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Journal

Proceedings of the Royal Society B, 281(1795)

ISSN

0962-8452

Authors

Turner, Wendy C
Kausrud, Kyrre L
Krishnappa, Yathin S
et al.

Publication Date

2014-11-22

DOI

10.1098/rspb.2014.1785

Peer reviewed

PROCEEDINGS OF THE ROYAL SOCIETY B

rspb.royalsocietypublishing.org

Research

Cite this article: Turner WC *et al*. 2014 Fatal attraction: vegetation responses to nutrient inputs attract herbivores to infectious anthrax carcass sites. *Proc. R. Soc. B* **281**: 20141785. http://dx.doi.org/10.1098/rspb.2014.1785

Received: 20 July 2014
Accepted: 1 September 2014

Subject Areas:
ecology, health and disease and epidemiology, behaviour

Keywords:
anthrax, camera traps, disease transmission, foraging ecology, host–pathogen contact, parasite avoidance

Author for correspondence:
Wendy C. Turner
e-mail: wendycturner@gmail.com

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2014.1785 or via http://rspb.royalsocietypublishing.org.

Royal Society Publishing

Fatal attraction: vegetation responses to nutrient inputs attract herbivores to infectious anthrax carcass sites

Wendy C. Turner[1,2], Kyrre L. Kausrud[1], Yathin S. Krishnappa[1], Joris P. G. M. Cromsigt[3,4], Holly H. Ganz[2,5], Isaac Mapaure[6], Claudine C. Cloete[6,8], Zepee Havarua[7], Martina Küsters[9], Wayne M. Getz[2,10] and Nils Chr. Stenseth[1]

[1]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, PO Box 1066 Blindern, Oslo 0361, Norway
[2]Department of Environmental Science, Policy and Management, University of California, 137 Mulford Hall, Berkeley, CA 94720-3112, USA
[3]Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Skogsmarksgränd, Umeå 90183, Sweden
[4]Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth, South Africa
[5]Genome Center and Department of Evolution and Ecology, University of California, Davis, CA, USA
[6]Department of Biological Sciences, Faculty of Science, and [7]Department of Animal Science, Faculty of Agriculture and Natural Resources, University of Namibia, Private Bag 13301, Windhoek, Namibia
[8]Etosha Ecological Institute, Ministry of Environment and Tourism, Etosha National Park, PO Box 6, Okaukuejo, Namibia
[9]Berkeley Etosha Anthrax Research Project, Swakopmund, Namibia
[10]School of Mathematical Sciences, University of KwaZulu-Natal, Private Bag X54001, Durban 4000, South Africa

Parasites can shape the foraging behaviour of their hosts through cues indicating risk of infection. When cues for risk co-occur with desired traits such as forage quality, individuals face a trade-off between nutrient acquisition and parasite exposure. We evaluated how this trade-off may influence disease transmission in a 3-year experimental study of anthrax in a guild of mammalian herbivores in Etosha National Park, Namibia. At plains zebra (*Equus quagga*) carcass sites we assessed (i) carcass nutrient effects on soils and grasses, (ii) concentrations of *Bacillus anthracis* (BA) on grasses and in soils, and (iii) herbivore grazing behaviour, compared with control sites, using motion-sensing camera traps. We found that carcass-mediated nutrient pulses improved soil and vegetation, and that BA is found on grasses up to 2 years after death. Host foraging responses to carcass sites shifted from avoidance to attraction, and ultimately to no preference, with the strength and duration of these behavioural responses varying among herbivore species. Our results demonstrate that animal carcasses alter the environment and attract grazing hosts to parasite aggregations. This attraction may enhance transmission rates, suggesting that hosts are limited in their ability to trade off nutrient intake with parasite avoidance when relying on indirect cues.

1. Introduction

Factors that affect host foraging ecology can be fundamental to disease dynamics, by regulating parasite transmission [1]. For a variety of host–parasite systems, hosts are infected with parasites by ingesting free-living parasite stages along with food or are parasitized while foraging. Where parasites can be detected, these parasite-inhabited locations can be avoided by foraging hosts, and anti-parasite behaviours can have a similar or greater effect on animal foraging patterns than anti-predator behaviours [2–4]. In fact, behavioural avoidance of parasite exposure can be more important than immunity in reducing infection in a population [5]. If parasites cannot be detected directly, as is likely to be the case for microparasites and many macroparasite larvae, hosts must rely on parasite-associated cues to avoid parasite infection. Faecal matter

is an important cue for the potential presence of parasites with faecal–oral transmission, and how faeces affects herbivore foraging decisions and parasite risk has been extensively studied (e.g. [6–10]). Given that faeces can have a positive effect on nutrients available to vegetation, herbivores face a trade-off between nutrient acquisition and parasite exposure when foraging near faeces-contaminated patches [9,11]. Analogous to faeces, animal carcasses represent detectable potential sources of parasites and nutrients in the environment, yet no studies have assessed herbivore foraging responses to carcass sites and what role these may have in disease transmission.

Foraging is often heterogeneously distributed across a landscape. At smaller scales, nutrient hotspots—characterized by increased levels of nitrogen, phosphorus and several important minerals [12]—spatially concentrate mammalian herbivores in grazing systems [13]. Such nutrient hotspots have been connected to abiotic heterogeneity, such as volcanic soil and catenal effects [12,14], as well as biotic drivers, such as nutrient concentration by herbivores [15,16]. Animal carcasses are important biotic agents that create localized nutrient pulses while at the same time aggregating parasites in the environment. Carcasses can create nutrient hotspots that can persist for several years, altering soil fertility and vegetation response [17–19]. However, it has yet to be determined how herbivores respond to these hotspots, including whether lingering visual or olfactory cues from a carcass serve as a deterrent to herbivores or if these nutrient-rich sites eventually become preferred foraging locations. In selecting carcass-generated nutrient hotspots, herbivores face a trade-off between increased nutrient intakes and a risk of infection by environmental parasites. Avoidance of or attraction to carcass sites, and the relative time scales of these behaviours, may strongly influence parasite transmission rates to susceptible individuals.

We evaluated herbivore behavioural responses to carcass-mediated nutrient hotspots and how these may affect host–parasite contacts over a 3-year period, in a guild of mammalian herbivores in Etosha National Park (Namibia) that succumb to the bacterial pathogen *Bacillus anthracis* (BA). BA is the causative agent of anthrax, a virulent disease that can kill herbivorous hosts within two weeks of a lethal exposure [20] (although sublethal exposures do occur [21]). BA is an environmentally transmitted pathogen that forms hardy spores, which can persist for years in the environment [22]. The environmental persistence of BA has long been associated with soil properties, weather and climate characteristics (e.g. [23]), and more recently with interactions with invertebrates and microbiota [24,25]. However, factors affecting parasite survival only represent one part of host–parasite contacts. The other part, which in grazing herbivores has been poorly studied, is how, where and when mammalian hosts contact BA in the environment.

Anthrax is endemic in Namibia and considered part of the natural ecosystem in Etosha National Park, allowing for ecological studies of this host–parasite relationship that could not be conducted in areas where outbreaks are managed and carcass sites decontaminated. We conducted a longitudinal study at marked plains zebra (*Equus quagga*) carcass sites from 2010 to 2013, to assess the effect and duration of (i) carcass nutrients on soil fertility, grass quality and grass biomass, (ii) BA concentrations on grasses and in soil at anthrax carcass sites, and (iii) herbivore presence and foraging activity at anthrax carcass and non-carcass grassland control sites using motion-sensing camera traps.

2. Material and methods

(a) Study area and carcass site selection

This study was conducted in Etosha National Park, Namibia, a semi-arid savannah with seasonal rains falling primarily between November and April (detailed description of study area in [26]). The years of study represent the range of rainfall values in central Etosha, with one of the highest rainfalls on record (2011: 705 mm), average rainfall years (2010: 390 mm and 2012: 378 mm) and a drought year (2013: 222 mm). Anthrax cases in Etosha are recorded annually, with a peak in the cases occurring towards the end of the rainy season (March–April) [22,26].

We focused on adult zebra (2+ years old) carcass sites, because most anthrax cases observed in Etosha are in zebras [22,26], and to standardize carcass body size and its nutrient influence at observed sites (details in the electronic supplementary material; typical carcass site shown in figure 1). In total, 43 carcass sites were selected to assess carcass nutrients, BA concentrations or herbivore foraging. Carcass sites for the nutrient study ($n = 8$) were all sites that tested negative for BA, to protect human health during sampling and analysis. Anthrax-positive carcass sites were used for camera traps ($n = 13$) and for BA sampling ($n = 21$). These sites were spread over a 300 km^2 area in central Etosha (electronic supplementary material, figure S1), with the mean minimum distances between neighbouring sites of 4.7 km for the nutrient study, 4.5 km for the camera study and 2.0 km for the BA study.

(i) Carcass effects on soil and grasses

Carcass sites for the nutrient study included six formed in 2010 and one each in 2011 and 2012 (month of death from January to June). Sites were sampled once per year at the end of the growing season (late March/early April) to evaluate the effect of the carcass on soil nutrients and grass quality and biomass. Samples were not collected in the year of death, only the following years, to have one full growing season for grasses to respond to carcass nutrients. Sampling occurred in 2011–2013 and individual sites were sampled up to three times.

Vegetation samples at carcass sites were collected from three sampling zones radiating out from the marking stake: 0–3 m, 3–6 m and 6–9 m (electronic supplementary material, figure S2). The 0–3 m sampling zone represents the location of highest disturbance where most carcass fluids were deposited. Vegetation harvesting for plant biomass was conducted along two transect lines oriented 180° apart. Plant quadrats (80 × 80 cm) were placed in the centre of each sampling zone along the transect lines and all above-ground plant biomass was harvested. Grass biomass estimates for each sampling zone are averages of the two replicate quadrats. Soil cores of 10 cm in depth were collected at the centre of the site near the marking stake (0 m; centre of the digesta pile) and in the centre of each of the plant sampling zones in four directions radiating out from the carcass sites (electronic supplementary material, figure S2). All soil samples from one sampling zone were pooled for analysis. Dry weights of clipped grass samples (leaves, stems and inflorescences) were recorded from each quadrat and grasses were analysed for percentage nitrogen, while soil samples were analysed for percentage nitrogen, pH, organic matter, P, K, Mg, Ca and Na (see the electronic supplementary material for details). Grass nitrogen was only assessed for the 2010 sites, 1 and 2 years after death; grass biomass in the drought year (2013) was insufficient for protein analyses.

(ii) *Bacillus anthracis* concentrations at carcass sites

Twenty-one anthrax-positive adult zebra carcass sites were marked between 2010 and 2012, and a subset of these sites was sampled in 2012 ($n = 7$ sites) and 2013 ($n = 19$ sites) to assess BA concentrations. Sites were considered anthrax-positive if

Figure 1. A typical zebra anthrax carcass site a few days after death in Etosha National Park, Namibia. Scavengers have consumed soft tissue, denuded the surrounding vegetation and dispersed the remains. Note the digesta pile at the centre, marked with the stake, and the partial skeleton visible in the upper left outside the denuded area.

diagnostic blood swabs from the carcass tested positive for BA (determined through culture with isolates confirmed by PCR [27]). As herbivores could potentially ingest BA at a carcass site by grazing on grass leaves, by inadvertently consuming grass roots when grazing or by ingesting soil for trace minerals [26], we sampled the above-ground grass parts, grass roots and the soil surrounding the plants separately to assess if levels of BA contamination varied among these different locations in the environment. Each carcass site was sampled between mid-February and early April. The dominant grass species within 1 m of the marking stake was sampled, and three replicates of this species were collected for analysis at each site. Plants were dug from the soil and carefully shaken to remove soil clods, the roots were clipped and placed in a 50 ml centrifuge tube, and the above-ground parts were placed in a separate 50 ml tube. A sample of the soil surrounding each plant was collected. Samples were refrigerated prior to analysis, with plant samples cultured for BA within 2 days and soil samples within a month of collection. The grass species collected included *Enneapogon desvauxii*, *Chloris virgata*, *Eragrostis nindensis*, *Monelytrum luederitzianum* and *Aristida adscensionis*, all of which are consumed by zebras [28].

The concentration of BA in all samples was assessed via bacterial culture in serial dilution on PLET agar using standard soil protocols [20] (details in electronic supplementary material). Colonies of BA were identified morphologically; in the cases where the identification was uncertain, the colony was streaked on blood agar for confirmation tests to determine if the colony was non-haemolytic, had penicillin sensitivity and was lysed by gamma phage [20]. The number of colony-forming units (CFU) was estimated relative to the sample weight (CFU g^{-1}), as plant samples were not a standard weight (all soil samples were 5 g).

(iii) Herbivore use of carcass sites

We used motion-triggered camera traps to monitor herbivore activity in 13 anthrax carcass sites and 13 matched control sites. Controls were placed 100 m from each carcass, with the direction oriented to retain similar landscape features to the carcass site. The location of each anthrax carcass site was marked with rocks placed 2.5 m from the centre in four directions (electronic supplementary material, figure S3) defining a standardized grazing 'patch' and providing depth of field for evaluating animal presence from photographs. Control sites were likewise marked with rocks to monitor the same-sized grazing patch as for carcass sites. Each camera was placed 12 m from the centre of the site and 1.2 m above the ground. The cameras were programmed to take photos continuously without delay between sequential triggers of the motion sensor, with 10 photos taken at 1 s intervals for each trigger (using either Reconyx RC55 Rapidfire or PC 800 Hyperfire cameras, with the same model used for matched carcass–control pairs). We focused this study on five herbivore species most commonly observed as anthrax cases in Etosha (table 1).

