

## ECOLOGY OF THE ARMADILLOS *CABASSOUS UNICINCTUS* AND *EUPHRACTUS SEXCINCTUS* (CINGULATA: DASYPODIDAE) IN A BRAZILIAN CERRADO

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We report on aspects of the ecology and natural history of 2 species of armadillos commonly found in a cerrado remnant in southeastern Brazil—the naked-tailed armadillo (*Cabassous unicinctus*) and the 6-banded armadillo (*Euphractus sexcinctus*). Armadillos were captured in pitfall traps or by hand, double-marked, and the habitat (campo sujo, campo cerrado, and gallery forests), season, and time of capture were recorded. We also recorded the sex and age of all armadillos, and reproductive condition of females. Population densities were estimated as 0.27 and 0.14 individuals/ha for *C. unicinctus* and *E. sexcinctus*, respectively. *E. sexcinctus* did not preferentially use any of the habitats included in the study area, whereas *C. unicinctus* preferentially used habitats with a more complex vegetation structure, such as gallery forests. *C. unicinctus* was diurnal and *E. sexcinctus* was mainly nocturnal. Neither species changed its activity pattern with season, but *C. unicinctus* was more active in months with decreased abundance of arthropods—the main food resource consumed by this species. Both species of armadillos appeared to reproduce year-round. Differences in habitat use and daily activity between *C. unicinctus* and *E. sexcinctus* suggest spatial and temporal displacement between these species.

Key words: armadillo, Brazil, *Cabassous unicinctus*, closed population models, *Euphractus sexcinctus*, neotropical savanna, niche overlap, population ecology, xenarthrans

Spatial and temporal displacement among sympatric species often occurs and may facilitate their coexistence (Levin 1999, 2003; Levin and Pacala 1997). For example, similar species are expected to vary in their use of habitats as well as in the timing of daily and seasonal activities (Carothers and Jaksic 1984). Thus, a fundamental step to describe a system composed of 2 or more similar species that are potential competitors is to determine their placement along relevant ecological axes (Levin and Pacala 1997).

Armadillos (Dasypodidae) are the most diverse group in number of species and geographic range among the xenar-

thrans, comprising 21 species that are distributed from the southern United States to Argentina and Chile (Gardner 1993; Nowak 1991). Although highly diversified and geographically widespread, knowledge of the ecology and natural history of armadillos is derived primarily from work done with the 9-banded armadillo (*Dasybus novemcinctus*) in the United States (McDonough and Loughry, in press). These studies have yielded much information on the biology of *D. novemcinctus*, such as diet, reproduction, space use, and activity patterns (Baker 1943; Breece and Dusi 1985; Clark 1951; Layne and Glover 1977, 1985; Sikes et al. 1990; Storrs et al. 1988; Wirtz et al. 1985) as well as behavior and causes of mortality (Loughry and McDonough 1996; McDonough 1994, 1997, 2000; McDonough and Loughry 1995, 1997a, 1997b). In contrast, knowledge of the ecology and natural history of other armadillo species is scarce, especially for species occurring in Brazil (e.g., Bezerra et al. 2001; Redford 1994; Schaller 1983).

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In Brazil, armadillos are relatively common and occur in a number of biomes, such as the Atlantic and Amazon rain forests, pampas, pantanal, caatinga, and cerrado (Wetzel 1985). Armadillos are particularly common in the cerrado—a tropical savanna hotspot of diversity comprising different habitats and a highly seasonal environment (Oliveira-Filho and Ratter 2002; Silva and Bates 2002)—where 6 species are usually found, namely, *Cabassous unicinctus*, *C. tatouay*, *D. novemcinctus*, *Dasytus septemcinctus*, *Euphractus sexcinctus*, and *Priodontes maximus* (Redford 1994; Wetzel 1985). Despite being a conspicuous and important component of the mammal community of the cerrado (Redford 1994), virtually nothing is known on the ecology and natural history of the species inhabiting this biome in Brazil.

The aim of this paper is to report on various aspects of the ecology and natural history of 2 armadillo species commonly found in a cerrado remnant in southeastern Brazil—the naked-tailed armadillo (*C. unicinctus*) and the 6-banded armadillo (*E. sexcinctus*). Both species feed heavily on insects, which suggest that they may be potential competitors (V. Bonato, in litt.). Therefore, we expect that these species differ in habitat use and daily and seasonal activities in order to reduce competition. The following questions were addressed in this paper: Do the armadillos differentially use any habitats included in the cerrado of the study area? Are the armadillos nocturnal or diurnal? Does the activity of the armadillos change with seasons? We also present data on the density and reproductive activity of the armadillos in the study area.

