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Factors Affecting Invasive Species Abundance: the Barbary Ground Squirrel on Fuerteventura Island, Spain

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Marta López-Darias and Jorge M. Lobo (2008) Factors affecting invasive species abundance: the Barbary ground squirrel on Fuerteventura Island, Spain. *Zoological Studies* **47**(3): 268-281. We assessed the determinants of habitat selection by the Barbary ground squirrel (*Atlantoxerus getulus*) at Fuerteventura (Canary Is., Spain). We implemented general linear model (GLM) procedures to analyze the relationships between squirrel abundances and 4 kinds of variables related to the biological requirements of the species (environment, food resources, biotic interactions, and refuge/shelter). We performed a variance partitioning analysis between the most explicative categories to explore correlation patterns. The time of year and weather conditions of the census clearly influenced the number of individuals observed. Shelter variables were the best correlates of both the abundance of squirrels and the number of their scat. Although food resources were less important, the presence of certain plant species was correlated with squirrel abundance, while general environmental variables and interactions with other mammals did not affect its distribution. These results improve our understanding of the ecology and the establishment of this highly successful introduced species, providing basic knowledge for use with future management strategies in the Canarian Archipelago.
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Key words: *Atlantoxerus getulus*, Biological invasion, Canary Is., General linear model, Habitat selection.

Much has been written to explain the successful colonization and establishment of marine and terrestrial invasive species. How this colonization and establishment occur is a complicated issue as these processes highly vary among groups. Finding a global theory is difficult since a successful invasion requires a species to pass through different stages, including transport, introduction, and establishment phases (Williamson 1996). Because social and biological mechanisms operating at each stage might differ, the influence of any trait may vary according to the stage at which it is evaluated (Kolar and Lodge 2001, Jeschke and Strayer 2006). Traits affecting the 1st 2 stages (transport and introduction) remain less explored and most likely involve numerous social aspects (see Jeschke and Strayer 2006). However, many features have been described to explain success in the establishment stage. These features can be grouped in 2 main types of factors: i) those related to the attributes of the resident community and ii) those associated with the characteristics of the invader. The attributes of the resident community include species richness, nutrient status, disturbance regime (Crawley 1987, Levine and D'Antonio 1999, Rejmánek 1999, Kneitel and Perrault 2006), competition and facilitation interactions (e.g., Holmgren et al. 1997, Rousset and Lepart 2000), and vegetation structure (e.g., Wiser et al. 1998, Miller et al. 2002). Invader characteristics related to success include the general demographics of the species (e.g.,

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Lodge 1993, Hee et al. 2000), a species' ability to change its behavior or development (e.g., Holway et al. 1998), morphometric or biological attributes (e.g., Rejmanek and Richardson 1996, Lloret et al. 2005, Jeschke and Strayer 2006), the potential for hybridization (Figueroa et al. 2003), any allelopathic advantages against resident species (Callaway and Ridenour 2004), and genetic diversity (Lindholm et al. 2005) or reduction of the invader (Tsutsui et al. 2000). Other hypotheses have been offered to explain the success of an invader species including the enemy-release hypothesis (the invaders are released from the effects of their natural enemies, parasites, pathogens, and predators in the new environment; see Torchin et al. 2003, Colautti et al. 2004) and the evolution of increased competitive ability hypothesis (Blossey and Notzold 1995).

Biologists have traditionally been interested in studying factors related to the distribution and abundance of species. To understand the establishment and colonization success of an invasive species, the relevance of different types of variables must also be determined, which in turn allows the design of appropriate management actions (see Shah 2001, Veitch and Clout 2002, Towns and Broome 2003, Genovesi 2005, Martins et al. 2006). However, the relevance of biological or environmental requirements is generally assessed individually (i.e., the disturbance regime by Levine and D'Antonio 1999 or vegetation structure by Bellingham and Coomes 2003). Herein, we examined the explanatory capacity of a high number of probable influential variables on the local abundance of the African Barbary ground squirrel *Atlantoxerus getulus* (Linnaeus, 1758), which has invaded Fuerteventura I., Canary Is., Spain. The Barbary ground squirrel is an optimal example for exploring mechanisms underlying the success of invaders on islands; this study may also provide essential data for the success of future eradication plans suggested for the Canarian Archipelago (see Group of Experts on Invasive Alien Species 2002). The Barbary ground squirrel, a rodent native to Morocco and Algeria (Aulaugnier and Thévenot 1986, Kingdon 1997), was introduced in 1965 as a pet to Fuerteventura I. (Machado 1979, Machado and Domínguez 1982). Since then, it has successfully colonized the entire island, occupying almost all terrestrial landscapes, partially thanks to human activities that favored its transport and introduction within the island (Machado and Domínguez 1982, pers. data). In spite of having a relatively good knowledge of these processes, we are yet unaware of the factors determining the distribution and abundance of this species. Ecological information from its native range is scarce; the limited data available suggest that the Barbary ground squirrel is found in rocky areas in its African distribution range, including: i) rocky-slope habitats of the Northern Toubkal mountain range, at elevations of 1000-4000 m; ii) *Argania spinosa* forests (Petter and Saint-Girons 1965); and iii) rocky areas of the Sahara Desert (Valverde 1957). A set of presence data is also available for its native range (see López-Darias et al. 2008), although no descriptions of factors affecting its abundance or distribution are provided. A preliminary unpublished study performed on Fuerteventura I. concluded that the squirrel was more abundant in the lower-middle zone of typical U-shaped valleys, and near stone walls and cultivated areas, compared to higher areas of slopes (Machado and Domínguez 1982). However, this elementary and relatively scarce information is insufficient. In this study, we attempt to provide the 1st basic quantitative information on factors influencing the current abundance and distribution of this small invasive mammal on Fuerteventura I.

