



Habitat use by armadillos in agroecosystems of central Argentina: does plot identity matter?

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In agroecosystems, the use of cultivated plots by mammals depends on habitat structure as well as on the degree of species specialization. In the Pampas of Argentina, during the last 2–3 decades, there has been a continuing expansion of cropland. The aim of this study was to analyze how the identity and characteristics of agricultural plots may have affected the activity of 2 species of armadillos (*ChaetophRACTUS villosus* and *DasyPUS hybridus*) in a rural landscape. We carried out 4 sampling sessions between December 2011 and June 2013, surveying 175 plots during spring–summer and 194 during fall at 25 different sites in the Pampas of Buenos Aires province, Argentina. In each plot, we surveyed for signs (burrows and holes) along a 600×6 m transect in order to assess armadillo activity and measured 4 habitat structural variables. As expected, there were structural differences between types of agricultural plots. Across all plots, a total of 6,654 armadillo signs were found (*C. villosus* = 5,009, *D. hybridus* = 1,645). Generalized linear mixed models revealed that during both seasons, the type of plot explained much of the variation in armadillo activity, except during spring–summer for *D. hybridus*. *C. villosus* had higher use of plots with a longer history of non-tillage (e.g., soybean), while there was more evidence of *D. hybridus* activity in plots with less human intervention (e.g., grasslands), especially during fall. Overall, *D. hybridus* and *C. villosus* were more sensitive to the particular structural features of plots rather than to the kind of land use practiced (crop field or rangeland). These results have important implications for future management decisions in the Pampas region because during the last decades, farming of soybeans has expanded at the expense of grasslands, and this change appears to have differentially affected these 2 species of armadillos.

En agroecosistemas el uso por parte de los mamíferos de lotes cultivados depende de la estructura del hábitat y del grado de especialización de las especies. En las Pampas de Argentina durante los últimos 30 años ha ocurrido una continua expansión de la superficie cultivada. El objetivo de este estudio fue analizar cómo la identidad y características de los lotes pueden afectar la actividad de dos especies de armadillos (*ChaetophRACTUS villosus* y *DasyPUS hybridus*) en un paisaje rural. Hicimos cuatro muestreos entre diciembre de 2011 y junio de 2013, incluyendo 175 lotes durante primavera-verano y 194 lotes durante otoño, de 25 localidades diferentes en la región Pampeana de la provincia de Buenos Aires. En cada lote registramos signos de la actividad de los armadillos (madrigueras o cuevas y hozaduras) a lo largo de una transecto de 600×6 m y caracterizamos cada lote midiendo cuatro variables de la estructura del hábitat. Existieron diferencias estructurales entre los diferentes tipos de lotes. Encontramos un total de 6.654 rastros de armadillos (*C. villosus* = 5.009, *D. hybridus* = 1.645). Modelos lineales generalizados mixtos revelaron que a lo largo de todo el estudio la identidad de los lotes explica la variación en la cantidad de evidencias de los armadillos, excepto durante primavera-verano para *D. hybridus*. *C. villosus* hace un mayor uso de lotes con historia más larga de siembra directa (soja) mientras que existen evidencias de que *D. hybridus* tiene más actividad en lotes con menor frecuencia de intervención humana, como los pastizales, especialmente durante otoño. En resumen *D. hybridus* y *C. villosus* son más sensibles a la identidad del lote antes que al tipo de uso. Estos resultados tienen un importante impacto en futuras decisiones de uso en la región

Pampeana, ya que durante las últimas décadas el cultivo de soja se ha expandido en detrimento de los pastizales y esto está afectando diferencialmente a, por lo menos, estas dos especies de armadillos.

