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Original investigation

Aboveground activity, reproduction, body temperature and weight of armadillos (Xenarthra, Chlamyphoridae) according to atmospheric conditions in the central Monte (Argentina)

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ABSTRACT

Hairy armadillos are generalist species widely distributed in South America. Three of these species, *Chaetophractus vellerosus, C. villosus* and *Zaedyus pichiy*, are sympatric in the arid central Monte. The objective of this study is to make a contribution to current knowledge about these species, the ecological interactions among them and their responses to arid environments. Aboveground activity, rectal temperature, body weight and reproductive status were measured in wild populations. The influence of seasonal and daily atmospheric conditions were estimated through generalized linear models. Seasonality affected the *Z. pichiy* reproduction cycle, body weight and aboveground frequency of occurrence. There was a higher frequency of animals with low body weight in late winter and spring, mostly breeding animals. Armadillos regained body weight in autumn, but their aboveground frequency decreased. Females showed higher weight variability than males in autumn. Daily atmospheric temperature proved to be the most relevant weather condition for *Z. pichiy*, with a positive influence on aboveground activities and body temperature. This species had the broadest range of body temperature, without relation to body weight. Typical dry and clear days of the central Monte were favorable conditions for *Z. pichiy* activity. Its diurnal activity had a higher probability of occurrence at twilight, and nocturnal activity occurred during summer. Presence of *C. vellerosus* was positively influenced by atmospheric temperature, whereas presence of *C. villosus* was not influenced by any weather condition. Differences in the use of solar radiation could represent a partial temporal segregation, promoting the coexistence of these sympatric species.

Introduction

Armadillos are the living members of an ancient phylogenetic group of mammals (Cingulata) externally distinguished by the dorsal carapace covering the body (Wetzel et al., 2008), which determines the ecological lifestyle of these animals (Superina and Loughry, 2012). Ancestral digging habits are retained by all extant armadillos, and they are expressed in a broad range from semi-fossorial to strictly subterranean habits (Gaudin and Croft, 2015; Vizcaíno and Milne, 2002; Vizcaíno et al., 1999). Armadillos have a remarkable low metabolic rate and poor thermoregulatory abilities (McNab, 1985, 1980). This relative heterothermia supposes measurable responses to changes in weather conditions, such as low environmental temperatures (Redford and Eisenberg, 1992) and number of annual freeze days (Taulman and Robbins, 2014). The seasonality observed in reproductive patterns (Loughry et al., 2015) is probably a response to environmental stimuli in terms of sunlight and temperature rhythms, as observed in other mammal species (Gilmore, 1981).

Euphractinae (Chlamyphoridae) includes four species with similar ecological requirements (Gibb et al., 2016; Abba et al., 2015). Euphractines are widely distributed across diverse habitats of temperate South America (Wetzel et al., 2008). Their generalist diets include plants, insects and small vertebrates obtained by digging (Redford, 1985). Euphractines construct burrows as other armadillo species, they are primarily nocturnal and largely asocial, and individuals are usually widely scattered from one another (McDonough and Loughry, 2008; Loughry and McDonough, 2013). Generalist habits and behavioral flexibility would increase the probability of survival of species inhabiting harsh habitats (Greenberg, 1990).

Chaetophractus vellerosus Gray 1865, *C. villosus* Desmarest 1804 and *Zaedyus pichiy Desmarest 1804* are euphractine species widely distributed in Argentina (Fig. 1). *Chaetophractus vellerosus* and *Zaedyus pichiy* inhabit arid environments, whereas *C. villosus* inhab-

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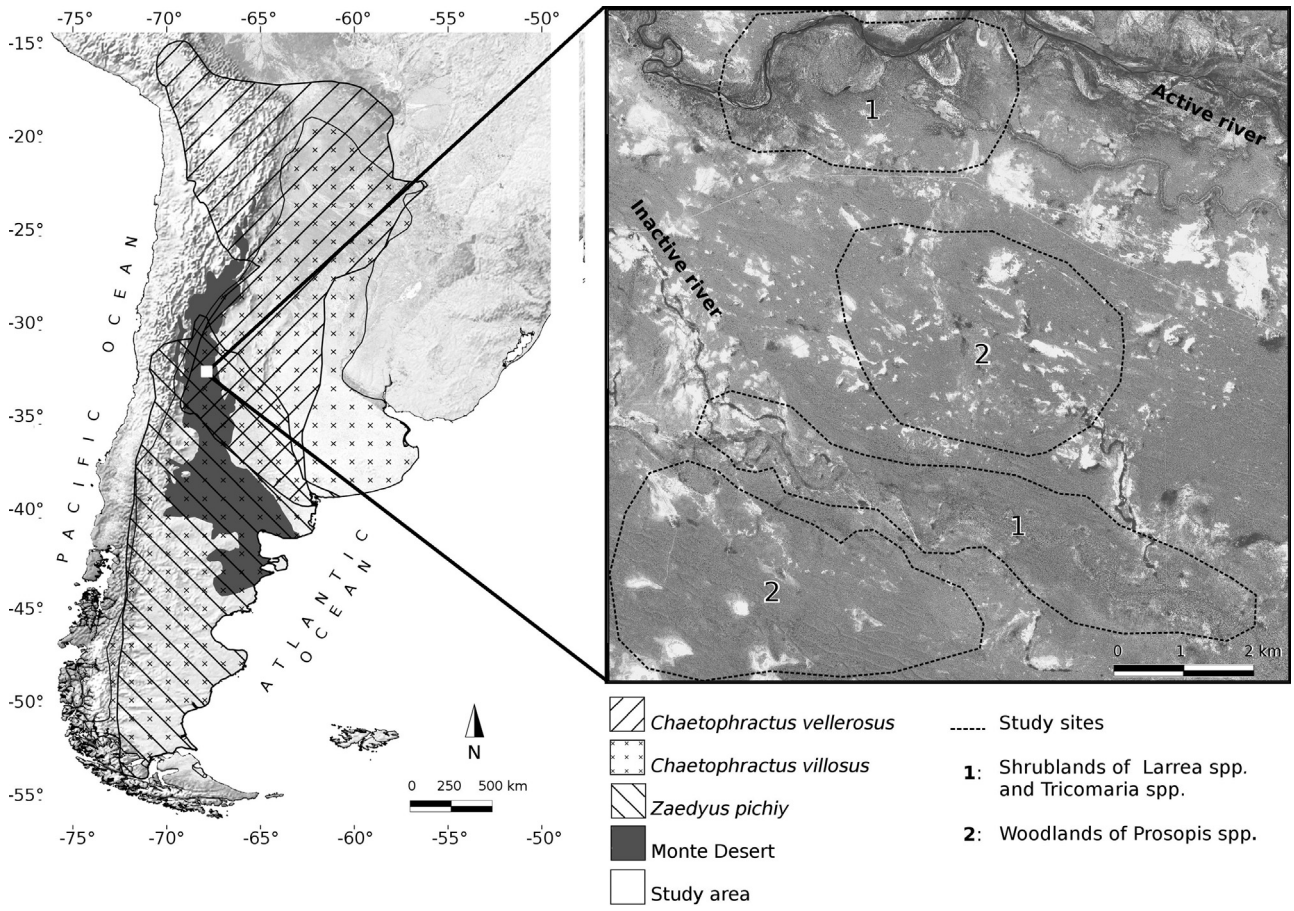

