



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



GfÖ

GfÖ Ecological Society of Germany,  
Austria and Switzerland

Basic and Applied Ecology 14 (2013) 320–328

Basic and  
Applied Ecology

www.elsevier.com/locate/baae

## Multi-scale patterns of habitat use by wild boar in the Monte Desert of Argentina

M. Fernanda Cuevas<sup>a,b,\*</sup>, Ricardo A. Ojeda<sup>a</sup>, Fabian M. Jaksic<sup>b</sup>

<sup>a</sup>Grupo de Investigaciones de la Biodiversidad, IADIZA, CCT CONICET, CC 507, 5500 Mendoza, Argentina

<sup>b</sup>Center for Advanced Studies in Ecology and Biodiversity (CASEB), Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Received 21 September 2012; accepted 26 March 2013  
Available online 3 May 2013

### Abstract

A large number of protected areas worldwide have been impacted by biological invasions, threatening the biodiversity they aim to protect. The wild boar (*Sus scrofa*) is one of the most threatening invasive species in Argentina, already occupying many ecoregions, including the central Monte Desert. However, there are no studies regarding the use that wild boars make of this invaded biome and what factors (climate or landscape) determine or contribute to the establishment of this species. The objectives of this study were to assess habitat use of the wild boar at spatial and temporal scales in the central Monte Desert, and to assess if climatic factors influence its abundance. Our results show that, at habitat-level the wild boar exhibited preferences for a particular habitat (*Larrea* shrubland) for feeding. At microhabitat-level, we found a positive association between herb cover and wild boar presence. In addition, we found a strong and positive association between the number of days with low temperatures and the number of wild boar signs registered. Therefore, we consider that in the central Monte Desert, habitat selection by wild boars is most likely determined by a maximization of food intake and a minimization of exposure to high temperature.

### Zusammenfassung

Eine große Anzahl der weltweit geschützten Gebiete wurden durch biologische Invasionen beeinflusst, welche die Biodiversität bedrohen, die geschützt werden soll. Das Wildschwein (*Sus scrofa*) gehört zu den bedrohlichsten invasiven Arten in Argentinien und besetzt bereits viele Ökoregionen einschließlich der zentralen Montewüste. Dennoch gibt es keine Untersuchungen in Bezug auf die Nutzung dieses Bioms durch die Wildschweine und zu den Faktoren (Klima oder Landschaft), welche die Besiedlung bestimmen oder einen Beitrag dazu liefern. Ziel dieser Untersuchung war es abzuschätzen, wie die Wildschweine das Habitat in der zentralen Montewüste auf räumlichen und zeitlichen Skalen nutzen und ob klimatische Faktoren die Abundanz beeinflussen. Unsere Ergebnisse zeigen, dass die Wildschweine für die Nahrungsaufnahme auf der Habitatebene eine Präferenz für ein bestimmtes Habitat (*Larrea*-Buschland) zeigen. Auf der Mikrohabitatebene fanden wir eine positive Beziehung zwischen

\*Corresponding author at: Grupo de Investigaciones de la Biodiversidad, IADIZA, CCT CONICET, CC 507, 5500 Mendoza, Argentina.  
Tel.: +54 261 5244168; fax: +54 261 5244001.

E-mail address: fcuevas@mendoza-conicet.gob.ar (M. Fernanda Cuevas).

dem Deckungsgrad der Krautschicht und der Anwesenheit von Wildschweinen. Zusätzlich fanden wir eine starke, positive Beziehung zwischen der Anzahl der Tage mit niedrigen Temperaturen und den registrierten Spuren von Wildschweinen. Daher vermuten wir, dass die Habitatselektion der Wildschweine am ehesten durch eine Maximierung der Nahrungsaufnahme und eine Minimierung der Hitzeexposition gekennzeichnet ist.

© 2013 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

**Keywords:** *Sus scrofa*; Arid lands; Ecology; Spatial use

## Introduction

Biological invasions are considered one of the main threats to natural ecosystems (Vitousek, D'antonio, Loope, Rejmanek, & Westbrooks 1997). A primary focus of invasion biology is assessing the impact of exotics on native species, communities and ecosystems (Williamson 1996). The wild boar (*Sus scrofa*) has been considered as one of the “worst” invaders, and several factors have been identified as affecting the abundance and distribution of this species, including climatic and ecological factors, human activities, and topography (Jedrzejewska, Jedrzejewski, Bunevich, Milkowski, & Krasinski 1997; Acevedo, Escudero, Muñoz, & Gortázar 2006). For example, in Italy hunting pressure affects the spatial behaviour of this species by modifying the location of resting sites (Scillitani, Monaco, & Toso 2009). In western Spain, rainfall influences the breeding biology of wild boars, where the number of pregnant sows increases in rainy years (Fernández-Llario & Mateos-Quesada 2005). In northeastern Spain, wild boar abundance was higher at higher altitudes (Acevedo et al. 2006). Further, heterogeneous landscapes may favour higher densities. This could be because these landscapes have a greater diversity of food resources and higher availability of refuges than homogenous landscapes (Fernández-Llario 2004; Acevedo et al. 2006).

Because wild boars lack sweat glands, patterns of habitat use in arid lands are led by the physiological need for free water and by a behavioural response to increased environmental temperature (Dexter 2003). The wild boar satisfies its water requirements by drinking free water, from metabolic pathways, and from the moisture content of the forage (Baber & Coblenz 1986; Rosell, Fernández-Llario, & Herrero 2001). Thus, this species must rely on behavioural thermoregulation to maintain favourable heat balance in hot environments (Baber & Coblenz 1986). The wild boar modifies its behaviour throughout the seasons, being crepuscular and nocturnal during summer, and crepuscular and diurnal during winter (Barrett 1978; Baber & Coblenz 1986). Moreover, it makes seasonal movements, having a larger home range in low resource seasons than in seasons with high resource availability (Singer, Otto, Tipton, & Hable 1981; Bertolotto 2010; Hayes, Riffell, Minnis, & Holder 2009). The quality of their habitat is related to the availability of free water, food abundance and vegetation cover (Barrett 1982). During high-temperature seasons, wild boars are associated with sites closer to water resources and higher vegetation cover. During the wet season, wild boars show

preference for places with a larger abundance of forbs and annual grasses. Furthermore, in winter the dependence on free water decreases and therefore the availability of food becomes more important (Barrett 1982; Baber & Coblenz 1986).

