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*Habitat Relations*

# The Utility of Normalized Difference Vegetation Index for Predicting African Buffalo Forage Quality

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**ABSTRACT** Many studies of mammalian herbivores have employed remotely sensed vegetation greenness, in the form of Normalized Difference Vegetation Index (NDVI) as a proxy for forage quality. The assumption that reflected greenness represents forage quality often goes untested, and limited data exist on the relationships between remotely sensed and traditional forage nutrient indicators. We provide the first study connecting NDVI and forage nutrient indicators within a free-ranging African herbivore ecosystem. We examined the relationships between fecal nutrient levels (nitrogen and phosphorus), forage nutrient levels, body condition, and NDVI for African buffalo (*Syncerus caffer*) in a South African savanna ecosystem over a 2-year period (2001 and 2002). We used an information-theoretic approach to rank models of fecal nitrogen ($N_f$) and phosphorus ($P_f$) as functions of geology, season, and NDVI in each year separately. For each year, the highest ranked models for $N_f$ accounted for 61% and 65% of the observed variance, and these models included geology, season, and NDVI. The top-ranked model for $P_f$ in 2001, although capturing 54% of the variability, did not include NDVI. In 2002, we could not identify a top ranking model for phosphorus (i.e., all models were within 2 $AIC_c$ of each other). Body condition was most highly correlated ($R^2_{adj} = 0.75$; $P \leq 0.001$) with NDVI at a 1 month time lag and with $N_f$ at a 3 months time lag ($R^2_{adj} = 0.65$; $P \leq 0.001$), but was not significantly correlated with $P_f$. Our findings suggest that NDVI can be used to index nitrogen content of forage and is correlated with improved body condition in African buffalo. Thus, NDVI provides a useful means to assess forage quality where crude protein is a limiting resource. We found that NDVI accounted for more than a seasonal effect, and in a system where standing biomass may be high but of low quality, understanding available nutrients is useful for management. © 2012 The Wildlife Society.

**KEY WORDS** African buffalo, fecal indicators, forage quality, NDVI, remote sensing, savanna, South Africa, *Syncerus caffer*.

Understanding forage and diet quality is fundamental to understanding ruminant population dynamics and developing effective management strategies (Grant et al. 2000). Forage quality affects ruminant population vital rates (Cebrian et al. 2008), including adult survival, juvenile survival, and pregnancy rates (Cook et al. 2004). Thus, assessing forage quality is valuable for integrating environmental characteristics with population dynamics. However, relating forage quality to population dynamics requires dietary data collected over multiple years and landscape-scale vegetation sampling can be expensive and logistically complicated, hence, the appeal of indexing forage quality using remotely sensed metrics of vegetation like Normalized Difference Vegetation Index (NDVI).

Managers have used NDVI to assess large-scale patterns in vegetation quality, net primary productivity (NPP), and biomass, with mixed results (e.g., Box et al. 1989, Beck et al. 1990, Markon and Peterson 2002, Moreau et al. 2003, Santin-Janin et al. 2009). Although NDVI has been used as a proxy for forage quality in multiple studies, particularly for ruminants (Boone et al. 2006; Pettorelli et al., 2007, 2011; Jachmann 2008), little has been done to assess the validity of this application. Previously, NDVI has been correlated with reproductive timing and success in both African buffalo (*Syncerus caffer*; Ryan et al. 2007) and elephants (*Loxodonta africana*; Wittemyer et al. 2007, Trimble

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et al. 2009). Similar relationships between NDVI and population dynamics have been demonstrated in a swallow (*Hirundo rustica*; Saino et al. 2004) and an Argentine rodent (*Akodon azarae*; Andreo et al. 2009).

Fecal indices as indicators of ruminant diet are useful for assessing range quality in African savannas (Arman et al. 1975, Sinclair 1977, Erasmus et al. 1978). Fecal nitrogen ($N_f$) and fecal phosphorus ($P_f$) measurements are correlated with body condition, variation in forage quality, and spatial distribution of African buffalo in savanna ecosystems at a variety of spatial and temporal scales (Sinclair and Gwynne 1972, Grant et al. 2000, Macandza et al. 2004, Winnie et al. 2008). Fecal indices are an attractive alternative to direct sampling of forage quality for several reasons; they are 1) easier to acquire at small spatial scales, 2) less expensive to analyze, and 3) directly reflect the dietary decisions of target species. Although fecal indicators are widely used in ruminant studies (Leslie et al. 2008), they are impractical to collect at large spatial scales for long periods of time. Hence, quantifying the relationship between fecal indicators and NDVI would benefit large-scale management of ruminant populations.

African buffalo are protein limited (Sinclair 1977), meaning that protein content and forage phenology are useful measures for population management. Protein, measured as nitrogen, is the most limiting nutrient for grazers (Bell 1971, Owen-Smith and Novellie 1982, Prins 1996). Fecal nitrogen content is highly correlated with forage digestibility (Greenhalgh and Corbett 1960, Leslie and Starkey 1985, Bartiaux-Thill and Oger 1986), dietary protein concentration (Moir 1960*a*, Mould and Robbins 1981, Wofford et al. 1985, Irwin et al. 1993), intake quantity (Arnold and Dudzinski 1963), and changes in live cattle mass (Grant et al. 1996).