Cameras were mounted at carcass/control sites for 11–26 months (mean 20 months), monitoring different locations between March 2010 and March 2013, including eight carcass sites formed in 2010, three from 2011 and two from 2012. After removing non-informative data (from cameras knocked down by animals, battery or memory card failure, or human error) there were 10 996 days of observations. These 26 cameras were triggered a total of 119 226 times and 6.5% of these were by the five herbivore species within the 20 m^2 patches. In total, within the patches there were 11 783 triggers of springbok, 5196 of zebra, 1043 of wildebeest, 455 of gemsbok and eight of elephant. Given the paucity of data for elephants and that none were observed foraging within the patches, this species was not considered further.

To quantify herbivore grazing events in carcass and control patches, we evaluated photographs at the level of the individual trigger, counting the number of individuals observed in the patch and the number grazing within a 10-photo series (all behavioural assessments were done by W.C.T.). An individual was recorded as grazing if a bite was observed, or from a series of photographs with the individual's head down and moving at grass height as if biting, plucking and chewing. We therefore focus on site use, looking at animal presence and grazing events observed at carcass and control patches. We did not attempt to quantify potential exposures for individual animals, owing to the difficulty of following an individual within a group through sequential triggers. Owing to the length of the study, the number of people involved and the amount of image data produced, we built custom software for efficient data management, annotation

Table 1. Anthrax cases in Etosha National Park, 1968–2011, and population estimates from an aerial survey, 2012.

scientific name	common name	anthrax confirmed	anthrax suspected	total	% of all confirmed cases	population estimate (95% CI)
Equus quagga	plains zebra	1586	346	1932	52.3	16 174 (13 310–19 038)
Connochaetes taurinus	blue wildebeest	660	224	884	21.8	2482 (1622–3342)
Antidorcas marsupialis	springbok	384	70	454	12.7	12 267 (10 110–14 424)[a]
Loxodonta africana	African elephant	297	225	522	9.8	2810 (2042–3578)
Oryx gazella	gemsbok	38	9	47	1.3	5298 (4356–6240)
—	all other species	67	38	105	2.2	—

[a]The springbok population estimate is a considerable underestimate, apparent in the number of visitations by species at camera sites.

and extraction [29] (described in the electronic supplementary material).

(b) Data analysis

We used linear mixed models (LMMs) to assess factors affecting soil P, N, pH, Na, K, Mg, Ca and organic matter. As fixed effects we included the effect of the carcass (from sampling distance) and site age (1, 2 or 3 years post-mortem) as continuous variables, and sampling year as a categorical variable, while controlling for variation among sites using carcass site as a random effect. Sampling year and the interaction between distance and site age were initially included in all models, but excluded from the final model if non-significant. One exception to these methods is for soil P, where the carcass exhibited a strong effect on P evident only at the 0 m sampling distance, and dropping to presumably baseline levels for all other distances (1.5–7.5 m). Therefore for the P model, we compared sampling distance as a categorical variable comparing the inner versus the midpoint of the other sampling distances (0 m versus 4.5 m). We log-transformed soil N, P, Na, K, Mg and Ca measurements to reduce heteroscedasticity in model residuals.

Factors affecting grass biomass at the negative carcass sites were assessed using a LMM, with fixed effects of site age and sampling distance (1.5, 4.5 and 7.5 m) as continuous variables, sampling year as a categorical variable, and the interaction between distance and site age. The random effects included carcass site and a variable to account for heterogeneity in the variance of biomass estimates among sampling years [30]. The effect of the carcass on grass N 1 and 2 years after death was evaluated using LMMs, with sampling distance as a categorical fixed effect and carcass site as a random effect.

Grass and soil sampling at anthrax-positive carcass sites found BA in at least one sample at 20 of 21 sites tested (the negative site was excluded from analysis). The three replicate samples from each carcass site were averaged by sample type for analysis. The concentration of BA spores (CFU g^{-1}) found on above-ground grass components and roots were each compared with the background levels in soil using Wilcoxon rank sum tests ($n = 28$ paired samples; some sites were sampled in both years). We then evaluated whether CFU g^{-1} decreased with the age of the site after death (1–3 years) for grass, root and soil samples using Kruskal–Wallis rank sum tests as the count data were highly overdispersed.

The herbivore site use data were analysed based on herbivore presence (N individuals present per camera trigger) and grazing (G individuals per trigger seen grazing) summed daily per site per patch type (carcass versus control) for the four herbivore species separately. If one camera from a site was not collecting data for a period of time, data from the paired camera during that time interval was excluded to avoid biasing comparisons by patch type. Because the distance between control and carcass patches is much smaller than the daily distance covered by all species, each daily observation was regarded as independent of the previous day's observations (see electronic supplementary material, figure S4 for autocorrelation structure).

To analyse the multivariate and presumably nonlinear relationships between site use, time and patch type, we used a statistical nonlinear regression model known as a generalized additive model (GAM) with a non-parametric smoother function [31]. We looked for differences in mean site use, differences in seasonality and differences in trends over time since host death. In the nomenclature below, we let $f(X|Y)$ represent the penalized non-parametrical smoother function estimated for a continuous variable X given a categorical variable Y. In our model below, we use N_t and G_t to represent the number of animals present and the number grazing, respectively, in site S on day t; T to represent the day since start of the first camera series, to account for the effects of events in time that occur across sites (e.g. a drought); J to represent the Julian day depending on site S (i.e. site-specific seasonality); A to represent the time since animal death depending on type of patch; and C to represent a binary variable of patch type (carcass or control). The model also includes constants a as a site-specific intercept and b as the effect of C on the fitted relationship. To account for overdispersion, a quasi-Poisson error family with a logarithmic link was used when modelling N or G, and quasi-binomial error family with a logit link in the logistic regression of $G|N$, essentially allowing an independent variance to mean ratio in the models. Thus, the models for zebra and springbok were of the form

$$\ln(N_t) = a_s + f_1(T) + f_2(J_t|S) + f_3(A_t|C) + bC + \varepsilon_{i,t} \quad (2.1)$$

and

$$P(G|N) = \frac{1}{1 + e^{-\beta}}, \quad (2.2)$$

where

$$\beta = a_s + f_4\left(\sqrt{N_t}\right) + f_5(T) + f_6(J|S) + f_7(A_t|C) + cC + \varepsilon_t \quad (2.3)$$

and

$$\ln(G_t) = a_s + f_8(T) + f_9(J_t|S) + f_{10}(A_t|C) + bC + \varepsilon_{i,t}. \quad (2.4)$$

The value of the site-specific constants a and the effect of patch type b differ between equations (2.1), (2.3) and (2.4). The error terms ε denote quasi-Poisson-distributed (equations (2.1) and (2.4)) or quasi-binomial (equation (2.3)) error families. In equation (2.3), the N term is square-root-transformed to stabilize variance. For wildebeest and gemsbok the smaller number of observations meant that the interaction between Julian date and site was unreliable (f_2, f_6 and f_9), and thus the effect of Julian date was fitted as one effect without the interaction with site. The spatial autocorrelation was surprisingly low, as shown by the non-parametric correlograms (electronic supplementary material, figure S4) with a max $\rho < 0.19$ for N, and no significant spatial autocorrelation whatsoever for a difference measure of site-specific differences, $D = G_{A,d} - G_{C,d}/N_{A,d} + N_{C,d}$.

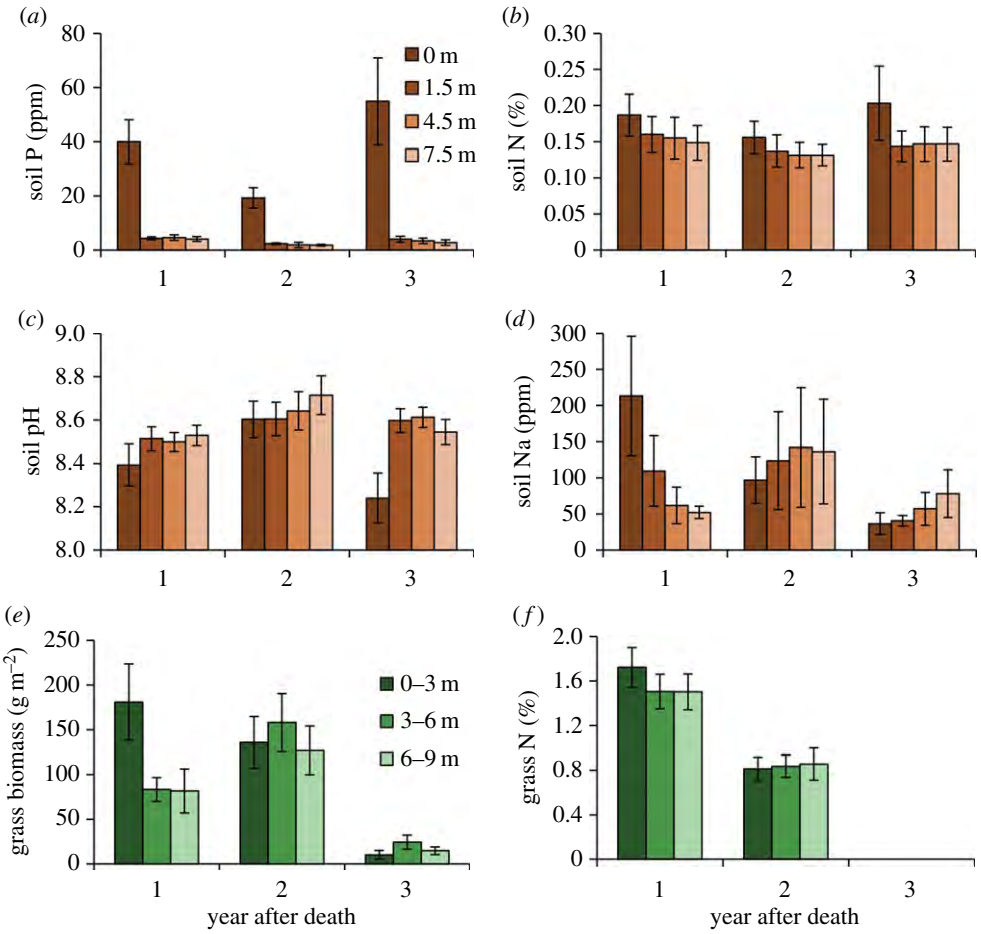

Figure 2. Effects of zebra carcasses on average soil concentrations of (*a*) phosphorus, (*b*) nitrogen, (*c*) pH and (*d*) sodium at four sampling distances (0, 1.5, 4.5 and 7.5 m), and on (*e*) grass biomass and (*f*) nitrogen from three sampling zones (0–3, 3–6 and 6–9 m).

3. Results

(a) Carcass effects on soil and grasses

Soil P was significantly higher at the inner distance (0 m) where the carcass was opened than at the outer distances and did not decline significantly over the 3 years of study (distance: $p < 0.0001$; site age: $p = 0.6201$; figure 2*a*). Soil nitrogen decreased significantly with distance from the carcass centre, a pattern that persisted for 3 years (distance: $p < 0.0001$; site age: $p = 0.1026$; figure 2*b*). Soil pH increased with distance from the carcass centre ($p = 0.0096$; figure 2*c*), with no effect of site age ($p = 0.6458$). Soil Na decreased significantly with distance from the carcass centre, an effect only observed 1 year after death (distance: $p = 0.0075$; site age: $p = 0.0001$; distance × site age: $p = 0.0063$; figure 2*d*). Soil K significantly decreased with distance from the site centre (distance: $p = 0.0156$); however, this effect was not strongly evident due to variation in K estimates among sites and years (site age: $p = 0.0212$; 2012 versus 2011: $p < 0.0001$; 2013 versus 2011: $p < 0.0001$; electronic supplementary material, figure S5). There was no detected effect of the carcass on soil Ca, Mg or organic matter (see electronic supplementary material, figure S5; full statistical results of soil analyses in electronic supplementary material, table S1). No effect of Ca in particular is probably due to removal of bones from the site, so that the nutrient influx came primarily from body fluids.

Grass biomass at carcass sites was significantly higher at the inner (1.5 m) distance although this effect was only apparent 1 year after death (distance: $p = 0.0231$; site age: $p = 0.2504$; distance × site age: $p = 0.0245$; figure 2*e*). There was no significant difference in grass biomass estimates recorded in an above-average and an average rainfall year (2011 versus 2012: $p = 0.6444$). However, there was a highly significant effect of year on grass biomass owing to a drought in 2013 (2011 versus 2013: $p < 0.0001$; figure 2*e*). Grass nitrogen was significantly higher 1 year after death at the inner distance (1.5 m versus 4.5 m distances: $p = 0.0520$; 1.5 m versus 7.5 m distances: $p = 0.0491$; figure 2*f*), although by 2 years after death, there was no statistically significant effect of the carcass on grass nitrogen (full statistical results of grass analyses in electronic supplementary material, table S2).