The wild boar was introduced to Argentina in 1906 for hunting purposes (Daciuk 1978), and at present it occupies a broad range of habitats, from the Patagonian forests and humid pampas to arid and semiarid regions. The negative effects of wild boar as an invasive species and ecosystem engineer are well known around the world, not only because of the damage inflicted on agricultural crops (Seward, Vercauteren, Witmer, & Engeman 2004; Wilson 2004), but also for the damage caused to the native biota (Bratton 1975; Arrington, Toth, & Koebel 1999; Tierney & Cushman 2006). Studies from Argentina show that in northern Patagonia the wild boar causes a reduction in seed survival and seedling regeneration of the native conifer *Araucaria araucana* (Sanguinetti & Kitzberger 2010). In the Monte Desert, its rooting behaviour significantly reduces plant cover of herbs, perennial grasses and shrubs, and decreases plant richness and diversity (Cuevas, Mastrantonio, Ojeda, & Jaksic 2012). Furthermore, disturbed soils showed less compaction, more moisture, a lower C/N ratio, and higher content of mineral nitrogen than undisturbed soils, thus generating an increase in soil degradation by wind erosion (Cuevas et al. 2012).

Understanding habitat preferences and patterns of habitat use by invasive species can be critical when making management and conservation decisions (Simberloff, Parker, & Windle 2005). In Argentina, regarding habitat use by wild boar, a previous study in Patagonia showed that they used low elevations and forests of *Nothofagus dombeyi* and *N. antarctica* (Schiaffini & Vila 2012). But there are no studies regarding habitat use and what factors (climatic or landscape) determine or contribute to the presence or sustainability of this species in arid lands such as the Monte Desert. Based on published records, it could be expected that the presence of wild boar is associated with the proximity of free water and high availability of herbs (the main food type in its diet), and that its activity (measured as number of wild boar signs) be lower during the wet season (higher food resource) than in the dry season. The objectives of this study were: (1) to assess habitat use of wild boar at spatial and temporal scales, specifically, whether there are any differences among habitat types, vegetation structure, and seasons, and (2) to assess whether climate factors influence wild boar activity.

## Material and methods

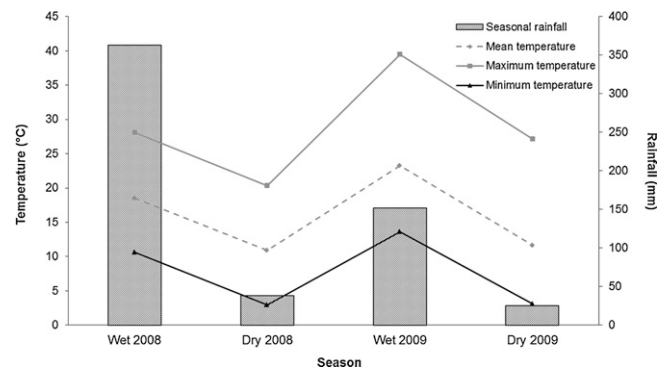
### Study area

Our study was conducted in the Man and Biosphere Reserve of Ñacuñán (34°02' S, 67°58' W; 13,200 ha), located in the central Monte Desert, Argentina. The landscape is characterized by a heterogeneous mosaic of vegetation patches. Dominant habitats are *Prosopis* woodland, *Larrea* shrubland, and sand dunes, which represent 69%, 24% and 7% of the Reserve, respectively (Roig & Rossi 2001).

The climate is semiarid and strongly seasonal, with hot wet summers and cold dry winters. Mean annual precipitation is 326 mm. Mean annual temperature is 15.6 °C, with a maximum annual mean of 23.8 °C and a minimum annual mean of 7.6 °C. The wet season goes from November to April and the dry season spans from May to October (Labraga & Villalba 2009). Precipitation and temperature data for the study period are shown in Fig. 1.

