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#### Marked reduction in body size of a wood mouse population in less than 30 years

Running head: Wood mouse body size decline in SW Spain

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**Abstract:** Thermoregulation, metabolism and life history of species are affected by body size and shape. Based on specimens of the wood mouse Apodemus sylvaticus that were collected at Doñana National Park in 1978-81 and 2006-07, we tested for changes between these periods in body mass, body size, and allometry. Furthermore, we used data from 1978-81, when more specimens were available, to evaluate the sexual dimorphism of adults. Between the two periods and regardless of age, the most striking reduction in size in both females and males concerned the body mass (females -29.5%, males -36%) and ear length (-20% for both sexes). Although less pronounced (3-4%), we also found a significant reduction in the total cranial and the condyle-basal lengths of females but not of males. No change was evident for the zygomatic width and the diastema length and for the head-body and hind foot lengths in either sex. The allometric relationships between the measured traits and the head-body length in adults did not change between the two periods. Males were larger than females in all the measured traits except the zygomatic width and the ear length. No sexual dimorphism was evident relative to the static allometry of adults. We speculate that a major determinant of this reduction may have been a shortage in suitable resources. Overall, this study confirms and extends previous findings on male-biased sexual size dimorphism and reveals a dramatic decline in body mass, which is likely linked to the observed reduction in species abundance at Doñana. The extent and rapidity of the observed morphological changes raise concerns about the conservation of Doñana ecosystems and pose questions for future research on the ecological processes that caused these changes.

**Keywords:** *Apodemus sylvaticus*; European wood mouse; Doñana National Park; allometry; sexual dimorphism.

#### **INTRODUCTION**

An animal's body size is a central feature that reflects several physiological and lifehistory traits, such as metabolic rate, fasting endurance, growth rate, interspecific competition, lifespan and fecundity (Calder, 1984). Spatial and temporal variation in the body size of animals within and among species has been reported worldwide for a large number of endothermic, ectothermic, aquatic and terrestrial species. Moreover, the relationship between body size variation and ongoing climate change has been demonstrated in an increasing number of studies (reviewed in Sheridan & Bickford, 2011), to such an extent that reduced body size is often referred to as the third universal response to global warming, after variation in phenology and species distribution (Gardner et al., 2011). It has been suggested that variation in an animal's body size may be due to direct or indirect effects of climate. Direct effects may arise because the ratio between surface and volume regulates heat dissipation, a phenomenon at the foundation of well-known and still debated eco-geographical hypotheses (e.g. Bergmann's and Allen's rules). As an example, Yom-Tov (2001) showed a marked decline in the tarsus length and body mass of four passerines in Israel over 50 years, which he related to the direct effect of increased temperatures. A number of indirect mechanisms have been suggested to explain how recent climate changes could affect the body size of birds and mammals (Yom-Tov and Geffen, 2011). Among these, great importance has been attributed to variation in predation, habitat fragmentation, interspecific competition, and food availability. For instance, the body mass of great tits *Parus major* in Britain was found to decline along with higher predation pressure over five decades (Gosler et al., 1995). In addition, the body size of three small mammal species, after anthropogenic

transformation of a temperate rainforest, was considerably smaller in fragmented than in non-fragmented habitats (Lomolino and Perault, 2007). At Doñana National Park (SW Spain), the location of the present study, nine skull traits in males of Iberian Lynx *Lynx pardinus* declined in size over the last century as a possible consequence of habitat fragmentation and inbreeding depression (Pertoldi et al., 2005). The availability of trophic resources seems to play an especially important role in body size variation, as shown by an extensive review of studies on this topic (Yom-Tov and Geffen, 2011). An example of the effect of trophic resources on body size comes from Yom-Tov & Yom-Tov (2012), who found a marked increase in skull size in red foxes *Vulpes vulpes* over the 20th century, which paralleled an increase in food availability. Analogously, dietary improvement was considered responsible for the increase in the overall size of Alaskan masked shrews *Sorex cinereus* and the skull size of two Japanese rodents during the twentieth century (Yom-Tov and Yom-Tov, 2005, 2004).

