

FEEDING ECOLOGY OF FIVE NEOTROPICAL UNGULATES: A CRITICAL REVIEW

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ABSTRACT

In addition to shedding light on underlying ecological processes, studies about animal diets are useful for guiding the design of species conservation projects. This study presents general characterizations of the diets of five neotropical ungulates, the lowland tapir (*Tapirus terrestris*), the red brocket deer (*Mazama americana*), the grey brocket deer (*Mazama gouazoubira*), the collared peccary (*Pecari tajacu*) and the white-lipped peccary (*Tayassu pecari*). In addition, a critical review of methodological procedures used in this field of ecology is presented. A number of methodological limitations were identified in this review, which may help guide future research in this field. The predominant types of studies reviewed focused on analyses of fecal matter and stomach contents. Direct observation of foraging, while difficult to implement, has revealed interactions among ungulates and other mammals that are otherwise difficult to observe. The general foraging patterns of various species and the main ecological roles of the species in the various environments where they occur were also observed. A list of plant species and families is also presented here to aid researchers and conservation practitioners in accessing resources about the main items in the ungulate diets discussed in this study.

Key words: Fauna; Diet; Methods; Foraging Patterns; Large Mammals.

RESUMO

Além de revelar processos ecológicos subjacentes, estudos sobre a dieta de espécies da fauna também geram informações úteis para o delineamento de projetos visando a conservação das mesmas. Esta revisão apresenta uma caracterização geral da dieta de cinco ungulados neotropicais, a anta (*Tapirus terrestris*), o veado mateiro (*Mazama americana*), o veado catigueiro (*Mazama gouazoubira*), o cateto (*Pecari tajacu*), e o queixada (*Tayassu pecari*), juntamente com uma avaliação crítica dos procedimentos metodológicos que têm sido adotados nesse campo do conhecimento ecológico. Algumas limitações metodológicas foram identificadas, o que pode servir de base de reflexão para pesquisas futuras nessa área. As análises do conteúdo fecal e estomacal predominaram entre os estudos. Já o método de observação direta do forrageio, apesar da sua difícil aplicação, foi ímpar ao revelar interações entre ungulados e outros mamíferos ainda pouco conhecidas da Ciência. Padrões gerais no forrageio das espécies também foram evidenciados, assim como os principais papéis ecológicos que as mesmas podem desempenhar nos diferentes contextos ambientais em que ocorrem. Uma lista de espécies e famílias botânicas também é apresentada, e visa facilitar o acesso de pesquisadores e de ambientalistas aos recursos que até o momento são tidos como os principais itens da dieta desses animais.

Palavras-chave: Fauna; Dieta; Métodos; Padrões de Forrageio; Mamíferos de Grande Porte.

INTRODUCTION

This paper presents a critical review of literature on the diets of five species of Neotropical ungulates (*Tapirus terrestris*, *Mazama americana*, *Mazama gouazoubira*, *Pecari tajacu* and *Tayassu pecari*). The ungulates mainly display frugivorous, granivorous, folivorous and grazing habits (Eisenberg & Redford 1999). They may act as seed predators or dispersers or as seedling predators (Howe & Smallwood 1982), and they often help control the growth and primary productivity of herbaceous and woody elements in different ecosystems (McNaughton *et al.* 1988, Augustine & Frelich 1998).

The wide geographic range, relative adaptability

to anthropogenic environments and high mobility of this group of ungulates (Eisenberg & Redford 1999) also makes it possible to assess the ecological implications of these species' feeding habits and diet on landscape dynamics, at both the local ecosystem and biome scales. In fact, it has already been empirically shown that the abundances of these species have direct and indirect effects on the population dynamics, structure and composition of plant communities in the Neotropics (Terborgh & Wright 1994, Asquith *et al.* 1997) and other regions (Stoner *et al.* 2007).

In addition to hunting, the main threats to the Neotropical ungulates are habitat degradation, loss and fragmentation (Cullen *et al.* 2000, Robinson & Bennett

2000, Peres 2001). Habitat fragmentation not only isolates local populations but also directly affects the amount of plant food resources available for ungulate populations by reducing plant species richness (Collinge 1996). The predominance of secondary forests in tropical regions and their effects on regional fauna have also been widely discussed in the conservation literature (DeWalt *et al.* 2003, Wright & Muller-Landau 2006, Bowen *et al.* 2007, Gardner *et al.* 2007, Prado *et al.* 2014). Further investigation of the foraging patterns of animals in these novel environmental contexts is needed. The widespread habitat modification and fragmentation occurring in the Neotropics points to a need for additional ecological studies that address current environmental conditions and are based on improved, high-quality research methods, such as standardized and independent observations.

Accordingly, the specific objectives of this review were the following: (1) to record and compare the number of samples used by these studies (i.e. number of feces, stomachs, and/or foraging observation events) and the spatial and temporal coverage of data collections; (2) to characterize the species' diets in this group; (3) to list the most commonly consumed plant species and families in the different biomes where the species occur; and (4) to identify the ecological processes underlying the group's diets as well as to discuss their implications for conservation.

METHOD

Methods for the Literature Search and Analysis

This review was restricted to studies that characterized species' diets in a systematic manner, as opposed to more general observations of foraging habits. In addition, only studies involving *in situ* data collection with direct evidence of consumption were included in the review. Literature was obtained through a search in the *ISI Web of Science* database (<http://www.isiwebofknowledge.com>) with the following combination of terms for each species: "*species' scientific name*" *and* (*diet or feeding ecology or feeding habits or nutrition or foraging ecology or food niche or foraging behavior*). The same search was then repeated using the species' common name. Therefore, 14 combinations of terms were used for each of the five study species. The searches were performed without specifying the time period during which the studies were published.