Studies have also shown that $P_f$ concentration is a good indicator of dietary phosphorus intake in cattle and wildlife (Moir 1960*b*, 1966; Belonje 1980; Belonje and van den Berg 1980; Holechek et al. 1985; Wrench et al. 1997). Phosphorus can have a large effect on daily weight gain in cattle, and deficiency can hamper growth and reproduction in large mammalian herbivores (Grasman and Hellgren 1993). The relationship between phosphorus and body condition is complicated by the nitrogen budget of the animal. Grant et al. (1996) found that phosphorus supplementation increased average daily weight gain of cattle only when nitrogen concentrations were above 1.2%, and Bortolussi et al. (1996) found that low digestible nitrogen depressed phosphorus absorption, resulting in increased $P_f$. Furthermore, van Niekerk and Jacobs (1985) showed that if dietary nitrogen was limited, then increases in dietary phosphorus had a negative effect on feed intake and live mass change in cattle. Therefore, a balance between dietary nitrogen and dietary phosphorus is required for herbivores to maintain body mass.

Our objectives were to 1) elucidate relationships between NDVI and forage quality for African buffalo, and 2) determine the relative importance of NDVI for predicting forage quality compared to season or geology. We first confirmed that fecal nutrient indices correlated to forage nutrient indices. We then investigated the temporal correlation between $N_f$, $P_f$, NDVI, and body condition. Next, we used model selection to assess the relative utility of NDVI in predicting $N_f$ and $P_f$, compared to simply knowing season and region of the park. Lastly, we examined the prediction intervals of the top ranked model to estimate if the model was applicable to the range of nutrient values observed in this system.

## STUDY AREA

Kruger National Park (KNP; 19,000 km$^2$, 200–840 m elevation) is located in northeast South Africa, with an underlying geology of basaltic and granite-derived soils (Fig. 1). Sandy soils are derived from granite and have high permeability and infiltration (Venter and Gertenbach 1986) resulting in broad-leaf savanna and a herbaceous layer of moderate forage quality in the uplands, a dense herbaceous layer with few trees on the midslopes, and a productive grass layer with thorny shrubs on the foot slopes of drainages (Grant et al. 2000). Basaltic-derived soils are mineral rich, clayey, and have low infiltration. In KNP, the vegetation found on basalts is mopane (*Colophospermum mopane*) shrubland in the north and knobthorn (*Acacia nigrecens*) and marula (*Scelocarya birrea*) savanna in the south (Venter and Gertenbach 1986). Basaltic areas have greater grass production than granitic areas, leading to more frequent burning (Grant et al. 2000).

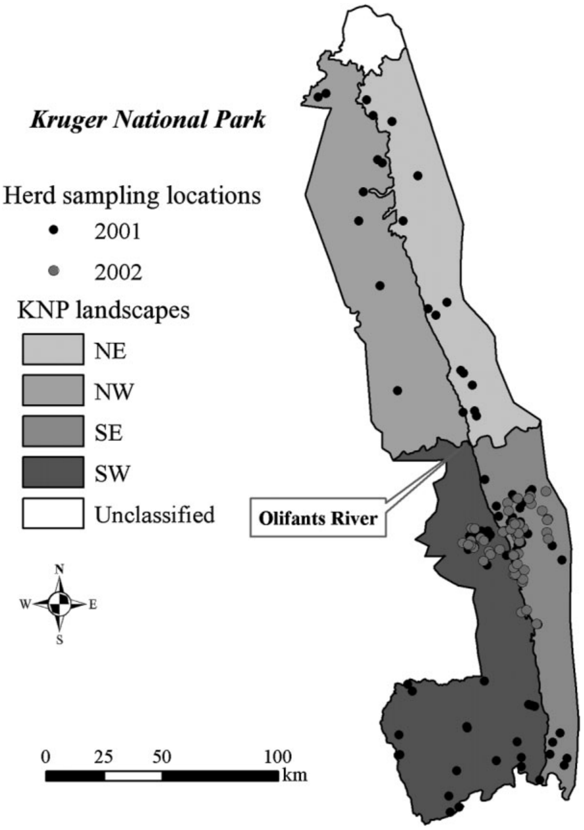

**Figure 1.** Kruger National Park (KNP), South Africa, showing African buffalo herd-sampling locations by year (2001 and 2002). Western landscapes are granite and eastern are basalt; the Olifants River (marked centrally) demarcates the north–south divide in the park.

