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Ecological differences between two sympatric species of armadillos (Xenarthra, Mammalia) in a temperate region of Argentina

Agustín M. ABBA and Marcelo H. CASSINI*

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Morpho-physiological specialization related to foraging can act as constraints on behaviour and ecological patterns of abundance and distribution. We tested this prediction in two species (weeping or screaming hairy armadillos *Chaetophractus vellerosus* Gray, 1865 and mulitas *Dasypus hybridus* Desmarest, 1804) that represent the two subfamilies of armadillos (Dasypodidae, Xenarthra): Euphractinae and Dasypodinae. The first subfamily possesses a well-developed masticatory apparatus that is considered primitive within the Xenarthra, while Dasypodinae show reductions in various aspects of cranial morphology. We sampled signs (burrows and foraging holes) and captured both species on 34 farms randomly selected in the north-eastern Pampas region of Argentina. We analyzed several niche dimensions. The two species showed significant differences in habitat use, seasonal patterns and diet. Weeping armadillos were generalists in their diet and active throughout the year. They were associated with calcareous-sand soil, as expected for a burrowing animal of the deserts. They tolerated a wide range of environmental conditions. We found that mulitas are myrmecophagous, and that they demonstrated a reduction in body temperature and activity during the cold season. As expected from their geographical distribution, mulitas used mainly vegetation with high cover and were associated with humic soils. Niche segregation between the two species of armadillos appeared to originate from different degrees of dietary specialization.

GEMA Group, DCB, Universidad Nacional de Luján, Rutas 5 y 7, 6700 Luján, Argentina (CONICET), e-mail: mhcassini@yahoo.com.ar

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Introduction

Structural and functional foraging specializations that enhance the ability to use certain food types, may also entail costs of being less efficient in exploiting other food resources (Darwin 1859). Foraging specialization not only affects daily food composition but other behavioural

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* Corresponding author

and ecological characteristics of a species. A well-established ecological effect of specialization is that it shifts species toward a higher risk of extinction, due to high vulnerability to environmental change. It also influences the biogeographical pattern of distribution; specialists typically exhibit smaller ranges than generalist species (ie it is difficult to find invasive species that are specialists), because they depend on the distribution of a limited set of food types (Gaston 2003). Foraging specialization also influences social systems and population dynamics. For example, nectar feeding is linked to some of the most extreme examples of social systems, like eusociality of bees and strict territoriality of hummingbirds (Krebs and Davies 1997). In both cases, social behaviours appear to improve food acquisition. Population demography of specialists can be closely linked to the dynamics of their prey (eg in phytophagous insects; Mayhew 1997).

Understanding the evolution of specialization is one of the classical themes of evolutionary ecology. Several theories have been proposed to explain how species become specialists (eg Brown and Wilson 1956, Maynard-Smith 1966, MacArthur and Levins 1967, Levins 1968, Rosensweig 1981). Specialist strategies usually derive from constraints on the behaviour and ecology of animals. In this paper we explore the relation between foraging specialization and several aspects of the ecological niche of armadillos, a typical member of Neotropical mammalian fauna.

Armadillos (Dasypodidae), anteaters and sloths, form the order Xenarthra (Delsuc *et al.* 2002). They are among the most distinctive of Neotropical mammals and several species show typical dietary specializations. Sloths are strictly arboreal folivores while anteaters specifically fed on ants, termites or honey, depending on species and environments (Redford and Eisenberg 1992). Anteaters have developed many anatomical adaptations for myrmecophagy such as and elongated rostrum, loss of teeth and well-developed tongues (Reiss 2000). Xenarthra typically exhibit a low metabolic rate that has been interpreted as a means of compensating for the use of low quality food (McNab 1984).

