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Incorporating secondary metabolites, tannin-binding proteins, and diet breadth into carrying-capacity models for African elephants

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ABSTRACT

Elephant populations have been historically difficult to manage and have sometimes been subjected to drastic management procedures. One way to monitor elephant populations to estimate a sustainable carrying capacity is through the use of standing-crop carrying-capacity models. Previous carrying-capacity models designed for grazers have posed issues when applied to browsers such as elephants, predicting much higher carrying-capacity estimates than are realized in nature. This might be attributed to the level of plant secondary metabolites, which limit the available nitrogen in browse material that browsers and mixed feeders encounter while foraging. Many browsers and mixed-feeders, including elephants, have a physiological mechanism to tolerate a portion of encountered tannins in the form of salivary tannin-binding proteins. We constructed an optimal-foraging model for carrying capacity for elephants that incorporates the negative effects of plant secondary metabolites and the partial neutralization of these chemicals by the tannin-binding affinity of elephant saliva. In addition, our model includes diet breadth and dietary contribution of browsed species, browse quality, and the available standing crop of browsed species. Ultimately, our model produced more plausible estimates of elephant carrying capacity when compared with estimates that use 100% nitrogen availability and use. Moreover, as the key variables needed for the model can be obtained easily, our model is not site-specific or limited to elephants, but rather can be applied to a wide range of browsing herbivores across a number of reserves of different sizes.

1. Introduction

African elephant (*Loxodonta africana*) populations present many management challenges (Kerley and Shrader, 2007; Midgley et al., 2005; Whyte et al., 1998). In southern Africa, elephant numbers are estimated to be about 20,000 individuals and are increasing by about 4% per year (Blanc, 2007, 2008; Blanc et al., 2005). Through their foraging, elephant populations can have negative impacts on the landscape (Conybeare, 2004; Guldemond and van Aarde, 2008; Kerley and Landman, 2006; Valeix et al., 2011). The primary reason for their negative effects on vegetation is that elephants require 100–200 kg of vegetation per day to meet their energetic needs and protein requirements (Guy, 1976; Osborn, 2004; Wyatt and Eltringham, 1974). In addition to the large quantities of vegetation that they consume, they can also be destructive foragers, often breaking, pushing over, or otherwise damaging trees (Midgley et al., 2005). While this destructive behaviour does create important habitat features for a host of other species, it can limit resources for other herbivores (Pringle, 2008).

Due to their impacts on the landscape, elephant populations have been subjected to drastic and invasive management techniques to limit local populations, including contraception, relocation, and culling (Kerley and Shrader, 2007; van Aarde et al., 1999; Whyte et al., 1998). Within Africa, protected areas are challenged to establish a balance between number of elephants and available resources. One approach to monitor and manage this issue is the use of carrying-capacity models for mammalian herbivores based on the available standing crop (biomass) in an area to predict the number of individuals that could be supported (e.g. Jones and Sandland, 1974; Hobbs and Swift, 1985). This has been done for a number of species, primarily grazers (Harlan, 1958; Jones and Sandland, 1974; Mott, 1960; Riewe, 1961; Sandland and Jones, 1975).

Many of the early models assume a simple linear relationship between live weight gain per animal or live weight gain per hectare and stocking rate (number of mammalian herbivores in an

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area) (Cowlishaw, 1969; Jones and Sandland, 1974; Riewe, 1961; Sandland and Jones, 1975). However, others suggest a more curvilinear relationship between live weight gain per animal or hectare and stocking rate (Owen and Ridgman, 1968). Most of these early models use live weight gain (per animal or hectare), a known relation of animal production, to predict optimum carrying capacity (Jones and Sandland, 1974). There are differing opinions as to which of these early theoretical models reflect the most accurate relationship between carrying capacity and animal gain (Jones and Sandland, 1974; Sandland and Jones, 1975).

Until the 1980s, there were very few carrying-capacity models that could be applied to wild herbivores. This was mainly because a corresponding number of Livestock Units (LU), an equivalent measure for all livestock based on their metabolic requirements, was never defined (Meissner, 1982). Meissner (1982) made one of the first attempts to form equivalent LUs for wild animals such as blesbok (*Damaliscus pygargus phillips*), buffalo (*Syncerus caffer*), zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), and elephants in an effort to more accurately predict carrying capacity based on metabolic requirements for each species and age-classes within each species. While this model was one of the first to include explicit values for wild animals, one key factor remained constant: all models assumed that foraging areas are homogenous in nutrient availability as well as nutrient utilization by animals. However, Hobbs and Swift (1985) incorporated explicit forage-quality values (e.g. nitrogen and metabolizable energy) into an optimal foraging model of carrying-capacity. The Hobbs and Swift (1985) model yielded a more precise representation of realized carrying capacity as a function of animal foraging choices and available nutrients. Forage quality and availability can vary both spatially and temporally, which can influence foraging animals' intake rates (Ungar and Noy-Meir, 1988) and selectivity (Sinclair and Gwynne, 1972). By incorporating site- and species-specific values of forage to a carrying-capacity model, Hobbs and Swift (1985) allowed for a more realistic estimate of what optimal carrying capacity should be for an area.

