



ORIGINAL INVESTIGATION

Influence of extrinsic variables on activity and habitat selection of lowland tapirs (*Tapirus terrestris*) in the coastal sand plain shrub, southern Brazil

Luiz Gustavo R. Oliveira-Santos*, Luiz Carlos P. Machado-Filho, Marcos Adriano Tortato, Luisa Brusius

Laboratory of Applied Ethology-Depto. de Zootecnia e Desenvolvimento Rural, Universidade Federal de Santa Catarina, Rodovia Admar Gonzaga, 1346, CEP 88.034-001, Florianópolis – SC, Brazil

Received 11 September 2008; accepted 28 May 2009

Abstract

The objectives of this research were to: 1. evaluate the circadian activity patterns of lowland tapirs (*Tapirus terrestris*) throughout the seasons and 2. study the influence of moonlight, temperature and rainfall on the activity patterns and habitat selection of this species, in the coastal sand shrub in southern Brazil. From June 2005 to June 2006, eight tapirs were monitored in a large enclosure containing open and vegetation-covered areas, using four camera traps. Differences in activity patterns within seasons were found. Tapir predominately presented nocturnal-crepuscular activity; however, they differed in the winter, with cathemeral activity patterns. Covered areas were mostly used during periods of extreme temperatures, with less diurnal and more nocturnal activities within these areas, on hotter days. Activity in open areas mainly occurred during periods of intermediate temperatures, both during the day and in the night. Moonlight intensity did not influence nocturnal activities. On days of precipitation of 34 mm or more, there was no record of open-area activities, despite constant activity in covered-area.

© 2009 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Keywords: Behaviour; Circadian rhythmic; Moonlight; Rainfall; Temperature

Introduction

Tapirs (*Tapirus terrestris* L., 1758) are among the largest neotropical mammals, weighing from 150 to 300 kg (Padilla and Dowler 1994). They are found from the north of South America all the way down to the northern portion of Argentina, occupying both closed forests and open environments (Emmons 1990; Eisen-

berg and Redford 1999). They are selective herbivores, rarely seen in natural environments due to their solitary habits. They have highly sensitive auditory and olfactory senses (Eisenberg and Redford 1999; Medici 2001) and are usually associated to bodies of water.

Tapirs spend most of their active time consuming great quantities of plants, mostly foraging in secondary and open areas (Naranjo 1995; Salas and Fuller 1996; Foerster and Vaughan 2002; Tobler 2002). Selection for such areas is probably due to the greater availability of vegetable biomass within accessible heights (Janzen 1982; Bodmer 1989, 1990). In such environments of greater exposition, the tapir needs to keep thermal and water balance, as well as develop anti-predation

*Corresponding author. Rua 21 de Setembro, 1880-Bairro Nossa Senhora de Fátima-Caixa Postal 109-Corumbá, MS-Brasil-79320-900-Embrapa Pantanal-Laboratório de Vida Selvagem.

E-mail address: gu_tapirus@hotmail.com (L.G.R. Oliveira-Santos).

strategies. For thermal and water balance, the tapir, as other thermal-independent animals, can use physiological mechanisms to either alter their activity or habitat selection patterns (Schmidt-Nielsen 2005). On the other hand, when individuals are occupying open areas, anti-predation strategies can be related to activity changes triggered by moonlight (Lockard and Owings 1974; Kaufman and Kaufman 1982; Downer 2001). In open areas, predators can detect, approach and capture their prey more easily because their ability to escape and hide is usually decreased (see review by Lima and Dill 1990).

Large ungulates, such as the tapir, have been classified, according to van Schaik and Griffith's (1996) early classification, as cathemeral organisms, presenting sporadic and random activity throughout the 24 h of the day. However, a study in Bolivia has recorded a great amount of nocturnal activity in a *T. terrestris* population (Gómez et al. 2005). Moreover, despite some diurnal activity in Costa Rica, *T. bairdii* was reported to have mainly nocturnal-crepuscular patterns as well (Williams 1984; Foerster 1998). Based in this plasticity in the activity pattern of tapirs, we hypothesized that they could change their activity and/or habitat selection depending on different extrinsic variables, optimizing the energetic cost to water and thermal balance and decreasing predation risk. We believed that temperature and rainfall could be important variables related to water and thermal balance, while the moonlight could be related to predation risk. Therefore, this study was aimed at evaluating year-round circadian rhythms of the tapir, and to study the effect of the extrinsic variables – temperature, rainfall and moonlight – on the activity patterns and habitat selection of this species.

Material and methods

Study area

The study was conducted in a 160 ha fenced enclosure, at the Serra do Tabuleiro State Park (STSP), in southern Brazil (27°50'S and 48°50'W). The predominant climate, according to the Köppen system, is meso-thermic humid (Cfa type), with hot summers. Annual precipitation is approximately 1600 mm, with no defined dry season. February has historically been the rainiest month (averaging 210 mm) and June, the driest (averaging 68 mm). The average annual temperature is 19 °C. January is generally the hottest month (averaging 25 °C, range = 20–38 °C) and July (averaging 15 °C, range = 4–25 °C) the coldest (GAPLAN 1986).