Fig. 1. Geographic distribution of *Chaetophractus vellerosus*, *C. villosus* and *Zaedyus pichiy* (IUCN SSC, 2016 modified according to Abba, pers. comm.; Abba et al., 2014a; Superina and Abba, 2014a), location of the study area and characteristics of sampled sites.

its a broad variety of habitats (Abba and Cassini, 2008; Wetzel et al., 2008). Although their geographical distributions are not clearly bounded by environmental variables (Abba et al., 2012), optimal habitats of *C. vellerosus* and *Z. pichiy* are associated with different seasonal climatic patterns, whereas distribution of *C. villosus* is mainly associated with temperate conditions and isothermality (Seitz et al., 2016). The three species share a narrow belt of arid ecosystems corresponding to the Monte, Espinal and Pampas ecoregions of Argentina (IUCN SSC, 2016; Abba et al., 2014a; Superina and Abba, 2014a). With a similar conservative fundamental niche (Wiens and Graham, 2005), it is expected that these sympatric species will require similar resources. However, a stable coexistence among species requires resource partitioning (Tilman, 2007; Walter, 1991) through mechanisms that ecologically separate each species from the other (Chesson et al., 2004). The first study about the sympatry of these species in the arid Espinal ecoregion found that *C. vellerosus* was a rare species, whereas *C. villosus* and *Z. pichiy* were more abundant (Crespo, 1944).

The objective of this study is to contribute to current knowledge about armadillo ecology and to examine resource partitioning among three sympatric species (*Chaetophractus vellerosus*, *C. villosus* and *Zaedyus pichiy*). According to the current knowledge about these species, three hypotheses were postulated concerning (1) the influence of seasonal environmental changes on the activity, reproduction and body weight of armadillos; (2) the influence of daily weather conditions on the aboveground presence and body temperature of armadillos; and (3) the resource partitioning among them (Table 1). The relevance of these topics lies in providing necessary ecological background information about armadillos inhabiting arid environments, such as the central Monte, for a future assessment of the local conservation status of their populations.

Material and methods

Study area

The study area (32°17' S, 67°40' W, 497–519 m.a.s.l.) is located in the Monte phytogeographical province, most specifically in the Low Monte ecoregion (Burkart et al., 1999). Six species of armadillo were registered in the study area (Seitz, 2013), which is nearly half of all species documented for Argentina. This area is a priority for the conservation of xenarthrans in arid ecosystems due to high species richness (Tognelli et al., 2011). The area has a temperate climate (mean annual temperature of 18 °C, range from −11 °C to 45 °C) with continental conditions (56 °C of annual amplitude, most of the year with 16 °C of daily amplitude). An annual average of 40 freeze days occurs from May (autumn) to September (spring). A water deficit caused by scarce rainfall (mean annual precipitation: 152 mm) and high solar radiation characterizes this arid climate (ratio between precipitation and potential evapotranspiration: 0.12). The region has a regime of subtropical rainfalls, with 60% of precipitation occurring during summer. Two climatic seasons can be identified: a warm-humid season (spring-summer), and a cold-dry season (autumn-winter, IADIZA Environmental Network, 2017, meteorological data from 1971 to 2017). This climate determines two seasonal periods of relatively high (summer) and low (winter) plant productivity (Bisigato et al., 2009), fauna diversity and abun-

Table 1
Hypotheses and predictions used to build *a priori* models based on the knowledge of armadillo species, with their response variables and predictor variables (codes between brackets).