Files that could not be obtained in digital format from the *ISI Web of Science* platform were obtained from the <http://scholar.google.com> website or from the *Universidade de São Paulo* (USP) online and physical journal collection (<http://www.usp.br/sibi/>). Finally, the *Tapir Specialist Group* (TSG) library (<http://atrium.tapirs.org/>) was consulted to refine the search for studies on the lowland tapir. Only journal articles and book chapters were considered. The search was performed in 2010, updated in 2013, and returned a total of 127 studies. Following the examination of its objectives and methods, only 68 studies matched with criteria of inclusion herein adopted.

The analysis unit used in this review was the "diet record," which represented the data collected on the diet of each ungulate at a given study site. This unit was independent of the number of papers produced from the same data in the diet record. The review is structured as follows. First, the methodological aspects of the studies are discussed. Second, the diet of each animal is characterized in terms of the relative importance of different parts of the plants consumed. Finally, the species' foraging patterns are presented, and the ecological aspects of their diets are discussed.

General Characteristics of the Study Species

The lowland tapir (*T. terrestris*) is the largest Neotropical terrestrial mammal, is generally solitary and is found at low densities (Eisenberg & Redford 1999). Given its relatively low reproductive rate, hunting has been one of the main threats to the survival of this species in recent decades (Bodmer *et al.* 1994). Tapirs have extensive home ranges ranging from 150 ha to 400 ha (Tobler *et al.* 2009), which also makes this species highly vulnerable to habitat loss and fragmentation. Regarding diet, the lowland tapir feeds mostly on fibrous vegetative plant material but also ingests many fruits and seeds (Barcelos *et al.* 2013).

The red brocket deer (*M. Americana*) is found from southern Mexico to northern Argentina and is more common in forests and wet areas, whereas the grey brocket deer (*M. gouazoubira*) is also common in open and dryer areas and is found from Panama to northern Argentina (Eisenberg & Redford 1999). The home range of these cervids may reach approximately 100 ha (Maffei & Taber 2003). With relatively high population recruitment rates, these species are among the group of Neotropical large mammals least affected by hunting (Robinson & Redford 1986, Robinson & Bennett 2000).

The collared peccaries (*P. tajacu*) are the most widely distributed Neotropical ungulates, occurring from the southern U.S. to northern Argentina. They live in groups of up to 50 individuals (Judas & Henry 1999). This species' home range may vary between 10 ha and 1000 ha (Taber *et al.* 1994, Judas & Henry 1999, Carrillo *et al.* 2002, Keuroghlian *et al.* 2004). White-lipped peccaries (*T. pecari*) form large groups of 50 to 400 individuals (Altrichter & Almeida 2002, Keuroghlian *et al.* 2009) and move over large distances (up to 13 km per day). Their home ranges vary from 1000 ha to 10,000 ha (Kiltie & Terborgh 1983, Bodmer 1990, Fragoso 1998, Fragoso 1999, Altrichter & Almeida 2002, Carrillo *et al.* 2002, Keuroghlian *et al.* 2004, Jácomo *et al.* 2013). The collared and white-lipped peccaries have similar diets but occupy different habitats (Bodmer 1991a) or exploit the landscape on different spatial scales (Fragoso 1999). Both species use the strength of their jaws to break open hard seeds and are able to break down the seeds by fermentation in their stomachs (Bodmer 1991b).

RESULTS AND DISCUSSION

Sampling Design and Procedures Used in the Studies

A total of 68 published studies (53 diet records in the field) were analyzed in this review. The studies were published between 1959 and 2013. The review included 15 diet records for the lowland tapir, eight for the white-lipped peccary, 17 for the collared peccary, four for the red brocket deer and nine for the grey brocket deer (Figure 1). The studies were performed in 13 countries from the southern U.S. to northern Argentina. Desert (Arizona, USA) and arid (southern Texas, USA) areas were represented in the studies, in addition to

Tropical Rain Forest (Atlantic Forest, Amazon, Brazil/French Guiana), Semideciduous Tropical Forest, Chaco Forest (Argentina), Deciduous Tropical Forest (Mexico), Pantanal (Brazil) and transition areas between Semideciduous Forest and Cerrado (Brazil).

Only 29 diet records (55% of the total records) reported the size of the area where the study was performed. The size of the study areas varied from 200 ha to 1,523,400 ha. The size of the effective sampling area within the study area (area where feces and stomachs were searched and foraging direct observations were performed) was only reported in five diet records (10%) (Salas & Fuller 1996, Fragoso & Huffman 2000, Kufner *et al.* 2008, Talamoni & Assis 2009, Serbent *et al.* 2011) (Table 1), ranging from 1500 m² to 82,500 m² in size (mean=51,000 m², standard deviation=30,019 m²).

In addition, only nine records (17%) specified the number of sampling sites per ecological unit on the landscape studied (Eddy 1961, Salas & Fuller 1996, Henry *et al.* 2000, Santos *et al.* 2005, Kufner *et al.* 2008, Talamoni & Assis 2009, Serbent *et al.* 2011, Hibert *et al.* 2011, Barcelos *et al.* 2013). Only six records (11%) indicated the stage of regeneration of the forest in which the study occurred (Richard *et al.* 1995, Fragoso & Huffman 2000, Richard & Juliá 2001, Gayot *et al.* 2004, Hibert *et al.* 2011, Barcelos *et al.* 2013) (Table 1). This paucity of data makes it difficult to perform a rigorous assessment of the role of secondary forests in the foraging pattern of large mammals (Dunn 2004). Information about the conservation status of the study areas was also limited. Only 12 records (22%) mentioned the type and degree of anthropogenic disturbance at the study site (Table 1). Agriculture, livestock production and logging were the most common anthropogenic activities in the study areas.