The landscape is composed of coastal salt-marsh vegetation covering sand dunes, with sparse areas of marshes and of either permanent or temporary lakes (Klein 1981). From satellite imaging and posterior field confirma-

tion, vegetation was classified according to four types: arboreal, herbaceous-shrubby, scrubby and grassy-brushy salt marsh. The arboreal salt-marsh is in an advanced stage of regeneration, representing 20% of the area. It has a 5 meter canopy and a dense understory, with bushes, lianas and epiphytes. The herbaceous-shrubby presents some temporary lakes during the wet season (spring-summer) and represents 41% of the marsh area. Sedges (*Lagenocarpus* sp.) and grasses occupy most of the area, with some isolated bushy concentrations of Melastomataceae (*Miconia* sp. and *Tibouchina* sp.), Myrtaceae (*Psidium Cattleianum*), and Clusiaceae (*Clusia parviflora*). The scrubby vegetation covers 8% of the area and is predominantly formed by trees (*Dodonaea viscosa* – Sapindaceae), which can achieve approximately 3 meters of height, and by bushes of the herbaceous-shrubby vegetation. The grassy-brushy covers 31% of the area and is formed by wetland plants, predominantly surrounded by sedges (*Cyperus* sp.).

Study animals

Eight tapirs were studied, 7 adults (3 males and 4 females) and a male calf, living in semi-captivity, breeding freely and without veterinary assistance. Their diet consists of the diverse natural resources of the area (Oliveira-Santos et al. 2005) with a supplement of squash, tapioca, cabbage, papaya and horse feed (Bevilaqua and Tortato 2003). This supplement is made available two or three times a week, is not sought for by all individuals, and is yet shared with other park animals, mainly rheas (*Rhea americana*) and capybaras (*Hydrochaeris hydrochaeris*).

Camera trap sampling

Between June 2005 and June 2006, four digital passive infrared (Tigrinus®) camera traps were used to monitor 14 sample stations: four in the arboreal salt-marsh, four in the herbaceous-shrubby vegetation, three in the scrubby vegetation and three in the grassy-brushy salt marsh. To optimize data collection, the sample stations were placed on trails which presented indirect evidence (tracks, footprints and feces) of the tapirs (Borges and Tomas 2004). Once the sample stations were pre-defined to the four habitats, we looked for sites with similar probability of capture in the whole semi-captivity, selecting those sites which were wind- and sunlight protected and with evident tapir trails. A minimum distance of 200 m was established between sample stations. The camera traps were placed on trees with bungee cords, facing the trails. The traps were programmed to monitor movements for 24 h, and the cameras to register the time and date of each recording.

We exchanged the camera-trap stations weekly, following a randomly selected and previously defined

chronogram for each vegetation area. Each vegetation area was monitored with a sample effort (in traps-day) in proportion to the available area. The same effort was maintained for each season. A more adequate sample design could increase the number of stations in the larger areas instead of increasing the sample effort in trap-days. This protocol was not applied because of camera-trap mechanism's constraints. Camera-traps did not function adequately with exposure to high wind and sunlight, counter-indicating the increase in the number of sample station in open areas. In fact, it is more difficult to detect tapir trails in open areas than in forested areas. Thus, we did not find more sites in open areas with evident trails, to standardized the capture probability between open and covered areas.

Extrinsic variables

The extrinsic variables studied were temperature, rainfall and moonlight intensity. The meteorological data used (rainfall and temperature) were daily records of the meteorological station of Epagri, at Palhoça, Santa Catarina state, which is located within the same coastal plain of the study area (10 km away). To evaluate the effect of the intensity of the moonlight on tapir behavior, a linear scale of natural numbers from 0–15 was created, where each day had a certain value (v). The scale began on the first day of the new moon ($v = 0$) and received increasingly higher values up to the first day of the full moon ($v = 15$). From the second day of the full moon ($v = 14$), each day thereafter received a lower number, up to the last day of the last quarter of the moon ($v = 1$). This scale was based on the assumption that the variation of moonlight is linear.

Data analysis

The arboreal and the scrubby salt-marsh areas were considered covered areas and the herbaceous-shrubby and the grassy-brushy areas were considered open areas. This classification system was made according to similar plant coverings. The characteristic of open or covered vegetation was supposed to be the main plant variable, which influenced activity and selection of habitat among different conditions of extrinsic variables (Mourão and Medri 2007).

As tapirs are solitary animals (Padilla and Dowler 1994) and usually walk at about 200–300 meters/hour (Foerster 1998; Tobler 2008), records with a minimum interval of 1 h between photographs, at each sample station, were considered independent (Gómez et al. 2005; Di Bitetti et al. 2006). Each photograph received a value for moonlight intensity (v), temperature ($^{\circ}\text{C}$) and accumulated rainfall (mm) for that day. Photographs taken one hour before and one hour after sunset and sunrise were considered of crepuscular activity. Photos

taken within the period of one hour after sunrise to one hour before sunset were considered of diurnal activity. Finally, those taken within the period encompassing one hour after sunset and one hour before sunrise were considered of nocturnal activity. For analysis of the influence of moonlight intensity on tapir activity, only nocturnal recordings were considered. Time of sunrise and sunset were accessed on the Moonrise 3.5 program (Sidell 2002).

