NUTRITIONAL PHYSIOLOGY OF DUIKERS: A SYNTHESIS

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Introduction

Duikers (*Cephalophus* and *Sylvicapra* spp) form a guild of small antelope inhabiting the forests of sub-Saharan Africa. Local duiker communities are diverse, with 17 species ranging 10-fold in body mass (3 – 80 kg.)[21] Duikers can be adversely affected by forest management and hunting, thus 15 species are listed in the International Union for the Conservation of Nature red list of threatened animals.[12, 15, 18] Duikers are known for their largely fruit diets, and are classified as concentrate selectors according to ruminant feeding strategy scheme of Hofmann. [8, 12,13]. Because small ruminants (< 15 kg) have a high ratio of metabolic rate to fermentation capacity, they are expected to select and require low-fiber, nutrient dense concentrate diets.[6]

In captivity, zoos have attempted to satisfy the nutritional requirements of duikers by feeding them fruit and other concentrates. Traditionally zoos have treated their duikers as virtual omnivores, feeding them a diet consisting of items such as monkey chow, raw meat, apples, grapes, carrots, yams, lettuce and alfalfa (*Sativa medicago*.)[2] However, these diets are typically higher in sugar (80-90% DM), starch and protein, and lower fiber (1-4% dry matter, DM) than natural diets. These differences have often led to nutrient imbalances and health problems in zoos.

Developing a frugivorous browser pellet/diet that incorporates the special digestive needs of duikers and better duplicates the chemical components of native foods may improve health of captive duikers, but requires a better understanding of the nutritional physiology of these small ruminants. Here, I review recent studies of nutritional physiology of duikers, including diet constituents and selection, nutrient requirements, and their ability to harvest, digest, and pass a variety of foods.

Digestive anatomy

Duikers are considered the most primitive of all living African antelopes with a large brain relative to body size.[27] They also have unusually large and wide mouths for picking large fallen fruits. Dukers have relatively large parotid salivary glands that presumably produce proline-rich salivary proteins, which selectively bind to tannins and other phenolics compounds in fruits and leaves.[10, 13, 21, 23] Their rumen is small, simple, S-shaped and densely papillated, thus adapted for rapid turnover of food with a high fermentation rate.[13] The omasum is reduced, containing 6-8 leaflets with a horny papillation. Duikers may use a ventricular groove to shunt high-quality ingesta into the

omasum, thus reducing loss of protein and energy to the rumen microbes.[14] Duikers have a relatively large hindgut that may supplement fermentation in the rumen.

Diet selection

Duikers eat from 25 – 89% fruit, averaging 70 - 80%, with the rest of their diets consisting of flowers, leaves, stems and fungi.[3, 8] A small amount (up to 0.71%) of the contents of duiker stomachs included insects. Juveniles tend to eat more leaves than adults. The size of fruit ingested increases with duiker size, and fruit consumption increases with fruit availability.[8] Duikers ingest all edible fallen fruits, whether whole or parts discarded by arboreal frugivores, and each species consumes a large variety of fruit species. Some studies suggest that the amount of foliage increases with animal size, but others have found equal fruit use but a decreasing use of animal matter with duiker size. [8, 17]

Nutrient composition of wild diets

In contrast to frugivore/concentrate diets fed in zoos, most wild fruits contain a woody, often lignified endocarp protecting a highly nutritious non-toxic endosperm. An analysis of 22 fruits and 45 types of foliage consumed by duikers in natural habitats showed that wild fruits eaten by duikers contained relatively low starch (< 1% DM) and sugar (< 50% DM), with 2-15 times more sugar than starch.[7,11, 17, 20, 21] Both wild fruit and foliage contained moderate to high fiber (24-68% DM neutral detergent fiber, NDF, and 10-50% DM acid detergent fiber, ADF). Tropical fruits also contain a moderate amount of pectin ranging from 3.5 to 12.1%, averaging 5.6 ± 3.3%, which is highly digestible and a rich source of potential energy.[19] Crude protein was higher in leaves (< 20%) than fruits (<10%), but both were higher than protein content in domestic fruits (1-4%.)[7] More than 80% of the food samples contained phenolics, especially condensed tannins that precipitate proteins and reduce protein digestibility, found rarely found in domestic fruits.

