

K. Leus

Feeding babirusa (*Babyrousa babyrussa*) in captivity

Abstract

This paper reviews the available information on stomach anatomy, digestion, foraging behavior and diet of wild and captive babirusa. Based on this information, suggestions for changes in the diet of captive babirusa are formulated, which will then need to be assessed.

*Published information suggests that wild babirusa show a marked preference for fruit supplemented with leaves, herbaceous material and a fair amount of animal material as well as mineral-rich soil and water. Behavioral observations on wild and captive babirusa indicated that they usually practice surface foraging, that rooting only takes place in loose soil, that they stand on their hind legs to reach food in higher places and that males tend to monopolize food when animals are fed together. Although unilocular, the babirusa stomach contains an enlarged area of mucus-producing cardiac glands (> 70 % of internal surface area v. 30 % in *Sus scrofa*) with a pH between 5.3 and 6.4 and populations of microorganisms. The true gastric glands are confined to a small gastric unit. Results from two independent digestibility studies on captive babirusa were in concordance with the general characteristics of non-ruminant forestomach fermenting frugivore/concentrate selectors. Passage time experiments suggested that no part of the digestive tract selectively held digesta longer than any other part and that caecocolonic fermentation may be less important in the babirusa than in the Eurasian wild pig. Analyses of the diets offered to babirusa in zoos worldwide revealed a very wide spread in nutritional values. The zoo diets were low in fiber and most zoos fed excess protein and energy. Browse was offered in a non-systematic way. Using the above information and adapted prediction equations suggestions*

for changes in the diet of captive babirusa were formulated, which will then need to be assessed.

Keywords

diet, digestion, nutrition, fermentation, pig

1. Introduction

The babirusa (*Babyrussa babyrussa*) is a remarkable pig endemic to the Indonesian islands of Sulawesi, Buru and the Sula and Togean island groups. The only subspecies currently kept in captivity, *B. b. celebensis*, has been protected under Indonesian law since 1931 (Dammerman 1950, Setyodiwiryo 1959), is included under Annex A of the Convention on International Trade of Endangered Species (CITES) and is registered as vulnerable in the IUCN red list of endangered species (Baillie and Groombridge 1996). The Sulawesi babirusa is threatened in the wild mainly by commercial hunting for the bush meat market, but also by habitat degradation and deforestation (Manansang et al. 1996, Clayton et al. 1997, Clayton and Milner-Gulland 1999). The subspecies is the subject of an international conservation breeding program (Plasa 1998).

Despite having been kept in captivity for at least 200 years, extremely little is known about the nutritional requirements of these animals. However, during the last ten years a number of studies have been carried out on babirusa in captivity which provide us with certain "clues" about what the requirements of these animals might be. Using recent data on stomach anatomy, digestion, foraging behavior and diet of wild and captive babirusa, as well as adapted prediction equations this paper will attempt to formulate a recommended diet for babirusa in captivity which will then need to be tested and refined.

2. Foraging behaviour and diet in the wild

The available information on the composition of the diet of wild babirusa has recently been reviewed (Leus 1996). Further information can be found in Clayton (1996). All information is fairly descriptive and qualitative. Nevertheless, it appears that babirusa have a preference for fruits and seeds but also consume a variety of leaves, grasses, invertebrates and small vertebrates.

The babirusa differs from other pigs by the lack of a well developed rostral bone and as a consequence is only able to root in loose soil or mud (Macdonald 1993). This may imply that roots are less important in the diet of the babirusa compared to that of the other wild pigs. Instead, the foraging behavior of the babirusa mainly exists out of walking around with the nose close to the ground or probing with its nose through the loose leaf litter (Leus and Vercammen 1996). In addition, babirusa have been observed browsing leaves on trees while standing on their hind legs unsupported or with their front legs leaning against the tree trunks (Macdonald and Leus 1995). A number of older reports state that the species tends to live in swampy and marshy areas and along rivers

(Leus 1996). Marsh vegetation is therefore a likely part of the diet. Similarly, babirusa are known to occur at altitudes of at least 1000 m. It is highly likely that they frequent the lower montane forests which are often dominated by Fagaceae trees known for their crops of acorns and chestnuts (Leus 1994, 1996).