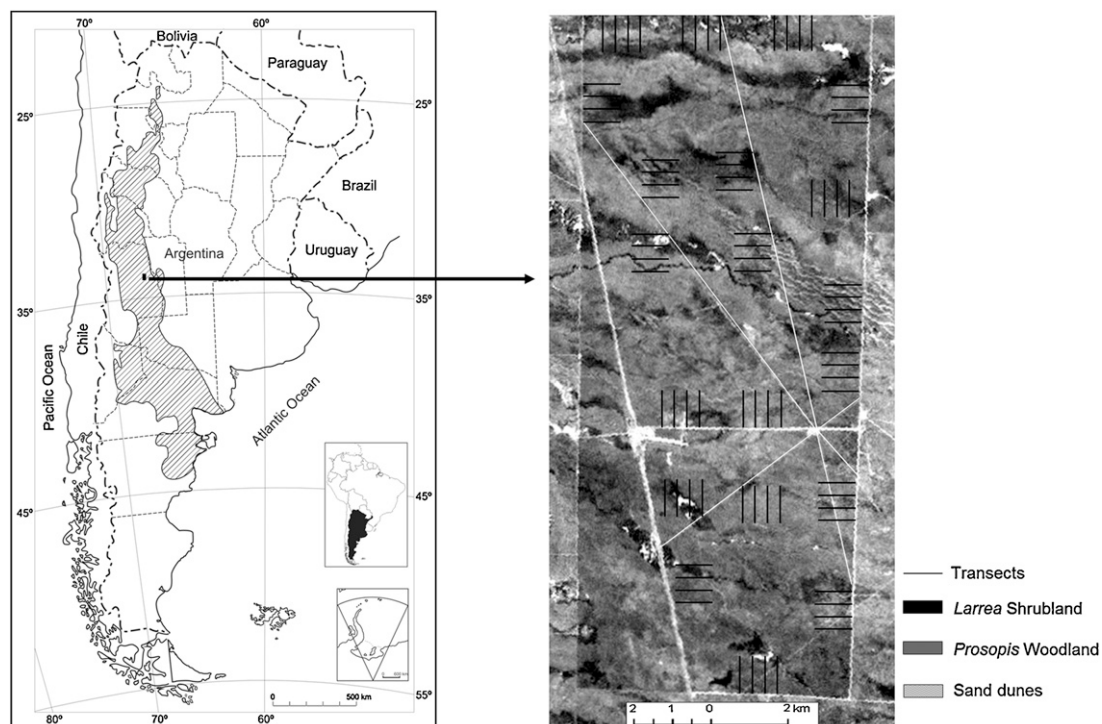
### Sampling design

Sampling was conducted twice a year (wet and dry season) during 2008 and 2009 to determine habitat use through wild boar signs. We established 20 large plots (1 km<sup>2</sup>) within the study area (7 km × 17.5 km), covering all habitat types. Due to the spatial heterogeneity of habitats, one large plot could



**Fig. 1.** Maximum, mean and minimum temperature, and seasonal rainfall, during the 2-year period of study (2008 and 2009) in the MaB Reserve of Ñacuñán.

contain one, two or three habitat types. These large plots were systematically established considering the logistics of access to the different transects (at least the first transect); the minimum distance between these large plots was 1 km. At each large plot we set up four 1-km linear transects and fresh (new) wild boar signs (tracks, nests, faeces and rooting) were recorded within 2.5 m on either side of each transect (Fig. 2). When a sign was encountered, a small plot (square shape; 50 m<sup>2</sup>) was set up. Along the same transects, we established small plots where wild boar signs were absent. We chose the location of non-used plots through the random selection of the distance travelled from the beginning of the transect



**Fig. 2.** Map of Argentina showing the Monte Desert biome (hatched area). Satellite image (LANDSAT 5 TM, spatial resolution 30 m) showing the inner and perimeter roads (white lines) and the location of transects (black lines) at three available habitats in the MaB Reserve of Ñacuñán.



or from the last established plot. This travelled distance was different at each transect in each sampling season. The establishment of these non-used plots took into account used plots and considered the minimum distance among plots. All small plots were placed a minimum of 250 m apart from each other (Abaigar, del Barro, & Vericad 1994). At each small plot (used and non-used plots), plant species composition and plant cover were recorded using a modified point-quadrat method with two transects of 10 m length (Passera, Dalmasso, & Borsetto 1983). The following environmental variables were assessed: percentage cover of herbs, grasses, sub-shrubs (shrubs <100 cm tall), shrubs (>100 cm tall), trees, total cover, litter, bare soil and type of habitat. Anthropogenic variables were also recorded at each small plot, including distance to nearest water source, nearest human habitation, and nearest road. These variables were measured using ArcGis Explorer software. All transects were surveyed once a season and none of the small plots were resampled more than once because the establishment of these small plots depended on the presence of wild boar signs found at each sampling season. During the entire period of study we measured 673 small plots (used and non-used plots) where the three habitats were well represented in each season because the percentage of each habitat ranged from 60 to 70% for *Prosopis* woodland, 20 to 30% for *Larrea* shrubland, and 7 to 10% for sand dunes, compared with the habitat proportions in the Reserve (see description of study area). We performed different analyses separately for each season and year (wet season 2008, dry season 2008, wet season 2009, and dry season 2009), firstly to quantify patterns of habitat selection of wild boars in the study area, and secondly because there were differences in climatic conditions between the two study years (Fig. 1).

## Statistical analyses

### Habitat characterization

The habitat types were characterized using Principal Component Analyses (PCA) with vegetation data obtained from all small plots. The following variables were used for the analyses: percentage of bare soil, litter, herbs, grasses, sub-shrubs, shrubs, and trees. This allowed us to examine which variables best explained the differences in structure among the three habitats found in the study area.

### Habitat use

To detect differences of wild boar signs between wet and dry seasons we applied a Mann–Whitney test. We analyzed habitat use at two different spatial levels: a habitat-level that considered the three main habitats (*Prosopis* woodland, *Larrea* shrubland, and sand dunes), and a microhabitat-level where environmental and anthropogenic variables measured at each selected small plot were considered. Habitat

availability was calculated as the proportion of small plots belonging to each of the three major vegetation communities present in the study area (Finlayson et al. 2008).

Wild boar behaviour at habitat-level was measured through two types of signs, rooting and tracks. We considered that rooting indicated that wild boar used the place as a feeding site, while tracks indicated that the habitat was used for moving from one place to another (displacement). To detect patterns of habitat use at this level, we used Chi-squared goodness of fit test to determine whether there was a significant difference between the observed frequency of small plots with signs and the expected use of the different habitat types. Expected frequencies were calculated taking into account the spatial availability of each habitat type. When significant differences were found, we applied Bonferroni confidence intervals for each frequency of occurrence of each type of wild boar sign in each habitat (Broomhall, Mills, & du Toit 2003; Liu et al. 2005). This analysis allowed us to determine which type of habitat was selected or not selected (i.e., the use was proportional or not to what was available) by the wild boar. If the expected proportion lay outside the interval, we concluded that the expected and actual use were significantly different and thus allowed us to determine preference by the species (if the proportion of usage was greater than expected) or avoidance (if the proportion of usage was lower than expected) (Neu, Randall Byers, & Peek 1974; López-Cortés, Cortés, Miranda, & Rau 2007).