Key words: *Chaetophractus*, crop fields, *Dasyplus*, perturbation, rangeland, soybean

Habitat use is the way an individual or population exploits biological and physical resources within a particular space (Krausman 1999). In agroecosystems, the use of cultivated plots by mammals (at least for small species) depends on habitat structure (Jacob 2008) as well as on the degree of species specialization (Coda et al. 2015). Numerous studies have highlighted the role of plot identity (e.g., different types of crops, rangelands, etc.) as an important influence on plot use (Bilenca et al. 2007; Escudero et al. 2014; Gonthier et al. 2014). In addition, the activity of livestock in rangeland paddocks can influence the availability of resources by inducing changes in vegetation structure through grazing (Eldridge et al. 2016).

In the Pampas of central Argentina, agriculture has played an important economic role since Spanish colonization in the 16th century, with consequent changes to the landscape (Ghersa et al. 1998; Viglizzo et al. 2011). In particular, there has been a significant intensification of agriculture and continued expansion of cropland, with no-till systems and genetically modified glyphosate-resistant soybean being especially favored (Viglizzo et al. 2011). No-till helps to maintain soil moisture, so this practice is often repeated in the same plot year after year, which allows for an increase in soil structure (Trigo and Cap 2003). In the Pampas, plot identity may also reflect the history of agricultural practices: plots of soybean, wheat, and barley usually have a long history of non-tillage, whereas plots of corn and sunflower show an alternation of non-tillage and conventional systems (Álvarez et al. 2015). Other types of plots include pastures and grasslands, which typically remain intact over several years because they are less frequently perturbed (Bilenca et al. 2012).

Several studies in the Pampas of Buenos Aires province have shown the effect of agricultural activities on wildlife, including birds (Codesido et al. 2013), rodents (Bilenca et al. 2007; González-Fischer et al. 2011), and armadillos (Abba et al. 2007, 2015). For example, previous studies on rodent species revealed that variation in population abundance was related to plot identity (Busch et al. 1984; Mills et al. 1991). Plot identities were the result of several attributes, such as vegetation structure, farming practices, history of use, and availability of resources (Bilenca et al. 2007; Jacob 2008; Coda et al. 2015).

In the Pampas of Buenos Aires province, the most common armadillos species are *Chaetophractus villosus* (large hairy armadillo) and *Dasyplus hybridus* (southern long-nosed armadillo) (Abba et al. 2007; Abba and Vizcaíno 2011; Abba et al. 2015). *C. villosus* is crepuscular to nocturnal and is present in a wide variety of habitats including grasslands, savanna, forest, agroecosystem, and degraded habitats (Abba and Vizcaíno 2011). Its diet includes many types of prey, such as invertebrates, small vertebrates, vegetables, and carrion (Redford 1985; Abba and Cassini 2008). *D. hybridus* is diurnal and typically found in grasslands but is also present, albeit less commonly,

in woodlands, and some degraded habitats (Abba and Vizcaíno 2011). Its food habits are similar to those of *C. villosus*, but with a strong tendency to myrmecophagy (Abba et al. 2011).

In a previous work, we analyzed the general effect of land use on the activity of these 2 species and found that they responded differentially to agriculture intensification. *C. villosus* seemed to respond favorably by showing more activity in croplands (Abba et al. 2015) to the point where it is even sometimes considered a pest (Abba and Vizcaíno 2011). In contrast, *D. hybridus* was affected by intensive agriculture, with more activity in plots with active livestock use and less in croplands (Abba et al. 2015). However, while we were able to detect a general impact of agriculture on these 2 species, we could not examine how finer variation in plot characteristics might have influenced activity and plot use (Abba et al. 2015). That is the aim of the present study, in which we analyzed how the identity of plots affected the activity of armadillos in a rural landscape.