Harvesting, intake and rumination

Small ruminants are expected to consume 3-5% body weight per day.[9] In captive trials, Malinga found that blue duikers (3-4 kg, *Cephalophus monticola*) ate about 1.3% of their body mass (0.721 – 2.31 g/kg), and grey duikers (*Sylvicapria grimmia*, 7-11 kg) ate 3.3% of theirs (2.88 – 4.02 g/kg).[17] In other studies offering a wide variety of fruits and foliages, blue duikers (4 kg) ate 21-199 g DM/day (.5 – 5% body mass).[25, 26] Captive blue duikers required at least 800 KJ/day digestible energy (DE) to maintain mass, but consumed up to 2560 KJ DE/day. [25]

Harvesting rates by blue duikers depended on the bite size obtained and fibrousness of forage, and corresponded well with interspecific scaling relationships for herbivores consuming fresh alfalfa.[24, 26] Duikers invested similar number of chews per g when consuming fresh foliage, but chewed about 40% slower for herbivores of similar size.[25, 26]

By consuming whole figs that offered large bites, blue duikers were able to consume domestic figs (*Ficus carica*) 6-8 times faster than they could strip leaves from willow or crop bites of alfalfa.[26] Blue duikers were also able to chew figs, which contained less fiber, faster than the foliage. Therefore, to meet their daily energy requirements in captivity, duikers only had to forage for 15 minutes on figs, whereas they had to forage for over 2.5 hours on alfalfa and 2.45 h on willow (*Salix lasiandra*.)[26] Likewise, Hart found that blue duikers could fill their rumen in only 8 minutes when feeding on the largest wild fruits (5.1-10 cm), but it took 83 min to fill their rumen on very small fruits (0.5-1 cm).[11] It took the larger bay duiker (*C. dorsalis*, 21 kg), 8 times longer to fill its gut on the small fruits than it did the blue duiker, and thus the bay duiker tended to avoided small fruit. Therefore, the smaller the duiker and the larger the fruit, the more time the animal has to search for rarer, more nutritional food items.

Free-ranging duikers spend about half their time stationary, becoming active for only short feeding bouts during the day to fill their small rumen quickly and maintain territorial boundaries.[3, 17] They then retreat to a bedsite to ruminate. The larger red duikers (*C. natalensis,* 12 kg) needed more time to find food, and thus were more mobile, and had larger, overlapping home ranges.[3]

Each day, blue duikers spent 4-5 times longer ruminating higher fiber foliage diets (alfalfa – 4 hr, willow- 6 hr) than the domestic fig diet (1 hr.)[26] They spent more time chewing each bolus and ruminated more boluses per day on foliage. Rumination time increased with fiber content and daily intake.

Mean retention time

Small ruminants are expected to retain ingesta in their digestive tract for a relatively short time, and thus digest it to a lesser extent.[6] However, mean retention time (MRT) for blue duikers eating alfalfa (30 hr) and figs (40 hr) was similar to MRT for ruminants as large as 100 kg.[26] Similarly, Maxwell duikers (*C. maxwelli*, 9 kg) had a relatively long MRT of 42 hr.[4] Mean retention time of cell wall in the blue duiker's digestive tract declined with increasing NDF and cellulose content of the diet.[26] MRT for the liquid ingesta was equal for blue duikers consuming domestic figs, alfalfa and willow (23.4 ± 2.0 hr.)