Hypothesis	Predictions	Response variables	Predictor variables
1. Seasonal changes in climate and food availability in the central Monte are expected to influence aboveground activity, reproduction and body weight of armadillos.			
1.a. Seasonal variations in aboveground activity were previously reported for *Chaetophractus vellerosus* (Abba et al., 2011; Cuéllar, 2008; Greegor, 1985) *C. villosus* (Abba and Cassini, 2008; Roig and Henriquez, 1984) and *Zaedyus pichiy* (Superina and Abba, 2014b).	Aboveground activity of these species will increase during spring-summer.	Aboveground frequency of occurrence of each species	Seasonality (SEA)
1.b. Seasonal changes in food availability are expected to influence body weight especially for *Z. pichiy*, that build up fat as energy reserve before hibernation (Superina and Abba, 2014b).	Body weight will increase when food availability is high (summer-autumn), especially before hibernation.	Body weight of *Z. pichiy*	Seasonality (SEA)
1.c. Most armadillo species have a seasonal reproduction (McDonough and Loughry, 2008), particularly documented for *C. vellerosus* (Abba et al., 2011; Cuéllar, 2008; Greegor, 1985) and *Z. pichiy* (Superina and Abba, 2014b).	Breeding activity will be bounded to late winter and spring.	Proportion of reproductive animals	Seasonality (SEA)
2. Daily changes in weather conditions are expected to influence the aboveground activity and body temperature of armadillos.			
2.1. *C. vellerosus* and *Z. pichiy* positively respond to external temperature (Superina and Abba, 2014b; Abba et al., 2011), whereas *C. villosus* is relatively independent (Roig and Henriquez, 1984).	Aboveground activity of *C. vellerosus* and *Z. pichiy* will increase with high external temperatures, without influence in *C. villosus*.	Aboveground presence of each species	Atmospheric temperature (TEM)
2.2. Seasonal shifts from summer nocturnal habits to winter diurnal habits were observed in *Chaetophractus* spp. (Abba et al., 2011; Abba and Cassini, 2008), whereas *Z. pichiy* maintained diurnal habits (Superina and Abba, 2014b).	Aboveground activity of *Z. pichiy* will increase with high solar radiation, without influence in both *Chaetophractus* spp.	Aboveground presence of each species	Solar radiation (RAD)
2.3. Typical species of arid environments (*C. vellerosus, Z. pichiy)* are affected by dry and clear days, whereas *C. villosus* is not restricted by climatic trends considering its extensive distribution range (Seitz et al., 2016; Superina and Abba, 2014b; Greegor, 1975).	Aboveground activity of *C. vellerosus* and *Z. pichiy* will increase with high barometric pressure and low air humidity, without influence in *C. villosus*.	Aboveground presence of each species	Barometric pressure (BAR) Air humidity (HUM)
2.4. Given the low capability to thermoregulate, environmental temperature influences the body temperature of armadillos independently of their body weight (McNab, 1985, 1980).	Body temperature will increase with high external temperatures, without influence of body weight.	Rectal temperature	Atmospheric temperature (TEM) Body weight (WEI)
3. A resource partitioning among these related species is expected in sympatry, in order to avoid a potential competence.			
3.1. Generalist species contract or expand their niche breadth in order to partitioning resources and avoiding competition (Pianka, 1981). Coexistence among potential competitors is promoted by temporal and spatial variability, trophic complexity and other ecological interactions (Tilman, 2007).	Aboveground presence will differ among these sympatric species in terms of the most relevant weather variables, and the range of shared variables used.	Overlapping among species in their aboveground presence	Relevant weather conditions for each species (main predictors detected modeling the Hypothesis 2)

dance (Seitz, 2013). The xerophytic vegetation is represented by shrub steppes with dominance of *Larrea* spp., and open woodlands of *Prosopis* spp. where groundwater is accessible. The Chaco ecoregion influences flora and fauna in the study area (Abraham et al., 2009). Regarding armadillos, this area is part of an ecotone, with presence of characteristic species of Patagonia and Monte (*Zaedyus pichiy*) as well as of the Chaco ecoregion (*Chaetophractus vellerosus*) (Sosa and Vallvé, 1999).

Field design

Preliminary surveys in the study area (Seitz, 2013) confirmed the sympatry of three euphractine species (*C. vellerosus*, *C. villosus* and *Z. pichiy*). Seasonal surveys were carried out on 10 occasions, from March 2010 to November 2011. Four sampling sites of 12 km^2 were selected to account for the environmental heterogeneity of the area (Fig. 1). Surveys utilized fixed transects that were sampled in the same sequence during each sampling occasion. Each sampling site was surveyed over three consecutive days, with a different 4-km transect covered each day. Transects were traversed by two observers 50 m apart, while two trained muzzled dogs searched for armadillos on each side of the transect. According to recorded geopositions of observed armadillos, dogs searched up to 100 m around observers. Therefore, each transect sampled around 1 km^2. Sampling was contingent upon the authorization of an indigenous community living in the area, whose main activity consists of herding goats. Admission to the sites was regulated by the movement of the goats. Consequently, access to the sampling sites was restricted at times, resulting in a seasonally unbalanced sampling effort (30 transect-days in spring and in summer, 12 transect-days in autumn and in winter). In total, transects were surveyed for 419 h, with 66% of these hours occurring during daylight [10:00 to 19:00–20:00 (in autumn-winter and spring-summer, respectively)], 14% at twilight (19:00–20:00 to 20:00-21:00) and 20% at night (20:00–21:00 to 4:00).

Whenever possible, adult animals were caught to measure their body weight (n = 67), rectal temperature (digital thermometer Citizen CTA-301c; n = 45), morphometric measures (standardized in Abba et al., 2011), and reproductive status (see Superina et al., 2009). The proportion of reproductive animals (*i.e.* number of breeding animals with respect to all caught adults) allowed the estimation of reproductive activity.

Seasonality was defined as: winter (mid-June to mid-September), spring (mid-September to mid-December), summer (mid-December to mid-March) and autumn (mid-March to mid-June). The unbalanced sampling among seasons was corrected for the EM algorithm, calculated as an iterative computation of maximum-likelihood via expectation-maximization steps (Dempster et al., 1977). Daily weather conditions were measured for each sampled hour with the continuous variables atmospheric temperature (°C), solar radiation (Wm^2), air humidity (%), and barometric pressure (hPa). Atmospheric data were obtained from *El Mateo*, a weather station located inside the study area. Data accuracy was checked using data from other nearby weather stations of the central Monte (IADIZA Environmental Network, 2017).

