Journal of Arid Environments 72 (2008) 2017–2025

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas?

Y. de Beer, R.J. van Aarde *

Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

A R T I C L E   I N F O

Article history:
Received 11 February 2008
Received in revised form
17 June 2008
Accepted 2 July 2008
Available online 13 August 2008

Keywords:
FRAGSTATS
Landscape metrics
Patchiness
Randomly located ranges
Water point density

A B S T R A C T

Elephants live in heterogeneous landscapes where their search for resources may increase individual survival. The uneven distribution of such resources may be linked to landscape heterogeneity. We therefore hypothesized that landscape heterogeneity determines elephant home range location and size in Etosha National Park, Khaudum Game Reserve and Ngamiland District 11. We used landscape maps to quantify landscape heterogeneity based on five metrics calculated using FRAGSTATS and compared these for elephant and randomly located ranges within the study areas. We further related elephant range size to the landscape metrics and water point density. The elephants located their home ranges in areas with relatively high Patch density, Landscape shape index and Shannon diversity index, and relatively low Largest patch index and Contagion. Elephants therefore seem to locate their home ranges in areas of the landscape where higher levels of heterogeneity occur during wet and dry seasons. Home range size decreased with increasing water point density and heterogeneity and water distribution influence elephant space utilisation. Management of elephants should therefore be directed at ensuring the inclusion of heterogeneous landscapes in conservation areas and at reconsidering water management policies that may influence home range sizes and landscape selection.

1. Introduction

Elephants roam across heterogeneous landscapes where they search for resources that may enhance their individual survival. Within the landscape, vegetation patches (homogenously vegetated areas that differ from the surrounding landscape) vary in their composition and spatial arrangement and this complexity represents landscape heterogeneity (Turner et al., 2001). Aspects of landscape heterogeneity can be measured through an assessment of patch characteristics. Hierarchy theory predicts that resource selection at smaller scales (i.e. plant parts or species) will cause an aggregate selection response at larger scales (O'Neill et al., 1986). The combination of preferred plant resources within vegetation patches may consequently elicit a selection response at the landscape level. Landscape heterogeneity may therefore benefit large herbivores through an increased stability of food resources (Illius and O'Connor, 1999). This may enhance their opportunities to achieve nutritional balance and to avoid toxin accumulation (Jachmann, 1989; Owen-Smith, 1988).

As large-bodied mixed feeders, elephants include low-quality plant matter in their diets (Owen-Smith, 1988). However, to maximise their energy intake there should be a trade-off between selection for scarce, high-quality resources and the

* Corresponding author. Tel.: +27 12 420 2753; fax: +27 12 420 4523.
E-mail addresses: ydebeer@zoology.up.ac.za (Y. de Beer), rjvaarde@zoology.up.ac.za (R.J. van Aarde).

0140-1963/$ - see front matter
doi:10.1016/j.jaridenv.2008.07.002

utilisation of lower quality resources that are presumably more abundant (Illius, 2006). Spatial and temporal variability in habitat quality can therefore influence individual fitness which, at the population level, shows up in demographic responses such as age-specific fecundity and survival (Sibly and Hone, 2003; Wang et al., 2006). During critical periods, such as the dry season, elephants may rely on 'key-resources' (e.g. Gaylard et al., 2003; Smit et al., 2007) that are sought after regardless of the spatial distribution of other resources (Illius, 2006). Water may be such a key-resource (see Harris et al., 2008).

The home range is expected to reflect the elephant's nutritional requirements (e.g. Schoener, 1981), especially for cows that are less restricted by social interactions than bulls (Owen-Smith, 1988). For elephants, nutritional constraints should be more pronounced as the dry season progresses. In theory, elephants are therefore expected to increase the size of their home ranges during the dry season to include the resources otherwise available during the wet season within smaller areas. Contradictory to this, elephants tend to concentrate their foraging activities in areas close to water during the dry season (Chamaillé-Jammes et al., 2007; de Beer et al., 2006; Gaylard et al., 2003; Leggett, 2006; Osborn and Parker, 2003; Redfern et al., 2003; Smit et al., 2007) and they then conceivably depend on lower quality food (Owen-Smith, 1988). The restriction imposed by the distribution of water as a 'key-resource' (see Illius, 2006) may therefore coincide with selection for areas with higher food resource availability within the landscape, which may consequently determine the location of elephant home ranges.