Our study area, Doñana National Park (DNP hereafter), is a large protected area in SW Spain that has undergone significant changes in its plant and animal communities over the last several decades (Ferreras et al., 2011; Muñoz-Reinoso, 2001; Rendón et al., 2008). A recent study (Santoro et al., 2016) revealed that the community richness of small mammals in a core area of DNP considerably shrank over the last 40 years and that high temperatures and low rainfall related negatively to the abundance of a rodent, *Apodemus sylvaticus*. Over the same period, while larger rodents became increasingly rare in the area (e.g. garden dormouse *Elyomis quercinus* and wood mouse *A. sylvaticus*), a smaller species (Algerian mouse *M. spretus*), is now by far the most commonly trapped species (see also Moreno et al., 2016). The decline in the area of the European rabbit *Oryctolagus cuniculus*, after the first outbreak of Rabbit Hemorrhagic

Disease in 1984-89 (Moreno et al., 2007), has been detrimental to the abundance of specialist predator species, such as *L. pardinus* and the Iberian imperial eagle *Aquila adalberti*, which feed on rabbits (Ferrer and Negro, 2004; Gil-Sánchez and McCain, 2011). However, at the same time, there has been an increase in the abundance of other predator species like the common genet *Genetta genetta* and Egyptian mongoose *Herpestes ichneumon* (Delibes *et al.*, 1992; Palomares *et al.*, 1996) for which small mammals represent an important part of the diet (Ferreras et al., 2011). Finally, during the last few decades we have observed a consistent deterioration of the habitat conditions in the Doñana Reserve probably due to a progressive desiccation process ongoing in the area. One example of these changes comes from the cork oak *Quercus suber* which has declined considerably in the Doñana Reserve (García et al., 2011). The acorns of this tree are likely a main trophic source (Sunyer et al., 2016) and a major determinant of population dynamics in *Apodemus* species (Montgomery, 1989).

The profound transformations of Doñana ecosystems may have exerted an effect on body size and, therefore, on the life history traits of inhabiting species. We hypothesize that, as a direct consequence of climate warming or in response to above mentioned deteriorating trophic conditions, the wood mouse body size has declined in the area over the study period (i.e. between 1978 and 2007). In support of this hypothesis we note that such a reduction in body size would have affected vital rates (survival and reproduction) and would therefore be in line with the observed loss of abundance of the wood mouse at Doñana (Moreno et al., 2016; Santoro et al., 2016). We are aware of a single study in Doñana National Park that investigated temporal changes in the body size of an animal species, the Iberian lynx (Pertoldi et al., 2005). In the present study, we aim to assess whether the body size of a small mammal species in Doñana, the wood mouse, has

declined between two periods spanning less than 30 years. For this purpose, we used morphometric measures taken from specimens collected at Doñana in 1978-81 and 2006-07 to investigate the temporal dynamics of: (i) body mass, (ii) body size (eight morphometric traits), (iii) and allometry of cranial and extremity traits relative to body length. Finally, (iv) to address the paucity of information on sexual dimorphism in this species, we evaluated differences between adult females and males in size, mass and allometry.

#### **MATERIAL AND METHODS**

#### **Study species**

The wood mouse (family Muridae), *Apodemus sylvaticus*, is a rodent that rarely exceeds 40 g with a long tail, equal or longer to the head and body length, and long hind legs typical of highly mobile species (Jubete, 2007). A moderate sexual dimorphism has been described with males larger and heavier than females (Alcántara and Díaz, 1996; Rosário and Mathias, 2004). The wood mouse is widely distributed across Europe, Asia and northern Africa and is one of the most abundant small mammal species inhabiting the Iberian Peninsula and Balearic Islands (Jubete, 2007). In the Iberian Peninsula, the species is mainly found in woodlands, but also in shrubby or herbaceous areas

(Camacho and Moreno, 1989). It is among the main prey of many raptors, carnivorous mammals, snakes and other generalist species like boars, herons and storks and, at Doñana, it was noted as the most hunted prey after rabbits in the 1980s (Kufner, 1986).

In the western Palearctic the size of the wood mouse increases from north to south (Alcántara, 1991). This has been interpreted as a case of character displacement due to competition with the slightly larger yellow-necked mouse *Apodemus flavicollis* (Alcántara, 1991). Moreover, *A. sylvaticus* presents gigantism in the islands, which has been interpreted as the result of scarce competition for resources and limited predation pressure (Sara and Casamento, 1995).