MATERIALS AND METHODS

Study area.—Our study area extends $\approx 225,000$ km² (500 km north to south, 450 km east to west; 33–39°S, 57–63°W; Fig. 1) in the Pampas region of Buenos Aires province (central Argentina). This region is basically a huge, flat plain with habitat differences due to land-use patterns. For example, in some areas, croplands have replaced the native vegetation, while other areas remain as natural grassland or have a mixture of crops and animal husbandry (Codesido et al. 2013). The dominant crops in the study area are soybean, wheat, corn, barley, and sunflowers, all under non-tillage. Non-tillage involves activities such as sowing, agrochemical applications (e.g., herbicides, pesticides, etc.), and harvest. These practices are applied constantly to the same plots, resulting in lands with a high frequency of perturbation (Satorre 2005). On the other hand, rangelands have less human impacts, with natural or seminatural grasslands representing the most stable habitats, while pastures of alfalfa, ryegrass, and clover are more frequently perturbed (e.g., agrochemical applications).

The climate is warm-temperate, with mean temperatures varying between 15°C in the south and 18°C in the north. Annual rainfall decreases from 1,000 mm in the NE to 800 mm in the SW. The interannual variability of rainfall is quite high, with extensive rainfall or drought in some years (Scian et al. 2006). According to data provided by the Servicio Meteorológico Nacional of Argentina (SMN, Exp_144540), the 1st year of our study was considered a normal period of rainfall (≈ 800 – 900 mm), whereas the 2nd year was exceptionally wet ($\geq 1,200$ mm). Thus, interannual rainfall variation was considered in our analyses (see section on “Statistical analyses” below).

Sampling of armadillos and plot characterization.—We studied the 2 most common armadillo species of the Pampas:

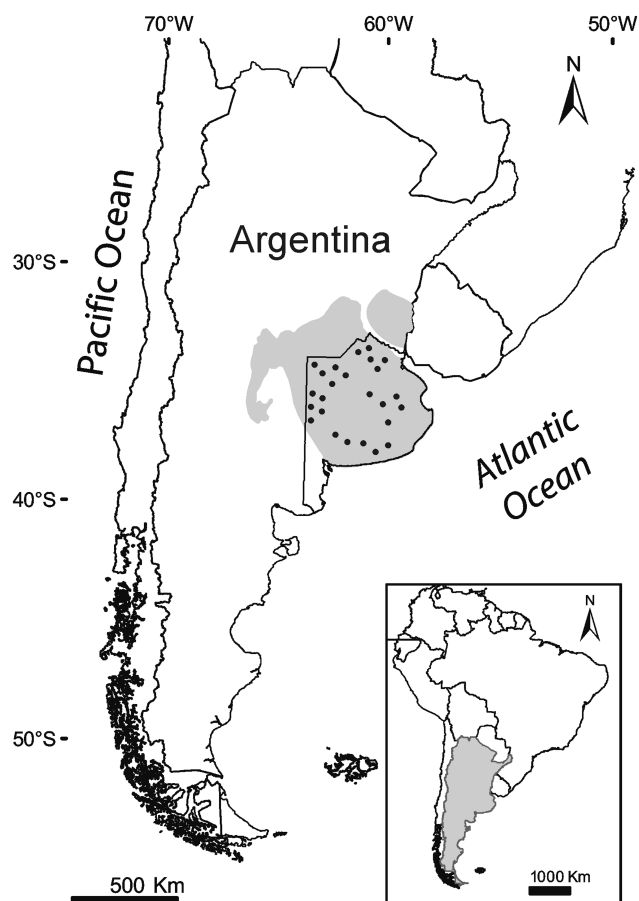


Fig. 1.—General location of the Pampas region (gray shading) and Buenos Aires province; black points indicate approximate locations of the survey sites.

C. villosus and *D. hybridus*. Both are active throughout the year and are semi-fossorial, digging 1 or more burrows in which they sleep. While active, both species leave their burrows to engage in a number of activities, such as reproduction, dispersal, movements to another territory, and so on. Most prominent among these is their search for food, which entails making numerous holes in the ground with the foreclaws (Abba 2008; Abba et al. 2011).