Captive babirusa in a semi-natural enclosure showed the ability to very carefully select and obtain certain plants and plant parts. The most frequently consumed food items were unripe cherry fruits and bramble leaves (Leus and Vercammen 1996).

Babirusa in the wild visit volcanic salt licks to drink large quantities of the salty water and to lick the stones and ingest the soil (Patry et al. 1995, Clayton 1996). The specific mineral and vitamin requirements of the babirusa are still unknown.

3. Digestive anatomy

Like the stomach of other pigs, the babirusa stomach consists of one large compartment without any segmentation. However, the stomach of the babirusa is not only much enlarged, but more than 70 % of its internal surface area is lined with mucus producing cardiac glands, compared to about 30 % in *Sus scrofa*. The true gastric only occupies about 12–17 % of the stomach surface. The cardiac gland region has a pH suitable for the survival of microorganisms that are present in high numbers in both the surface mucus layer and the luminal mucus (Langer 1973, 1988, Leus 1994, Leus et al. 1999, Leus and Macdonald [unpubl. observ.]). A frequently discussed function of such microorganisms is bacterial fermentation of plant structural components by means of enzymes, which the host is unable to produce itself (Costerton et al. 1987). The cardiac gland area of the babirusa is therefore likely to be a fermentation area. Only two groups of animals appear to share with the babirusa the possession of an enlarged and elongated stomach part lined almost exclusively with cardiac glands: the colobine monkeys and macropodid marsupials (kangaroos and wallabies) (Langer 1988, Moir 1968, Bauchop 1978, Gemmel 1977).

Forestomach fermenters usually show a system of folds, blindsacs or narrow constrictions in the stomach which slow down the passage of digesta and which separate the fermentation chamber from the low pH of the gastric gland area (Langer 1988). No such structures were found in the babirusa stomach. Furthermore, data on passage time of chyme through the gastrointestinal tract of the babirusa suggested (because of only a single marker excretion peak) that no part of the digestive tract selectively held digesta longer than any other part and that the transit time of digesta for the babirusa is not longer than that for the domestic pig (Leus 1990, Conklin and Dierenfeld 1994). The large size of the cardiac gland area in the babirusa stomach may however allow sufficient separation of the food ingested from the acid and pepsin produced in the "gastric unit", for a long enough time to allow some microbial fermentation to take

place. If fermentation time is indeed limited, breakdown of NDF and ADF may be less efficient than that shown by other forestomach fermenters.

4. Digestibility

Two digestibility studies were carried out on the babirusa (Conklin and Dierenfeld 1994, Leus 1994, 1997) and in both cases the animals did not readily consume the amount of hay or dried grass offered as a source of fiber. Grass may therefore not be a palatable feedstuff for the babirusa.

When consuming a zoo diet (mostly composed of low fiber grain and fresh fruit and vegetables), the babirusa digested the NDF and ADF fractions of the diet equally well (Conklin and Dierenfeld 1994). Babirusa consuming a barley-soya basal diet with dried grass added as a source of fiber digested NDF slightly better than ADF although the difference appeared to become smaller the more grass was added (Leus 1994).

When babirusa and domestic pigs (Large White \times Landrace) were fed the same barley-soya basal diet with added dried grass, babirusa digested the NDF from dried grass origin equally well and the NDF from the whole diet (barley-soybean + dried grass) better than the domestic pigs. In contrast, the babirusa digested the ADF from the whole diet (barley-soybean + dried grass) as well as the domestic pigs but were less able to digest the ADF from the dried grass alone (Leus 1994, 1997).