In addition, we provide an example of how to select and sample areas for exhaustive monitoring of a species' presence and abundance, collecting data to explore relationships of a species' abundance with environmental and biological factors. Processing an exhaustive compilation of field sampling and geographic information system (GIS) variables with generalized linear models (GLMs) and applying variation partitioning techniques, we estimated and compared the relevance of different groups of explanatory variables (environment, food resources, refuge/shelter, and biological interactions) at different scales (landscape, plot, and subplot) to the abundance and distribution of the Barbary ground squirrel on Fuerteventura I. These results provide some understanding of the abundance of this invasive species on Fuerteventura I., and can serve as a foundation for developing future management strategies to mitigate the detrimental effects of this species.

MATERIAL AND METHODS

Study area

Fuerteventura I. is the 2nd largest island (with an area of approximately 1660 km^2), the 2nd lowest in elevation (807 m), and the closest to Africa (around 115 km away) of the highly biodiverse Canarian Archipelago (Médail and Quézel 1999; 27°- 29°N, 13°- 18°W; Fig. 1). The island has an arid climate and semi-desert habitats, with a mean annual temperature of around 20°C (Dorta 2005) and mean annual precipitation of < 100 mm. Fuerteventura is the oldest island in the archipelago (20.4 ± 0.4 Ma; Carracedo et al. 2005, Criado 2005), and high erosion has resulted in an abundance of interior tapering cliffs, usually no more than 600 m in elevation, surrounded by extensive flatlands. Large extensions of biogenic sand, called "jable", and numerous stone walls characterize the landscape (Rodríguez 2005 and references therein). The island flora has been altered by the exploitation of wood resources, intensive livestock grazing, and the introduction of exotic herbivores (Rodríguez 2005). Fuerteventura I. is currently dominated by substitution vegetation, and small patches of native vegetation are relegated to inaccessible or unfavourable areas (Rodriguez 2005). Nevertheless, the island supports a wide variety of endemic floral and faunal species (Izquierdo et al. 2004), and some of the Canary Is. ecosystems are well represented only on this island.

Survey design

Correctly selecting sampling plots to yield a representative sample of environmental and vegetation variability is essential to ensure the reliability of species distribution models (Hortal and Lobo 2005). We conducted a principal component analysis (PCA) to describe environmental variations prior to the selection of sampling plots, using 4 climatic (annual precipitation, mean annual temperature, minimum winter temperature, and maximum summer temperature) and 1 topographic variables (elevation). Environmental variables were extracted from the digital cartography of the Spanish Instituto Nacional de Meteorología (http://www.inm.es/). Only 1 factor presented an eigenvalue exceeding 1 (4.24), which explained 84.75% of the total variability. Factor scores were positively related to annual precipitation and elevation, but negatively related to the 3 temperature variables. First, we established the number of plots (circles with a radius of 100 m) that 1 person could feasibly sample (n = 300). Subsequently, we calculated the number of 100 x 100 m UTM squares (Universal Transverse

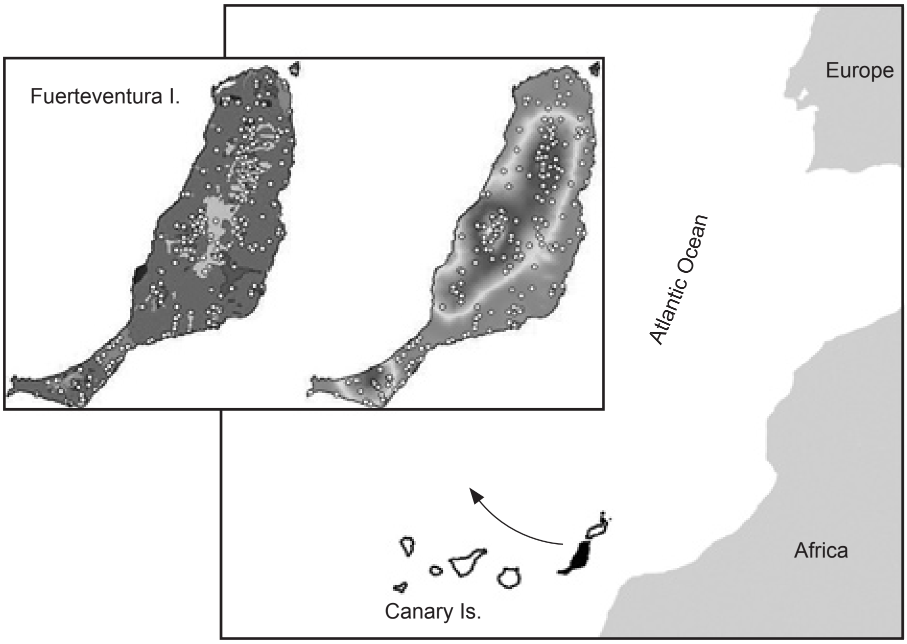

Fig. 1. Geographic location of Fuerteventura Island within the Canarian Archipelago, showing the position relative to the African continent and mainland Iberian Peninsula. On Fuerteventura Island, the locations of sampled plots (dots) within different vegetation types (left; vegetation categories following Ruiz 1980) and across the principal component dimension that covers the climatic and elevational variation on the island are shown (right; blue for lower elevations and mean annual precipitation and red for higher elevations and mean annual precipitation; see text).

