

Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*)

RICHARD E. BODMER*

Large Animal Research Group, Department of Zoology, University of Cambridge,
34A Storey's Way, Cambridge CB3 0DT

(Accepted 17 October 1989)

(With 4 figures in the text)

Large non-ruminant ungulates consume the more abundant low-quality forage because this gives them the advantage of reducing search effort. However, large-bodied herbivores would be predicted to search for high-quality fruit patches if these patches were of large size and the fruits rich in nutrients. Diets of lowland tapir (*Tapirus terrestris*), a large non-ruminant of the Amazon basin, were examined from animals of north-eastern Peru to investigate this relationship between high-quality fruit, lower-quality browse and searching behaviour. Lowland tapir consumed on average 33% fruit, which is relatively high for a large non-ruminant ungulate. The fruit portion of lowland tapir diets was dominated by the nutritious *Mauritia flexuosa* (Palmae) drupes, which were selected by tapir more frequently than other fruit types. *M. flexuosa* palms grow in virtually monotypic stands and occur in larger patches than other fruit trees used by terrestrial herbivores of the Amazon. Lowland tapir encountered fruits more frequently when ranging in *M. flexuosa* palm forests than in non-palm forests, because they changed their searching behaviour once they entered palm forests by turning more abruptly. It appears that lowland tapir can consume greater proportions of fruit than other large non-ruminant ungulates, because they exploit a nutritious fruit that occurs in large patches and that meets the energy demands of their large body size.

Contents

	Page
Introduction	121
Materials and methods	122
Preparation of samples for laboratory analysis	122
Analysis of samples	122
Analysis of searching behaviour	124
Identification and analysis of plants	124
Fruit availability and selection ratios	124
Results	124
Discussion	127
References	128

Introduction

Foraging strategies of herbivores are determined by the balance between the costs of searching for food and exposure to predators and the food's nutritional quality (Belovsky, 1978; Crawley, 1983; Stephens & Krebs, 1986). Low-quality forages usually consist of plant parts that have large proportions of cellulose, in contrast to high-quality forages that consist of accessible soluble and

* Present address: Dept. Zoologia, Museu Paraense Emilio Goeldi, Caixa Postal 399, 66.040 Belém, PA, Brazil

storage carbohydrates, proteins, or fats (Van Soest, 1982; Demment & Van Soest, 1985). Large non-ruminant herbivores are efficient at digesting low-quality forage per unit time, because their large digestive systems allow both long retention and rapid throughput (Demment & Van Soest, 1985). Large ungulates use the strategy of consuming large quantities of the more abundant low-quality forage rather than lesser quantities of the scarcer high-quality forage (Bell, 1971; Foose, 1982). The use of abundant forage has the important advantage of reducing search effort. It appears likely that large non-ruminant ungulates would not meet their nutritional demands if they concentrated on searching for scarce high-quality forage (Demment & Van Soest, 1985).

There could be several circumstances where large non-ruminant herbivores would search for high-quality foods. These include situations where high-quality food is found in sufficiently large patches to overcome the costs of searching, where foods have sufficient nutritional value for the energy gain from each food item to outweigh the costs of searching, and where high-quality foods are superabundant. In the case of high-quality food items that do not meet these requirements, the prediction would be that large non-ruminant herbivores would eat them when they came across them, but would not go out of their way to search for them.

Whether foraging by lowland tapir (*Tapirus terrestris*) agrees with the above predictions and how these animals alter their searching behaviour in relation to high-quality fruit is examined in this paper. The lowland tapir (150 kg) is the only large-bodied non-ruminant herbivore of the Amazon ecosystem. From the previous discussion it would be predicted that this ungulate would consume large quantities of lower-quality browse accompanied by smaller quantities of higher-quality fruits. This was investigated by examining species of preferred fruits and their distribution in the forest. Searching behaviour of the lowland tapir was then examined to determine how they were selectively searching for fruit in large patches.

Materials and methods

The study was conducted in lowland plain rainforests of north-eastern Peru in an area approximately 500 km², situated 100 km south-east of the city of Iquitos (Fig. 1). The 2 major rivers that occur in the study area include the black water Rio Tahuayo and the white water Quebrada Blanco.

Stomach and caecal contents of lowland tapir were collected from animals shot by local hunters of the Rio Tahuayo-Quebrada Blanco study area (Bodmer, Fang & Moya Ibanez, 1988) and faecal samples were collected during forest censuses.

