ARTICLE

Seasonal variation in foraging behaviour of plains zebra (*Equus quagga*) may alter contact with the anthrax bacterium (*Bacillus anthracis*)

Zepee Havarua, Wendy C. Turner, and John K.E. Mfune

Abstract: Pathogens transmitted via the environment are often aggregated in space, and seasonal variation in wildlife foraging behaviour may alter contact rates with environmental pathogens. The soil-borne bacterium *Bacillus anthracis* Cohn, 1872 causes anthrax, and herbivores acquire gastrointestinal anthrax by ingesting spores. Therefore host foraging behaviour could be a fundamental component of anthrax epidemiology. This study investigated seasonal changes in bite density and diet of plains zebras (*Equus quagga* Boddaert, 1785) in relation to anthrax seasonality in Etosha National Park, Namibia, where most zebra anthrax cases are observed in wet seasons. The diet of zebras shifted from more short grasses during the wet season to more tall grasses in the dry season, suggesting a greater potential for soil ingestion in wet seasons. Zebras also foraged most intensively in the wet season with the number of bites/step declining through the dry season. This higher bite density in wet seasons may lead individuals to ingest greater concentrations of the pathogen if foraging in a localized infectious area. Although sex and reproductive state affected bite density, no sex difference in anthrax occurrence was observed. This study demonstrates how considering variation in host foraging behaviour may enhance our understanding of disease seasonality for pathogens with foraging-dependent transmission.

Key words: *Bacillus anthracis*, disease transmission, Etosha National Park, *Equus quagga*, foraging ecology.

Résumé : Les pathogènes transmis par l'intermédiaire du milieu sont souvent concentrés dans l'espace, et les variations saisonnières du comportement d'alimentation des animaux sauvages peuvent modifier les taux de contact avec des pathogènes de l'environnement. La bactérie du sol *Bacillus anthracis* Cohn, 1872 cause le charbon, et les herbivores contractent le charbon gastro-intestinal en ingérant des spores. Le comportement d'alimentation de l'hôte pourrait donc être un élément fondamental de l'épidémiologie du charbon. L'étude s'est penchée sur les variations saisonnières de la densité de coups de mâchoire et du régime alimentaire des zèbres des plaines (*Equus quagga* Boddaert, 1785) et leur relation avec la saisonnalité du charbon dans le parc national d'Etosha (Namibie), où la plupart des cas de charbon chez les zèbres sont observés durant les saisons humides. Le régime alimentaire des zèbres passait d'une plus grande abondance d'herbes courtes durant la saison humide à plus d'herbes hautes durant la saison sèche, ce qui se traduirait par un plus grand potentiel d'ingestion de sol durant les saisons humides. L'alimentation des zèbres était en outre plus intense durant la saison humide, le nombre de coups de mâchoire/de pas diminuant au fil de la saison sèche. La densité accrue de coups de mâchoire durant les saisons humides pourrait mener les individus à ingérer de plus grandes concentrations du pathogène s'ils s'alimentent dans une zone infectée. Bien que le sexe et l'état reproducteur aient une incidence sur la densité de coups de mâchoire, aucune différence entre les sexes n'a été observée en ce qui concerne la fréquence du charbon. L'étude démontre comment la prise en considération des variations du comportement d'alimentation des hôtes peut améliorer la compréhension de la saisonnalité des maladies pour les pathogènes dont la transmission dépend de l'alimentation. [Traduit par la Rédaction]

Mots-clés : *Bacillus anthracis*, transmission de maladies, parc national d'Etosha, *Equus quagga*, écologie de l'alimentation.

Introduction

Long-lived pathogens that are transmitted via the environment are often aggregated in space (e.g., *Bacillus anthracis* Cohn, 1872 causing anthrax: Dragon et al. 2005; prion PrP^Sc causing chronic wasting disease: Saunders et al. 2012). However, the mechanisms through which wildlife hosts contact these pathogens are often poorly understood. Here, we explore the role of herbivore foraging behaviour in influencing seasonal variation in contact with the anthrax bacterium. Anthrax is a highly virulent zoonotic disease in livestock and wildlife that occurs nearly worldwide (WHO 2008). Immunization has led to a global decline in livestock anthrax cases in many parts of the world, but anthrax remains enzootic in many national parks and game-ranching areas (Hugh-Jones and de Vos 2002). In herbivores, transmission is thought to be through the gastrointestinal or inhalational route (WHO 2008). However, it is generally assumed that herbivores acquire gastrointestinal an-