To assess the relevance of these results for the digestive mechanisms of the babirusa, the following three considerations should be taken into account:

- In the domestic pig, only small amounts of volatile fatty acids (VFA's – the products of bacterial fermentation) are produced in the cranial half of the stomach. By far the largest proportion of VFA's is produced in the caecum and colon (Argenzio and Southworth 1974, Clemens *et al.* 1975). Correspondingly, it was found that almost all cellulose and 80 % of hemicellulose digestion occurs in the large intestine of the domestic pig (Keys and DeBarthe 1974). Babirusa consuming a zoo diet showed low metabolic fecal nitrogen losses which, together with the lack of a secondary marker excretion peak in the transit time study, led to the suggestion that caeco-colonic fermentation may be less important in the babirusa than in the other pigs (Conklin and Dierenfeld 1994).
- In the peccary, another forestomach fermenter and close relative of the pigs, it was shown that although 30 % more VFA's were present in the forestomach compared to the caecum and colon, practically no cellulose digestion occurred in the forestomach (Shively *et al.* 1985, Lochmiller *et al.* 1989). It was therefore concluded that peccaries ferment more easily digestible plant cell components such as hemicellulose in the forestomach whereas the digestion of cellulose is restricted to the caecum and colon (Lochmiller *et al.* 1989).

If caeco-colonic fermentation is indeed less important in the babirusa and if digestion of cellulose in pigs and peccaries occurs in the caecum and colon, then we would expect less efficient digestion of cellulose by the babirusa. Still, if forestomach fermentation is more important in the babirusa than in the domestic pig, one might expect this forestomach fermentation to make up for the less efficient caeco-colonic fermentation as far as the digestion of cellulose is concerned. However, as was discussed above, the anatomical structure of the stomach (unilocular without internal folds or constrictions) will most likely not allow a very efficient fermentation of cellulose. The forestomach fermentation may therefore not be able to make up for the reduced caeco-colonic fermentation in case of ADF fibers originating from food sources such as dried grass or hay which have fairly tough fibrous components. Another possibility is that the babirusa, like the peccary, does not show any cellulose digestion in the forestomach despite the bacterial fermentation occurring in this region and relies entirely on caeco-colonic fermentation for the digestion of this food component.

The above considerations, together with the observation that babirusa appear better able to digest NDF from a largely grain-based diet than domestic pigs, but appear less able to digest ADF from dried grass origin than domestic pigs, strongly suggest that the babirusa is a non-ruminant forestomach fermenting frugivore/concentrate selector. The fact that in the study by Conklin and Dierfeld (1994) ADF and NDF were equally well digested might be related to the fact that the babirusa's ability to digest fiber was not sufficiently challenged because the hay component ("the" fibrous product) in the diet offered was largely ignored.

5. Zoo diet survey

Between March 1991 and May 1993 all zoos with babirusa (16 in Europe, 7 in the USA and 2 in Indonesia) were sent a questionnaire requesting information on the constituents of the diet, the daily amounts fed, the preferences of the animals and the way in which the food was offered. Results from 19 zoos (containing 38 male and 41 female babirusa) were of a sufficiently detailed nature that they could be analyzed for their nutritional contents using published values and prediction equations. The exact method of analysis can be found in Leus (1994) and in Leus and Morgan (1995) where a short report of the results is presented.

The food items offered were divided into 4 categories: 1) fruit and vegetables (F&V), 2) commercial pellets, grains, bread, nuts and oils (P&G), 3) animal products (AP) and 4) browse (grass, hays, branches, leaves etc.). The babirusa received a very wide range of food items: 57 different F&V, 27 P&G, 6 AP and 42 different browses were offered to the animals. In most zoos the diet was built up around a relatively fixed set of core items (such as apple, banana, oranges, carrots, lettuce, leek, yams and potatoes, commercial pellets and grains) which were easily available all year round. These core items were then supplemented with smaller amounts of seasonal fruits, vegetables and browse. Information

on the amounts and types of browse offered was too vague to allow calculation of the percentage of browse in the diet in relation to the other food categories. The data shown below are for the daily diet of adult male and adult female babirusa without the browse.

Table 1 shows the mean amounts of the different food categories offered to the babirusa as well as the nutritional composition of this offered diet. As is obvious from the large standard deviations there was a huge range in the amounts and proportions of the different food items fed. In fact, the range of values for the different nutrients offered is so wide that it is impossible that all these diets are answering the nutritional requirements of the animals. Some zoos offer too much, others not enough. On average, the diet consisted of $\frac{2}{3}$ fruit and vegetables and $\frac{1}{3}$ commercial pellets (for herbivores, horses or pigs) and other grain products. Nine zoos added small amounts of animal products (minced meat, one day chicks, invertebrates, eggs, fish, mice, rats) to the diet on some days of the week.

