2013; Potvin and Huot, 1983; Wallmo et al., 1977). The carrying capacity concept is a productivity-based theory developed for domestic herbivores that, when applied in a wildlife context, needs to be adapted to different management objectives and for indigenous herbivores. The concept is generally considered unsuitable for describing plant-herbivore dynamics in systems with substantial environmental variance (e.g. semi-arid systems characterized by high degrees of climatic unpredictability; McLeod, 1997). Thus, considering the stochastic nature of most natural systems, this concept may be of limited use in many instances. Therefore, it is critically important to assess the

outputs of such models against empirically derived observations to identify discrepancies and shortcomings of the model if they are to be of any value.

A well-documented approach to modeling herbivore abundances is that of Boshoff and colleagues (Boshoff et al., 2001, 2002a, 2002b; Boshoff and Kerley, 2001) — a spreadsheet model that is based on habitat-specific forage availability estimates and the forage requirements of the herbivore community. It uses adaptations of the agriculture-based Large Stock Unit (LSU) approach using LSU equivalents for indigenous herbivores. (See Appendix C, available online at <http://dx.doi.org/10.1016/j.jaridenv.2014.06.004>; Meissner, 1982). While, the LSU approach has been applied elsewhere (e.g. Bothma et al., 2004; Flinders, 1988; Heady and Child, 1994; Landsberg et al., 1992; Robinsen and Bolen, 1989), it has not been tested in the peer-reviewed literature.

Here we assess whether the forage productivity-based modeling approach of Boshoff and colleagues (Boshoff et al., 2001, 2002a) produces reliable estimates that reflect the abundance patterns of a medium- to large-sized herbivore community at a local scale in a semi-arid region. In this way, we validate the use of the approach for wildlife management applications in a highly variable system, and thus by extension lend support to its use in relatively homogenous systems. We further adjust the modeling in an attempt to address a recognized shortcoming of Boshoff et al.'s (2001, 2002b) approach — i.e. the apparent overestimation of small species abundances. Thus our contribution is two-fold — validating the simple modeling approach to estimating herbivore abundances and addressing a recognized shortcoming.

2. Materials and methods

2.1. Study area description

The c. 280 km² Samara Private Game Reserve (Samara; 24°50'19.60"E, 32°21'41.67"S) is located approximately 30 km south-east of Graaff-Reinet, in the eastern Karoo, South Africa. At the time of the study, the property included a 62 km² game-fenced area. The reserve exhibits a great diversity of landscapes and vegetation types, where open plains give rise to the steep ridges of the Great Escarpment and Southern African Plateau. The region is semi-arid with 300–400 mm mean annual rainfall.

Samara comprises representative areas of four of South Africa's biomes: Albany thicket, Savannah, Grassland and Nama-karoo (Mucina and Rutherford, 2006, Fig. 1), incorporating eight distinct vegetation types and two azonal vegetation units (modified from Vlok et al., 2003; Van Cauter et al., 2005). For the purpose of this study, the vegetation types, detailed descriptions of which can be found in Van Cauter et al. (2005), are described as mammal habitats. Albany thicket is characterised by dense, evergreen, semi-succulent and thorny vegetation which is relatively impenetrable in an undisturbed state. Samara contains five thicket habitat types: Succulent and Non-succulent Valley thicket as well as Mesic and Temperate thicket are all poorly stratified habitats of dense, evergreen woody trees and shrubs (Eberhardt, 1978; Mucina and Rutherford, 2006) that form the forage production base. Succulent valley thicket is dominated by *Portulacaria afra* (an important forage plant for many browsing herbivores) while it is much less prominent in Non-succulent valley thicket. Mesic thicket and Temperate thicket contain relatively fewer palatable plant species than the Valley thicket types (Le Roux et al., 1994; Palmer, 1989). Xeric succulent thicket is characterised by an open mosaic of thicket bush clumps (containing *P. afra*) and karroid shrubs (Stuart-Hill, 1992). The Savanna biome is represented only by Woodland which comprises a discontinuous tree layer with a grassy understory intermixed with a few karroid species (Van Cauter et al.,

2005). The Grassland biome refers to short and simply-structured herbaceous vegetation dominated by grass species. It is represented on Samara by Sweet grassland, dominated by grass species which remain palatable throughout the year (Van Oudtshoorn, 1999). Nama-karoo is represented only by Open dwarf shrubland which is found on plains and is dominated by dwarf shrubs intermixed with grasses and other small arid-adapted plant forms (Mucina and Rutherford, 2006, Fig. 1). The two azonal units are mosaics of Temperate thicket and Sweet grassland and Sour grassland (i.e. dominated by grass species of low nutritional value, especially outside of the growth season; Van Oudtshoorn, 1999), respectively. They are characterized by distinct bushclumps interspersed with open fields of grass (Van Cauter et al., 2005).

Habitat types are distributed in a fairly predictable pattern across the landscape with Sweet grassland and the mosaic units occurring along the plateau, while Temperate thicket is restricted to the upper ridges at the edge of the plateau. Mesic thicket is limited to an isolated patch on the upper slope of the escarpment while Valley thicket types occur along slopes. The latter are abutted by Xeric succulent thicket at the base of the escarpment and Open dwarf shrubland on the plains (Fig. 1; Van Cauter et al., 2005; Vlok et al., 2003). Although many of these habitat types have remained relatively undisturbed, some areas (mostly Xeric succulent thicket and the Temperate thicket/grassland mosaics) show signs of transformation owing to past land-use regimes (i.e. goat and sheep farming).

The game-fenced area within which the study was conducted incorporates areas of the plateau, escarpment and the plains at the foot of the escarpment. Three habitat types are unique to the game-fenced area, namely: Temperate thicket/Sour grassland mosaic, Mesic thicket and Sweet grassland, while Woodland and Open dwarf shrubland are found exclusively outside the game-fenced section. All other habitat types were found both inside and outside the game-fenced section.

At the time of the study, Samara supported 12 medium and large herbivore species (Table 1), all of which were present in the game-fenced section (Van Cauter et al., 2005). In addition, three carnivore and two omnivore species were confirmed to be present on the property.

2.2. The model basics

Following Boshoff et al. (2001, 2002a), we modeled the predicted abundances of the medium- to large-sized herbivore community (see Table 1) of the game-fenced area of Samara. The approach was based on allocating a conservatively estimated carrying capacity, which is generally a reduction of the recommended agricultural capacity. Forage resources in each mammal habitat were allocated to the different foraging guilds (i.e. grazers, browsers, and mixed-feeders) based on the graze/browse ratio of that habitat and then equally among species within each guild. Forage productivity has the potential to vary with season in some habitats. This is accounted for in the agricultural carrying capacity estimates (Anonymous, 1985). However, we also addressed this variability by considering surrogates for productivity (e.g. rainfall seasonality, soil nutrient status, grass component, topography) along with vulnerability to herbivore impacts when applying the reduction factor to the agricultural carrying capacity for each habitat. Thus, habitats with a higher degree of seasonality in productivity and/or vulnerability were reduced by a larger degree (up to 70% in some cases) than those with a more consistent forage base or which were relatively less vulnerable ($\geq 30\%$). Mammal habitats were derived from vegetation types, which were identified and mapped for the whole property at 1:50 000 scale, employing an expert-based approach using aerial photography. The resultant map was ground-truthed and drawn boundaries were found to deviate by a mean 28.4 m

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