Preparation of samples for laboratory analysis

Stomach, caecal and faecal samples were either washed while still fresh or stored labelled in a 30-gallon drum of 5% formaldehyde. Fresh stomach and caecal samples were weighed before washing. All samples were washed by being emptied into a 0.2 mm² mesh cloth that was thoroughly rinsed in fresh water. Samples were then labelled, placed in trays, and air-dried at 30–34 °C for approximately 14 days. If mould started to form during drying, 10% formaldehyde was lightly sprayed over the sample. When thoroughly dried, the contents were placed in air-tight plastic bags and stored for further analysis. This method of preservation was very successful, with only 1% of samples turning mouldy during storage.

Analysis of samples

A total of 44 samples from lowland tapir were analysed. Food types were determined by selectively removing all particles greater than 5 mm², either by hand or by using a wire mesh with a 5 mm² grid size. These

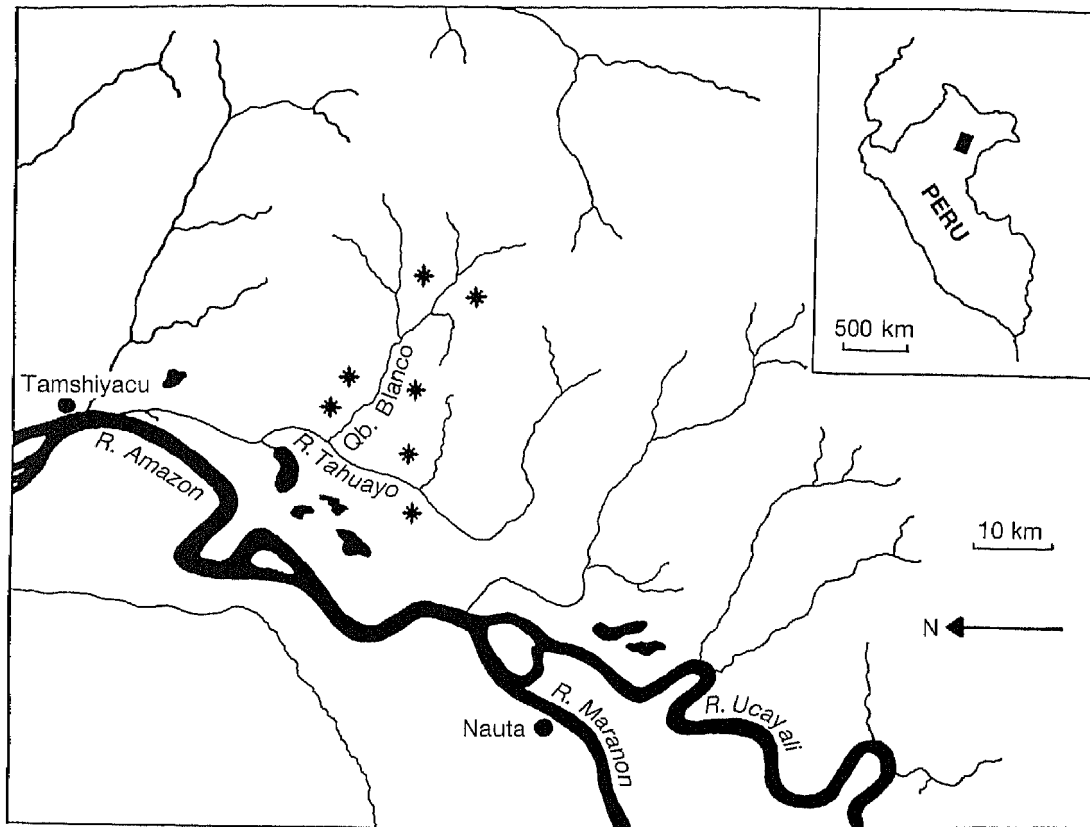


FIG. 1. Map of the study area; stars indicate the locations where lowland tapir trails were followed.

large particles were then separated into individual types and weighed, and a portion was mounted on cardboard with glue in order to be identified later. The rest of the sample was considered as small particles. Percentage occurrence of food types was calculated by determining the number of samples that contained each specific type.

Food-part data were analysed by determining the proportion of fruit, leaf and fibre within each sample. This was done for each sample by randomly removing between 10 and 20 g of the small particles and dividing them into fruit, leaf and fibre. Each of these divisions was weighed and the proportion of each extrapolated to the entire sample of small particles. The large particles were also separated into food parts and weighed. Calculation of food parts was finally completed by adding the corresponding parts of the small-particle and large-particle analyses.

