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BLACK RHINOCEROS (*DICEROS BICORNIS*) NATURAL DIETS: COMPARING IRON LEVELS ACROSS SEASONS AND GEOGRAPHICAL LOCATIONS

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Abstract: Although excessive iron storage in black rhinoceros (*Diceros bicornis*) has been a cause for continuous concern over the last four decades and differences in the iron content of diet items fed in captivity and in the wild have been documented, no reports exist on the iron content of the total diet ingested by free-ranging animals. Here, the results of field studies using backtracking to record the ingested diets of black rhinoceros from three habitats across three seasons are reported. Levels of iron and of condensed tannins, which might reduce iron availability, averaged at 91 ± 41 ppm dry matter and 3.0 ± 1.0% dry matter, respectively, across all habitats and seasons. Although geographic and seasonal variation was significant, these differences are of a much lower magnitude than differences between the averages of these diets and those fed to black rhinoceros in captivity. The results can provide guidelines for the iron content of diets designed for black rhinoceros and suggest that the effect of tannins in these species should be further investigated.
Key words: black rhinoceros, natural diet, iron, hemosiderosis, tannin.

INTRODUCTION

Over the past decades, much attention has focused on the nutrition of rhinoceros species in captivity due to possible links with a number of pathologies, particularly in black rhinos.[2–4,6,7,10–13] Hemosiderosis, hemolytic anemia, ulcerative dermatitis, peripheral vasculitis, and overall impaired immune function[32] are all suspected to be linked to an inadequate diet and more precisely to mineral and fatty acid imbalances, vitamin deficiencies, and antioxidant status.[12] In captive black rhinoceros, excessive iron storage has been demonstrated regularly at necropsy[13,27,34,36] and has been linked to many apparently idiopathic conditions of captive black rhinoceros that have not been documented in wild black rhinos or their grazing counterparts, the white and Indian rhinoceros.[34,35]

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One of the commonly stated hypotheses concerning the susceptibility of black rhinoceros to excessive iron storage disease is the relatively higher (available) iron content of the diet of captive versus wild animals. Generally, it is thought that animals living on low-iron diets in the wild did not evolve adaptations that prevent excessive iron absorption. In the case of the black rhinoceros, the effect of a generally low dietary iron level and the presence of substances that additionally reduce iron availability, such as tannins, have been suggested to contribute to a generally low content of available iron in the natural diet.[3] A difference between diets fed in captivity and diet items ingested by free-ranging black rhinos appears evident.[3,6] Diets fed in captivity that were analyzed averaged 374 ± 224 ppm iron on a dry matter basis (ranging from 98 to 1,009 ppm),[3] but individual diet items in the wild averaged 82 ± 61 ppm (ranging from 12 to 215 ppm).[14,19] However, these two sets of data cannot be compared directly, because the different quantities ingested of the individual diet items in the wild were not known, making a calculation of the content of the overall diet of the animals impossible. Additionally, a quantitative estimate of the iron content of free-ranging black rhino diets that takes the seasonal changes in chemical composition into consideration and that compares different habitats has not been conducted.

In a study aiming at understanding whether nutritional limiting factors were responsible for the differences in reproductive success between black rhino subpopulations in Southern Africa, the seasonal changes in the dietary chemical contents were documented for three black rhino populations showing contrasting reproduction performance in three different habitats. In this article, the seasonal variations in the dietary iron content in these three free-ranging black rhino populations are presented and compared with values reported for captive black rhino diets.

METHODS

The study was carried out in the Waterberg Plateau Park in North Central Namibia (20°30′S and 17°15′E), the Tswalu Kalahari Reserve in the Northern Cape, South Africa (27°04′S and 22°10′E), and the Great Fish River Reserve in the Eastern Cape, South Africa (32°50′S and 26°30′E). The vegetation at the Waterberg Plateau Park is part of the "Tree Savannah and Kalahari Dry Woodland" vegetation type of Namibia. The mean annual rainfall is 412 mm, with a standard deviation of 129 mm.[15] The rainy season starts in November and ends in March. At Tswalu Kalahari Reserve, the vegetation primarily consists of Shrubby Kalahari Dune Bushveld on the plains and Kalahari Mountain Bushveld in the mountains and hills.[31] Mean annual rainfall is 280 mm, with a standard deviation of 154 mm (records maintained in the park). Rainfall occurs from December to April, with the greatest rainfall in December and the least rainfall in July. The Great Fish River Reserve lies within the Thicket Biome of the Eastern Cape Province. The vegetation is characterized by dense thicket (clumps of thorny and succulent shrubs).[30] The mean annual rainfall is 435 mm (records maintained in the park). The rain normally occurs from October until November and from March until May. However, seasons are not clearly defined, and the reserve, which is located at the junction between the winter rainfall and summer rainfall areas, often gets winter rains.