## MATERIALS AND METHODS

*Study area.*—Fieldwork was done at the Estação Ecológica de Itirapina (EEI), located in Itirapina (22°15'S, 47°49'W), São Paulo State, southeastern Brazil. The study area covers an area of 4,500 ha of natural cerrado (savannalike) vegetation. The cerrado vegetation comprises 5 different vegetation physiognomies, namely, campo limpo (clean field), campo sujo (dirty field), campo cerrado (closed field), cerrado sensu stricto, and cerradão (closed woodland—Oliveira-Filho and Ratter 2002). These physiognomies differ in density and composition of plants of the woody layer (trees and large shrubs) and the ground layer (subshrubs and herbs), forming a continuum from open and dry grassland to dense forest (Goodland 1971; Oliveira-Filho and Ratter 2002; Silva and Bates 2002). Riparian forests also occur throughout the cerrado and 4 different forms are recognized, namely, gallery forests, riverine forests, alluvial forests, and valley forests. These forests differ in physiognomy and floristic composition, which result from variation in topography, drainage characteristics, and soil properties (Oliveira-Filho and Ratter 2002).

Most of the area of the EEI is occupied by campo sujo, campo cerrado, and gallery forests. Campo sujo is a grassland with scattered shrubs, small trees (2–3 m tall), and acaulescent palms. Campo cerrado is an open scrubland where the trees are small (3–6 m), but taller and denser than in campo sujo (Goodland 1971; Oliveira-Filho and Ratter 2002; Silva and Bates 2002). Gallery forests are narrow forest strips alongside

streams and are flanked by the cerrado vegetation (Oliveira-Filho and Ratter 2002). These forests are evergreen, have trees 10–20 m tall, and have low and dense understory vegetation (Silva and Bates 2002).

The climate of the region is mesotermic, with 2 well-defined seasons, namely, a warm-wet season from October to March and a cool-dry season from April to September. During this study, the monthly rainfall and the mean monthly temperature ranged, respectively, from 125 to 423 mm and 23.7°C to 25.4°C in the warm-wet season, and from 5 to 122 mm and 16.4°C to 22.1°C in the cool-dry season. Four armadillo species occur at the EEI, *D. septemcinctus*, *D. novemcinctus*, and the most abundant *C. unicinctus* and *E. sexcinctus*.

*Data collection.*—Individuals of *C. unicinctus* and *E. sexcinctus* were monitored in an area of about 500 ha within the EEI from September 1999 to May 2001. Captures of the armadillos were done on 5 consecutive days every 15 days, for a total of 210 days of fieldwork. The armadillos were captured by hand when sighted foraging (from 0600 h to 0200 h) and by 72 pitfall traps with drift fences left open for 24 h and checked every morning (Jones et al. 1996). Eighteen 45-m-long lines containing 4 pitfall traps each (100-liter plastic pails; 65 cm tall × 50 cm in diameter; 15 m apart) were set up at the study area. There were 6 lines (100–500 m apart) in each type of habitat (campo sujo, campo cerrado, and borders of gallery forests). The drift fences were made of plastic mesh fixed with sticks, and were 50 cm tall, with an additional 10 cm buried in the soil. The armadillos captured were double-marked with a numbered ear tag (National Band and Tag Co., Newport, Kentucky) and adhesive silver reflective tape (Scotchlite, 3M Co., St. Paul, Minnesota). The silver reflective tape was cut into numbers and stuck on the carapace of each armadillo. At each capture, the habitat, season, and time of capture as well as the sex, age, and reproductive condition of the armadillos were recorded. Armadillos were classified as juveniles when their carapaces were soft. Reproductive condition was recorded for females only and they were classified as reproductive when they had swollen nipples and increased abdomen volume (Loughry and McDonough 1996). Recaptures and resightings were included as independent data points because of the small sample size obtained in this study. Trapping and handling methods followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

The pitfall traps also were used to sample arthropods from mid-May 2000 to mid-May 2001. On the 1st day of each trapping session, the pitfall traps were cleaned and left open for 24 h. All arthropods captured after this 24-h period were collected and preserved in 70% ethanol. The arthropods collected were transported to the laboratory where they were identified to the level of order. To estimate the monthly abundance of arthropods in terms of biomass, the number of individual arthropods of each order collected in each month was multiplied by their average weight in the study area (V. Bonato, in litt.).

