Determinants for the Diet of Captive Agoutis (*Dasyprocta* spp.)

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KEYWORDS

- Dasyprocta
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Sparse attention in the literature has been given to the considerations for an appropriate, practical diet for captive animals of the genus *Dasyprocta* (order Rodentia, family Dasyproctidae, common name agouti). *Dasyprocta* includes 11 extant species distributed throughout Central America, South America, and some associated islands (Coiba Island Panama, Roatan Island Honduras, and the Lesser Antilles). The species name, common name and average weights of the species in this genus are listed in **Table 1**.^{1,2} These species are terrestrial rodents that prefer neotropical savannas and evergreen forests.^{3,4} All species of *Dasyprocta* are diurnal⁵ and are classified as scatter-hoarding frugivores.^{6–9} Current species holdings in zoos that participate in the International Species Information System (ISIS) include *Dasyprocta azarae, D cristata, D fuliginosa, D leporine* (and subspecies), *D mexicana, D prymnolopha*, and *D punctata* (and subspecies).¹⁰

Species in the genus *Dasyprocta* resemble pacas but they are larger and more slender.¹¹ *Dasyprocta* are not burrowers,^{8,11,12} although they use crevices or existing burrows for birthing and raising pups.^{11–13}

DIET CLASSIFICATION

There is much evidence supporting classification of *Dasyprocta* species as a frugivore.^{6–9} For example, *D leporine* is reported to have a wild diet that is 87% fruit, 6% animal matter, 4% fibrous foods, and 2% leaves.^{8,9} There is an equal—if not overwhelming—amount of evidence that species of *Dasyprocta* are omnivores, however.

Dasyprocta, as members of the order Rodentia, have the generalist feeder, rodent dentition to support an omnivorous adaptation.¹⁴ Similar to most caviomorphs, the

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| Table 1 Species name, common name, and average weights of species in the genus <i>Dasyprocta</i> | | |
|---|-------------------------|---|
| Species | Common Name | Average Weight (kg) |
| Dasyprocta azarae | Azara's agouti | 2.7 ¹¹ |
| | | 2–4 ¹ 3.8 ² |
| Dasyprocta coibae | Coiban agouti | |
| Dasyprocta cristata | Crested agouti | |
| Dasyprocta fuliginosaª | Black agouti | 3.5–6 ⁵ |
| Dasyprocta guamara | Orinoco agouti | |
| Dasyprocta kalinowskii | Kalinowski's agouti | _ |
| Dasyprocta leporina ^a | Brazilian agouti or | 3.0–5.9 ¹³ |
| | orange-rumped agouti | 2.7 ^{2,6,11} 4 0–5 8 ⁸ |
| Dasyprocta mexicana | Mexican agouti | 2.0–4.0 ⁵ |
| Dasyprocta prymnolopha | Black-rumped agouti | 3.1–4 kg ¹¹ |
| Dasyprocta punctata ^a | Central-American agouti | 3.0–5.2 ⁵ |
| | | $3.1-4^{11}$ 2- $a^{1,27}$ |
| Dasyprocta ruatanica | Ruatan Island agouti | |

^a There are subspecies.

dental formula of *Dasyprocta* species is I 1/1, C 0/0, P 1/1, M 3/3.¹¹ The incisors are continuously growing with restricted enamel on the anteroventral surface that is resistant to compressive strain and has a sharp edge for shaving and chiseling.¹⁴ The jaw can move forward and create two occlusions: the incisors occlude (for gnawing and chiseling) but the cheek teeth do not, or the cheek teeth occlude (for mastication) and the incisors do not. When the incisors are occluded and used for chiseling nonfood items, the skin of the upper lip can close off the mouth cavity to prevent entry of nonfood material. In general, the upper incisors can cut vegetation and pierce invertebrates or the flesh of vertebrates, and the lower incisors can cut and shear food, including flesh. The cheek teeth are used for grinding and chewing foods, including animal and plant foods.