Armadillos are characterized by moveable, horny bands between bony plates that cover the dorsal and lateral surfaces of the thorax and abdomen (McNab 1980). Two distinct subfamilies have been described within Dasypodidae (Delsuc *et al.* 2002): Dasypodinae and Euphractinae. Most Euphractinae possess a well-developed masticatory apparatus (eg skull large, broad and heavier; mandible heavy, condyle elevated, angular process well developed and expanded, etc.), that it is considered primitive within the Xenarthra, while Dasypodinae show reductions in various aspects of cranial morphology, including the number of teeth (Smith and Redford 1990). *Dasypus*, the only genus of the subfamily, resembles a small armoured anteater, with its elongated head and laterally compressed body (Smith and Redford 1990). Based on its cranial morphology, it has been described as being 'poised in the road of myrmecophagy' (Patterson 1975).

Redford (1985) studied the diet of several members of these two clades and found, as expected from the morphology of masticator apparatus, that Euphractinae are largely omnivorous-carnivorous while most Dasypodinae are insectivorous. An exception to this rule is *Dasypus novemcinctus* that shows an omnivorous diet (Smith and Redford 1990).

We investigated two representative species of two clades of Dasypodidae: the weeping or screaming hairy armadillo *Chaetophractus vellerosus* Gray, 1865 and the mulita or southern long-nosed armadillo *Dasypus hybridus* Desmarest, 1804. Most aspects of their ecology were unknown, including diet composition. We studied them for three years in a coastal fringe of the Pampas region of Argentina, which is a sympatric portion of the biogeographical distribution of both species (the eastern edge of the distributio*n of C. vellerosus* and southern limit for *D. hybridus*, Fig. 1). Mulitas and weeping armadillos show low levels of overlap in their geographical distribution, and are associated with different eco-regions. While *C. vellerosus* is associated mainly with semi-deserts, *D. hybridus* is found in humid sub-tropical and temperate regions. For weeping armadillos the study area represented a more benign, wet environment than they are normally found. In contrast, for mulitas, the region was harsher and colder. Foraging specializations and low metabolic rates of sloths, anteaters and *Dasypus* armadillos have been considered constraints on the distribution of these species, which inhabit tropical and subtropical areas of South America (McNab 1980). Therefore for *D. hybridus*, living in a temperate region like the Pampas should represent a metabolic challenge due in part to substantial reduction in food availability and temperature during the winter.

Species can coexist in environments with a heterogeneous distribution of resources, due to two main reasons: because they are specialized to use different resources or because they select different resources (Rosenzweig 1981). Niche partitioning produced by resource selection is known as "the ghost of competition." Niche specialization can be produced by two mechanisms: by character displacement, which is the evolutionary consequence of long-term interspecific competition (the "ghost of competition past"), and by allopatric divergence that results when species evolved in different types of environments, and they became sympatric only in a narrow portion of their range (Lack 1971) or due to recent migration processes or invasions. In summary, there is a similar ecological pattern that can be produced by three different mechanisms. This makes finding causes of niche segregation difficult. At least two methods have been proposed for distinguishing between niche partitioning and niche specialization: removal experiments and multiple regressions (Morris 1989).

The other distinction between the "ghost of competition past" and allopatric divergence is less frequently analyzed. The latter hypothesis postulates that, if two species evolved in different ecosystems (such as semiarid steppes and humid grasslands), two patterns are expected: (1) they should use resources and habitats differently (niche partitioning), but also that (2) these differences should reflect their different origins. This simple prediction requires analyses of the geographical distribution of the sympatric species and of their morphological, physiological and behaviourial adaptations that reflects their different specializations. We tested these ideas using two species of armadillos in a marginal region of the Argentinean Pampas as a model.