Statistical analyses

The effects of seasonality on aboveground presence and frequency of each species were analyzed using both binary (observed and not observed animals) and continuous (number of animals recorded per km^2) variables. The influence of daily weather conditions on aboveground presence or absence was analyzed for each hour tracked. Variation in rectal temperature was compared with body weight and weather temperature at the moment of capture. Reproductive status of individuals was examined according to season and weather temperature at the moment of capture (Table 1).

The exploratory data analysis (Tukey, 1977) tested the distribution of raw data and the collinearity between explanatory variables, in order to select the adequate theoretic distribution of the response variable, and to eliminate predictor variables that strongly correlated ($r \geq 0.70$). All predictions were tested using generalized linear models (Crawley, 2007; McCullagh and Nelder, 1989). Gamma distribution and log link function were used in models for rectal temperature, body weight and reproduction of *Z. pichiy*, given the negative asymmetry of distributions (Shapiro test $W = 0.92$, $W = 0.91$ and $W = 0.51$ respectively, $p < 0.05$). Due to the high number of transects without observed animals, the relation of seasonality to aboveground activity was tested using gamma-binomial hurdle models (Frees, 2011). Gamma error distribution and log link function modeled the frequency of occurrence, whereas binomial error distribution and logit link function modeled the aboveground presence. Similarity among species regarding the probability distributions of frequency was tested with Kolmogorov-Smirnov procedure (Crawley, 2007). The interspecific overlap in the use of shared variables was estimated using Horn's index R_o (Horn, 1966) once the relevant weather conditions were identified for each species.

Information-theoretic procedures were applied to evaluate models (Burnham and Anderson, 2002). Hurdle models of frequency and presence related with seasonality were compared against null models. When response variables were explained by weather, we considered all possible combinations of predictors, and several candidate models were obtained with additive combinations of predictor variables. Once the Akaike's information Criterion corrected for small sample size (AIC_c) was calculated for each model, a comparison was made using ΔAIC_c (*i.e.* the difference between the lowest AIC_c obtained and the AIC_c of each other model) and w_i (the AIC_c weight of each model, as the relative likelihood that this is the best of all models considered). Parameter likelihood (*i.e.* the support for each predictor variable) was evaluated summing w_i across all models that contained it; parameter estimates were model-averaged, based on the w_i of all candidate models. Confidence interval limits at 95% (CI) of parameter estimates were calculated in order to supplement parameter-likelihood evidence of important effects.

To measure the consistency of continuous data response to the gamma model, meaning the predictive ability of models, goodness of fit was measured with two-sample Cramer-von Mises U test (Michelangeli et al., 2009). A theoretical distribution with the same shape and scale parameters of the continuous data response was compared against distribution frequencies, and evaluated with p-values. The fit of binomial models to presence was analyzed with receiver operating characteristic (ROC) analysis, characterizing the performance of a model through the area under the curve (AUC). True and false positive rates were calculated by sampling total presence-absence data to train models with 75% of data, and test with 25% of remaining data. Good predictive ability is associated with AUC closer to 1 than to 0.5 (Fawcett, 2006). Statistical analyses were carried out using R (http://www.r-project.org/). Values are reported as $x \pm SE$ except where noted. All tests were two-tailed, and differences were considered significant at $p < 0.05$.

Results

Influence of seasonality on aboveground frequency, body weight and reproductive activity

We caught 74% of all observed animals (N = 91). The highest sampling success was obtained for *Z. pichiy* (0.37 animals/km, CI = 0.28-0.47, N = 61), followed by *C. villosus* (0.20 animals/km, CI = 0.12-0.28, N = 20) and *C. vellerosus* (0.10 animals/km, CI = 0.05-0.17, N = 10). *C. villosus* differed from both *C. vellerosus* and *Z. pichiy* in the distribution function of aboveground frequency (Kolmogorov-Smirnov test $D = 0.1$ and $D = 0.2$ respectively, both $p < 0.05$), whereas distributions of *C. vellerosus* and *Z. pichiy* did not differ significantly ($D = 0.3$, $p > 0.05$).

The frequency of occurence was adequately modeled according to seasonality for *C. vellerosus*, *C. villosus*, and *Z. pichiy* (Cramér-von Mises test $U = 0.08$, $U = 0.05$ and $U = 0.09$, $p < 0.05$). Nearly half of all variation in *Z. pichiy* frequency of occurrence ($w_i = 0.45$; $AIC_c = -0.7$) was accounted for by seasonality, whereas it was not relevant for the other two species (see Appendix). According to parameter estimates and confidence intervals of each level of the factor, the aboveground frequency of *Z. pichiy* was lower in autumn than in other seasons ($CI_{autumn} = -2.35; -0.37$, see Appendix in Supplementary material). The parameter of discrepancy indicated a slight overdispersion in Pearson residual errors ($\Phi = 1.19$), corresponding to outlier values in spring (Fig. 2).