To check if the circadian activity patterns had a uniform distribution throughout the day (cathemerality), the Rayleigh test of the Oriana 2.0 program (Zar 1996) was adopted. To compare the proportions of diurnal, nocturnal and crepuscular activities between seasons and types of vegetation, the G Test (Zar 1996) was used. The criteria used to define if the activity pattern was cathemeral or not was a statistical test. A cathemeral pattern was defined when uniform circular distribution of the records around the clock was found (Rayleigh test). If no cathemerality was found, tapirs were classified as nocturnal ($>70\%$ of recordings at night), nocturnal-crepuscular (45–70% of the recordings at night and $>20\%$ crepuscular), crepuscular-diurnal ($<45\%$ of recording at night and $>20\%$ crepuscular) or diurnal ($<45\%$ of recording at night and $<20\%$ crepuscular).

Linear regressions were used to check if there was a relationship between activity and moonlight and temperature. In these cases, because we aimed to evaluate changes in the activity pattern on different habitats, diurnal and nocturnal recordings in open and covered areas were analyzed separately. Since we categorized the daily accumulated rainfall, and activity was measured in frequency of records, the Pearson correlation test or Kolmogorov-Smirnov test would not be adequate to the rainfall effect analyses. Then, in this case, we used graphics analyses to compare open and covered areas. Activities were defined according to the frequency of records found in each category of moonlight, daily mean temperature or of daily accumulated rainfall. For all cases, the frequency was calculated by dividing the number of records in each category by its respective sample effort in number of traps-day. We used the frequency of records as a surrogate of activity to avoid biased results, because the unequal sampling effort in each class or category of moonlight, daily mean temperature or daily accumulated rainfall.

Results

Circadian activity patterns

An effort of 1,213 traps-days was made, and 157 tapir photographs were taken. There were differences in the

circadian activity patterns of the different seasons of the year ($G = 18.882$, $P = 0.004$) (Table 1). Tapirs predominantly presented nocturnal-crepuscular activity throughout the year (Fig. 1). Only during winter there was a cathemeral behavior observed, for no difference in the distribution of records throughout the hours of the day was found ($Z = 0.584$, $P = 0.504$). Despite the major nocturnal activity in the open areas (72%), in relation to covered areas (54%), there were no differences between the distribution of activities within these areas ($G = 3.137$, $P = 0.217$). In both areas, the pattern was typically nocturnal-crepuscular.

Influence of extrinsic variables

Nocturnal tapir activity had no effect from moonlight in open ($R^2 = 0.02$, $N = 16$, $P = 0.57$) nor covered areas ($R^2 = 0.02$, $N = 16$, $P = 0.58$). In covered areas, diurnal activity decreased as the daily mean temperature increased ($R^2 = 0.84$; $N = 16$; $P < 0.01$; diurnal activity = $-0.011 \times \text{temperature} + 0.283$) (Fig. 2a). Inversely, nocturnal activity was noted to increase during hot days ($R^2 = 0.33$; $N = 16$; $P = 0.02$; nocturnal activity = $0.012 \times \text{temperature} - 0.092$). In open areas, the majority of the records were made in intermediate temperatures (15–20 °C), irrespective of the time of day (Fig. 2b). No activity was recorded in open areas on days with precipitation above 34 mm (Fig. 3a). Nonetheless, in covered areas, activity was recorded even on the rainiest days (65–74 mm) (Fig. 3b).

Discussion

Circadian activity patterns

Results indicated mainly nocturnal-crepuscular tapir activity. This pattern has already been reported in

studies of lowland tapirs (Maffei et al. 2002; Gómez et al. 2005), as well as with other species of the same genus (Williams 1984; Foerster 1998; Lizcano and Cavelier 2000; Holden et al. 2003). Our results do not corroborate the idea that the tapir has cathemeral activity, which is characteristic of various selective grazing ungulates (van Schaik and Griffiths 1996). According to these authors, body size is the main factor for variation in activity patterns. Therefore, large herbivore mammals would be cathemeral to achieve intake according to energy requirements.

Another factor that may be relevant in explaining activity patterns is interspecific diet competition, which may occur between mammals and birds (Gómez et al. 2005). In our study, tapirs co-occurred with capybaras and rheas. However, no interspecific competition was noticed, as tapirs would forage in different places and on different plants (mainly shrubs in open and covered areas; Padilla and Dowler 1994) from those used by capybaras and rheas (mainly grasses in open areas). Anti-predator strategies are also supposed to explain activity patterns. In this study, however, there were no tapir predators, and some studies have not found tapir activity related to any anti-predation strategy (Weckel et al. 2006).