(b) *Bacillus anthracis* concentrations at carcass sites

Bacillus anthracis was found in all three sample types: in soil, on grass roots and on above-ground grass components. Across all sites irrespective of age, there were significantly lower concentrations of BA on grasses above ground than in the soil ($p = 0.0027$), but no significant difference in concentrations between grass roots and soil ($p = 0.5651$). When comparing how BA concentrations varied with site age, the concentrations of BA present on grass roots or in soil did not differ significantly among the site ages sampled ($p = 0.1337$; soil: $p = 0.2507$; figure 3). However, the concentrations of BA on the above-ground component of grasses did decrease significantly from younger to older sites ($p = 0.0029$; figure 3). Therefore, 1 year after death there was no significant difference in the concentration of spores among sample types

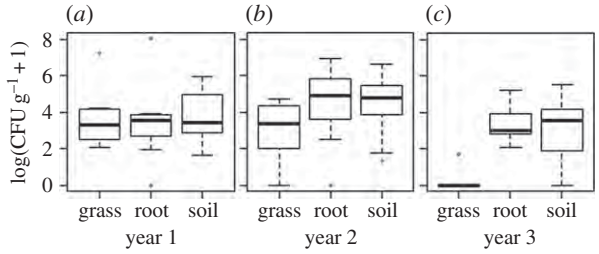

Figure 3. Concentrations of *Bacillus anthracis* on grass, root and surrounding soil at carcass sites (*a*) 1 year, (*b*) 2 years and (*c*) 3 years after animal death. Here 'grass' refers to the above-ground component. Concentrations are quantified as colony forming units (CFU) g^{-1} of sample material and averaged for replicate samples from each site.

($p = 0.9680$), but by 2 and 3 years after death, spore concentrations significantly differed among the sample types (2 years after death: $p = 0.0307$; 3 years after death: $p = 0.0082$). This pattern was driven by the decline in BA spore concentrations on the above-ground component over time, which dropped to near zero on 3-year-old sites (figure 3).

(c) Herbivore use of carcass sites

Four species were present in the camera-monitored patches in sufficient numbers to be included in analyses: springbok ($N =$ 17 516 animal events), zebra ($N = 7452$), wildebeest ($N = 1611$) and gemsbok ($N = 595$). These animal events (N) are the number of individuals observed within a patch during a single trigger of the motion sensor, summed over all triggers.

Multivariate nonlinear models indicated some initial avoidance of the carcass patches after host death, especially for zebra, but the effect was small and transient (figure 4*a–d*). However, with time the situation reversed, and zebra and springbok exhibited clear and significant preferences for grazing in carcass patches compared with control patches ($p < 0.001$; figure 4*e,f,i,j*), resulting in a disproportionate tendency to forage in the potentially infectious patches in the first year after death of the focal animal. The results for wildebeest are more ambiguous, as fewer data existed; however, a greater tendency towards grazing in carcass patches was apparent ($p < 0.01$; figure 4*g,k*). The results suggest that for zebra, springbok or wildebeest encountering a site where a zebra has died within the last year, an animal is up to four times more likely to graze at the potentially infectious carcass patch than at a random grassland patch nearby (figure 4*e–g*). Gemsbok showed no clear foraging preferences; if anything, they displayed an avoidance of carcass patches (though with the smaller amount of data this trend is uncertain: $p < 0.1$; figure 4*l*). Carcass and control patches seemingly became indistinguishable again for grazers from 1.5 to 2.5 years after death of the focal animal (figure 4). This seems to match the time scale of carcass effects detected in grass biomass and nitrogen, and early preference for grazing at carcass sites would significantly increase the odds of anthrax transmission from grazing in the first year after death. Full GAM results are in the electronic supplementary material, appendix S.

In evaluating the potential biological impact of these results for our understanding of BA transmission, it is important to consider the variation among sites in their attractiveness to herbivores, because it could be argued that a preference for grazing at carcass patches might be most substantial in marginal, nutrient-poor areas where little grazing occurs anyway. If strong attraction was only observed at sites with few herbivore visitations, this would indeed lessen the importance of foraging preference for carcass sites in BA transmission. However, there were no significant correlations between the abundance of animals (N) visiting camera sites and the relative differences among sites in grazing preference between carcass and control patches (Spearman's $\rho < 0.3$, $p > 0.1$). While there was site-specific variation in grazing preference between the carcass and control patches, this was independent from the average number of animals present per day. Thus, the preference for carcass patches seems likely to be representative and valid for Etosha's grassland plains, and therefore likely to be ecologically significant for BA transmission in this system.

The number of visitations and grazing events were also assessed in relation to seasonality (by Julian date) and distance to water, but no predictive models (GAMs) of visitation rates could be built using distance to water as a meaningful predictor. While strong seasonal effects in site use are evident (electronic supplementary material, figure S6), the differences in seasonality among sites are not easily explained by the shortest distance (or weighted sum of distances) to surface water.

4. Discussion

The aims of our study were to determine (i) whether herbivores could be exposed to BA when grazing at anthrax carcass sites, (ii) whether herbivores preferentially feed at or avoid anthrax carcass sites, (iii) the duration of processes identified under (i) and (ii), and (iv) the potential importance of carcass sites for foraging-based disease transmission in grazing herbivores. We found that nutrients from carcasses positively alter the environment in ways that are attractive to some, but not all herbivore species, and that anthrax carcass sites represent a significant risk of exposure to BA for grazing herbivores. The time scales of peak site infectivity and attractiveness coincide in the first year after death—evidence that selective foraging may be particularly important in sustaining BA transmission in endemic anthrax areas. When host foraging responses to parasite-associated cues vary with time, the success of the avoidance period in reducing or preventing infection depends upon the lifespan of the parasite in the environment. Here we describe an infection-avoidance mismatch for herbivores foraging at anthrax carcass sites, but this has also been observed for other parasite-associated cues. For example, herbivores most strongly avoid foraging near fresh faeces [8,32], but it can take weeks before nematode eggs in faeces develop into infectious larvae and migrate onto surrounding vegetation [8]. Therefore, if hosts rely on indirect cues to assess temporal changes in parasite risk, trading off parasite avoidance with food acquisition in high-parasite/high-quality foraging locations may be an imperfect strategy.

Animal carcasses represent a significant and localized pulse of nutrients into the environment, which can lead to increased herbivory on plants fertilized by carcasses (e.g. cicada carcasses [33]). Previous studies of ungulate carcass effects on soil and vegetation have been conducted only in temperate or arctic environments [17–19,34], and Towne [17] suggested that abundant scavenger communities would reduce the nutrient effect of carcasses in tropical systems. In our subtropical system, however, we found that carcasses created clear and biologically significant effects on soil P, N and

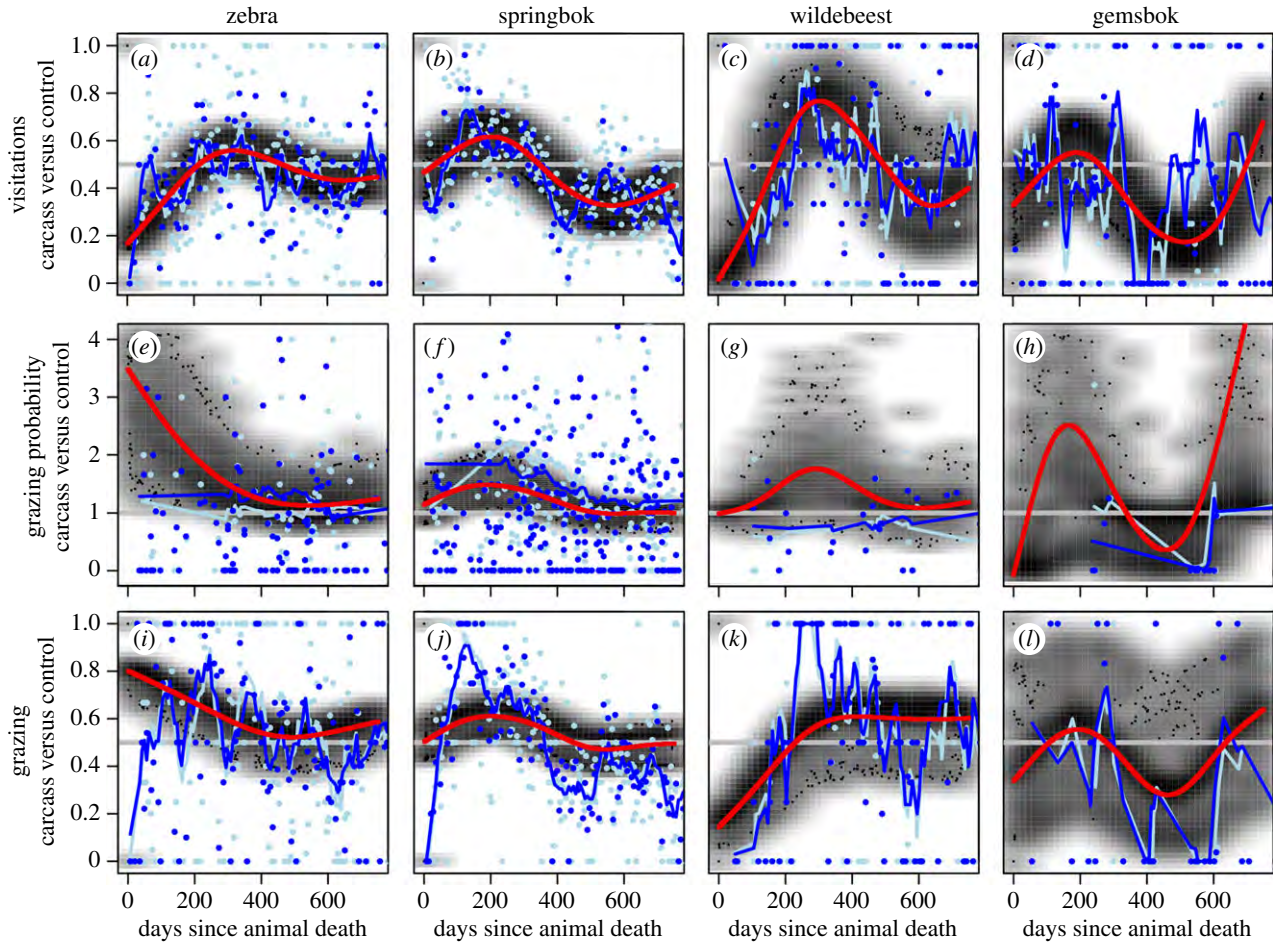

Figure 4. The effect of anthrax carcasses on site visitations and grazing behaviour for zebra, springbok, wildebeest and gemsbok. The upper panels ($a-d$) show the proportion of site visitations that occur at carcass versus control patches over time since animal death (equation (2.1)). The middle panels ($e-h$) show the ratio of foraging probability at carcass versus control patches (equations (2.2) and (2.3)), given that an animal is present in the patch (i.e. $P(G_a|N_a)/P(G_c|N_c)$, where presence in anthrax carcass versus control patches is denoted by N_a and N_c, and grazing events in anthrax carcass versus control patches by G_a and G_c, respectively). The lower panels ($i-l$) show the proportion of all observed grazing events that occur in carcass patches (equation (2.4)). Across all plots, red lines show the mean predicted effect of days after host death on visitation or grazing behaviour between carcass and control patches as predicted by the GAMs. The greyscale density clouds indicate a range of these predicted model effects, from bootstrap data drawn independently from the observed ranges of the variables to give an idea of the relative magnitude of the effects (details in electronic supplementary material). The blue circles and lines show the raw response variable data aggregated at 3-day (light blue) and 7-day (dark blue) intervals with smoothing lines. The horizontal grey lines indicate the no-difference line between carcass and control patches: values above this line indicate a preference for ($a-d$) visiting or ($e-l$) grazing at carcass patches, below indicate a preference for control patches.

pH for at least 3 years post-mortem, with shorter-term effects on soil Na, K, grass biomass and grass N, despite very swift consumption of soft tissue by scavengers [35]. After body fluids have entered the environment, scavenger removal of the carcass remains may actually enhance the chances of subsequent herbivory, because the presence of skin and bones on the site might provide a visual cue that deters herbivory, or at least prevent vegetation re-growth beneath the remains.

Experimental lethal doses for ingested anthrax are high in herbivores (around 10^7–10^8 spores [20]), therefore transmission depends on BA aggregating in the environment and the behaviour of potential hosts at these aggregations. BA spores are known to be concentrated in soils at anthrax carcass sites and can persist there for several years [22,36], patterns that are not affected by scavenger presence or exclusion [37]. Despite the hypothesized importance of grazing in BA transmission [20,38], this is the first study to examine levels of BA contamination on grasses in the natural environment. We found that the above-ground component of grass holds BA spores, and 1 year after death the concentrations on grasses were as high as in soil. However, although spore concentrations remained high in soil and on grass roots over the 3 years of study, by the second year after death concentrations on grasses above ground were significantly lower, and by the third year they were near zero. This indicates that herbivores can be exposed to relatively high concentrations of BA from grazing at carcass sites in the first year when nutrient-rich vegetation has regenerated. If herbivores consume grass roots as well as above-ground components when grazing, they can also be exposed to high BA spore concentrations throughout the second year. This opens the door to species-specific and seasonal differences in exposure risk to BA based on variation in foraging ecology [26,28].