Average body weight of *Z. pichiy* (Table 2) was 8.2% higher than previously reported (Superina and Abba, 2014b), with the heaviest animals weighting up to 13% more than previously documented [mean-maximal weight (gr): 1064–1700 versus 977–1500, respectively]. Variation in body weight was better explained by seasonality ($w_i = 0.77$; $AIC_c = 720.2$; see Appendix) than by atmospheric temperature. The minimal model only included seasons and it explained 28% of body weight variation. Gamma models adequately predicted the response, with errors normally distributed ($W = 0.8$, $p > 0.05$). Body weight significantly increased in autumn ($CI_{autumn} = 6.88, 7.49$) and decreased during winter-spring ($CI_{winter} = -0.49, -0.03$; $CI_{spring} = -0.64, -0.19$; see Appendix in Supplementary material). The predicted distribution slightly overestimated weight loss during winter-spring, and underestimated the weight gain in summer (Fig. 3a). Males were heavier than females (Mann-Whitney test $U = 195$, $p < 0.05$), particularly during summer-autumn ($U = 70.5$ $p < 0.05$, Fig. 3), but not during winter-spring ($U = 23.5$ $p > 0.05$). The mean weight of *Chaetophractus* spp. (Table 2) was similar to that previously reported (Greegor, 1985; Abba et al., 2011) and the number of sampled animals was not sufficient to build models.

The proportion of breeding individuals of *Z. pichiy* was associated with seasonality ($w_i = 0.72$; $AIC_c = 33.9$; see Appendix), with 28% of explained variation. Once breeding males started the repro-

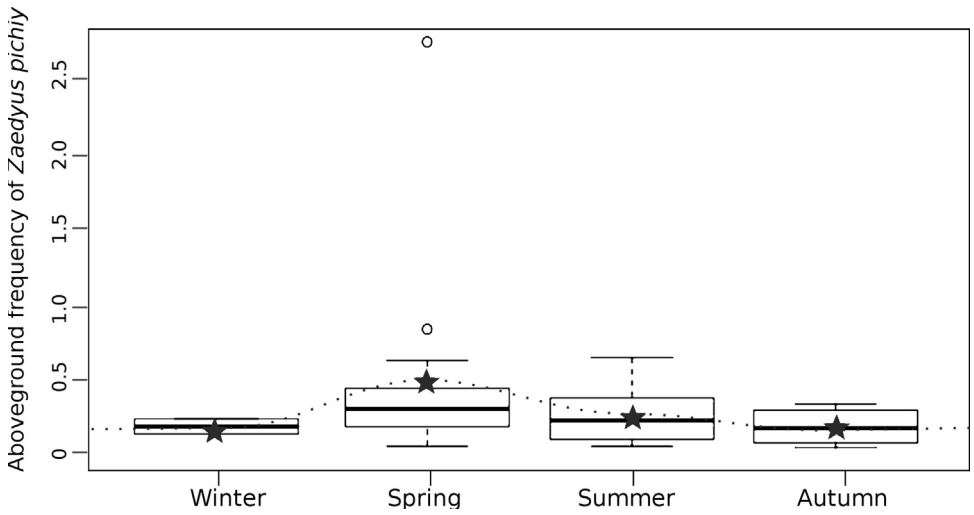

Fig. 2. Box plot of *Zaedyus pichiy* aboveground frequency (animals/km) in each season. Outliers (dots), means (stars) and intra-seasonal variation (vertical lines) represent predicted values of gaussian distribution of probabilities.

Table 2
Basic statistics of rectal temperature and body weight for each armadillo species: average (av.), standard deviation (SD), range of data (range), and number of sampled individuals (N).

	Chaetophractus vellerosus				*Chaetophractus villosus*				*Zaedyus pichiy*			
	av.	SD	range	N	av.	SD	range	N	av.	SD	range	N
Rectal temperature (°C)												
	36.25	1.71	34.00–38.00	4	36.00	0.81	35.00–37.00	4	36.60	1.61	33.00–39.00	37
Body weight (grams)												
Total	816	90	700–950	5	2464	380	1900–2900	11	1064	315	650–1700	51
Females	850	87	800–950	3	2507	406	1900–2900	7	954	269	670–1500	21
Males	765	92	700–830	2	2387	375	2000–2800	4	1147	330	650–1700	30

ductive cycle in late winter, the number of breeding animals increased until spring (CI_{winter} = 0.05, 0.85; CI_{spring} = 0.11, 0.72; see Appendix), and some males showed injuries probably due to intraspecific aggressiveness. Receptive females were found around spring equinox (±3 days). Breeding males of *Chaetophractus* spp. were found from early to late spring. However, the small sample of individuals prevented us from carrying out statistical analysis.

Influence of daily weather conditions on aboveground presence and rectal temperature

The aboveground presence explained by weather conditions was adequately fit with a gamma distribution in hurdle models for the three species. Temperature, solar radiation, air humidity and barometric pressure were not strongly correlated, and distinctively explained the presence of *Chaetophractus* spp. and *Z. pichiy*.

The best model for *C. vellerosus* included a positive effect of temperature (above 28 °C) and a negative one for radiation (below 300 mW) (w_i = 0.37; AIC_c = 89.3, see Appendix; Fig. 4). The minimal adequate model matched with the best model (CI_{TEM} = 0.01, 0.41; CI_{RAD} = $-7.0e^{-3}$, -1.0^{e-3}; see Appendix) and explained 11.9% of variation. Predictive ability of the minimal model was slightly better than random (AUC = 0.60). Logistic output for *C. vellerosus* minimal model fit well for radiation but not for temperature (Fig. 4).

Solar radiation explained 10.3% of the *C. villosus* presence (see Appendix). Although the first candidate model associated presence to radiation and pressure (w_i = 0.29; AIC_c = 151.4), the minimal adequate model only included the negative effect of radiation (CI_{RAD} = -0.01, $-2.0e^{-3}$). Predicted radiation fit well to observed data, expecting higher probabilities of presence below 400 mW (Fig. 4). ROC curves analysis indicated no predictive power in the *C. villosus* minimal model (AUC = 0.50).