Based on our results, differences in activity patterns between seasons are more likely to be related to changes in temperature and rainfall throughout the year. Low temperatures, associated with high precipitation, led tapirs to be uniformly active throughout the day. Conversely, on days with high temperatures and high precipitation, activity was concentrated in the cooler periods of the day (at night and twilight). No differences were noted in the activity patterns of the tapirs in either open or covered areas, although in open areas we recorded less diurnal and crepuscular activity.

Influence of extrinsic variables

Lizcano and Cavelier (2000) and Downer (2001) reported an increase in the activity of the Andean mountain tapir (*T. pinchaque*) with the increase in moonlight, in either forest or saline environments. Normally, carnivore prey decrease activity during full moon as an anti-predation strategy, mainly in open environments (Lockard and Owings 1974; O'Farrell 1974; Kaufman and Kaufman 1982; Price et al. 1984). However, this pattern is not always found (Benedix 1994; Vieira and Baumgarten 1995; Bittencourt et al. 1999). In the present study, there was no effect of the moonlight on the activity of the tapir. Apparently, the intensity of the moonlight was of little importance both due to the absence of natural potential predators and to the fact that tapir mostly use olfactory and auditory

Table 1. Distribution of photographic records of tapirs by period of day (crepuscular, nocturnal and diurnal), for each season, and in the open and covered areas.

Season	Registers			
	Crepuscular (%)	Nocturnal (%)	Diurnal (%)	Total
Autumn	4 (12)	28 (85)	1 (3)	33
Winter	11 (21)	25 (48)	16 (31)	52
Spring	12 (32)	18 (49)	7 (19)	37
Summer	6 (17)	25 (72)	4 (11)	35
Total	33 (21)	96 (61)	28 (18)	157
Area				
Open	8 (16)	35 (72)	6 (12)	49
Covered	25 (23)	61 (57)	22 (20)	108
Total	33	96	28	157

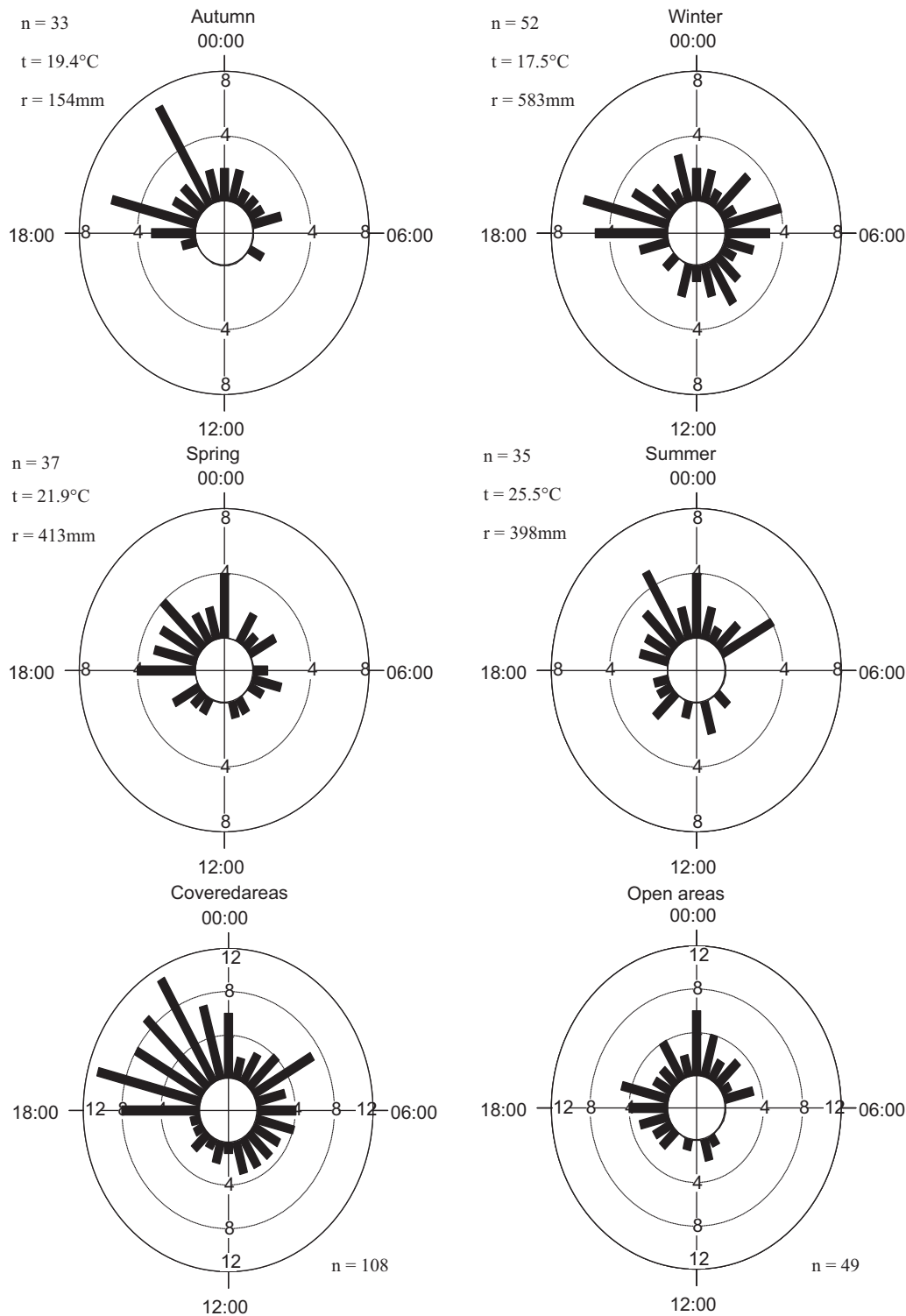


Fig. 1. Distribution of photographic recordings of the tapirs throughout the day each season and in the open and covered areas. The bars correspond to the number of recordings at each hour of the day. n = total number of recordings, t = temperature average, r = accumulated rainfall.

