Utilization of Shrubs for Forage and Shelter by Marsh Deer (*Blastocerus dichotomus)* in Jataí Ecological Station, Brazil

An analysis of stable carbon isotopes and of GPS tracking data

Linda Orrell

Supervisor: Jung, Jens
Department of Animal Environment and Health

Sveriges lantbruksuniversitet
Fakulteten för veterinärmedicin och husdjursvetenskap
Veterinärprogrammet

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SUMMARY

The South American marsh deer (*Blastocerus dichotomus)* is a wetland living species which is in risk of extinction in the wild. Since not much is known about its requirements concerning habitat and forage, this study aims at their choice of forage and habitat, with focus on use of shrubs available for shelter and forage. The study was performed in Jataí Ecological Station, São Paulo state, Brazil. I examined if marsh deer, like many other deer species, chose bed-sites in close proximity to large shrubs, which can provide cover from weather and predators. GPS-data from two marsh deer equipped with GPS-collars was analyzed to find the bed-sites of the deer. The bed-site coordinates were plotted on a map divided into vegetation zones with different densities of shrubs. The density and duration of bed-sites in each different vegetation zone was calculated. The results showed that the marsh deer did prefer bed-sites close to shrubs but not when shrubs become too dense. An analysis of stable carbon isotopes in hair taken from 30 marsh deer from two different populations was also performed to show the proportion between browse and grass ingested. These results estimated that only 4 - 14 % of the marsh deer's diet consists of grasses. However, it is not possible to tell from this type of analysis if the browse ingested consists of forbs or shrubs and if the marsh deer also feed on aquatic plants. No differences were seen between populations and genders.

SAMMANFATTNING

Den sydamerikanska sumphjorten är en våtmarkslevande art som är utrotningshotad i det vilda. Eftersom inte mycket är känt angående dess behov gällande habitat och föda syftar den här studien mot deras födo- och habitatval med fokus på deras utnyttjande av buskar för skydd och föda. Studien genomfördes i Jataí Ecological Station i delstaten São Paulo, Brasilien. Jag undersökte om sumphjorten, liksom många andra hjortdjur, väljer legor i närheten av stora buskar som kan ge skydd från väder och rovdjur. GPS-data från två hjortar utrustade med GPS-halsband analyserades för att lokalisera hjortarnas legor. Legornas positioner plottades på en karta indelad i vegetationszoner med olika busktäthet. När tätheten och durationen av legorna i varje vegetations zon beräknades visade det att sumphjortarna föredrar legor nära buskar men inte när busktätheten blir för hög. En analys av stabila kolisotoper i hår från 30 sumphjortar från två populationer utfördes också för att visa proportionen mellan intag av blad och gräs. Dessa resultat visade att enbart 4 – 14 % av sumphjortens diet består av gräs. Med denna typ av analys är det däremot inte möjligt att avgöra om löven de äter kommer från örter eller buskar och om sumphjorten också äter akvatiska växter. Ingen skillnad sågs mellan olika populationer eller kön.

SUMÁRIO

O cervo do pântanal sul Americano (Blastocerus dichotumus) vive em condicao úmida, está sendo ameacada, com riso de extincao na selva. Este estudo visa ganhar um conhecimento mais próximo nas suas escolhas por habitat e forragem, com foco na avaliacao do uso de arbustos disponíveis para abrigo e busca de alimento. O estudo é executado na estação ecológica de Jataí, estado de São Paulo, Brasil. Eu examinei se os cervos do pântano, assim como outras espécies de cervos, escolheram camas-locais na proximidade de grandes arbustos, que podem fornecer protecao contra as intempéries e os predadores. Dois cervos do pântano foram equipados com colares com GPS, estes dados foram analisados para encontrar as camas-locais dos cervos. As coordenadas das camas-locais foram plotadas em um mapa e dividido em polígono, com densidades diferentes dos arbustos. Uma relação entre o número de cama-locais em cada polígono e o tamanho de cada polígono foi calculada; o cervo do pântanal prefere sítios proximo de arbustos, mas não areasa com alta densidade de arbustos. A análise das camas-locais é baseada somente em dados de uma estação chuvosa, sendo que uma diferença sazonal na seleção destas camas-locais é possível. Uma análise de isótopos estáveis do carbono em amostras de pêlos de 30 cervos do pântano, de duas populações diferentes, foi executada para mostrar a proporção entre pastar e amostra ingerida. Estes resultados, em meu estudo, mostraram que somente de 4 – 14 % pastam. Nenhuma diferença foi encontrada entre as populações dos dois diferentes cervos do pântano e genero. A amostra ingerida consiste provavelmente de arbustos pequenos e possivelmente plantas aquáticas.

INTRODUCTION

About the marsh deer

Anatomy and ecology

The marsh deer (*Blastocerus dichotomus)* is the largest species of the cervidae family in South America, reaching an average shoulder height of 130 cm and an average weight of 100 kg for females and 130 kg for males (Figueira et al, 2005). It is adapted to a life in wetland habitats and riverine areas that are seasonally flooded, preferring a water depth of 30-60 cm. An adaptation to a life in wetland habitats is seen in the anatomy of their hoofs. They have extended toes which can spread up to 10 cm apart and in between there is a strong interdigital membrane, preventing them from sinking into the mud. With the exception of females with their young, the marsh deer is mainly a solitary living animal. Occasionally groups of up to five animals have been spotted. The fawns are predated by wild canines, felids and snakes and the adults by jaguars (Pinder & Grosse, 1991).