Further support for classification of *Dasyprocta* species as omnivores is the dentition wear patterns described in wild caviomorph rodents. In one study, a lack of distinctive wear patterns prevented diet specialization classification of wild *Dasyprocta* as a frugivore, folivore, hard-object specialist, browser, or grazer.¹⁵ The dental wear patterns, or lack of patterns, seem to support that these animals are not specialist feeders.

Information provided by field studies also supports classification of *Dasyprocta* species as omnivores. For example, wild *Dasyprocta* eat:

Fruit: citrus fruit and coconuts^{7,16}; avocado, mango, pineapple, tomato, papaya, melon⁷; Syagrus romanzoffiana (Queen palm, Arecaceae).⁴

Plants: leaves,^{3,9} flowers,^{3,16} roots.³

Grains: corn, rice.16

Nuts and seeds: fruit seeds,³ almonds,³ Astrocaryum standleyanum (black palm) seeds,¹⁷ brazil nuts (*Bertholletia excelsa*),¹⁸ dry palm pyrenes (eg, *Bactris*

acanthocarpa, B excelsa, bactris palm),^{18,19} Hymenaea courbaril L (guapino, locust) seeds,²⁰ Ormosia arborea (Legumindae) and Mimusop coriacea seeds,²¹ S romanzoffiana.⁴

Animal Matter: invertebrates.^{3,9,13,22}

Various researchers also report omnivory in *Dasyprocta*. For example, during the fruit season, *Dasyprocta* ate a diet of 37% fruit pulp and 44% fruit seeds supplemented with plant and animal matter. In the off-season, food caches (mostly seeds) and roots were eaten as well as plant and animal matter.^{3,9,13,17,22} With some variation due to climate and location, fruiting season is from March to June. In addition, there is little to no evidence of dietary specialization in either female or male *Dasyprocta*. The lack of dietary variation between the sexes in *Dasyprocta* can probably be attributed to the sharing of territories and common food sources for males and females.^{9,13,20,23} The evidence supporting omnivory in *Dasyprocta* species, in general, affects other determinants of dietary requirements in captives.

GASTROINTESTINAL TRACT

There is a lack of detail describing the physiology of the gastrointestinal tract (GIT) of *Dasyprocta* species, which might be attributed to the assumption of frugivory and assumptions of homology with species that have been studied, such as the guinea pig (*Cavia porcellus*) and the paca (*Agouti paca*). These assumptions of frugivory and of homology with other species mean that there is a tendency for literature to rely on existing information for other species. At this time, there is also a lack of any evidence of cecotrophy.

ENDOGENOUS ASCORBIC ACID

There is some conflicting evidence for the physiologic ability of *Dasyprocta* species to endogenously synthesize ascorbic acid. In support of the need for a dietary source of ascorbic acid, the assumption of classification as a frugivore would indicate lack of an evolutionary ability to endogenously create ascorbic acid.⁷ Captive *Dasyprocta* seem to preferentially select foods high in ascorbic acid and this may indicate an inability to synthesize ascorbic acid.⁷ Such an apparent preference may only indicate a preference for the palatability of those foods higher in ascorbic acid, however (eg, mango, pineapple).

Classification as an omnivore supports endogenous ascorbic acid synthesis in *Dasyprocta*. In addition, because fruits are only available for 4 to 5 months per year, it is questionable how *Dasyprocta* species obtain sufficient dietary sources of ascorbic acid during the off-season. A study on the biosynthesis of ascorbic acid in the acouchi and agouti further supports endogenous ascorbic acid synthesis in *Dasyprocta*. This study reports that both species have the ability to produce endogenous ascorbic acid.²⁴

SCATTER-HOARDING BEHAVIOR

Dasyprocta species are terrestrial scatter-hoarders and various studies report similar caching behavior.^{8,9,23,25} In general, seeds (and nuts) are cached one at a time after the pulp of a fruit is eaten or discarded^{8,20,23} and retrieved at some point after the fruiting season.^{9,23} Retrieval can be as long as 8 months after burial.²³ Caches are covered with soil and usually a leaf or twig is placed on top after burial in a hole 2 to 8 cm deep.²³