The camera trap study provides further support that transmission of BA is foraging-based and species-specific. Forage selection is hierarchical, from large-scale seasonal movements through daily movements for water, forage, rest and predator avoidance, down to step-by-step decisions about potential food items within sensory range. Our results suggest that the forage selection processes that cause overrepresentation of grazing in infectious patches take place on the very fine scale of step-by-step decisions. There were signs of early avoidance of carcass nutrient patches after death, the length of which is likely to depend upon when the first rainfall (and thus plant

regrowth) occurs relative to the time of death. However, should a herbivore encounter a recently created carcass patch, it is still more likely to graze there than at a nearby grassland patch, a pattern that was particularly strong for zebra. From around 10 months onwards herbivores were as likely to visit carcass patches as control patches, yet were still more likely to graze when visiting carcass patches. After approximately 2 years, attraction to the carcass patches disappeared, and the patch types seem indistinguishable to grazers. Attraction strength varied among species, with zebra, springbok and wildebeest showing periodically strong preferences for grazing at anthrax carcass patches (up to four times the frequency of grazing events in carcass patches relative to control patches in the first year). Similarly, we did not detect any significant preference for carcass patches by gemsbok, which compared with the other herbivore species examined are rarely found as anthrax mortalities. In future research, we will evaluate transmission probabilities, and the timing and intensity of anthrax outbreaks among herbivore species.

Southern Africa has the greatest genetic diversity of BA and is hypothesized to be its geographical origin [39]. Therefore, the environmental conditions in our study area may represent the environment in which the bacterium evolved much of its current life history. A recent experiment demonstrates that BA spores in soil enhance grass seedling establishment, and that even small additions of blood increase grass height [40]. This may indicate a BA–grass mutualism whereby BA benefits from a quick regeneration of nutrient-rich grasses at carcass sites to attract herbivorous hosts. Although not evaluated in this study, exsanguination from anthrax carcasses [41] could lead to a greater localized nutrient release than from non-anthrax carcasses, where blood coagulates in tissues that are subsequently consumed and dispersed by scavengers. From an evolutionary perspective, the life-history strategy of environmental transmission by BA essentially releases its virulence evolution from the constraint of host preservation. On the contrary, killing a host as quickly as possible may increase transmission probabilities, by avoiding a prolonged period of non-transmission in a weakened host. Thus, beyond its ability to produce fulminant infections in hosts, BA seem highly adapted to a life-history strategy of exploiting grazing herbivores.

In conclusion, we find that host foraging responses to carcass sites are dynamic, changing with time from avoidance to attraction to no preference, with the strength and duration of these behavioural states varying among herbivore species. The avoidance period may be sufficient to reduce contact with parasites that only persist for short times in the environment. However, for long-persisting disease agents (such as BA, prions and some coccidia), the ability to survive beyond the initial period of carcass site avoidance may lead to more transmission events than would be expected by chance. These results demonstrate how host foraging ecology and behaviour can affect host–parasite contacts and, ultimately, transmission of environmental parasites in a multi-host natural disease system.

Data accessibility. Data from this study have been made publically available at the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.m49k6.

Acknowledgements. We thank the Ministry of Environment and Tourism in Namibia for providing permission to conduct this research. We are grateful to the scientific staff and managers at the Etosha Ecological Institute for logistical support and assistance, particularly to W. Kilian, S. Kötting, G. Shatumbu, W. Versfeld, R. Aingura, P. Ndumbu, M. Kasaona, E. Ithana, N. Kanime and many others who accompanied our researchers in the field. We greatly appreciate those who assisted with data collection: K. Amutenya, Z. Barandongo, N. Barker, S. Bischoff, K. Dean, R. Easterday, R. Ho, F. Jatamunua, N. Pries, H. Schønhaug and S. Thong. We thank S. Bellan for useful discussions about the research and two anonymous reviewers whose comments improved this paper.

Funding statement. Funding was provided by NSF OISE-1103054 (to W.C.T.), NIH GM083863 (to W.M.G.) and CEES funds (to W.C.T.).

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Supplementary Material

Supplementary Material and Methods
Supplementary References
Supplementary Figures 1-6
Supplementary Tables 1-2
Appendix S: GAM results

Supplementary Material and Methods

Marked carcass site selection

Potential study sites were visited at least a week after death to assess if the site could be included in the study, after allowing time for scavengers to consume the soft tissue from the carcass. Scavenger feeding locations were characterized by the destruction of vegetation (figure 1 and figure S1), the presence of scavenger feces and vulture feathers, as well as hair, digesta, and bone fragments from the carcass (scavenger species consuming carcasses are described in Bellan et al. [1]). Sites where scavengers dragged the carcass across multiple feeding locations were excluded, as the nutrient effect at any single location would be reduced; however, at none of the selected sites did the skeleton remain within the vegetation-denuded area. Of the potential carcass sites visited, 74.1% were marked; the others were rejected because of multiple feeding locations (13.0%), or owning to location within the disturbed area near watering points (7.4%) or roads (5.6%). Although anthrax carcasses may hemorrhage blood from body orifices, scavengers open carcasses first from the soft tissue around the anus and groin, depositing much of the digesta and body fluids into the soil from these exit points. This area of fluid concentration was designated as the center of the carcass site and marked with a metal stake (figure 1). To determine the size of carcass sites for sampling, we measured the long and short axis of 49 scavenged adult zebra carcass sites. The area where digesta was deposited into the soil was 2.1±1.6m by 1.4±0.6m (mean±SD) and the area of plant disturbance was 4.9±1.4m by 4.0±1.0m. All marked sites were from adult zebra carcasses, with the exception of one carcass site in the camera trap study which was from an adult wildebeest in 2012.

Grass and soil nutrient analyses

The Kjeldahl method was used to assess the percentage of nitrogen in grass and soil samples and was conducted at the Analytical Laboratory Inc. in Windhoek, Namibia. All other soil analyses were conducted at the Ministry of Agriculture, Water and Forestry Laboratory in Windhoek, including soil pH, organic matter, P, K, Mg, Ca and Na using standard methods [2].

Bacterial culture

The concentration of *B. anthracis* in soil samples was assessed via bacterial culture in serial dilution on PLET (polymyxin B sulfate, lysozyme, EDTA and thallous acetate) agar, methods adapted from standard protocols [3, 4]. For the soil samples, five grams of homogenized soil was combined with 45ml 0.1% sodium pyrophosphate in a 50ml centrifuge tube then vortexed at maximum speed for 15 minutes to break up soil clumps and separate BA cells from soil particles. Samples were then centrifuged at 300 *g* for 2 minutes to settle larger soil particles and the supernatant transferred to a new centrifuge tube and centrifuged at 3000 *g* for 15 minutes to pellet the sample. The pellet was resuspended in 5ml of 0.1% peptone water or sterile distilled water (no significant difference in colony forming units (CFU) was observed between these two treatments; Turner, unpublished data). One ml of the resuspended pellet was used to create the

serial dilutions from 10^0 to 10^{-5} (the number of dilutions plated depended on the site age and sample type), and 100µl of the selected dilutions was plated directly (without heat treating the samples). Plates were incubated at 30°C for four days. Grass or root samples were cultured following the soil protocol. However, these samples were not a standard weight, so the count estimates were adjusted based on the weight of each individual sample to calculate CFU/g (mean and range of sample weights: above ground samples 1.50g (0.07-5.91g), root samples 1.51g (0.03-11.7g)).

Colonies of *B. anthracis* were identified morphologically, and plates were examined and BA colonies counted after two and four days. The day four assessment was to confirm the day two counts, particularly for colonies that were small at the day two count. In cases where the identification of a colony was uncertain, the colony was streaked on blood agar for confirmation tests to determine if the colony was non-hemolytic, had penicillin sensitivity and was lysed by gamma phage [3]. The number of CFU/g was determined for all dilutions that were countable (not overgrown or with too many to count). Quantification of the CFU/g of soil or vegetation was based on the plate with the smallest dilution in the dilution series that had CFU counts of 30-300 colonies, or the lowest dilution with colonies, if all counts were smaller than 30.

Photo data storage, extraction and software

Due to the length of the study, the number of individuals involved and the amount of image data produced, we built a custom software for efficient data management, annotation and extraction [5]. Photo storage cards were collected from cameras during routine battery replenishments. The cards were then attached to a computer to enable the data management software to download images directly from the card and prepare it for annotation. Students and researchers would then be presented with an intuitive web-based interface to tag downloaded photographs with species and behavioral information. These data were then extracted, with each image being annotated with information such as camera, site, species, presence/absence in the patches, behavior and each photo's own metadata as written by cameras at actuation.

The main goals of the software were to be scalable and to have a robust process for data collection and storage, to counter human errors which are difficult to avoid on any medium-scale or large-scale projects. Using the popular client-server software architecture, the data were securely stored on a web server and custom interfaces were built for specific tasks. The on-demand reporting that was possible because of using a relational database management system like MySQL enabled us to have insight into data as they were coming in and being annotated. The web-interface provided platform independence to field volunteers and researchers alike, and at least four different computer operating systems were used seamlessly during this study.

This software, called Aardwolf, is a multi-platform, open-source software. Binaries are available at http://sourceforge.net/projects/aardwolf/; sources are available at https://github.com/yathin/aardwolf.

Additional detail on Figure 4

The GAM models (equations (2.1)-(2.4), see model statistics and parameter estimates) were summarized in figure 4 to show the effect of anthrax carcasses on site visitations and grazing behavior for zebra, springbok, wildebeest and gemsbok over time. To visualize the effect size of the variables patch type and time since death, bootstrap data were generated at the daily scale with 3000 data points drawn independently from the observed ranges of the variables. To not give undue weight to less visited sites, the probability of sampling each site was proportional to

the total number of individuals (*N*) visiting both carcass and control patches at each site divided by the number of days the camera was functional.

In figure 4, the upper panels (A-D) show the proportion of site visitations that occur at carcass versus control patches over time since animal death as predicted by equation (2.1). The red line shows the estimated effect of time on the number of visitations at carcass patches relative to control patches, so that if the number of daily visitations predicted from equation (2.1) is denoted E_N and split into $E_{N,a}$ and $E_{N,c}$ depending on whether it is a carcass or control patch respectively, the red line shows the fraction of daily visitations expected to be occurring at carcass patches (i.e. $E_{N,a}/ E_N$). The grey shading shows the same, only shown as grey density shading for the bootstrapping data, thus giving a visual presentation of the variance in the predictions and the relative effect of carcass versus control site over time. The blue circles and lines show the raw response variable data aggregated at 3-day (light blue) and 7-day (dark blue) intervals with smoothing lines. The horizontal gray lines indicate the no-difference line between carcass and control sites: values above this line indicate a preference for carcass sites, below indicates a preference for control sites.

The middle panels (E-H) show the ratio of foraging probability at carcass versus control patches (equations (2.2) and (2.3)), given that an animal is present in the patch (i.e., $P(Ga|Na)/ P(Gc|Nc)$, and grazing events in anthrax carcass vs. control patches *Ga* and *Gc*, respectively). The density shading and lines otherwise follow the same methods as the upper panels.

The lower panels (I-L) show the resulting proportion of all observed grazing events that occur in carcass patches relative to control patches (equation (2.4)). The red lines show the estimated effect of time on the number of grazing events at carcass patches relative to control patches, so that if the number of daily grazing events predicted from equation (2.4) is denoted E_G and split into $E_{G,a}$ and $E_{G,c}$ depending on whether it is a carcass or control patch respectively, the figure shows the fraction of daily visitations expected to be occurring in carcass sites (i.e. $E_{G,a}/ E_G$) using the same methods as the upper panels.