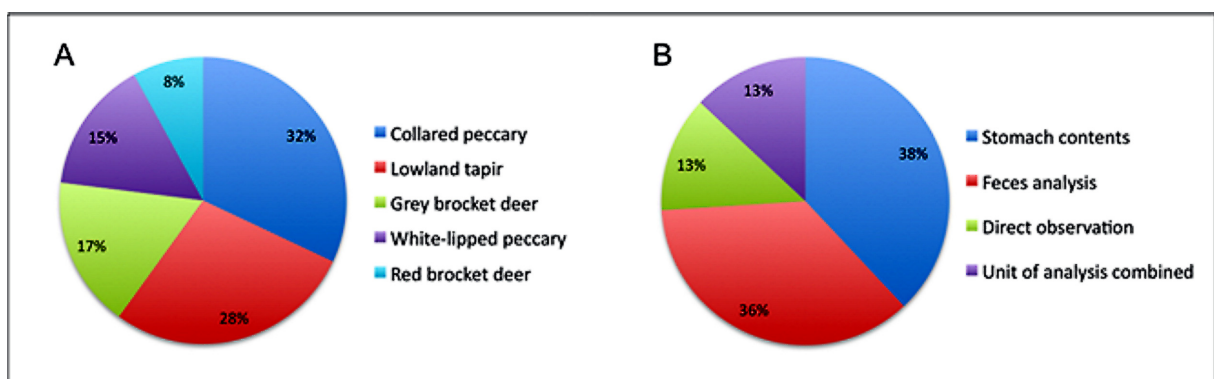


Figure 1. Proportion of diet records for each ungulate analyzed in this review (A). Proportion of ungulate diet records that adopted each unit of analysis above listed (B). Data based on 53 ungulate diet records.

Table 1. Number and proportion of ungulate diet records reporting basic information about study area and data collection procedures adopted (data based on 53 diet records).

METHODOLOGICAL TOPICS	NUMBER OF DIET RECORDS (%)
Duration of data collection reported	35 (66)
Size of the study area informed	29 (55)
Conservation status of the study area informed	12 (23)
Number of sampling sites used on the landscape informed	9 (17)
Stage of forest succession in the study area reported	6 (11)
Size of the effective sampling area* reported	5 (9)
Sampling sufficiency analysis presented	5 (9)

* area where feces and stomachs were searched and foraging direct observations were performed

The time period of data collection was explicitly reported in 36 records (68%) and ranged from three to 78 months (mean=20.8, median=16, standard deviation=16.3 months) (Table 1). Twenty records (38%) used stomach contents as the unit of analysis, 19 (36%) were based on fecal analyses, and seven (13%) were based on direct observations. Combinations of various analyses were also used (Figure 1). The number of stomach content samples used in each study varied from five to 121 (mean=35, median=31, standard deviation=25.9 samples), and the number of fecal samples varied from 10 to 356 (mean=117, median=104.5, standard deviation=91.3). Of the 13 records that included direct observation as a sampling method, only one record reported the number of observation events used in the research (82 events) (Santos *et al.* 2005).

Only five diet records (about 9% of the total) addressed the issue of sampling sufficiency (Table 1), three studies for the lowland tapir, and two for both the grey brocket and the red brocket deer. Based on collectors' curve approach (plotting accumulated number of the species against sampling effort), the studies for the lowland tapir showed that 53 fecal samples (Hibert *et al.* 2011), 94 fecal samples (Barcelos *et al.* 2013), and even 135 fecal samples (Tobler *et al.* 2010) could not be adequate to estimate the diet richness of this ungulate. Regarding deer species, Gayot *et al.* (2004) observed that 28 stomachs of the red brocket and that 34 stomachs of the grey brocket were both insufficient to assess suitably these ungulates diet (in terms of plant species). Conversely, Branam *et al.* (1985) suggested that 57 red brocket deer's stomachs could be adequate to this aim. No record diet for the white-lipped peccary and the collared peccary reported such methodological aspect of the research.

In summary, the main limitations of these studies were related to a lack of information about the number of sampling sites and the size of the sampling areas. This criticism does not apply to the studies that used stomach content analyses because in these cases, the samples were obtained from local hunters. However, studies that use analyses of fecal samples and direct observation methods can easily include basic information about sampling design and procedures.

Methods of Diet Analysis

Diet records for the lowland tapir showed predominance of fecal sample analyses (used alone or in combination with other methods in 82% of the records), with only a few examples of stomach content analyses (18%) and direct observation of foraging (18%). The lowland tapir tends to defecate repeatedly in specific locations in the forest (Fragoso 1997, Fragoso & Huffman 2000, Hibert *et al.* 2011) and defecates in large amounts, allowing for feces to be easily obtained over prolonged periods. The large quantity of seeds in the feces and the high degree of preservation of the seeds after defecation also makes fecal sample collection the preferred sampling method. On the other hand, the lowland tapir is usually found at low population densities (Eisenberg & Redford 1999). As a result, this mammal is less common than other species in the diets of local hunting communities, making stomach content samples difficult to obtain, and direct observation nearly impossible in the natural environment.

Diet studies for the collared and white-lipped peccaries show that researchers used preferentially stomach content analysis (used in 52% of the records), followed by fecal analysis (40%) and direct observation of foraging (40%). The few records for the diet of the red brocket deer were based on stomach

content analyses (Branan *et al.* 1985, Bisbal 1994, Bodmer 1991b, Gayot *et al.* 2004). These studies were conducted in rural communities in the Amazon where the species is often abundant and widely hunted, thereby facilitating access to butchered stomachs for analysis (Branan *et al.* 1985, Bisbal 1994, Bodmer 1991b, Gayot *et al.* 2004). Studies of the grey brocket deer mostly relied on stomach content analyses (used in 55% of the records) (Stallings 1984, Branan *et al.* 1985, Bodmer 1991b, Bisbal 1994, Gayot *et al.* 2004), followed by fecal analyses (33%) (Kufner *et al.* 2008, Pinder 2004, Serbent *et al.* 2011) and direct observation (22%) (Richard *et al.* 1995, Richard & Juliá 2001).

Overall, for the five ungulates, the analysis of fecal or stomach samples was the most common type of analysis (Figure 1). Fecal samples are generally easier to obtain, but stomach samples are easier to obtain in area where there are indigenous communities hunting the animals. Direct observation of foraging was shown to be unique because it allows for the identification of diet items that are not preserved in stomach contents or in feces. However, direct observation is only feasible in specific contexts, such as with semi-captive animals or in open environments where the animals can be observed at a distance.