Mercator System) for each of the 11 vegetation categories present on the island (Fig. 1; digitalized and adapted following Ruiz 1980). The square root of the area covered by each vegetation category was used to divide the total number of plots (n = 300) among the different categories, in order to devote a proportionally lower sampling effort in the most common vegetation types and obtain data from those rare but representative vegetation categories. The number of sample plots per vegetation category varied from 3 to 121 (mean ± SD; 27 ± 33). Subsequently, the plots were regularly distributed within each vegetation category according to the gradient expressed by the PCA factor, in order to guarantee that all of the climatic and ecosystem diversity of the island was represented (Fig. 1).

Subplot selection and area characterization

As 71 plots were located in urban or highly disturbed areas (Fig. 1), we successfully sampled 229 plots. Each plot was located using a Garmin III Plus global positioning system (GPS). Within each plot, 21 subplots of 2.25 m^2 each separated by a 5 m distance were selected; 4 subplots towards each of the cardinal directions, established with a Suunto compass, and an additional subplot at the central point (Fig. 2). In each subplot, we established a 1.5 x 1.5 m area, laid out perpendicular to the axis of each direction (Fig. 2), within which we measured a number of variables selected to account for previously known biological requirements of the species.

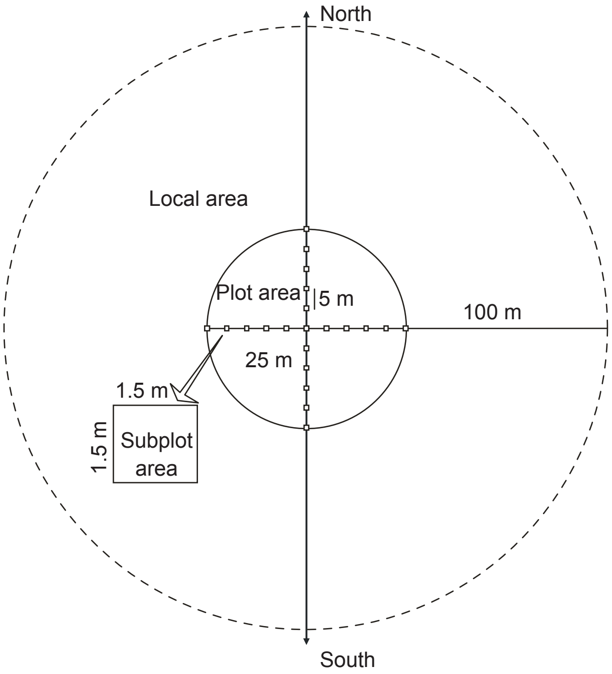

Fig. 2. Schematic representation of the subplot selection method in each plot.

Explanatory variables

We compiled data on 4 types of variables related to the environment, food resources, refuge/shelter, and biological interactions which possibly influence the distribution and abundance of this species. These explanatory variables were measured at 3 different spatial scales: landscape (approx. 1 km^2), plot (10,000 m^2), and subplot (2.25 m^2; see Appendix 1) because relevant factors capable of explaining a biological attribute can act at different scales (Rosenzweig 1995).

Environmental climatic and topographic data were extracted for each plot. The annual average temperature and precipitation data were from the digital cartography of the Spanish Instituto Nacional de Meteorología (http://www.inm.es/) at a 100 x 100 m resolution. We also used the environmental factor previously extracted by the PCA to summarize the environmental characteristics of each plot. The elevation of each plot was estimated from a digital elevation model interpolated from topographic digitized contours at 20 m contour intervals using Idrisi Kilimanjaro software (Clark Labs 2004). The slope and aspect of each plot were also measured using a Suunto compass and a clinometer. As the squirrel abundance could be influenced by the type of vegetation, the main type present in the landscape around each plot from those present on the island (badland, town, jable, stony slope, flat area, abandoned cultivation, cultivation, ravine, or abandoned cultivation terrace) were included as dummy variables (with a value of either 0 or 1).

Food resource variables were extracted at the 3 scales considered. The Barbary ground squirrel is predominantly herbivorous (Machado and Domínguez 1982) and does not use vegetation as shelter. Therefore, we considered plant cover to be a good proxy for food resources. In each subplot, we recorded data on the herbaceous, shrub, and tree cover (percentage of area covered in each subplot), maximum and minimum plant height, and soil type. We also noted dominant plant species (the species occupying a higher percentage of cover in each subplot) and all plant species present in each subplot to assess any potential plant-animal relationships. Snails are also an important protein source for the Barbary ground squirrel (Machado and Domínguez 1982). Thus, we counted the number of live individuals of each snail species present in each subplot. Samples were taken during the dry season when live snails were less abundant, so we also counted the number of dead snail individuals as a measure of the potentiality of the area to support snails. We quantified dominant live and dead snails into 2 categories: large (longest axis > 1.5 cm) and small (< 1.5 cm), to account for the supposed preference of squirrels to feed on larger snails. Additionally, we considered distances to cultivated areas, roads, urban areas, and isolated houses as a measure of food availability, since squirrels take advantage of crops (Machado and Domínguez 1982) and domestic animal food. These variables were included in the analysis as continuous ones (at the plot scale), but also as dummy variables (at the landscape scale) representing the presence or absence of these categories in the landscape around each plot. Last, the dominant vegetation type in the landscape of each plot was included as a dummy variable taking into account the 11 vegetation types recognized on the island (see Ruiz 1980).