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thrax by ingesting *B. anthracis* spores together with food or water (Turner et al. 2013). Large experimental lethal doses for gastrointestinal anthrax (10^7–10^8 spores in herbivores; WHO 2008) imply that animals must ingest large quantities of spores to induce a fatal infection. Although water sources have been found to contain *B. anthracis* (Ebedes 1976), animals are unlikely to ingest a lethal dose of spores from the relatively low quantities of *B. anthracis* found in water samples (Lindeque and Turnbull 1994). These studies suggest that anthrax transmission in herbivores is primarily via forage ingestion, and thus forging ecology may play an important role in the seasonality of anthrax.

Many infectious diseases, including anthrax, exhibit seasonality (Altizer et al. 2006; Turner et al. 2013), and forage resources also fluctuate seasonally (Owen-Smith 2002). If the timing of transmission depends upon foraging ecology, then fluctuations in resources may create predictable variability in foraging behaviour which affects the transmission of *B. anthracis* to susceptible hosts. In our study system of Etosha National Park, Namibia, sporadic anthrax cases are observed throughout the year, with a peak in incidence occurring during the late wet season (Lindeque and Turnbull 1994; Beyer et al. 2012; Turner et al. 2013).

Although a link between foraging behaviour and anthrax seasonality has been suggested for several different locations (Dragon and Rennie 1995; Wafula et al. 2008), no studies have yet evaluated the seasonality of host foraging ecology and whether the timing of "riskier" foraging behaviours for anthrax transmission relates to the timing of disease outbreaks. Where foraging behaviour has been suggested to be an important risk factor in anthrax outbreaks, this has generally been under dry conditions, either from wilting of vegetation forcing animals to graze closer to the soil (Dragon and Rennie 1995; Wafula et al. 2008) or from ingestion of dry, spiky vegetation that may cause lesions in the gastrointestinal tract (Beyer and Turnbull 2009; Hugh-Jones and Blackburn 2009; WHO 2008). Grazing of wilted grasses close to the soil surface may have contributed to the timing of anthrax outbreaks during the dry season in American bison (*Bison bison* (L., 1758)) in Wood Buffalo National Park, Canada (Dragon and Rennie 1995), and in hippopotamus (*Hippopotamus amphibius* L., 1758) in Queen Elizabeth National Park and Mburo National Park in Uganda (Wafula et al. 2008). However, foraging as a risk factor is not only important during dry or drought conditions; Wafula et al. (2008) noted that an anthrax outbreak in plains zebra in Queen Elizabeth National Park occurred when zebra were foraging on lush green grasses at the beginning of the rains. In general, contact with *B. anthracis* from the soil is more likely to occur when an herbivore forages close to the soil surface than when it feeds on taller vegetation.

We investigated how seasonal changes in foraging ecology relate to the seasonal timing of anthrax infections in plains zebra (*Equus quagga* Boddaert, 1785). In particular, we examined seasonal differences in zebra diet composition and bite density. Since the location of all previous anthrax carcasses in the landscape cannot be known, we do not examine foraging specifically in relation to carcass sites, but instead examine general aspects of foraging behaviours that may alter the risk of exposure. Although there is increasing evidence that *B. anthracis* may be active outside of mammalian hosts (Saile and Koehler 2006; Schuch and Fischetti 2009; Dey et al. 2012), there is not yet evidence that the quantities of spores in the environment fluctuate seasonally. Therefore, we assume that spore abundance in the soil does not vary seasonally and that any differences in exposure will be due to host behavioural changes.

With seasonal shifts in diet selection, herbivores are likely to experience different levels of risk of contacting soil-borne pathogens depending on which foods are selected. This may be particularly true for mixed-feeding herbivores that have dramatic shifts in the species consumed, from primarily grazing to browsing in different seasons. What may be less apparent, however, is the contribution of foraging behaviour to exposure risk for herbivore species that graze throughout the year, such as the plains zebra. Although grass biomass may be lower during dry than wet seasons, zebras may feed closer to ground level during wet seasons if feeding on short, nutritious grasses than during dry seasons if they shift to consuming higher biomass, tall-grass species. To determine if zebras feed on shorter vegetation during the anthrax season than in other seasons, we recorded the species consumed by zebras in different seasons. We hypothesize that grazing closer to the ground surface may put zebras at higher risk of exposure to *B. anthracis* in the soil during wet seasons than dry seasons. This hypothesis is consistent with recent work showing that zebras ingest more soil per day in wet seasons than in dry seasons (Turner et al. 2013).