It is worth highlighting an innovative use of mixed methods that included (1) direct foraging observation to identify the plants consumed by lowland tapirs; (2) a molecular analysis of fecal samples to identify plant fragments and (3) recording ecological knowledge of local population. This mixed methodology was applied by Hibert *et al.* (2011) in a study of the diet of the lowland tapir in French Guiana in an area with indigenous Wayãpi communities. These are highly complementary approaches, and molecular analysis of animal diets is a technique with a large amount of potential that has yet to be explored. In addition, Prado *et al.* (2013) also have argued toward the efficacy of an ethnoecological approach in ungulate diet studies.

Diet of the Lowland Tapir

The lowland tapir was shown to consume fruits, leaves, fibers, twigs, stems and flowers. In the Peruvian Amazon, fruits, leaves and fibers were found in similar proportions in the tapir's diet (Bodmer 1990, 1991a). In French Guiana, samples of tapir diets contained a larger proportion of fibrous material (Henry 2000), and the tapirs in this region consumed a greater

diversity of leaves (measured by the number of identified species) than fruits (Hibert *et al.* 2011).

In a mosaic of Semideciduous Forest and Igapó Forest in Bolivia, an analysis of the tapir's diet found a predominance of leaves, followed by fibers and fruits (Herrera *et al.* 1999). Higher consumption of fibers than other foods was observed in southeastern Brazil (Talamoni & Assis 2009). For feces found in sandbank vegetation on the Brazilian coast, leaves were present in almost 50% of the feces, and stem fragments were present in 40% (Santos *et al.* 2005). The same study showed that the tapirs fed primarily on herbaceous and shrub species that were common in the early stages of forest regeneration.

In general, a larger portion of the plant biomass is available to fauna during early stages of succession compared to more advanced stages (Bowen *et al.* 2007). Indeed, *T. terrestris* and *T. bairdii* have often been observed foraging in patches of secondary vegetation (Naranjo 1995, Salas & Fuller 1996, Foerster & Vaughan 2002, Tobler 2002). The same pattern has been observed in other animal groups (Bowen *et al.* 2007), reinforcing the hypothesis that tropical secondary forests may benefit part of the fauna (Wright & Muller-Landau 2006).

The tapir's diet comprises mainly vegetative plant parts. All of the studies except Bodmer (1990, 1991a) found that leaves and fibers were the most commonly consumed items, with fruits and seeds playing a smaller role, regardless of biome, habitat type or sampling method. In fact, non-ruminant large herbivores such as the tapir can efficiently digest low-quality food, especially plant fibers (Demment & Van Soest, 1985). The feeding strategy of these animals is to forage large quantities of food with low nutritional value, which is usually abundant, rather than a smaller quantity of food with higher nutritional value (Bodmer 1990) (*e.g.*, fruit pulp and seeds), which require a greater energy investment during foraging.

While fibers were the predominant plant part in most tapir diets, in the Peruvian Amazon these ungulates were found to consume large proportions of fruits from monotypic clumps of the palm *Mauritia flexuosa* (Bodmer 1990). Given the considerably reduced foraging costs in this context, the benefits of frugivory seem to have been maximized, resulting in greater fruit intake by the tapirs (Bodmer 1990). The palm clumps, which are typically associated with historic and prehistoric processes of human occupation

(Balée 1987, 1993; Politis 2001), may play an important role in the foraging dynamics of many animal species and are an interesting topic of research for combined ecological, anthropological and archaeological studies.

Diets of the Red and Grey Brocket Deer

The small number of studies of the red brocket deer showed that this species is predominantly frugivorous in the Amazon, although its diet also includes flowers, fungi and arthropods, which are often found in the samples in small proportions (Bodmer 1991a, Bisbal 1994, Gayot *et al.* 2004). The diet of the grey brocket deer includes fruits, leaves, fibers, flowers, roots, bark, shoots, stalks, twigs, minerals, fungi and animals. In the Amazon, fruits represented between 70 and 90 of the grey brocket deer's diet (Bodmer 1991a, Gayot *et al.* 2004), based on analyses of stomach content. However, a fecal analysis in the Pantanal (Brazil) showed that 90% of the species' diet was composed of leaves (Pinder 2004). Although the differences in the results of these studies could be attributed to differences in methods (namely, differences between stomach content and fecal analyses), it is also possible that this species is more frugivorous or more folivorous in different contexts. Further investigation is required to answer this question.

In the Chaco region of Argentina, tree and shrub elements dominated the diet of the grey brocket deer (Kufner *et al.* 2008). A similar pattern, but with increased importance of succulent species, was observed in the same region during a period of intense water stress (Serbent *et al.* 2011). In the phytogeographic province of Loa Yungas (Argentina), the diet of this species consisted of easily digestible and energy-rich food, including fruits, seeds, young leaves, shoots and flowers. Other elements were found in the diet during the period when the most nutritious items were scarce (Richard & Juliá 2001).

In the same study, the grey brocket deer was also observed feeding on ticks from the species *Haemaphysalis kohlsi* (Ixodida, Ixodidae), which were found on other deer and a tapir, and was also observed feeding on an unidentified lepidopteran (Richard & Juliá 2001). Earthy substances (geophagia), bird bones (osteophagia) and animal excrement (coprophagia) were also observed to be food items, in addition to salt and tiles from an old building site. The ingestion

of minerals in general may be related to the processing of toxic secondary plant compounds. The fact that bones were observed in the stomach contents of a pregnant female and that eating earthy substances is more common among females has led other authors to hypothesize that there is an association between the consumption of minerals, such as calcium, and the specific nutritional requirements of pregnancy (Richard & Juliá 2001). This type of information could only have been obtained using direct observation of foraging. Therefore, the use of this method is recommended for future studies, even though it is known to be difficult to implement *in situ*.

