Mammalia 74 (2010): 247–255 © 2010 by Walter de Gruyter • Berlin • New York. DOI 10.1515/MAMM.2010.007

Use of vertical space by small mammals in gallery forest and woodland savannah in south-western Brazil

Wellington Hannibal[1] and Nilton C. Caceres[2,]*

[1] Departamento de Biologia, Universidade Federal de Mato Grosso do Sul-UFMS, Aquidauana, MS, 79.200-000, Brazil, e-mail: wellingtonhannibal@gmail.com
[2] Laboratório de Ecologia de Mamíferos e Aves, Departamento de Biologia, CCNE, Universidade Federal de Santa Maria-UFSM, Santa Maria, RS, 97.110-970, Brazil

*Corresponding author

Abstract

We examined the community composition and abundance of small mammals in the vertical strata of gallery forests and woodland savannahs in south-western Brazil. Captures were carried out during the winter and summer months of 2006/2007. Traps were set in three transect lines per habitat, with 10 capture stations on each line. Each station had three traps: on the ground, in the understorey (2–3 m in height), and in the canopy (8–10 m) in each physiognomy. With an effort of 3600 trap-nights, 11 species of small mammals were captured, which were distributed differently regarding the forest physiognomies and utilisation of vertical strata. The species showed a high degree of habitat segregation in the two physiognomies, with only the climbing-rat *Rhipidomys macrurus* found in both habitats. The correspondence analysis revealed that *Caluromys philander* occurred mostly in the canopy; *Cryptonanus agricolai*, *Marmosa murina*, and *Oecomys bicolor* in the understorey; and *Gracilinanus agilis* and *Nectomys rattus* on the ground. The utilisation of traps in different strata increased species richness in the Cerrado biome, showing that the small-mammal community is distributed along the vertical complexity of the forest and even in different physiognomies, enabling more species to coexist.

Keywords: Cerrado biome; coexistence; environmental complexity; marsupials; rodents.

Introduction

The abundance, richness, and diversity of species in small-mammal communities in the Neotropics can be related to the heterogeneity and complexity of the habitat (August 1983, Fernandez and Gentile 1999, Grelle 2003, Vieira and Palma 2005).

Small mammals can be classified into four guilds in relation to their vertical activity. One guild comprises strictly terrestrial species; a second guild comprises scansorial species that mainly use the ground and the lower strata of the forest; the third guild comprises scansorial species that use the ground, the understorey, and the canopy as well; and the fourth guild is formed mainly by arboreal species. Differences in vertical habitat utilisation are indeed a result of the interspecific competition (Vieira and Monteiro-Filho 2003, Begon et al. 2006).

In Brazil, studies related to the vertical forest utilisation by small mammals have been performed mostly in the Atlantic Forest (Vieira 1998, Graipel 2003, Graipel et al. 2003, Grelle 2003, Vieira and Monteiro-Filho 2003) and in the Amazon Forest (Malcolm 1991, 1995, Lambert et al. 2005). The community structure of small-mammal species regarding vertical forest utilisation in the Cerrado biome has remained unknown.

Most of the studies on small-mammal ecology carried out in the Cerrado biome have focussed on habitat heterogeneity (Alho 1981, Mares et al. 1986, 1989, Lacher and Alho 2001, Bonvicino et al. 2005, Ribeiro and Marinho-Filho 2005, Vieira and Palma 2005), and none of them has treated the vertical forest complexity. This could be related to the more heterogeneous landscape of the Cerrado biome, although discernible habitat complexity can be easily seen in the gallery forests and woodland savannahs.

The aim of this study was to examine the community composition and abundance of small mammals along the vertical strata in gallery forests and woodland savannahs of south-western Brazil. Our hypotheses were that: (1) Are species segregated on a vertical gradient? If not, is this because woodland savannah is not stratified, and/or is this because canopy is very low? These questions are based on the fact that the Cerrado biome has woodland formations with highly variable canopy height ranging from 14 to 30 m, sometimes exhibiting a complex physiognomy (Ribeiro and Walter 1998). In the study region, canopy height of woodland savannah ranges from 7 to 12 m on average (Caceres et al. 2010), being lower than expected. Thus, based on this, our questions would be explained by a weak or no evidence of segregation in the vertical space, at least in this region. (2) Are species composition and relative abundance of the small-mammal community in vertical strata similar between two vegetation physiognomies (gallery forest and woodland savannah)? This study was carried out in south-western Brazil, a region in the southern portion of the Cerrado biome which remains unknown with regard to small-mammal ecology and mainly community structure. In addition, we examined environmental factors related to vegetation complexity in both physiognomies, to examine their influence on the faunal structure.

Material and methods

Study area

The study areas comprised three replicates for both the gallery forest (GF1, GF2, GF3) and woodland savannah (WS1, WS2, WS3) physiognomies, located in two adjacent municipalities within the southern Cerrado biome. For gallery forest, the first and second sites were set at the Córrego das Antas stream, GF1 (20°27′18″ S, 55°34′6″ W), and at its tributary, 400 m distant, the Córrego do Jamil, GF2 (20°27′19″ S, 55°33′52″ W); the third site, 10 km distant from these, was set at the Córrego da Divisa, GF3 (20°27′16″ S, 55°29′52″ W). All these streams are tributaries of the Aquidauana River (Figure 1). Concerning woodland savannah, the first site was located in one 40-ha fragment, WS1 (20°31′15″ S, 55°17′55″ W), and the other two 3 km distant from this site, situated in a 400-ha remnant. The distance between these two other sampling sites (WS2: 20°33′27″ S, 55°17′44″ W; WS3: 20°33′47″ S, 55°17′49″ W) was 800 m within the 400-ha savannah remnant (Figure 1). The minimum distances among the three sampling sites in gallery forests were 400 m between GF1 and GF2, and the maximum distance was 7 km between GF2 and GF3. The study area comprised a maximum linear distance of 35 km between the GF1 and WS3 sites.