Supplementary References

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Supplementary Figures

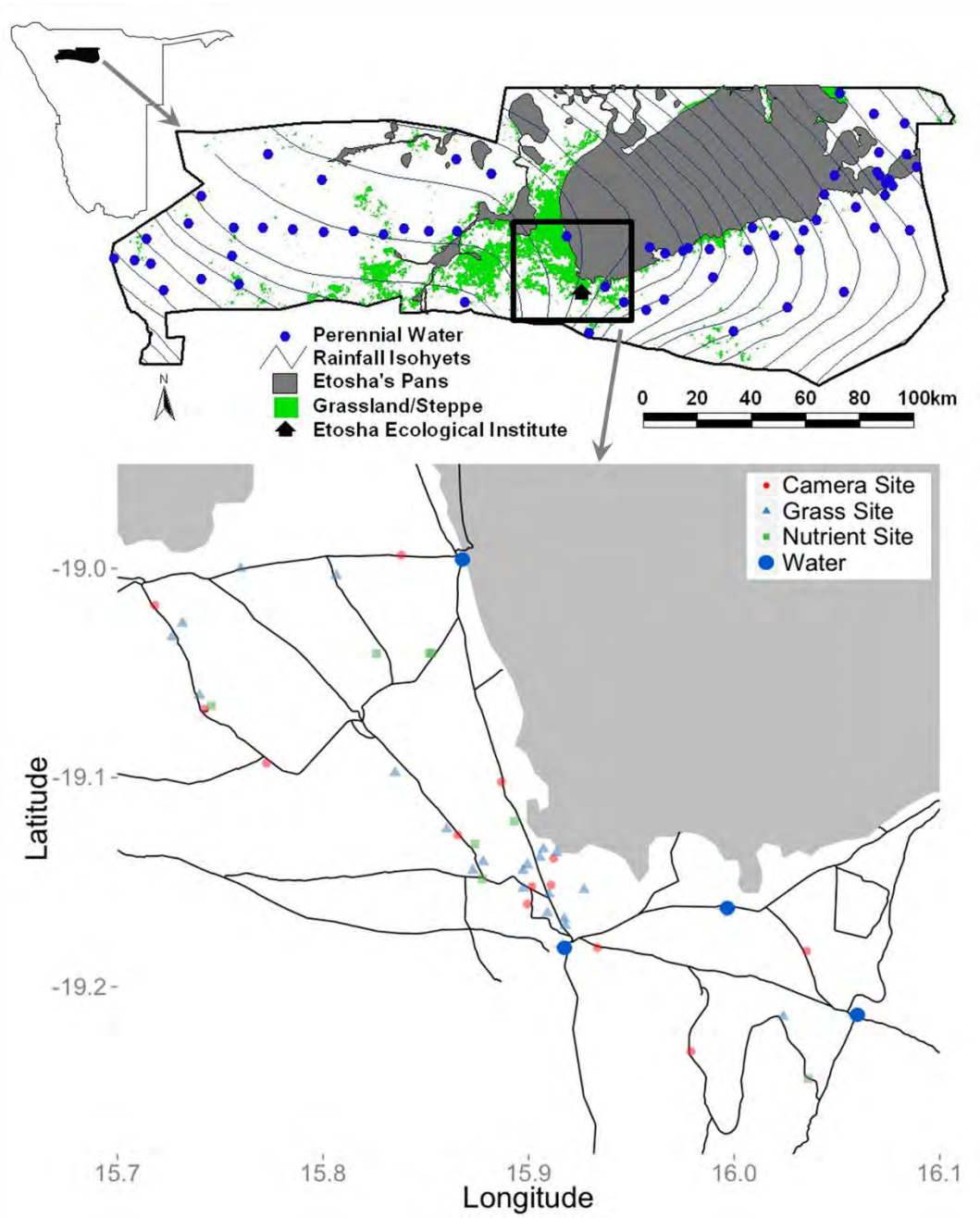

Figure S1. Etosha National Park in northern Namibia. The study area was located on the grassland and dwarf shrub savanna plains (in green) on the south-west edge of the main salt pan. The zoomed map shows the locations of marked carcass sites, the road network and perennial watering points in the study area. The three types of marked carcass sites include those used as camera trap sites (camera sites, *N*=13), soil and grass nutrient sites (nutrient sites, *N*=8) and sites for assessing the concentration of *Bacillus anthracis* on grasses (grass sites; *N*=21).

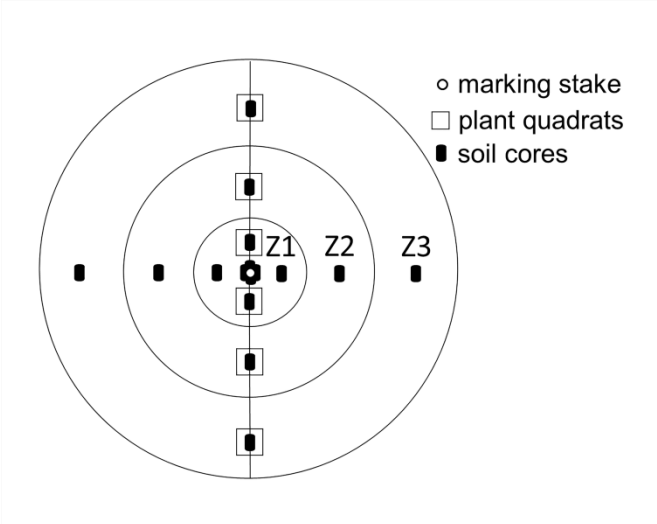

Figure S2. The sampling design for the carcass nutrient study. The three sampling zones are Z1: 0-3m, Z2: 3-6m, Z3: 6-9m.

Figure S3. A carcass site five days after death with rocks marking the grazing patch for the camera study, April 2012.

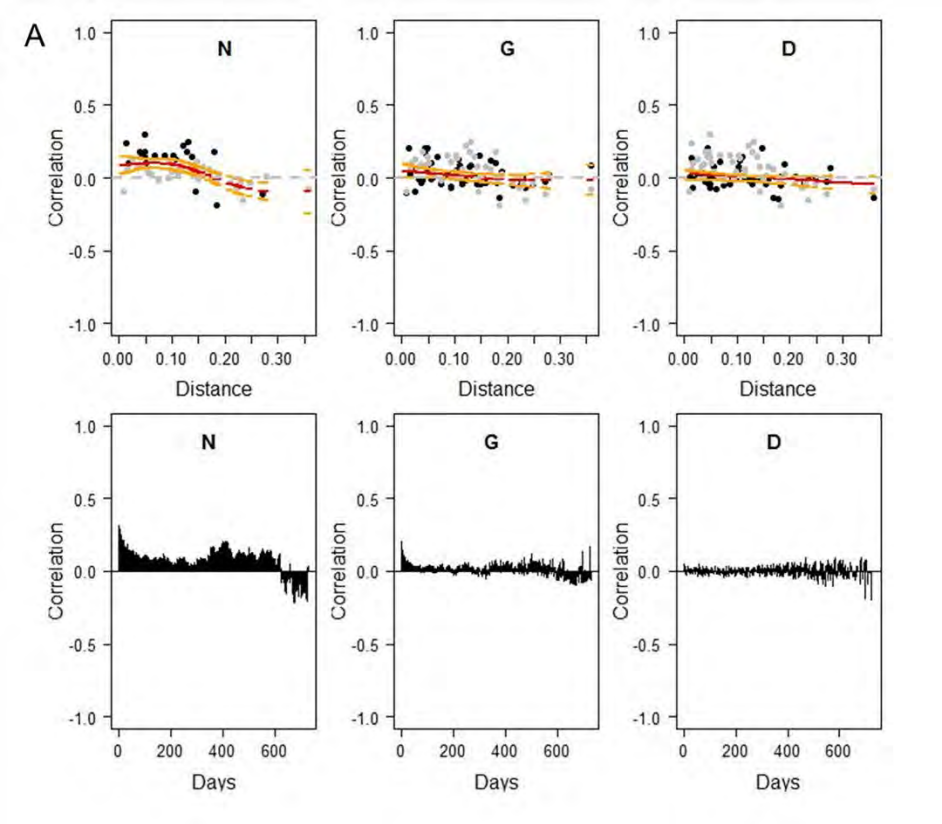

Figure S4. Correlograms for A) zebra, B) springbok and C) wildebeest. Spatial autocorrelation was measured by pairwise non-parametric (Spearman) correlations between N, G or D (summed over both patches from a site) compared to Euclidian distance between sites on the latitude-longitude grid (upper panels). Temporal autocorrelation at time lag *x* (lower panels) was measured as the non-parametric (Spearman) correlation between $N_{i,t}$ and $N_{i,t-x}$. N_t represents the number of visitations (i.e. animals visible in a patch in a camera trigger) per day, and G_t the number of visiting animals that are observed grazing in the patch. To measure any autocorrelation in difference in patch preference we also use a derived measure, $D = \frac{G_{A,d} - G_{C,d}}{N_{A,d} + N_{C,d}}$. For gemsbok, not enough data existed to make valid autocorrelation estimates.

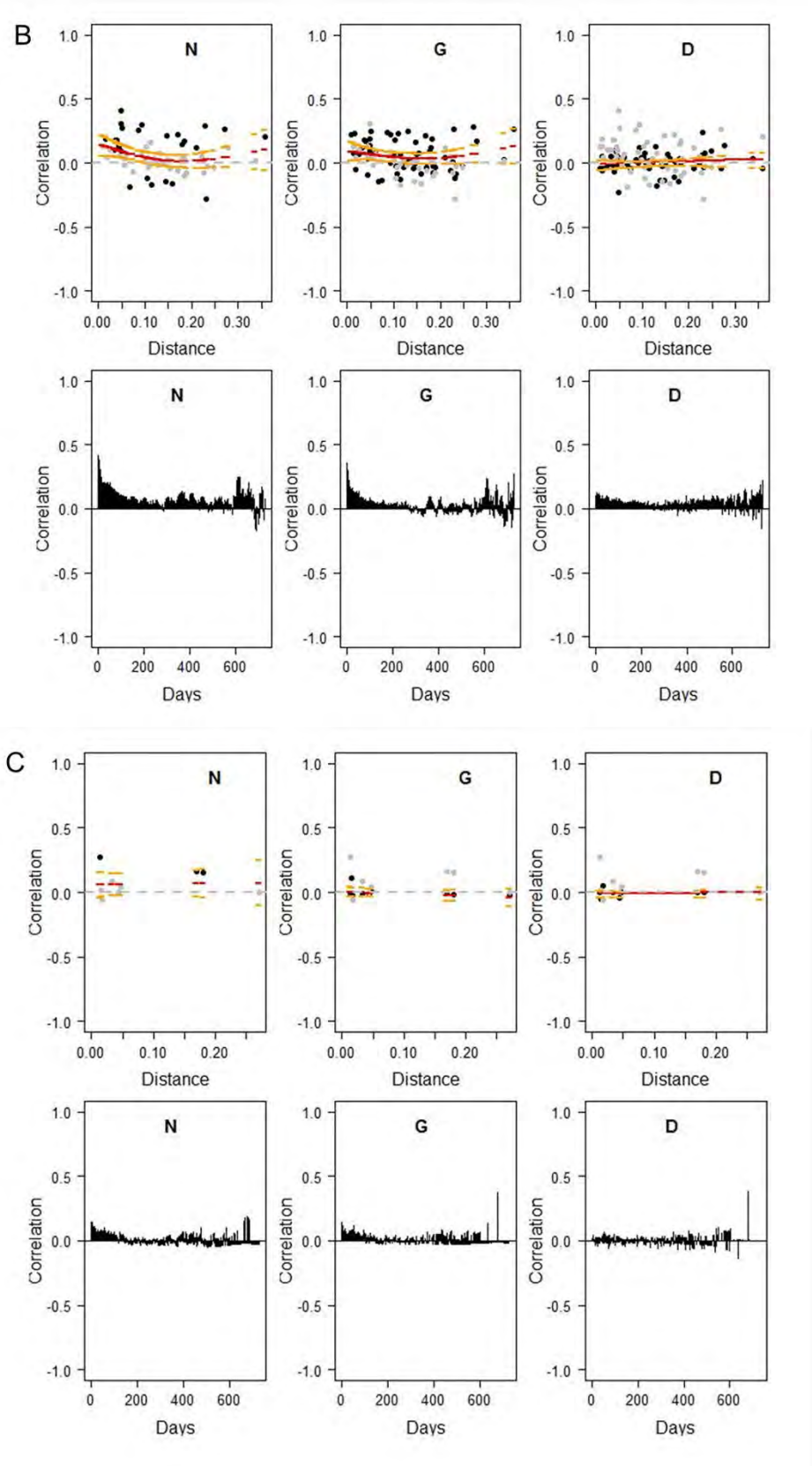

Fig. S4. Continued

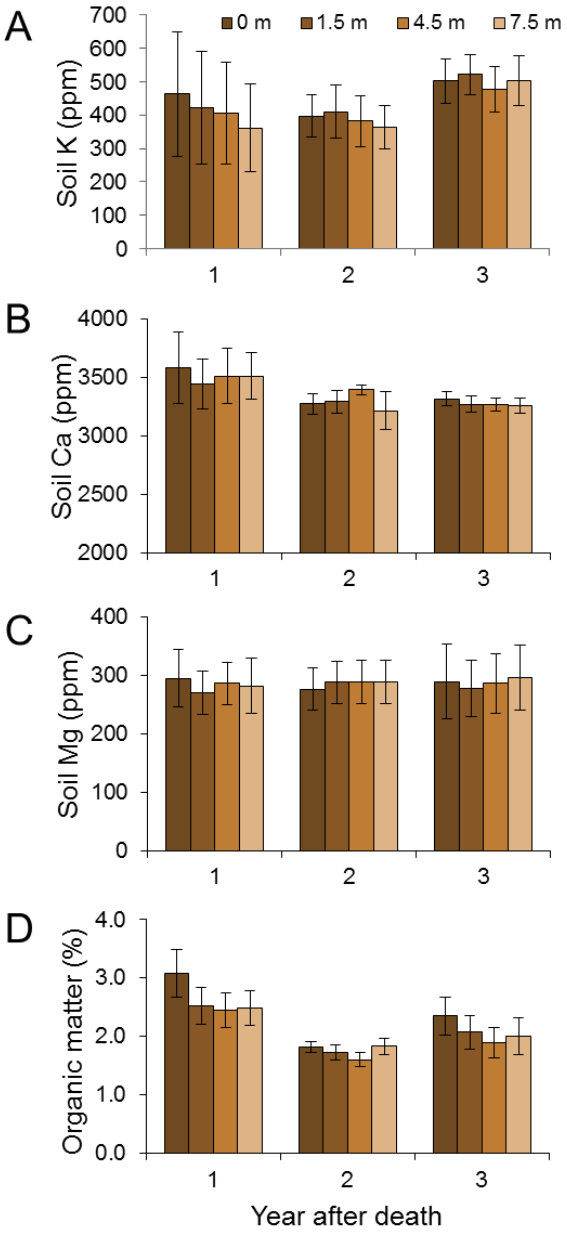

Figure S5. Average soil concentrations of A) potassium, B) calcium, C) magnesium and D) organic matter at four sampling distances (0, 1.5, 4.5 and 7.5m) from the center of zebra carcass sites one, two and three years after death.