senses, whereas vision seems to have a secondary role (Padilla and Dowler 1994).

It seemed that the tapirs used the behavioral strategy of altering their activity and habitat selection to avoid

the extremes of temperature. During the hottest days, tapirs decreased their diurnal in covered areas, and compensated with an increase in nocturnal activity. In this case, diurnal or nocturnal activity was related to

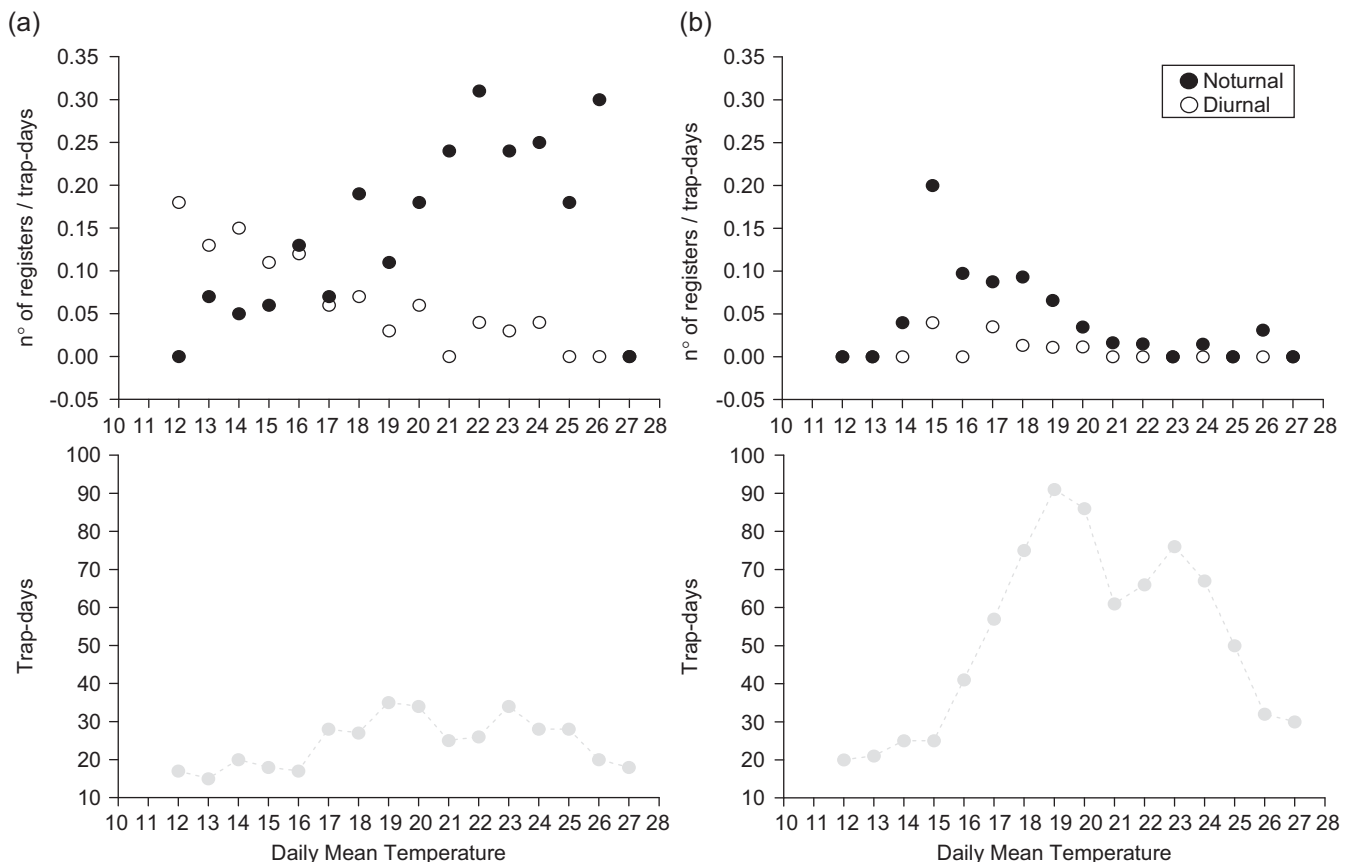


Fig. 2. Relationship between the frequency of records of tapirs and the daily mean temperature, and the sample effort (in trap-days) by daily mean temperature. (a) Diurnal and nocturnal records (above) and the sample effort (below) in covered areas. (b) Diurnal and nocturnal records (above) and sample effort (below) in open areas.

temperature, not to photoperiod. In other hand, diurnal and nocturnal activities in open areas were concentrated within the periods of intermediate temperatures (15–22 °C). These results support the hypothesis that the activity and habitat selection flexibility of tapirs could be merged to keep the thermal and water balance throughout the landscape.