Animal trapping

Captures were made quarterly, during August/September and November/December 2006, and February/March and May/June 2007, evenly encompassing both dry and wet seasons. The trapping campaigns extended for 5 days in each field

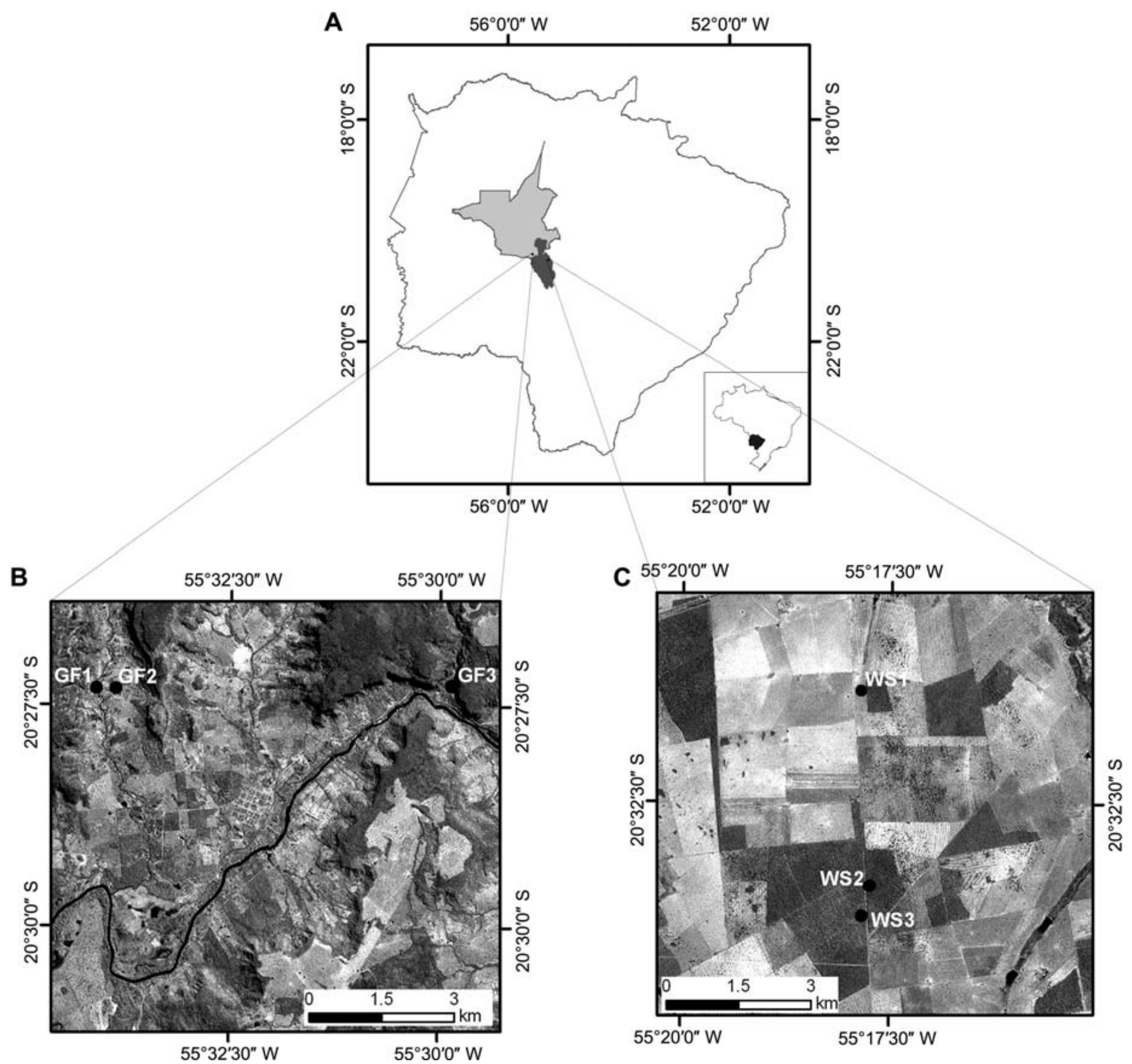

Figure 1 (A) Map of the State of Mato Grosso do Sul, Brazil, showing the municipalities of Aquidauana (clear grey) and Dois Irmãos do Buriti (dark grey); (B) aerial photograph showing the three points of gallery forest (GF1, GF2, and GF3); (C) aerial photograph showing the three points of woodland savannah (WS1, WS2, and WS3).

phase for both gallery forest and woodland savannah, totalling four field phases for each sampling site.

Captures were made in the two physiognomies (gallery forest and woodland savannah) by placing one transect line at each site (GF1, GF2, GF3, WS1, WS2, and WS3), each one comprising 10 sampling stations. Each sampling station comprised three traps: one on the ground, one in the understorey (2–3 m), and another in the canopy (8–10 m), totalling 90 traps installed per physiognomy (30 on the ground, 30 in the understorey, and 30 in the canopy). The distance between adjacent capture stations along a given transect line was 20 m. The traps were of two different types and sizes: small (7.5×9×30 cm) and large (12×14×40 cm) Sherman traps, and small (13×13×34 cm) and large (17×17×45 cm) Young traps. The traps were installed alternately so that each trap type and size was used in the different strata and physiognomies. The canopy traps were hung from a rope system that made it possible to connect them easily to the branches.

The bait used was a mixture of banana, squash, bacon, and cod liver oil, which had been previously used successfully in the region (Caceres et al. 2010).

Traps were examined every morning for captures. The method we utilised was capture, mark (with ear perforation by means of small round holes) (Monteiro-Filho and Abe 1999), and recapture. Some individuals that we could not identify with certainty in the field were removed for systematic identification.

Species were identified according to the nomenclature utilised by Wilson and Reeder (2005), with addition of other systematic studies (Bonvicino et al. 1996b, 2002a,b, Voss et al. 2005, Carmignotto and Monfort 2006). Animals collected were identified and deposited at the Universidade Federal de Santa Maria mammal collection.

Environmental parameters

The forest structure was measured for six vegetation parameters at each capture station. (1) Stratification was measured as an imaginary vertical column with a diameter of 3 m, counting how many butleries (coverage planes) were formed in that column up to the canopy. (2) Branch density was defined as the number of tree branches present in this last column. (3) Canopy density was measured at five points at each capture station, one at the central point and the other four at a distance of 3 m (to the north, south, east, and west), by counting leave obstruction in a mirror containing 37 small squares corresponding to 100% of the canopy area. (4) Tree, (5) shrub, and (6) liana densities were measured by counting individuals/structures to a 3-m radius from the central point of the sampling station. These environmental parameters are important factors in determining the forest quality for Neotropical small mammals (Pardini et al. 2005). To assess our hypotheses, tree density was measured and intended as a parameter that correlates with canopy height in the region, as there is a direct correlation between these two variables in woodland savannah (Caceres et al. 2010). In addition, vertical complexity was evaluated by the stratification variable.