Refuge/shelter variables were also measured at the 3 scales and included, because dry walls or stones have been suggested to be essential for the success of the colonization process by this species (Machado and Domínguez 1982, P. Gouat pers. comm.). In each subplot, we recorded the total number, and maximum height and width of stone heaps, as well as the total stone cover (%). Since the larger the stones, the larger the spaces between stones, and the larger the number of potential shelters, we also noted partial stone cover (%) of 4 sizes (< 10, 10-30, 30-50, and > 50 cm in diameter). In addition, we counted the number of stone dry walls in each subplot, also incorporating the occurrence of potential shelter for squirrels as a categorical variable (none, some, few, and many). Soil penetrability in each subplot was also included as a categorical variable (sandy, clay, sandy-clay, jable, rocky, rocky-jable, pyroclastic, pyroclastic-sandy, and cultivated), taking into account the presence of *A. getulus* underground burrows (aside from inside-wall burrows). Furthermore, we also included refuge/shelter variables for each plot using the mean or summed values of subplot measures (see Appendix 1): the number of potential shelters for squirrels, number of stone dry walls, type of stone dry wall (categorical: longer or shorter than 100 m), number of ravines, type of ravine (categorical: small, medium, or large), number of stone heaps, maximum height of stone heaps, and maximum width of stone heaps. At the landscape scale we measured the occurrence of stone heaps (categorical: none, some, few, and many) and the number of abandoned houses.

Last, as explanatory variables capable of explaining the relevance of biological interactions, we counted the number of feral goat/sheep or rabbit scat in each subplot, accounting for a possible association or exclusion of squirrels by the most abundant mammals on the island. Sheep and feral goat scat, which are virtually indistinguishable, were counted together, while fresh scat (more colorful and harder) were recorded separately as a measure of the recent presence of goats/sheep and rabbits.

Ground squirrel census

We carried out a squirrel census in a radius of 200 m around the center of all plots between July and Oct. 2005. After arriving at the census point, the observer remained still for 10 min, which was previously established as the amount of time needed for this squirrel species to reestablish activity. We counted the number of squirrels observed during 2 consecutive 10 min periods, and the total number recorded was the sum of the observations in the 2 periods, with no individual counted twice. Making this count without marking the squirrels was feasible because they tend to stay outside the nest during most of the daytime and also remain still for many minutes, usually on the same rock. We also quantified the number of squirrel scat in each plot as an additional measure of their activity as an indirect measure of squirrel abundance. The landscape of Fuerteventura is mainly flat, and open brush is commonly the main type of vegetation, so squirrel detectability was not dependent on habitats in our case.

Previous authors suggested that this species' diurnal activity is highly dependent on time and weather; they observed that these squirrels never hibernate (Petter and Saint-Girons 1965, Machado and Domínguez 1982). For that reason, in addition to limiting all census efforts to hot sunny days, we measured weather variables at the moment of sampling (average and maximum wind speed, air temperature, and humidity) with a Kestrel 3500 pocket weather meter 5 min before each census.

Statistical methods

We used GLMs to summarize the relationships between the abundance of squirrels or scat and the explanatory variables. GLMs are an extension of classical linear regression models that allow for non-linearity in the data, a range of distributions of independent variables other than a normal distribution, and categorical variables (McCullagh and Nelder 1989). We assumed logarithmic relationships between the dependent and explanatory variables (the link function), and a Poisson error distribution of the dependent variable. As a first step, we regressed the dependent variable (number of observed squirrels in each plot, or the number of squirrel scat against the specific weather conditions at the moment of sampling, as well as against the date and hour. We extracted the residuals of this regression, as we considered that they represented variation in the number of squirrels or scat after eliminating the influence of daily weather conditions. We used these residuals as the dependent variable in subsequent regressions.

Subsequently for both squirrel abundance and scat, we regressed all explanatory variables one by one against these residuals. In order to account for nonlinear relationships between the predictors and the dependent variable, we examined the statistical significance of linear, quadratic, or cubic functions of each continuous variable. This analysis was carried out to estimate only the most relevant variables. Next, we performed backward-stepwise selections on previously identified significant variables ($p < 0.01$) belonging to the same type (environment, food resources, biological interactions, and refuge/shelter). This analysis was carried out to estimate the explanatory capacity of each type of variable. To obtain an estimation of the explanatory capacity of all variables considered, a new backward-stepwise selection procedure was applied to the previously selected variables of each type. As we considered a huge number of variables, our aim was not to find the best model with the most correct parameters, but to obtain a reliable estimate of the relevance of the different types of variables. The percentage of deviance retained by the model (Dobson 1990) was used as an estimate of the percentage of the variation explained. To avoid overparameterization in the models, we only selected statistically significant variables that explained > 2% of the total variability. The residuals of the complete model so obtained were checked for autocorrelations, since 1 or several important spatially structured explanatory variables can be left out if they are spatially autocorrelated (Cliff and Ord 1981, Legendre and Legendre 1998, Keitt et al. 2002).