To detect patterns of habitat use at microhabitat-level, we applied multiple logistic regressions through a Generalized Linear Model (GLM). First, we built one model including the two years of study to detect the year and season effects, and then we built one model for each sampling season (wet season 2008, dry season 2008, wet season 2009, and dry season 2009) to detect patterns of habitat selection of wild boars. We used R 2.15.0 software (R Development Core Team, 2012) with packages MASS (Venables & Ripley 2002), ncf (Bjørnstad 2009) and spdep (Bivand 2012). The response variable was presence/absence of wild boar signs and the explanatory variables were environmental and anthropogenic variables measured in selected plots. We used a binomial error distribution and a logistic link function (Crawley 1993). As the response variable at any one small plot could reflect response values at surrounding small plots, we included in the models the spatial autocorrelation. When violations of independence do occur, alternative models that account for dependence in the residuals should be used (Keitt, Bjørnstad, Dixon, & Citron-Pousty 2002). This is achieved through the extension of generalized linear models by adding a distance-weighted function of neighbouring response values to the model's explanatory variables. This extra parameter is known as the autocovariate (Autocovariate model) (Dormman et al. 2007). To do that we first applied a GLM for binomial data. Then we calculated the spatial autocorrelation (Moran's I) for the residuals model, and finally we used this new autocovariate in a new generalized linear model.

## Influence of climatic factors

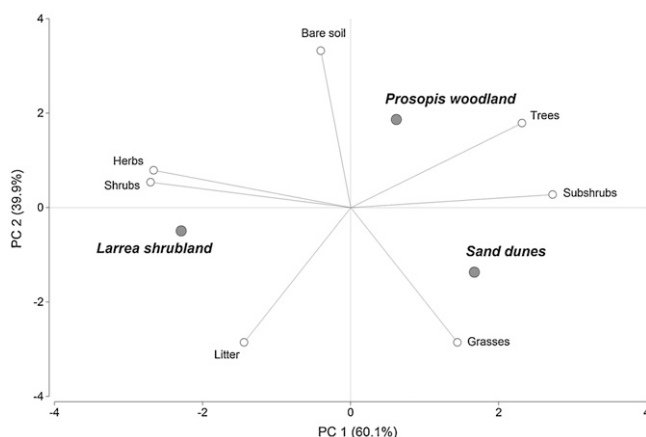
To determine which climate variables could be related to the abundance of wild boar signs in each sampling season, we applied a GLM using as response variable the number of signs found in each season. The explanatory variables were precipitation of sampling season, precipitation of the previous season, number of days with rain, mean temperature, maximum mean temperature, minimum mean temperature, and number of days with temperatures lower than 10 °C (Porter & Gates 1969; Acevedo et al. 2006). We used a Poisson error distribution and a logarithmic link function (Crawley 1993).

For habitat selection and for the influence of climatic factors models, several models were contrasted considering all combinations of the predictors; the null model (model including only the constant) was included. Akaike's Information Criterion, corrected for small sample size (AICc), was used as a measure of the fit of a model. Model comparison was based on the differences in AICc values ( $\Delta\text{AICc}$ ), so when  $\Delta\text{AICc}$  values were greater than two units, the model with the lowest AICc could be considered as a statistically better description of the process that generated the data. We also calculated normalized Akaike weights ( $w_i$ ) for each model, this value being interpreted as the probability of that model is the best one among the models valuated (Burnham & Anderson 2004).

## Results

### Habitat characterization

The PCA of habitat structure extracted two components accounting for 100% of variation (Fig. 3). PC1 represents 60.1% of the total variation, with PC2 having the remaining 39.9%. PC1 was positively associated with sub-shrubs and trees and negatively associated with herbs and shrubs. PC2



**Fig. 3.** Biplot of habitat and vegetation variables resulting from a principal component analysis (PCA) in the MaB Reserve of Nacuñán.

was positively associated with bare soil and negatively associated with litter and grasses. This analysis showed that *Larrea* shrubland was characterized by the presence of herbs, shrubs and litter, *Prosopis* woodland was associated with bare soil and trees, and sand dunes with sub-shrubs and grasses.

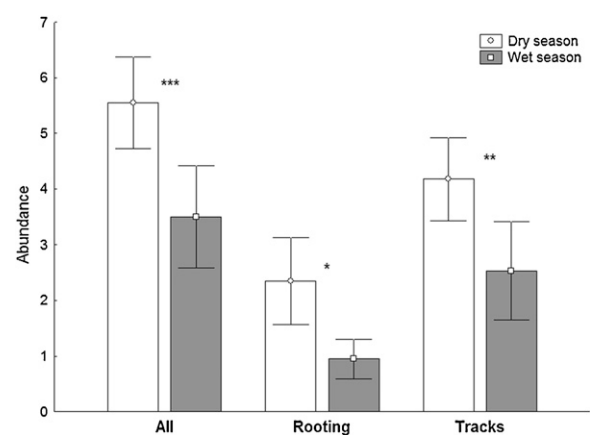
### Habitat use

The abundance of wild boar signs (all, rooting and tracks) was significantly higher during the dry than the wet seasons (Fig. 4).

At the habitat-level, the observed frequency of rooting signs was significantly different from expected use of the three habitat types in all seasons and years (wet season 2008:  $\chi^2 = 16.83$ ,  $df = 2$ ,  $p < 0.001$ ,  $n = 27$ ; dry season 2008:  $\chi^2 = 6.51$ ,  $df = 2$ ,  $p = 0.012$ ,  $n = 35$ ; wet season 2009:  $\chi^2 = 11.18$ ,  $df = 2$ ,  $p = 0.004$ ,  $n = 11$ ; dry season 2009:  $\chi^2 = 7.89$ ,  $df = 2$ ,  $p = 0.019$ ,  $n = 19$ ; Table 1). Bonferroni confidence intervals showed that *Larrea* shrubland was used more than expected by chance during the entire study period, indicating that wild boars prefer this habitat for rooting. *Prosopis* woodland was used less than expected by chance only during wet season 2008 and dry season 2009, which means that wild boars avoided this habitat for feeding (Table 1).