Lethal doses of *B. anthracis* for herbivores are known to be high and such high concentrations of *B. anthracis* spores are only likely to be encountered at sites of previous anthrax mortalities (Lindeque and Turnbull 1994; Dragon et al. 2005). Carcasses create nutrient hotspots (Towne 2000; Bump et al. 2009) and nutrient hotspots attract herbivores (Ben-Shahar and Coe 1992; Grant and Scholes 2006). When an herbivore encounters a site that previously had an anthrax carcass, the probability that the individual contacts a lethal dose of *B. anthracis* will depend upon its behaviour while in the infectious area. In general, abundant, green, and nutritious vegetation may allow grazers to forage more intensively at high nutrient sites and in the wet season, which could lead to foraging-based seasonal differences in pathogen exposure when foraging at a carcass site. We examine seasonal differences in zebra bite density, defined as the number of bites taken per step, and consider how higher bite densities may influence contact with a spatially aggregated pathogen such as *B. anthracis*. We recorded bite density at a spatial and not temporal scale (i.e., per unit step and not time), given that the area of contamination at a carcass site is quite localized, covering only a few metres around where the carcass was located (Dragon et al. 2005). We explore how seasonal differences in bite density and diet selection of zebras may relate to the wet season timing of anthrax outbreaks in Etosha National Park.

Materials and methods

Study area

The study was conducted in central Etosha National Park, Namibia, in Okaukuejo and Halali, two neighbouring management sections, from December 2009 to November 2010. Three seasons are recognized in Etosha: hot, wet (November–April); cool, dry (May–July); hot, dry (August–October) (le Roux et al. 1988). The mean annual rainfall for Okaukuejo was 369 mm and for Halali it was 424 mm from 1966 to 2011 (Etosha Ecological Institute (EEI) rainfall records). Etosha's vegetation varies from dwarf shrub savanna and grasslands, which occur around extensive salt pans, to thorn-bush and woodland savanna, with much of the park covered with mopane (*Colophospermun mopane* (Kirk ex Benth.) Kirk ex J. Léonard) trees and shrubs. The dominant grasses in the study area are *Enneapogon desvauxii*, *Aristida adscensionis*, *Eragrostis nindensis*, *Eragrostis porosa*, *Chloris virgata*, *Urochloa brachyura*, *Eragrostis echinochloidea*, *Tragus racemosus* (L.) All., and *Monelytrum luederitzianum*, and the dominant dwarf shrubs are *Leucosphaera bainesii*, *Cyathula hereroensis* = *Cyathula lanceolata*, *Monechma tonsum*, *Monechma genistifolium*, and *Petalidium englerianum* (le Roux et al. 1988). Plains zebra are the main anthrax host species in Etosha, representing over 50% of all recorded anthrax mortalities (Turner et al. 2013). Grazers and mixed feeders form 98.3% of all confirmed anthrax cases in the park, while browsers make up only 1.7% of the total cases (EEI mortality records 1976–2010).