There were no significant differences in the proportions of fruit, leaf and fibre between the stomach ($n = 15$), caecal ($n = 4$), and faecal ($n = 25$) samples (ANOVA, all combinations $P > 0.2$). These samples were therefore lumped during the dietary analyses. Caecal samples were collected from the same animals as stomach samples and were treated as independent samples. This was justified because there is approximately 30 h difference between food in the stomach and caecum, determined from the passage rate of food in lowland tapir guts (Foose, 1982).

Analysis of searching behaviour

Searching behaviour of lowland tapir was analysed by calculating the degree of turning which a tapir made every 10 m along its trail. This was done by following 58 different tapir trails and recording 570 directional changes, 433 in non-palm forests and 137 in palm forests. The rate at which fruit was encountered within each 10 m was recorded while the animals' trails were being followed. The rate of encountering fruits was also recorded during 400 10-m sections of straight vegetational transects. Transects always had a directional change equal to zero.

Identification and analysis of plants

Fruit and seed samples were compared and identified with the assistance of Rodolfo Vasquez at the herbarium of the Universidad Nacional de la Amazonia Peruana and by the book written by van Roosmalen (1985). Samples were identified to family, genus, or species levels.

Pulp and seed weights were obtained by drying fruits at 30–34 °C for a continuous period of 14 days, removing the pulp from the seed with a scalpel or small pocket knife and recording the dry weights of each.

Strength of seeds was measured by cracking them with an Instron 1122 to determine load at breaking point (*p*).

Residual fruit production, or fruit production minus those fruits consumed by arboreal frugivores, was measured with fruit traps following Smythe (1970) and Terborgh (1983). Fruit traps, each with an area of 1 m², were set at 20 m intervals along straight transects at a height of 0.5 m. Fifty traps were placed in *terra firme* (dry land) forests and 50 in mixed floodplain/palm forests. Fruit traps were emptied twice a month and the contents were put into 2 separate bags, one for *terra firme* traps and the other for floodplain/palm traps. Fruits were separated from leaves and stems, placed in labelled trays and dried for 14 days at 30–34 °C. When thoroughly dried, fruits were put in air-tight plastic bags for further analysis.

Fruit availability and selection ratios

Availability of fruits was calculated by the number of months that a fruit type occurred in either *terra firme* or floodplain/palm fruit traps. The proportion of a given fruit type available in the habitat was then calculated from the entire data set of monthly occurrences.

Food selection ratios were calculated by the index developed by Ivlev (1961). Values between 0 and 1.0 indicated increasing positive selection for that fruit type, whereas values between 0 and –1.0 indicated increasing negative selection, consumption being at frequencies lower than availability (Cock, 1978). Selection ratios for red brocket deer (*Mazama americana*), grey brocket deer (*Mazama gouazoubira*), collared peccary (*Tayassu tajacu*) and white-lipped peccary (*Tayassu pecari*) of *M. flexuosa* fruits were used for comparison (Bodmer, 1989).

Results

Lowland tapirs consumed large quantities of fruit for their body size. Stomach, caecal and faecal samples contained 33 ± 17.3% fruit and 66 ± 17.4% leaf and fibre. Leaf and fibre were consumed in greater proportions than fruit ($F_{1,82} = 73.7$, $P < 0.001$).

The fruit consumed by the lowland tapir was dominated by the pulp of the *Mauritia flexuosa* drupe, which occurred in 76.3% of the lowland tapir samples. The next most common fruit consumed by the tapir was the *Jessenia* sp. drupe that occurred in 23.7% of the samples. The only other fruits occurring in more than 10% of the tapir samples were *Scheelea* sp. (13.2%), Sapotaceae (10.5%), and Araceae (10.5%) (Fig. 2).