The mean annual rainfall in KNP is 550 mm, and a north–south rainfall gradient contributes to landscape heterogeneity, wherein the south receives approximately 40% more annual rain than the north (Gertenbach 1980). Annual rainfall follows a unimodal pattern; a wet season from October to March and a dry season from April to September (Ryan and Getz 2005, Ryan and Jordaan 2005, Ryan et al. 2007). To portray and control for season within our data, we split the year into 4 periods: early wet season (Oct–Dec), late wet (Jan–Mar), early dry (Apr–Jun), and late dry (Jul–Sep). During the 2 calendar years of our study, rainfall differed substantially, with 641 mm in 2001 (Jan–Dec) and 288 mm in 2002 (Jan–Dec). Hence, we were able to evaluate the utility of NDVI during wet and dry years.

## METHODS

### Fecal Sample Collection

We used 2 fecal sample datasets, each collected and analyzed for nitrogen and phosphorus content with the same protocol and equipment. We collected samples by locating buffalo herds, either visually from a vehicle and then tracking them, or by radio-telemetry for herds that were the focus of a longer-term dataset. We collected all fecal samples within 12 hours of deposition, by gloved hand, to ensure consistent measurement (Leite and Stuth 1994). We took samples from the center of intact dung piles to reduce any contamination or double-sampling. We air dried samples until they could be transported to an oven where they were dried to a constant weight at 60° C. We collected 10 dung samples at each herd-sampling event, and did not use samples contaminated with dung beetles or fly larvae.

We collected 1 dataset in March and between July and October 2001, partly in conjunction with another study (Caron et al. 2003). These data were from 50 separate herds that were distributed throughout KNP (Fig. 1) and represented late-wet and late-dry season habitat use at a broad spatial scale. We collected the other dataset from the Satara Region (Central-South) of KNP (Fig. 1). The Satara region spans granite and basalt-derived soils from the eastern limit of KNP at the Lebombo Mountains to the western park boundary (see Fig. 1). We collected this dataset from 3 to 4 herds between February 2001 and December 2002, and the number of samples varied by month (Table 1). We only used herd-level samples in which $\geq$5 dung samples yielded data, and we averaged the data by herd. These combined datasets yielded 146 total herd-level fecal samples for our analyses.

### Measurement of Fecal N and P ($N_f$ and $P_f$)

The Near Infrared Spectroscopy (NIRS) technique is less expensive and more rapid than traditional wet lab methods for analyzing fecal samples, and we found it to be a reliable alternative (see Appendix 1). We used NIRS to determine nitrogen and phosphorus concentrations (expressed as g/100 g or %) in fecal material until May 2002. We used wet lab methods, that is, the traditional Kjeldahl wet lab for nitrogen and the Molybdovanadate colourmatic method for phosphorus (Holechek et al. 1982, Leite and Stuth 1990, Lyons and Stuth 1992, Lyons et al. 1995, Foley et al. 1998), on samples collected after May 2002. We used the wet lab results to calibrate the NIRS technique (Appendix 1).

To assess whether samples analyzed for $N_f$ and $P_f$ reflected dietary nitrogen and phosphorus in the feeding patch on which they were obtained, we used data from forage species samples collected between April and December 2002 as part of other studies on forage preferences (Macandza et al. 2004) and habitat structure (Bowers 2006) for African buffalo. Although we did not directly measure passage time for these buffalo, data from cattle suggest that over a range of feed quality, passage time varies from 46 hours to 48 hours (Oshita et al. 2008). In the Bowers (2006) study, buffalo herds were followed and representative forage from buffalo feeding patches was clipped and stored for analyses. We analyzed the samples of forage, both grazed and ungrazed stems, for nitrogen and phosphorus content (expressed as g/100 g or %) using the standard Kjeldahl technique (Association of Official Analytical Chemists 1975). We compared these data, pooled monthly, to mean $N_f$ and $P_f$ values during the same months ($n = 9$) for the same herds.

### Remotely Sensed Vegetation Greenness

We derived remotely sensed vegetation data were derived from the 1-km Advanced Very High Resolution Radiometry (AVHRR) imagery collected by the National Oceanic and Atmospheric Association (NOAA). The AVHRR sensors are on polar orbiting satellites scanning the earth twice per day, providing global coverage since 1981, and have proven useful for monitoring vegetation (Tucker et al. 1986, Townshend 1994). The NDVI is derived from the visible and near-infrared light reflected by vegetation (Tucker 1979) and is calculated from the near infrared (NIR) and red (RED) bands of satellite imagery as:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{RED}}{\mathrm{NIR} + \mathrm{RED}}$$

We received post-processed NDVI data through agreement with the Agricultural Research Council, Institute for Soil, Climate and Water (ARC-ISCW), South Africa. Daily imagery was processed at ARC-ISCW as described in Wessels et al. (2004) using an 8-bit 0–255 scale, with 255 coded as a cloud and atmospheric interference layer. To minimize clouds in the images, the data were re-sampled to dekads (10- to 13-day intervals), yielding 2 or 3 cloud-free images per month, which were averaged by 1.1-km$^2$ resolution pixels as described in previous studies in a nearby reserve (Ryan et al. 2006, 2007). We used the same methods for KNP, with a more recent time-series (2000–2003). The NDVI tends to plateau at relatively low Leaf Area Index, even in grasslands, which must be accounted for when using NDVI as a predictor of forage quality (Fan et al. 2009), particularly in areas with trees or dense shrub. In our analyses, we used ln(NDVI) to portray this response. We divided KNP into 4 regions (areas approximately 3,200–5,900 km$^2$), and took the average monthly NDVI value across the region for each herd. The 4 KNP regions are based on the east–west divide between granite and basalt geology, and the