Regarding tracks we did not find any difference between frequencies of tracks in the different habitats during both seasons and years of study (wet season 2008:  $\chi^2 = 1.81$ ,  $df = 2$ ,  $p = 0.4$ ,  $n = 42$ ; dry season 2008:  $\chi^2 = 5.12$ ,  $df = 2$ ,  $p = 0.08$ ,  $n = 63$ ; wet season 2009:  $\chi^2 = 0.85$ ,  $df = 2$ ,  $p = 0.65$ ,  $n = 59$ ; dry season 2009:  $\chi^2 = 2.01$ ,  $df = 2$ ,  $p = 0.37$ ,  $n = 104$ ), which means that for displacement wild boars used the three available habitats proportionally.

At the microhabitat-level, autocovariate models based on  $\Delta\text{AICc}$  and  $w_i$  revealed that there was a positive and significant effect of year (2009), dry season and herb cover on wild boar signs (Table 2). Models for each sampling season showed that herb cover was the most important factor



**Fig. 4.** Mean ( $\pm 2\text{SE}$ ) abundance of wild boar signs (all, rooting, tracks) for wet and dry seasons (combined from 2008 and 2009) in the MaB Reserve of Nacuñán. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

**Table 1.** Simultaneous confidence intervals using the Bonferroni approach for wild boar habitat use at the habitat-level based on rooting signs recorded in the MaB Reserve of Ñacuñán during the wet and dry seasons of 2008 and 2009. An asterisk indicates the expected proportions of use that fell outside the confidence interval. The habitat in bold is that preferred by boars.

Season	Category	Expected proportion of use	Observed proportion of use	95% Confidence interval
Wet 2008	<i>Prosopis</i> woodland	0.60	0.33	0.110–0.532*
	<b><i>Larrea</i> shrubland</b>	<b>0.31</b>	<b>0.67</b>	<b>0.426–0.859*</b>
	Sand dunes	0.09	0	
Dry 2008	<i>Prosopis</i> woodland	0.69	0.54	0.342–0.744
	<b><i>Larrea</i> shrubland</b>	<b>0.20</b>	<b>0.40</b>	<b>0.202–0.598*</b>
	Sand dunes	0.11	0.06	(–) 0.037–0.151
Wet 2009	<i>Prosopis</i> woodland	0.70	0.36	0.017–0.712
	<b><i>Larrea</i> shrubland</b>	<b>0.22</b>	<b>0.64</b>	<b>0.289–0.983*</b>
	Sand dunes	0.08	0	
Dry 2009	<i>Prosopis</i> woodland	0.63	0.37	0.104–0.632*
	<b><i>Larrea</i> shrubland</b>	<b>0.29</b>	<b>0.58</b>	<b>0.308–0.850*</b>
	Sand dunes	0.08	0.05	(–) 0.069–0.175

affecting wild boar presence (Table 3). This association was positive and significant in three of four samplings. The cover of shrubs, sub-shrubs, and litter was negatively associated with wild boar signs. During the dry season 2009, the model revealed that a lower cover of grasses and a larger distance to the nearest road were positively associated with wild boar signs. For all models the autocovariate was significant, which means that there was spatial autocorrelation.

### Influence of climatic factors

The GLM constructed based on  $\Delta AICc$  and  $w_i$  showed that the abundance of wild boar signs was positively associated with the number of days with temperature lower than 10 °C. This means that the greater the number of days with such temperatures, the greater the abundance of signs (Table 4).

### Discussion

Previous studies have demonstrated that ecological and climatic factors, human activities, and topography, affect the distribution and abundance of ungulate populations (Jedrzejewska et al. 1997; Fernández-Llario 2004;

Fernández-Llario & Mateos-Quesada 2005; Acevedo et al. 2006; Scillitani et al. 2009). In this 2-year study, habitat use at habitat-level showed that wild boars, based on rooting signs, exhibited a strong preference for *Larrea* shrubland in both dry and wet seasons. Habitat use at microhabitat-level showed a positive association between herb cover and wild boar signs. The model built for the dry season of 2009 differed from other models because that season was the driest during the entire study period; thus, we could not include herb cover because of its low availability in the environment leading to that variable containing many zeroes. Although weather conditions were very different between years (Fig. 1), we still found a positive effect between herb cover and wild boar signs, meaning that wild boars showed a strong association of habitat use at habitat-level for *Larrea* shrubland and at microhabitat-level for herb cover. Indeed, these components are related: *Larrea* shrubland is the habitat associated with high herb cover (as PCA showed). Considering that rooting is the main means of boars to searching food, and that herbaceous plants are their most important food and the only one in wild boar's diet for which positive selection could be demonstrated (Cuevas, Novillo, Campos, Dacar, & Ojeda 2010; Cuevas, Ojeda, Dacar, & Jaksic 2013), we conclude that wild boars prefer *Larrea* shrubland for feeding. On the

**Table 2.** Influence of year, season and environmental and anthropogenic variables on wild boar habitat use at the microhabitat-level using all signs and logistic models during the wet and dry seasons in the MaB Reserve of Ñacuñán.

Model	AICc	$\Delta AICc$	$w_i$	$K$
<b>Yr: 2009<sub>(+)</sub>*** + Se:dry<sub>(+)</sub>*** + Litter<sub>(-)</sub>** + Grasses<sub>(-)</sub> + Herbs<sub>(+)</sub>*** + Sub-shrubs<sub>(-)</sub> + sac<sub>(+)</sub>***</b>	<b>768.28</b>	<b>0</b>	<b>0.542</b>	<b>8</b>
Yr: 2009 + Se:dry + Litter + Herbs + sac	769.97	1.69	0.232	6
Yr: 2009 + Se:dry + Litter + Grasses + Herbs + Sub-shrubs + D.water + D.road + sac	770.49	2.21	0.18	10

Predictor variables are: year (Yr: 2008 and 2009), season (Se: dry and wet), litter, herbs, grasses, sub-shrubs, shrubs, distance to nearest water source (D.water), and distance to nearest human habitation (D.human), distance to nearest road (D.road) and autocovariate (sac).  $K$  is the number of estimated parameters. Models are ordered by  $\Delta AICc$ ; only models with  $\Delta AICc \leq 3$  are shown. For the selected model (in bold), positive association for a given variable is indicated by (+), negative by (–). \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

**Table 3.** Habitat selection at the microhabitat-level using wild boar signs (All) and logistic regression models during the wet and dry seasons in the MaB Reserve of Ñacuñán.