#### **Study Area**

Doñana National Park covers 54,252 ha (Fig. 1). This protected area is a mosaic of ecosystems and is considered among the most important biodiversity hotspots in Europe. The climate is Mediterranean sub-humid (annual rainfall  $\approx$  500-600 mm) with two marked seasons: winters mild and wet (January mean T  $\approx$  10°C), and summers hot and dry (August mean T  $\approx$  25 °C). Three main biotopes exist in the area: sand dunes, scrublands, and marshlands (Valverde, 1958), with the latter representing the largest ecosystem in the park that is strongly influenced by seasonal flooding. Sand dunes are parallel to the coast and are influenced by the mobility of the substrate. Scrublands are mainly dominated by Mediterranean species.

#### Data

All data, available in Docampo et al. (2018), came from 1026 individuals (416 females and 602 males) collected at different times of the year over two periods (1978-81 and 2006-07) and preserved in the Doñana Biological Station Collection. A standard procedure was followed when dead specimens are collected during trapping programs of small mammals. The capture date (day, month and year), type of trap used (snap- or live-traps), and zone together with the sex, weight and body measures (head-body

length, hind foot, ear and tail lengths) are recorded immediately after the individuals' death. Therefore, the bodies of dead individuals are frozen and stored in the Doñana Biological Station Collection until the moment they are dissected by the taxidermist who annotates data about the interior organs (e.g. gonads) and, subsequently, preserve in the Collection only the skin and the skull of each specimen. In 2016, we complemented the data existing on these specimens by assessing the age and taking measurements of the skull. As a result, we obteined an individual data about the weight and eight morphometric traits (four cranial and four external). The weight was measured by mean of a precision dynamometer (Pesola). The body traits measured were: headbody length (HBL), from the tip of nose to the base of the tail; hind foot length (FL), from the back of the heel to the tip of the fingers; ear length (EL), from the proximal sinus to the distal end; and tail length (TL), from the tip to the base. The cranial measurements (Fig. 2 a, b) were: cranial total length (CTL), from the nasal end (rhinion) to the point of farthest occipital (ophistion); condyle-basal length (CBL), from the proximal end of the occipital condyles to the prognathion; zygomatic width (ZW), between the cheekbone salient points (zygion-zygion); and diastema length (DL). All length measurements were taken with a digital caliper to the nearest 0.1 mm. Individuals were classified into five age classes following Felten's (1952) criteria based on the degree of wearing of the upper molars assessed by visual examination with a stereoscopic microscope (Fig. 2 c). For this study, specimens without information on sex were discarded (see Table 1 for details on sample size).

The collection specimens used in this study were collected using two types of traps: snap-traps ( $\approx$ 80%) and live-traps ( $\approx$ 16%, note that in this case they were individuals who died in the trap accidentally); this information was not available for the remaining

portion of specimens ( $\approx 4\%$ ). In the first period (1978-1981) both methods were used whereas in the second period (2006-2007) all the specimens were captured in live-traps. Regardless of the capture method, all specimens came from five zones within DNP in the same biotope (scrublands). A preliminary analysis excluded any relationship between the zone of capture and the morphometric variables examined in this study.

#### **Statistical analyses**

First, we tested for a change between the two periods in: (i) body mass, (ii) body size (head-body, cranial and extremity lengths) (iii) and allometry. The trap type was included in the analyses to account for potential size selectivity, or size-dependent trapinduced mortality, of the two types used in the study. These analyses were run separately for each sex to facilitate interpretation of results. Second, we tested (iv) sexual dimorphism relative to the body size, body mass and allometry. For the latter analyses, to prevent the potential confounding effect of the period of specimen collection, we used only data from 1978-1981 when data from more individuals were available. In addition to the sexual dimorphism analyses, to avoid heterogeneity due to different ontogenetic stages (Klingenberg, 2016), we considered only data from adults (age classes 4 and 5) for analyses of (static) allometry and sexual dimorphism.

Continuous variables were scaled (mean= 0, SD= 1) previous to the analyses to improve model convergence and make the effect size of different predictors comparable. To test for temporal changes in body mass and size (i and ii), we defined "period" as a categorical predictor divided into "period 1" and "period 2", where "period 1" includes 1978, 1979, 1980, 1981 and "period 2" includes 2006 and 2007. Note that the choice of these two periods was opportunistic inasmuch as it referred to the years, in old and