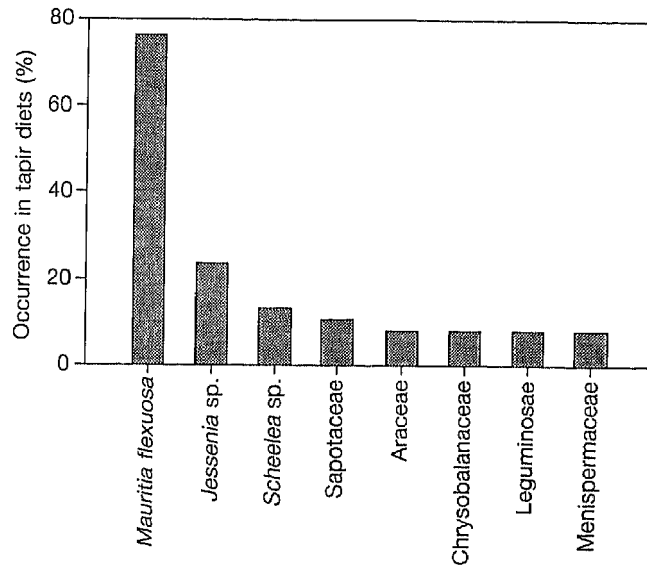


FIG. 2. The percentage occurrence of fruit types in stomach, caecal and faecal samples of lowland tapir. Only fruits that occurred in three or more of the 44 samples are depicted.

The lowland tapir preferred the *M. flexuosa* drupe to other fruit types and showed a considerably greater preference for it than did any other ungulate species. Indeed, the selection ratio for *M. flexuosa* fruit by the lowland tapir was more than double that for the second most preferred fruit, Sapotaceae (Fig. 3). Selection ratios by white-lipped and collared peccaries for

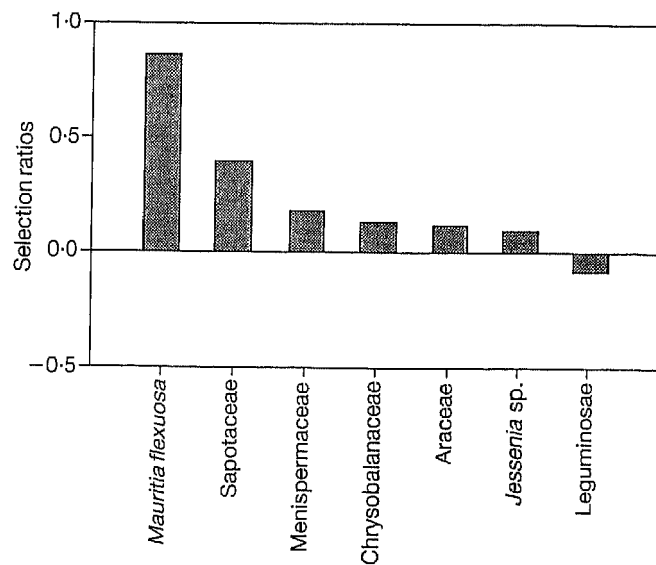


FIG. 3. Selection ratios of fruit types consumed by lowland tapir. *Scheelea sp.* has been omitted because of its absence from fruit traps.

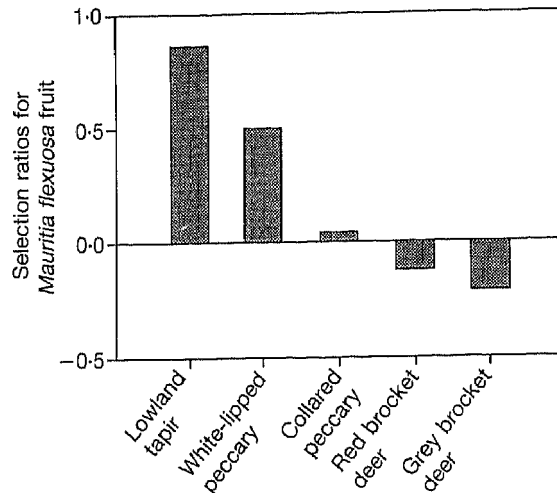


FIG. 4. Selection ratios of Amazon ungulates for *Mauritia flexuosa* palm fruits.

M. flexuosa were both positive, whereas those by the red and grey brocket deer were both negative (Fig. 4). *Jessenia* sp. was the second most common fruit in the diet of the lowland tapir and was very common in the study area. This fruit had a selection ratio close to zero, suggesting that the tapirs consumed it in proportion to the rate of encounter and with no active searching.

Mauritia flexuosa palms occur in larger patches than other fruit trees used by terrestrial mammals of the Amazon and have a much greater tendency to grow in clumps than other palm species (Kiltie & Terborgh, 1983) (Table I). *M. flexuosa* palms grow in swampy habitats, often in virtually monotypic stands. Fruits of *M. flexuosa* were present throughout most of the year (78%) in the fruit traps of the floodplain/palm habitats but did not occur in any of the *terra firme* fruit traps. *M. flexuosa* palm swamps occupy approximately 2.35% of the forests in the Peruvian Amazon (COREPASA, 1986).