Nutrient digestibility

Despite current theory that suggests small ruminants cannot digest plant fiber as efficiently and large ones, duikers digest fiber as efficiently as do large herbivores on many diets.[1, 4-6, 10, 11, 25, 26] Within duikers, body size is not correlated with ability to digest fiber.[7, 11] For example, grey duikers had a higher crude fiber and DM digestibility than the much larger domestic sheep (40 kg), Thompson's gazelles (*Gazella thomsonii*, 9-21 kg) and elands (*Tauratragus oryx*, 130-300 kg).[1] Even blue duikers, the smallest in the guild, digested forages from 10% to 50% NDF with 5-20% of the NDF comprised of indigestible acid detergent lignin (ADL), as thoroughly as do larger ruminants.[25] Duikers seem particularly able to digest fiber in domestic figs and native fruits. Virtually all of the non-ADL parts of domestic figs and wild fruits were digested by blue duikers,

and blue and bay duikers digested NDF fiber in domestic figs and wild native figs (*F. capensis*) and wild *Croton humanianus* better than expected for ruminants foraging on leaf and stem diets.[21,25] These small ruminants may achieve this unexpected fiber digestibility by rumen bypass that allows acid digestion of hemicellulose in the true stomach and subsequent fermentation in the hindgut, greater maceration of plant material during ingestion, or greater surface: volume ratio in the small and heavily-papillated gut.[1,4]

However, the duiker's small, simple rumen likely limits its ability to digest very high fiber grasses. For example, when blue duikers were fed bermudagrass hay (*Cynodon dactylon*, 72% NDF) and Kentucky 31 tall fescue (*Festuca arundinacea*, 47% NDF), particles of chewed grass hay escaped the reticulo-omasal orifice and were trapped by the pylorus, causing impaction and death of one blue duiker on each diet.[16]

Protein requirements

Duikers have a relatively low protein (nitrogen, N) requirement in relation to larger ruminants.[7] Blue duikers (2.6 g N/kg DM, and Maxwell's and bay duikers (1.43-1.65 g N/kg DM), and grey duikers (3.63 g N/kg DM) all had lower metabolic fecal nitrogen than the ruminant average (5.1±0.8 g N/kg DM).[1, 4, 23, 25] However, the endogenous urinary nitrogen of blue duikers (194 mg/kg$^{0.75}$/d) exceeded the mean for ruminants (93 ± 40 mg N/kg$^{0.75}$/d.)[23, 25] Regardless, blue duikers required only 643.3 mg N/kg$^{0.75}$/d to maintain nitrogen balance.[25] Non-reproductive male blue duikers were able to maintain nitrogen balance on a diet of domestic figs containing only 6.4% CP.[26] Therefore, if food intake is unrestricted, duikers require a minimum protein content in their diet of about 4%, but would need to eat relatively large quantity if given low N foods.

Tolerance of tannins

Duikers seem to tolerate high-tannin diets better than many herbivores. Although protein and cell wall digestion by bay and blue duikers was lower in higher tannin diets, the protein-precipitating capacity of tannins found in 9 foods fed blue duikers did not consistently reduce the digestibility of neutral detergent solubles and NDF.[10, 21, 25] Tannins did reduce protein digestion in blue duikers, but to a lesser extent than was found in larger ruminants such as deer and elk.[23] Duikers likely have physiological adaptations to handle tannins in forages, such as salivary-binding proteins and larger livers.[7]

Conclusions

The native diet of duikers consisting largely of wild fruits should not be confused with the low-fiber, high-sugar domesticated fruits developed for the human palate.[7] However, duikers are not simply small cattle either. Recent work has shown that duikers can handle large amounts of NDF and relatively low protein. In captivity, duikers are most successful on browser diets relatively low in cellulose and higher in rapidly fermenting substrate such as hemicellulose, pectin and simple carbohydrates.[7] Tannin and lignified

browse may be especially important in maintaining health. Duikers do not require a dietary protein requirement > 12%.

Currently, several zoos and research facilities have successfully fed duikers diets of about 14% CP and 31% NDF that include a herbivore pellet such as Mazuri® Browser Maintenance 5654 (Purina Mills, St. Louis, Missouri), fresh browse, alfalfa hay, and a limited amount of fresh vegetables such as spinach or broccoli, squash, sweet potatoes, carrots, and banana peels.[2, 7, 22, 25]

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