Table 1. Data used to study the relationships between Normalized Difference Vegetation Index (NDVI) and forage quality for African buffalo, Kruger National Park, South Africa, 2001–2002.

| Year | Season | Month | Number of herds | Forage quality | Fecal samples | Body condition | NDVI |
|---|---|---|---|---|---|---|---|
| 2001 | Late Wet | Feb | 2 | | | X | X |
| | Late Wet | Mar | 25 | | X | X | X |
| | Early Dry | Apr | | | | | X |
| | Early Dry | May | | | | | X |
| | Early Dry | Jun | | | | | X |
| | Late Dry | Jul | 2[a] | | X | X | X |
| | | | 7[b] | | X | | X |
| | Late Dry | Aug | 6 | | X | X | X |
| | | | 6 | | X | | X |
| | Late Dry | Sep | 5 | | X | X | X |
| | | | 11 | | X | | X |
| | Early Wet | Oct | 12 | | X | X | X |
| | | | 1 | | X | | X |
| | Early Wet | Nov | 10 | | X | X | X |
| | Early Wet | Dec | | | | | X |
| 2002 | Late Wet | Jan | | | | | X |
| | Late Wet | Feb | | | | | X |
| | Late Wet | Mar | | | | | X |
| | Early Dry | Apr | 3 | | X | X | X |
| | | | 2[c] | X | X | | X |
| | Early Dry | May | 5 | | X | X | X |
| | Early Dry | Jun | 5 | | X | X | X |
| | | | 2 | X | X | | X |
| | Late Dry | Jul | 4 | | X | X | X |
| | | | 2 | X | X | | X |
| | Late Dry | Aug | 8 | | X | X | X |
| | | | 2 | X | X | | X |
| | Late Dry | Sep | 11 | | X | X | X |
| | | | 2 | X | X | | X |
| | Early Wet | Oct | 10 | | X | X | X |
| | | | 2 | X | X | | X |
| | Early Wet | Nov | 11 | | X | X | X |
| | | | 2 | X | X | | X |
| | Early Wet | Dec | 3 | | X | X | X |
| | | | 2 | X | X | | X |
| 2003 | Late Wet | Jan | 2 | X | X | | X |

[a] Samples from 3 to 4 herds; buffalo did not maintain distinct herds over the time period, although we identified 3–4 main groupings.

[b] Data collected in conjunction with another study (Caron et al. 2003), thus separated for the months in which both datasets were collected (Jul–Oct). We excluded 2 of the original Caron et al. (2003) study samples, because of low fecal sample size.

[c] Data collected as part of Bowers (2006), classifying vegetation; 2 herds were repeatedly the subject of forage quality sampling.

north–south divide at the Olifants River, which is the northern boundary of the Satara region (Fig. 1).

## Body Condition

We collected body condition scores monthly from February 2001 to December 2002 from the 3 or 4 herds in the Satara region. We identified herds with radio collars that were placed on some herd members. We did not score every herd each month and did not repeatedly score herds within a month. The scoring method was adapted from Prins (1989, 1996), using a 1–5 scale where 1 is poor and 5 is good condition, based on visual observations of skeletal protrusions at the pelvis, flank, ribs, neck, and spine (described fully in Caron et al. 2003). Body condition scoring was conducted by 1 researcher (P. Cross) from video of herds crossing roads. To eliminate confounding relationships between condition, age, and parturition status we only used the mean score of females estimated to be >5 years old, without calves. Although we did not collect condition scores simultaneously with fecal collection, they are from the same 3 or 4 herds in the same months, and are assumed to represent the effect of forage quality on body condition.

## Analyses

We used Pearson's correlation coefficient (Zar 1999) to evaluate the relationships between mean monthly dietary nitrogen and $N_f$, and dietary phosophous and $P_f$. We sampled 2 African buffalo herds 9 times from April 2002 to January 2003 (Table 1). Within a herd, we treated monthly samples as independent for correlation analyses. As passage time for buffalo is assumed to be 46–48 hours, comparable to cattle (Oshita et al. 2008), we assumed that buffalo feeding selection and corresponding habitat indicators were independent across months.

We used cross-correlations, that is, correlating 2 time-series by monthly time lags (Crawley 2010), to obtain the greatest correlation coefficients for mean monthly body condition with NDVI, $N_f$, and $P_f$. Within a month

($n = 15$), we sampled anywhere from 2 to 25 herds (Table 1). We subsequently modeled relationships with the greatest significant correlation coefficient using generalized linear models (GLMs; Bolker 2008).