It is important mentioning that Richard and Juliá (2001) performed their observations in a semi-captive environment, which may be an alternative to *in situ* observations in natural habitat. Their study was performed in a fenced area of ~20 ha, belonging to a protected area of ~200 ha. The area consisted of pastures, shrub and secondary forest habitats, and the authors found out that the grey brocket deer consumed mainly young leaves, fruit and flowers, comprising 73 botanical species in total. However, Richard and Juliá (2001) did not address how this semi-captive context could or not affect the density and healthy of this ungulate in the area. Therefore, it was not assessed the potential influence of this specific environmental context on the foraging habits of the grey brocket deer observed by the authors.

Diet of the Collared Peccary

Of the diet records for the collared peccary, 13 (76%) addressed the relative importance of different items in the diet. In the Arizona desert, fibers represented 96% of the total volume of stomach samples, and the consumption of roots was considered common. The ingestion of vegetative parts of herbaceous species was significant during periods of low availability of other resources (Eddy 1961). A seasonal pattern was observed in Texas (USA), with greater consumption of herbaceous species in autumn, cacti in spring, herbaceous species and grasses in winter and herbaceous species and cacti in summer (Ilse 1995). The cactus *Opuntia engelmannii* was especially important in the collared peccary's diet, both in the desert region of Arizona and the arid regions of southern Texas (USA), accounting for 80 to 95% of the species' diet in those regions (Neal 1959, Eddy 1961, Everitt *et al.* 1981).

A greater proportion of roots (47.9%) and leaves (41.2%) were recorded in the collared peccary's diet in Mexico (Martínez-Romero & Mandujano 1995). Roots were also the primary item in the collared peccary's diet in Costa Rica (McCoy *et al.* 1990, Martínez-Romero & Mandujano 1995). In summary, the diet of the collared peccary was found to be composed mainly of leaves and roots in North and Central America, regardless of the methods used. In contrast, studies from South America showed that this species was predominantly frugivorous in this region. These findings were based on the three methods used for diet analysis and represented a wide geographical gradient, ranging from northern South America to southeastern Brazil (Bodmer 1991a, Barreto *et al.* 1997, Salazar 2007, Keuroghlian & Eaton 2008, 2009; Desbiez *et al.* 2009).

Collared peccaries in Bolivia were observed ingesting ticks found on other individuals of their group. These animals also consumed bird feathers (species from Tinamidae and Caprimulgidae), which is most likely due to the carcassivorous habit of this species (Salazar, 2007) and deserves further investigation. The consumption of an infant collared peccary by an adult was also observed (Salazar, 2007). Another study, carried out in Venezuela, showed a strong association between groups of collared peccaries and wedge-capped capuchins (*Cebus olivaceus*). The primates were present in 39 of the 86 observations of collared peccaries, who appeared to be following the primates and consuming the fruits discarded by them (Robinson & Eisenberg 1985).

Diet of the White-Lipped Peccary

The review of studies of the white-lipped peccary indicated that its diet was composed of fruits, leaves, fibers, flowers, roots, stem, fungi, soil and animals. The literature also showed a consistent pattern of frugivory from Central America to southeastern Brazil (Bodmer 1991a, Barreto *et al.* 1997, Altrichter *et al.* 1999, 2000, 2001; Salazar 2007, Keuroghlian & Eaton 2008, Desbiez *et al.* 2009), regardless of the methods employed.

The peccary was a seed predator for over 95% of the seeds in the Peruvian Amazon (Bodmer 1991b). In Costa Rica, the peccary was a predator of the seeds of 30 species, and a seed dispersal agent for only two species (Altrichter *et al.* 1999). In Costa Rica, earthworms were an important item in the peccary's

diet, and this phenomenon may also occur in other habitats. However, the consumption of earthworms is rarely recorded because of the difficulty of observing earthworms in the stomach content and feces of ungulates (Altrichter *et al.* 2000). Again, the direct observation method is useful here in that it allows for recording the consumption of items that are absent from fecal and stomach content analyses.

In Bolivia, ticks and bird feathers (from the families Tinamidae and Caprimulgidae) were also found in the stomachs of white-lipped peccaries (Salazar 2007). Two opportunistic feeding habits related to the behavior of other mammals were recorded: (1) preferential foraging at the base of "objects" on the forest floor, such as trees, exposed roots, deadwood, vines and rocks, where rodents had deposited palm seeds (*Astrocaryum* sp.) (Kiltie 1981, Peruvian Amazon) and (2) consumption of palm seeds (*Maximiliana maripa*) directly from the feces of the lowland tapir (Fragoso 1999).

Ecological Considerations of Species' Diets

The predominantly herbivorous foraging habit of the lowland tapir, which is associated with a certain degree of selectivity (Salas & Fuller 1996) and with foraging in patches of secondary vegetation (Naranjo 1995, Salas & Fuller 1996, Foerster & Vaughan 2002, Tobler 2002, Oliveira-Santos *et al.* 2010, Chalukian *et al.* 2013, García *et al.* 2012), plays an important role in the dynamics of forest regeneration because this species' foraging habit favors certain plant species over others. In terms of seed dispersal through frugivory, tapirs ingest seeds and defecate them whole (Bodmer 1991b, Barcelos *et al.* 2013). However, the feces are commonly deposited in flooded areas, which prevent the germination of many of the seeds (Bodmer 1991b, Fragoso & Huffman 2000, Quiroga & Roldan 2001).

In the Amazon, the tapir's movement over large distances and habit of defecating repeatedly in specific spots in the forest can result in the formation of clumps of *M. maripa* palm (Fragoso 1997). This observation suggests that the lowland tapir may also modify vegetation composition across landscapes at a scale of tens of kilometers. As one of the last Neotropical megafauna, the lowland tapir disperses seeds in a unique pattern, and its extinction would certainly eliminate this type of interaction with the vegetation, as no other native mammal would play the same

ecological role in the Neotropics (Fragoso 1997, O'Farrill *et al.* 2013).