Data analysis

For characterising small-mammal community structure, two variables were utilised in each physiognomy: composition and abundance. The capture success (number of captures divided by the total effort, multiplied by 100) was calculated for each vertical stratum.

Small-mammal species with at least five captures were used to examine the degree of association between faunal composition/abundance and utilisation of the vertical strata. For this purpose, Correspondence Analysis was performed (Past Software; Hammer et al. 2001), followed by a χ^2-test (Bioestat 4.0 Software; Ayres et al. 2005), because this allows one to examine the significance of these associations.

We utilised the t-test to examine the differences between the environmental vegetation parameters at the 60 capture stations (30 in gallery forest and 30 in woodland savannah) during the wet season only, because during the dry season stratification and foliage density were not present in the woodland savannah. Pearson's linear correlation analysis was used to examine the degree of relationship among the six vegetation parameters sampled at the 39 capture stations for which small mammals were captured. Both tests were applied using the Bioestat Software 4.0 (Ayres et al. 2005). Pearson's correlation test was used prior to the subsequent analyses, to exclude auto-correlated variables.

To examine the degree of association among small mammals and environmental parameters, we used small-mammal species with at least five captures in total. Environmental parameters were: physiognomy (gallery forest and woodland savannah), season (dry and wet) and vegetation parameters that were retained after the Pearson's correlation analysis for auto-correlated variables. The test used was the Canonical Correspondence Analysis (Past Software; Hammer et al. 2001). Relationships among environmental and faunal parameters were assessed by means of the Bartlett test (Bioestat 4.0; Ayres et al. 2005).

Results

For a total sampling effort of 3600 trap-nights, 58 captures representing 50 individuals belonging to 11 species (six marsupials and five rodents) were made in the two physiognomies. An equal number of species was recorded for the two physiognomies (n=6). Three (27%) of the 11 species were captured exclusively in arboreal traps (Table 1). According to stratum, trapping success was high in the understorey for gallery forests and high on the ground for woodland savannah.

In gallery forest, 33 captures were made, representing 28 individuals (capture success=1.8%; sampling effort=1800 trap-nights). We captured three marsupial species and three rodent species in the gallery forests. Among marsupials, *Marmosa murina* occurred in all three strata but mainly in the understorey; *Micoureus constantiae* was captured only once, in the understorey; and *Caluromys philander* was captured mainly in the canopy. Among rodents, *Nectomys rattus* was exclusively terrestrial; *Rhipidomys macrurus* was captured only once, in the understorey; and *Oecomys bicolor*

Table 1 Number of individuals and capture success of small mammals in gallery forest and woodland savannah of south-western Brazil.

Species	Gallery forest			Woodland savannah		
	Ground	Understorey	Canopy	Ground	Understorey	Canopy
Didelphimorphia						
Caluromys philander[a]	0	2	4 (1)	0	0	0
Cryptonanus agricolai	0	0	0	1	5	0
Gracilinanus agilis	0	0	0	6 (1)	3 (1)	0
Marmosa murina	2	5 (1)	0 (2)	0	0	0
Micoureus constantiae[a]	0	1	0	0	0	0
Thylamys macrurus	0	0	0	1	0	0
Rodentia						
Necromys lasiurus	0	0	0	1 (1)	0	0
Nectomys rattus	6	0	0	0	0	0
Oecomys bicolor	2	4 (1)	1	0	0	0
Rhipidomys macrurus[a]	0	1	0	0	0	1
Thrichomys pachyurus	0	0	0	4	0	0
Capture success (%)	1.66	2.50	1.33	2.50	1.50	0.16
Total captures	10	15	8	15	9	1

Parentheses indicate recapture numbers.
[a]Indicates species captured only in arboreal traps.

occurred in all three strata but mainly in the understorey (Table 1).

In woodland savannah, 25 captures representing 22 individuals were made (1.4%; 1800 trap-nights). We captured three marsupial species and three rodent species in this physiognomy. Among marsupials, *Gracilinanus agilis* was captured both on the ground and in the understorey, but mainly on the ground; *Cryptonanus agricolai* was captured more in the understorey; and *Thylamys macrurus* was captured only once, on the ground. Among rodents, *Necromys lasiurus* and *Thrichomys pachyurus* occurred exclusively on the ground; whereas *R. macrurus* was the only species recorded in the canopy of the woodland savannah, and also the only species recorded in both physiognomies.

The first two axes extracted from the Correspondence Analysis explained 99.5% of the total variance in the use of vertical strata among the 39 capture stations where animals were caught. The χ^2-test showed a high degree of association among the small-mammal species and their utilisation of vertical strata (χ^2=35.48; DF=10; p=0.0001). The marsupial *G. agilis* and the rodent *N. rattus* were associated with the ground, representing 52% of the captures in this stratum. The marsupials *C. agricolai* and *M. murina* and the rodent *O. bicolor* were associated with the understorey, representing 67% of captures in this stratum; this was the most species-rich stratum. *Caluromys philander* was the only species associated with the canopy, being captured only in gallery forests, and representing 56% of the captures in this stratum (Figure 2).

Branch density and tree density were the only parameters that did not show a difference between the two physiognomies (p>0.05). Shrub density was significantly higher in woodland savannahs, whereas stratification, lianas, and mainly foliage density were significantly higher in gallery forests (Table 2).

We obtained only positive correlations between each vegetation parameter, i.e., between stratification and canopy density (r=0.36; p=0.02), trees and shrubs (r=0.32; p=0.04), and branches and canopy density (r=0.34; p=0.04), showing that these correlated parameters would have the same effect when used in the canonical analysis. Thus for the canonical analysis between fauna and environment, the following vegetation parameters were used: stratification, tree density, liana density, and branch density.