We randomly selected 25 sites distributed throughout our study area (Fig. 1). At each site, we selected 4 independent plots: 2 stubble crop fields and 2 rangelands with livestock. The mean size \pm SE of plots was 45 ± 2 hectares (range: 15–316 ha). Within each plot, we walked transects measuring 600×6 m and counted signs of armadillo activity (burrows and foraging holes—see Abba et al. 2007, 2015). Signs could be distinguished at the species level by considering 1) the general shape of the sign in the case of foraging holes and 2) the width and shape of the entrance in the case of burrows (see Abba et al. 2007, 2015).

To characterize each plot, we measured 4 structural habitat variables: vegetation height (in stubble plots this corresponded to stalk height), cover (percentage of soil covered by vegetation in rangeland and percentage of soil covered by stubble mulch), depth (in crop plots = the depth of stubble mulch, in

rangeland = litter depth), and soil hardness. To acquire the data, we used a ring of 0.25 m^2 that was thrown down randomly four times in each plot. We then measured the structural variables within the ring (INTA PRECOP 2015). We measured height and depth with a tape measure (cm), cover was estimated visually, and soil hardness was obtained with a soil tester (penetrometer). The 4 sets of values were averaged to generate the mean characteristics of each plot.

We did 4 surveys to estimate armadillo activity: 2 during spring–summer (December 2011–January 2012; the same 2 months again the following year) and 2 during fall (April–May 2012 and May–June 2013). Thus, each site was surveyed twice each season over 2 years, but sampling was carried out in different plots each time to avoid replication of data points. In rangeland, we surveyed pastures and natural or seminatural grasslands; in cropland, we surveyed winter crop stubbles (wheat, barley) during spring–summer and summer crop stubbles during fall (soybean, corn, sunflower; fields with less common crops such as oats, rye, and peanut were excluded from our analyses due to small sample size). We analyzed data from 369 plots: 175 during spring–summer (79 stubble crop and 96 rangelands) and 194 during fall (94 stubble crop and 100 rangelands).

Statistical analyses.—Separate analyses were conducted for each season (spring–summer and fall). In order to describe the variation between plots, we applied a principal component analysis (PCA) considering the 4 structural habitat variables (variables with factor loadings greater than 0.65 were considered as contributing to a particular component). Differences in vegetation structural characteristics among plots were compared by means of analysis of variance (if it was necessary, variables were transformed to ensure normality and homoscedasticity assumptions) or Kruskal–Wallis tests (Zar 2010).

To test the role of plot identity on armadillo activity, we used a generalized linear mixed model (GLMM) with a negative binomial distribution of count data (Pinheiro and Bates 2000), because the variance was much greater than the mean. Separate models were built for each species and for each season. One explanatory variable was plot identity (during spring–summer with 4 categories: barley, wheat, pasture, and grassland; 5 during fall: soybean, sunflower, corn, pasture, and grassland). Identity was specified as a fixed effect, whereas year (2 levels: year 1 = normal rainfall and year 2 = wet) was treated as a random effect in order to control for possible climatic influences on armadillo activity.

Models were evaluated with information-theoretic procedures (Burnham and Anderson 2002). Akaike's information criterion corrected for small sample size (AIC_c) was calculated for each model (Burnham and Anderson 2002), with the AIC_c weight of a model (w_i) representing the relative likelihood that the specific model was the best of the suite of all possible models. We calculated 95% confidence intervals (CIs) for coefficients of each level of the explanatory variables; a CI that did not include 0 indicated a statistically significant effect on armadillo activity (Burnham and Anderson 2002). Statistical analyses were carried out using package “glmmADMB”

(Fournier et al. 2012) implemented in R software, Version 3.2.2 (R Development Core Team 2015).