We analyzed several niche dimensions: habitat use, seasonal patterns of activity, diet, and thermoregulatory activity. Based on the hypothesis that foraging morphology constrains significant aspects of species ecology, we tested the following predictions: (1) Mulitas should be dietary specialists, with a large proportion of ants (termites are not common in the Pampas), while weeping armadillos should be dietary generalists. (2) Considering that myrmecophagy is an adaptation for tropical and subtropical regions where food availability and temperature are relatively stable year round, mulitas in the Pampas should reduce activity during the winter, while weeping armadillos should present a similar level of activity throughout the year. (3) Considering that weeping armadillos normally live in semi-desert environments (Fig. 1), it is expected that they would prefer sandy soils to dig their

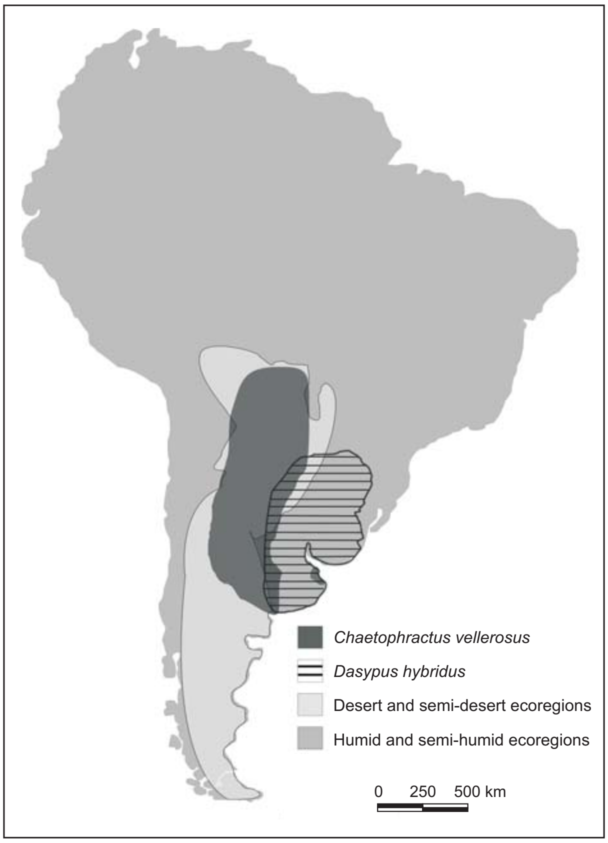

Fig. 1. Map showing the distribution of *C. vellerosus*, *D. hybridus* and two major habitats of South America: deserts and semi-deserts, and humid and semi-humid eco-regions.

burrows in comparison to mulitas. (4) The sum of all the behavioural and ecological differences in niche traits should result in habitat segregation between the two species.

Material and methods

Study area

The study was carried out in the East part of the Pampas grasslands (Argentina) between 35°34'S 57°17'W and 35°00'S 57°51'W. The study area has a disjunctive population of *C. vellerosus* that is separated by 500 km from the principal distribution of the species (Fig. 1). The weather is moderate-warm and humid with mean annual temperature of 16.2°C and 1035 mm of annual precipitation. The annual prevailing wind intensity is around 12 km/h, predominantly from the east and secondarily from the northeast and northwest (Hurtado *et al.* 2003).

The study area was fragmented in units of private farms. Farms were considered the unit of land use. In maps (1:25 000) 34 farms were selected randomly (Abba *et al.* 2007). The main farm activity is husbandry of beef cattle on natural grassland, with crops (eg alfalfa, corn, sorghum, *Lolium*, *Paspalum*, etc.) found on less than 10% of the land (León *et al.*1984).

The study area is also inhabited by a third species of armadillos, *Chaetophractus villosus*. We did not include this species in the analysis because we captured only a small number of individuals that precluded any systematic comparison with the other two species (see below). Abba *et al.* (2007) indicated that of the three species *C. villosus* shows the greatest generalist tendencies; therefore, it is expected that this species has a similar effect both on *C. vellerosus* and *D. hybridus* in the study area.