*Estimation of population density and statistical analyses.*—The capture–recapture history data of the armadillos *C. unicinctus* and *E. sexcinctus* were used to estimate their population size in the sampled area with closed population models

(Otis et al. 1978; Pollock et al. 1990). For each species, data on all trapping occasions within a given trimester were pooled to form a single trapping occasion per trimester, yielding a total of 6 trapping occasions. Discriminant analysis for model selection implemented in program CAPTURE was used to select the best model to describe the capture probabilities and estimate the population size of each species (White et al. 1982). Population density estimates were computed by dividing the population size estimates by the size of the sampled area (about 500 ha).

For each species, chi-square tests were used to test if the armadillos occurred uniformly among the habitats of the study area, daytime periods (4-h intervals from 0600 h to 0200 h), and seasons. The expected number of captures in each habitat was computed by multiplying the total number of captures by the proportion that each habitat occupied in the sampled area (campo sujo: 0.68; campo cerrado: 0.26; gallery forest: 0.06). Such proportions were computed using a curvimeter on a scaled map of the sampled area. The expected number of captures in each daytime period was computed by multiplying the total number of manual captures done in the daylight hours by 0.60 and those done in the nighttime hours by 0.40. The expected number of captures in each season was computed by multiplying the total number of captures by the proportion of months in each season during which fieldwork was done (warm-wet: 0.57; cool-dry: 0.43). Poisson regression was used to test whether the number of captures of armadillos was related to the abundance of arthropods in terms of biomass, with the significance of the biomass of arthropods as a predictor variable being tested with the Wald statistics ( $z$ —McCullagh and Nelder 1989). This analysis was done for *C. unicinctus* only because its diet is composed of more than 90% of arthropod biomass (V. Bonato, in litt.). Logistic regressions were used to test if the probability of an individual female *C. unicinctus* to be reproductive was related to season. This analysis was not done for *E. sexcinctus* because of the small number of females captured ( $n = 4$ ).

## RESULTS

**Density and habitat use.**—A total of 44 individuals of *C. unicinctus* (22 males, 17 females, and 5 of unidentified sex) and 25 individuals of *E. sexcinctus* (20 males, 4 females, and 1 of unidentified sex) were captured during the study period. Two (50%) of 4 juveniles of *C. unicinctus* were captured during the warm-wet season and the others during the cool-dry season. Only 2 juveniles of *E. sexcinctus* were recorded during the cool-dry season of the study period.

Population closure was not rejected for the population of *C. unicinctus* ( $Z = -1.12$ ,  $P = 0.13$ ) or for the population of *E. sexcinctus* ( $Z = -1.58$ ,  $P = 0.06$ ). The equal catchability model,  $M_{0c}$ , and heterogeneity model,  $M_{1h}$ , were selected as the best models to describe the capture probabilities and estimate the population size of *C. unicinctus* and *E. sexcinctus*, respectively. Although the simple model  $M_0$  was selected to estimate the population size of *C. unicinctus*, White et al. (1982) suggest that, in this case, model  $M_{1h}$  should be used to estimate the population size because it is more robust than