The best model for *Z. pichiy* included all weather variables (w_i = 0.67; AIC_c = 332.5, see Appendix in Supplementary material) and agreed with the retained model (CI_{TEM} = 0.03, 0.25; CI_{RAD} = $-3.0e^{-3}$, $-1.0e^{-3}$; CI_{HUM} = -0.07, $-1.0e^{-3}$; CI_{BAR} = $8.0e^{-3}$, 0.15), explaining 7.3% of variation. Aboveground presence increased with temperature and pressure, whereas humidity and radiation had negative effects. Predicted values fit well to observed values (Fig. 4), probability of presence increased with temperatures above 17 °C and humidity below 60%, showing higher variation at temperatures higher than 35 °C. This species was present across the entire range of radiation, with minimal predicted presence at highest radiation and showing maximal probabilities around 300 mW. ROC analysis detected an adequate ability of minimal model to predict presence (AUC = 0.75).

The mean rectal temperature was similar for the three species, but they differed in terms of range amplitudes (Table 2). *Z. pichiy* was the most variable species, its rectal temperature was adequately modeled with gamma error distribution (U = 0.21). The best model retained only external temperature as an explanatory variable (w_i = 0.75; AIC_c = 137.4; see Appendix), accounting for 21.5% of variation. Rectal temperature linearly increased with external temperature, with a predicted slope of 0.22 (Fig. 5), whereas body weight had no incidence on it. Rectal temperature of *Chaetophractus* spp. were not modeled due to the small sample of individuals.

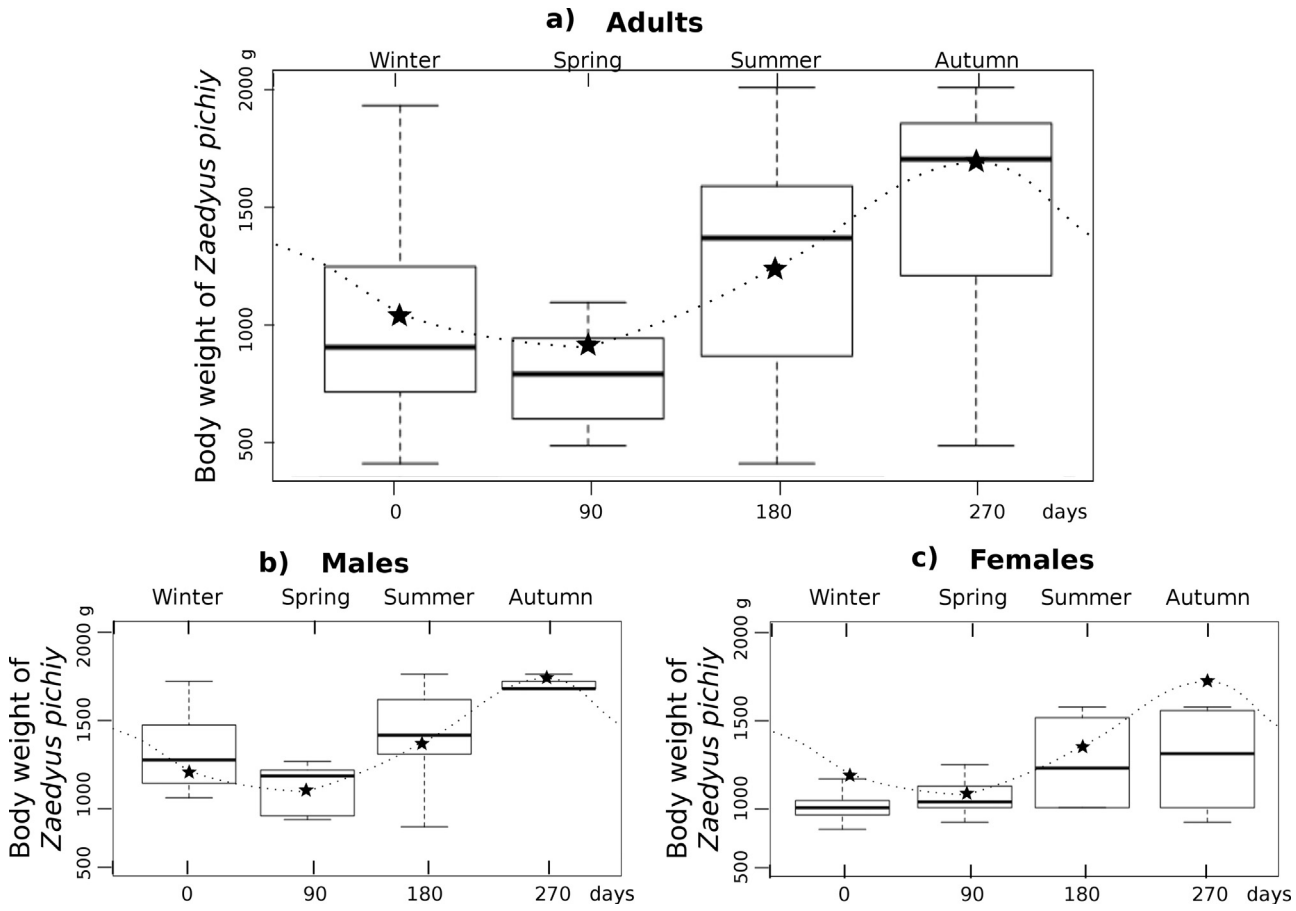

Fig. 3. Box plot of *Zaedyus pichiy* body weight in each season, for all adult individuals sampled (n = 51), males (n = 30) and females (n = 21). Means (stars) and intra-seasonal variation (vertical lines) represent predicted values of gaussian model.