Table 1

Average amount (g/day) of food (Total fresh weight), fruit and vegetables (F&V), pellets and grains (P&G), animal products (AP), dry matter (DM), crude protein (CP), Fat, englyst fiber (EF) and digestible energy (DE) offered to babirusa in 19 zoos in Europe and North America. (%BW = percentage of body weight; %DM = percentage of dry matter; CP:DE = protein to digestible energy ratio)

	Male	%BW	%DM	Female	%BW	%DM
Total	3128 ± 928	3.5		2733 ± 798	4.5	
F&V	2151 ± 983			1856 ± 831		
P&G	878 ± 577			806 ± 512		
AP*	209 ± 233			148 ± 113		
DM	1069 ± 481	1.2		956 ± 425	1.6	
CP	162 ± 109		15.2	142 ± 84		14.9
Fat	63.9 ± 44.9		6.0	54.4 ± 32.4		5.7
EF	209 ± 136		19.6	184 ± 120		19.2
DE	14.4 ± 6.6			13.0 ± 5.7		
CP:DE	11.3 ± 3.2			10.9 ± 3.2		

* Average of nine zoos that offered animal products.

In the study by Conklin and Dierenfeld (1994), the animals showed a dry matter intake of 1.2 % of their body mass. The wet weight intake was about 2.3 % of Body weight. If we assume an average weight of 90 kg for males and 60 kg for females then the average amount of dry matter offered to male babirusa is equal to the observed intake whereas that offered to the females is

higher. The average wet weight offered to the babirusa as a percentage of body weight was much higher than the intake observed by Conklin and Dierenfeld (1994).

No data are available on the protein and energy requirements of the babirusa. Using prediction equations for the domestic pig based on the protein weight in the body (Whittemore 1993), the babirusa maintenance requirements for crude protein and digestible energy (DE) were calculated and can be found in table 2 (for details of calculations see Leus 1994, Leus and Morgan 1995). The average weight of a male babirusa was taken to be 90 kg and that of a female babirusa 60 kg. A state of maintenance can be defined as a situation where the body composition of the animal remains stable, the animal is not producing any products e.g. milk and it is not performing any work on its surroundings (McDonald et al. 1981). In other words, very active animals, growing animals and pregnant or lactating sows have higher requirements. Nevertheless, a number of zoos appear to be feeding their animals up to four times the required amount of protein and up to two times the amount of digestible energy. As a consequence many babirusa in captivity are obese.

Table 2

Predicted maintenance requirements for CP and DE for an average male (90 kg) and female (60 kg) babirusa in comparison to a Large White domestic pig of similar size. Predictions according to equations in Whittemore (1993). (CP: DE ratio = protein to energy ratio)

Maintenance requirement for:	90 kg Babirusa	90 kg Large White	60 kg Babirusa	60 kg Large White
CP	82 g/day	110 g/day	55 g/day	73 g/day
DE	10.8 MJ/day	13.5 MJ/day	8.0 MJ/day	9.9 MJ/day
CP:DE ratio	7.6 g CP/MJ DE	8.1 g CP/MJ DE	6.9 g CP/MJ DE	7.3 g CP/MJ DE

Mature animals have a smaller need for protein because there is no longer any above maintenance lean tissue growth, but have a higher need for energy to sustain body maintenance activities (McDonald et al. 1981, Whittemore et al. 1993). Mature animals will therefore require a smaller protein:energy ratio in the diet than young growing animals. A protein:energy ratio of 13 gCP/MJ DE is considered to be appropriate for pregnant adult female domestic pigs or growing domestic pigs above 80 kg (Whittemore 1993). The required protein:energy ratio for an adult non-gestating, non-lactating babirusa can therefore be expected to be much lower than that. Indeed, if the ratio is calculated from the predicted CP and DE requirements (see Table 2) then we obtain 7.6 and 6.9 g CP/MJ DE for a 90 kg and 60 kg babirusa respectively. No zoo fed a diet with a ratio that was much lower than the predicted values. However, in the

majority of institutions, both male and female animals were receiving a protein to energy ratio that was much higher than this predicted value.