The explanatory variables used in multiple regression models are often correlated. Although determining causal factors using correlative techniques is always a delicate task (MacNally 2000), correlations can constitute key materials and the basis for more-sophisticated experimental proposals. When interested in forecasting the dependent variable, this collinearity is not a concern because the objective is to maximize the explanatory variability of the model (Legendre and Legendre 1998). Conversely, if we aimed to correctly estimate the regression coefficients (the independent contributions of each explanatory variable on the dependent one), this collinearity would force us to discriminate the pure effect of 1 variable when the effect of the others had been taken into account. Partial regression (Legendre and Legendre 1998) allowed us to measure the amount of variation attributed exclusively to each variable, and the variation that may have indifferently been attributed to a group of explanatory variables. This variation partitioning method was applied to squirrel abundance in order to estimate the unique contributions of environmental, food resource, and refuge/shelter variables, and the percentages of variability accounted for different combinations of these variables (see Borcard et al. 1992 or Lobo et al. 2001). We used the STATISTICA 6.0. package (StatSoft 2001) for all statistical computations.

RESULTS

Influence of prevailing weather variables

Of the sampling variables, only the quadratic function of the date, the quadratic function of air temperature, and the cubic function of average wind speed were selected in the backward-stepwise analysis, accounting for 19.7% of the total deviance in the number of observed squirrels. The number of squirrel excrement, regressed against the date and prevailing weather conditions at the time of sampling, accounted for 11.5% of the total variability. Residuals of these functions were retained and used in subsequent analysis as dependent variables, independent of weather conditions during each plot sampling.

Explaining squirrel excrement

Twenty-five significant variables explained more than 2% of the total variability in excrement number, the most relevant being the presence, number, and characteristics of stone heaps in each plot, and shelter and ravine presence (Table 1). A complete model, including all of these significant variables, explained 45.1% of the total variability. The addition of spatial variables did not improve the model predictions, and the residual autocorrelation was not significant at any lag distance.

Explaining squirrel abundances

Only 3 significant environmental variables accounted for more than 2% of the total deviance (Table 2); landscape type (a dummy variable) explained most of the total deviance (7.5%). Backward selection of all such significant variables explained around 12% of the total variability.

Thirty-eight significant food resource variables accounted for more than 2% of the total variability each, and among these only 13 accounted for more than 4% of the total variability each (Table 2). The dominance and presence of some plant species of the genus *Asparagus*, *Rubia*, *Kleinia*, *Salvia*, or *Matthiola*, individually explained more than 5% of the total variability. The distance to cultivated areas, which was negatively related to squirrel abundance, was the most important among non-plant variables. A complete model including all significant trophic variables accounted for almost 37% of the total variability.

Shelter variables presented the greatest

Table 1. Explanatory variables accounting for more than 2% of the variability in the number of Barbary ground squirrel scat on Fuerteventura I. We noted the deviance of each variable considered alone, as well as the percentage of the deviance explained. The type of significant function and the sign of each term are indicated for continuous variables. All of these variables were statistically significant ($p < 0.001$)

Variable	Function	Sign	Deviance	Percent (%) deviance
Full deviance			12,839.1	
Presence of stone heaps in subplots			10,837.4	15.59
Maximum height of stone heaps	quadratic	+ -	10,933.3	14.84
Number of stone heaps in each locality			11,126.6	13.34
Landscape type			11,225.1	12.57
Presence of shelters in each locality			11,398.3	11.22
Presence of shelters in each plot			11,418.2	11.07
Slope	quadratic	- -	11,460.8	10.73
Width of stone heaps	quadratic	+ -	11,518.3	10.29
Presence of ravines			11,523.8	10.24
Number of stones > 50 cm	cubic	+ - +	11,744.9	8.52
Vegetation type			11,886.6	7.42
Soil type			12,031.5	6.29
Presence of shelters in each subplot			12,036.1	6.25
Number of dry walls in each locality	quadratic	+ -	12,069.8	5.99
Number of dry walls in each plot	quadratic	+ -	12,102.2	5.74
Ravine type			12,175.9	5.16
Stone cover		+ -	12,223.9	4.79
Number of stones 10-30 cm		+ - +	12,257.1	4.53
Number of stones 30-50 cm			12,350.2	3.81
Presence of dry walls			12,381.1	3.57
Herbaceous cover	cubic	+ - +	12,393.0	3.47
Presence of abandoned houses			12,469.6	2.88
Distance to cultivated areas	quadratic	+ -	12,508.4	2.58
Elevation	cubic	- + -	12,545.7	2.28
Presence of stone heaps in each plot			12,571.7	2.08

explanatory capacity. Qualitative variables representing the number of shelters showed a significant relevance (plot shelters accounted for 29.5% of the total deviance). Also, the explanatory capacity of those quantitative variables related to the number, type, and distance to dry walls should be highlighted (Table 2). The complete model from these significant shelter variables explained 40.8% of the total variability.

Last, biological interaction variables were not relevant and accounted for only 5.6% of the total variability of squirrel abundance. The cubic function of fresh rabbit droppings and the quadratic function of the number of fresh rabbit dung were the only significant variables selected by the backward-stepwise method that explained > 2% of the variability (4.4% and 2.4%, respectively).