Sign survey

From 12 December 2003 to 19 October 2004, an area of approximately 70 ha of each farm was surveyed, using the following methods. Two observers walked in a straight line, 20-m apart, and observed 10 m of both sides of each line, locating burrows. The direction of transect was selected at random and started near the principal access. Observers walked for 5 h at a speed of approximately 3.5 km/h, controlled with a GPS. The same approach has been used to estimate the habitat use of numerous different species of burrowing animals (detailed description in Abba *et al.* 2007). Two types of burrows were identified for the two species: complex structures or home burrows and simple structures or foraging holes (Abba *et al.* 2005). Features that allowed discrimination of burrows between species were width and shape of the entrance, as well as direct observations of animals digging. The width of the entrance was used because width showed significant differences among the 3 species present in the study area (Abba *et al*. 2007).

When a burrow or a hole was found, the following variables were measured: (1) Type of vegetation (within a 5-m radius around the burrow): grassland, pasture, native woodland and exotic woodland. "Grassland" is a mixture of native species of grasses with foreign and exotic species of different herbaceous plants (mainly *Cynara cardunculus*, *Cardus acanthoides*, *Lolium perenne*, *Festuca arundinacea*, *Phalaris aquatica, Trifolium repens*) (León *et al.* 1984), and was used mainly for husbandry of beef cattle. "Pastures" were cultivated grasses (commonly *Lotus, Melica*, and *Paspalum*) also used for husbandry. "Native woodland" or "talar" is a sub-climax community of xeric species (Parodi 1940, Cabrera 1949). This community developed in a narrow fringe area of mid-to late Holocene beach ridges (ancient sand dunes) and extends along the north-eastern margin of the Pampas plain. These coastal deposits form elongated hills up to 6 m above the surrounding plain, composed of sand and marine mollusc shells (Cavallotto 2002). The physiognomic of the "talar" is similar low woodland with shrubby trees of 3 to 6 meters high, with a low vegetation substrate of shrubs and herbs. The dominant species are xeric plants, in general the principal species is the "tala" *Celtis tala*, accompanied for *Jodina rhombifolia*, *Acacia caven*, *Scutia buxifolia*, *Schinus longifolia* and *Sambucus australis* (Parodi 1940, Cabrera 1949, Vervoorst 1967). "Exotic woodlands" are relatively small patches of trees like *Eucalyptus* and *Populus*; (2) Type of soil: calcareous, sand, humus or gravel. Soils were differentiated by color and texture, following Soil Survey Staff (1999); (3) Plant cover: high (> 66%), medium, and low (< 33%), which was determined following the Braun Blanquet (1979) method. Low vegetation was finally not present in the study area, and (4) Plant height: high (> 20 cm) and low (< 20 cm), determined as an average of plant heights measured at five points in a 5 m of radius around the sign.

Captures of armadillos

Captures were conducted in 150 ha sampling areas located in four fields that were selected based on our previous sign survey. Fields had to show abundant evidence of the presence of armadillos. Two of them possessed a large extent of soil fringes of Holocene beach ridges. In the other two areas, humic soils dominated.

Capturing and marking techniques of similar species of armadillos were developed by McDonough and Loughry (see McDonough and Loughry 1997, Loughry and McDonough 1998). From February 2006 to February 2007, four seasonal diurnal samplings were conducted from 08:00–09:00 h to 19:00–20:00 h for four days each in the four fields selected. Two field observers walked 30-m-wide transects until the whole sampling area was covered. The resulting effort was 64 hours per field per season (4 days × 16 person hrs) and a total of 1024 hours (64 × 4 fields × 4 seasons). During the survey, all visible animals were captured and processed, all remains of dead animals were collected, and all burrows with signs of recently activity (eg accumulation of grass, remove soil) were sampled to check for the presence of armadillos; this check consisted of a revision of the initial 50 cm of burrow. Animals were captured by hand or in a net and burrows were checked by hand or on occasion, by opening the first 50 cm with a shovel.