Fig. 1. Number of confirmed anthrax cases (caused by the bacterium *Bacillus anthracis*) by sex in adult plains zebras (*Equus quagga*) from 1974 to 2010, observed in the three seasons (hot, wet season: November–April; cool, dry season: May–July; hot, dry season: August–October).
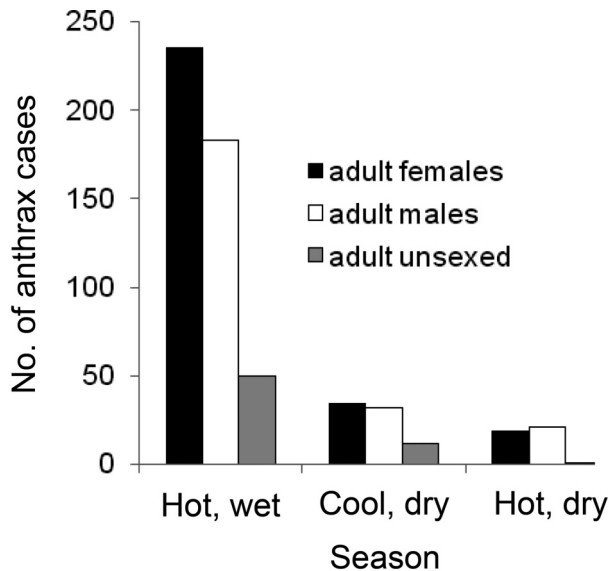
than the hot, dry season ($t_{[235]} = -5.381$, $P = <0.001$; Fig. 2). Time of day, temperature, and vegetation type had no significant effect on the number of bites/step taken by zebras when season was included in the model (time of the day: $F_{[1,359]} = 0.093$, $P = 0.759$; temperature: $F_{[1,359]} = 0.119$, $P = 0.730$; vegetation: $F_{[4,359]} = 1.720$, $P = 0.162$). Temperature was significantly related to the number of bites/step if the variable season was not included in the model ($F_{[1,359]} = -1.675$, $P < 0.001$). Either variable could be used to describe seasonal variation in the number of bites/step; however, this study was designed around specific seasons and thus the variable season was retained in the model and the variable temperature was removed. There was no significant difference in the number of bites/step taken by males and nonlactating females (males: $n = 146$; nonlactating females: $n = 92$; $t_{[236]} = 1.462$, $P = 0.067$; Fig. 2). However, lactating females took significantly more bites/step than nonlactating females (lactating females: $n = 122$; $t_{[212]} = 1.026$, $P = 0.023$; Fig. 2).

Diet composition of zebra

Twenty-five different plant species (19 grass species: Table 1; 6 woody shrub species: Table 2) were recorded in the diet of zebras. Two short-grass species, *Enneapogon desvauxii* and *Eragrostis nindensis*, were the most commonly grazed grass species throughout the year. Comparing consumption of short to tall grasses, zebra consumed short grasses significantly more often in the wet season than in the dry seasons ($\chi^2_{[2]} = 23.0$, $P < 0.001$; Fig. 3). Tall-grass species like *Urochloa brachyura*, *Chloris virgata*, *Setaria verticillata*, *Enneapogon cenchroides*, *Monelytrum luederitzianum*, and *Cenchrus ciliaris* were consumed in all seasons, but their consumption increased in the dry season along with other tall-grass species such as *Fingerhutia africana* and *Heteropogon contortus*, which were not consumed during the hot, wet season (Table 1). The contribution of woody shrubs to zebra diet did not differ significantly among seasons ($\chi^2_{[2]} = 1.21$, $P = 0.546$; Fig. 3).

Discussion

Anthrax is an ancient disease documented since biblical times and was the first disease attributed to a microorganism (Schwartz 2009). Despite being a disease long known to humans, the role of host behavioural traits in anthrax transmission has remained cryptic. This study assessed whether seasonal variation in zebra foraging behaviour could affect exposure to anthrax, a soil-borne pathogen. For both foraging measures examined in this study (i.e., bite density and diet selection), seasonal variation in foraging behaviour pointed towards higher exposure to *B. anthracis* during wet seasons—the season of peak anthrax mortality for zebra in Etosha. These results are supported by studies showing that zebras ingest more soil per day (Turner et al. 2013) and are more likely to have an anti-anthrax antibody titre (Cizauskas et al. 2014) during wet seasons than during dry seasons. Although our study does not provide definitive proof that foraging behaviours are linked to anthrax seasonality, taken together, these seasonal correlations are strongly suggestive of a role of foraging ecology in exposure to *B. anthracis*.

Foraging behaviour

Zebras foraged more intensively in the wet season, consuming more bites of grass for each step taken while foraging than in the dry seasons. Increasing bite density when available biomass and quality are at a peak and seasonal water is readily available maximizes forage intake while allowing more time for reproductive and vigilance activities, since parturition and mating both peak in the wet season (Brooks and Harris 2008).