METABOLIC RATE

The metabolic rate of *Dasyprocta* species varies according to territorial conditions or the housing conditions of captives.¹⁶ For example, males bonded to a female are more active and have higher respiration rates and body temperatures (use more energy) than animals housed alone, male/male or all-male groups, or male and female non-bonded pairs. The activity of bonded males seems to be related to territoriality, and behaviors include digging, scrape-marking, and scenting.²⁶ Adult males defend their territory against any male at any time but adult females only defend their territory when food is scarce.¹¹

An equation for estimating basal metabolic rate for *Dasyprocta* species from 2.7 to 3.3 kg is $8.78 \times \text{weight (kg)}$.²⁷ In general, females weigh more than males.⁹

APPARENT DIETARY REQUIREMENTS

Studies on the captive diets of *Dasyprocta* are nonexistent. Captive *Dasyprocta* are reported to eat carrots, potatoes, cassava, and cooked ground beef.²³ In general, they eat meat only if cooked but this does not mean they will not eat uncooked flesh. For example, a group of captive *Dasyprocta* killed and ate an adult male *Liomys pictus* (painted spiny pocket mouse).²³

The high proportion of seeds and nuts in the diets of wild *Dasyprocta* along with the selection of foods higher in energy and lower in water content in captive animals⁷ suggest a preference for foods that offer sufficient protein and fats. Protein and fats are minimally available in most fruit pulp.³ For example, avocado is a preferred food of captive *Dasyprocta* and this fruit is high in protein and fat.⁷

Dietary fiber levels for wild *Dasyprocta* seem to be consistent year-round, because of the availability of fruit when in season and the consumption of roots and plant matter during the off-season.⁹ A suggested level of dietary crude fiber for a 2.7 kg animal is 157 g crude fiber/kg dry matter feed (DM).²⁸ Calculation of dietary fiber levels must be based on fruit without peels, because of the penchant of *Dasyprocta* to peel fruit before ingestion.²³

Captive *Dasyprocta* seem to prefer foods high in ascorbic acid.⁷ Again, whether the preference is for the ascorbic acid or the palatable fruit (mango, papaya, melon, oranges, pineapple, and tomato) remains to be determined.

Dasyprocta prefer eating either on elevated surfaces or under and within vegetation. They eat by sitting on their haunches and holding food with their forepaws. Food is often examined and tasted before ingestion, and spherical food or objects from 1.5 cm to 15 cm in diameter seem to be the most appealing.²³ The practice of handling and tasting food before ingestion is probably a form of examination and determination for suitability as a food. For example, wild *Dasyprocta* do not eat seeds containing quinolizidine alkaloids (QA) although they do cache these seeds.²⁹ QAs can disrupt neural function and they are also a teratogen.²¹

LIFE STAGE NUTRITION: REPRODUCTION

Sexual maturity in *Dasyprocta* can occur as early as 6 months of age.⁸ Gestation is approximately 120 days and the precocial pups (one to two) are born furred with their eyes open.^{11,23,30} Neonates weigh about 22.7 g, and the young are tolerated within a territory even after weaning.^{23,31} The mating season of wild *D punctata* is February to April,²³ but in captivity *D punctata* often has two litters per year with about 4 months between litters.^{8,11}

In the wild, pregnant *Dasyprocta* increase the amount of seeds (protein, fat, and energy) in their diets.³ In captive guinea pigs (*C procellus*), another precocial rodent, the average daily energy intake during gestation was 16% greater than normal intake and energy intake while lactating was 92% greater than normal intake.¹² Female agoutis were observed to continue nursing pups as long as 7 weeks post partum.²⁹ As with many species, lactating females should be fed ad lib to guarantee provision of sufficient energy.