To assess whether NDVI helped explain more of the variability in $N_f$ and $P_f$ than could be accounted for by season or location alone or in combination, we used an information-theoretic approach (Burnham and Anderson 2002). We created GLMs predicting $N_f$ and $P_f$ in 2001 and 2002, incorporating different combinations of seasonality (3 seasons in each year), latitude (north and south in 2001 only), geology (granite and basalt), and ln(NDVI) (Table 2). We included seasonality as a single factor in the model comparisons, that is, either all 3 seasons or none. We used Akaike's Information Criterion corrected for small sample size ($AIC_c$) and Akaike weights to rank models. We viewed models with $\leq 2$ $AIC_c$ from the top-ranking model as informative (Burnham and Anderson 2002). We used $F$-tests to assess model goodness-of-fit and to identify biologically relevant parameters in the models. We report parameter estimates for the top-ranking models (Table 3). We performed statistics in JMP 8.0.2 (SAS Institute, Inc., Cary, NC), and R (Version 2.3.1; R Foundation for Statistical Computing, Vienna, Austria).

# RESULTS

Monthly $N_f$ and dietary nitrogen were correlated (Pearson's $r = 0.98$, $n = 9$, $P \leq 0.001$), as were monthly average $P_f$ and dietary phosphorus (Pearson's $r = 0.85$, $n = 9$, $P = 0.004$; Fig. 3). These results imply that $N_f$ and $P_f$ are useful surrogates for dietary nitrogen and dietary phosphorus for African buffalo in KNP. The percentages of $N_f$ and $P_f$ were greater than corresponding dietary values (Fig. 2) as expected because of metabolic fecal nutrients.

## Body Condition

Observed body condition of African buffalo cows was correlated with NDVI (body condition $= 0.98 \times \text{NDVI} - 1.65$, $R^2_{adj} = 0.44$, $F_{\text{ratio}} = 16.58$, $P \leq 0.001$). Additionally, cross-correlation showed significant associations between body condition and NDVI, with NDVI measured up to 4 months preceding body condition data identified as biologically meaningful ($P \leq 0.05$; Fig. 3). The best predictor was NDVI from the month preceding body condition data (body condition $= 1.17 \times \text{NDVI}_{t-1} - 2.55$, $R^2_{adj} = 0.75$, $F_{\text{ratio}} = 56.93$, $P \leq 0.001$; Fig. 3). Cross-correlations between body condition and $N_f$ were biologically meaningful ($P \leq 0.05$) for 2–4 months lags, with a correlative peak at 3 months (body condition $= 0.97 + 1.39 \times N_{f(t-3)}$, $R^2_{adj} = 0.65$, $F_{\text{ratio}} = 27.19$, $P \leq 0.001$; Fig. 3). We concluded $P_f$ was not significantly correlated with body condition scores at any time lags.

## Models of $N_f$, $P_f$, and ln(NDVI)

The highest ranked model for $N_f$ in 2001 included ln(NDVI), geology, and season ($R^2 = 0.61$, $F_{4,81} = 32.21$, $P \leq 0.001$; Table 2). A competing model ($\Delta AIC_c \leq 2$) included latitude; however, the parameter estimate was deemed uninformative ($P = 0.49$). The highest ranked model for $N_f$ using the 2002 data also included ln(NDVI), geology, and

**Table 2.** Candidate model rankings for predicting fecal nitrogen ($N_f$) and fecal phosphorus ($P_f$) for African buffalo, Kruger National Park, South Africa, in 2001 and 2002.

| Model[a] | $K$[b] | $AIC_c$ | $\Delta AIC_c$[c] | $w_i$[d] |
|---|---|---|---|---|
| $N_f$ | | | | |
| 2001 | | | | |
| ln(NDVI) + geology + season | 5 | −41.07 | 0 | 0.71 |
| ln(NDVI) + geology + season + latitude | 6 | −39.21 | 1.86 | 0.28 |
| ln(NDVI) + geology | 3 | −31.03 | 10.04 | 0.01 |
| ln(NDVI) | 2 | −29.08 | 11.99 | 0.00 |
| Geology + season + latitude | 5 | −23.68 | 17.39 | 0.00 |
| 2002 | | | | |
| ln(NDVI) + geology + season | 5 | −78.95 | 0 | 1.00 |
| ln(NDVI) + geology | 3 | −52.40 | 26.55 | 0.00 |
| ln(NDVI) | 2 | −52.16 | 26.79 | 0.00 |
| Geology + season | 4 | −34.87 | 44.08 | 0.00 |
| $P_f$ | | | | |
| 2001 | | | | |
| Geology + season + latitude | 5 | −112.84 | 0 | 0.46 |
| ln(NDVI) + geology + season | 5 | −112.38 | 0.46 | 0.36 |
| ln(NDVI) + geology + season + latitude | 6 | −111.03 | 1.81 | 0.18 |
| ln(NDVI) + geology | 3 | −59.85 | 52.99 | 0.00 |
| ln(NDVI) | 2 | −54.22 | 58.62 | 0.00 |
| 2002 | | | | |
| ln(NDVI) | 2 | −105.64 | 0 | 0.35 |
| ln(NDVI) + geology | 3 | −104.72 | 0.92 | 0.22 |
| Geology + season | 4 | −104.93 | 0.71 | 0.25 |
| ln(NDVI) + geology + season | 5 | −104.35 | 1.29 | 0.18 |

[a] NDVI, Normalized Difference Vegetation Index.