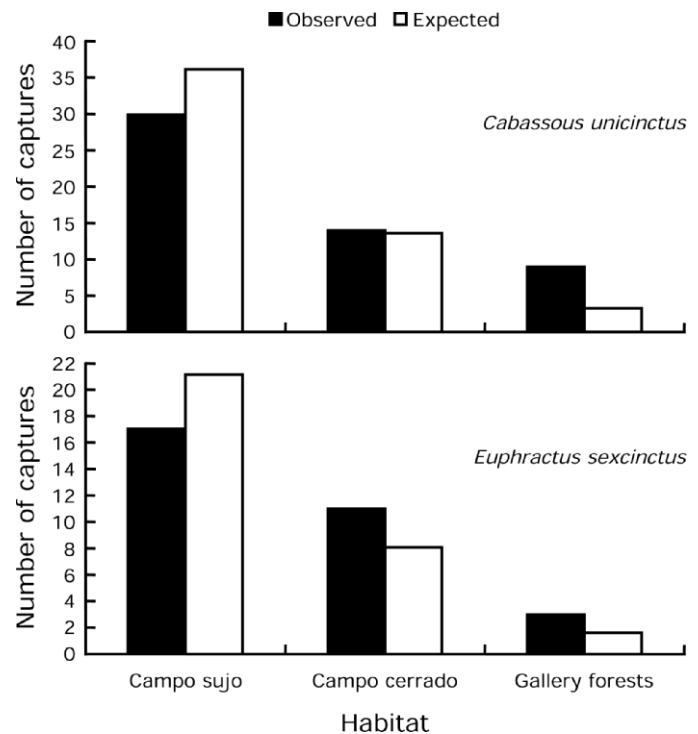


FIG. 1.—Observed and expected number of captures of *Cabassous unicinctus* and *Euphractus sexcinctus* in the campo sujo, campo cerrado, and gallery forests of the cerrado of the Estação Ecológica de Itirapina, southeastern Brazil.

model  $M_0$ . Hence, the estimates presented here for the 2 armadillo species were computed based on model  $M_{1h}$  and equaled 133 (95% confidence interval [95% CI], 101–179) individual *C. unicinctus* and 68 (95% CI, 47–106) individual *E. sexcinctus*. Density estimates for *C. unicinctus* and *E. sexcinctus* equaled 0.27 and 0.14 individuals/ha, respectively.

Most of the captures of both *C. unicinctus* and *E. sexcinctus* occurred in campo sujo, followed by campo cerrado and gallery forests (Fig. 1). The number of captures of *C. unicinctus* differed from that expected within each habitat ( $\chi^2 = 11.67$ ,  $d.f. = 2$ ,  $P < 0.01$ ; Fig. 1), with more captures occurring in the gallery forests than expected ( $\chi^2 = 11.33$ ,  $d.f. = 1$ ,  $P < 0.001$ ; Fig. 1). In contrast, the number of captures of *E. sexcinctus* did not differ significantly from that expected within each habitat ( $\chi^2 = 2.56$ ,  $d.f. = 2$ ,  $P = 0.28$ ; Fig. 1).

**Daily, seasonal, and reproductive activity.**—A large number of manual captures of active individuals of *C. unicinctus* occurred during the daylight hours (about 97%) and only 1 during the night (Fig. 2a). Active individuals of this species were captured significantly more frequently in the daylight hours, mainly from 1000 h to 1400 h, than expected ( $\chi^2 = 17.47$ ,  $d.f. = 1$ ,  $P < 0.001$ ; Fig. 2a). In contrast to *C. unicinctus*, active individuals of *E. sexcinctus* were frequently captured during both the daylight and nighttime hours ( $\chi^2 = 2.67$ ,  $d.f. = 1$ ,  $P = 0.10$ ; Fig. 2c).

The number of active individuals of *C. unicinctus* and *E. sexcinctus* captured were similar between the warm-wet and cool-dry seasons ( $\chi^2 = 0.57$ ,  $d.f. = 1$ ,  $P = 0.45$ ; Fig. 2b;  $\chi^2 = 1.55$ ,  $d.f. = 1$ ,  $P = 0.21$ ; Fig. 2d). Although this result shows