The first two axes of the Canonical Correspondence Analysis between faunal and environmental parameters corresponded to 97% of the total variance (ϕ=14.79; DF=38; p=0.01). The wet season was not important in explaining variance, being associated with axis 2 (explaining only 15.5% of the variation). Axis 1 alone could explain 81.6% of the variance. Axis 1 could best explain most of the vari-

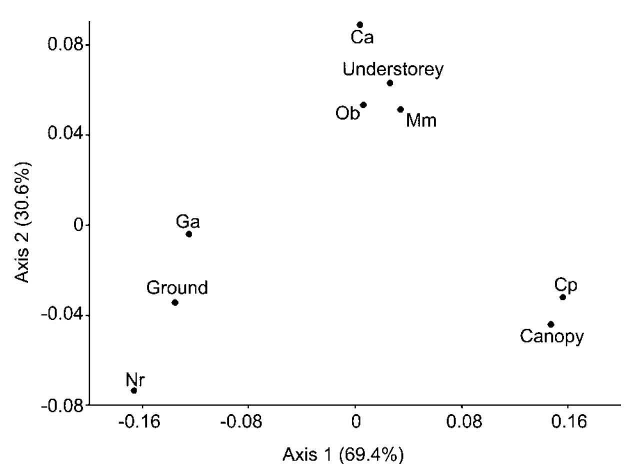

Figure 2 Correspondence Analysis (χ^2=35.48; DF=10; p=0.0001) associating small mammal species with the vertical strata in gallery forest and woodland savannah physiognomies of south-western Brazil. Legends for species: Cp=*C. philander*, Ca=*C. agricolai*, Ga=*G. agilis*, Mm=*M. murina*, and rodents: Nr=*N. rattus* and Ob=*O. bicolor*.

Table 2 Means and standard deviations for data of vegetation parameters measured during the wet season at 60 capture stations of both physiognomies studied (gallery forest and woodland savannah) of a Cerrado region in south-western Brazil.

	Woodland savannah	Gallery forest	t-Test	p-Value
Stratification	1.2±0.4	1.6±0.6	-2.3799	0.02*
Number of trees	2.6±0.9	2.1±1.2	1.8522	0.07
Number of shrubs	5.9±1.6	4.8±2.2	2.2302	0.03*
Number of branches	2.5±1.0	2.9±1.2	-1.3504	0.18
Canopy density (%)	78.9±15.4	90.4±10.7	-3.3537	0.001**
Number of lianas	1.3±1.3	2.6±2.8	-2.3618	0.02*

*p<0.05; **p<0.01.

ation, accounting for differences between fauna and physiognomies during the dry season, which was the season when most captures happened. There was a marked association between *C. agricolai* and *G. agilis* with the woodland savannah, as well as another important association between *C. philander*, *M. murina*, *N. rattus*, and *O. bicolor* and gallery forests. Liana density was the best environmental descriptor for those species correlated with the gallery forest, observing axis 1 (Figure 3, right).

Discussion

Our balanced sampling at different forest heights for the two physiognomies added real knowledge on small mammal community structure, provided that similar studies no longer used this protocol.

Several studies have pointed out the importance of arboreal captures for the evaluation of the species composition of small-mammal communities (Malcolm 1995, Graipel 2003, Grelle 2003, Vieira and Monteiro-Filho 2003, Lambert et al. 2005). Ecological studies carried out elsewhere in the Cerrado biome have not used traps in the understorey or in the canopy (Alho 1981, Mares et al. 1986, Vieira 1999, Lacher and Alho 2001, Briani et al. 2004, Bonvicino et al. 1996a, 1997, 2005, Ribeiro and Marinho-Filho 2005), showing that arboreal small-mammal species can be neglected in focal regions, as reported by Rodrigues et al. (2002).

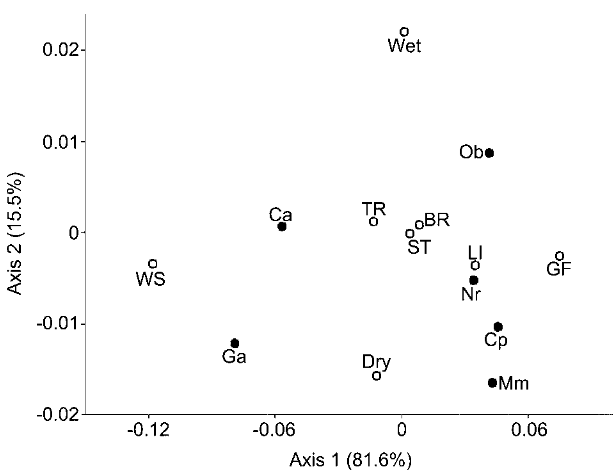

Figure 3 Canonical Correspondence Analysis showing the association (ϕ=14.79; DF=38; p=0.01) between faunal (black point) and environmental parameters (white point) in a region of the Cerrado biome in south-western Brazil. Legends for species: Cp=*C. philander*, Ca=*C. agricolai*, Ga=*G. agilis*, Mm=*M. murina*, Nr=*N. rattus*, and Ob=*O. bicolor*; for environmental parameters: WS=woodland savannah and GF=gallery forest; season: dry and wet; vegetation parameters measured: TR=tree density, ST=stratification, LI=liana density, BR=branch density.

Therefore, the use of traps in different forest strata allows adequate sampling of small mammals by enabling the capture of arboreal species (e.g., *R. macrurus*, *M. constantiae*, and *C. philander*, which were exclusively captured in arboreal traps here, or other, mostly arboreal ones) that have not previously been recorded in studies in the Cerrado (e.g., Mares et al. 1986, Bonvicino et al. 1996a, Vieira 1999, Lyra-Jorge et al. 2001, Briani et al. 2004, Ribeiro and Marinho-Filho 2005).

Despite the low abundance found in this study (11 species; effort of 3600 trap-night), the present species richness was similar to other studies carried out in savannah physiognomies of the Cerrado biome, which have found nine species (effort: 14,102 trap-night; Vieira 1999) and 10 species (effort: 4120 trap-nights; Briani et al. 2004), as examples. If we compared only gallery forest, the richness was the same than that found in other areas of the Cerrado (Lacher and Alho 2001). Our study had a similar pattern of capture success when compared with other studies carried out in the Cerrado biome, being around 2–5% (Alho 2005). Our relatively low abundance was as a result of the sampling protocol used, which has prioritised equal sampling in each vertical stratum. As most of the captures of small mammals are expected for the low, ground stratum (Graipel 2003, Vieira and Monteiro-Filho 2003, Lambert et al. 2005), this protocol would lead in fact to low rates of captures, by sampling mainly in quality rather than in abundance. However, as mentioned earlier and will be discussed later, species richness and composition did not suffer with this, provided that expected, cursorial species were found in our study when compared with a study carried out earlier in the region (Caceres et al. 2010), except for one species of *Calomys*. By contrast, our study revealed new species for the region, with the addition of three arboreal species, *C. philander*, *M. murina*, and *M. constantiae*.