[b] Number of estimable model parameters.

[c] Difference in value between Akaike's Information Criterion for small sample sizes ($AIC_c$) of the current model and the best model.

[d] Akaike weight: the probability that the current model is the best model.

**Table 3.** Parameter estimates from the 2 top-ranked generalized linear models for predicting fecal nitrogen ($N_f$) in African buffalo, Kruger National Park, South Africa, 2001–2002.

| Model | Parameter | Estimate | SE | $R^2$ |
|---|---|---|---|---|
| $N_f$ (2001) | Intercept | −2.87 | 0.98 | 0.61 |
| | ln(NDVI)[a] | 0.92 | 0.21 | |
| | Season (early wet) | 0.15 | 0.04 | |
| | Season (late wet) | −0.16[b] | 0.09 | |
| | Season (late dry) | 0.01[b] | 0.06 | |
| | Geology (granite) | 0.06 | 0.02 | |
| | Geology (basalt) | −0.06 | 0.02 | |
| $N_f$ (2002) | Intercept | −2.87 | 0.51 | 0.65 |
| | ln(NDVI) | 0.93 | 0.12 | |
| | Season (early wet) | 0.11 | 0.02 | |
| | Season (early dry) | −0.16 | 0.03 | |
| | Season (late dry) | 0.04[b] | 0.03 | |
| | Geology (granite) | 0.06 | 0.02 | |
| | Geology (basalt) | −0.06 | 0.02 | |

[a] NDVI: Normalized Difference Vegetation Index.

[b] Parameter is not significant.

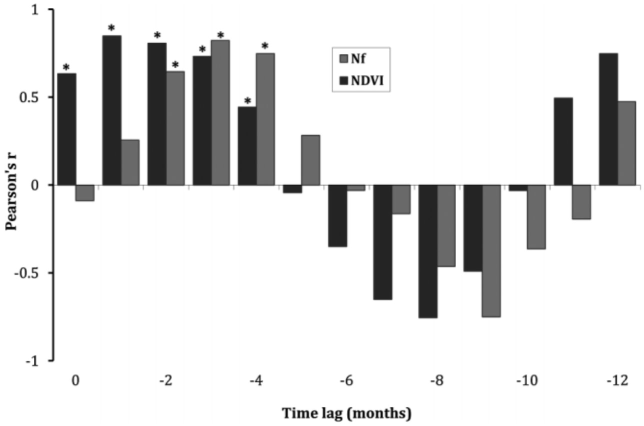

**Figure 3.** Cross correlations (Pearson's *r*) between Normalized Difference Vegetation Index (NDVI) or fecal nitrogen ($N_f$) and African buffalo body condition by month (number of months between the collection of body condition data and either NDVI or $N_f$), in Kruger National Park, South Africa, 2001–2002. Asterisks indicate significant ($P \leq 0.05$) correlations.

season ($R^2 = 0.65$, $F_{4,55} = 25.09$, $P \leq 0.001$; Table 2). We found a positive relationship between $N_f$ and ln(NDVI) in both years (2001: estimate = 0.92, SE = 0.21; 2002 estimate = 0.93, SE = 0.12), and a positive relationship between $N_f$ and the early wet season (2001 estimate = 0.15, 0.15, SE = 0.04; 2002 estimate = 0.11, SE = 0.02), but this was not significant for the late wet season in 2001 or late dry seasons in both years. In 2002, we found a negative relationship with the early dry season (estimate = −0.16, SE = 0.03). In both years, we found $N_f$ had an equal positive relationship with granite landscapes, and a negative relationship with basalt (2001, 2002: granite estimate = 0.06, SE = 0.02; basalt estimate = −0.06, SE = 0.02; Table 3). Prediction intervals for modeled $N_f$ consistently overlapped actual $N_f$ measurements, with lower $N_f$ observed during summer (generally Jun–Oct) in both years (Fig. 4).

The highest ranked 2001 model for $P_f$ included geology, season, and latitude, but not ln(NDVI) ($R^2 = 0.54$, $F_{4,81} = 23.83$, $P \leq 0.001$; Table 2). We also identified 2 competing models ($\Delta AIC_c \leq 2$); 1 including ln(NDVI), and 1 excluding latitude (Table 2). The highest ranked 2002 model for $P_f$ was the ln(NDVI) model ($R^2 = 0.07$, $F_{1,58} = 4.22$, $P = 0.045$), and all candidate models competed (Table 2). Akaike weights were consistently <0.46 and hence no clear top-ranking model could be identified. Our results indicate that substantial variation in $P_f$ was unaccounted for in models using NDVI, geology, and season in KNP.