Fats make proportionally the largest contribution to the DE of the diet and the transfer of dietary fats to body fats is a very efficient process costing the animal very little energy (Whittemore 1993). Considering the problems with obesity in captive babirusa, care should be taken not to feed large amounts of energy. In particular, preventing the feeding of animals by the public may contribute to this. For example, 50 g of peanuts (about half the average packet for sale) contributes 1.23 MJ DE.

Although no data are available on the requirements for fiber, a fiber content of about 19 % of dry matter appears very low for a forestomach fermenter. Daily inclusion of common European and North American browses would significantly improve the amount of fiber consumed (Nijboer and Dierenfeld 1996). As was stated above grasses and hays appear to be less palatable to the babirusa.

Browse offered to the babirusa came in many forms and shapes. A list of the different types of browse offered and the parts eaten can be found in Table 3. A number of zoos did not specify the species of browse fed and their accounts were included under the general terms branches, grass, hay and leaves. In some zoos alfalfa hay was eaten completely whereas others stated that the animals tried to pick out the leaves and would sometimes chew the stems but not eat them. Many zoos offered fresh branches, grass, herbs or alfalfa during the spring and summer seasons and fed dried branches and hays during the winter. The inclusion of browse in the diet was often not on a regular or controlled basis.

Table 3
List of browse items offered to babirusa in 19 zoos
in Europe and North America.

Scientific name	English name	Form	Parts eaten	No. zoos
	Branches	fresh	bark, leaves, twigs, buds	8
	Grass	fresh	entirely	9
	Hay	dry	entirely	4
	Leaves	fresh and dry	entirely	2
<i>Acacia</i> sp.	Acacia	branches fresh	leaves only	3
<i>Acer pseudoplatanus</i>	Sycamore	branches fresh	bark, leaves, twigs	1
<i>Acer rubrum</i>	Red maple	branches fresh	?	1
<i>Acer saccharinum</i>	Silver maple	branches fresh	?	1
<i>Acer saccharum</i>	Sugar maple	branches fresh	?	1
<i>Alnus</i> sp.	Alder	branches fresh	?	1

Table 3
List of browse items offered to babirusa in 19 zoos
in Europe and North America. (continued)

<i>Avicennia germinans</i>	Mangrove	branches fresh	?	1
<i>Betula</i> sp.	Birch	branches fresh	bark, leaves, twigs, buds	3
<i>Celtis occidentalis</i>	Hackberry	branches fresh	?	1
<i>Corylus</i> sp.	Hazel	branches fresh	leaves	1
<i>Crataegus</i> sp.	Hawthorn	branches fresh	leaves	1
<i>Fagus grandifolia</i>	American beech	branches fresh	?	1
<i>Fagus</i> sp.	Beech	branches fresh	leaves	1
<i>Ficus benjamina</i>	Weeping fig	branches fresh	?	1
<i>Forsythia</i> sp.	Forsythia	branches fresh	?	1
<i>Fraxinus</i> sp.	Ash	branches fresh	bark, leaves, twigs	1
<i>Gymnocladus dioica</i>	Kentucky coffee tree	branches fresh	?	1
<i>Hibiscus rosa</i>	Hibiscus	branches fresh	?	1
<i>Hordeum vulgare</i>	Hydroponic barley	fresh	entirely	1
<i>Liquidambar styraciflua</i>	Sweetgum	branches fresh	?	1
<i>Malus</i> sp.	Crabapple	branches fresh	?	1
<i>Medicago sativa</i>	Alfalfa	fresh and dry	entirely	9
<i>Morus alba</i>	White mulberry	branches fresh	?	1
<i>Morus</i> sp.	Mulberry	branches fresh and dry	leaves, bark	1
<i>Musa</i> sp.	Banana	leaves	?	1
<i>Phleium pratense</i>	Timothy hay	dry	?	3
<i>Phyllostachys aurea</i>	Golden bamboo	branches fresh	?	1
<i>Populus alba</i>	White poplar	branches fresh	?	1
<i>Populus euramericana</i>	Poplar	branches fresh	bark, leaves, twigs, buds	2
<i>Quercus rubra</i>	American oak	dried leaves	leaves	1
<i>Quercus</i> sp.	Oak	branches fresh and dry	leaves, bark	2
<i>Robinia pseudoacacia</i>	Black locust	branches fresh	?	1