With regard to the classification of the use of vertical stratum by small mammals (Vieira 2006b), species using mainly or exclusively the ground are placed in a ''cursorial'' guild, which in the study area included the marsupials *T. macrurus* and *G. agilis* and the rodents *N. rattus*, *N. lasiurus*, and *T. pachyurus*. *Thylamys macrurus* was considered scansorial, utilising mainly the ground but capable of regularly using the understorey (Carmignotto and Monfort 2006, Caceres et al. 2007b). *Gracilinanus agilis* was associated with the ground here, although it was captured in the understorey as well; but our report is not in accordance with a previous classification (Vieira 2006b), which considered the species to be arboreal. This could be related to two facts: (1) the canopy height of woodland savannah is low in the region (averaging 7–12 m; Caceres et al. 2010), being least complex (Table 2), with ground and canopy staying very close to each other, and (2) a great part of its captures occurred in the dry season here (valid also for the marsupials *C. philander* and *M. murina*; see Figure 3, axis 2), when individuals would need to move over a wider range of the three-dimensional space, including the ground level, to locate available resources (Caceres et al. 2002). The dry season is poorer in food resources (Malcolm 1995, Wells et al. 2004, Martins et al. 2006) corroborating this foraging behaviour, which is thought to facilitate capture of some species. Indeed, the congeneric species *G. microtarsus* has a more arboreal habitat, often occupying the canopy in the Atlantic Forest (Passamani 2000, Vieira and Monteiro-Filho 2003). Considering the rodents that occurred on the ground, *N. rattus* showed a cursorial habit here, similar to its congener *N. squamipes* from the Atlantic Forest (Lambert et al. 2005, Pardini et al. 2005, Graipel et al. 2006). *Necromys lasiurus* was captured only on ground level, showing its well-known cursorial habit, where 100% of its movements after capture have occurred on this level (Vieira et al. 2005). Although *T. pachyurus* was captured only on the ground in this study, its congener *T. apereoides* is considered semi-arboreal (Reis and Pessoa 2004). *Thrichomys* species in fact have cursorial and semi-arboreal habits (Oliveira and Bonvicino 2006, Bonvicino et al. 2008), but with a cursorial habit for *T. pachyurus* here (N.C. Caceres unpublished data).

The marsupials *C. agricolai*, *M. murina*, and *M. constantiae* and the rodents *O. bicolor* and *R. macrurus* were associated with the understorey, being considered scansorial or arboreal species here. These categories (Vieira 2006b) include species that utilise the ground and understorey at a similar rate, but with occasional use of the canopy, such as *M. murina* here (Lambert et al. 2005, Vieira 2006b). *Micoureus constantiae* is considered essentially arboreal, utilising the canopy more than the ground or the understorey (Vieira 2006b). Partially corroborating this, studies of *M. paraguayanus* in the Atlantic Forest have shown that this species utilises the understorey more than the ground (Graipel et al. 2006) or uses the understorey and canopy at similar rates (Goulart et al. 2006). In a different pattern (similar to *G. agilis*), *M. constantiae* was captured on the ground of a disturbed woodland savannah area elsewhere (Caceres et al. 2007a), which could be related to the forest structure of this area, which is probably less complex and leads arboreal species to descend more to the ground. Another hypothesis could be related to spatial segregation (Caceres and Monteiro-Filho 2006), where species of *Micoureus* tend to occupy mainly a lower stratum than those species of the genus *Caluromys*, which preferentially occupies the canopy (Charles-Dominique et al. 1981, Atramentowicz 1988, Julien-Laferrière 1995, Lambert et al. 2005). Therefore, *M. constantiae* was classified here as a generalist species, utilising with similar frequency all three strata (ground, understorey, and canopy), following Vieira (2006b).

The predominance of captures of *O. bicolor* in the understorey is in accordance with the results found for the genus in areas of the Amazon Forest. In the southern Amazon Forest, congeneric species were also captured mainly in the understorey (Lambert at al. 2005), the same pattern seen in French Guyana (Mauffrey and Catzeflis 2003) and the Atlantic Forest (Vieira and Monteiro-Filho 2003). Therefore, species of *Oecomys* could be considered as semi-arboreal with substantial use of the understorey (Ochoa 2000, Lambert et al. 2005), but sometimes descending to ground level (Bizerril and Gastal 1997, Mauffrey and Catzeflis 2003).

Rhipidomys macrurus was the only species captured in the canopy of the woodland savannah. The genera comprise arboreal species, which use the canopy more than the ground level (Ochoa 2000, Mauffrey and Catzeflis 2003, Vieira and Monteiro-Filho 2003, Lambert et al. 2005). This is in accordance with its remarkable body adaptations for arboreal life (such as the longer tail and whiskers, and larger eyes; N.C. Caceres personal observation), which make possible better exploitation of a three-dimensional habitat in trees. Specific movement behaviours in trees allow these arboreal animals to succeed in tasks related to habitat use (Vieira 2006b). Interestingly, *R. macrurus* was reported as a generalist in the use of vertical strata in the southern Amazon Forest (Lambert et al. 2005), and was the only species found in both physiognomies here.

Caluromys philander was the main species in this study to show a prominent association with the forest canopy, proving its essentially arboreal habit (Malcolm 1991, Julien-Laferrière 1995, Passamani 2000, Grelle 2003), and corroborating the classification of Vieira (2006b). However, the species can also be captured even in a low forest stratum (Charles-Dominique et al. 1981, Atramentowicz 1988, Julien-Laferrière 1995, Lambert et al. 2005). This could be a factor of seasonal regimes of climate and resources, leading the species to occasionally exploit the ground and understorey for feeding (see Caceres et al. 2002 for similar data).