recent times, when more data (collected within different research campaigns) were available for our analyses. To analyze the temporal variation and sexual dimorphism relative to body mass and size (objectives i, ii, and iv), we used linear mixed-effects models (function *lmer* from *lme4* package; Bates et al., 2015). Second, we included "year" as a random factor to control for any random variation across years. The statistical significance of each predictor was computed by means of a Likelihood Ratio Test with a Chi square distribution (function *anova*) as recommended for linear mixed models (Bolker et al., 2009). For the analysis of change in allometry (iii) and sexual dimorphism relative to allometry (iv), we fitted standardized major axis regressions (function sma from package smatr; Warton et al., 2012) that minimize residual variance both in X and Y dimensions. Our findings were robust to the presence of collinearity issues, influential observations and to obvious deviations from homoscedasticity or normality of response variables. For the analyses of temporal change in body size (objectives i and ii) and of sexual dimorphism (objective iv), we used the Holm-Bonferroni method for multiple comparisons (Holm 1979) to adjust the p-values of the focal predictors (i.e. respectively of "period" and "sex"). Note that each analysis had a slightly different sample size depending on how many specimens were available with complete information for all the variables (response and predictors) in the model (Table 1). All the analyses were performed in R version 3.1 (RStudio Team, 2017). The complete R code used to perform the analysis is provided as supplementary information (file S1).

*I. Temporal change in Body mass* – We defined "body mass" as the response variable, "period" as the focal predictor (i.e. that for which we wanted to test the effect), "month" (of capture), "age", head-body length, and "trap type" as the control variables, and

"year" as the random intercept. The list of control variables was defined to infer the difference, if any, between the body mass between periods net of any difference explainable by the control variables. Control variables were chosen among those for which data were available to us and of which we a priori supposed might relate to the body mass. While age is an individual characteristic obviously related to the body mass, the month of capture could reflect different trophic resource availability. For this analysis, the "head-body length" was also in the list of control variables to prevent spurious differences among individuals' body mass due to the differences in their total length.

*II. Temporal change in morphometric lengths* – We used the same approach described in the previous section except that the head-body length was not one of the controlling variables given that it was one of the response variables. We performed a separate analysis for each morphological trait as a response variable in order to assess for which morphometric traits, if any, the temporal reduction was specific.

*III. Allometry* – To calculate the relative growth of the measured traits relative to the growth in the body length, we used the Huxley expression:  $y=ax^b$ , where *y* is a measurement of overall length (HBL in our case), *x* is a measurement of a specific morphological trait, and *b* is the allometric coefficient (Huxley, 1932). All the measurements were previously log-transformed to obtain a linear relationship: log (y) = log (a) + b\*log (x), with a slope of b and an intercept of log (a). The allometric coefficient *b* is therefore interpretable as the relative growth of *x* with respect to the growth of *y* (*b*=1, isometry; *b*<1, negative allometry; and *b*>1, positive allometry). Per each trait and period, we estimated the allometric coefficient (relative to the Head-Body Length, HBL) and tested for isometry and whether it changed between the two periods.

*IV. Sexual dimorphism* – To test for sexual dimorphism in body size (morphometric lengths) and mass we ran an analysis for each body trait and one for body mass. We defined the morphometric trait as a response variable, "sex" as the focal predictor, and "year" and "month" as random intercepts. To test for sexual dimorphism in allometry, we compared allometric coefficients of each sex by using standardized major axis regressions (function *sma* from package *smatr*).

#### RESULTS

*I. Body mass* – The body mass of both sexes declined remarkably with, in the second period, the females being 29.5% and males 36.2% lighter than in the first period (according to the models' fitted values) (Table S1).

*II. Body size* – The length of some of the measured morphometric traits decreased between the two periods with the most remarkable reductions being evident for ear. In particular, we found a significant reduction among females in two cranial traits and ear [according to the models' fitted values: cranial total length = -4.1%; condyle-basal length = -3.4%; zygomatic width = -3.1% (marginally significant); ear length = -21.3%] and, among males, of ear (EL = -21.8%) (Figure 3, Table S1).

*III. Allometry* – We found a marginally significant change in allometry only among females that, relative to HBL, would have longer skulls (CTL) in the second than in the first period (Table S2). No other changes in allometry were found between the two periods.

*IV. Sexual dimorphism* – Adult males were significantly heavier (on average 14.3%) than females. In absolute terms, this pattern was qualitatively similar for all the

measured traits (Table S3; males longer than females: HBL = +3.8%; CTL = +1.3%; CBL = +1.4%; DL = +1.8%; FL = +3.3%; TL = +2.5%) except the zygomatic width and the ear length, for which we did not find significant differences between males and females. We did not find significant differences in the allometric coefficients of adult females and males (Table S4).