Season		Model	AICc	$\Delta$ AICc	wi	K
Wet	2008	Herbs <sub>(+)</sub> <sup>**</sup> + Shrubs <sub>(-)</sub> + sac <sub>(+)</sub> <sup>***</sup>	190.82	0	0.450	4
		Litter + Herbs + Shrubs + sac	191.65	0.83	0.297	5
		Herbs + sac	192.24	1.42	0.181	3
		Litter + Herbs + Shrubs + D.human + D.road + sac	193.07	2.25	0.146	6
		Litter <sub>(-)</sub> <sup>*</sup> + Herbs <sub>(+)</sub> <sup>**</sup> + Sub-shrubs <sub>(-)</sub> + sac <sub>(+)</sub> <sup>***</sup>	146.78	0	0.414	4
Dry	2009	Litter + Herbs + sac	147.24	0.46	0.329	5
		Litter + Herbs + Sub-shrubs + D.human + sac	148.61	1.83	0.166	6
		Litter <sub>(-)</sub> + Herbs <sub>(+)</sub> <sup>*</sup> + Sub-shrubs <sub>(-)</sub> <sup>*</sup> + sac <sub>(+)</sub> <sup>***</sup>	188.72	0	0.319	5
		Herbs + Sub-shrubs + sac	189.35	0.63	0.233	4
		Litter + Grasses + Herbs + Sub-shrubs + sac	189.29	0.57	0.240	6
	2008	Litter + Grasses + Herbs + Sub-shrubs + D.water + sac	190.57	1.85	0.127	7
		Grasses <sub>(-)</sub> + D.road <sub>(+)</sub> + sac <sub>(+)</sub> <sup>***</sup>	178.36	0	0.273	4
		Litter + D.road + sac	179.1	0.74	0.188	4
		Litter + Grasses + D.road + sac	179.37	1.01	0.164	5
		D.road + sac	179.42	1.06	0.161	3
		Litter + Grasses + D.human + D.road + sac	180.76	2.4	0.082	6
		Litter + D.human + D.road + sac	180.8	2.44	0.081	5

Predictor variables are: litter, herbs, grasses, sub-shrubs, shrubs, distance to nearest water source (D.water), and distance to nearest human habitation (D.human), distance to nearest road (D.road) and autocovariate (sac). *K* is the number of estimated parameters. Models are ordered by  $\Delta$ AICc; only models with  $\Delta$ AICc  $\leq$  3 are shown. For the selected model (in bold), positive association for a given variable is indicated by (+), negative by (-). \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

other hand, based on tracks, we did not find habitat selection throughout the study period. This suggests that wild boars use – for moving from one place to another – the three habitat types in proportion to their availability.

Taking into account our sampling design we cannot confirm the avoided habitats. This is because although these sites were not used during the sampling period, it does not necessarily mean they have not been used prior to our study. Because we know that rooting remains in the soil at least 4 years, we can confirm that our non-used plots were really so. But that our results are accurate only for the period of study.

Several works have described selection by wild boars at the habitat level (Baber & Coblenz 1986; Barrett 1982; Abaigar et al. 1994; Boitani, Mattei, Nonis, & Corsi 1994; Honda 2009; Schiaffini & Vila 2012). Such selection includes mainly forests and grasslands. Although these studies have not evaluated selection at the microhabitat-level, the presence of wild boars in some places has been related to the availability of food and shelter. Bertolotto (2010) evaluated habitat use by wild boars and found that they preferred forests at the habitat level, but did not find a selection at the microhabitat-level. Abaigar et al. (1994) found a positive selection for forests at a habitat level using tracks, but did not find a pattern of habitat use from rooting.

On the other hand, our climatic model was built with only one variable: “number of days with temperature less than 10 °C”. This means that there is a positive and significant association between the number of days with low temperature and the number of wild boar signs registered in the reserve. As we mentioned above, temperature and availability of free water are two important factors for wild boar population

distribution and abundance. The association between wild boar abundance and temperature has been described by other authors (Jedrzejewska et al. 1997; Dexter 1998; Geisser & Reyer 2005; Acevedo et al. 2006; Honda 2009). In several cases, when the temperature is high wild boars are restricted to areas with dense vegetation cover and close to water resources (Dexter 1998; Acevedo et al. 2006). In our study, we did not find a strong association with free water as reported by other authors (Baber & Coblenz 1986; Barrett 1978; Abaigar et al. 1994; Dexter 1998, 2003). But the activity and/or daily movements of wild boars in periods or seasons of high temperature were indeed reduced. This could be observed in the wet season, where the number of signs was lower than in the dry season. Temperature could be a limiting factor in wild boar activity, especially

**Table 4.** Logarithmic regression model using climatic variables for abundance of wild boar signs (All) during both years of study in the MaB Reserve of Ñacuñán.