Distribution and status

Historically the marsh deer has been distributed in an area stretching from the southern banks of the Amazon River and west of the Atlantic Forest highlands to the northern parts of Argentina and Uruguay and into parts of Peru and eastern Bolivia (Figueira et al, 2005). The number of marsh deer has been drastically reduced, its reduction in global range distribution has been estimated to 65 % during the last four decades (Weber & Gonzales, 2003). The Pantanal Wetland, a 160,000 km^2 relatively undisturbed ecosystem in southern Brazil, now holds the largest remaining population of marsh deer (Pinder, 1996). This population was estimated to approximately 36,000 individuals in the early nineties (Mauro et al, 1998). In the Iberá wetland in Argentina, the second largest wetland in South America and the other major stronghold for the marsh deer, the number of marsh deer was estimated to approximately 1,000 in 1992 (Beccaceci, 1994). The species is believed to be extinct in Uruguay with no sighting since 1958. Many of the remaining populations are small and isolated due to habitat loss and fragmentation (Marquez et al 2006). An estimate of the total Brazilian population was made 1994 by Pinder resulting in the number 50,950 with only 1,300 animals in protected areas (Andriolo et al, 2005). The species is listed as vulnerable on the Red List of the International Union for Conservation of Nature (IUCN), which means it is likely to become endangered if nothing is done to improve their situation (Varela et al, 2002). Marsh deer is listed as endangered in Brazil (Andriolo et al, 2005).

Threats

The largest threat to the species is the loss of wetland habitat, mainly from the construction of hydroelectrical power-plants. The closing of dams inevitable leads to the destruction of the floodplains in the flooded area (Pinder 1996). The expansion of farmland also propose a threat, partly through habitat loss and habitat fragmentation but also through a closer contact between cattle and deer, exposing the deer to diseases such as brucellosis, babesiosis, foot-and-mouth disease, bluetongue, epizootic hemorrhagic disease and endo- and ectoparasites (de Oliveira et al, 2005). The marsh deer has also been exposed to excessive hunting and hide trade. This is now forbidden and the marsh deer is included in the CITES list, Appendix I, which bans all kind of trading with the species (CITES, 2008), but poaching still occurs (de Oliveira et al, 2005).

The importance of suitable bed-sites

Many deer species seek out bed-sites that shield them from weather extremes and provide protection from predators and they are located non-randomly within the deer's home-range (Kufeld et al, 1988; Ockenfels & Brooks, 1994; Millspaugh et al, 1997; Strohmeyer et al, 1999; Germaine et al, 2004).

A suitable bed-site can contribute to the deer's thermoregulation, which is a critical function for their survival. In the tropics the hot climate means that animals have to dissipate excess heat energy to maintain the right body core temperature. Physiologically, the main way to handle this heat load is by sweating, but this causes water losses and has high energy costs. Animals can also regulate their temperature by altering their behaviour. One way to do this is to lower activity levels during the hottest part of the day, another way is to seek thermal cover, like bed-sites with a good canopy closure, to avoid direct solar radiation (Ockenfels & Brooks, 1994).

Concerning predation, a bed-site that provides good concealment can have both positive and negative effects. It lessens the risk of predation by reducing the risk of detection and by physically obstructing the predator's attack. But a good hiding place can also delay the deer's detection of the predator and obstruct the deer's escape. However, in studies on a variety of deer species, the advantages of a good cover seem to outweigh this disadvantage in most cases (Mysterud & Ostbye, 1999).

This study will examine the marsh deer's bed-sites proximity to shrubs. Living in a hot climate it would be reasonable to expect the marsh deer to take advantage of the shade provided by the shrubs when choosing their bed-sites. Not much has been found in the litterature concerning the marsh deer's choice of bed-sites. Pinder (1996) observed that marsh deer often rested in the grasslands around the marshes along the Paraná River and were less often seen in the shrubs. According to Voss et al (1981, cited in Pinder & Grosse, 1991) they prefer to rest in tall grasses and patches of sedges.

Marsh deer – grazer or browser?

Ruminants are commonly classified as grazers, browsers or intermediate feeders (Gordon, 2003). However, the definition for grazers and browsers can vary between authors. In this paper a grazer is defined as an animal that mainly feeds on monocot plants (grasses, sedges) whereas a browser mainly feeds on dicot plants (forbs, shrubs, trees) (Gordon, 2003; Sponheimer et al, 2003b; Codron et al, 2007). Hence, feeding of the ground does not automatically place a ruminant species as a grazer since they could be feeding on forbs or small shrubs rather than grasses or sedges. In the remaining of this paper the term grass is going to include both grasses and sedges.

Another way to classify the feeding strategy of ruminants is through a morphophysiological approach. Based on differences in their digestive systems they can be divided into three overlapping feeding categories: grass and roughage eaters (mainly grazers), concentrate selectors (mainly browsers) and intermediate feeders (mixing grass and browse). Each of these categories has a digestive system well adapted to a different kind of diet (Hofmann, 1989).

Considering species of the cervidae family they have mainly been reported to be either concentrate selectors like roe deer, moose, white-tailed deer and mule deer or intermediate feeders like elk and fallow deer (Mysterud & Ostbye, 1999). Few species are reported to be grazers; one of them is the taruca in the Andes (Weber & Gonzales, 2003).