Table 3

List of browse items offered to babirusa in 19 zoos in Europe and North America. (continued)

<i>Salix babylonica</i>	Weeping willow	branches fresh	?	1
<i>Salix nigra</i>	Black willow	branches fresh	?	1
<i>Salix</i> sp.	Willow	branches fresh	bark, leaves, twigs, buds	4
<i>Trifolium</i> sp.	Clover	fresh	entirely	1
<i>Viburnum</i> sp.	Fragrant honey-suckle	branches fresh	?	1
<i>Vitis vinifera</i>	Grape	branches fresh	?	1
<i>Zea mais</i>	Corn stems	fresh and dried	entirely	1
<i>Zea mais</i>	Corn stems with cobs	fresh and dried	entirely	2
<i>Zingiber</i> sp.	Torch ginger	?	?	1

6. Recommendations/conclusions

6.1 Diet composition

Taking all of the above into account, proposed criteria for a diet are set out in Table 4. Because the babirusa is a non-improved pig species which has a slower growth than domestic pigs, reaches a smaller mature size and has problems with obesity in captivity, the CP and DE energy levels were raised only slightly above the predicted levels for requirements.

As far as dry matter is concerned, the diet below could be achieved by feeding 46 % fruit and vegetables, 27 % commercial pellets and 27 % browse on an as fed basis. However, most commercial pellets used for babirusa today are too rich in protein and energy so that with a 27 % ration, the animals would receive too much protein and energy. Because most of the dry matter fed is derived from the P&G fraction, further reduction of this fraction to bring down the protein and energy content of the diet makes it very difficult to obtain the required intake of DM unless extremely large amounts of fruit, vegetables and browse are fed. The challenge will be to either locate a pellet that is not too rich in protein and energy, or to devise a new pellet that can replace the pellet and browse fractions.

6.2 Browse

For browse, products such as grass and hays have proved to be fairly unpalatable and more difficult to digest. Preference should be given to temperate browse species. However, care should be taken with species such as willow (*Salix* sp.). As is the case with langurs (*Colobinae*), the babirusa will ingest

long strips of the bark that may form a fiber ball in the stomach, as was the case with one female babirusa in Antwerp. The bacterial fermentation of browse will provide an additional supply of protein and energy. The relative contribution of this to the total protein and energy intake can not yet be estimated with the information available.

Table 4

Proposed criteria for a test diet for an average male (90kg) and female (60kg) babirusa in captivity. BW = Body Weight; DM = Dry Matter, CP = Crude Protein, DE = Digestible Energy, CP:DE ratio = protein to energy ratio, NDF = Neutral Detergent Fiber, ADF = Acid Detergent Fiber.

	90 kg babirusa	60 kg babirusa
Total DM intake	1.2% BW = 1080g	1.2% BW = 720g
CP	90g / day	60g / day
DE	11.8 MJ / day	9 MJ / day
CP:DE ratio	7.6	6.9
NDF/ADF	daily browse	daily browse

6.3 Method of feeding

When fed together, males often tend to monopolize the female's food unless she is in oestrous. The main part of the diet, especially the nutritious pelleted ration, should therefore be fed separately. Pieces of fruit and vegetables should be distributed across the floor and in between the bedding and other ground cover and feeding times should be spread over the day so that the animals can perform their normal foraging behavior (walking around with the nose close to the ground) as much as possible. Browse can also be an important enrichment item and must not only be fed at ground level but can also be offered at higher levels so that the animals have to reach high and if necessary stand on their hind legs to reach for food. Because many of the favorite items fed to animals by the public are high fat and high energy items, feeding of animals by the public should be avoided as much as possible.