In open areas, both higher and lower temperatures are physiological challenges to thermal and water balance (Schmidt-Nielsen 2005). Thus, the covered areas were selected in the extremes of temperature. However, in these areas, tapirs were more nocturnal in hotter days and more diurnal in the colder days. The decrease of diurnal activity and increase of nocturnal activity during higher temperatures was also related to large and medium mammals as lynxes (Beltrán and Delibes 1994), jackals (Ferguson et al. 1988), bears (Garshelis and Pelton 1980), martens (Zielinski et al. 1983) and badgers (Fowler and Racey 1988). In intermediate temperatures, tapirs used both covered and open areas, but the open areas were used in these temperatures only. In this sense, mammals as giant anteaters are also active during day and night hours, depending on the temperature. In hot

days, giant anteaters move mainly at night and rest during the day inside forest patches (Medri e Mourão 2007), showing a similar example of activity and habitat selection changes according the temperature.

Tapirs can also avoid high temperatures by selecting shaded and humid environments (Alger et al. 1998), decreasing activity during the hottest periods of the day (Lizcano and Cavelier 2004), or searching for rivers, lakes or ponds (Herrera et al. 1999; Lizcano and Cavelier 2000; Novarino et al. 2005). The resting inside lakes and rivers in higher temperatures has been recorded in large African (e.g. see Estes 1992; hippopotamus, elephants, rhinoceros) and American mammals (e.g. Alho et al. 1987; capybaras). On other hand, in open habitats, the Andean tapir (*T. pinchaque*) showed strictly crepuscular activity, as a strategy to shun the extreme cold of Andean nights (Acosta et al. 1996; Downer 1996).

Generally speaking, covered environments were used during the extremes of temperature, whereas open environments were preferred during intermediate temperatures. Because covered areas can keep temperatures low, up to 8 °C on hot days, as well as high, up to 5 °C

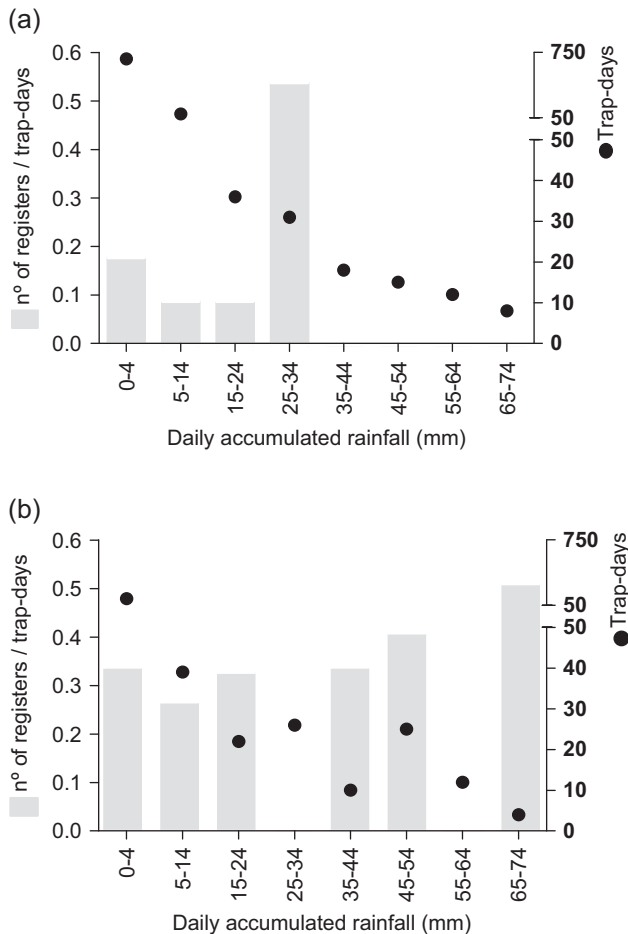


Fig. 3. Number of photographic records by sample effort (in trap-days) in different classes of daily accumulated rainfall in (a) open areas and (b) covered areas.

on the coldest days (Mourão and Medri 2007), forest environments, similarly to burrowing in small mammals (Medri 2008), can be used to thermal regulation.

Rainfall patterns also influenced the selection of habitat. During strong rainfall, the more constant use of covered areas, in contrast to the open areas, can be interpreted as selection for shelter against intense rain. Strong rainfall, and lasting for long periods of time, can lead to a sudden drop in the superficial body temperature. Moreover, it can make the weak vision of the tapir more difficult and, in addition, affect both its sense of smell and hearing. In such cases, the canopy covering can function as thermal protection as well as safety for a more assured sense of orientation.