## DISCUSSION

Prior studies have used NDVI as a proxy for ruminant forage quality without validation. We found NDVI was correlated with body condition measures and $N_f$, but not $P_f$. We also found that $N_f$ was correlated with dietary nitrogen, and thus we suggest that NDVI is a useful predictor of dietary quality for African buffalo. This is a useful finding in an ecosystem

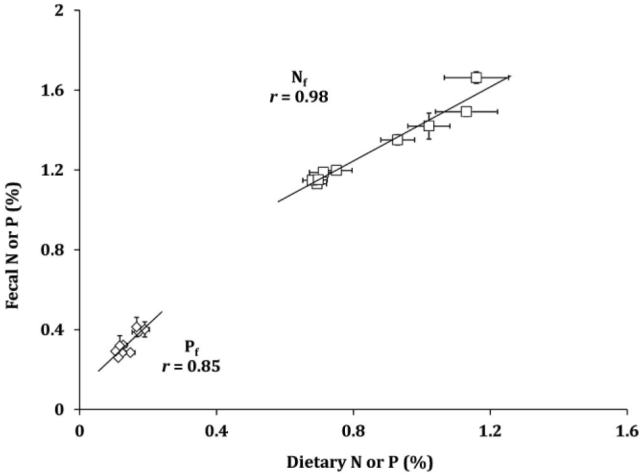

**Figure 2.** Correlations of mean monthly fecal nitrogen ($N_f$; squares) and phosphorus ($P_f$; diamonds) with dietary nitrogen and phosphorus for African buffalo in Kruger National Park, South Africa, 2001–2002. Pearson's *r* is given for each nutrient, and standard errors are shown for both axes.

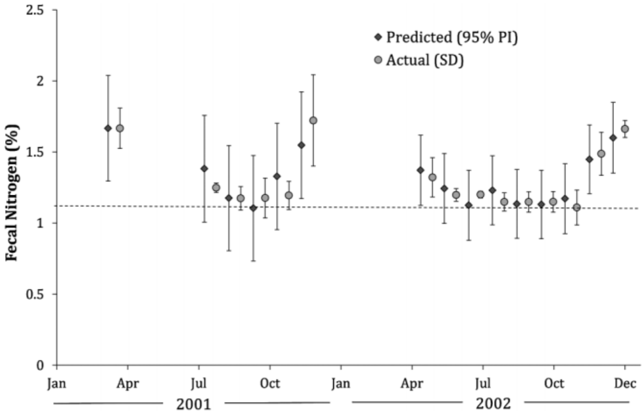

**Figure 4.** Mean actual (with standard deviation; SD) and predicted (with 95% prediction intervals; PI) fecal nitrogen ($N_f$) of African buffalo in Kruger National Park, South Africa for the top-ranked regression models in 2001 and 2002. Dashed line corresponds to minimum dietary needs for buffalo ($N_f = 1.2$).

where the crude protein content of forage is a limiting resource for members of the grazing community. The relationship between NDVI and fecal nutrients has been investigated in at least 2 temperate herbivore systems (Christianson and Creel 2009, Hamel et al. 2009). We are unaware of any other African studies that linked NDVI to $N_f$.

A peak in $N_f$ during the peak growing season has been observed in studies of ruminants on semi-arid and arid landscapes, including domesticated cattle on rangeland (Senft et al. 1987) and desert (Becerra et al. 1998) and for tropical ruminants in parks (Jhala 1997, Padmalal et al. 2003). A corresponding peak in NDVI values reflects the early green growth of plants, which is low in tannins, high in digestible fiber, and allows uptake of plant crude protein; but it does not represent a biomass peak. A positive relationship between $N_f$ and body condition in buffalo was observed by Grant et al. (2000), and measured directly in cattle (Grant et al. 1996). Although we were unable to weigh African buffalo in our study, the body condition index of cows was positively correlated with time-lagged NDVI. Peak $N_f$ preceded peak body condition by 3 months in our study, and peak NDVI preceded the peak in body condition by a month. The positive correlation peaks for both NDVI and $N_f$ with body condition at 1–3 months time lags corroborate our regression models that demonstrated NDVI is a useful predictor of $N_f$ levels. Buffalo in this region calve around the time of peak NDVI (Ryan et al. 2007), and lactation is the most energetically demanding season of the annual life history cycle for cows (Sinclair 1977, Prins 1996). We suggest that sufficient forage biomass accumulation in addition to increased quality may cause the lagged response we found between NDVI, $N_f$, and body condition. The NDVI reflects new growth, but buffalo are bulk grazers, therefore accumulation of sufficient vegetation quantity in addition to high quality may be necessary to achieve good body condition.