A problem that existed for the implementation of carrying-capacity models was that they were appropriate for grazers (eat grasses) only, which has posed issues when applied to browsers (eat woody plants such as trees and shrubs). In general, browsers encounter plants that have higher concentrations of protein than do grazers, which is beneficial for mammalian herbivores (Mattson, 1980; Van Soest, 1994). However, the woody plants that browsers feed on are generally quite well defended by secondary metabolites (i.e. not used for primary metabolism of the plant – Herms and Mattson, 1992). Grazers, on the other hand, usually encounter plants (grasses) with lower protein concentrations than woody plants but these plants are less well-defended by secondary metabolites than are woody plants (Chesselet et al., 1992). This often results in the failure of applying carrying-capacity models designed for grazers such as cattle and sheep to browsing mammals (i.e. because browsers encounter higher levels of secondary metabolites in their forage than do grazers). The reason for this problem with carrying-capacity models is that plant secondary metabolites (PSMs), especially tannins, typically reduce the amount of available nitrogen/crude protein in the forage (Robbins et al., 1991). As a result, grazing models applied to browsers and/or mixed-feeders typically overestimate carrying capacity because they assume that all nitrogen is available in browse material and thus generate substantially higher carrying-capacity estimates than can be realized in nature (Windels and Hewitt, 2011).

Windels and Hewitt (2011) developed a model based on the Hobbs and Swift (1985) model to predict the carrying capacity of browsers and mixed-feeders. In doing so, they took into account the amount of secondary metabolites in available browse species, which should improve carrying-capacity estimates. They found that by including the effects of plant secondary metabolites on protein and energy, their model yielded lower, and more realistic estimates of carrying capacity. While Windels and Hewitt's (2011) model produced plausible estimates of carrying capacity for white-tailed deer (*Odocoileus virginianus*) in Mexico, there is a challenge to their approach. This approach includes the need to assess the amount of non-protein nitrogen. The % crude protein is conventionally calculated by weighting nitrogen by 6.25 for each plant species. However, not all nitrogen is proteinaceous (Mattson, 1980). This is a fairly complex process and would most likely not be feasible for resource managers to conduct for all plant species eaten by specific herbivores.

A factor that has not been extensively explored in previous carrying-capacity models is the tannin-binding affinity of a browser's saliva. Many mammalian species have adapted to browsing on tannin-rich plant species via the production of salivary tannin-binding proteins (McArthur et al., 1991; Shimada, 2006). These salivary proteins bind to released tannins before the tannins can bind to nitrogen released from the digesting plant material, neutralizing some of the negative impacts of tannins (McArthur et al., 1991; Shimada, 2006). The tannin-binding affinity of saliva can vary among species (Clauss et al., 2005). Each animal species that frequently encounters tannins can neutralize different levels of tannins (Clauss et al., 2005). Thus, access to different proportions of nitrogen by browsers is species-dependent. This adjusted available nitrogen value would then influence the estimated carrying capacity of an area. As a result, we aim to explore the addition of this factor into a carrying-capacity model to examine if this yields a more precise representation of carrying capacity.

To generate an improved carrying-capacity model for elephants, we conducted an in-depth study of elephant foraging behaviour during the dry season. This is the most food-limiting season for mammalian herbivores due to low nutrient quality and lower food availability. Moreover, it is the critical period that determines how many animals an area can support sustainably (Coe et al., 1976; Owen-Smith, 2002b). Employing Hobbs and Swift's (1985) concept of incorporating explicit nutritional values, we used their model as a framework for our carrying-capacity model. We also focused on the negative effects of plant secondary metabolites (which Hobbs and Swift (1985) did not address) and the neutralization of these chemicals by the tannin-binding affinity of elephant saliva. In addition, our model includes diet breadth and dietary contribution of browsed species, browse quality, and the available standing crop of browsed species. We aimed to develop a tool that protected areas and conservation/management bodies would be able to implement. Due to the robustness of the model, it is not intended to be site-specific and potentially could be generalized for other large mammalian browsers.

2. Methods

Carrying-capacity models require a priori knowledge about foraging behaviour, including information about intake rate (g/day), plant species preference (proportion contribution), available nitrogen in each plant species eaten (forage quality) (g nitrogen/g dry matter), the available biomass of each plant species (g/ha), and the tannin-binding affinity of the saliva of the model's target species. To gather these data, we studied a population of semi-tame elephants near Bela Bela in the Limpopo province, South Africa. These six elephants (male: $N = 3$, female: $N = 3$) were between 10 and 20 years old during the duration of our study and ranged from ~2.2 to 3.5 tonnes in weight. None of the female elephants were pregnant or nursing nor were the males in musth. All observations were made during the winter dry season (June–August 2013), when the animals fed exclusively on browse, and did not graze.