According to Tomas and Salis (2000) the literature is contradicting concerning the marsh deer's feeding habits. Some studies found that marsh deer mainly feed on grasses whereas others have stated that they mainly are browsers. Marsh deer has also been reported to ingest a lot of aquatic plant species. Investigations of rumen contents have also contradicted each other. Some rumens have contained mainly grass and some mainly leaves, so the question if the marsh deer is a grazer or a browser has not yet been completely answered. Going through the English literature there are only two studies found on the marsh deer's feeding habits. These two studies both conclude that the deer ingest more browse than grass (Tomas & Salis, 2000; Costa et al, 2006).

The analysis of stable carbon isotopes

Direct observation and micro-histology, i.e. examination of remnants of ingested plant parts in faeces, are two methods used to determine the marsh deer's diet in previous studies (Tomas & Salis, 2000; Costa et al, 2006). One disadvantage of determining a species diet through direct observation solely is that since this method usually record eating time rather than amount of ingested forage it is difficult to quantify the amount eaten of each type of plant species. Also the results can be biased by the observer since it can be hard to spot exactly what plant species and which part of the plant the animal is eating, especially when observing from larger distances. The use of micro-histology is a different approach to find out which species the animal has been ingesting but the exact amount of each species consumed is still difficult to determine (Holechek et al, 1982).

One semi-quantitative way to find out what kind of forage an animal has been eating is through the analysis of stable carbon isotopes in animal tissue. This reveals the proportion between grass and browse ingested and helps determine if the animal is mainly a grazer or a browser (West et al, 2006). The use of stable isotope analyses in studies of animal feeding ecology is based upon the fact that different food sources have different stable isotope ratios and that the stable isotope ratios in animal tissues are proportional to the stable isotope ratios in their diet (Jardine et al, 2006). Isotopes are atoms of the same element but with different number of neutrons leading to a difference in atom weight and also a slight difference in reaction time in chemical reaction. Some isotopes are prone to radioactive decay, some are not. The ones who do not undergo radioactive decay are called stable isotopes. Carbon, the element analyzed in this study, has two stable isotopes, ^{12}C and ^{13}C. They are after consumption traceable in animal tissues like blood, bone, collagen and hair, leaving a chemical fingerprint of the food consumed (West et al, 2006).

Plants have two major ways of photosyntesis, called C3 and C4. In the tropics almost all grasses and sedges are C4 plants (high elevation grasses excepted) whereas bushes, forbs and trees are C3 plants (Cerling et al, 2003). Due to different chemical pathways C3 plant species are more depleted in ^{13}C compared to those with C4 photosynthesis. The analysis of stable carbon isotopes in herbivore tissue will therefore reveal what kind of plants the animal has been eating. The analysis of stable carbon isotopes is becoming an increasingly common way to investigate if a herbivore in the tropics are a grazer, browser or a mixed feeder (West et al, 2006)

In this study stable carbon isotopes in hair, taken from 30 marsh deer in two different habitats, have been analyzed to find out the proportion between grazing and browsing. An analysis of stable carbon isotopes has, to my knowledge, never before been performed on marsh deer.

Background to the study

The construction of the Porto Primavera dam in Paraná River 1998 led to the destruction of the wetland habitat for a population of approximately 1,000 marsh deer (Pinder, 1996). This was the last remaining population of marsh deer in Säo Paulo state. In this state the marsh deer is now classified as critically endangered. To face the situation a group of scientists formed the Marsh Deer Reintroduction Project. Its purpose is to conserve the marsh deer in Säo Paulo state through reintroduction of captured deer from the Porto Primavera population into remaining floodplains where the original population has disappeared. Five of the captured deer, two males and three females, were reintroduced into Jataí Ecological Station (Figueira et al, 2005). The deer have reproduced since then and in 2006 there were approximately 20 marsh deer in the area (José Maurício Barbanti Duarte, personal communication).

The researchers behind the Marsh Deer Reintroduction Project, led by José Maurício Barbanti Duarte from the department of Animal Technology, University of Jaboticabal, São Paulo, have continuously been recapturing animals from the Jataí-population since the reintroduction. Their purpose has been to monitor the population regularly in order to follow population growth and animal welfare. This study was planned and carried out in collaboration with the Brazilian research group.

Aim of the study

Even though the marsh deer may be threatened by extinction there is not much detailed knowledge about its requirements considering diet and habitat (Tomas & Salis, 2000). This study aims at gaining a closer knowledge of the marsh deer's utilization of shrubs for foraging and shelter. The questions I want to find the answers to are the two following:

1. Does the density of marsh deer's bed-sites differ in areas with different shrub densities and if so, do they locate the majority of their bed-sites in areas with a high or low shrub density?

2. Is the marsh deer a grazer, browser or an intermediate feeder?

Through the analysis of the bed-sites proximity to shrubs I will discuss if the marsh deer uses shrubs for shade or hiding. Since many other deer species have been shown to use shrubs for shelter I find it likely that the marsh deer will too. Through the analysis of stable carbon isotopes I will show the proportion between browsing and grazing foraging. My expectation is that the marsh deer ingest more browse than grass, since this would be in line with most of the previous studies performed. This information may lead to a closer understanding of the marsh deer's needs concerning suitable habitats and be of aid in the selection of additional protected areas in the future.