The ears of the animals were marked with ear tags (National Band and Tag Company, Newport, KY), and a temporary marker (a sticker fixed on the shell) was used for following the animals after releasing and for avoiding recapturing on the same day. After marking, the following data were recorded: age and sex (pup, juvenile, adult female, adult male) using size and sexual maturity (Loughry and McDonough 1996, McDonough *et al.* 1998), rectal temperature, total length and other partial body measurements, skin samples, natural marks and abnormalities, and behaviour immediately before and after the capture. At the point of capture the following environmental data were taken: temperature, type of vegetation, type of soil, type of vegetation, plant cover and plant height as previously described in methods section.

Burrow association with signs of low disturbance

The study area was largely modified by agricultural activity. Livestock grazing and crops were not distributed homogeneously. At a micro-habitat level, there were patches of unmanaged land, ie areas around fences, buildings and trees. When fields were not used for agricultural purposes for several years, the vegetation community changed and some species became dominant: cockleburs *Xanthium*, cardoons (*Carduus acanthoides* and *Cynara cardunculus*) and "brooms" (*Baccharis notosergila* and *Baccharis trimera*). These unmanaged patches did not suffer livestock trampling and agricultural ploughing, thus they represent stable microhabitats. The association of burrows with signs of low disturbance was measured as positive when a fence, a building, a tree or any of the three plants that indicated low disturbance were present at less than 3 m from the burrow.

Diet analysis

Most armadillos defecated at the moment when they were captured and these feces were used for diet analysis. Feces were cleaned and filtered to eliminate soil remains, using methods described in literature (Greegor 1980, Anacleto and Marinho-Filho 2001). Food fragments were analyzed with magnifying glasses. Samples were dried until reaching constant weight and weighed with digital balance (0.01 g, ES-200A). Item identification was based on a reference collection, consultation with specialists and from literature (Orrego Aravena 1974, Morrone and Coscarón 1998, Cicchino 2006). Fecal analysis is a standard method for evaluating diet composition of many animal species. However, it has limitations, especially because it can underestimate the role of prey with soft bodies that do not leave solid remains in feces. For example, earthworms and some larvae of insects could represent a significant prey item of armadillos, however their detection in feces could be low.

One hundred nineteen and 33 fecal samples of *C. vellerosus* and *D. hybridus*, respectively, were analyzed. Data composition was expressed as percentages of samples with the type of food item or as an estimated percentage of bulk based on a scoring system of 1–10 to assess the importance of each prey item in a discrete piece of feces (1 being a trace item and 10 a piece entirely composed of one single prey category). The score for each category was multiplied by the dry weight of the piece of feces. The resulting figures for each category from all pieces of feces were then summed and expressed as a percentage value of all prey categories (Wise *et al.* 1981).

The extent of habitat and diet use was calculated with standardized Levin's index: $(1/\sum p_i^2) - 1) / (S - 1)$, where p_i is the proportion of resource i, and S is the amount of resource. To analyze the overlap in diet we use percentage overlap (Krebs 1989).

Results

One hundred nineteen and 33 fecal samples of *C. vellerosus* and *D. hybridus*, respectively, were analyzed. In 100% of feces of both species,