Lactating females took significantly more bites/step than males or nonlactating females (Fig. 2), which is in accordance with previous research on zebra during the wet season (Neuhaus and Ruckstuhl 2002). Specific nutrient demands of lactation may drive lactating females to increase their bite density and to seek forage of higher quality than males and nonlactating females. While lactating females of some species may compensate by reducing metabolic expenditures (e.g., by reducing locomotor activities: Miller et al. 2006; fasting: Mellish et al. 2000; entering periodic torpor: Racey and Speakman 1987) or by increasing metabolic efficiency (Mellish et al. 2000), females of most species are expected to increase nutrient intake during lactation (Bunnell and Gillingham 1985).

In our study, the diet of zebra was dominated by two short-grass species, *Enneapogon desvauxii* and *Eragrostis nindensis* (Table 1). Zebra diet shifted from a higher proportion of short-grass species in the wet season to a higher proportion of tall-grass species in the dry season (Fig. 3), a finding in accordance with recent work on zebra diet selection in Hluhluwe-iMfolozi Park, South Africa (Arsenault and Owen-Smith 2011). This dietary shift may represent a survival strategy for zebras to achieve their nutrient requirements in dry seasons by consuming larger quantities of poorer quality, more available forage than to seek higher quality, sparsely available forage (Arsenault and Owen-Smith 2011).

Foraging and anthrax seasonality

Bacillus anthracis concentrations in the environment are highly localized around carcass sites (Lindeque and Turnbull 1994; Dragon et al. 2005). If carcass sites serve as the primary source of lethal infections, then the probability that an herbivore contracts anthrax depends, among other factors, on the timing and frequency of its encounters with anthrax carcass sites and its behaviour while at these sites. Animal carcasses create intensive localized nutrient pulses that can affect soil fertility and vegetation quality for multiple years following death (Towne 2000; Bump et al. 2009). Herbivores have a well-defined spatial awareness of patch location and can orient their movements towards high-quality patches within a landscape of heterogeneous sward resources (Shipley et al. 1996; Brooks and Harris 2008). Linking foraging behaviours to carcass sites assumes that herbivores are not deterred from feeding at carcass sites as a result of visual or olfactory cues from the carcass. Anecdotal evidence suggests that herbivores do indeed feed at carcass sites (Towne 2000), an observation supported by findings that zebras preferentially graze at anthrax carcass sites compared with nearby control grassland sites, a

Fig. 2. Number of bites/step taken by adult female and male plains zebras (*Equus quagga*) while foraging in different seasons. Female zebras are separated by reproductive status into those that were lactating or not lactating. Numbers above bars indicate sample size. Values are presented as means ± SE.
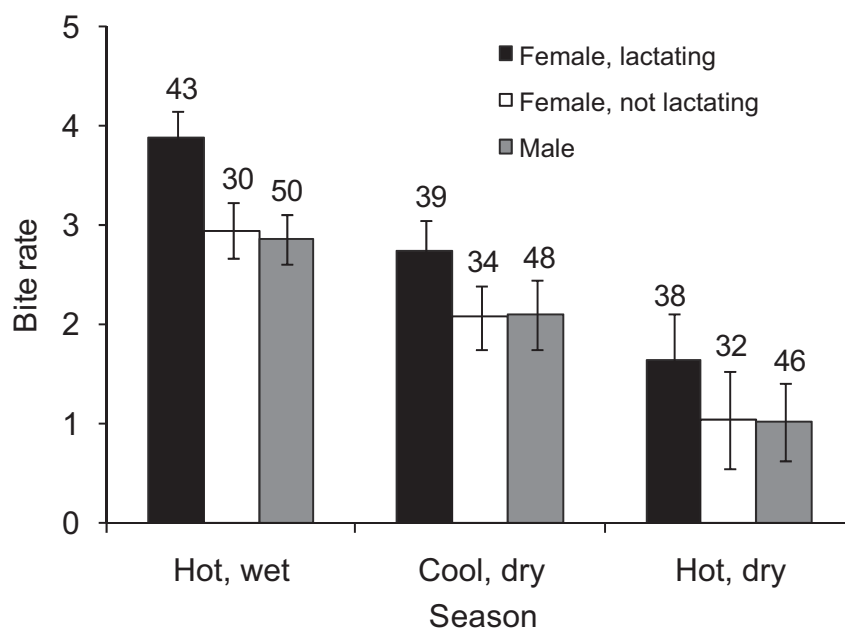

Table 1. Grass species consumed by plains zebras (*Equus quagga*) in Etosha National Park, Namibia, presented as percentages of total grass selection in each season.