MATERIALS AND METHODS

Study area

The Jataí Ecological Station is a protected area managed by the Instituto Florestal, situated in Louis Antonio, São Paolo State (21º33'S/47º45'W and 21º37'S/47º51'W). The study area consists of the floodplains along the Mogi-Guaçú River inside the protected area, and of three privately owned marshes, in connection to Jataí (Figueira et al, 2005). The largest and most important of these marshes, which contains the bulk of the reintroduced population, is a private floodplain area named Capão-da Cruz (1,512 ha) at the western border of the Jataí Ecological Station (Duarte, personal communication). Jataí has a total area of 9,010 ha which is covered by cerrado vegetation and a rich aquatic mosaic including lowlands, streams, marginal lagoons, and floodplains (Figueira et al, 2005). The entire study area is surrounded by sugarcane plantations, roads and forests.

The capture

Three female marsh deer named Andrea, Bruna and Julia were captured on the 28-29th of October 2006 with a technique called "Bulldogging" developed solely for this species by Duarte and his colleagues Each deer is chased with a helicopter until exhaustion, or for a maximum of ten minutes, whereupon two men jump off the helicopter onto the deer and wrestle it to the ground. The deer is then held down for about fifteen minutes, allowing a third person to sample blood and hair, to put an ear tag and the GPS-collar on it. Even though this procedure might seem stressful for the animal and therefore unethical, it is considered by the Brazilian research team that developed it to be the least dangerous way to capture the animals. Anaesthetics cannot be used due to the risk of drowning in the marsh (Duarte, personal communication).

Analysis of bed-sites

GPS-collars

The three marsh deer were tagged with GPS collars (Tellus Remote GSM, Televilt, Lindesberg, Sweden). The collars were configured following the Tellus GPS System User Manual (revised Aug 7th, 2006) using TPM software (Televilt, Lindesberg, Sweden). The coordinate system was UTM.

The GPS-positions of the deer were recorded and stored in the collars with a chosen time interval, five minutes for Bruna and Julia and ten minutes for Andrea. An activity measurement, which described the number of changes in collar position, vertically and horizontally, during the time it took for the collar to obtain the GPS fix, was also recorded. If the animal is inactive, a low number of position changes in the collar position are expected. If the animal is active a higher number of changes during the fix attempt are expected.

Julia and Bruna were recaptured in July 2007. Julia's collar was then removed and the data was downloaded from the collar. The collar had collected data until it ran out of battery on February 17th, 2007. Bruna had by the time of the capture lost her collar and hence all the data was lost. Andrea has not yet been recaptured and is probably still wearing her collar, but it ran out of battery December 2nd, 2006 and records no more data. However, her data has been downloaded from the Televilt database, thanks to an SMS-function on her collar.

Study period and climate

The climatic conditions in the area are divided into a distinct dry (November-April) and wet season (May-October) (Santos et al, 2001). This study was conducted during the wet season. GPS tracking data was collected from the 28th of October 2006 to the 17th of February 2007. The length of the study period differed for the two focal deer. From the collar of one of them, Andrea, data was received only until the 2nd of December 2007, whilst from the collar of Julia data was collected during the entire study period. The average monthly precipitation in the area is approximately 175 mm in November and February and 250 mm in December and January. The average monthly maximum and minimum temperatures during November-February are approximately 30ºC and 20ºC respectively. During the dry season the average monthly maximum temperature is 25-30ºC and the average monthly minimum temperature 12-18ºC. The average monthly precipitation during the dry season varies between 30-120 mm (Allmetsat, 2008).

Data treatment

The downloaded data files contained some probably inaccurate data. The first step in the data treatment was hence to remove any such errors. Rows assigned "Time Out" were commonly occurring, denoting that the positions were not fixed within the time limit, and that the position was therefore not recorded. In addition, the data set sometimes contained incorrect date or time recordings, or GPS positions that were way out of the study area. GPS positions could also be obviously wrong in the sense that the deer seemed to have moved a distance of several hundred meters in one direction only to be back at almost exactly the original position five minutes later. All these rows had to be manually deleted from the data set before doing any kind of analyses. In addition, all data registered before the 30th of October was removed, taking into account that the deer's behaviour might have been affected by stress from being captured during the first few days.

The measurements of horizontal (X) and vertical (Y) neck movement were added together to an "activity column", to receive a measurement of the deer's total level of neck movements with respect to change of collar position both vertically and horizontally. The activity value varied from 0 to 142, but was in 83 % of recordings between 0 and 10; only less than 4 % exceeded 20.

Using the UTM coordinate system, in which locations are measured in meters, made it possible to calculate the distance in meters between each recorded position. Each position was subtracted from the position of the previous measurement, resulting in a positive or negative distance for northing and easting. Using Pythagoras' theorem ($a^2 + b^2 = c^2$), the distance between the two points was then calculated. This calculated distance might be shorter than the real walked distance since we cannot assume that the deer moved between the two points in a straight line. On the other hand, even when the deer is laying on the same spot the radio collars calculates a walked distance of a few meters due to measurement errors. Hence, the calculated distance still gives a fairly good indication on how far the deer has walked.

The capturing of marsh deer and data processing described above took place before I started my degree project. This work was done by the Brazilian research team and three Swedish students, Lina Lehndahl, Josefin Ragge and Josefine Larsson. I used their data to calculate and localize the positions of bed-sites of the deer.

Localization of bed-sites

The GPS tracking data was used to localize Julia's and Andrea's bed-sites. The criteria chosen for a bed-site were:

1. Duration of one hour or more.

2. An activity level of 0, 1 or 2. A higher value was accepted if the previous and following value was 0, 1 or 2.

3. A maximum of 11 meters between each recorded position. A higher value was accepted if it was matched with a similar value in the opposite direction in the following recording. The coordinates of the first of those two values were excluded from the following calculations since the high value was considered to be an incorrect measurement. A higher value has also been accepted in the first row of each bed-site, since it represents meters walked from the last position before the deer arrived at the bed-site.