Relationships between animals and environment are meaningful in determining species distribution and segregation, as is the case of small mammals here, seen in axis 1 (Canonical Correspondence Analysis, Figure 3) which could explain most of the data variation. There was an important relationship between selected small-mammal species (*C. philander*, *M. murina*, and *O. bicolor*) and gallery forest, which could be related to the higher complexity seen in this physiognomy, with higher density of lianas and canopy density, and a greater vertical stratification. The density of these structural parameters helps to connect different portions of the three-dimensional vertical strata, and help arboreal animals (such as those listed above) to move between arboreal patches.

Lianas, branches, and foliages also help by providing more vertical complexity to the forest habitats. This relationship occurred mainly in gallery forest rather than in woodland savannah in the study region (Table 2) and elsewhere (Marimon and Haridasan 2005), as lianas are rare, and canopy density and stratification levels were low in the savannahs studied. This explains, in part, the low number of fully arboreal small mammals found in savannahs when compared with gallery forests here (Table 1).

Woodland savannah is a physiognomy constituted by a large number of shrubby cerrado (*sensu stricto*) plant species mixed with gallery forest species. Thus, its forest canopy is shorter, ranging from 7 to 20 m, whereas the mean height of the gallery forest canopy varies between 20 and 30 m (Ribeiro and Walter 1998, Marimon and Haridasan 2005). Here, during the wet season the gallery forest had a denser canopy density (90%) than the woodland savannah (79%). In addition, the canopy in woodland savannah was broadly open during the dry period in the study region because of intense leaf fall. All these observations are supported by other studies carried out here (Caceres et al. 2010) and elsewhere (Ribeiro and Walter 1998, Marimon and Haridasan 2005), comparing the structures of both types of physiognomies. These factors could affect arboreal species distribution in woodland savannah, where arboreal habitat patches must be less connected, impeding the movements of small arboreal mammals there, and possibly favouring the existence of more cursorial species, such as *T. macrurus*, *N. lasiurus*, and *T. pachyurus*, which were all collected on the ground of the arboreal savannah here. By contrast, the low canopy height observed here for the woodland savannah (7–12 m height; Caceres et al. 2010) could explain the lower number of arboreal species in this physiognomy (e.g., *C. agricolai*), and even the unexpected major use of the ground level by *G. agilis*. We thus suggest that the spatial segregation between these morphological similar species, *G. agilis* and *C. agricolai*, is given in part by the vertical use of strata.

Studies in tropical South America have confirmed that small-mammal distributions in landscapes are mostly different and varied, varying with different vegetation physiognomies, forest densities, and water presence, showing the close relationship of mammals and habitat structure (August 1983, Fernandez and Gentile 1999, Lyra-Jorge et al. 2001, Grelle 2003, Vieira and Monteiro-Filho 2003). Our strong differentiation in species composition between the habitats of savannah and gallery forest leads us to infer about other reasons for this differentiation. An important reason is vegetation history and biogeographic processes involved when forests and savannahs advanced or retracted over the landscape in the recent past (Vivo and Carmignotto 2004), carrying species and forcing adaptation to each one of these different vegetations in the Cerrado biome (Johnson et al. 1999).

The Cerrado biome supports a mostly distinct fauna of small mammals associated with the two main forest physiognomies: gallery forest and woodland savannah in the southern portion of the biome. The complexity in these forest physiognomies, regarding their structural differences, is thought to be responsible for the vertical habitat utilisation by the small-mammal communities. The balanced utilisation of traps for sampling in different forest strata increased the conventional, expected species richness, showing that small mammals are spatially segregated along the vertical strata. To different degrees, both forest physiognomies (woodland savannah and gallery forest) found in the Cerrado biome are in part responsible for the patterns of high biodiversity commonly recognised for the biome (Myers et al. 2000). These physiognomies are better considered as complementary to each other, rather than a single ecological unit, when viewed in terms of species composition of their small-mammal faunas.

Acknowledgements

We thank Arlindo F. Béda, Dimitrius A.C. Cavalcante, and José Rímoli for field assistance, Raffael G. Oliveira, and Vitor M. Bacani for map assistance, Sandra M. Hartz and Maurício E. Graipel for fruitful comments on an early version of the manuscript, and one anonymous referee for their helpful assistance in its final version. This manuscript is a result of a Master's Dissertation in Zoology carried out in the ''Programa de Pós-Graduação em Biodiversidade Animal'', UFSM, Santa Maria, Brazil. N.C.C. is a CNPq-research fellow.

References

Alho, C.J.R. 1981. Small mammal populations of Brazilian Cerrado: the dependence abundance on diversity habitat complexity. Rev. Bras. Biol. 41: 223–230.

Alho, C.J.R. 2005. Intergradation of habitats of non-volant small mammals in the patchy Cerrado landscape. Arq. Mus. Nac. 63: 41–48.

Atramentowicz, M. 1988. La frugivorie opportuniste de trois marsupiaux didelphidés de Guyane. Rev. Ecol. (Terre Vie) 43: 47–57.

August, P.V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64: 1495–1507.

Ayres, M., M. Ayres Jr., D.L. Ayres and A.S. Santos. 2005. Bioestat 4.0: aplicações estatísticas nas áreas das ciências biológicas e médicas. Sociedade Civil Mamirauá, Belém. pp. 291.

Begon, M., C.R. Townsend and J.L. Harper. 2006. Ecology from individuals to ecosystems. 4ª ed. Blackwell Publishing, Oxford, United Kingdom. pp. 738.

Bizerril, M.X.A. and M.L.A. Gastal. 1997. Fruit phenology and mammal frugivory in *Renealmia alpina* (Zingiberaceae) in a gallery forest of central Brazil. Rev. Bras. Biol. 57: 305–309.

Bonvicino, C.R., R. Cerqueira and V.A. Soares. 1996a. Habitat use by small mammals of upper Araguaia River. Rev. Bras. Biol. 56: 761–767.

Bonvicino, C.R., P.S. D'Andrea, R. Cerqueira and H.N. Seuánez. 1996b. The chromosomes of *Nectomys* (Rodentia, Cricetidae) with 2n=52, 2n=56, and interspecific hybrids (2n=54). Cytogenet. Cell Genet. 73: 190–193.