Despite the precociality of the pups, they will nurse even while eating solid food.¹² In the wild, at 1 day old, pups nurse, groom, and search leaf litter.²⁹ The lactating female does not provide the pups with solid food, but the pups do follow her and eat from her foods. Learning is probably a dominant factor in food choice, although pups eventually explore and eat foods not introduced by the dam.²⁹

DIABETES

Rodent species have been used for decades as models for human diabetes.³¹ In addition, wild caviomorph rodents (not including *Dasyprocta* species) have a low physiologic activity of insulin (1%–10% of the activity of most mammals),³² and in serum glucose tests, caviomorph species produced more insulin than most mammals.³¹ The current hypothesis states that the higher insulin response in these species is a compensatory mechanism for the lower physiologic activity of their insulin.³¹ This compensatory response may also predispose them to developing diabetes, however.³³

Field studies support the hypothesis that a higher insulin response in caviomorph species may predispose them to diabetes. Three wild caviomorph individuals, two *Abrocoma bennetti* (chinchilla rat) and one *Microcavia niata* (Andean Mountain cavy), had abnormal serum glucose concentration values and cataracts, and all three animals were obese. These are typical symptoms of diabetes.³³ A captive agouti diagnosed with diabetes was also obese and had cataracts.³¹

Extrapolating these findings to *Dasyprocta* species suggests that captives are at extremely high risk for developing diabetes, especially when fed as frugivores. Diabetes in general has become nearly epidemic in captive wild animals. For example, diabetes was once only believed to be a risk factor for sedentary, obese nonhuman primates.^{34,35} Diabetes is increasingly identified in captive animals of other species, however.³⁶

DENTAL CARIES AND PATHOLOGY

Studies of wild *Dasyprocta* suggest that captives are at high risk for developing dental caries and dental pathology. Dental caries were found in wild populations of cavio-morphs, and this seems related to dietary carbohydrates (mainly those containing fructose, glucose, and sucrose)^{37,38} that promote plaque and bacteria.³⁹ Dental caries have been induced in laboratory animals by feeding a soft diet high in carbohydrates.⁴⁰ In wild populations of caviomorphs, frugivores had the highest incidence of dental caries (10.5%–19.8%) in comparison with grazers (1.1%–8.7%).³⁸ Moderate fresh fruit consumption actually decreases the incidence of dental caries in humans.⁴¹

SUMMARY

Although there is no existing research on the dietary physiology and nutrition of captive *Dasyprocta* species, there are several recommendations that can be made for feeding captives. These include:

Feed as omnivores: There is overwhelming evidence that these species are omnivorous despite a preference for fruit when given food choices. Captive diets should have a high percentage (40% as fed) of foods providing protein and fats (avocado, seeds, nuts, legumes) supplemented with plant matter (40% as fed). Other foods, such as corn, oats, rice, rye, wheat, roots (carrots, parsnips), grasses, leaves, hibiscus flowers, and grains should be fed at about a 10% as-fed level. An estimated dietary crude fiber for a 2.7 kg animal is approximately 157 g crude fiber/kg DM.²⁷ Fruit and insects should be provided as environmental enrichment at approximately 10% of foods (as fed).

- Provide opportunities for caching: Scatter-hoarding seems to be an innate behavior of *Dasyprocta* species. In captivity, caching of food would provide activity at the time of burial and later when food is retrieved. Most exhibits could accommodate an area of dirt of sufficient depth for this activity.
- Prevent obesity: Caviomorph species are prone to obesity. Vigilant body condition scoring and weighing is the only way to reliably monitor weight gain or loss. In addition, provision for activity, such as caching opportunities, mazes, elevations, burrows, and puzzle boxes with novel items, encourages activity and energy use.
- Gestation and lactation: The dietary percentage of foods providing protein and fats (seeds, nuts, and so forth) should be increased for gestating females, and the energy content should be increased by at least 16%.¹² Food should be provided ad lib for lactating females.
- Prevent the development of diabetes: Current evidence suggests that wild and captive caviomorphs are at risk for diabetes. To date, it seems that caviomorphs produce more insulin than most mammals to compensate for the lower physiologic activity of their insulin.³¹ This atypical physiologic factor may predispose *Dasyprocta* to developing diabetes. Feeding captive *Dasyprocta* as omnivores and feeding a diet low in fermentable carbohydrates seems to be preventative.³³
- Prevent dental caries: Individuals in wild populations of frugivorous caviomorphs had a 10.5%–19.8% incidence of dental caries.³⁸ This information seems to support that if fed as frugivores, captive *Dasyprocta* are also at high risk for developing dental caries. Feeding captive *Dasyprocta* as omnivores and feeding a diet low in fermentable carbohydrates seems to be a preventative.