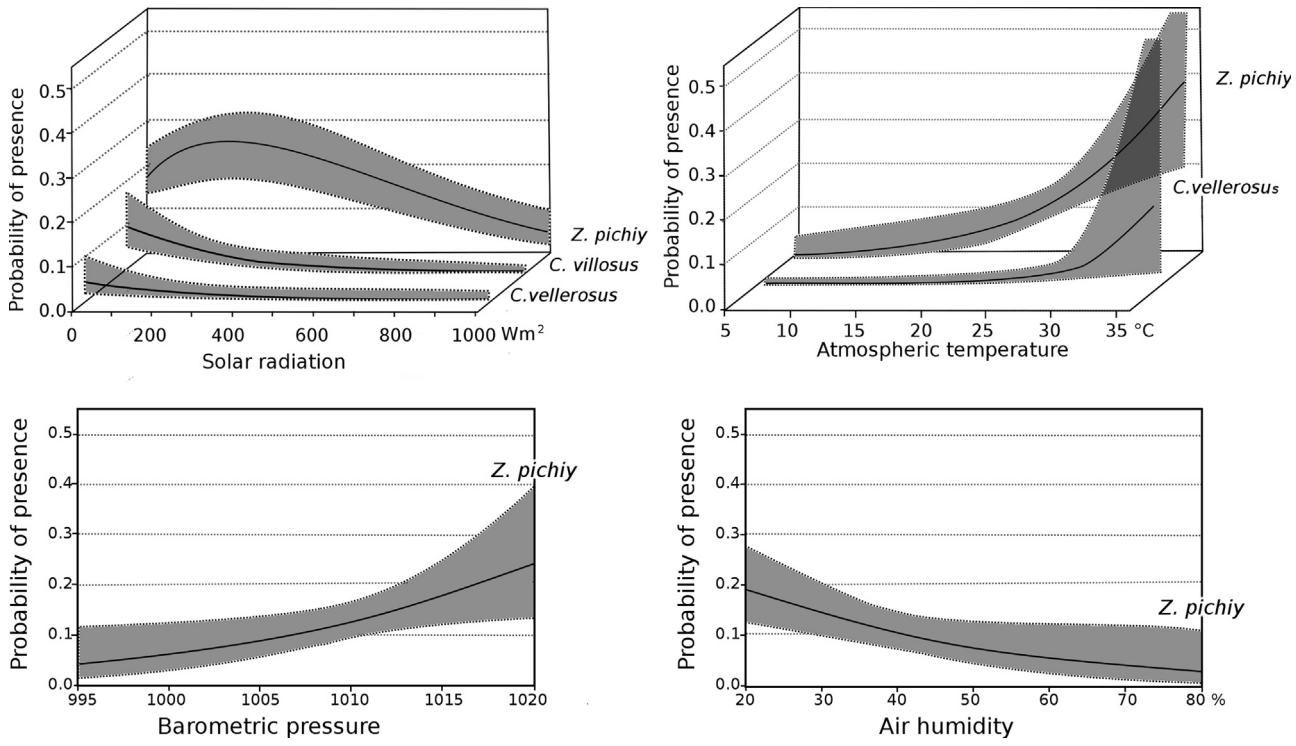

Fig. 4. Fitted values (lines) and standard errors of gamma predictions (shade area) of variables composing the minimum adequate weather model for each species.

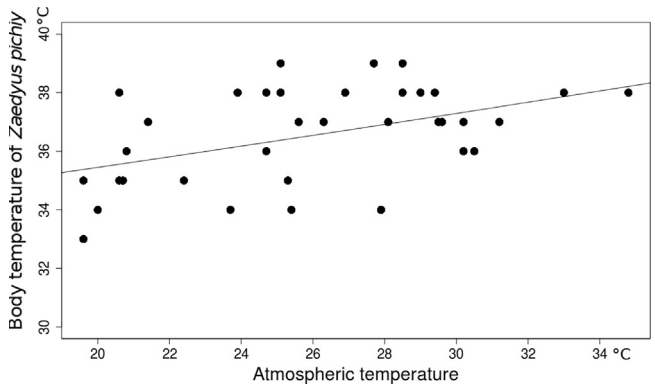

Fig. 5. Body temperature of *Zaedyus pichiy* according to atmospheric temperature observed (dots, n = 37) and predicted by gamma model (line).

Overlap among species in the used range of environmental conditions

Considering solar radiation as an explanatory variable of aboveground presence in the best model for each armadillo species (Fig. 4), the Horn index detected a high overlap between *Zaedyus pichiy* and *C. vellerosus* ($R_0 = 0.90$), followed by the overlap between *Chaetophractus* species ($R_0 = 0.78$) and between *C. villosus* and *Z. pichiy* ($R_0 = 0.69$).

Weather temperature was included in the best models for *Z. pichiy* and *C. vellerosus* (Fig. 4). Even though the presence of both species increased with high temperature, the overlap index was moderate ($R_0 = 0.56$).

Discussion

Seasonal and daily conditions of the central Monte influenced the aboveground activity of the three species of armadillos differently: *Z. pichiy* was responsive to all evaluated variables, *C. vellerosus* was affected by atmospheric temperature and solar radiation, and C. *villosus* was not influenced by seasonality or any weather variable. These results suggest an interaction among species through their shared resources, and a probable time partitioning in their diel activities. However, our results about *Chaetophractus* spp. are preliminary due to the small sample of animals found in the study environment.

Effects of seasonality

The three species showed aboveground activity all year round, as almost all euphractine species do (Loughry et al., 2015). Seasonality influenced the aboveground frequency of occurrence of *Z. pichiy*, showing a decrease in autumn, which indirectly agrees with predicted higher activity during spring-summer, meanwhile no seasonal changes were detected in frequencies of occurrence of *Chaetophractus* spp. Seasonality also affected the reproductive cycle and body weight of *Z. pichiy*, which may reflect its hibernation requirements (Hatcher, 1903 cited in McNab, 1980). As predicted, breeding animals were observed in late winter and spring, whereas body weight increased in autumn and decreased in winter.