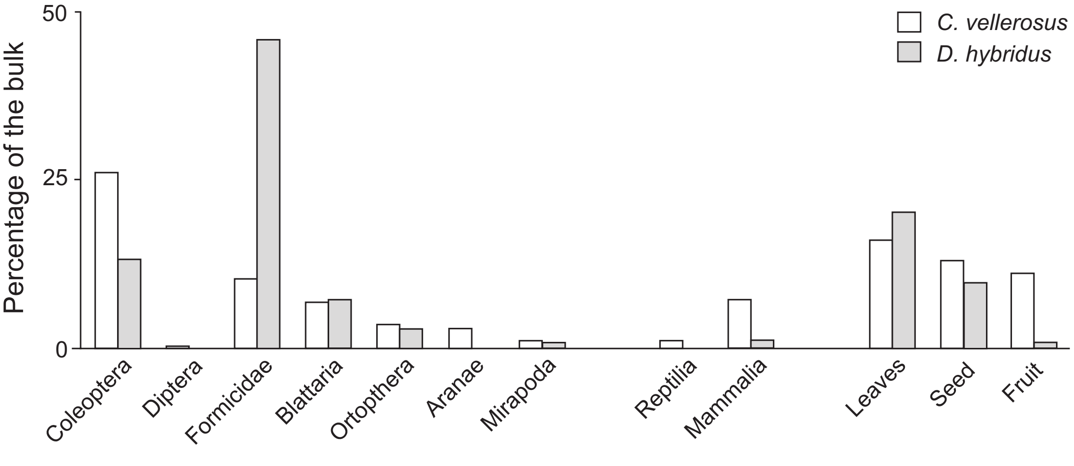

Fig. 2. Diet of weeping armadillos *C. vellerosus* and mulitas *D. hybridus* estimated as the percentage volume for 12 categories of components from the total bulk. Both species differed in their patterns of diet composition.

Table 1. Frequencies of observations (signs and captures) at different soil types, plant covers and sites with or without signs of disturbance, and results of contingency analyses. Sign data were also presented in Abba *et al*. (2007). WA – Weeping armadillos. * – Low cover was not present in the study area.

		Signs			Captures		
		WA	Mulitas	χ^2 (p)	WA	Mulitas	χ^2 (p)
Soil	Calcareous	750	196	711.0 (< 0.0001)	129	2	140.9 (< 0.0001)
	Humic	75	579		7	45	
Plant cover*	Medium	623	92	657.5 (< 0.0001)	56	0	27.9 (< 0.0001)
	High	199	681		80	47	
Signs of disturbance	Without	107	167	38.4 (< 0.0001)			
	With	90	34				

there were remains of insects and plants, indicating that these are the main component of their diet. Vertebrates were present in almost 30% of the feces of weeping armadillos while there were only traces in less than 1% of the feces of mulitas. Weeping armadillos showed a varied diet with coleopterans as the main prey but with important representation of other prey types such as ants, cockroaches and plants (Fig. 2). Mulitas seem to specialize in eating ants and also consumed large amounts of plant material. The food niche breath of *C. vellerosus* (Levin index = 0.47) was more than double that of *D. hybridus* (Levin index = 0.20). In addition, diet overlap was mid- to high percentage (61%).

Partitioning in habitat use by the two species was analysed (Table 1). Both signs and animal distribution indicated that weeping armadillos preferred calcareous soils while mulitas preferred humic soils. Vegetation cover was relatively high in the study area, especially in the four fields were armadillos were captured (there were no areas with cover less than 33%). Under these conditions, weeping armadillos utilized sites with relatively low cover in comparison to mulitas, which were found in high cover. In other studies conducted with this species the general pattern observed was similar (González *et al.* 2001, Cuellar 2008). Finally, mulitas utilized areas of low disturbance more than *C. vellerosus.*

We also conducted analysis on seasonal variations of abundance of armadillos. Ratios of armadillos that were captured outside the burrows in cold (autumn and winter) and warm (spring and summer) seasons were: 56:38 for *C. vellerosus* and 7:34 for *D. hybridus*. Again, there was a different pattern between species. Weeping armadillos were active throughout the year, while the presence of mulitas was significantly reduced during the cold season because they stayed in their burrows. Two 2-factor GLM-ANOVAs were conducted with body temperature and body mass as dependent variables, and species and season and independent variables (Table 2). Body temperatures were similar between species and were lower in cold seasons than in warm seasons (Fig. 3a). Body mass was lower in cold than in warm seasons only for weeping armadillos but not for mulitas (Fig. 3b). For weeping armadillos body temperature and mass were positively correlated (r = 0.30, p = 0.004).

Table 2. ANOVA analyses with body temperature and body weight as dependent variables and species and season as independent variables.