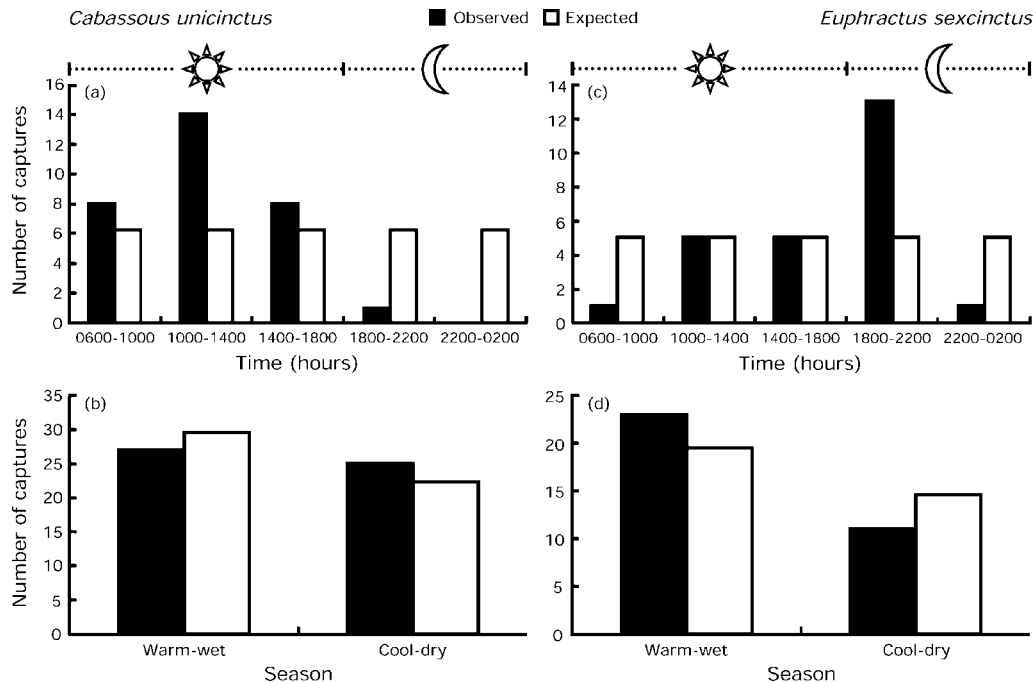


FIG. 2.—Observed and expected number of captures of *Cabassous unicinctus* and *Euphractus sexcinctus* during a and c) the daylight hours and b and d) in each season in the cerrado of the Estação Ecológica de Itirapina, southeastern Brazil. Panels a and c show the number of manual captures only.

that the activity of *C. unicinctus* did not differ between seasons, the number of captures per month seemed to increase with the decrease in arthropod biomass (Fig. 3). The Poisson regression showed that the biomass of arthropods was significantly related to the number of captures of *C. unicinctus* per month ( $z = 4.58$ ,  $d.f. = 1$ ,  $P = 0.03$ ).

Three (50%) of 6 female *C. unicinctus* captured in the warm-wet season were reproductive, whereas 7 (64%) of 11 females captured in the cool-dry season were reproductive. The probability of an individual female *C. unicinctus* to be reproductive was not influenced by season (logistic regression:  $\chi^2 = 0.30$ ,  $d.f. = 1$ ,  $P = 0.59$ ). As for *E. sexcinctus*, only 1 female was captured in the warm-wet season and 3 in the cool-dry season; all of them were reproductive.

## DISCUSSION

**Population density.**—Although the closure test showed that the populations of *C. unicinctus* and *E. sexcinctus* can be assumed to be closed during the study period, it is very unlikely that no births, deaths, or migration of armadillos into and out of the sampled area occurred and that their population size did not change. However, if changes in population size were small during the study period, then the assumption of population closure upon which closed population models are based can still hold (White et al. 1982). The long life span of armadillos relative to the duration of this study and their low reproductive and recruitment rates (Loughry and McDonough 1996; Nowak 1991; Redford 1994; Redford and Wetzel 1985), as well as potential barriers (lakes) to their migration into and out of the study area, suggest that changes in population size of

*C. unicinctus* and *E. sexcinctus* during the study period were probably small. Although hunting pressure on South American populations of armadillos has been reported (Cuellar, in press; Loughry and McDonough 1998), there was no evidence of armadillos killed by humans inside or near the EEI during the period of this study. Therefore, the population size and density estimates for *C. unicinctus* and *E. sexcinctus* at the sampled area obtained through the use of closed population models can be considered relatively accurate.

This is the 1st study to report on an estimate of population size for the armadillo *C. unicinctus*, which occurred at densities of 0.27 individuals/ha in the cerrado area studied here. This estimate showed that *C. unicinctus* is more abundant in the study area than *E. sexcinctus*, which occurred at densities of 0.14 individuals/ha. An observed density of *C. unicinctus* twice as high as that of *E. sexcinctus* could be the result of competitive interactions, hunting selection for a particular species, or distinct recruitment rates between these armadillo species (Cuellar, in press; Loughry and McDonough 1998). However, more data from South American populations of armadillos are needed to evaluate between these alternatives.