4. A standard deviation of no more than 5.0 meters for all the recordings of northing and easting coordinates in each bed-site.

An example of a bed-site marked in the data-set can be seen in figure 1.

When the bed-sites had been localized in the data-set a mean value was calculated for the coordinates of each bed-site creating a GPS-point for each bed-site. The duration for each bed-site was also calculated.

Northing	Easting	Meters walked	Activity level	Bed-site no
7611724	202450	12	6	
7611728	202459	10	13	
7611809	202424	88	2	
7611751	202461	69	2	
7611729	202479	28	0	294
7611729	202473	6	6	294
7611732	202473	3	0	294
		22	0	294
7611726	202474	24	0	294
7611731	202473	5	0	294
7611728	202474	3	0	294
7611732	202479	6	0	294
7611729	202473	7	0	294
7611731	202480	7	1	294
7611731	202480	0	3	294
7611731	202481	1	0	294
7611718	202471	16	10	
7611734	202484	21	11	
7611698	202451	49	10	

Figure 1. An example of the marking of a bed-site in the data-set. Note the low values in the columns “meters” and “activity” and the low variation in the northing and easting coordinates in the bed-site marking compared to the recordings before and after the marked bed-site.

Vegetation zones

The study area was divided into different vegetation zones with the aid of satellite pictures, acquired from the National Land Survey of Sweden, and aerial photographs. One of the satellite pictures showed the area in infrared, making it easier to distinguish different types of vegetation from each other. In the aerial photographs, taken from a height of 200 m, single larger shrubs were clearly visible. These photographs were stitched together, using the program Autostitch, to create a high resolution map over the area. This map was then compared to the satellite pictures. The area was divided into four vegetation zones:

1. No shrubs
2. Open shrub (< 50 % shrubs)
3. Closed shrub (> 50 % shrubs)
4. Forest (> 50 % trees)

The vegetation zone called “no shrubs” had a vegetation of grass, forbs, small shrubs (not visible on the aerial photographs), reeds or aquatic plants. The GPS-point of each bed-site was plotted in this map. Comparing the percentage of bed-sites in different vegetation zones made it possible to tell which zones Julia and Andrea preferred and which they avoided. Figure 2 displays the area of distribution of the different vegetation zones and the locations of the bed-sites.

The division into different vegetation zones was performed in the computer program ArcGIS version 9.2 and was made by another student, Josefine Ragge, for her degree project.

Figure 2. This map shows the area of distribution of the different vegetation zones in the study area and the location of the bed-sites. The different patterns represents forest (dense green circles), closed shrub (dense green dots), open shrub (thin green circles) and no shrubs (plain light green). Bed-sites are marked with black dots.

Analysis of stable carbon isotopes

Whenever a marsh deer has been captured for scientific reasons in Jataí Ecological Station a hair sample has been collected. Hair samples have also been taken from the marsh deer in the Porto Primavera population before the relocation. These hair samples have been stored in alcohol ever since. Thirty of these hair samples were sent to Iso-Analytical Limited, a stable isotope laboratory in Sandbach, UK. Thirteen of the samples were from the Jataí population and the other seventeen came from the Porto Primavera population. At Iso-Analytical approximately 500 µg of each hair sample was analyzed for stable carbon isotopes using the EA-IRMS technique (elemental analyzer isotope ratio mass spectrometry). Each sample were put into a tin capsule and sealed. The samples were then combusted and the resulting CO_2 gas was analyzed for stable carbon isotopes in a Europa Scientific 20-20 IRMS.

The results are reported using the standard stable isotope terminology where carbon isotopes ratios are expressed in delta notation (difference between sample and standard) as parts per thousands (West et al, 2006):

$$\delta^{13}C(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

R is the ratio of the minor to major isotope, $\delta^{13}C/\ \delta^{12}C$, as measured by mass spectrometry. All results are reported relative to the standard Vienna-Pee Dee Belemnite (West et al, 2006).

A dual-mixing model was used to convert hair $\delta^{13}C$ values to estimates of % C4 grass ingested (Codron et al, 2006):

$$\left(\delta^{13}C_{C3\ plant} + \Delta\delta^{13}C - \delta^{13}C_{hair}\right)/\left(\delta^{13}C_{C3\ plant} - \delta^{13}C_{C4\ plant}\right)$$

$\Delta\delta^{13}C$ is the isotope fractionation between diet and hair, here the value +3.2 ‰ has been used (Sponheimer et al, 2003a). Different endpoint values for C3 plants have been tried in the equation above, -27 ‰ (global mean), -29 ‰ and -31 ‰. The reason for this is that C3 plant species can be more or less depleted in ^{13}C in different environments (Cerling et al, 2003) and no local values are available for Jataí Ecological Station. The C4 end-point value varies less between different environments and hence the global mean of -12 ‰ has been used (West et al, 2006). To clarify with an example; if the global means are used as end-point values a $\delta^{13}C$ value of -23.8 ‰ in the hair samples would indicate a pure browse diet whereas a $\delta^{13}C$ value of -8.8 ‰ would indicate a pure grass diet.

RESULTS

Analysis of bed-sites

In total 460 bed-sites were found, 104 for Andrea and 356 for Julia. Of these 460 bed-sites only 353 were used in the analysis below due to demarcation of the home-range areas in the satellite pictures. With the criteria chosen for a bed-site Andrea was bedded 26 % of the time and Julia 20 %. The dominating activity level when the marsh deer were at the bed-sites was 0 (83.4 %), only 1.8 % of the recordings exceeded level 5.