Grass species	n	Percent consumed per season			Grass classification
		Hot, wet	Cool, dry	Hot, dry	
Anthephora schinzii Hack.	12	2.5	4.6	2.5	Short
Aristida adscensionis L.	12	1.7	3.1	5.4	Tall
Aristida congesta Roem. & Schult.	13	0.8	3.8	5.9	Short
Cenchrus ciliaris L.	25	10.5	6.1	4.5	Tall
Chloris virgata Sw.	20	3.3	7.7	6.7	Tall
Enneapogon cenchroides (Licht. ex Roem. & Schult.) C.E. Hubb.	20	5.0	3.5	6.5	Tall
Enneapogon desvauxii P. Beauv.	79	29.0	23.8	11.5	Short
Eragrostis echinochloidea Stapf	10	1.7	0.8	5.8	Tall
Eragrostis nindensis Ficalho & Hiern	34	17.1	11.5	7.7	Short
Eragrostis porosa Nees	23	4.1	7.6	7.5	Tall
Eragrostis sabinae Launert	10	5.0	2.3	0.8	Short
Eragrostis trichophora Coss. & Durieu = *Eragrostis cylindriflora* Hochst.	9	3.3	1.1	2.5	Tall
Fingerhutia africana Lehm.	9	0.0	0.8	5.8	Tall
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.	7	0.0	1.5	4.2	Tall
Monelytrum luederitzianum Hack.	11	1.7	2.3	5.0	Tall
Setaria verticillata (L.) P. Beauv.	13	2.5	7.2	6.2	Tall
Tragus Haller	8	3.3	2.3	1.2	Short
Triraphis purpurea Hack.	7	2.5	0.8	2.8	Short
Urochloa brachyura (Hack.) Stapf	28	6.0	9.2	7.5	Tall

Note: *n* is the total number of times the plant species was observed being consumed. Sampling months for the hot, wet season were March–April, for the cool, dry season were May–June, and for the hot, dry season were August–September. Grass species are classified as tall (>50 cm) or short (<50 cm) based on the height of the mature plant (measurements based on Müller 2007).

pattern which is strongest the first year after death (W.C. Turner. unpublished data).

If a foraging herbivore enters a vegetated carcass site, the chance of exposure to a lethal *B. anthracis* infection will depend in part upon its bite density while in the infectious area. All else being equal, an animal that takes more bites/step is more likely to contact *B. anthracis* at a carcass site than one that takes fewer bites/step and quickly passes out of the infectious area. We found that zebras take, on average, 3.5 bites/step while foraging in the wet season compared with 1.8 bites/step in the hot, dry season. The area of contamination around an anthrax carcass site is quite

localized, at approximately 7 m × 7 m (from two carcass sites sampled for spatial variation in *B. anthracis* distribution: Dragon et al. 2005). Although zebra step lengths while foraging have not been published, if we assume an equal step length in either season, then from our bite rates zebras would take nearly twice as many bites if foraging in a contaminated area in the wet season than in the dry season. An assumption of equal step length across seasons may not be credible, although if zebra step length differed between seasons, we hypothesize that step lengths would increase with decreasing food availability in the dry season. If this hypothesis holds, then seasonal differences in step length would

Table 2. Percentage of woody shrub species consumed by plains zebras (*Equus quagga*) in Etosha National Park, Namibia, in each season presented relative to total shrub selection per season.

Shrub species	*n*	Percent consumed per season		
		Hot, wet	Cool, dry	Hot, dry
Catophractes alexandri D. Don	20	23.4	23.5	24.1
Cyathula hereroensis Schinz = *Cyathula lanceolata* Schinz	10	12.1	13.2	15.3
Leucosphaera bainesii (Hook. f.) Gilg	17	38.5	39.0	43.0
Monechma genistifolium C.B. Clarke	8	12.2	12.0	3.3
Monechma tonsum P.G. Mey.	6	4.4	2.3	3.3
Petalidium englerianum (Schinz) C.B. Clarke	8	9.4	10.0	11.0

Note: *n* is the total number of times the plant species was observed being consumed. Sampling months for the hot, wet season were March–April, the cool, dry season were May–June, and the hot, dry season were August–September.

