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Supplement: coprophagy in leporids and other mammalian herbivores

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In reviewing coprophagy (more precisely, reingestion: ingesting own faeces directly from the anus) in mammalian herbivores (Hirakawa, 2001), I stated that the Capybara (*Hydrochaerus hydrochaeris*) does not have a colonic separation mechanism, nor does it practise reingestion, following Hörnicke & Björnhag (1980). After publishing this article, Professor Ian Hume in Australia informed me that the Capybara has a selective retention (i.e. separation) mechanism, does practise coprophagy and introduced me to an article (Borges, Dominguez-Bello & Herrera, 1996) that I had overlooked. I then found two other articles that described coprophagy in the Capybara (Herrera, 1985; Mendes *et al*., 2000). In this supplement, I briefly describe the reingestion pattern in the Capybara and revise my previous overview of coprophagy in mammalian herbivores.

The Capybara's daily rhythm of reingestion in the wild (Herrera, 1985) is very similar to that in leporids. The Capybara typically rests in the morning, grazes in the late afternoon and evening, and spends nights alternately grazing and resting. Reingestion is practised during daytime resting periods (07:00–14:00), while most faeces are voided during grazing at night (Ojasti, 1973). Although Herrera's nocturnal observations were not continuous, the observations by Mendes *et al*. (2000) on Capybaras in captivity confirm that reingestion does not occur during the night. The described sequence of reingestion behaviour in the Capybara (Herrera, 1985) is also similar to that in leporids and other reingesting herbivores. The reingested 'pasty' faeces are richer in protein and poorer in gross fibre than the voided 'oval-shaped' faeces (Mendes *et al*., 2000). The description indicates that the two types of faeces are both nutritionally and morphologically differentiated, hence they are what I have referred to as soft and hard faeces in my review. It also suggests that the soft faeces (caecotroph) are an amorphous type, not a 'capsule' type covered with a tough membrane (Hirakawa, 2001). Whether the Capybara also reingests hard faeces is not known. Borges *et al*. (1996) stated that the nitrogen and neutral detergent fibre (NDF) contents in the caecum, colon and stomach of the Capybara dynamically change over a day, suggesting the existence of a separation mechanism.

Overall, the daily reingestion rhythm and digestion style in the Capybara are amazingly similar to those observed in leporids, the Coypu (*Myocastor coypus*) and the Ringtail Possum (*Pseudocheirus peregrinus*). Accordingly, the Capybara should be grouped together with them in fig. 5 in Hirakawa (2001). Figure 6 in Hirakawa (2001) should also be revised as shown in Fig. 1 here. The Capybara is certainly the largest mammalian herbivore to practise reingestion. Professor Hume (personal communication) further suggested that the Common

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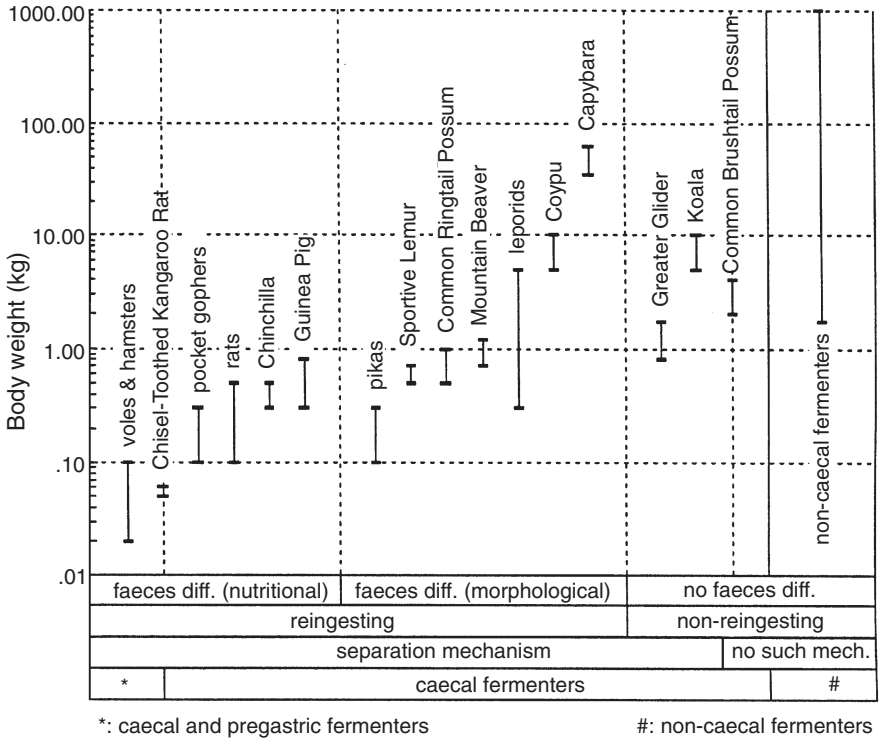