When all variables previously shown to be

Table 2. Explanatory variables accounting for more than 4% of the variability in Barbary ground squirrel abundance, grouped by the 3 main types of explanatory variables considered (environment, shelter, and food resources). For continuous variables, the type of significant function and the sign of each term are indicated. For qualitative variables, the results of a univariate ANOVA are presented. All of these continuous variables were statistically significant ($p < 0.001$). The percentage of deviance accounted for by each variable and by a backward-stepwise procedure carried out on all variables of the same type (backward-selected model) are also included. * and *** indicate levels of significance of < 0.05 and < 0.001, respectively, by *F*-test

	Variable	Percent (%) explained deviance	Type of function	Sign	
Environment	Landscape type	7.49			$F_{(8,220)} = 2.06^{*}$
	Elevation	3.49	quadratic	+ -	
	Aspect	2.52	quadratic	+ -	
	Backward-selected model	12.18			
Trophic resources	D-*Asparagus nesiotes*	9.73	linear	+	
	P-*Asparagus nesiotes*	9.35	linear	+	
	D-*Rubia fruticosa*	7.67	cubic	+ - +	
	P-*Klenia neriifolia*	7.26	quadratic	- +	
	P-*Salvia aegypciaca*	6.92	linear	-	
	P-*Mattiola bolleana*	6.48	linear	-	
	Distance to cultivated areas	4.96	linear	-	
	P-*Sisymbrium erisiomides*	4.96	linear	+	
	P-*Atractylis cancellata*	4.85	quadratic	+ -	
	P-*Caralluma buchardii*	4.71	linear	+	
	P-*Dipcadi serotinum*	4.39	linear	-	
	D-*Euphorbia* spp.	4.3	quadratic	+ -	
	Vegetation type	4.15			$F_{(9,219)} = 0.93^{ns}$
	Backward-selected model	26.86			
Shelter	Local shelter	29.55			$F_{(3,225)} = 24.89^{***}$
	Distance to walls	16.43	cubic	+ - +	
	Local walls	11.9	cubic	+ - +	
	Long walls	11.37	quadratic	+ -	
	Plot shelter	10.63			$F_{(3,225)} = 7.55^{***}$
	Short walls	10.57	quadratic	+ -	
	Type of ravine	7.2			
	Ravines	4.22	quadratic	+ -	
	Sandy soil	4.29	quadratic	+ -	
	Walls	4.29	quadratic	+ -	
	Backward-selected model	40.81			

significant were modeled together, 55.35% of the total variability of squirrel abundance was accounted for (Table 3). The addition of spatial variables did not improve model predictions, and a residual autocorrelation was not significant at any lag distance. Partial regression of the 3 main types of explanatory variables (environmental, food resource, and refuge/shelter) showed that the contribution of each type of variable alone was similarly small (Fig. 3). Approximately 19% of the total variability could be indistinctly attributed to any of the 3 types of variables. The majority (34%) of variations in squirrel numbers could be explained by the joint influence of trophic and shelter variables, while a small percentage of the variability (approximately 11%) could jointly be explained by environmental and shelter variables. Last, the fraction of the variability explained at the same time by environmental and trophic variables was large and negative (nearly -22%), indicating that these 2 variables together may have a synergistic effect on squirrel abundance, explaining more than the sum of their individual effects (see Legendre and Legendre 1998). Similar partial regression results were obtained when the number of excrement was used as the dependent variable (not shown).

DISCUSSION

A clear result emerges from our analysis: biological requirements of the Barbary ground squirrel may explain a large amount of its distribution. As this species is an invader, recognition of these variables will be central to understanding its capacity for establishment. Although habitat selection by animals is difficult to model due to the high number of variables possibly influencing it, the results of our model help explain the main variables affecting the squirrel's distribution and abundance on Fuerteventura I. According to what we initially suspected, shelter variables explained a large proportion of the variation in the abundance of *A. getulus*, while environmental variables were less important. In general, analysis of both scat and squirrel abundances across the island highlighted the

Table 3. Parameters of the complete backward-selected model in which all of the explanatory variables are considered together after a previous selection carried out on variables of the same type (environment, food resources, and shelter; Table 2). This complete model explained 55.35% of the total variability of squirrel abundance. Superscripts indicate the quadratic term of the function. The levels of each of the considered categorical variables are included. The Wald statistic is a test of significance of the regression coefficients. *, **, and *** indicate levels of significance < 0.05, < 0.01, and < 0.001, respectively

	Level of the factor	Parameters	Wald	
Intercept		1.360	310.85	***
Local shelter	Middle	0.189	12.11	***
Local shelter	Few	-0.243	12.95	***
Local shelter	None	-0.607	39.36	***
Type of landscape	Flat area	0.278	12.15	***
Type of landscape	Abandoned cultivation	0.284	7.03	**
Type of landscape	Abandoned terrace	-0.684	13.12	***
P-*Salvia aegyptiaca*		0.160	13.79	***
P-*Sicymbrium erysimoides*		0.038	13.48	***
P-*Atractylis cancellata*		0.102	15.36	***
P-*Atractylis cancellata*^{2}		-0.007	15.03	***
Rabbit latrines with fresh dung		-0.204	7.79	**
Rabbit latrines with fresh dung^2		0.047	8.67	**
Sandy soil		0.021	7.86	**
Vegetation type	*Euphorbia regis-juvae*	-0.299	7.02	**
Vegetation type	Psamophyllous	0.646	15.97	***
Vegetation type	Scrub of Compositae	-0.353	5.27	*

importance of variables related to the availability of shelter (e.g., dry walls, ravines, and stone heaps). For instance, the number of shelters explained about 30% of the abundance variability, accounting for more variation than the complete models of environmental or food resource variables. Nevertheless, the inherent correlation among naturally occurring variables hindered our search for causal relationships (MacNally 2000). Our variation-partitioning analysis suggested that we cannot distinguish among the majority of variable types to elucidate their individual explanatory capacities.