REFERENCES

- 1. Redford KH, Eisenberg JF. Mammals of the neotropics, The Southern Cone: Chile, Argentina, Uruguay. Chicago: University of Chicago Press; 1992.
- 2. McNab MK. The influence of food habits on the energetics of eutherian mammals. Ecological Monographs 1986;56:1–20.
- 3. Henry O. Frugivory and the importance of seeds in the diet of the orange-rumped agouti (*Dasyprocta leporine*) in French Guiana. J Trop Ecol 1999;15:291–300.
- Guimarães PR, Lopes PFM, Lyra ML, et al. Fleshy pulp enhances the location of Syagrus romanzoffiana (Arecaceae) fruits by seed-dispersing rodents in an Atlantic forest in southeastern Brazil. J Trop Ecol 2005;21:109–22.
- 5. Emmons LH, Feer F. Neotropical rainforest mammals: a field guide. 2nd edition. Chicago: University Press; 1997.
- 6. Arends A, McNab BK. The comparative energetics of caviomorph rodents. Comp Biochem Physiol A Mol Integr Physiol 2001;130:105–22.
- Laska M, Baltazar JML, Luna ER. Food preferences and nutrient composition in captive pacas, Agouti paca (Rodentia, Dasyproctidae). Mamm Biol 2003;68: 31–41.

- 8. Dubost G, Henry O, Comizzoli P. Seasonality of reproduction in the three largest terrestrial rodents. Mamm Biol 2005;70(2):93–109.
- Dubost G, Henry O. Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. J Trop Ecol 2006;22: 641–51.
- 10. ISIS. International Species Information System. Available at: www.ISIS.org. Accessed December 2008.
- 11. Eisenberg JF, Redford KH. Mammals of the neotropics: the central neotropics, vol. 3. Chicago: The University of Chicago Press; 1999.
- 12. Kunkele J. Energetics of gestation relative to lactation in a precocial rodent, the guinea pig (*Cavia procellus*). J Zool (Lond) 2000;250:533–9.
- Dubost G. Ecology and social life of the red acouchy, *Myoprocta exilis*; comparison with the orange-rumped agouti, *Dasyprocta leporina*. J Zool 1988;214: 107–23.
- 14. Landry SO Jr. The Rodentia as omnivores. Q Rev Biol 1970;45(4):351-72.
- 15. Townsend KEB, Croft DA. Enamel microwear in caviomorph rodents. J Mammal 2008;89(3):730–43.
- 16. Lee TE Jr, Hartline HB, Barnes BM. Dasyprocta ruatanica. Mammalian Species 2006;800:1–3.
- 17. Hoch GA, Adler GH. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). J Trop Ecol 1997;13:51–8.
- Peres CA, Schiesari LC, Diasleme CL. Vertebrate predation of Brazil-nuts (*Bertholletia excelsa, Lecythidaceae*), an agouti-dispersed Amazonian seed crop: a test of the escape hypothesis. J Trop Ecol 1997;13:69–79.
- 19. Silva MG, Tabarelli M. Seed dispersal, plant recruitment and spatial distribution of Bactris acanthocarpa Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. Acta Oecol 2001;22:259–68.
- Guimarães PR Jr, Gomes BZ, Ahn YJ, et al. Cache pilferage in redrumped agoutis (*Dasyprocta leporina*) (Rodentia). Mammalia 2005;69(3–4): 431–4.
- Panter KE, Keeler RF. Quinolizidine and piperidine alkaloid teratogens from poisonous plants and their mechanism of action in animals. Vet Clin North Am Food Anim Pract 1993;9(1):33–40.
- 22. Silvius KM. Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: granivory or "grubivory"? J Trop Ecol 2002;18:707–23.
- 23. Smythe N. The natural history of the Central American agouti (*Dasyprocta punc-tata*). Smithsonian Contrib Zool 1978;257:1–52.
- 24. Yess NJ, Hegsted DM. Biosynthesis of ascorbic acid in the acouchi and agouti. J Nutr 1967;92(3):331–3.
- 25. Guimarães PR Jr, Kubota U, Zacarias B, et al. Testing the quick meal hypothesis: the effect of pulp on hoarding and seed predation of *Hymenaea courbaril* by red-rumped agoutis (*Dasyprocta leporine*). Austral Ecol 2006;31:95–8.
- Korz V, Hendrichs H. Spontaneous behavior and body temperature in male Central American agoutis (*Dasyprocta punctata*) under different social conditions. Physiol Behav 1995;58(4):761–8.
- 27. Huesner AA. Size and power in mammals. J Exp Biol 1991;160:25-54.
- 28. Langer P. The digestive tract and life history of small mammals. Mamm Rev 2002; 32(2):107–31.
- 29. Guimarães PR Jr, Jose J, Galetti M, et al. Quinolizidine alkaloids in *Ormosia arborea* seeds inhibit predation but not hoarding by agoutis (*Dasyprocta leporina*). J Chem Ecol 2003;29(5):1065–72.