RESULTS

During both seasons, plots were structurally different from one another (Table 1). This was underscored by the PCA results, which showed clear separation among plots (Fig. 2). In spring–summer, the first 2 components accounted for 67.6% of the total variance and separated grasslands and pastures from stubble plots of barley and wheat. The 1st axis (38.4% of the variance) did so on the basis of depth, with increasing depth in stubble plots, while the 2nd axis (29.2% of the variance) did so on the basis of height, with grassland and pastures having higher vegetation height (Fig. 2). In fall, the first 2 components of the PCA accounted for 62% of the total variance. The 1st axis explained 32% of the variance and was associated with depth and soil hardness, which separated corn stubble (highest stubble depth) from grassland, pastures, and stubbles of soybean and sunflower (Fig. 2). The 2nd axis (30% of total variance) represented a gradient of vegetation height and cover, with grassland and pastures showing the highest values and stubbles of soybean and sunflower the lowest (Fig. 2).

Table 1.—Mean (\pm SE) vegetation structural characteristics of plots surveyed in the Pampas of Buenos Aires province, central Argentina. Sample sizes are in parentheses. The depth data presented for pastures and grasslands correspond to litter depth. Significant differences among plots in each season are indicated in bold and results of a posteriori comparisons are indicated with different letters. Analysis of variance or Kruskal–Wallis tests ($P < 0.01$ —Zar 2010).

Season	Variables	Barley (34)	Wheat (45)	Pasture (57)	Grassland (39)	
Spring–summer	Height (cm)	19.9 \pm 1.4 b	32.9 \pm 1.3 a	40.3 \pm 3.2 a	39.2 \pm 5.1 a	
	Depth (cm)	3.6 \pm 0.3 a	3.5 \pm 0.3 a	2.1 \pm 0.2 b	1.7 \pm 0.2 b	
	Cover (%)	70.9 \pm 3.5 ab	68.6 \pm 2.9 b	72.7 \pm 2.7 ab	80.3 \pm 2.9 a	
	Soil hardness (cm)	15.7 \pm 1.1 a	16.2 \pm 0.8 a	9.3 \pm 0.5 b	9.8 \pm 0.8 b	
Fall		Soybean (54)	Sunflower (13)	Corn (27)	Pasture (66)	Grassland (34)
	Height (cm)	13.6 \pm 1.8 c	27.8 \pm 5.9 b	45.1 \pm 2.8 a	28.7 \pm 2.3 b	31.3 \pm 3.9 b
	Depth (cm)	4.0 \pm 0.2 b	3.7 \pm 0.5 b	5.6 \pm 0.4 a	1.9 \pm 0.1 c	1.8 \pm 0.2 c
	Cover (%)	67.6 \pm 3.0 b	35.4 \pm 6.0 c	72.0 \pm 4.4 b	76.1 \pm 2.8 b	90.0 \pm 1.7 a
	Soil hardness (cm)	22.3 \pm 0.6 a	19.3 \pm 1.3 ab	21.3 \pm 0.8 a	16.0 \pm 0.7 b	19.5 \pm 1.0 a