Data were collected at the Waterberg Plateau Park (May–November 2004 and 2005) and at Tswalu Kalahari Reserve (April–December 2004 and 2005). For the Great Fish River Reserve, the diet profile data were collected from May through November 2002. Plant samples from the Great Fish River Reserve were collected in May, September, and November 2005.

Because it is extremely difficult to follow rhinos during the day and because they feed mainly at night, an indirect observation method called "backtracking" was used.[18,26] Attempts were made to select tracks so that the areas used by black rhinoceros in the respective reserves were represented evenly. The basis of this technique is to follow footprints left by black rhino and record all fresh signs of browsing activity (termed "feeding stations"[21]). Tracking was performed by experienced field scouts. A fresh track from the previous night was located early in the morning and followed backwards. At each feeding station, the number of bites was recorded for each plant species, as well as the plant parts consumed. Bites were identified by the characteristic "pruning" of vegetation, in which the twig is cut off by the proximal molars, leaving a distinctive diagonal cut that is easily detectable.[26] Recent browsing was distinguished from older use by comparing the color of the wood at the point of bite.[16] A bite could be a single severed twig or a group of severed twigs within a hypothetical circle of 10 cm in diameter. At the Waterberg Plateau Park, 138 feeding tracks were successfully followed, 146 at the Tswalu Kalahari Reserve, and 71 at the Great Fish River Reserve.

The study period was classified into three seasonal subdivisions in relation to rainfall, phenologic stage of plant species consumed, and dietary profile. The seasons at the Waterberg Plateau Park were defined as follows: early dry (May–June), late dry (July–September in 2004 and July–October in 2005), and new leaf flushing period (October in 2004 and November in 2005). At Tswalu, seasons were defined as follows: early dry (April–June), late dry (July–September), and flushing period (October–December). At the Great Fish River reserve, seasons were defined as follows: early dry (May–June), late dry (July–September), and flushing period (October–November).

The diameter of every twig bitten by the rhinos was grouped into different diameter classes (<3 mm, 3–<6 mm, 6–<10 mm, 10–<20 mm, 20–<30 mm, 30–40 mm, and >40 mm). In order to estimate the dry mass consumed of each plant species, diameter/dry mass regression equations were developed for leaves and twigs of the species that contributed 80% of the bites along each feeding track.[24] The total dry mass contribution of leaves and stems of a given species was calculated by applying the appropriate regression equation to the standard mean diameter for each twig diameter class and then multiplying this value by the total number of twigs recorded in that same diameter class for that species. The total dry mass contribution for a species is the sum of the dry mass of leaves and stems estimated in each diameter class. For the plant species for which diameter/dry mass regressions were not developed (20% of the remaining bites), the regressions

Table 1. Seasonal variation of the iron content in the diet of three free-ranging black rhinoceros (*Diceros bicornis*) populations.

	Early dry season	Late dry season	Flushing period
Waterberg Plateau Park	61.2 ± 8.7^{aA}	49.5 ± 10.9^{bA}	50.7 ± 8.3^{bA}
Tswalu Kalahari Reserve	100.2 ± 14.8^{aB}	136.7 ± 47.0^{bB}	175.0 ± 31.5^{cB}
Great Fish River Reserve	76.4 ± 14.2^{C}	86.1 ± 19.0^{C}	84.2 ± 20.0^{C}

Seasonal averages (in ppm dry matter) and standard deviation within a row, means with different lowercase superscript differ significantly from each other; within a column, means with a different uppercase superscript differ significantly from each other (analysis of variance with Bonferroni posthoc test).

developed for species similar in structure and shape were used to calculate their dry mass contribution to the diet.

Only the plant species contributing a minimum of 80% of the dry mass ingested by each rhino during the early dry season, late dry season, and flushing period were analyzed. Air-dried samples were ground through a 0.5 mm screen. Leaves and stems were analyzed separately. Iron was analyzed using inductively coupled plasma optical emission spectrometry (Bemlab, Cape Town 7130, South Africa). Condensed tannins (CTs) were analyzed using acid butanol assay, as described in the Tannin Handbook.[22] Sorghum tannin was used as a standard.