Both of the cervid species studied here were mostly frugivorous-granivorous in the Amazon. The brockets consume whole seeds, break down the hard parts of the seeds during rumination and process the chemical compounds in the seeds through pre-gastric fermentation in the rumen (Bodmer 1991b). The apparently greater dependency of the red brocket deer on fruits makes this species more vulnerable to habitat degradation and fragmentation because one of the consequences of these processes is decreased plant species richness, which decreases fruit and seed availability in fragmented habitat (Collinge 1996). On the other hand, the apparently folivorous habit of the grey brocket deer in the Pantanal (Brazil) (Pinder 2004) suggests that in addition to frugivory and granivory, this species may consume seedlings and vegetative parts of herbs, shrubs and young tree species, depending on its environment.

The diet of the collared peccary was composed mainly of leaves and roots in North and Central America (Neal 1959, Ilse 1995, Eddy 1961, McCoy *et al.* 1990, Martínez-Romero & Mandujano 1995, Everitt *et al.* 1981) and of fruits and seeds in the southern portion of the continent (Bodmer 1991, Barreto *et al.* 1997, Salazar 2007, Keuroghlian & Eaton 2008, Desbiez *et al.* 2009, Keuroghlian *et al.* 2009). It was also observed that seed predation by collared peccaries is more common than seed dispersal (Bodmer 1991b, Beck 2006). White-lipped peccaries also play a limited role in seed dispersal (Bodmer 1991b, Altrichter *et al.* 1999, Beck 2006). This species forms large groups of hundreds of individuals that forage over vast areas, depend on a large variety of habitats, and follow temporal variations in resource availability to meet their needs during the different times of the year (Fragoso 1998, 1999, Keuroghlian *et al.* 2009, Reyna-Hurtado *et al.* 2012). This foraging pattern makes this species highly vulnerable to impacts from anthropogenic activities that occur at the same landscape scale as the foraging scale of the animals (Fragoso 1999), such as extensive agriculture and livestock production. Indeed, reports of population decline and local extinction of this species in areas of agricultural use are not uncommon (Peres 1996a, 2001; Cullen *et al.* 2000, Azevedo & Conforti 2008, Keuroghlian *et al.* 2013).

Discrete Foraging Patterns of Ungulates

The studies reviewed here also described how foraging strategies result in interactions between mammals, as in the case of the white-lipped peccary, whose foraging pattern following the distribution of seeds (*Astrocaryum* sp.) deposited by rodents (Kiltie 1981) and who also consumed seeds directly from the feces of the lowland tapir (Fragoso 1999). The collared peccary was found to display similar behavior by following groups of wedge-capped capuchins, and it was suggested that the peccaries may have eaten of the fruits discarded by these animals (Robinson & Eisenberg 1985). Similarly, the grey brocket deer has been observed feeding on ticks on a lowland tapir (Richard & Juliá 2001).

These observations of ungulate foraging have revealed interactions among mammals that are otherwise difficult to observe. In fact, these types of interactions are considered to be rare because of a lack of observations of similar behaviors. However, a comprehensive literature review shows that opportunistic interactions such as the one observed between collared peccaries and wedge-capped capuchins may be more common than has been previously thought. Similar types of foraging interactions have been observed between ungulates and primates in India and Ceylon (Robinson & Eisenberg 1985), between birds and primates (Zhang & Wang 2000, Kuniy *et al.* 2003, Boinski & Scott 1988, Heymann 1992), between birds and coatis (*Nasua nasua*) (Beisiegel 2007), between birds and other ungulates (Marcus 1985, Peres 1996b), between primates and coatis, and between primates and tayras (*Eira barbara*) (Haugaasen & Peres 2008).

Geophagous, osteophagous (bird bones) and coprophagous habits were also recorded for the grey brocket deer (Richard & Juliá 2001), and bird feathers were found in the stomachs of collared and white-lipped peccaries (Salazar 2007). Interviews with rural residents also provided evidence of feathers in the digestive tract of cervids in Atlantic Forest (south-eastern Brazil) (Vogliotti 2003, Prado *et al.* 2013). These unusual foraging habits, though little studied, may be important in the diet of some ungulates. Because these strategies likely address physiological needs that are not yet well understood, manipulated experiments examining the nutritional physiology of these species in captivity, in addition to direct observations of foraging *in situ*, would be valuable methods for future research.

Final Considerations

A list of plant species and families (see supplementary file 1) was created to facilitate access for researchers and conservation practitioners to information about the plants that are currently considered the main food sources for the ungulates in this study. The review allowed for an assessment of current knowledge about the diet of these species in the different environments where they are found, including the identification of little-understood foraging patterns that require additional studies. This review also reveals important limitations regarding adoption and description of data collection procedures used in these studies. About 30% of the studies analyzed do not report the duration of the data collection and almost 50% do not inform the size of the study area. In addition, most of the studies do not present any information about conservation status in the study area. Besides, less than 10% of them report the size of the effective sampling area or address the issue of temporal or spatial sampling sufficiency (Table 1).

In animal diet studies, information about the relationship of the sampling effort (i.e. number and size of sampling sites) to different elements on the landscape can be useful, especially in highly heterogeneous environments where the quantity and spatial arrangement of sampling sites may have significant effects on the diet composition record. Indeed, this kind of information can support key decisions and practices concerning the conservation of ungulate species. In addition, diet studies have shown great variation in terms of the number of samples and the time period for sampling, which compromise any further effort to compare diets within and between species. There was also a lack of studies from Neotropical environments of great concern for conservation, such as the Brazilian Caatinga and Cerrado. Finally, in order to improve our ecological knowledge about these ungulates, and make its conservation programs more effective, future diet studies ought to overcome the set of current methodological limitations herein discussed.

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ANNEX 1

Table 1. The most common plant taxa in the diets of five ungulates, listed in alphabetic order of botanical family.