In our study, we hypothesized that landscape heterogeneity and water distribution are determinants of the location and size of elephant home ranges in arid savannas. The apparent selection for variables that are encapsulated by landscape heterogeneity metrics may explain the uneven distribution of elephants across landscapes as an outcome of their preferences for certain habitats. Moreover, by identifying how landscape heterogeneity and water distribution affects the spatial dynamics of elephants we may be able to predict how elephants will respond to areas in which they do not occur at present. This may facilitate initiatives to improve conservation management plans that incorporate aspects of landscape ecology (see Damschen et al., 2006; van Aarde and Jackson, 2007).

2. Materials and methods

2.1. Study region

The Etosha National Park, Khaudum Game Reserve and Ngamiland District 11 (henceforth, referred to as Etosha, Khaudum and NG11, respectively), occur within the arid to semi-arid savanna regions of southern Africa (see Sankaran et al., 2005). At the time of the study, Etosha was a fenced off conservation area that stretched over 22,270 km^2 in north-central Namibia. Khaudum extended over 3841 km^2 in north-eastern Namibia along part of the international border between Namibia and Botswana. The NG11 lay along the Okavango Panhandle in north-western Botswana and stretched over 4704 km^2 within a controlled hunting concession.

Situated along the 19°S latitude, annual rainfall generally increased from ~200 mm in the west (Etosha) to ~650 mm in the east (NG11). Rainfall in the region was erratic and annual rain fell mostly between November and April (Data provided by the Ministry of Environment and Tourism, Namibia; Meteorological Services, Botswana).

Mopane (*Colophospermum mopane*) woodlands dominated in Etosha (Lindeque, 1988). In Khaudum, *Burkea africana* and *Baikiaea plurijuga* woodlands on the sand dunes and *Terminalia sericea*, *Acacia* species and *Combretum* species in the inter-dune valleys characterised the patchy vegetation of the reserve (Weaver and Skyer, 2005). In NG11, mopane woodlands dominated along the panhandle but *Burkea africana* and *Baikiaea plurijuga* woodlands were also prominent within the area (Mendelsohn and el Obeid, 2004).

Elephant numbers in Etosha have remained relatively stable (~2000 elephants) since the 1980s (Etosha Ecological Institute, unpublished data). Since the provisioning of water in Khaudum, elephant numbers in the reserve increased rapidly from a guestimated 80 in 1976 to the present population in excess of 3000 (Weaver and Skyer, 2005). In NG11, 3579 elephants occurred during the 2003 dry season and 1060 during the 2004 wet season (Jackson et al., 2008).

2.2. Elephant home ranges

Home ranges were estimated from location data obtained from satellite GPS units that were fitted to adult cows living in different breeding herds in Etosha ($n = 6$), Khaudum ($n = 6$) and NG11 ($n = 4$). The GPS units (model AWT SM2000E) provided accuracy within 15 m (Ott, 2007) and GPS error was reduced by using kernel density estimates instead of the locations as individual points (Dussault et al., 1999).

Elephant home ranges were calculated for two dry (May–October) and two wet seasons (November–April) in each of the study areas using the Animal Movement extension (Hooge and Eichenlaub, 1997) of ArcView GIS 3.3 (ESRI, Inc. 2002). We used the 95% fixed kernel density estimate with least square cross validation (LSCV) smoothing (Börger et al., 2006; Seaman and Powell, 1996; Seaman et al., 1999). The minimum and maximum sample size for an elephant in this study was 49 and 178 locations, respectively.