The dietary content of iron and CTs for each individual rhino was calculated by multiplying the mean ($n = 5$) value of the concentration of each chemical component in leaves and stems of each plant species by the respective dry mass ingested of each plant part.

The significance level was set at 0.05. All statistical analyses were performed using the SPSS 15.0 (SPSS Inc., Chicago, Illinois 60606, USA) statistical software package. Proportional data were arcsine transformed prior to analysis. The feeding tracks were the independent replicates. Differences between seasons in terms of dietary iron content were tested using one-way analysis of variance. Posthoc significant differences were tested using the Bonferroni test.

RESULTS

Iron content in the diet of black rhinos at Waterberg decreased from the early dry to the late dry season before increasing slightly during the flushing period (Table 1). The dietary iron content was significantly higher during the early dry season than during the late dry season and flushing period. Dietary iron content at Tswalu increased from the early dry season to the flushing period, during which it peaked at 175 ppm on a dry matter basis. The seasonal average iron contents in the diet of black rhinos at Tswalu were significantly different for each one of the three seasons. At the Great Fish River Reserve, dietary iron content increased slightly during the late dry season but remained relatively constant throughout the dry season and flushing period. There were no significant differences between the three seasons.

The average dietary iron content at Tswalu was higher than the average at the other two study sites for each one of the three seasons. The average iron content was the lowest at Waterberg for each one of the three seasons. Dietary iron contents for each season were significantly different between sites.

Dietary CT content at Waterberg decreased from the early dry to the late dry season before rising again during the flushing period (Table 2). The seasonal average CT contents at Waterberg were significantly different for each one of the

Table 2. Seasonal variation of the condensed tannin content in the diet of three free-ranging black rhinoceros (*Diceros bicornis*) populations.

	Early dry season	Late dry season	Flushing period
Waterberg Plateau Park	4.3 ± 0.5^{aA}	4.3 ± 0.5^{bA}	3.4 ± 0.6^{cA}
Tswalu Kalahari Reserve	1.8 ± 0.7^{aB}	1.7 ± 0.7^{aB}	2.8 ± 1.6^{bAB}
Great Fish River Reserve	3.3 ± 1.6^{aC}	3.4 ± 1.5^{aA}	1.9 ± 1.7^{bB}

Seasonal averages (in % dry matter) and standard deviation within a row, means with different lowercase superscript differ significantly from each other; within a column, means with a different uppercase superscript differ significantly from each other (analysis of variance with Bonferroni posthoc test).

three seasons. At Tswalu, the CT content in the diet of black rhinos remained relatively constant during the dry season (early and late dry season) before increasing sharply during the flushing period. Condensed tannin content during the flushing period was significantly higher than during the early or late dry season. At the Great Fish River Reserve, dietary CT content remained constant during the dry season (early and late dry) before decreasing dramatically during the flushing period. The CT level during the flushing period was significantly lower than during the early or late dry season. There was no significant difference between the early and late dry seasons.

Condensed tannin levels in the diets during the early dry season were significantly different between each study site. During the late dry season, the CT level in the diet of black rhinos at Tswalu was significantly lower than at the Great Fish River Reserve and Waterberg. There was no significant difference between CT levels at Waterberg and the Great Fish River Reserve. During the flushing period, dietary CT contents were significantly different between Waterberg and the Great Fish River Reserve. There were no significant differences in the CT levels between Waterberg and Tswalu and between Tswalu and the Great Fish River Reserve.

DISCUSSION

The results of this study must be considered with some caution as to how representative they are for black rhinos in general, or for the vegetation consumed in each of these reserves in particular, because regardless of efforts to achieve a correct inventory of the actual feeding behavior in the reserves, a complete representation of rhino feeding behavior due to the tracks followed cannot be guaranteed. Nevertheless, these results represent the best estimate of a total dietary mineral intake of free-ranging rhinos available to date. At Waterberg, the decrease in dietary iron content towards the late dry season corresponds to a dramatic drop in dietary leaf/twig ratio (close to zero) as deciduous species eaten during the early dry season shed their leaves and are not replaced by evergreen species but by different deciduous species, mainly leafless *Combretum psidioides* and *Grewia avellana*. At Tswalu, the peak in dietary iron content during the flushing period is the result of an increased consumption of *Rhigozum trichotomum*, which has a higher iron concentration than other plant species eaten during that time of year. The consumption of *R. trichotomum* at Tswalu increased from 1.5% during the early dry season to 5.4% during the late dry season and to 16.3% of the total dry mass during the flushing period. The vegetation and therefore the diet at the Great Fish River Reserve consist mostly of succulents that remain green throughout the year; seasons are not well marked, because the reserve lies at the junction between the winter and summer rainfall areas, which can explain the lack of seasonality in the dietary iron content for this site.