BOTANY FAMILY	BOTANY SPECIES	T.	M.	M.	P.	T.	REFERENCES
		TERRESTRIS	AMERICANA	GOUAZOUBIRA	TAJACU	PECARI	
Agavaceae	<i>Yucca treculeana</i>				X		24, 26
Agavaceae	<i>Agave palmeri</i>				X		28, 29
Alismataceae	<i>Echinodorus rostratus</i>				X		26
Anacardiaceae	<i>Spondias mombin</i>	X					7
Anacardiaceae	<i>Spondias</i> sp.					X	35
Anacardiaceae	<i>Anacardium excelsum</i>					X	35
Anacardiaceae	<i>Schinus</i> sp.			X			13
Annonaceae	*	X					1
Apocynaceae	<i>Pacouria guianensis</i>	X					7
Apocynaceae	<i>Hancornia speciosa</i>					X	31
Araceae	*					X	35
Araliaceae	<i>Schefflera decaphylla</i>		X				10
Arecaceae	<i>Mauritia</i> sp.	X					2
Arecaceae	<i>Syagrus romanzoffiana</i>	X			X	X	3, 6, 21, 32
Arecaceae	<i>Astrocaryum</i> sp.	X					7
Arecaceae	<i>Mauritia flexuosa</i>	X					8, 9
Arecaceae	<i>Maximiliana maripa</i>	X					8
Arecaceae	<i>Jessenia</i> sp.	X					9
Arecaceae	<i>Scheelea</i> sp.	X					9
Arecaceae	<i>Attalea phalerata</i>				X	X	20, 31, 33
Arecaceae	<i>Euterpe edulis</i>					X	32
Arecaceae	<i>Oenocarpus bacaba</i>		X				10
Balanophoraceae	<i>Langsdorffia hypogaea</i>				X		20
Bombacaceae	<i>Catostemma fragrans</i>		X				10
Bombacaceae	<i>Eriotheca</i> sp.		X				10
Bromeliaceae	<i>Bromelia balansae</i>				X	X	20, 31
Cactaceae	*			X			12
Cactaceae	<i>Cereus</i> sp.				X		20
Cactaceae	<i>Opuntia lindheimeri</i>				X		24, 25, 26
Cactaceae	<i>Ferocactus wislizeni</i>				X		27
Cactaceae	<i>Carnegiea gigantea</i>				X		27
Cactaceae	<i>Opuntia engelmannii</i>				X		27, 28, 30
Cactaceae	<i>Ferocactus wislizeni</i>				X		28
Caesalpiniaceae	<i>Eperua falcata</i>		X				10
Caesalpiniaceae	<i>Swartzia panacoco</i>		X				10
Cannabaceae	<i>Celtis pallida</i>				X		28
Capparaceae	<i>Capparis retusa</i>			X			19
Capparaceae	<i>Capparis speciosa</i>			X			19
Caryophyllaceae	*			X			16
Cecropiaceae	<i>Cecropia obtusa</i>		X				10
Cecropiaceae	<i>Cecropia sciadophylla</i>		X				10
Celastraceae	<i>Maytenus spinosa</i>			X			12, 13
Chrysobalanaceae	<i>Licania operculipetala</i>					X	35

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BOTANY FAMILY	BOTANY SPECIES	T. TERRESTRIS	M. AMERICANA	M. GOUAZOUBIRA	P. TAJACU	T. PECARI	REFERENCES
Clusiaceae	<i>Symphonia globulifera</i>		X				11
Commelinaceae	<i>Commelina nudiflora</i>					X	31
Convolvulaceae	<i>Ipomoea muricata</i>				X		29
Cyclanthaceae	<i>Cyclanthus bipartitus</i>		X				10
Cyperaceae	<i>Cyperus</i> sp.				X		29
Ericaceae	<i>Arctostaphylos pungens</i>				X		29
Fabaceae	*	X					1
Fabaceae	<i>Dimorphandra mollis</i>	X					4
Fabaceae	<i>Enterolobium schomburgkii</i>	X					8
Fabaceae	<i>Swartzia</i> sp.		X				11
Fabaceae	<i>Inga</i> sp.			X		X	14, 35
Fabaceae	<i>Swartzia benthamianna</i>			X			18
Fabaceae	<i>Caesalpinia paraguarensis</i>			X			19
Fabaceae	<i>Mimosa</i> sp.				X		20
Fabaceae	<i>Desmodium barbatum</i>				X		20
Fabaceae	<i>Prosopis glandulosa</i>				X		24
Fabaceae	<i>Pithecellobium flexicaule</i>				X		25
Fabaceae	<i>Cercidium microphyllum</i>				X		27
Fabaceae	<i>Prosopis juliflora</i>				X		27, 28
Fabaceae	<i>Acacia greggii</i>				X		28
Fabaceae	<i>Mimosa obtusifolia</i>					X	31
Fabaceae	<i>Pithecellobium saman</i>					X	36
Fabaceae	<i>Cassia moschata</i>	X					8
Fagaceae	<i>Quercus arizonica</i>				X		28, 29
Heliconiaceae	<i>Heliconia</i> sp.					X	35
Humiriaceae	<i>Sacoglottis cydonioides</i>	X					7
Lauraceae	*				X	X	21, 32
Lecythidaceae	<i>Eschweilera</i> sp.		X	X			10, 14
Lecythidaceae	<i>Lecythis persistens</i>			X			14
Malpighiaceae	<i>Byrsonima orbignyana</i>					X	31
Malvaceae	<i>Bombax spectabile</i>		X	X			11, 18
Malvaceae	<i>Sida santamarensis</i>			X			15
Malvaceae	<i>Sida rhombifolia</i>			X			16
Malvaceae	<i>Sida</i> sp.				X		20
Malvaceae	<i>Waltheria albicans</i>				X		20
Malvaceae	<i>Guazuma ulmifolia</i>				X		23
Malvaceae	<i>Quararibea asterolepis</i>					X	35
Melastomataceae	*	X					5
Melastomataceae	<i>Bellucia grossularioides</i>			X			18
Meliaceae	<i>Carapa guianensis</i>		X				10
Meliaceae	<i>Guarea grandifolia</i>		X				10
Moraceae	<i>Ficus</i> sp.	X	X	X		X	2, 10, 14, 35
Moraceae	<i>Perebea</i> sp.	X					2

Continued...