TABLE I

The tendency of palm trees to clump was determined from quadrats of 66 × 10 m located 4 km inland from the Manu River, Peru. The information presented below is from Kiltie & Terborgh (1983). A value of 1.0 indicates perfectly even spacing, whereas increasing values reflect increasing amounts of clumping

Species	Spacing index
<i>Jessenia</i> sp.	1.0
<i>Astrocaryum macrocalyx</i>	1.4
<i>Scheelea</i> sp.	2.0
<i>Euterpe</i> sp.	2.2
<i>Oenocarpus</i> sp.	3.0
<i>Iriartea ventricosa</i>	3.2
<i>Socratea durissima</i>	3.5
<i>Mauritia flexuosa</i>	22.1

Mauritia flexuosa fruits are nutritious oval drupes of approximately 2–3 cm long by 1–2 cm wide. Pulp makes up 37.9% of the entire fruit ($n=12$). The seeds are very strong and require a load of 408 ± 59 kg to reach their breaking point ($n=3$). The pulp is nutritionally rich and consists of 53.2% fat, 43.0% carbohydrate, and 3.8% protein (Lopes *et al.*, 1980). The tapir appear to digest only the pulp portion of the drupes. During feeding trials with two captive adult tapir the pulp was stripped off the fruit and the seeds were always spat out. Intact seeds of *M. flexuosa* were found in two faecal samples.

Lowland tapir can consume large quantities of *M. flexuosa* fruits, because they change their searching behaviour once they enter the palm swamps in order to increase the rate of encountering fruit. Lowland tapir encountered fruits more frequently in *M. flexuosa* palm forests, with an encounter rate of 37%, than in the non-palm forests, with an encounter rate of 5.4% (Goodness of fit test, $G=79.4$, $P<0.001$). This increase in the tapir's ability to find fruits in palm forests appears to be due to some aspect of their searching behaviour and not to overall fruit abundance, because during straight transect walks fruit was encountered at the same rate in the palm forests (9.4%) as in the non-palm forests (4.4%) (Goodness of fit test, $G=3.08$, $P=0.08$). In accordance with this observation, in the palm forests fruits were encountered at greater rates by lowland tapir than during the transect walks (Goodness of fit test, $G=24.8$, $P<0.001$), and in non-palm forests fruits were encountered at similar rates by tapir as during transect walks (Goodness of fit test, $G=0.31$, $P=0.5$). One aspect of the lowland tapir's searching behaviour that appears to be directly related to the rate at which they encounter *M. flexuosa* fruits is the degree of turning whilst ranging in the different forest types. Thus the tapir made more abrupt turns every 10 m in *M. flexuosa* palm forests ($34 \pm 29^\circ$) than in non-palm forests ($17 \pm 15^\circ$) ($U=20114$, $P<0.001$).

Discussion

Large non-ruminant herbivores often consume large proportions of low-quality foods: for example, Baird's tapir (Terwilliger, 1978), black rhinoceros (Goddard, 1968), greater one-horned rhinoceros (Laurie, 1982), and most if not all of the wild equids (Janis, 1976). Large non-ruminant herbivores appear to maintain their nutritional requirements by consuming large quantities of the abundant low-quality foods. The post-gastric (caeco-colic) fermentation allows rapid passage of forage, whilst their gut volume allows for relatively long retention. Using this strategy large-bodied ungulates gain maximum extraction of low-quality foods per unit time (Foose, 1982; Demment & Van Soest, 1985).

In comparison to other large non-ruminant ungulates the lowland tapir consumes relatively large quantities of fruit. The results of this paper suggest that tapir use a type of fruit, *M. flexuosa*, that occurs in monotypic clumps and thus maximizes the benefits of frugivory by minimizing searching costs. In *M. flexuosa* palm forests lowland tapir make many abrupt turns and have a high rate of fruit encounter, whereas in non-palm forests lowland tapir turn less sharply and have a low rate of fruit encounter. In following lowland tapir trails through the forest it sometimes appeared as if the animals were going from one *M. flexuosa* palm swamp to another via non-palm forests and in several areas there appeared to be worn tapir trails connecting different palm swamps.

The amount of fruit consumed by large non-ruminant ungulates depends on the size of the fruit clumps and on the nutritional quality. Baird's tapir, for example, consume large amounts of browse and very little fruit from the understorey of Barro Colorado Island (Terwilliger, 1978). Barro Colorado Island does not have large monotypic clumps of fruiting trees like *M. flexuosa*

patches of the Amazon (Smythe, 1970; Foster, 1982) and this could explain the absence of large amounts of fruit from the diet of Baird's tapir.