Fig. 3. Diet composition of plains zebras (*Equus quagga*). Percentages are shown for short grass species (<50 cm) and tall grass species (>50 cm) based on the height of the mature plant (measurements based on Müller 2007), and for shrub (woody) species recorded in zebra diet.
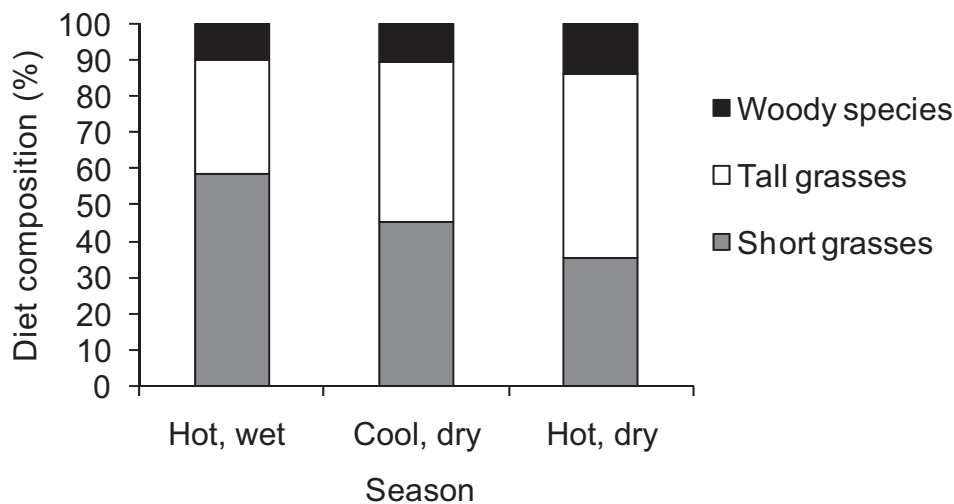
further enhance seasonal differences in potential foraging-based contacts with the anthrax bacterium while feeding at a carcass site.

The higher bite rates and preference for short grasses observed in the wet season may put zebra at a higher risk of contact with soil-borne pathogens with a higher chance to ingest a lethal dose of *B. anthracis* spores while foraging. This is supported by recent evidence that zebras ingest more soil in wet than dry seasons (Turner et al. 2013). In combination, the seasonal variation in zebra bite density and diet selection suggest a greater risk of contacting *B. anthracis* during wet seasons, which is in accordance with observed mortality patterns in Etosha (Fig. 1).

Adult males are often more likely to die of anthrax than adult females (WHO 2008). A male bias in disease risk is a pattern seen for a variety of pathogens, because of reproductive stressors leading to increased susceptibility of males and (or) behavioural differences between males and females in exposure (Zuk and McKean 1996). The greater bite density for lactating females compared with other adults could indicate that lactating females have a higher risk of exposure to *B. anthracis* while foraging than males or nonlactating females. However, we found no significant difference in anthrax mortalities between male and female zebra in Etosha. Any increased exposure risk for lactating females may be offset by a higher susceptibility of males, or the bite density differences observed between lactating females and other adults may not be sufficient to create observable differences in exposure risk between the sexes. Since mortalities were not classified by female reproductive status, we could not evaluate an effect of lactation status on anthrax risk for females.

A role for foraging in the timing of anthrax outbreaks has been previously suggested, particularly in regards to dry season an-

thrax outbreaks, as a result of herbivores feeding on wilted or dry and spiky vegetation (Dragon and Rennie 1995; WHO 2008; Beyer and Turnbull 2009; Hugh-Jones and Blackburn 2009). This study has demonstrated that it is not just foraging conditions that may be relevant to anthrax transmission, but that variation in foraging behaviour, in particular diet selection, may also alter seasonal exposure to soil-borne pathogens such as *B. anthracis*. In addition to anthrax, an ecological examination of animal foraging behaviour may aid our understanding of disease dynamics for a variety of other pathogens and parasites that have foraging-dependent transmission rates (e.g., strongyle nematodes, *Clostridium botulidium* van Ermengem, 1896, ticks, fungal spores; Hall et al. 2007).

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