- 30. Galef BG, Clark MM. Non-nurturent functions of mother-young interaction in the agouti (*Dasyprocta punctata*). Behav Biol 1976;17:255–62.
- Montiani-Ferreira F, Pachaly JR, Lange RR, et al. Cataract and diabetes in an agouti. In: Anais 15th Congresso Panamericano de Caencias Veterinarias. Campo Grande: Pan American Association of Veterinary Sciences; 1996. p. 71.
- 32. Opazo JC, Soto-Gamboa M, Bozinovic F. Blood glucose concentration in caviomorph rodents. Comp Biochem Physiol A Mol Integr Physiol 2004;137:57–64.
- 33. Garca-Rubi E, Calles-Escandon J. Insulin resistance and type 2 diabetes mellitus—evidence for a role of insulin. Arch Med Res 1999;30(6):459–64.
- 34. Diamond J. The double puzzle of diabetes. Nature 2003;423:599-602.
- 35. Sandrick K. Zoo nutrition: a walk on the wild side. J Am Diet Assoc 2001;101(8): 868–9.
- Sanchez C, Bronson E, Deem S, et al. Diabetes mellitus in a cheetah: attempting to treat the untreatable? In: Proceedings of the American Association of Zoo Veterinarians/American Association of Wildlife Veterinarians. 2005. p. 101–3.
- 37. Pollard MA. Potential cariogenicity of starches and fruits as assessed by the plaque-sampling method and an intraoral cariogenicity test. Caries Res 1995; 29:68–74.
- 38. Sonea K, Koyasuc K, Tanakab S, et al. Effects of diet on the incidence of dental pathology in free living caviomorph rodents. Arch Oral Biol 2005;50:323–31.
- 39. Navia JM. Experimental periodontal disease. Animal models in dental research. Alabama: University of Alabama Press; 1977. p. 312–37.
- 40. Miles AEW, Grigson C. Variations and diseases of the teeth of animals. Cambridge (UK): Cambridge University Press; 1990.
- 41. Edgar WM. Extrinsic and intrinsic sugars: a review of recent UK recommendations on diet and caries. Caries Res 1993;27(Suppl):64–7.