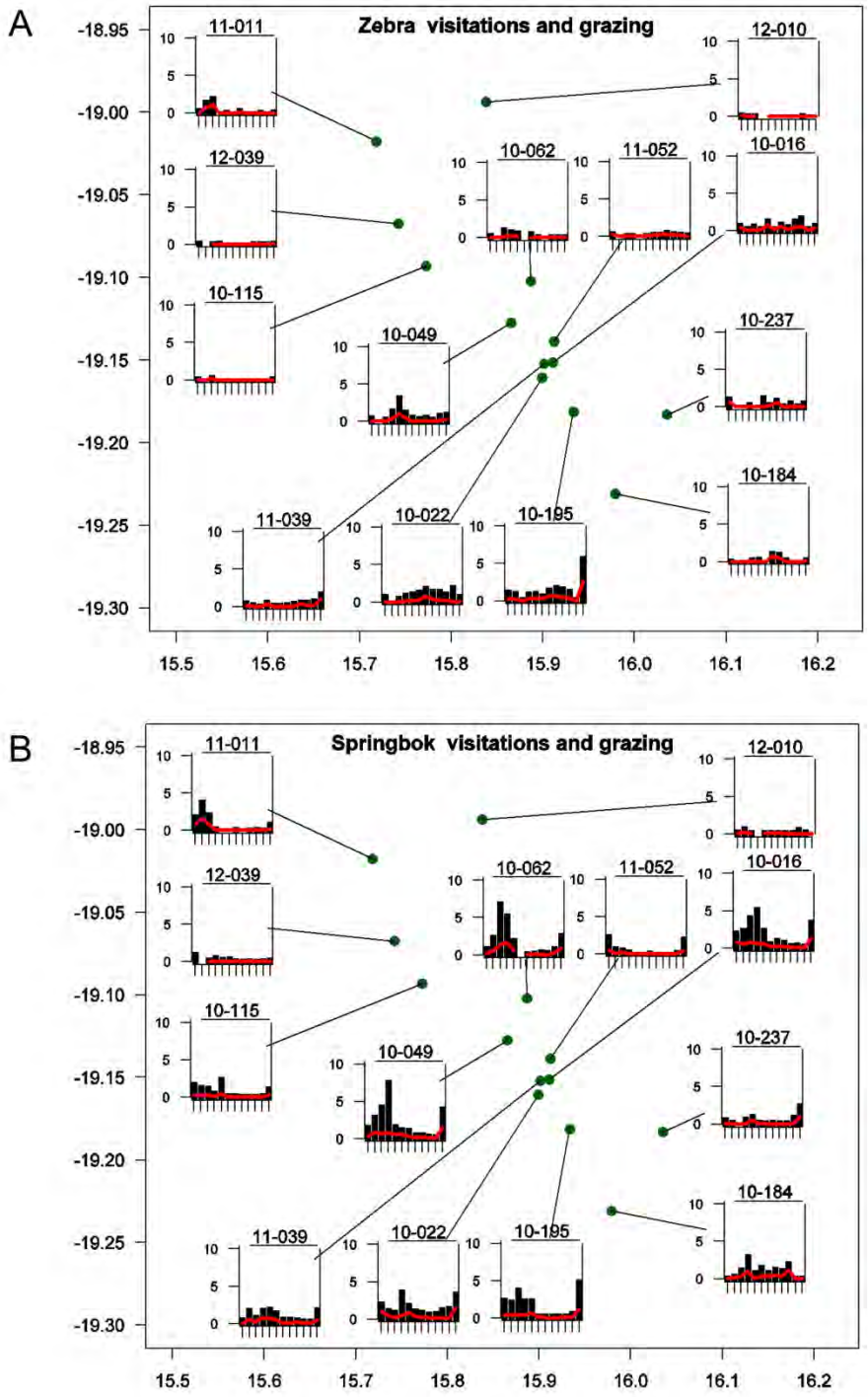

Figure S6. Seasonality and differences among sites in herbivore visitations and grazing events for A) zebra, B) springbok, C) wildebeest and D) gemsbok. The green dots represent a matched carcass-control pair on a Latitude-Longitude grid. In the inset plots, black bars are the mean monthly number of animals observed per day at the sites (from January-December) for each site (summed over both patch types, and corrected for days of available data) and the red line is the predicted proportion of grazing events per day by month for the site (combined for carcass and control patches) from equation (2.4) (see Methods).

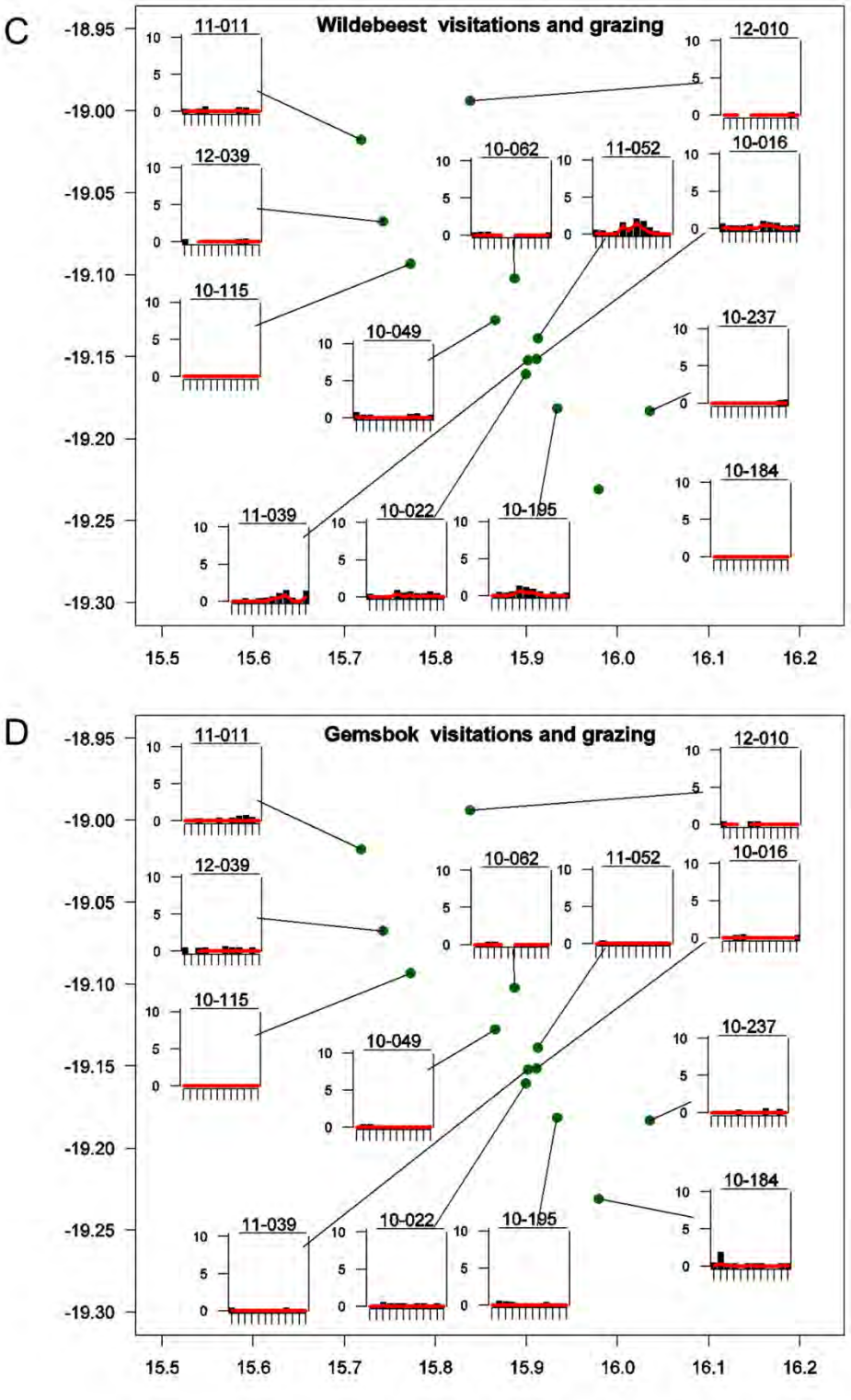

Fig. S6. Continued

Table S1. Linear mixed model results for fixed effects in soil analyses. All models started with sampling distance, site age, year and distance*age as fixed effects and carcass site as a random effect. Year and the distance*age interaction were excluded from the final model if they did not signicantly improve the model fit (based on AIC values).

response	coefficients	estimate	SE	*t*-statistic	*p*-value
log_P	intercept	1.513	0.153	9.9	<0.0001
	distance	-0.228	0.022	-10.6	<0.0001
	site age	-0.032	0.064	-0.5	0.6201
log_N	intercept	-0.829	0.058	-14.3	<0.0001
	distance	-0.010	0.002	-4.8	<0.0001
	site age	0.014	0.008	1.7	0.1026
pH	intercept	8.501	0.076	111.5	<0.0001
	distance	0.020	0.008	2.7	0.0096
	site age	-0.014	0.029	-0.5	0.6458
log_Na	intercept	2.452	0.200	12.3	<0.0001
	distance	-0.102	0.037	-2.8	0.0075
	site age	-0.334	0.080	-4.2	0.0001
	distance*site age	0.049	0.017	2.8	0.0063
log_K	intercept	2.526	0.056	45.1	<0.0001
	distance	-0.006	0.002	-2.5	0.0156
	site age	-0.133	0.056	-2.4	0.0212
	year(2012 vs 2011)	0.261	0.060	4.4	<0.0001
	year(2013 vs 2011)	0.580	0.113	5.1	<0.0001
log_Ca	intercept	3.538	0.016	214.4	<0.0001
	distance	-0.001	0.001	-0.5	0.5883
	site age	0.046	0.016	2.9	0.0045
	year(2012 vs 2011)	-0.107	0.018	-6.1	<0.0001
	year(2013 vs 2011)	-0.154	0.031	-4.9	<0.0001
log_Mg	intercept	2.405	0.058	41.7	<0.0001
	distance	0.002	0.001	1.1	0.2809
	site age	0.010	0.006	1.6	0.1074
organic matter†	intercept	3.103	0.279	11.1	<0.0001
	distance	-0.014	0.011	-1.2	0.2297
	site age	-0.359	0.208	-1.7	0.0890
	year(2012 vs 2011)	-0.605	0.287	-2.1	0.0390
	year(2013 vs 2011)	0.024	0.455	0.1	0.9576

†The organic matter model contains an additional random effect, to account for heterogeneity in variance among years.

Table S2. Linear mixed model results for fixed effects in grass analyses. All models are fit with carcass site as a random effect; the grass biomass model included a random effect to account for heterogeneity in variance among sampling years.

response	coefficients	estimate	SE	*t*-statistic	*p*-value
grass biomass	intercept	148.069	24.004	6.2	<0.0001
	distance	-8.189	3.495	-2.3	0.0231
	site age	-10.062	8.652	-1.2	0.2504
	year (2012 vs 2011)	11.179	24.077	0.5	0.6444
	year (2013 vs 2011)	-105.796	21.062	-5.0	<0.0001
	site age * distance	3.025	1.305	2.3	0.0245
grass nitrogen (2011)‡	intercept	1.723	0.165	10.4	<0.0001
	distance (4.5m vs 1.5m)	-0.217	0.098	-2.2	0.0520
	distance (7.5m vs 1.5m)	-0.220	0.098	-2.2	0.0491
grass nitrogen (2012) ‡	intercept	0.813	0.117	6.9	<0.0001
	distance (4.5m vs 1.5m)	0.023	0.052	0.4	0.6653
	distance (7.5m vs 1.5m)	0.042	0.052	0.8	0.4446

‡ For grass N we did not assess site age or year effects, because grass N can vary considerably among successive measurements due to various abiotic and biotic factors [6] and grass N data were only available for the six carcass sites formed in a single year (2010). Instead, we tested the effect of the carcass one and two years after death (2011 and 2012, respectively) treating sampling distance as a categorical variable.

Appendix S: Generalized Additive Model results of visitations (equation (2.1)), grazing given present (equations (2.2) and (2.3)) and grazing (equation (2.4)) for zebra, springbok, wildebeest and gemsbok. Model variables include: type (carcass/control), site (individual IDs with YR-NUM codes from Park mortality records), time (days since start of the study), timeAD (days since animal death), jday (Julian day), with interactions as specified in the data analysis section.