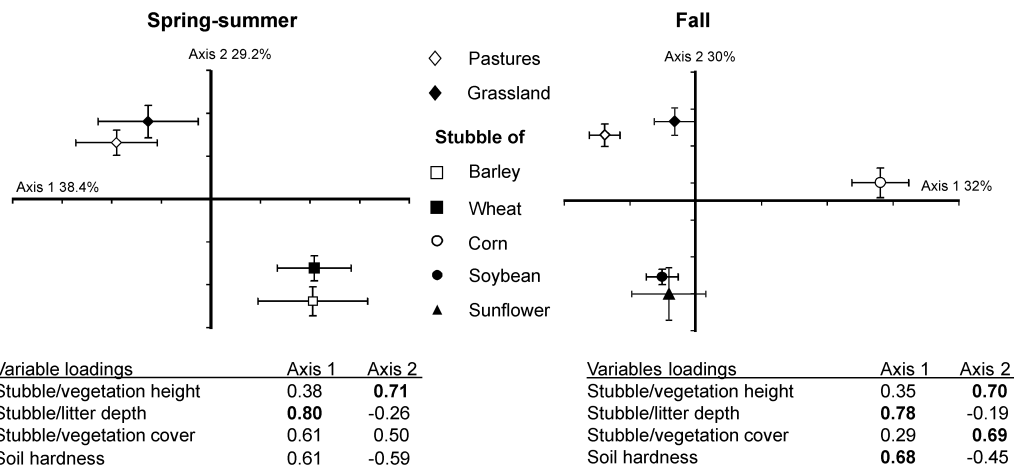


Fig. 2.—Results of principal component analyses (PCA) of the 4 variables measured in each plot in the Pampas of Buenos Aires province. PCA results are shown separately for each sampling season. Variables with factor loadings greater than 0.65 were considered to contribute to the component.

A total of 6,654 armadillo signs were found. *C. villosus* was the most active species with 5,009 signs and a mean of 11.6 ± 1.3 signs per plot during spring–summer ($n = 175$) and 15.4 ± 1.5 during fall ($n = 194$). Plot identity explained variation in the number of signs of *C. villosus* ($w_i = 0.611$; $AIC_c = 1144.4$; see Supporting Information S1), with significantly more activity in barley plots than in pasture or grassland during spring–summer (Fig. 3). Plot identity also explained variation in signs of *C. villosus* during fall ($w_i = 0.997$; $AIC_c = 1410.9$; see Supporting Information S2), with a higher use of soybean than grassland plots (Fig. 3). In both seasons, plots used the most by *C. villosus* (i.e., barley and soybean) were structurally similar in that they had the lowest vegetation height (Table 1).

For *D. hybridus*, we recorded a total of 1,645 signs, with a mean of 5.9 ± 1.4 signs per plot during spring–summer ($n = 175$) and 3.1 ± 0.6 during fall ($n = 194$). As observed in *C. villosus*, the identity of plots explained variation in signs of *D. hybridus* during fall ($w_i = 0.909$; $AIC_c = 680.8$; see Supporting Information S2) with grasslands showing the highest level of activity (Fig. 3). The remaining 4 plot types all had low and statistically indistinguishable levels of activity (Fig. 3). In spring–summer, plot identity did not explain variation in

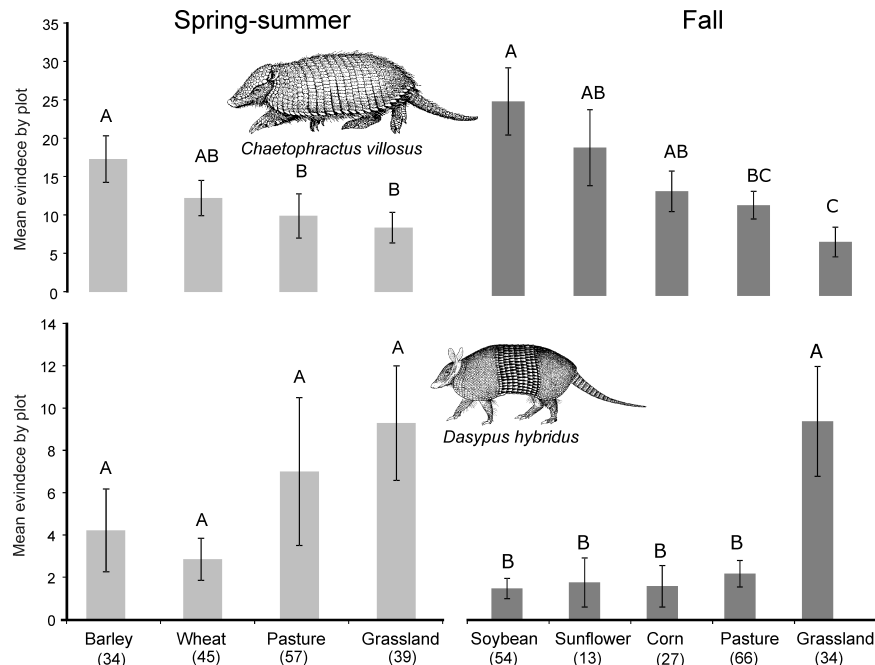


Fig. 3.—Mean \pm SE of armadillo signs (top, *Chaetophractus villosus*; bottom *Dasypus hybridus*) in the Pampas of Buenos Aires province, classified by season and plot identity (number of plots are in parentheses). Letters indicate that confidence intervals of coefficient estimates were different between plot types. Illustration modified from Díaz and Barquez (2002).