The estimate of 0.14 individuals/ha for *E. sexcinctus* in the cerrado area studied here is lower than that estimated for this species in the Brazilian pantanal using enumeration methods, which equalled 0.57 individuals/ha (Schaller 1983). On the other hand, the density of *E. sexcinctus* in EEI is greater than that estimated based on census methods in the Bolivian chaco, which was 0.012 individuals/ha (Cuellar, in press). This remarkable contrast among intraspecific population densities is likely due to variation in local competitive forces (Loughry and McDonough 1998), hunting pressure (Cuellar, in press; Loughry and

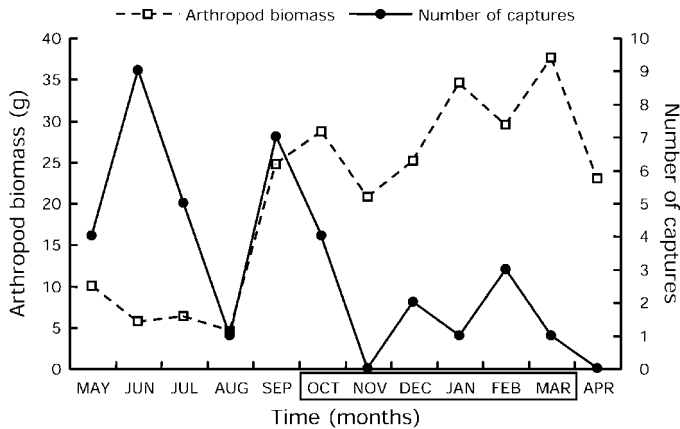


FIG. 3.—Monthly biomass (g) of arthropods and number of captures of *Cabassous unicinctus* in the cerrado of the Estação Ecológica de Itirapina, southeastern Brazil, from mid-May 2000 to mid-May 2001. Data collected in mid-May 2000 and mid-May 2001 were pooled. Months within rectangles span the warm-wet season.

McDonough 1998), or limiting resources. In the EEI, competitive interactions with other xenarthrans, such as other species of armadillos and anteaters, is more likely than hunting pressure to be generating the observed patterns of density.

The proportion of juveniles in the populations of *C. unicinctus* and *E. sexcinctus* was 9% and 8%, respectively. Studies of age structure of populations of *D. novemcinctus* in the United States revealed a density of juveniles ranging from 3% to 16% (Loughry and McDonough 1996). Although comparisons among population structure of different species of armadillos should be made carefully, it could be expected that densities of juvenile *C. unicinctus* and *E. sexcinctus* in the EEI might be underestimated because juveniles of armadillos appear to remain close to their natal burrow and are more vigilant than adults (Loughry and McDonough 1996).

**Habitat use and activity patterns.**—The armadillos *C. unicinctus* and *E. sexcinctus* have been reported to occur in a number of different habitats, such as lowland humid forests, riparian forests, and semiarid and savannalike habitats (Cuellar, in press; Meritt 1985; Redford and Wetzel 1985; Wetzel 1985). Both species of armadillos used several habitats in the cerrado of the EEI, including the cerrado physiognomies campo sujo and campo cerrado, and gallery forests. Although the number of captures of *E. sexcinctus* in the campo sujo, campo cerrado, and gallery forests occurred in proportion to the distribution of these habitats in the sampled area, the number of captures of *C. unicinctus* was disproportional to the occurrence of these habitats. Captures of *C. unicinctus* were more frequent than expected in the gallery forests. These findings suggest that *C. unicinctus* occurs more frequently in habitats with a more complex vegetation structure because the woody layer of the campo cerrado and gallery forest is denser and more diversified than that of the campo sujo (Goodland 1971; Oliveira-Filho and Ratter 2002; Silva and Bates 2002).

Studies based on sightings and burrow density have shown that Brazilian armadillos occur at higher abundances in hardwood and riparian habitats than in grassland (McDonough

et al. 2000). Differences in the use of habitats could occur because of at least 3 possible alternatives. First, armadillos are usually located in areas supporting dense plant growth because this could provide them with valuable protective cover (Clark 1951). In fact, the majority of the mammalian fauna in cerrado uses gallery forests as a refuge (against predators or fire) and as food and water sources (Redford and Fonseca 1986). Second, differences in habitat use may be correlated with the nature of the soil and litter layer (Layne and Glover 1977). Armadillos might be more frequent in gallery forests because these areas have soil that is easy to dig in (McDonough et al. 2000). Third, prey availability also would seem a logical explanation for differences in habitat use (McDonough et al. 2000).

Even though several captures of *E. sexcinctus* occurred in the daylight hours, as previously reported by Cuellar (in press), Redford and Wetzel (1985), Schaller (1983), and Carter (1985), the high number of captures during the nighttime hours suggests that the activity of *E. sexcinctus* is mainly nocturnal in the cerrado area studied here. Although *C. unicinctus* has been regarded as a nocturnal species based on data collected in Paraguay and Argentina (Meritt 1985), the results reported here clearly demonstrate that *C. unicinctus* was mainly diurnal in the cerrado. A similar finding was reported by Carter (1985) from another area in Brazil.