6.4 Further studies

Because no data are available on the nutritional composition of the diet in the wild, experimentation will be necessary to try out and refine the recommended diet. In addition, there is an urgent need for feed intake data of the current diets being fed, including the browse fraction. Equally urgent and essential are quantitative diet studies in the wild. Their habit of visiting volcanic salt licks may

point to specific mineral requirements and further studies in this field are certainly required.

Nutritional studies on this fascinating pig are not only essential for practical management reasons but will also allow us to reveal the mechanisms of their interesting digestive mechanisms.

Acknowledgements

Many thanks to all the people who played an essential role in the production of the papers that contributed to the present work, in particular Dr. Alastair A. Macdonald, Dr. Colin Morgan, Dr. Ilias Kyriazakis, Mr. Paul Vercammen and all the veterinary, curatorial and keeper staff of the European and North American zoos. The financial support of the Commission of the European Community and the Development Trust of the University of Edinburgh is gratefully acknowledged.

References

- Argenzio, R.A., M. Southworth 1974: Sites of organic acid production and absorption in gastrointestinal tract of the pig. *Am. J. Physiol.* 228: 454–460.
- Baillie, J., B. Groombridge, (eds.) 1996: *IUCN Red List of Threatened Animals*. Gland: IUCN.
- Bauchop, T., 1978: Digestion of leaves in vertebrate arboreal folivores. In: (G. Montgomery, ed.) *The Ecology of Arboreal Folivores*. Washington DC: Smithsonian Institution Press. pp. 193–204.
- Clayton, L.M., 1996: *Conservation Biology of the Babirusa, Babyrousa babyrussa, in Sulawesi, Indonesia*. Unpubl. PhD thesis. Oxford: University of Oxford.
- Clayton, L., M. Keeling, E.J. Milner-Gulland 1997: Bringing home the bacon: a spatial model of wild pig hunting in Sulawesi, Indonesia. *Ecological Applications* 7: 642–652.
- Clayton, L., E.J. Milner-Gulland 1999: The trade in wildlife in North Sulawesi, Indonesia. In: (E.L. Bennett, J.R. Robinson, eds.) *Blood on the leaves: evaluating the sustainability of hunting in tropical forests*. Columbia: Columbia University Press.
- Clemens, E.T., C.E. Stevens, M. Southworth 1975: Sites of organic acid production and pattern of digesta movement in gastrointestinal tract of swine. *J. Nutr.* 105: 759–768.
- Conklin, N.L., E.S. Dierenfeld 1994: Digestibility and passage of a zoo diet fed to babirusa (*Babyrousa babyrussa*). *Zool. Garten N.F.* 64: 357–365.