To understand protein needs of herbivores, crude forage protein and fecal output can be compared. Sinclair (1975, 1977) quantified minimal dietary protein requirements of African buffalo and wildebeest (*Connochaetes taurinus*) in the Serengeti at 5–6%. In KNP, dry season $N_f$ persisted around 1.2% (4.4% crude protein; see Fig. 4). Grant et al. (1996) found that for cattle, phosphorus supplementation only induced weight gain above 1.2% dietary nitrogen. Thus, African buffalo in KNP may be living at or below their minimum dietary protein requirement as they over-winter.

Fecal nitrogen may lose utility as an indicator of forage quality in extreme environmental conditions. After sustained periods of low dietary nitrogen, such as an extended dry period or temperate winter, grazers deplete fat stores and catabolize muscle leading to increases in $N_f$ (Cook et al. 2004). Thus, using $N_f$ as an indicator of diet quality when resources are most limiting may be difficult. The predictive models for $N_f$ fit our data, but with broad prediction intervals (see Fig. 4). This is likely because of a combination of few data points and a preponderance of dry season data. We expect that additional data would allow us to capture more of the variation, and reduce the prediction intervals.

We suspect that levels of $P_f$ may be affected by seasonal changes in absorption rates, likely in interaction with nitrogen levels. We found $P_f$ was not correlated with body condition or NDVI, suggesting that phosphorus availability is more appropriately measured using direct forage or fecal indicators in KNP. Our regression models suggested that NDVI did not improve our ability to predict $P_f$ beyond simply using geology and season (Table 2).

African buffalo are primarily grazers, and because of their body size and ruminant gut morphology have been called supreme bulk grazers (Owen-Smith and Cumming 1993), implying that their feeding strategy is to maximize biomass intake. In a savanna ecosystem, as the dry season progresses available forage lignifies and becomes unpalatable to the point where even a bulk grazer must become selective (Macandza 2004, Winnie et al. 2008). In buffalo, this selectivity may not be restricted to periods of low quality food; Sinclair and Gwynne (1972) found that during field trials, buffalo in the Serengeti selected the best forage even when pastures contained abundant, high quality forage. Though buffalo will occasionally browse on woody shrubs (Vesey-Fitzgerald 1974, Stark 1986, Ryan et al. 2007), isotopic analyses suggest that woody browse likely represents only a small proportion of their diet (Halley and Minagawa 2005).

## MANAGEMENT IMPLICATIONS

We examined the potential for a more cost-effective means of predicting protein and phosphorus availability to herbivores on large landscapes. We concluded NDVI is a useful predictor of $N_f$ level, which in turn reflects forage nitrogen level, and is correlated with body condition of African buffalo, but lags NDVI by 1 month. We found NDVI was not useful as an indicator of $P_f$ levels, and performed poorly in model comparisons based solely on underlying geology and seasonality. We recommend that NDVI be combined with geology and season to improve estimation of nitrogen availability and ultimately body condition in African buffalo. We revealed time-lagged effects of green vegetation to body condition of female buffalo, which we suggest is the result of early high quality, but low quantity food availability. We caution managers that although NDVI serves as a predictor of forage quality for large ruminants, the role of forage quantity is also informative.

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## APPENDIX 1: NEAR INFRARED SPECTROMETRY METHODOLOGY AND CALIBRATION

We used Near Infrared Spectrometry (NIRS) to determine nitrogen and phosphorus concentrations in all samples collected through April 2002 (Holechek et al. 1982; Leite and Stuth 1990, 1995; Lyons and Stuth 1992; Foley et al. 1998), and wet lab methods on samples from May to December 2002. We collected NIRS data using an NIRS model 5000 monochromator (Foss NIR Systems, Silver Springs, MD), scanning from 11,000 nm to 25,000 nm using 2 nm increments. We ground fecal samples using a Retsch model SM1 mill (Dusseldorf, Germany) with a 1-mm sieve, and scanned samples twice. We took an average measurement value with a root mean square (RMS) limit of 35 nm between scans. For each set of samples, we computed the bounds of spectral measurements. We eliminated 7 samples for calibration that had extreme spectra.

We used 80 samples for NIRS instrument calibration. We obtained wet lab nitrogen and phosphorus values for the 80 samples by the combustion method for nitrogen and by Molybdovanadate colourmatic method for phosphorus (Wenzel and Likens 1991). Using WinISI version 1.5 (Infrasoft International, State College, PA) for chemometric calibration analysis, we chose the best calibration equation (Shenk and Westerhaus 1991, Lyons and Stuth 1992, Leite and Stuth 1995, Lyons et al. 1995). The lab technique using NIRS was shown to capture a significant and high proportion of the variance of the wet-lab measured nitrogen ($r^2 = 0.97$, $n = 77$, $P \leq 0.001$; Standard error of calibration [SEC] = 0.04, Standard error of calibration validation [SECV] = 0.05) and phosphorus ($r^2 = 0.83$, $n = 74$, $P \leq 0.001$; SEC = 0.04, SECV = 0.05). Because of the high correlation between NIRS and traditional techniques, we used the results from the 2 methods interchangeably.

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