Intraspecific variation in activity time throughout the ranges of these species is the result of local adaptation of individuals that potentially shift their activities to times when food and potential mates are available, or to avoid risk of predation and severe weather conditions (McDonough and Loughry 1997b). Additionally, activity of armadillos seems to be influenced by endogenous rhythms. McNab (1980) reported that *Cabassous* regulates body temperature rather precisely at warm temperatures, whereas *E. sexcinctus* maintains body temperatures at a lower temperature range. Therefore, both species of armadillos found in EEI seem to have their activity mainly influenced by endogenous rhythms given that *C. unicinctus* is commonly active during the day when mean temperatures are approximately 25°C and *E. sexcinctus* during the evening, when mean temperatures are about 10°C lower.

Although the activity of both *C. unicinctus* and *E. sexcinctus* did not differ between seasons, the activity of *C. unicinctus* changed on a monthly timescale and was significantly related to the biomass of arthropods. A larger number of captures of *C. unicinctus* occurred during months of decreased arthropod biomass, suggesting that the naked-tailed armadillo was more active under conditions of food limitation. This finding indicates that when food abundance is low, individuals of *C. unicinctus* probably traverse larger areas and spend more time foraging in order to supply their energetic and nutritional requirements, as predicted by optimal foraging theory (Schoener 1971).

Examination of our data showed that reproduction in *C. unicinctus*, and possibly in *E. sexcinctus*, was not seasonal and that both species may be able to reproduce year-round in the cerrado. Cuellar (in press) reported that *E. sexcinctus* from Bolivian chaco exhibited a short, concentrated reproductive season at the end of the dry season and maximum fecundity rates at the 1st month of wet season. Although patterns of

reproduction did not differ strikingly between these species, patterns of habitat use and activity suggest the possibility of competitive displacement at our study site. The hypothesis that the patterns we observed are due to competitive interactions between these species, and thus facilitate their coexistence, deserves further investigation.

### RESUMO

Nesse trabalho são apresentados dados sobre a ecologia e a história natural de 2 espécies de tatu comumente encontrados em uma área de cerrado do sudeste do Brasil—o tatu-de-rabomole-pequeno (*Cabassous unicinctus*) e o tatu-peba (*Euphractus sexcinctus*). Os tatus foram capturados manualmente ou em armadilhas de interceptação-e-queda e foram duplamente marcados. Em cada captura, foram registrados o habitat (campo sujo, campo cerrado e mata de galeria), a estação e a hora da captura. Também foram registrados o sexo e a idade de todos os tatus, e a condição reprodutiva das fêmeas. As densidades populacionais foram estimadas em 0,27 e 0,14 indivíduos/ha para *C. unicinctus* e *E. sexcinctus*, respectivamente. *E. sexcinctus* não apresentou preferência por habitats, ao passo que *C. unicinctus* apresentou uma preferência por habitats com uma estrutura vegetacional mais complexa, como as matas de galeria. *C. unicinctus* apresentou atividade diurna, ao passo que *E. sexcinctus* apresentou atividade principalmente noturna. Nenhuma das espécies apresentou diferenças sazonais em atividade, mas *C. unicinctus* foi mais ativo nos meses com baixa abundância de insetos—o principal recurso alimentar consumido por essa espécie. Ambas as espécies de tatus aparentemente se reproduzem ao longo de todo o ano. As diferenças no uso de habitat e atividade diária entre *C. unicinctus* e *E. sexcinctus* sugerem a ocorrência de deslocamento espacial e temporal entre essas espécies.

### ACKNOWLEDGMENTS

We thank G. Giralde, R. J. Sawaya, C. A. Brasileiro, M. C. Kiefer, A. Tozetti, and L. A. Anjos for helping with fieldwork. D. Zanchetta and M. Martins provided logistical support. S. Hyslop reviewed the English of the manuscript. An anonymous reviewer provided helpful comments. We are deeply indebted to W. J. Loughry for comments and suggestions that went a long way to improving the quality of the manuscript. T. S. Carter was instrumental in providing much needed literature. VB (00/01371-2), GM (02/00381-0), and EGM (03/10639-7) were supported by scholarships from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Brazil). SFR is partially supported by a fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil). This research was supported by grants from FAPESP.

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Submitted 24 June 2006. Accepted 23 May 2007.

Associate Editor was Gerardo Ceballos.