#### DISCUSSION

Our findings show a clear body size reduction in a wood mouse population, which took place in less than 30 years and was especially remarkable for body mass. These findings are robust to several potentially confounding effects including sex, trap type, age and season of collection (see tables S5 and S6 for details on control variabes). Neither the observed changes can be attributed to close-in-time abrupt environmental changes as data from the two periods were concomitant with dry periods (dry years: 1979-81, and 2005). Unlike the body mass, we did not find a significant reduction in the total body length suggesting that specimens were thinner at the end of the study period. We suggest that the observed reduction in wood mouse body size may be a nutritionmediated response to the reduced availability of, or limited access to, trophic resources. Moreover, except for cranial width and ear length, we found male-biased size dimorphism in adults for all the measured traits, i.e. cranial, hind foot, tail, head-body lengths and body mass. We did not find allometric differences between sexes for any trait relative to the head-body length. As discussed in the literature for this species, male-biased sexual size dimorphism is likely an effect of stronger intrasexual competition among males (Alcántara and Díaz, 1996; Rosário and Mathias, 2004).

In recent years, there has been an increasing interest in the role of global change in body size variation. Several studies have shown cases of recent body size shrinkage, which has been attributed to direct and indirect consequences of climate change (Gardner et al., 2011; Sheridan and Bickford, 2011). Changes in temperature, rainfall, habitat types and connectivity may directly and indirectly affect species' phenotypes. The body size reduction in the wood mouse found in this study could be in line with Bergmann's thermoregulatory expectations given the warming climate at Doñana during the study period (see Santoro et al. 2016 for details). Supporting this hypothesis, the Doñana small mammal community suffered a marked loss of diversity with the Algerian mouse (*Mus spretus*), of smaller size and typically of warmer climates, increasing in abundance in sharp contrast with the fate of other species, including the wood mouse, which experienced a sharp decline in population size (Moreno et al., 2016; Santoro et al., 2016). Moreover, our analyses (Santoro et al., 2016) suggested that low rainfall and high temperatures were negatively correlated with the abundance of wood mouse in line with Bergmann's logic framework. On the other hand, the validity of another ecogeographical hypothesis, Allen's rule, was not supported by our findings as we also found a considerable reduction in ears' length that, together with tails', should have increased as a mechanism to dissipate heat under climate warming.

A debate exists about the validity of the so-called eco-geographical rules to explain temporal and even spatial gradients of species morphometric traits (McNab, 2010; Millien et al., 2006; Teplitsky and Millien, 2014). Instead of being mediated by thermoregulatory mechanisms, climate effects on phenotypic traits may be indirectly mediated by changes in the available resources due to environmental changes (e.g.

limiting resources), intra- and inter-specific competition, or increasing predation (McNab, 2010; White, 2008; Yom-Tov and Geffen, 2011).

The observed body mass reduction was beyond what could be explained by the estimated decline in size (e.g. the head-body length did not decline significantly), which suggests that the body of the wood mouse was remarkably thinner at the end of the study period. Therefore, this loss of weight might reflect deteriorating body conditions in line with the hypothesis of declining availability of resources. Overall, the reduction in body size could be a nutrition-mediated plastic or genetic response to declining food availability (Gardner et al., 2011). Such a change in food availability at Doñana could be due to local environmental changes. This is in line with the results obtained in an ongoing isotopic study (Santoro et al., in preparation) comparing the diet of wood and Algerian mice in the area during a period similar to the present study and which suggests a deterioration in the trophic resources used by the wood mouse. In this sense, it is worth noting that the observed relationship between climate and wood mouse abundance in the study area (Santoro et al., 2016) may be due to climate-related changes in the productivity of trophic resources on which the wood mouse feeds (Bogdziewicz et al., 2017; Díaz et al., 2010).

Alternatively, an increase in interspecific competition may have resulted in a shortage of food supplies for the disadvantaged species. This hypothesis is consistent with the simultaneous decline of *A. sylvaticus* and increase of *M. spretus* in the area (Moreno et al., 2016; Santoro et al., 2016), two species that may compete for resources and habitat (Bauduin et al., 2013; Cassaing et al., 2013). According to this hypothesis, capture-recapture data from the core area of Doñana National Park indicate that, since the appearance of *M. spretus* in the trapping records (1984-85), this species had a persistent

abundance peak in autumn, while the abundance peak of *A. sylvaticus* was delayed from autumn to winter (Moreno et al., 2016).