The number of bed-sites per ha and the duration of these bed-sites per ha have been calculated. The ratio of the percentage of bed-sites in each different vegetation zone to the percentage of the total area for each type of vegetation has also been calculated. Using this equation random distribution of bed-site would result in an index close to one in all the different zones. An index higher than one means that the proportion of bed-sites in this vegetation zone is higher than this zones proportional area and is indicating that the marsh deer prefer this habitat when they chose a bed-site. In the same way an index lower than one indicates that they avoid it. The results are presented in table 1.

The results show that the two marsh deer prefer to locate their bed-sites in closed shrubs (4.4 bed-sites/ha; index: 2.2), that they are indifferent to areas with open shrubs (1.9 bed-sites/ha; index 1.0) and that they avoid having their bed-sites in areas with no shrubs (1.2 bed-sites/ha; index: 0.6) or forest (1.3 bed-sites/ha; index: 0.6). The mean duration for bed-sites in the three shrubby vegetation zones was 93 minutes compared to 83 minutes in vegetation zones without shrubs.

Table 1. Results of the bed-site analysis

Vegetation zone	Size (ha)	% of total area	# bed-sites	% bed-sites	Mean duration (min)	Bed-sites/ha	%bed-site/% area	min/ha
No shrubs	51.0	28.8	61	17	83	**1.2**	**0.6**	99
Open shrub	69.5	39.3	134	38	91	**1.9**	**1.0**	175
Closed shrub	27.8	15.7	121	34	96	**4.4**	**2.2**	418
Forest	28.6	16.2	37	37	91	**1.3**	**0.6**	118

Analysis of stable carbon isotopes

The mean $\delta^{13}C$ value for all deer is -25.20 ‰ (SD=0.37 ‰). This value represents different amounts of C4 plants ingested depending on the C3 end-point value used. Three different C3 end-point values (-27 ‰, -29 ‰ and -31 ‰) have been tried because of the variation in $\delta^{13}C$ values in C3 plants in different environments. The results are presented in table 2. Using the global mean of -27 ‰ resulted in a diet consisting of more than 100 % C3 plants, which is clearly impossible. An end-point value of -29 ‰ is equivalent to 3.6 % C4 plants ingested and -31 ‰ to 13.7 %. No significant differences were seen between sexes or different ages. There was tendency between the two populations (for an endpoint value of -31 ‰ are mean values 14.3 ± 0.6 in Jataí vs. 13.3 ± 0.5 in Paraná, Anova GLM, F_3.52, P=0.074. Standard deviation for repeated measurements of laboratory reference samples (powdered bovine liver, sucrose and beet sugar) were less than 0.1 ‰.

Table 2. The mean of % C4 ingested with different C3 end-point values

End-point value, C3 (‰)	C4 ingested (%)
-27	-9.3
-29	3.6
-31	13.7

DISCUSSION

Looking at the selection of bed-sites in relation to shrubs, it seems that the two marsh deer in this study prefer bed-sites in close proximity to shrubs, although they sometimes chose bed-sites in more open habitats, and that they avoid forest. Concerning the feeding habits of the Jataí and Porto Primavera marsh deer populations the analysis of stable carbon isotopes suggests that they are mainly browsers, i.e. feeding on plant parts from dicot plant species.

The selection of bed-sites close to shrubs is in line with the expectation that the marsh deer, like many other deer species, would use the canopy of the shrubs to protect themselves from heat and predators (Kufeld et al, 1988; Ockenfels & Brooks, 1994; Millspaugh et al, 1997; Strohmeyer et al, 1999; Germaine et al, 2004). On the other hand they do not reflect the observations made by Pinder (1996) and Voss et al (1981, cited in Pinder & Grosse 1991) who observed marsh deer lying in the grass and not in the shelter of shrubs. However, these are not results of studies made on the marsh deer's choice of bed-sites but are mere occasional observations. It is probable that these observations are biased by the fact that the marsh deer would be easier to observe when they are lying in the grass than if they are hiding in the shrubs.

Living in the tropics, the main concern considering the climate would be to handle the heat. The most effective way for the marsh deer to do this would be to shield from the direct radiation from the sun by taking shelter in the shade (Ockenfels & Brooks, 1994). In the middle of the day, when the sun stands high, there would be no shade available in this habitat except under the canopy of the shrubs. The grassy vegetation, away from the shrubs, is taller than the deer in many places and could provide for shade earlier and later in the day when the sun stands lower, but in those hours the temperature would be lower and the need for thermal protection less.

To seek thermal cover is only a good way to handle heat if it provides net benefits of energy, that is when it does not take too much energy to travel between feeding and cover sites. This applies especially if the animal is bedded for only a short period of time. It is more likely for the animal to seek shelter the longer the bedding period lasts (Mysterud & Ostbye, 1999). In this study a slight difference in duration is seen between the duration of bed-sites in areas with (93 minutes) and without shrubs (83 minutes). Another method that deer use to relieve heat stress is to increase heat loss through conduction by the use of water (Mysterud & Ostbye, 1999). The marsh deer is living in a habitat where it can be tiring to walk. They have constant availability to water which would make it easier for them to control body temperature and they do not risk dehydration. Therefore it may cost less energy for them to stay close to their feeding sites instead of seeking shade on occasions when they are far away from areas with large shrubs. This may be an explanation to why they sometimes chose bed-sites in areas without shrubs.