- Costerton, J.W., K.-J. Cheng, G.G. Geesey, T.I. Ladd, J.C. Nickel, M. Dasgupta, T.J. Marrie 1987: Bacterial biofilms in nature and disease. *Ann. Rev. Microbiol.* 41: 435–464.
- Dammerman, K.W., 1950: Geschiedenis van de natuurbescherming in Indonesië. *Chronica Naturae* 106: 216–228.
- Gemmel, R.T., W. v. Engelhardt 1977: The structure of the cells lining the stomach of the tammar wallaby (*Macropus eugenii*). *J. Anat.* 123: 723–733.
- Keys, J.E., J.V. DeBarthe 1974: Cellulose and hemicellulose digestibility in the stomach, small intestine and large intestine of swine. *J. Anim. Science* 39: 53–56.
- Langer, P., 1973: Vergleichend-anatomische Untersuchungen am Magen der Artiodactyla (Owen, 1848). I. Teil: Untersuchungen am Magen der Nonruminantia (Suiformes). *Gegenbaurs morph. Jahrb.* 119: 514–561.
- Langer, P., 1988: *The mammalian herbivore stomach, comparative anatomy, function and evolution*. Stuttgart/New York: Gustav Fischer.
- Leus, K., 1990: *Inleidende studie tot de voedings- en verteringskarakteristieken van Babyrousa babyrussa L. (hertezwijn): met vermelding van gastro-intestinale parasieten*. Licentiaatsthesis (Unpubl. BSc thesis). Antwerp: Universitaire Instelling Antwerpen.
- Leus, K., 1994: *Foraging behaviour, food selection and diet digestion of Babyrousa babyrussa (Suidae, Mammalia)*. Unpubl. PhD thesis. Edinburgh: The University of Edinburgh.
- Leus, K., 1996: The habitat and diet of the Sulawesi babirusa (*Babyrousa babyrussa celebensis*). In: (J. Manansang, A.A. Macdonald, D. Siswomartono, P. Miller, S. Seal, eds.) *Population and Habitat Viability Assessment for the babirusa (Babyrousa babyrussa)*. Apple Valley: IUCN/SSC Conservation Breeding Specialist Group, pp. 121–143.
- Leus, K., C.A. Morgan 1995: Analyses of diets fed to babirusa (*Babyrousa babyrussa*) in captivity with respect to their nutritional requirements. *IBEX J.M.E.* 3: 41–44.
- Leus, K., P. Vercaemmen 1996: Behaviour of a male and female babirusa (*Babyrousa babyrussa*, Suidae, Mammalia) during the first few days after their move to a semi-natural enclosure. *Zool. Garten N.F.* 66: 133–155.
- Leus, K., A.A. Macdonald 1997: From babirusa (*Babyrousa babyrussa*) to domestic pig: the nutrition of swine. *Proc. Nutr. Soc.* 56: 1001–1012.
- Leus, K., G.P. Goodall, A.A. Macdonald 1999: Anatomy and histology of the babirusa (*Babyrousa babyrussa*) stomach. *C.R. Acad. Sci. paris, Sciences de la vie* 322: 1081–1092.
- Lochmiller, R.L., E.C. Hellgren, J.F. Gallagher, W. Varner, W.E. Grant 1989: Volatile fatty acids in the gastrointestinal tract of the collared peccary (*Tayassu tajacu*). *J. Mammal.* 70: 189–191.

- Macdonald, A.A., 1993: The Babirusa. In: (W.L.R. Oliver, ed.) *Status survey and conservation action plan for pigs, peccaries and hippos*. Gland: IUCN, pp. 161–170.
- Macdonald, A.A., Leus K. 1995. Creating a public understanding of the biology of the babirusa (*Babyrousa babyrussa*) within a caring zoo environment. *IBEX J.M.E.* 3: 37–40.
- Manansang, J., A.A. Macdonald, Siswomartono D, Miller P, Seal S. (eds.) Population and Habitat Viability Assessment for the babirusa (*Babyrousa babyrussa*). Apple Valley: IUCN/SSC Conservation Breeding Specialist Group.
- McDonald, P., R.A. Edwards, J.F.D. Greenhalgh 1981: *Animal Nutrition*. 3rd edition, Essex: Longman Group Ltd.
- Moir, R.J., 1968: Ruminant digestion and evolution. In: (C.F. Code, ed.) *Handbook of Physiology*, Section 6, Alimentary canal, Volume 5. Washington D.C.: American Physiological Society, pp. 2673–2694.
- Patry, M., K. Leus, A.A. Macdonald 1995: Group structure and behaviour of babirusa (*Babyrousa babyrussa*) in Northern Sulawesi. *Austr. J. Zool.* 43: 643–655.
- Plasa, L., 1998: *Internationales Zuchtbuch für den Hirscheber (International Studbook for the Babirusa) Babyrousa babyrussa*. Stuttgart: Wilhelma Zoologisch-botanischer Garten.
- Setyodiwiryo, K., 1959: Nature protection in Indonesia. *Proceedings of the Ninth Pacific Science Congress of the Pacific Science Association* 7: 18–20.
- Shively, C.L., F.M. Whiting, R.S. Swingle, W.H. Brown, L.K. Sowls 1985: Some aspects of the nutritional biology of the collared peccary. *J. Wildl. Manag.* 49: 729–732.
- Whittemore, C.T., 1993: *The Science and Practice of Pig Production*. Harlow: Longman.