Bonvicino, C.R., S.R. Freitas and P.S. D'Andrade. 1997. Influence of bordering vegetation, width, and state of conservation of gallery forest on the presence of small mammals. In: (L.L. Leite and C.H. Saito, orgs.) Contribuições ao Conhecimento Ecológico do Cerrado. Universidade de Brasília, Brasília. pp. 164–167.

Bonvicino, C.R., S.M. Lindbergh and L.S. Maroja. 2002a. Small non-flying mammals from conserved and altered areas of Atlantic Forest and Cerrado: comments on their potential use for monitoring environment. Rev. Bras. Biol. 62: 765–774.

Bonvicino, C.R., I. Otazu and P.S. D'Andrea. 2002b. Karyologic evidence of diversification of the genus *Trichomys* (Rodentia, Echimyidae). Cytogenet. Genome Res. 97: 200–204.

Bonvicino, C.R., B. Lemos and M. Weksler. 2005. Small mammals of Chapada dos Veadeiros National Park (Cerrado of Central Brazil): ecologic, kariologic, and taxonomic considerations. Rev. Bras. Biol. 65: 395–406.

Bonvicino, C.R., J.A. Oliveira and P.S. D'Andrea. 2008. Guia dos roedores do Brasil, com chaves para gêneros com caracteres externos. Organização Pan-Americana de Saúde, Rio de Janeiro. pp. 120.

Briani, D.C., A.R.T. Palma, E.M. Vieira and R.P.B. Henriques. 2004. Post-fire succession of small mammals in the Cerrado of central Brazil. Biodiv. Conserv. 13: 1023–1037.

Caceres, N.C. and E.L.A. Monteiro-Filho. 2006. Uso do espaço por marsupiais: fatores influentes, comportamento e heterogeneidade espacial. In: (N.C. Caceres and E.L.A. Monteiro-Filho, orgs.) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Universidade Federal de Mato Grosso do Sul, Campo Grande. pp. 203–214.

Caceres, N.C., I.R. Ghizoni Jr. and M.E. Graipel. 2002. Diet of two marsupials, *Lutreolina crassicaudata* and *Micoureus demerarae* in a coastal Atlantic Forest island of Brazil. Mammalia 66: 331–340.

Caceres, N.C., M.R. Bornschein, W. Hannibal and A.R. Percequillo. 2007a. Mammals of the Bodoquena Mountains, south-western Brazil: an ecological and conservation analysis. Rev. Bras. Zool. 24: 426–435.

Caceres, N.C., R.P. Napoli, W. Hannibal, J. Casella and G.S. Gazeta. 2007b. Natural history of the marsupial *Thylamys macrurus* (Mammalia, Didelphidae) in fragments of savannah in south-western Brazil. J. Nat. Hist. 41: 1979–1988.

Caceres, N.C., R.P. Napoli, J. Casella and W. Hannibal. 2010. Mammals in a fragmented savannah landscape in south-western Brazil. J. Nat. Hist. 44: 491–512.

Carmignotto, A.P. and T. Monfort. 2006. Taxonomy and distribution of the Brazilian species of *Thylamys* (Didelphimorphia: Didelphidae). Mammalia 70: 126–144.

Charles-Dominique, P., M. Atramentowicz, M. Charles-Dominique, H. Gérard, A. Hladik, C.M. Hladik and M.F. Prévost. 1981. Les mammiferes frugivores arboricoles nocturnes d'une forêt guyanaise: interrelations plantes-animaux. Rev. Ecol. (Terre Vie) 35: 341–343.

Fernandez, F.A.S. and R. Gentile. 1999. Influence of habitat structure on a streamside small mammal community in a Brazilian rural area. Mammalia 63: 29–40.

Goulart, F.V.B., F.L. Souza, H.B. Pavese and M.E. Graipel. 2006. Estrutura populacional e uso do estrato vertical por *Micoureus paraguayanus* (Didelphimorphia, Didelphidae) em fragmentos de Floresta Atlântica de planície no sul do Brasil. Biotemas 19: 45–53.

Graipel, M.E. 2003. A simple ground-based method for trapping small mammals in the forest canopy. Mast. Neotrop. 10: 177–181.

Graipel, M.E., J.J. Cherem, P.R.M. Miller and L. Glock. 2003. Trapping small mammals in the forest understory: a comparison of three methods. Mammalia 67: 551–558.

Graipel, M.E., J.J. Cherem, E.L.A. Monteiro-Filho and L. Glock. 2006. Dinâmica populacional de marsupiais e roedores no Parque Municipal da Lagoa do Peri, ilha de Santa Catarina, sul do Brasil. Mast. Neotrop. 13: 31–49.

Grelle, C.E.V. 2003. Forest structure and vertical stratification of small mammals in a secondary Atlantic forest, Southeastern Brazil. Stud. Neotrop. Fauna Environ. 38: 81–85.

Hammer, Ø., D.A.T. Haper and P.D. Ryan. 2001. Past: paleontological statistics software package for education and data analysis. Palaeontol. Electr. 4: 4–9.

Johnson, M.A., P.M. Saraiva and D. Coelho. 1999. The role of gallery forests in the distribution of cerrado mammals. Rev. Bras. Biol. 59: 421–427.

Julien-Laferrière, D. 1995. Use of space by the woolly opossum *Caluromys philander* (Marsupialia, Didelphidae) in French Guiana. Can. J. Zool. 73: 1280–1289.

Lacher Jr., T.E. and C.J.R. Alho. 2001. Terrestrial small mammal richness and habitat association in an Amazon forest-Cerrado contact zone. Biotropica 33: 171–181.

Lambert, T.D., J.R. Malcolm and B.L. Zimmerman. 2005. Variation in small mammal species richness by trap height and trap type in southeastern Amazonia. J. Mammal. 86: 982–990.

Lyra-Jorge, M.C., V.R. Pivello, S.T. Meirelles and M. Vivo. 2001. Riqueza e abundância de pequenos mamíferos em ambientes de cerrado e floresta, na Reserva Cerrado Pé-de-Gigante, Parque Estadual de Vassunuga (Santa Rita do Passo Quatro, SP). Naturalia 26: 287–302.

Malcolm, J.R. 1991. Comparative abundances of Neotropical small mammals by trap height. J. Mammal. 72: 188–192.