Diverse reasons can explain the importance of shelter. On the one hand, daily temperature variations greatly influence the behavior of *A. getulus* (Saint-Guirons 1953, Machado and Domínguez 1982), which becomes less active at low temperatures and high humidities. However, more research is needed to clarify this relationship between demographics and behavior, especially since our results also suggest that seasonality and wind speed affected the activity of the Barbary ground squirrel. In general, the metabolic rate of animals determines their resource requirements, as well as parameters such as growth rate and lifespan (Brown et al. 2004, see also Nagy 2001). Temperature is one of the main environmental variables influencing the metabolic rate (Speakman 1997 2000), as squirrels regulate their body temperature accordingly (Chappell and Bartholomew 1981). *Atlantoxerus getulus* maintains a body temperature of 36-39°C (Machado and Domínguez 1982), but temperature oscillations and a lack of shelter can lower its body temperature to 25°C, which can be lethal, or, conversely, raise it by 1-1.5°C, increasing the possibility of death by direct exposure to solar radiation (Machado and Domínguez 1982). Burrowing inside dry walls or stone heaps may be essential behavior that helps the squirrels maintain their thermal balance (Werner et al. 2005) during daily and seasonal temperature oscillations. This behavior is especially important in a semi-desert climate where small vertebrates cope with temperature extremes with a variety of physiological and behavioral solutions (Grenot 2001). On the other hand, some aspects of the reproductive requirements of *A. getulus* may also explain the relevance of shelter, since lactating females are obligated to stay near nest sites throughout most of the year. Juveniles spend approximately their 1st 5-6 wk inside burrows (Machado and Domínguez 1982), and females menstruate roughly every 4 mo (Poduschka 1974), with potentially 2 or even 3 broods a yr on Fuerteventura I. Thus, a continuous presence of females and their progeny around shelters should be expected. Finally, predation can also partially explain the relevance of shelters. Forty yr after being introduced, *A. getulus* has become prey for some native and introduced predators (*Felis catus*, *Buteo buteo*, *Corvus corax*, and *Falco tinnunculus*) and now plays an important role in the island's trophic webs. Thus, predator-escape behavior must be maintained (Bonenfant and Kramer 1996, Kramer and Bonenfant 1997), especially on an island such as Fuerteventura with an abundance of predators.

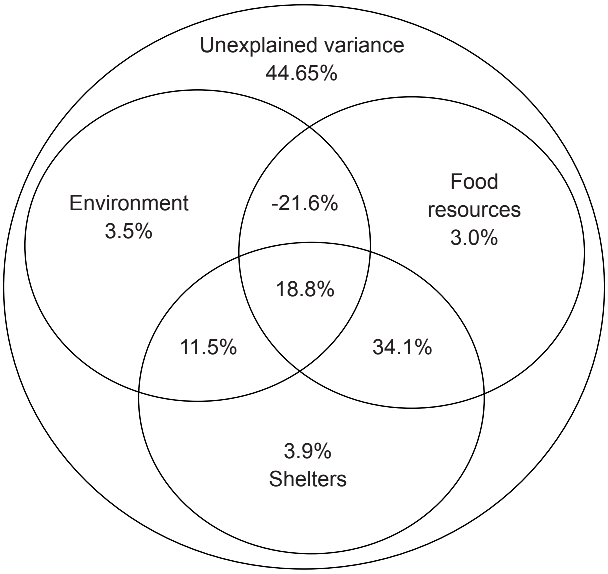

Fig. 3. Results of the variation partitioning process among the 3 main types of variables that explain Barbary ground squirrel abundance on Fuerteventura I.

The presence, abundance, width, and height of stone heaps best explained scat quantity. Different relevant variables accounting for scat and individuals may indicate differential uses of habitat for defecating and other activities. The previously described biological causal hypothesis accounting for the squirrel abundance in relation to the presence of stone heaps may also explain the occurrence of excrement. However, we suggest another complementary cause for such a relationship. Vigilance behavior has important implications for social animals (Edmunds 1974, Quenette 1990), and *A. getulus* is mainly a social species (Gouat and Yahyaoui 1999). Although its behavioral ecology is not well known, we do know that some individuals from each family group spend much of their time in active vigilance of the group movement area. These individuals stand or lie on walls or stone structures for long periods of time (sometimes for an hour) during the day. Similar behavior is also found in some months during the reproductive period, when males spend long periods standing on stone heaps constantly repeating particular acoustic signals. The same stone heaps are frequently used, suggesting that males select the highest stone heap as an observation point from whence they are better seen by females and are also able to observe and guard the surrounding area. Scat accumulated in these stone heaps may be the result of this behavior, a possible source of the relationship between stone heaps and squirrel excrement.

In general, dry walls were found to be good indicators of squirrel abundance. The presence of sandy soils was also positively correlated with squirrel abundance, possibly due substrate penetrability and ease of burrowing. Interestingly, the jable landscape, although highly penetrable, is the only significantly unsuitable habitat for the squirrel. These large extensions of organogenic sand are not crossed by stone dry walls, and stone heaps are quite unusual.