Model	AICc	$\Delta$ AICc	wi	K
<b><math>T^{\circ} &lt; 10_{(+)}^{***}</math></b>	<b>30.085</b>	<b>0</b>	<b>0.360</b>	<b>2</b>
Number of days with rain + $T^{\circ} < 10$	31.525	1.44	0.175	3
$T^{\circ} < 10 + Pp$	32.055	1.97	0.134	3
Number of days with rain	32.452	2.37	0.110	2

Predictor variables are: precipitation of sampling season (Pp), number of days with rain, maximum mean temperature ( $T^{\circ}$ max), and number of days with temperatures lower than 10 °C ( $T^{\circ} < 10$ ). *K* is the number of estimable parameters. Models are ordered by  $\Delta$ AICc, only models with  $\Delta$ AICc  $\leq$  3 are shown. For the selected model (in bold), positive association for a given variable in the model are indicated by (+), negative by (-). \*\*\*  $p < 0.001$ .



in arid lands, because boars lack sweat glands or other cooling physiological mechanisms for maintaining hydric and thermal balance. They require free water, shade, a diet rich in water, and/or a behavioural response to increased environmental temperatures (Rosell et al. 2001; Dexter 2003).

Therefore, we assume that wild boar's behaviour follows optimal foraging theory, where high temperature could have a negative effect on boar fitness, influencing habitat preference for foraging by reducing the activity of individuals for thermoregulation and hence of foraging to reduce energy expenditure. This type of behaviour has been reported from arid lands of Australia (Dexter 1998), where Dexter (2003) also found a reduction of body weight in summer. This is in line with Barret's (1978) finding that a 23–27% increase in wild boar weight occurred in California during winter, while Baber and Coblenz (1987) observed that kidney fat indices increased during autumn and winter. Variation in body weight is attributable to two constraints: places where the animal can forage and adaptive physiological response to increased temperature. In both cases, it results in a reduction of activity. However it would be interesting not only to carry out long-term studies and thus ascertain whether this ecological strategy endures over time, but also to increase the scale of the study area for a better understanding of wild boar habitat use on Monte Desert biome.

In conclusion, in arid lands such as the Monte Desert, where water is scarce and the exposure to high temperature is high, shade could be essential for the survival of this invasive species. Therefore, habitat selection by wild boars in arid lands could be determined by the maximization of food intake and the minimization of exposure to high temperatures. Considering the ecological strategies of wild boars in this environment and their impact (Cuevas et al. 2012), it is necessary to design a management strategy for this invasive species in Argentina.

## Acknowledgments

Special thanks to Carlos Cabrera and the long list of assistants who helped us with the fieldwork. To Soledad Albanese, Agustina Novillo and Veronica Chillo for their comments, and to Eugenia Periago for assisting in the English version of the manuscript. This project was part of the EU-funded research project ALARM (Settele et al. 2005) to develop and test methods and protocols for the assessment of large-scale environmental risks. Partially funded by CONICET (PIP 5944), SECYT (PICT 11768), Argentina, and FONDECYT-FONDAP 1501-0001, Chile.

## References

Abaigar, T., del Barro, G., & Vericad, J. R. (1994). Habitat preference of wild boar (*Sus scrofa* L., 1758) in a mediterranean

- environment. Indirect evaluation by signs. *Mammalia*, 58, 201–210.
- Acevedo, P., Escudero, M. A., Muñoz, R., & Gortázar, C. (2006). Factors affecting Wild Boar abundance across an environmental gradient in Spain. *Acta Theriologica*, 51(3), 327–436.
- Arrington, D. A., Toth, L. A., & Koebel, J. W., Jr. (1999). Effects of rooting by Feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage. *Wetlands*, 9, 535–544.
- Baber, D. W., & Coblenz, B. E. (1986). Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. *Journal of Mammalogy*, 67(3), 512–525.
- Baber, D. W., & Coblenz, B. E. (1987). Diet, nutrition, and conception in feral pigs on Santa Catalina Island. *Journal of Wildlife Management*, 51(2), 306–317.
- Barrett, R. H. (1978). The feral hogs on the dye creek ranch, California. *Hilgardia*, 46(9), 281–346.
- Barrett, R. H. (1982). Habitat preferences of feral hogs, deer, and cattle on a Sierra Foothill Range. *Journal of Range Management*, 35(3), 342–346.
- Bertolotto, E. (2010). Behavioural ecology of Wild Boar (*Sus scrofa*) in an Apennine environment, PhD thesis. Italy: Univerisdad de Sassari.
- Bivand, R. (2012). *SPDEP: Spatial dependence: weighting schemes, statistics and models*. R package version 0.5-45. <http://CRAN.R-project.org/package=spdep>
- Bjørnstad, O. N. (2009). *NCF: spatial nonparametric covariance functions*. R package version 1.1-3. <http://CRAN.R-project.org/package=nfc>
- Boitani, L., Mattei, L., Nonis, D., & Corsi, F. (1994). Spatial and activity patterns of Wild boars in Tuscany, Italy. *Journal of Mammalogy*, 75(3), 600–612.
- Bratton, S. P. (1975). The effect of the European wild boar, *Sus scrofa*, on Gray Beech Forest in the Great Smoky Mountains. *Ecology*, 56, 1356–1366.
- Broomhall, L. S., Mills, M. G. L., & du Toit, J. T. (2003). Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. *Journal of Zoology (London)*, 261, 119–128.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference. Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261–304.
- Crawley, M. J. (1993). *GLM for ecologists*. Oxford, UK: Blackwell Scientific Publications.
- Cuevas, M. F., Novillo, A., Campos, C., Dacar, M. A., & Ojeda, R. A. (2010). Food habits and impact of rooting behaviour of the invasive Wild boar, *Sus scrofa*, in a protected area of the Monte Desert, Argentina. *Journal of Arid Environment*, 74, 1582–1585.
- Cuevas, M. F., Mastrantonio, L., Ojeda, R. A., & Jaksic, F. M. (2012). Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. *Mammalian Biology*, 77, 299–306.
- Cuevas, M. F., Ojeda, R. A., Dacar, M. A., & Jaksic, F. M. (2013). Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. *Acta Theriologica*, 58, 63–72.
- Daciuk, J. (1978). Estado actual de las especies de mamíferos introducidos en la Subregión Araucana (Rep. Argentina) y grado de coacción ejercido en algunos ecosistemas surcordilleranos. *Anales de Parques Nacionales*, 14, 105–130.