The findings on the seasonal diet composition of the black rhinos of this study suggest that although significant differences do occur seasonally in free-ranging populations, these differences are far lower than the general discrepancy between diets of free-ranging and captive specimens. These latter discrepancies should therefore not be downplayed by assertions that seasonal differences in the wild may occur. The evident differences between individual geographic locations were also apparent in serum iron levels of free-ranging black rhinoceros from four different locations.[13] Although putative geographic differences should be considered when using limited data on one or a few subpopulations as a species-specific guideline, the magnitude of the variation between different geographic locations of free-ranging populations is far less than that between animals from captivity and the wild in general. Finally, it could be suggested that other iron sources (e.g., dust or grit adhering to plant parts, soil) are ingested by free-ranging black rhinoceros, which could increase the ingested iron in the wild. The available data, however, suggest that the ingestion of such components in black rhinoceros is comparatively low.[25]

Levels of CTs in the ingested diets were within the range of tannins reported previously for black rhinoceros forages.[2] Variation did occur between regions and seasons, indicating that no specific value for the general tannin content of black rhinoceros diets can be estimated. Black rhinoceros are probably adapted to dietary tannins, possibly due to detoxification mechanisms in the liver (which may be larger than that of white rhinoceros[28]) but also due to inducible salivary tannin-binding proteins.[5] In concert with in vitro and in vivo studies,[17,20,29,33,37] tannins might reduce the absorption of iron in black rhinoceros. Therefore, it has been suggested that browsing rhinos should benefit from the addition of tannins to their diet.[2,3,34] Experimental evidence for this is lacking so far.[3]

Although no influence of tannin supplementation ranging from 0.5% to 1.5% dry matter on iron digestibility could be demonstrated,[3] the reduction in digestibility could occur at the tannin levels observed in free-ranging diets (2.2–3.4% dry matter). Low doses of tannins may have some positive effects in black rhinoceros,[9,10] but the absence of relevant effect on digestion parameters[2,3] suggests that tannin concentrations evaluated so far were comparatively low or that effects of added tannins were not pronounced due to the presence of tannin-binding salivary proteins. Although further research appears warranted, these findings could indicate that for diets used in captivity, a generally low iron level, rather than an inclusion of tannins, might be the more appropriate first step.

Iron oversupplementation is a major area of concern in captive browsing rhinos, which suffer from a variety of uncommon disease syndromes that have been seen in association with iron overload.[32,34] Dietary iron content in zoos is extremely variable, ranging from 98 to 1,009 ppm dry matter, far above the recommended values for domestic horses (40–70 ppm dry matter).[3,6] Dietary iron contents at Waterberg (49.5–61.2 ppm dry matter) fall within this recommended range, whereas iron contents at the Great Fish River Reserve and Tswalu already exceed this range. At 374 ± 224 ppm iron in dry matter,[3] the average dietary iron reported for black rhino diets in zoos is two to five times higher than that observed in the diet of free-ranging rhinos. Ideally, the reasons for high iron levels in the individual diets used should be determined, and individual diet items with high iron levels should be excluded.[23] Particular attention needs to be paid to the composition of compound feeds and mineral supplements.[8] A lack of dietary fibers, both soluble and insoluble, in captive diets may also increase bioavailability of dietary iron in captivity. Although neutral detergent fiber (32–61% dry matter) and acid detergent fiber (17–39% dry matter) contents reported for zoo diets[1,2] are only slightly lower than the dry season average values reported for the three sites in this study (neutral detergent fiber 46–58%; acid detergent fiber: 32–43% dry matter),[24] acid detergent lignin values reported for the zoo diets are much lower (2–8% dry matter) than the acid detergent lignin content reported in this study (17–22% dry matter).

CONCLUSIONS

Seasonal variations in the dietary iron content of free-ranging rhino populations are inconsistent between areas and do not show a clear common seasonal pattern, with one site showing no seasonal changes and another site showing strong seasonal changes. Iron is clearly oversupplemented in captive diets, containing two- to fivefold the amount of iron observed in free-ranging diets. The absence of CTs and the lack of soluble and insoluble fibers in captive diets may increase further the bioavailability of dietary iron. In order to better estimate the actual available iron content in the diet of free-ranging rhinos, studies on the bioavailability of iron in indigenous browse diets are necessary.

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