Visitations, zebra:

```
Family: quasipoisson
Link function: log

Formula:
N ~ s(Time, k = 3) + s(JDay, by = Site, bs = "cp", k = 3) + s(TimeAD,
    by = Type, k = 5) + s(JDay, by = Type, k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.59458    0.19464  -8.192 2.82e-16 ***
TypeControl  0.13172    0.04305   3.060 0.002218 **
Site10-022   0.29767    0.07702   3.865 0.000112 ***
Site10-049   0.02712    0.08366   0.324 0.745809
Site10-062  -0.82434    0.12303  -6.700 2.18e-11 ***
Site10-115  -1.95026    0.25159  -7.752 9.79e-15 ***
Site10-184  -1.26577    0.25252  -5.013 5.45e-07 ***
Site10-195   1.37629    0.14935   9.215  < 2e-16 ***
Site10-237   0.71720    0.27567   2.602 0.009289 **
Site11-011  -1.91552    0.61179  -3.131 0.001746 **
Site11-039   2.21342    0.47622   4.648 3.39e-06 ***
Site11-052   1.23757    0.49947   2.478 0.013234 *
Site12-039   0.00000    0.00000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df     F  p-value
s(Time)              1.977  1.999 35.59 3.95e-16 ***
s(JDay):Site10-016   1.997  2.000 26.46 2.12e-12 ***
s(JDay):Site10-022   1.998  2.000 28.72 1.60e-13 ***
s(JDay):Site10-049   1.997  2.000 31.48 1.07e-14 ***
s(JDay):Site10-062   1.997  2.000 28.91 1.77e-13 ***
s(JDay):Site10-115   1.995  2.000 34.40 4.51e-16 ***
s(JDay):Site10-184   1.998  2.000 37.77  < 2e-16 ***
s(JDay):Site10-195   1.997  2.000 30.18 4.98e-14 ***
s(JDay):Site10-237   1.997  2.000 36.02  < 2e-16 ***
s(JDay):Site11-011   2.000  2.000 30.50 3.72e-14 ***
s(JDay):Site11-039   2.000  2.000 21.61 2.93e-10 ***
s(JDay):Site11-052   1.998  2.000 25.89 3.71e-12 ***
s(JDay):Site12-039   1.989  2.000 17.53 1.83e-08 ***
s(TimeAD):TypeCarcass 3.973  3.999 29.30  < 2e-16 ***
s(TimeAD):TypeControl 3.999  4.000 64.41  < 2e-16 ***
s(JDay):TypeCarcass  4.000  4.000 86.93  < 2e-16 ***
s(JDay):TypeControl  3.999  4.000 42.06  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.0501   Deviance explained = 18.4%
GCV score = 2.7541  Scale est. = 2.7419    n = 12138
```

Visitations, springbok:

```
Family: quasipoisson
Link function: log

Formula:
N ~ s(Time, k = 3) + s(JDay, by = Site, bs = "cp", k = 3) + s(TimeAD,
    by = Type, k = 5) + s(JDay, by = Type, k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -0.42988    0.07130  -6.030 1.69e-09 ***
TypeControl  0.18057    0.04458   4.051 5.14e-05 ***
Site10-022   0.06023    0.06673   0.903 0.366729
Site10-049   0.01482    0.05720   0.259 0.795638
Site10-062  -0.04239    0.07801  -0.543 0.586900
Site10-115  -1.14123    0.11534  -9.894  < 2e-16 ***
Site10-184  -0.46212    0.10519  -4.393 1.13e-05 ***
Site10-195   0.31069    0.08579   3.622 0.000294 ***
Site10-237  -0.67365    0.15666  -4.300 1.72e-05 ***
Site11-011  -2.97688    0.43565  -6.833 8.68e-12 ***
Site11-039   1.12467    0.16646   6.757 1.47e-11 ***
Site11-052  -2.11625    0.43049  -4.916 8.94e-07 ***
Site12-039   0.00000    0.00000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                           edf Ref.df       F  p-value
s(Time)               1.999388  2.000 175.756  < 2e-16 ***
s(JDay):Site10-016    0.000693  2.000   0.000 0.373817
s(JDay):Site10-022    1.969362  2.000  40.641  < 2e-16 ***
s(JDay):Site10-049    0.000220  2.000   0.000 0.714570
s(JDay):Site10-062    1.648800  2.000   3.437 0.014760 *
s(JDay):Site10-115    1.870156  2.000   7.897 0.000195 ***
s(JDay):Site10-184    1.946813  2.000  73.783  < 2e-16 ***
s(JDay):Site10-195    1.693832  2.000   8.039 5.30e-05 ***
s(JDay):Site10-237    1.916581  2.000  24.462 5.87e-12 ***
s(JDay):Site11-011    1.993549  2.000  53.778  < 2e-16 ***
s(JDay):Site11-039    1.824510  2.000   8.155 0.000112 ***
s(JDay):Site11-052    1.980685  2.000  30.629 3.33e-14 ***
s(JDay):Site12-039    1.834998  2.000  23.036 1.27e-11 ***
s(TimeAD):TypeCarcass 3.646094  3.917  19.788 9.24e-16 ***
s(TimeAD):TypeControl 3.974506  3.999  68.965  < 2e-16 ***
s(JDay):TypeCarcass   3.954131  3.998  95.914  < 2e-16 ***
s(JDay):TypeControl   3.989184  4.000 161.925  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.0816   Deviance explained = 24.7%
GCV score = 4.4762  Scale est. = 4.4597    n = 13040
```

Visitations, wildebeest:

```
Family: quasipoisson
Link function: log

Formula:
N ~ s(Time, k = 3) + s(JDay, bs = "cp", k = 3) + s(TimeAD, by = Type,
    k = 5) + s(JDay, by = Type, k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -2.35046    0.11991 -19.602  < 2e-16 ***
TypeControl -0.08050    0.06749  -1.193 0.232997
Site10-022  -0.34701    0.10343  -3.355 0.000796 ***
Site10-049  -0.45843    0.13032  -3.518 0.000437 ***
Site10-062  -1.31879    0.16510  -7.988 1.53e-15 ***
Site10-115  -3.86506    0.77432  -4.992 6.09e-07 ***
Site10-195   0.69632    0.14432   4.825 1.42e-06 ***
Site10-237  -0.99960    0.32548  -3.071 0.002139 **
Site11-011   0.06214    0.28660   0.217 0.828347
Site11-039   1.95291    0.28933   6.750 1.57e-11 ***
Site11-052   2.16288    0.28925   7.478 8.23e-14 ***
Site12-039   0.00000    0.00000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df      F p-value
s(Time)              1.992  2.000 33.914 2.1e-15 ***
s(JDay)              1.918  2.000 50.746 < 2e-16 ***
s(TimeAD):TypeCarcass 3.959  3.999 21.616 < 2e-16 ***
s(TimeAD):TypeControl 3.863  3.989 23.910 < 2e-16 ***
s(JDay):TypeCarcass   3.957  3.999 23.567 < 2e-16 ***
s(JDay):TypeControl   1.000  1.000  9.939 0.00162 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.0154   Deviance explained = 14.1%
GCV score = 1.1883  Scale est. = 1.1849    n = 9674
```

Visitations, gemsbok:

```
Family: quasipoisson
Link function: log

Formula:
N ~ s(Time, k = 3) + s(JDay, bs = "cp", k = 3) + s(TimeAD, by = Type,
    k = 5) + s(JDay, by = Type, k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -4.6514     0.1234 -37.709  < 2e-16 ***
TypeControl   0.5323     0.0893   5.960 2.59e-09 ***
Site10-022    0.5341     0.1682   3.175  0.00150 **
Site10-049   -0.9600     0.2423  -3.962 7.49e-05 ***
Site10-062    0.2389     0.1816   1.316  0.18835
Site10-115   -0.5617     0.2119  -2.650  0.00806 **
Site10-184    2.5248     0.1325  19.054  < 2e-16 ***
Site10-195    1.0537     0.1455   7.240 4.76e-13 ***
Site10-237    0.4831     0.1785   2.706  0.00683 **
Site11-011    0.5852     0.1178   4.969 6.84e-07 ***
Site11-039   -1.6835     0.2743  -6.138 8.61e-10 ***
Site11-052   -2.5383     0.2583  -9.828  < 2e-16 ***
Site12-039    0.0000     0.0000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                        edf Ref.df      F p-value
s(Time)               1.992  2.000  90.13  <2e-16 ***
s(JDay)               1.989  2.000 166.19  <2e-16 ***
s(TimeAD):TypeCarcass 3.836  3.982  66.24  <2e-16 ***
s(TimeAD):TypeControl 3.845  3.979 151.46  <2e-16 ***
s(JDay):TypeCarcass   3.977  3.999  90.53  <2e-16 ***
s(JDay):TypeControl   3.990  4.000 120.28  <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.0362   Deviance explained = 25.7%
GCV score = 0.36913  Scale est. = 0.36812   n = 11552
```

Grazing given present, zebra:

```
Family: quasibinomial
Link function: logit

Formula:
cbind(G, N - G) ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay,
    by = Site, bs = "cp", k = 3) + s(TimeAD, by = Type, k = 5) +
    s(JDay, by = Type, k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.15520    0.08219 -14.056  < 2e-16 ***
TypeControl -0.46472    0.03293 -14.110  < 2e-16 ***
Site10-022  -1.66586    0.07264 -22.933  < 2e-16 ***
Site10-049  -1.11444    0.06019 -18.516  < 2e-16 ***
Site10-062  -1.43098    0.11606 -12.330  < 2e-16 ***
Site10-115  -2.18447    0.29336  -7.446 1.03e-13 ***
Site10-184   0.48899    0.12256   3.990 6.65e-05 ***
Site10-195  -0.44368    0.06477  -6.851 7.71e-12 ***
Site10-237   0.20802    0.11484   1.811 0.070107 .
Site11-011   0.17039    0.20273   0.840 0.400653
Site11-039   0.56727    0.16282   3.484 0.000496 ***
Site11-052   1.60083    0.17759   9.014  < 2e-16 ***
Site12-039   0.00000    0.00000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                           edf Ref.df       F  p-value
s(sqrt(N))           1.928e+00  1.995 532.072  < 2e-16 ***
s(Time)              1.956e+00  1.997  17.504 2.66e-08 ***
s(JDay):Site10-016   1.923e+00  2.000  20.766 1.61e-13 ***
s(JDay):Site10-022   1.870e+00  2.000  31.411  < 2e-16 ***
s(JDay):Site10-049   1.931e+00  2.000  10.614 7.56e-07 ***
s(JDay):Site10-062   1.775e+00  2.000   9.604 5.85e-06 ***
s(JDay):Site10-115   1.989e+00  2.000  57.666  < 2e-16 ***
s(JDay):Site10-184   7.488e-01  2.000   0.818 0.091726 .
s(JDay):Site10-195   1.996e+00  2.000  12.670 6.64e-09 ***
s(JDay):Site10-237   1.374e+00  2.000   4.155 0.000907 ***
s(JDay):Site11-011   2.000e+00  2.000  21.109 1.72e-10 ***
s(JDay):Site11-039   7.611e-01  2.000   0.595 0.148159
s(JDay):Site11-052   5.553e-05  2.000   0.000 1.000000
s(JDay):Site12-039   1.156e-01  2.000   0.063 0.320184
s(TimeAD):TypeCarcass 3.676e+00  3.924  10.175 5.00e-08 ***
s(TimeAD):TypeControl 3.853e+00  3.980  14.549 9.00e-12 ***
s(JDay):TypeCarcass   3.973e+00  3.995  21.984  < 2e-16 ***
s(JDay):TypeControl   3.911e+00  3.980  25.620  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.331   Deviance explained = 28.4%
GCV score = 0.27732  Scale est. = 0.27623   n = 12138
```

Grazing given present, springbok:

```
Family: quasibinomial
Link function: logit

Formula:
cbind(G, N - G) ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay,
    by = Site, bs = "cp", k = 3) + s(TimeAD, by = Type, k = 5) +
    s(JDay, by = Type, k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.29735    0.08366 -15.507  < 2e-16 ***
TypeControl -0.27381    0.03457  -7.921 2.55e-15 ***
Site10-022  -0.06295    0.05305  -1.187 0.235428
Site10-049   0.02787    0.05176   0.538 0.590286
Site10-062   0.12636    0.05682   2.224 0.026181 *
Site10-115  -0.11311    0.07335  -1.542 0.123049
Site10-184   0.76454    0.08851   8.638  < 2e-16 ***
Site10-195   0.07144    0.08066   0.886 0.375784
Site10-237   0.45212    0.14119   3.202 0.001368 **
Site11-011  -0.17787    0.34574  -0.514 0.606941
Site11-039   1.27395    0.19290   6.604 4.15e-11 ***
Site11-052   0.88657    0.23597   3.757 0.000173 ***
Site12-039   0.00000    0.00000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                           edf Ref.df      F  p-value
s(sqrt(N))            1.981563  2.000 52.052  < 2e-16 ***
s(Time)               1.923727  1.989 33.485 4.19e-15 ***
s(JDay):Site10-016    1.913128  2.000 39.777  < 2e-16 ***
s(JDay):Site10-022    1.993720  2.000 37.549  < 2e-16 ***
s(JDay):Site10-049    1.930130  2.000 58.927  < 2e-16 ***
s(JDay):Site10-062    0.005639  2.000  0.001   0.7025
s(JDay):Site10-115    0.001549  2.000  0.000   0.6481
s(JDay):Site10-184    1.999351  2.000 41.447  < 2e-16 ***
s(JDay):Site10-195    1.997022  2.000 19.135 1.06e-09 ***
s(JDay):Site10-237    1.810484  2.000 22.973 6.01e-12 ***
s(JDay):Site11-011    1.976346  2.000 25.956 3.28e-12 ***
s(JDay):Site11-039    1.463054  2.000  2.103   0.0527 .
s(JDay):Site11-052    0.859352  2.000  0.893   0.1253
s(JDay):Site12-039    1.337806  2.000  2.906   0.0135 *
s(TimeAD):TypeCarcass 3.929204  3.994 21.141  < 2e-16 ***
s(TimeAD):TypeControl 3.110896  3.553 24.422  < 2e-16 ***
s(JDay):TypeCarcass   3.999153  4.000 42.971  < 2e-16 ***
s(JDay):TypeControl   3.999585  4.000 33.907  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.161   Deviance explained = 15.1%
GCV score = 0.46294  Scale est. = 0.46123   n = 13040
```