Resource variables were significantly related to squirrel abundance. It is worth highlighting that *A. getulus* frequently consumes and disperses seeds of some fleshy-fruited plant species (*Aparagus*, *Rubia*, *Opuntia*, *Lycium*, and *Prunus* spp.; Nogales et al. 2005, López-Darias and Nogales 2008). Other plants (*Euphorbia*, *Atractylis*, and *Mesembryanthemum* spp.) are also known to constitute an important part of the squirrel's diet. Distance to cultivated areas is also important, which agrees with the very opportunistic diet and use of crops by the species (Valverde 1957, Machado and Domínguez 1982). Although this squirrel is a predator of snails (Machado and Domínguez 1982), the squirrel's abundance did not depend on snail density, suggesting that snails are not an essential component of the squirrel's diet, or that their abundance is not a limiting factor for the Barbary ground squirrel on Fuerteventura.

Few environmental variables appeared to be relevant. Only 115 km separate Fuerteventura I. from the species' native distribution range, and the climate and landscape of the 2 areas are very similar. The latitude in the native distribution area (Aulaugnier and Thévenot 1986) overlaps that of the island. Moreover, the squirrel is present in a wide variety of Moroccan habitats between elevations of 1000 and 4000 m (Petter and Saint-Guirons 1965). Such a wide climate spectrum in the native distribution area suggests that only the sea barrier stopped the colonization of the Canarian Archipelago by this species. After its deliberate introduction to the islands, this species found no climate restrictions. A previous analysis suggested that all of the Canary Is. offer optimal habitats for this attractive pet (López-Darias et al. 2008), so that it could become a very pernicious invader. This situation is worthy of deep consideration, and plans need to be established to prevent the future expansion and establishment of this species throughout the archipelago.

Biological interaction variables did not seem to be highly relevant. No relationship between the squirrel's presence and the presence of rabbits or feral goats/sheep was detected. It would be useful to further examine the influence of squirrels on the presence of other mammals, especially rabbits (the islanders believe that rabbit populations declined after the squirrel's introduction) and the endemic shrew, *Crocidura canariensis* Hutterer, López-Jurado and Vogel, 1987, which is listed as vulnerable by the IUCN and is protected by Spanish law (Hutterer 2004). Although some of the proposed biological explanations need confirmation by means of specific behavioral and experimental studies, the majority of the significant relationships obtained can be explained by realistic biological mechanisms. Further, this work produced data that are very useful for understanding the species' ecology, and for elaborating future management strategies to control the populations on Fuerteventura I. and prevent its expansion throughout the Canarian Archipelago.

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Appendix 1. Measured variables grouped according to the 4 types considered (environment, food resources, biological interactions, and refuge/shelter). The scale at which each variable was measured is indicated by S for subplot, P for plot, and L for landscape. Variables types are indicated by 1 (quantitative) or 2 (categorical), showing each category for categorical variables. The procedure followed to measure subplot variables is indicated by A (subplot data were averaged for posterior analysis), S (data were summed), or D (variables were transformed to dummy ones). Italicized variables correspond to those used both as continuous and dummy binary ones

Type of variable	Scale	Variable name	Variable nature	Measurement method	Categories
Environment	P	Slope	1		
		PCA factor	1		
		Mean annual temperature	1		
		Mean annual precipitation	1		
		Elevation	1		
		Aspect	1		
	L	Landscape type	2		Badland, town, jable, stony slope, flat area, abandoned cultivation, cultivation, ravine, and abandoned cultivation terrace
Food resources	S	Herbaceous cover (%)	1	A	
		Scrub cover (%)	1	A	
		Tree cover (%)	1	A	
		Soil without vegetation (%)	1	A	
		Maximum plant height	1	A	
		Species of maximum height	2	D	Name of the species
		Minimum plant height	1	A	
		Species of minimum height	2	D	Name of the species
		All plant species present	2	D	Names of all species present
		Dominant plant species	2	D	Name of the dominant species
		Number of live snails	1	S	
		Type of live snails	2	D	Small, large
		Dominant type of live snails	2	D	Small, large
		Number of dead snails	1	S	
		Type of dead snails	2	D	Small, large
		Dominant type of dead snails	2	D	Small, large
	P/L	Distance to cultivated areas	1		
		Distance to roads	1		
		Distance to urban areas	1		
		Distance to isolated houses	1		
		Type of vegetation	2		See Ruiz (1980) 14 categories
Refuges/shelters	S	Number of stone heaps	1	S	
		Maximum height of stone heaps	1	A	
		Maximum width of stone heaps	1	A	
		Stone cover (%)	1	A	
		Stones smaller than 10 cm (%)	1	A	
		Stones 10-30 cm (%)	1	A	
		Stones 30-50 cm (%)	1	A	
		Stones larger than 50 cm (%)	1	A	
		Number of stone dry walls	1	A	
		Occurrence of potential shelters for squirrels	2	D	None, some, few, many
		Type of soil (penetrability)	2	D	Sandy, clay, sandy-clay, jable, rocky, rocky-jable, pyroclastic, pyroclastic-sandy, cultivated
	P	Number of potential shelters for squirrels	2		None, some, few, many
		Number of stone dry walls	1		
		Type of stone dry wall	2		Long, short
		Number of ravines	1		
		Types of ravines	2		Small, medium, large
		Number of stone heaps	1		
		Maximum height of stone heaps	1		
		Maximum width of stone heaps	1		
	L	Occurrence of stone heaps	1/2	D	None, some, few, many
		Number of abandoned houses	1		
Biological interactions	S	Number of old rabbit excrement	1	S	
		Number of fresh rabbit excrement	1	S	
		Number of rabbit latrines	1	S	
		Number of rabbit latrines with fresh excrement	1	S	
		Number of old goat/sheep excrement	1	S	
		Number of fresh goat/sheep excrement	1	S	