Contemporary theories on optimal foraging would predict that large-bodied non-ruminant herbivores should only resort to frugivory if the nutritional gains outweigh the searching costs (Stephens & Krebs, 1986). This study of the lowland tapir is an example of how a large-bodied tropical forest ungulate is able to maintain a higher rate of frugivory than would be predicted from foraging models by exploiting a nutritionally-rich fruit source that occurs in large patches.

I would like to thank the Ministerio de Agricultura, Peru, for granting permission to conduct the research and for providing logistic support. Drs George Rabb, Nigel Leader-Williams, Marcio Ayres and T. H. Clutton-Brock are thanked for their valuable discussions. Tula Fang, James Penn, Luis Moya, Dr Jaime Moro, Carlos Malaga and Filomeno Encarnación gave advice and support throughout the field work. Rodolfo Vasquez assisted with the identification of fruits. Drs Nigel Leader-Williams, R. J. Putman, Iain Gordon, David Chivers and Robin Gill reviewed the manuscript. This work was supported by grants from the Chicago Zoological Society and the G. B. Harris Foundation.

REFERENCES

- Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Scient. Am.* **255**: 86-93.
- Belovsky, G. E. (1978). Diet optimization in a generalist herbivore: the moose. *Theoret. Pop. Biol.* **14**: 105-134.
- Bodmer, R. E. (1989). *Frugivory in Amazon ungulates*. PhD thesis, University of Cambridge.
- Bodmer, R. E., Fang, T. G. & Moya Ibanez, L. (1988). Ungulate management and conservation in the Peruvian Amazon. *Biol. Conserv.* **45**: 303-310.
- Cock, M. J. W. (1978). The assessment of preference. *J. Anim. Ecol.* **47**: 805-816.
- COREPASA (1986). *Plan maestro de la Reserva Nacional Pacaya-Samiria*. Iquitos, Peru: Editorial e Imprenta DESA.
- Crawley, M. J. (1983). *Herbivory: the dynamics of animal-plant interactions*. Oxford: Blackwell Scientific Publications. (*Stud. Ecol.* **10**: 1-437.)
- Demment, M. W. & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* **125**: 641-672.
- Foose, T. J. (1982). *Trophic strategies of ruminant versus nonruminant ungulates*. PhD thesis, University of Chicago.
- Foster, R. B. (1982). Famine on Barro Colorado Island. In *The ecology of a tropical forest: seasonal rhythms and long-term changes*: 201-212. Leigh, E. G., Rand, A. S. & Windsor, D. M. (Eds), Washington, D. C: Smithsonian Institution Press.
- Goddard, J. (1968). Food preferences of two black rhinoceros populations. *E. Afr. Wildl. J.* **6**: 1-19.
- Ivlev, V. S. (1961). *Experimental ecology of the feeding of fishes*. New Haven: Yale University Press.
- Janis, C. M. (1976). The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution, Lawrence, Kans.* **30**: 757-774.
- Kiltie, R. A. & Terborgh, J. (1983). Observations on the behavior of rain forest peccaries on Peru: why do white-lipped peccaries form herds? *Z. Tierpsychol.* **62**: 241-255.
- Laurie, A. (1982). Behavioural ecology of the greater one-horned rhinoceros (*Rhinoceros unicornis*). *J. Zool., Lond.* **196**: 307-341.
- Lopes, J. P., Albuquerque, H., Silva, Y. & Shrimpton, R. (1980). Aspectos nutritivos de alguns frutos da Amazônia. *Acta amazon.* **10**: 755-758.
- Smythe, N. (1970). Relationships between fruiting seasons and seed dispersal methods in a Neotropical forest. *Am. Nat.* **104**: 25-35.
- Stephens, D. W. & Krebs, J. R. (1986). *Foraging theory*. Princeton, New Jersey: Princeton University Press.
- Terborgh, J. (1983). *Five New World primates: a study in comparative ecology*. Princeton, New Jersey: Princeton University Press.
- Terwilliger, V. J. (1978). Natural history of Baird's tapir on Barro Colorado Island, Panama Canal Zone. *Biotropica* **10**: 211-220.
- Van Roosmalen, M. G. M. (1985). *Fruits of the Guianan flora*. Netherlands: Institute of Systematic Botany, Utrecht University.
- Van Soest, P. J. (1982). *Nutritional ecology of the ruminant*. Corvallis, Oregon: O & B Books Inc.