Grazing given present, wildebeest:

```
Family: quasibinomial
Link function: logit

Formula:
cbind(G, N - G) ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay,
    bs = "cp", k = 3) + s(TimeAD, by = Type, k = 5) + s(JDay,
    by = Type, k = 5) + Type + Site

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -4.738e-01  1.005e-01  -4.714 2.46e-06 ***
TypeControl -5.731e-01  4.264e-02 -13.441  < 2e-16 ***
Site10-022  -6.258e-01  8.174e-02  -7.656 2.10e-14 ***
Site10-049  -1.374e-01  8.192e-02  -1.677  0.09357 .
Site10-062  -1.334e+00  1.196e-01 -11.152  < 2e-16 ***
Site10-115  -1.361e+02  1.403e+07   0.000  0.99999
Site10-195   3.319e-02  1.153e-01   0.288  0.77343
Site10-237   6.382e-01  2.195e-01   2.907  0.00365 **
Site11-011   1.491e-01  2.076e-01   0.718  0.47265
Site11-039   1.544e+00  2.233e-01   6.914 5.00e-12 ***
Site11-052   5.379e-01  2.223e-01   2.419  0.01556 *
Site12-039   0.000e+00  0.000e+00      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                           edf Ref.df      F  p-value
s(sqrt(N))           1.9330152  1.995 190.35  < 2e-16 ***
s(Time)              1.9963891  2.000  33.25 4.04e-15 ***
s(JDay)              0.0003358  2.000   0.00 3.16e-05 ***
s(TimeAD):TypeCarcass 3.9609992  3.999  33.90  < 2e-16 ***
s(TimeAD):TypeControl 3.9909103  4.000  41.40  < 2e-16 ***
s(JDay):TypeCarcass   3.9356653  3.997 138.27  < 2e-16 ***
s(JDay):TypeControl   3.4813514  3.853  30.06  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.317   Deviance explained = 27.7%
GCV score = 0.087721  Scale est. = 0.087446  n = 9674
```

Grazing given present, gemsbok:

```
Family: quasibinomial
Link function: logit

Formula:
cbind(G, N - G) ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay,
    bs = "cp", k = 3) + s(TimeAD, by = Type, k = 5) + s(JDay,
    by = Type, k = 5) + Type + Site

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -2.063e+00  1.254e-01 -16.444  < 2e-16 ***
TypeControl  4.226e-01  5.500e-02   7.684 1.67e-14 ***
Site10-022  -1.465e+00  1.396e-01 -10.494  < 2e-16 ***
Site10-049  -1.365e+02  2.616e+06   0.000        1
Site10-062  -1.377e+02  1.570e+06   0.000        1
Site10-115  -1.351e+02  2.177e+06   0.000        1
Site10-184  -7.047e-01  1.348e-01  -5.229 1.73e-07 ***
Site10-195  -6.202e-01  1.251e-01  -4.956 7.30e-07 ***
Site10-237  -1.642e+00  1.751e-01  -9.379  < 2e-16 ***
Site11-011   6.178e-01  9.715e-02   6.360 2.10e-10 ***
Site11-039   8.934e-01  1.478e-01   6.044 1.55e-09 ***
Site11-052   5.981e-01  1.398e-01   4.277 1.91e-05 ***
Site12-039   0.000e+00  0.000e+00      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df      F p-value
s(sqrt(N))           1.990  2.000 189.36 < 2e-16 ***
s(Time)              1.994  2.000 261.70 < 2e-16 ***
s(JDay)              1.990  2.000  28.41 2.2e-15 ***
s(TimeAD):TypeCarcass 3.978  3.999 156.40 < 2e-16 ***
s(TimeAD):TypeControl 4.000  4.000 238.27 < 2e-16 ***
s(JDay):TypeCarcass   3.958  3.973 109.42 < 2e-16 ***
s(JDay):TypeControl   3.247  3.492  32.53 < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.349   Deviance explained = 36.9%
GCV score = 0.013718  Scale est. = 0.013679  n = 11552
```

Grazing, zebra:

```
Family: quasipoisson
Link function: log

Formula:
G ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay, by = Site, bs = "cp",
    k = 3) + s(TimeAD, by = Type, k = 5) + s(JDay, by = Type,
    k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -3.65887    0.08019 -45.629  < 2e-16 ***
TypeControl -0.34432    0.02355 -14.621  < 2e-16 ***
Site10-022  -0.82249    0.06070 -13.551  < 2e-16 ***
Site10-049  -0.44576    0.04585  -9.723  < 2e-16 ***
Site10-062  -0.89629    0.09557  -9.378  < 2e-16 ***
Site10-115  -1.36410    0.21139  -6.453 1.14e-10 ***
Site10-184   0.24410    0.09901   2.465  0.01370 *
Site10-195  -0.13822    0.06271  -2.204  0.02753 *
Site10-237   0.55564    0.11312   4.912 9.14e-07 ***
Site11-011   0.60824    0.18577   3.274  0.00106 **
Site11-039   1.28190    0.19043   6.732 1.75e-11 ***
Site11-052   1.55906    0.19664   7.929 2.41e-15 ***
Site12-039   0.00000    0.00000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                           edf Ref.df         F  p-value
s(sqrt(N))           1.9995516  2.000 15847.054  < 2e-16 ***
s(Time)              1.9947542  2.000    27.380 1.37e-12 ***
s(JDay):Site10-016   1.9996050  2.000    13.684 4.03e-07 ***
s(JDay):Site10-022   1.9304856  2.000    67.523  < 2e-16 ***
s(JDay):Site10-049   1.9981793  2.000    30.513 1.50e-14 ***
s(JDay):Site10-062   1.5222983  2.000     4.425  0.00278 **
s(JDay):Site10-115   1.9892227  2.000    45.799  < 2e-16 ***
s(JDay):Site10-184   1.8383554  2.000    16.588 1.14e-08 ***
s(JDay):Site10-195   0.0003742  2.000     0.000  0.35952
s(JDay):Site10-237   1.8494515  2.000    39.157  < 2e-16 ***
s(JDay):Site11-011   1.8752719  2.000    11.819 2.59e-06 ***
s(JDay):Site11-039   1.6322498  2.000     5.030  0.00181 **
s(JDay):Site11-052   1.9468702  2.000    23.128 2.97e-11 ***
s(JDay):Site12-039   1.8466760  2.000     8.681 8.12e-05 ***
s(TimeAD):TypeCarcass 3.5287784  3.851    17.033 3.14e-13 ***
s(TimeAD):TypeControl 3.8957324  3.988    20.935  < 2e-16 ***
s(JDay):TypeCarcass   3.9886915  4.000    33.950  < 2e-16 ***
s(JDay):TypeControl   3.9978231  4.000    31.216  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.747   Deviance explained = 84.5%
GCV score = 0.25158  Scale est. = 0.25051   n = 12138
```

Grazing, springbok:

```
Family: quasipoisson
Link function: log

Formula:
G ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay, by = Site, bs = "cp",
    k = 3) + s(TimeAD, by = Type, k = 5) + s(JDay, by = Type,
    k = 5) + Type + Site

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -2.70956    0.07617 -35.572  < 2e-16 ***
TypeControl -0.13938    0.02706  -5.151 2.62e-07 ***
Site10-022  -0.01582    0.04102  -0.386 0.699796
Site10-049  -0.03936    0.04108  -0.958 0.338023
Site10-062  -0.18023    0.04882  -3.692 0.000224 ***
Site10-115  -0.41115    0.07231  -5.686 1.33e-08 ***
Site10-184   0.39632    0.07085   5.594 2.27e-08 ***
Site10-195  -0.02921    0.06641  -0.440 0.660070
Site10-237   0.36726    0.12517   2.934 0.003351 **
Site11-011  -0.52765    0.27629  -1.910 0.056187 .
Site11-039   1.60266    0.18558   8.636  < 2e-16 ***
Site11-052  -0.29445    0.27555  -1.069 0.285262
Site12-039   0.00000    0.00000      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                           edf Ref.df         F  p-value
s(sqrt(N))           1.9978674  2.000 11842.774  < 2e-16 ***
s(Time)              1.9699880  1.998    59.441  < 2e-16 ***
s(JDay):Site10-016   1.7055126  2.000     5.485  0.00124 **
s(JDay):Site10-022   0.0002108  2.000     0.000  0.74874
s(JDay):Site10-049   1.9304456  2.000    23.375 7.09e-12 ***
s(JDay):Site10-062   1.8305165  2.000    10.592 5.68e-06 ***
s(JDay):Site10-115   1.8908965  2.000    14.535 1.59e-07 ***
s(JDay):Site10-184   1.8517518  2.000    20.291 1.47e-10 ***
s(JDay):Site10-195   0.0001608  2.000     0.000  0.91582
s(JDay):Site10-237   1.5742012  2.000     7.617 6.43e-05 ***
s(JDay):Site11-011   1.9868161  2.000    60.386  < 2e-16 ***
s(JDay):Site11-039   1.8719176  2.000    24.507 2.36e-12 ***
s(JDay):Site11-052   1.9667379  2.000    31.577 1.04e-14 ***
s(JDay):Site12-039   1.7211644  2.000     5.535  0.00159 **
s(TimeAD):TypeCarcass 3.7471349  3.955    22.328  < 2e-16 ***
s(TimeAD):TypeControl 3.8356713  3.979    30.465  < 2e-16 ***
s(JDay):TypeCarcass  3.9906231  4.000    54.912  < 2e-16 ***
s(JDay):TypeControl  3.9696497  3.998    39.422  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.613   Deviance explained = 76.8%
GCV score = 0.44764  Scale est. = 0.44593   n = 13040
```

Grazing, wildebeest:

```
Family: quasipoisson
Link function: log

Formula:
G ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay, bs = "cp", k = 3) +
    s(TimeAD, by = Type, k = 5) + s(JDay, by = Type, k = 5) +
    Type + Site

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -4.409e+00  7.993e-02 -55.164  < 2e-16 ***
TypeControl -2.048e-01  3.174e-02  -6.453 1.15e-10 ***
Site10-022   1.182e-01  4.875e-02   2.424   0.0154 *
Site10-049  -1.268e-01  6.309e-02  -2.009   0.0445 *
Site10-062  -9.773e-01  1.090e-01  -8.963  < 2e-16 ***
Site10-115  -1.327e+02  7.762e+05   0.000   0.9999
Site10-195   4.311e-01  8.549e-02   5.043 4.67e-07 ***
Site10-237  -9.798e-02  1.733e-01  -0.565   0.5719
Site11-011   4.432e-01  1.918e-01   2.310   0.0209 *
Site11-039   1.047e+00  2.026e-01   5.169 2.40e-07 ***
Site11-052   9.439e-01  2.067e-01   4.567 5.00e-06 ***
Site12-039   0.000e+00  0.000e+00      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                        edf Ref.df        F  p-value
s(sqrt(N))            2.000  2.000 16602.56  < 2e-16 ***
s(Time)               1.000  1.000    20.59 5.75e-06 ***
s(JDay)               1.998  2.000    22.97 6.18e-11 ***
s(TimeAD):TypeCarcass 2.393  2.948    15.00 1.63e-09 ***
s(TimeAD):TypeControl 3.925  3.996    41.05  < 2e-16 ***
s(JDay):TypeCarcass   3.998  4.000    20.12  < 2e-16 ***
s(JDay):TypeControl   3.988  4.000    23.78  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.769   Deviance explained = 88.8%
GCV score = 0.10574  Scale est. = 0.10541   n = 9674
```

Grazing, gemsbok:

```
Family: quasipoisson
Link function: log

Formula:
G ~ s(sqrt(N), k = 3) + s(Time, k = 3) + s(JDay, bs = "cp", k = 3) +
    s(TimeAD, by = Type, k = 5) + s(JDay, by = Type, k = 5) +
    Type + Site

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -7.621e+00  9.995e-02 -76.254  < 2e-16 ***
TypeControl  2.608e-01  5.793e-02   4.502 6.80e-06 ***
Site10-022   7.174e-01  9.921e-02   7.232 5.08e-13 ***
Site10-049  -1.294e+02  2.719e+05   0.000   0.9996
Site10-062  -1.296e+02  3.032e+05   0.000   0.9997
Site10-115  -1.292e+02  2.739e+05   0.000   0.9996
Site10-184   1.622e+00  1.161e-01  13.966  < 2e-16 ***
Site10-195   1.014e+00  1.119e-01   9.063  < 2e-16 ***
Site10-237   5.176e-01  1.761e-01   2.939   0.0033 **
Site11-011   1.339e+00  9.167e-02  14.607  < 2e-16 ***
Site11-039   1.637e+00  1.401e-01  11.692  < 2e-16 ***
Site11-052   3.130e-01  1.300e-01   2.408   0.0161 *
Site12-039   0.000e+00  0.000e+00      NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df       F  p-value
s(sqrt(N))           2.000  2.000 7889.93  < 2e-16 ***
s(Time)              2.000  2.000  259.42  < 2e-16 ***
s(JDay)              1.989  2.000   14.16 5.42e-07 ***
s(TimeAD):TypeCarcass 4.000  4.000   84.32  < 2e-16 ***
s(TimeAD):TypeControl 3.920  3.996  139.28  < 2e-16 ***
s(JDay):TypeCarcass   3.989  4.000   32.25  < 2e-16 ***
s(JDay):TypeControl   3.984  3.999  115.87  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.609   Deviance explained = 82.4%
GCV score = 0.02068  Scale est. = 0.020619  n = 11552
```