Our study suggests the tendency of tapir to concentrate activity during night and crepuscular hours. However, they appear to have some flexibility in their behavior in response to environmental (extrinsic) factors, exhibiting behavioral adaptation to different climatic constraints. Open and covered areas are used year-round, and are influenced by temperature and

rainfall, while moonlight did not appear to influence the activity.

Acknowledgements

We acknowledge FAPESC (Research Support Foundation of Santa Catarina) (FCTP 3245/039) and CNPq (National Research Council) for financial support, and the FATMA (Environmental Foundation) team of the Visitors Centre from the State Park of Serra do Tabuleiro for their logistic support. We are grateful to Maria J. Hötzel, Maurício E. Graipel, Carlos A. Zucco, Guilherme Mourão and Peter G. Crawshaw Jr. for their comments on the manuscript.

References

- Acosta, H., Cavelier, J., Londono, S., 1996. Aportes al conocimiento de la biología de la anta de montaña, *Tapirus pinchaque*, en los Andes centrales de Colombia. *Biotropica* 28, 258–266.
- Alger, S.J., Vaughan, C., Foerster, C., 1998. Resting site micro-habitat selection by *Tapirus bairdii* during the dry season in Corcovado National Park, Costa Rica. *Vida Silvestre Neotropical* 7, 136–138.
- Alho, C.J.R., Campos, Z.M.S., Gonçalves, H.C., 1987. Ecologia de capivara (*Hydrochaeris hydrochaeris*, Rodentia) do pantanal: II-Atividade, sazonalidade, uso do espaço e manejo. *Brazilian Journal of Biology* 47, 99–110.
- Beltrán, J.F., Delibes, M., 1994. Environmental determinants of circadian activity of free-ranging Iberian lynxes. *Journal of Mammalogy* 75, 382–393.
- Benedix, J.H., 1994. A predictable pattern of daily activity by the pocket gopher *Geomys bursarius*. *Animal Behaviour* 48, 501–509.
- Bevilaqua, A.T.B., Tortato, M.A., 2003. Status, origin, and diet of captive lowland tapirs in the State of Santa Catarina – Southern Brazil. *Tapir Conservation* 12, 16–17.
- Bittencourt, E.B., Conde, C.F., Rocha, C.F.D., Bergallo, H.G., 1999. Activity patterns of small mammals in an Atlantic forest of southeastern Brazil. *Ciência e Cultura* 51, 126–132.
- Bodmer, R.E., 1989. Ungulate biomass in relation to feeding strategy within Amazonian forests. *Oecologia* 84, 547–550.
- Bodmer, R.E., 1990. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *Journal of Zoology* 222, 121–128.
- Borges, P.A., Tomas, W.M., 2004. Guia de rastros e outros vestígios de mamíferos do Pantanal. Embrapa Pantanal, Corumbá.
- Di Bitetti, M.S., Paviolo, A., De Ângelo, C., 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic forest of Misiones, Argentina. *Journal of Zoology* 270, 153–163.
- Downer, C.C., 1996. The mountain tapir, endangered “flag-ship” species of the high Andes. *Oryx* 30, 45–58.