Conclusion.

BOTANY FAMILY	BOTANY SPECIES						REFERENCES
		<i>T.</i> TERRESTRIS	<i>M.</i> AMERICANA	<i>M.</i> GOUAZOUBIRA	<i>P.</i> TAJACU	<i>T.</i> PECARI	
Moraceae	<i>Brosimum guianense</i>			X			14
Moraceae	<i>Morus nigra</i>			X			16, 17
Moraceae	<i>Brosimum</i> sp.					X	35
Moraceae	<i>Bagassa guianensis</i>		X				10, 7
Myristicaceae	<i>Virola kwatae</i>		X				10
Myristicaceae	<i>Virola surinamensis</i>		X	X			10, 14
Myristicaceae	<i>Virola michelii</i>			X			14
Myrtaceae	*	X			X	X	1, 21, 32
Olacaceae	<i>Ximenia americana</i>				X	X	20, 31
Onagraceae	<i>Ludwigia multinervia</i>	X					5
Opiliaceae	<i>Agonandra silvatica</i>		X				10
Phytolaccaceae	<i>Rivina humilis</i>				X		25
Piperaceae	<i>Piper</i> sp.	X					5
Poaceae	*				X	X	22, 34
Portulacaceae	<i>Portulaca mundula</i>				X		25, 26
Rhamnaceae	<i>Condalia microphylla</i>			X			13
Rhamnaceae	<i>Ziziphus oblongifolius</i>			X			19
Rubiaceae	*	X					1
Sapindaceae	<i>Paullinia capreolata</i>		X				10
Sapotaceae	<i>Pouteria</i> sp.	X	X				2, 11
Sapotaceae	<i>Pouteria egregia</i>		X				10
Sapotaceae	<i>Chrysophyllum prieurii</i>			X			14
Simaroubaceae	<i>Castela coccinea</i>			X			12, 19
Simmondsiaceae	<i>Simmondsia chinensis</i>				X		27
Solanaceae	*	X					1
Solanaceae	<i>Solanum viarum</i>				X	X	20, 31
Solanaceae	<i>Solanum triquetrum</i>				X		24, 25
Solanaceae	<i>Physalis viscosa</i>				X		24
Verbenaceae	<i>Vitex cymosa</i>				X	X	20, 31
Verbenaceae	<i>Phyla incisa</i>				X		26
Verbenaceae	<i>Phyla nodiflora</i>				X		26
Vitaceae	<i>Cissus rhombifolia</i>				X	X	23, 36

a: An item was considered common when it was found in more than 10% of the diet, measured as occurrence in stomach contents or feces, independent events of direct observation of foraging, proportion of time spent by a lowland tapir foraging on the plant, percentage of total dry weight of ingested food, or proportion of the item relative to the total number of ingested items. *: Not identified species. **Reference 1:** Talamoni and Assis (2009), Semideciduous Tropical Forest, Brazil; **2:** Tobler *et al.* (2010), Peruvian Amazon; **3:** Giombine *et al.* (2009), Semideciduous Tropical Forest, Brazil; **4:** Bizerril *et al.* (2005), Cerrado, Brazil; **5:** Santos *et al.* (2005), Atlantic Forest (Restinga Habitat), Brazil; **6:** Galetti *et al.* (2001), Semideciduous Tropical Forest, Brazil; **7:** Henry *et al.* (2000), Amazonia, French Guiana; **8:** Fragoso and Huffman (2000), Amazonia, Brazil; **9:** Bodmer (1990), Amazonia, Peru; **10:** Gayot *et al.* (2004), Amazonia, French Guiana; **11:** Branan *et al.* (1985), Amazonia, Suriname; **12:** Serbent *et al.* (2011), Semideciduous Forest, Argentina; **13:** Kufner *et al.* (2008), Chaco Forest, Argentina; **14:** Gayot *et al.* (2004), Amazonia, French Guiana; **15:** Pinder (2004), Pantanal, Brazil; **16:** Richard and Juliá (2001), Loa Yungas phytogeographic province, Argentina; **17:** Richard *et al.* (1995), Loa Yungas phytogeographic province, Argentina; **18:** Branan *et al.* (1985), Amazonia, Suriname; **19:** Stallings *et al.* (1984), Chaco, Paraguay; **20:** Desbiez *et al.* (2009), Pantanal, Brazil; **21:** Keuroglan and Eaton (2008), Semideciduous Tropical Forest, Brazil; **22:** Salazar (2007), Savannah, Bolivia; **23:** Barreto *et al.* (1997), Amazonia, Venezuela; **24:** Everitt *et al.* (1981), Arid Environment (Zachry Ranch), EUA; **25:** Everitt *et al.* (1981), Arid Environment (Gonzalez Ranch), EUA; **26:** Everitt *et al.* (1981), Arid Environment (Yturria Ranch), EUA; **27:** Eddy (1961), Arizona Desert (Tucson Mountain Park), EUA; **28:** Eddy (1961), Arizona Desert (Santa Rita Range), EUA; **29:** Eddy (1961), Arizona Desert (Canelo Hills), EUA; **30:** Neal (1959), Arizona Desert, EUA; **31:** Desbiez *et al.* (2009), Pantanal, Brazil; **32:** Keuroglan and Eaton (2008), Semideciduous Forest, Brazil; **33:** Keuroglan *et al.* (2009), Pantanal, Brazil; **34:** Salazar (2007), Savannah, Bolivia; **35:** Altrichter *et al.* (2000), Tropical Wet Forest, Costa Rica; **36:** Barreto *et al.* (1997), Amazonia, Venezuela.

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