One study made on elk living in a hot climate showed that they can be successful even with minimal thermal cover as long as they have adequate forage. In the study area sagebrush provided the only shade. Most elk were found either far away from or in the sagebrush. They used the sagebrush stands for thermal cover if they happened to be close by, but they did not walk long distances to find them. This suggests that the action of seeking thermal cover is an energy optimization process and is not always necessary if the availability of energy is abundant. This also means that the need of thermal cover may differ between populations depending on the access to accurate forage (McCorquodale et al, 1986).

One question does arise when looking at the results. If the marsh deer choose bed-sites in the shrubs because of the shade they provide, why do they avoid the forest which would also provide shade? The answer to this question could be that the vegetation zones defined as forests consists of very dense vegetation, difficult to penetrate (personal observation) and therefore it is possible that the marsh deer would lose more energy than they would gain if they chose bed-sites in this type of vegetation. The plant species available in vegetation with dense shrub may also be less suitable for foraging.

Another way for deer to handle heat is to alter their activity pattern, having their major activity periods during times of the day with lower temperatures and rest during the hot part of the day (McCorquodale et al, 1986). This is in line with Lehndal (in preparation), who found that the marsh deer in this area are mainly nocturnal.

Considering the bed-sites function as protection for predators, the shrubs would probably not make much of a difference in this habitat. Since the grass grows tall the visibility is low in many places even without the extra protection of the canopy of the shrubs. It is thinkable that the marsh deer in our study area can use these grasses for protection as well as shrubs. This strategy, to seek shelter from predators in tall grasses, has been observed among oribis in Serengeti, Tanzania (Mduma & Sinclair, 1994).

The results of the stable carbon isotopes analysis indicate that the marsh deer is a browser. However, it is not possible to distinguish different kinds of browse from each other, like forbs, fruits or woody shrubs, with this type of analysis (Cerling et al, 2003). The fact that the marsh deer are placing the majority of their bed-sites among large shrubs could indicate that these shrubs constitute their preferred forage, but not necessarily so. If their preferred type of forage grows somewhere else it could still be beneficial for them to travel to the shelter of the shrubs for their resting periods, even though doing this would cost them energy and give them less time at their feeding site. Therefore it is possible that the marsh deer also forage in other areas, ingesting, and perhaps preferring, forbs, small shrubs not visible on the aerial photographs and aquatic plants.

Concerning the analysis of stable carbon isotopes one disadvantage with this study is that no local $\delta^{13}C$ values for the plants in the area has been available. The global means are approximately -27 ‰ for C3 plants and -12 ‰ for C4 plants (West et al, 2006). However, using these figures as endpoint values resulted in a diet which consisted of more than 100 % browse which is clearly impossible. This result probably depends on the fact that C3 values can vary considerable in different ecosystems depending on light conditions and availability of water (Cerling et al, 2003).

C3 plants are more depleted in ^{13}C in plants with a good water supply, resulting in lower $\delta^{13}C$ values (Codron et al, 2005). Cerling et al (2003) reported that mesic ecosystems have a Δ_{C3-C4} separation of 16-17 ‰ whereas xeric ecosystems have a Δ_{C3-C4} separation of 14-15 ‰ in non-drought condition and 11-13 ‰ in drought conditions. Since the marsh deer inhabits habitats rich in water one can presume that the $\delta^{13}C$ values of the browse they ingest would be more negative than the global mean. The exact value is impossible to know without an analysis of the local plant species but since the study area has a very good supply of water one can assume a Δ_{C3-C4} separation of at least 17 ‰. This would result in an end-point value of -29 ‰. Using this value the marsh deer would only ingest 4 % grass. It is possible that a wetland ecosystem gives plants even more depleted in ^{13}C, no studies about feeding ecology in wetlands using stable carbon isotopes have been found. There are reports concerning other ecosystems, like rainforests, going as low as -31.4 ‰ (Cerling et al, 2003). Magnusson et al (2001) reported a mean $\delta^{13}C$ value of -30.4 ‰ in C3 plants in a Brazilian savannah. Therefore the figure -31 ‰ was also tried as an end-point value, giving a C4 ingestion of 14 %. So, whatever endpoint value used, grass is still only a minor food source.

Another source of error is the possibility of the presence of aquatic plants in the area. Marsh deer has been reported to eat aquatic plants in previous studies (Tomas & Salis, 2000). There are aquatic plants present in our study area, but not to a great extent (Dahlström, in preparation). The photosynthesis in aquatic plant parts submerged in water does not work under the same conditions as in terrestrial plants, resulting in $\delta^{13}C$ values that are not indicative of the photosynthetic pathway (Keeley & Sandquist, 1992). Therefore it can be difficult to draw any conclusion from an analysis of carbon stable isotope if the animal has been eating aquatic plants. In a review by Keeley and Sandquist (1992) there is a summarization of $\delta^{13}C$ values for a wide range of aquatic plants. It is most likely that the deer only would ingest floating and emerging parts of the aquatic plant species. The mean $\delta^{13}C$ value in these parts in the dicots was -28.8 ‰. This value is in the range of the C3 end-point values used. However the $\delta^{13}C$ value of all emerging and floating parts of the monocots (grasses and sedges) was -25.1 ‰, i.e. much lower than the C4 end-point value of -12 ‰. The monocots and dicots combined had a mean of -27.1 ‰. These values suggest that the heterogeneous group of aquatic plants probably would be interpreted as browse in an analysis of stable carbon isotopes. Since this group could include aquatic grasses, which than would be interpreted as browse, the results would show a false low percentage of grass ingested. If the marsh deer in this study feed on aquatic grass species the estimated result of 4 – 14 % grass ingested is too low.