	Body temperature		Body mass	
	F	p	F	p
Species	1.6	0.21	375.7	< 0.00001
Season	57.1	< 0.00001	1.6	0.20
Interaction	0.9	0.35	9.1	0.003

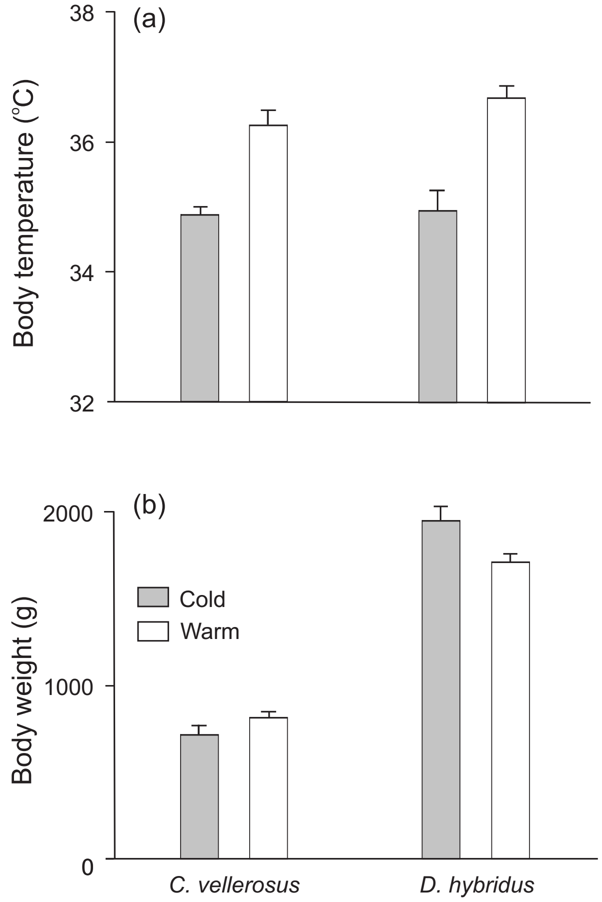

Fig. 3. Body temperatures (a) and body weight (b) for *C. vellerosus* and *D. hybridus* during cold and warm seasons.

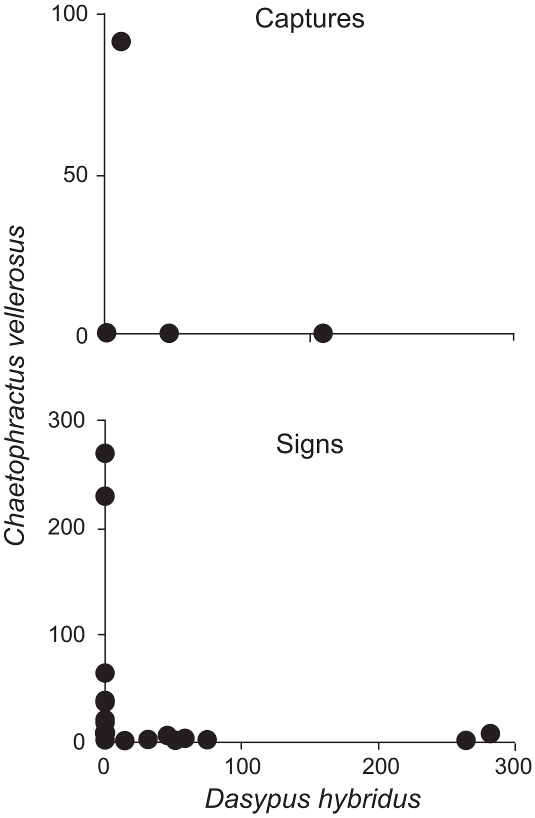

Fig. 4. Number of captures and signs of *C. vellerosus* (captures – 87, signs – 825) and *D. hybridus* (captures – 47, signs – 775). Each point corresponds to a surveyed field, four fields for captures, and 34 localities for sign surveys. Species showed a significant spatial segregation at local scale.

The relationship between the abundance of both species in different fields was analysed (Fig. 4). Weeping armadillos and mulitas showed an extreme level of segregation at a local level, both when signs and direct counts are used for estimated population abundance.