signs of *D. hybridus* (Null model, $w_i = 0.839$; $AIC_c = 735.5$; see Supporting Information S1), even though the use of grassland remained high (Fig. 3).

DISCUSSION

This is the 1st study to analyze the effect of plot identity on the activity of armadillos. Plot identity was clearly defined by vegetation structure and soil features, and it appeared that armadillos responded to this variation with species-specific differential use of habitats. Differential use of plots was particularly noticeable in fall, with both species exhibiting significantly more activity in certain plot types.

Regardless of season, *C. villosus* showed more activity in those plots with the lowest vegetation height (spring–summer= barley, fall= soybean). A similar response was observed in the 9-banded armadillo, *D. novemcinctus*, where it was proposed that a thick understory of shrubs and bushes might make it difficult for an armadillo to move through (Loughry and McDonough 2013). For *C. villosus*, a preference for plots with low vegetation also could be related to predator avoidance because plots with lower vegetation height may provide more opportunities to find possible refuges and escape routes (Abba 2008; Abba et al. 2011).

Chaetophractus villosus also showed high activity in plots with a longer history of non-tillage, such as soybean. As mentioned earlier, non-tillage maintains soil structure and allows for major development of stubble mulch, which in turn is thought to sustain a high abundance and diversity of arthropods (House 1989; Marasas et al. 1997; Kromp 1999; Lietti 2008), and earthworms (Kladivko 2001; Brown et al. 2003; Maitre

et al. 2012), both of which are important food items in the diet of *C. villosus* (Abba 2008; Abba and Cassini 2008).

In contrast to *C. villosus*, which is considered more of a generalist armadillo in terms of diet and habitat preferences (Redford 1985; Abba and Cassini 2008; Abba et al. 2015), *D. hybridus* is considered more of a specialist (Abba and Cassini 2008; Abba et al. 2011, 2015) and, as such, likely more sensitive to human perturbation. Our results confirm this perception because *D. hybridus* showed more activity in plots with less human impacts (i.e., grasslands). This response could be related to the fact that grasslands are the type of plots which receive less pesticide applications. As a result, they may be able to sustain larger numbers of ants (Underwood and Fisher 2006), which are the main food item of *D. hybridus* (Abba et al. 2011). If so, then the response detected in our study could reflect a decline in ant abundance in plots with high human intervention. As a final consideration, it should be taken into account that an important behavior of *Dasypus* species is the construction within the burrow of a nest made of dry weeds (Loughry and McDonough 2013), which are much more available in grasslands than in the other types of plots.

In the present study, we determined that *D. hybridus* and *C. villosus* are more sensitive to plot identity than just to land use. These results have important implications for future land management decisions in the Pampas region because during the last decades, agriculture, particularly the creation of soybean plots, has expanded dramatically, and primarily at the expense of grasslands. If this trend continues, our data suggest the abundance of *C. villosus* may increase, which may lead to ever more conflicts with humans, whereas *D. hybridus* may lose its favored habitat and could severely decline, to the point where it becomes an endangered species in this region.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author. **Supporting Information S1.**—Model selection based on ΔAIC_c comparison of generalized linear mixed model (GLMM) describing *Chaetophractus villosus* and *Dasyopus hybridus* activity in spring–summer.

Supporting Information S2.—Model selection based on ΔAIC_c comparison of generalized linear mixed model (GLMM) describing *Chaetophractus villosus* and *Dasyopus hybridus* activity in fall.

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