- Downer, C.C., 2001. Observations on the diet and habitat of the mountain tapir (*Tapirus pinchaque*). *Journal of Zoology* 254, 279–291.
- Eisenberg, J.F., Redford, K.H., 1999. *Mammals of the Neotropics. The central Neotropics*. University of Chicago Press, Chicago.
- Emmons, L.H., 1990. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago.
- Estes, R.D., 1992. *The behavior guide to African mammals*. University of California Press, Berkeley.
- Ferguson, J.W.H., Galpina, J.S., Vet, M.J., 1988. Factors affecting the activity patterns of black-backed jackals *Canis mesomelas*. *Journal of Zoology* 214, 55–69.
- Foerster, C.R., Vaughan, C., 2002. Home range, habitat use, and activity of Baird's tapir in Costa Rica. *Biotropica* 34, 423–437.
- Foerster, C.R., 1998. *Ecología de la anta centroamericana Tapirus bairdii en un bosque húmedo tropical de Costa Rica*. M.Sc. Thesis, Universidad Nacional, Costa Rica.
- Fowler, P.A., Racey, P.A., 1988. Overwintering strategies of the badger, *Meles meles*, at 57°N. *Journal of Zoology* 214, 635–651.
- GAPLAN, 1986. *Atlas de Santa Catarina. Aerofoto Cruzeiro S/A*, Rio de Janeiro.
- Garshelis, D.L., Pelton, M.R., 1980. Activity of black bears in the Great Smoky Mountains National Park. *Journal of Mammalogy* 61, 8–19.
- Gómez, H., Wallace, R.B., Ayala, G., Tejada, R., 2005. Dry season activity periods of some Amazonian mammals. *Studies on Neotropical Fauna and Environment* 40, 91–95.
- Herrera, J.C., Taber, A.B., Wallace, R.B., Painter, R.L.E., 1999. Lowland tapir (*Tapirus terrestris*) behavioural ecology in the southern Amazonian tropical forest. *Vida Silvestre Neotropical* 8, 31–37.
- Holden, J., Yanuar, A., Martur, D.J., 2003. The asian tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. *Oryx* 37, 34–40.
- Janzen, D.H., 1982. Seeds in tapir dung in Santa Rosa National Park, Costa Rica. *Brenesia* 19, 129–135.
- Kaufman, D.W., Kaufman, G.A., 1982. Effect moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). *Journal of Mammalogy* 63, 309–312.
- Klein, R.M., 1981. Fisonomia, importância e recursos da vegetação do Parque Estadual da Serra do Tabuleiro. *Sellowia* 33, 5–54.
- Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68, 619–640.
- Lizcano, D.L., Cavelier, J., 2000. Daily and seasonal activity of the mountain tapir (*Tapirus pinchaque*) in the Central Andes of Colombia. *Journal of Zoology* 252, 429–435.
- Lizcano, D.L., Cavelier, J., 2004. Using GPS collar to study Mountain tapirs (*Tapirus pinchaque*) in the Central Andes of Colombia. *Tapir Conservation* 13, 18–23.
- Lockard, R.B., Owings, D.H., 1974. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *Journal of Mammalogy* 43, 189–193.
- Maffei, L., Cuellar, E., Noss, A.J., 2002. Using camera-traps to assess mammals in the chaco-chiquitano ecotone. *Revista Boliviana Ecológica* 11, 55–65.
- Medici, E.P., 2001. Order Perissodactyla, family Tapiridae (Tapirs): biology. In: Fowler, M.E., Cubas, Z.S. (Eds.), *Biology, Medicine, and Surgery of South American Wild Animals*. Iowa State University Press, Iowa, pp. 363–376.
- Medri, I.M., 2008. *Ecologia e História Natural do Tatu-peba, Euphractus sexcinctus (Linnaeus, 1758), no Pantanal da Nhecolândia, Mato Grosso do Sul*. Ph.D. Thesis, Universidade Federal de Mato Grosso do Sul.
- Mourão, G., Medri, I.M., 2007. Activity of a specialized insectivorous mammal (*Mirmecophaga tridactyla*) in the Pantanal of Brazil. *Journal of Zoology* 271, 187–192.
- Naranjo, E.J., 1995. Abundancia y uso de habitat del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silvestre Neotropical* 4, 20–31.
- Novarino, W., Kamilah, S.N., Nugroho, A., Janra, M.N., Silmi, M., Syafri, M., 2005. Habitat use and density of the Malayan tapir (*Tapirus indicus*) in the Tarak Forest Reserve, Sumatra, Indonesia. *Tapir Conservation* 14, 28–30.
- O'Farrel, M.J., 1974. Seasonal activity patterns of rodents in a sagebrush community. *Journal of Mammalogy* 55, 809–823.
- Oliveira-Santos, L.G.R., Machado Filho, L.C.P., Tortato, M.A., Falkenberg, D.B., Hotzel, M.J., 2005. Diet of Tapirs (*Tapirus terrestris*) introduced in a salt marsh area of the Baixada do Massambu, State Park of the Serra do Tabuleiro – Santa Catarina, south of Brazil. *Tapir Conservation* 14, 22–27.
- Padilla, M., Dowler, R.C., 1994. *Tapirus terrestris*. *Mammalian Species* 481, 1–8.
- Price, M.V., Waser, N.M., Bass, T.A., 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* 65, 353–356.
- Salas, L.A., Fuller, T.K., 1996. Diet of the lowland tapir (*Tapirus terrestris* L.) in the Tabaro River valley, southern Venezuela. *Canadian Journal of Zoology* 74, 1444–1451.
- Schmidt-Nielsen, K., 2005. *Fisiologia Animal: adaptação e meio ambiente*. Santos Editora, São Paulo.
- Sidell, B.P., 2002. *Moonrise 3.5 (32Bit) Software*.
- Tobler, M., 2002. Habitat use and diet of Baird's tapirs (*Tapirus bairdii*) in a Montane Cloud Forest of the Cordillera de Talamanca, Costa Rica. *Biotropica* 34, 468–474.
- Tobler, M.W., 2008. *The ecology of the lowland tapir in Madre de Dios, Peru: using new technologies to study large rainforest mammals*. Ph.D. Thesis, University of Texas.
- van Schaik, C.P., Griffiths, M., 1996. Activity periods of Indonesian Rain Forest mammals. *Biotropica* 28, 105–112.
- Vieira, E.M., Baumgarten, L.C., 1995. Daily activity patterns of small mammals in the cerrado area from Brazil. *Journal of Tropical Ecology* 11, 225–262.
- Weckel, M., Giuliano, W., Silver, S., 2006. Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *Journal of Zoology* 270, 25–30.
- Williams, K., 1984. *The central american tapir in north-western Costa Rica*. Ph.D. Thesis, Michigan State University, Michigan.
- Zar, J.H., 1996. *Biostatistical analysis*. Upper Saddle River, New Jersey.
- Zielinski, W.J., Spencer, W.D., Barrett, R.H., 1983. Relationship between food habits and activity patterns of pine martens. *Journal of Mammalogy* 64, 287–316.