Discussion

Dasypus hybridus and *Chaetophractus vellerosus* showed distinct dietary ecology. While mulitas ate mainly ants and plants, weeping armadillos consumed a wide range of food types. In contrast, *C. vellerosus* showed the similar pattern of overall diet composition between different ecosystems of Argentina (there is no information available from other regions for *D. hybridus*).

Differences between species in diet composition were expected from their differences in anatomy and functionality of the feeding apparatus. Smith and Redford (1990) conducted a detailed analysis on these apparatuses comparing the two subfamilies of armadillos, showed that Dasypodidae have morphological adaptations to myrmecophagy while Euphractinae have a less differentiated rostrum as expected for a generalist.

D. hybridus and *C. vellerosus* showed distinct habitat use. Weeping armadillos were associated with calcareous-sand soil, as expected for a burrowing animal of the deserts. In contrast and as expected from their humic geographical distribution, mulitas used mainly vegetation with high cover and were associated with humic soils.

D. hybridus and *C. vellerosus* showed distinct seasonal patterns of activity. Weeping armadillos were active on a year-round basis as observed by Greegor (1985) in the Andalgalá monte desert, while mulitas significantly reduced activity during the cold season. In tropical areas, where food availability is high and climate is mild, *Dasypus* responded opportunistically to seasonal variations in prey (Redford 1985, McDonough and Loughry 2008). Ants and termites are more available, therefore, are consumed more intensively in the wet season. In our study area, ants are more abundant in the warm season. In the cold season, the combination of morphological constraints and severe weather probably impose a limit to the amount of food consumed by mulitas and on their ability to maintain body temperature. The solution that they appeared to find was to reduce activity. This result was expected considering that the study area was in the southern portion of their distribution. The combination of low activity within burrows and low body temperatures, are probably associated to a daily or seasonal torpor, as noted in *Zaedyus pichiy* (Superina and Boily 2007). This strategy apparently allows them to maintain a relatively stable body mass throughout the year. In contrast, weeping armadillos were active year-round and tolerated more variability in the environmental conditions.

A diet of *C. vellerosus* was previously studied in Monte Desert by Greegor (1980). The general pattern was similar between that region and the Pampas grassland (this study): plant material and insects were the most important prey types and were similarly represented, followed by vertebrates. Some differences within each prey type were found between seasons, as it expected from the contrasting climatic regions found in deserts and grasslands.

Smith and Redford (1990) cautioned against predicting behaviour and ecology based on morphology in Xenarthra. They postulated that the morphology of the masticatory apparatus of *D. novemcinctus* is adapted to myrmecophagy, however they exhibit a varied diet. Vizcaíno *et al*. (1998) questioned this approach by studying several extant and extinct members of armadillos. They showed that strict myrmecophagy is clearly predictable, and that the prediction for Dasypodinae is a trend towards preferring ants and termites rather than strict myrmecophagy. Our results support the contention espoused by Vizcaíno *et al*. (1998). *D. novemcinctus* is exceptional not only in the composition of their diet but in other aspects of their ecology and behaviour. For example, *D. novemcinctus* have the largest geographical range of the xenarthran species and are the only species that has invaded North America (Loughry and McDonough 1998).

In summary, for the two species of armadillos studied, different morpho-physiological adaptations were associated with distinct ecological traits. In our study, the consequence is a niche and spatial segregation between these species. In this case, niche partitioning did not evolve from inter-specific competition because most geographical ranges of *C. vellerosus* and *D. hybridus* do not overlap and they have evolved adaptations to different types of eco-regions. In most cases studied, morphological differentiation in foraging traits evolved by character displacement, and species can co-exist using different resources or habitats (Brown and Wilson 1956). There are many examples of character displacement; the first one published was probably that of the Galapagos finches (Darwin 1859). In this paper, we stress the importance of the ecological consequences of the adaptations of two species of armadillos rather than the evolutionary mechanisms through which they originated.

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