The onset of reproductive activity of *Z. pichiy* after hibernation (Superina and Abba, 2014b) could affect its body mass. Both biological events could represent a negative energy balance, accounting for the seasonal decrease of body mass when food resources are still scarce in the central Monte (Carrera et al., 2009).

The body mass of *Z. pichiy* increased after the breeding season, with heaviest animals observed in autumn, probably as a result of the summer increase of food availability for this omnivore (Seitz, 2013). The autumn decrease of aboveground activities may result from less time spent foraging once these animals have achieved an acceptable weight preparing for hibernation. The increase of insect diversity, and the dietary inclusion of *Prosopis* fruits during summer-autumn (Seitz, 2013), could account for the fact that *Z. pichiy* is slightly heavier in central Monte than in other studied environments. This link between two natives of the Monte could be mutually beneficial for both, e.g., by providing nutritional input for armadillos and seed dispersal for *Prosopis* spp.

Zaedyus pichiy presented nonbreeding individuals during the reproductive season, as observed in other armadillo species (*C. vellerosus* Abba et al., 2011; Cuéllar, 2008; Greegor, 1985; *C. villosus, Euphractus sexcinctus* Cuéllar, 2008; and *Dasypus novemcinctus* McDonough, 2000). Lactating females with offspring were observed during summer-autumn, as reported previously (Superina and Abba, 2014b). Age and nutritional status are conditions that seem to influence the onset of reproduction in armadillos (McDonough and Loughry, 2008). Sexual differences in reproduction and breeding requirements may affect the gaining of fat before hibernation, as weight in autumn was lower and more variable in females than in males.

Despite having more generalist habits and being less influenced by seasonality, *Chaetophractus* spp. was more scarce than *Z. pichiy*. Relative frequencies of these species could be influenced by other issues rather than seasonality in the central Monte, as their biogeographical histories and their interspecific relations.

Effects of daily conditions

Aboveground presence of each species responded differently to weather conditions. Differing from prediction, radiation negatively affected the presence of *C. vellerosus,* suggesting a prevalence of nocturnal habits in the study environments throughout the year. For this species, the predicted increase of aboveground presence in response to higher atmospheric temperature was supported. Greegor (1985) also suggested external temperature limiting the daily activity in the Monte. Despite this species is considered to be adapted to a xeric environment because of its ability to concentrate urine (Greegor, 1975), its aboveground presence was not influenced by typical dry and clear days of the central Monte. This result is consistent with the presence of *C. vellerosus* in humid habitats of the Yunga forests and the Pampas grassland (Abba et al., 2015; Carlini and Vizcaíno, 1987).

The presence of *C. villosus* was not affected by any daily variables. Being the most generalist euphractine species (Abba and Cassini, 2008; Poljak et al., 2010; Abba et al., 2014b), the non-response to weather conditions supports the prediction that climate has the minimal influence on the presence of *C. villosus*. The negative influence of solar radiation on its aboveground presence suggests a tendency to nocturnal habits, as occurs in other populations (Abba and Cassini, 2008).

Environmental temperature was the most relevant daily condition for *Z. pichiy*, with a positive influence on its aboveground presence and body temperature. Low humidity and high pressure were also favorable conditions for aboveground activity, supporting its predicted association to arid and semiarid climate (Superina and Abba, 2014b). As predicted, *Z. pichiy* was predominantly diurnal, with a higher probability of aboveground presence at twilight and night in summer. Nocturnal activity in *Z. pichiy* was also observed in captivity (Superina and Abba, 2014b and references therein). Other sources of heat such as soil temperature could also influence the aboveground presence of *Z. pichiy*. In fact, thermal inertia of sandy soils tends to accumulate solar energy during the day and lose heat during the night (Buchan, 1991). Thermal benefits of sandy soils in the central Monte could allow *Z. pichiy* a nocturnal access to feeding resources.

Among these armadillo species, *Z. pichiy* presented the broadest range of body temperatures, which were positively associated with environmental temperature but independent of body mass, as expected for small armadillos (McNab, 1985).

Resource partitioning among the armadillo species

Aboveground presence of each species responded distinctively both to weather conditions and the range-use of shared conditions, supporting the hypothesis of resource partitioning among related species in sympatry through temporal segregation. The relevance of solar radiation, with *C. villosus* and *C. vellerosus* being more nocturnal than *Z. pichiy*, suggests a temporal partition of activity patterns associated to the thermal requirements of each species. Diurnal activities in *Z. pichiy* could be ascribed with thermal benefits of radiation, given the relevance of external temperatures for the aboveground presence of this species.

Responses of armadillo species to atmospheric conditions could be associated to their respective biogeographic origins. The high number of individuals of *Z. pichiy* in the central Monte and its strong response to dry and clear days are ascribed to the association of this species with arid conditions. Indeed, *Z. pichiy* was found in fossil records associated with arid pulses at least since the Holocene (Vizcaíno et al., 1995 and references therein), and it has several adaptations to cold and dry habitats (Superina and Abba, 2014b). The ecological flexibility of *C. villosus* is reflected in its current wide geographic range and variable daily activity periods across regions and seasons (Abba et al., 2014b; Poljak et al., 2010; Abba and Cassini, 2008). This flexible daily cycle of *C. villosus* activity would facilitate its coexistence with *Z. pichiy*, the most diurnal species.

Our hypotheses were based on previous knowledge about these species, aiming to test them under the particular conditions of the harsh environment these closely related species share in the central Monte. Extreme conditions generally influence ecological responses, and generalist species usually change their activities in order to avoid interspecific competition. Our results support these assertions, particularly for *Z. pichiy*. Further studies are needed to reinforce our preliminary findings on *Chaetophractus* spp. in order to evaluate their population tendencies and to guide management actions for the local conservation of both species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.mambio.2017.11.008.

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