Malcolm, J.R. 1995. Forest structure and the abundance and diversity of Neotropical small mammals. In: (M.D. Lowman and N.M. Nadkarni, eds.) Forest canopies. Academic Press, San Diego, CA. pp. 179–197.

Mares, M.A., K.A. Ernest and D.D. Gettinger. 1986. Small mammal community structure and composition in the Cerrado Province of Central Brazil. J. Trop. Ecol. 2: 289–300.

Mares, M.A., J.K. Braun and D.D. Gettinger. 1989. Observation on the distribution and ecology of the mammals of the Cerrado grassland of central Brazil. Ann. Carnegie Mus. 58: 1–61.

Marimon Jr., B.H. and M. Haridasan. 2005. Comparação da vegetação arbórea e características edáficas de um cerradão e um cerrado *sensu stricto* em áreas adjacentes sobre solos distrófico no leste do Mato Grosso, Brasil. Acta Bot. Bras. 19: 913–923.

Martins, E.G., V. Bonato, H.P. Pinheiro and S.F. Reis. 2006. Diet of gracile mouse opossum (*Gracilinanus microtarsus*) (Didelphimorphia: Didelphidae) in a Brazilian Cerrado: patterns of food consumption and intrapopulation variation. J. Zool. Lond. 226: 21–28.

Mauffrey, J.F. and F. Catzeflis. 2003. Ecological and isotopic discrimination of syntopic rodents in a Neotropical rain forest of French Guiana. J. Trop. Ecol. 19: 209–214.

Monteiro-Filho, E.L.A. and A.S. Abe. 1999. Catchability of the white-eared opossum, *Didelphis albiventris*, in a disturbed area of southeastern Brazil. Arq. Ciên. Vet. Zool. UNIPAR 2: 31–35.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Ochoa, J.G. 2000. Efectos de la estracción de maderas sobre la diversidad de mamíferos pequeños em bosques de tierras bajas de la Guayana Venezolana. Biotropica 32: 146–164.

Oliveira, J.A. and C.R. Bonvicino. 2006. Ordem Rodentia. In: (N.R. Reis, A.L. Peracchi, W.A. Pedro and I.P. Lima, eds.) Mamíferos do Brasil. Universidade Federal de Londrina, Londrina. pp. 347–406.

Pardini, R., S.M. Souza, R. Braga-Neto and J.P. Metzger. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biol. Conserv. 124: 253–266.

Passamani, M. 2000. Análise da comunidade de marsupiais em Mata Atlântica de Santa Teresa, Espirito Santo. Bol. Mus. Biol. Prof. Mello Leitão 11: 215–228.

Reis, S.F. and L.M. Pessoa. 2004. *Thrichomys apereoides*. Mamm. Spec. 741: 1–5.

Ribeiro, J.F. and B.M.T. Walter. 1998. Fitofisionomias do bioma Cerrado. In: (S.M. Sano and S.P. Almeida, eds.) Cerrado: Ambiente e Flora. Embrapa-CPAC, Planaltina. pp. 87–166.

Ribeiro, R. and J. Marinho-Filho. 2005. Estrutura da comunidade de pequenos mamíferos (Mammalia, Rodentia) da Estação Ecológica de Águas Emanadas, Planaltina, Distrito Federal, Brasil. Rev. Bras. Zool. 22: 898–907.

Rodrigues, F.H.G., L. Silveira, A.T.A. Jácomo, A.P. Carmignotto, A.M.R. Bezerra, D.C. Coelho, H. Garbogini, J. Pagnozzi and A. Hass. 2002. Composição e caracterização da fauna de mamíferos do Parque Nacional das Emas, Goiás, Brasil. Rev. Bras. Zool. 19: 589–600.

Vieira, E.M. 1998. A technique for trapping small mammals in the forest canopy. Mammalia 62: 306–310.

Vieira, E.M. 1999. Small mammal communities and fire in the Brazilian Cerrado. J. Zool. 249: 75–81.

Vieira, M.V. 2006a. Locomoção, morfologia e uso do habitat em marsupiais neotropicais: uma abordagem ecomorfológica. In: (N.C. Caceres and E.L.A. Monteiro-Filho, orgs.) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Universidade Federal de Mato Grosso do Sul, Campo Grande. pp. 145–156.

Vieira, E.M. 2006b. Padrões de uso vertical do habitat por marsupiais brasileiros. In: (N.C. Caceres and E.L.A. Monteiro-Filho, orgs.) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Universidade Federal de Mato Grosso do Sul, Campo Grande. pp. 219–228.

Vieira, E.M. and E.L.A. Monteiro-Filho. 2003. Vertical stratification of small mammals in the Atlantic rain forest of south-eastern Brazil. J. Trop. Ecol. 19: 501–507.

Vieira, E.M. and A.R.T. Palma. 2005. Pequenos mamíferos de Cerrado: distribuição dos gêneros e estrutura das comunidades nos diferentes habitats. In: (A. Scariot, J.C. Sousa-Silva and J.M. Felfili, orgs.) Cerrado: Ecologia, Biodiversidade e Conservação. Ministério do Meio Ambiente, Brasília. pp. 265–282.

Vieira, E.M., G. Iob, D.C. Briani and A.R.T. Palma. 2005. Microhabitat selection and daily movements of two rodents (*Necromys lasiurus* and *Oryzomys scotti*) in Brazilian Cerrado, as revealed by a spool and line device. Mamm. Biol. 70: 359–365.

Vivo, M. and A.P. Carmignotto. 2004. Holocene vegetation change and the mammal faunas of South America and Africa. J. Biogeog. 31: 943–957.

Voss, R.S., D.P. Lunde and S.A. Jansa. 2005. On the contents of *Gracilinanus* Gardner and Creighton, 1989, with the description of a previously unrecognized clade of small didelphid marsupials. Am. Mus. Nat. Hist. 3482: 1–34.

Wells, K., M. Pfeiffer, M.B. Lakim and K.E. Linsenmair. 2004. Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia. J. Biogeogr. 31: 641–652.

Wilson, D.E. and D.M. Reeder. 2005. Mammal species of the world – A taxonomic and geographic reference. 3rd edn. The Johns Hopkins University Press, Baltimore, MD. pp. 21, 42.