- Dexter, N. (1998). The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. *Wildlife Research*, 25, 547–549.
- Dexter, N. (2003). The influence of pasture distribution, and temperature on adult body weight of feral pigs in a semi-arid environment. *Wildlife Research*, 30, 75–79.
- Dormman, C. F., McPherson, J. M., Araujo, M. B., Bivand, R., Bolliger, J., Carl, G., et al. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30, 609–628.
- Fernández-Llario, P. (2004). Environmental correlates of nest site selection by wild boar *Sus scrofa*. *Acta Theriologica*, 49, 383–392.
- Fernández-Llario, P., & Mateos-Quesada, P. (2005). Influence of rainfall on the breeding biology of Wild boar (*Sus scrofa*) in a Mediterranean ecosystem. *Folia Zoologica*, 54, 240–248.
- Finlayson, G. R., Vieira, E. M., Priddel, D., Wheeler, R., Bentley, J., & Dickman, C. R. (2008). Multi-scale patterns of habitat use by re-introduced mammals: A case study using medium-sized marsupials. *Biological Conservation*, 141, 320–331.
- Geisser, H., & Reyer, H. U. (2005). The influence of food and temperature on population density of Wild boar *Sus scrofa* in the Thurgau (Switzerland). *Journal of Zoology (London)*, 267, 89–96.
- Hayes, R., Riffell, S., Minnis, R., & Holder, B. (2009). Survival and habitat use of feral hogs in Mississippi. *Southeastern Naturalist*, 8(3), 411–426.
- Honda, T. (2009). Environmental factors affecting the distribution of the wild boar, sika deer, Asiatic black bear and Japanese macaque in central Japan, with implications for human-wildlife conflict. *Mammalian Study*, 34, 107–116.
- Jedrzejewska, B., Jedrzejewski, W., Bunevich, A. N., Milkowski, L., & Krasinski, Z. A. (1997). Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriologica*, 42(4), 399–451.
- Keitt, T. H., Bjørnstad, O. N., Dixon, P. M., & Citron-Pousty, S. (2002). Accounting for spatial pattern when modeling organism environment interactions. *Ecography*, 25, 616–625.
- Labraga, J. C., & Villalba, R. (2009). Climate in the Monte Desert: Past trends, present conditions and future projections. *Journal of Arid Environment*, 73, 154–163.
- Liu, X., Toxopeus, A. G., Skidmore, A. K., Shao, X., Dang, G., Wang, T., et al. (2005). Giant panda habitat selection in Foping Nature Reserve, China. *Journal of Wildlife Management*, 69, 1623–1632.
- López-Cortés, F., Cortés, A., Miranda, E., & Rau, J. R. (2007). Dietas de *Abrothrix andinus*, *Phyllotis xanthopygus* (Rodentia) y *Lepus europaeus* (Lagomorpha) en un ambiente altoandino de Chile. *Revista Chilena de Historia Natural*, 80, 3–12.
- Neu, C. W., Randall Byers, C., & Peek, J. M. (1974). A technique for analysis of utilization – Availability data. *Journal of Wildlife Management*, 38(3), 541–545.
- Passera, C. B., Dalmasso, A. D., & Borsetto, O. (1983). *Método de Point Quadrat Modificado*. Taller sobre arbustos forrajeros. Mendoza: FAO, IADIZA.
- Porter, W. P., & Gates, D. M. (1969). Thermodynamic equilibria of animals with environment. *Ecological Monographs*, 39(3), 227–244.
- Roig, F. A., & Rossi, B. (2001). Flora y vegetación. In S. Claver, & S. Roig-Juñent (Eds.), *El desierto del Monte: La Reserva de Biosfera de Ñacuñán* (pp. 41–75). Triunfar, Argentina: IADIZA, MAB, UNESCO.
- Rosell, C., Fernández-Llario, P., & Herrero, J. (2001). El Jabalí (*Sus scrofa* Linnaeus, 1758). *Galemys*, 13(2), 1–25.
- Sanguinetti, J., & Kitzberger, T. (2010). Factors controlling seed predation by rodents and non-native *Sus scrofa* in Araucaria araucana forests: Potential effects on seedling establishment. *Biological Invasions*, 12, 689–706.
- Schiaffini, M. I., & Vila, A. R. (2012). Habitat use of the wild boar, *Sus scrofa* Linnaeus 1758, in Los Alerces National Park, Argentina. *Studies on Neotropical Fauna and Environment*, 47(1), 11–17.
- Scillitani, L., Monaco, A., & Toso, S. (2009). Do intensive drive hunts affect wild boar (*Sus scrofa*) spatial behaviour in Italy? Some evidences and management implications. *European Journal of Wildlife Research*, 56(3), 307–318.
- Settle, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M., et al. (2005). ALARM (Assessing Large-scale Environmental Risks for biodiversity with tested Methods). *Gaia*, 14, 69–72.
- Seward, N. W., Vercauteren, K. C., Witmer, G. W., & Engeman, R. M. (2004). Feral swine impacts on agriculture and the environment. *Sheep & Goat Research Journal*, 19, 34–40.
- Simberloff, D., Parker, I., & Windle, P. N. (2005). Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment*, 3(1), 12–20.
- Singer, F. J., Otto, D. K., Tipton, A. R., & Hable, C. P. (1981). Home ranges, movements, and habitat use of European wild boar in Tennessee. *Journal of Wildlife Management*, 45(2), 343–353.
- Tierney, T. A., & Cushman, J. H. (2006). Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a California grassland. *Biological Invasions*, 8, 1073–1089.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. (fourth ed.). New York: Springer.
- Vitousek, P., D'antonio, C., Loope, L., Rejmanek, M., & Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, 21, 1–16.
- Williamson, M. (1996). *Biological invasions*. London, UK: Chapman & Hall.
- Wilson, C. J. (2004). Rooting damage to farmland in Dorset, southern England, caused by feral wild boar *Sus scrofa*. *Mammal Review*, 34, 331–335.