The results of this study confirm my expectations that marsh deer eat more browse than grass, although the amount of grass ingested seems to be lower than the findings in earlier studies, as in Costa et al (2006) and Tomas and Salis (2000), both performed in Pantanal. They reported a percentage of grass ingested somewhat higher than the result from this study, 19 % and 30 % respectively, compared to 4 – 14 %.

Costa et al (2006) made an observational diet study in Pantanal on marsh deer and pampas deer and found that they fed on 21 different plant species, choosing mainly new leaves and shoots. The diet consisted to 19 % of grass. To reach the same amount as them in this study a C3 end-point value of -32.5 ‰ would have to be used, which I find less probable since I have found no references to such a low end-point value in previous studies. However, it is possible, as mentioned earlier, that some of the browse in reality consists of aquatic grass species. Cerling et al (2003) also demonstrated that studies based on direct observation tend to overestimate the amount of grass ingested by browsers and of browse ingested by grazers. If this is true it is possible that Costa's result of 19 % grazing could be an overestimation.

Tomas and Salis (2000) performed a micro-histological analysis of faecal samples from marsh deer living in Pantanal, looking for remnants of plant species. They found that the marsh deer in their study fed mainly on the new growth of shrubs and earlier growth stages of aquatic plants and grasses, flowers were also readily consumed. In total, 40 ingested species were found. There were slight differences in species eaten between dry and wet season. Their diet consisted of 30 % monocots. This is two to seven times more grass than in this study and could be explained by the fact that most of the species ingested in Tomas and Salis (2000) study were aquatic plants. They concluded that the marsh deer is an intermediate feeder on the Hofmann scale.

When Hofmann (1989) classified ruminants as either concentrate selectors, grass and roughage eaters or intermediate feeders he did this looking at the differences in their digestive systems. Grass and roughage eaters are mainly grazers, consuming a lot of fibres. They have a large rumen and a long retention time, making it possible to digest cellulose and hemicellulose. Concentrate selectors are mainly browsers and eat a diet high in cell solubles, low in digestible fibres, but with a higher content of lignin, which is considered to be indigestible for all ruminants. A smaller rumen and a faster gastro-intestinal transit time make it difficult for them to digest structural fibres, but favour a rapid passage of lignin, leaving place for new browse. The intermediate feeders have a digestive system that morphologically and functionally lies in between the two already mentioned. They prefer a diet low in fibres but when the preferred source of forage go scarce, as in the winter or the dry season, their digestive system adapts and they switch to a diet with a higher fibre content.

Red brocket deer (*Mazama americana*) and grey brocket deer (*Mazama gouazoubirak*) are two South American deer species that have been reported to be concentrate selectors, with the ability to eat fibre and leaf in times of fruit scarcity (Gayot et al, 2004). The marsh deer has in comparision to these two *Mazama* species a longer gastro-intestinal transit time which should give it a higher ability to digest a diet rich in fibers (de Oliveira & Duarte, 2006).

The composition of stable carbon isotopes in hair reflects the diet eaten during the whole period of growth, that is a time period of several months (Sponheimer et al, 2003a) This fact make it difficult to tell if the marsh deer eats the same kind of forage all the year round. It is possible that they increase the amount of grass ingested in times when the nutrisious value of the forage changes or when availability of browse is lower. However, the small variations in $\delta^{13}C$ between the different hair samples taken at different times of the year suggests that the marsh deer mainly feed on the same composition of forage indifferent of season.

To find out more about the seasonal changes in the marsh deer's feeding habits one could perform an analysis of stable carbon isotopes in faeces collected over the year instead of hair. Faeces reflect the food eaten the last days instead of several months as with hair (Sponheimer et al, 2003a). Collecting faeces from marsh deer can be difficult though since they defecate in the water where their faeces are rapidly dissolved (Tomas & Salis, 2000). One could also perform a study based on microhistology; this would bring more information about exactly what species they are ingesting.

To find out more about the marsh deer's bed-site preferences it would be interesting to do a study where the micro-habitat of each bed-site is examined, preferably on recently used bed-sites. This could be made possible if additional marsh deer were equipped with GPS-collars with the SMS function, providing the research team with information about the deer's whereabouts close after it has been bedded.

CONCLUSIONS

The results of this study suggest that the marsh deer prefer bed-sites in shrubby areas even though they sometimes chose to rest in areas without shrubs. This indicates that spending time in the proximity of shrubs has to be favourable for the marsh deer in one way or another. Most probably they chose these locations because of the shelter the shrubs provide from heat and predators, but their feeding habits could also be of importance when making this choice. With the aid of the analysis of stable carbon isotopes the marsh deer were found to be browsers, ingesting only 4 – 14 % grass, although this result might be false low if they are feeding on aquatic grasses. So, it is possible that their bed-sites are located close to shrubs simply because these shrubs provide them with their preferred type of forage. However, it is impossible to tell how much of the browse ingested that consists of plant parts from shrubs. The marsh deer could also feed on forbs and aquatic plants; this might even make out the bulk of their forage. On those occasions when they chose bed-sites away from shrubs the constant availability of water, the high vegetation and the fact that the marsh deer in the area are mainly nocturnal could help them cope with the heat and predators. With the present results it seems likely that marsh deer prefer a habitat with shrubs available.

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