Fig. 1. Ranges of body weights of caecal and non-caecal fermenters arranged according to reingestion behaviour and faeces differentiation (revised from fig. 6 in Hirakawa, 2001). Although a forestomach fermentation chamber has not been reported for the Chisel-Toothed Kangaroo Rat (*Dipodomys microps*), I put it on the border line because I suspect the possibility from its body weight. The Common Brushtail Possum is also placed on the border because it may have a colonic separation mechanism. Body weights are from Walker (1964), MacDonald (1984) and Silva & Downing (1995).

Brushtail Possum (*Trichosurus vulpecula*), previously grouped together with the Capybara, may have some slight selective retention mechanism. If this suggestion is substantiated, the Common Brushtail Possum should perhaps be grouped together with the Koala (*Phascolarctos cinereus*) and Greater Glider (*Petauroides volans*) in Fig. 1 and the category previously consisting of the Common Brushtail Possum and Capybara may disappear. This would simplify the pattern of digestion styles in mammalian caecal fermenters as follows.

Among herbivorous mammals, all caecal fermenters, among which the Capybara is the largest, have a colonic separation mechanism and they are largely divided into three groups. The first group consists of species weighing less than 1.0 kg that produce only nutritionally differentiated faeces and practise reingestion. The second group includes larger species, between 0.1 kg and 100 kg, that produce not only nutritionally but also morphologically differentiated faeces and practise reingestion. The third group currently consists only of marsupial species (the Greater Glider, the Koala, and possibly the Common Brushtail Possum), which have a colonic separation mechanism but do not produce differentiated faeces or practise reingestion.

Further studies and information may necessitate revision of my overview of the reingestion and digestion styles in mammalian caecal fermenters. I hope that this work stimulates such studies and helps advance our understanding of this intriguing phenomenon. I thank

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REFERENCES

Borges, P.A., Dominguez-Bello, M.G. & Herrera, E.A. (1996) Digestive physiology of wild capybara. *Journal of Comparative Physiology B*, **166**, 55–60.

Herrera, E.A. (1985) Coprophagy in capybara, *Hydrochoerus hydrochoeris*. *Journal of Zoology, London*, **217**, 616–619.

Hirakawa, H. (2001) Coprophagy in leporids and other mammalian herbivores. *Mammal Review*, **31**, 61–80.

Hörnicke, H. & Björnhag, G. (1980) Coprophagy and related strategies for digesta utilization. In: *Digestive Physiology and Metabolism in Ruminants* (Ed. by Y. Ruckebusch & P. Thivent), pp. 707–730. MTP Press, Lancaster, UK.

Macdonald, D.W. (1984) *The Encyclopedia of Animals.* Equinox Ltd, Oxford, UK [Japanese edition 1986. Heibonsha Ltd Publishers, Tokyo, Japan].

Mendes, A.C., da Nogueira, S.S., Lavorenti, A. & Nogueira-Filho, S.L.G. (2000) A note on the cecotrophy behavior in capybara (*Hydrochaeris hydrochaeris*). *Applied Animal Behaviour Science*, **66**, 161–167.

Ojasti, J. (1973) *Estudio biológico del chiüguire o capibara*. Ediciones del Fondo Nacional de Investigaciónes Agropecuárias (FONAIAP), Caracas, Venezuela. [in Portuguese, quoted by Mendes *et al*. 2000].

Silva, M. & Downing, J.A. (1995) *Handbook of Mammalian Body Masses*. CRC Press, Boca Raton, FL.

Walker, E.P. (1964) *Mammals of the World*. Johns Hopkins University Press, Baltimore, MD [3rd edn revision by J.-L. Paradiso 1975].

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