At Doñana, the wood mouse is present in the diet of many species and is an important prey for several raptors and for generalist carnivores (Kufner, 1986). Predation pressure may have increased between the two periods, especially as a consequence of the severe crash in the European rabbit (O. cuniculus) population occurred in 1989 after an outbreak of Rabbit Hemorrhagic Disease (Moreno et al., 2007; Villafuerte et al., 1994). In fact, as a result, some generalist carnivores in the area, like *Meles meles* and Herpestes ichneumon, began to prey less on rabbits and more on other species including small mammals (Fedriani et al., 1998). There is also some evidence of an increase in the abundance of generalist carnivore species in the area, probably related to the decline of the lynx at Doñana (Palomares et al., 1996). Such an increase in predation may have affected the body size of wood mouse by means of two mechanisms. First, experimental evidence in the wood mouse indicates that an increased risk of predation may exert a negative effect on body mass via reduced food intake (Monarca et al., 2015). Second, body size reduction may also represent a response to increased predatory pressure because smaller individuals may have an advantage in escaping predation (Gosler et al., 1995) or because they may be less appealing to predators (Valverde, 1967). The observed marginally significant change in the cranial allometry between the two periods may also be related to changes in diet but we lack a plausible explanation for why this has occurred uniquely among (adult) females. To avoid any spurious effect due to the type of device used for capture we consider only individuals captured by live-traps and between January and April when more specimens were available in the dataset.

Whatever the causes of the observed decline in the body size of the wood mouse at Doñana, this change is probably related to the observed decline in wood mouse abundance, as phenotypic and demographic dynamics are often related in a causal manner (Ozgul et al., 2010). Poor trophic conditions may decrease the investment in reproduction thus reducing the number of pups and their survival. Furthermore, reproductive maturation may be reached at a certain weight (see e.g. Ueda and Takatsuki, 2005) and, therefore, this reduction in body mass may have exerted a detrimental effect on the reproduction of the species in the study area. This is compatible with our data if we consider that, in the first period, about 35.3% of captured individuals were subadults (age classes 1, 2 and 3) whereas this percentage was significantly lower in the second period declined to just 5.4% in the second period ( $\chi^2$ = 3.94, df=1, p< 0.05; details in file S1 - to avoid spurious effects of type of trapping device and month of capture we restricted this analysis to individuals captured by live traps between January and April when more specimens were available).

*Sexual dimorphism* – To the best of our knowledge, previous to the current study, sexual dimorphism in the wood mouse had been shown, with males being larger in body mass and condyle-basal length (Alcántara and Díaz, 1996; Rosário and Mathias, 2004). Our study confirms the larger size of males but broadens this finding by including differences in cranial total length, diastema, head-body length, and hind foot and tail lengths. Although other evolutionary causes could explain the male-biased dimorphism (see Ueda and Takatsuki, 2005 for a discussion on a related species), such as sexdifferential resource partitioning or reproductive role division, based on the species biology we think that the overall larger size of males is more likely a consequence of sexual selection being stronger in males (see also Díaz et al., 2010).

*Conservation implications* – Phenotypic and fitness components are strictly related within animal biology. In particular, body size is a phenotypic trait that affects mortality, intra- and inter-specific competition and breeding performance (Calder, 1984). Phenotypic and demographic responses to environmental variation are therefore linked, playing a crucial role in the ecological consequences of global change. In this regard, the loss of diversity and richness in the small mammal community shown in previous studies (Moreno et al., 2016; Santoro et al., 2016) and the wood mouse body size reduction presented here may be two facets of the same process. Overall, our findings should alert conservationists to the need of further studies to better understand the underlying mechanisms and the magnitude of these changes in the small mammal community in Doñana.

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**Figure 1 – Doñana National Park**. The continuous line represents the border of the National Park (marine portion excluded). Landsat 5 Thematic Mapper (26/04/2004) downloaded from Earth Explorer, infrared false color composition (RGB= 543). Kindly provided by the LAST-EBD group.

**Figure 2** – **Skull measurements.** A skull of a specimen of *Apodemus sylvaticus* collected at Doñana. **A**) Lateral view of the cranium, **B**) Dorsal view, **C**) Ventral view: *M1*, first upper molar; *M2*, second upper molar; *M3*, third upper molar.

Figure 3 – Temporal changes in morphometric measurements. Changes in females (A) and males (B) (in %) of eight morphological measures and weight between period 1 (1978-1981) and period 2 (2006-2007). Numbers next to measures refer to percentage of reduction between the 1<sup>st</sup> and 2<sup>nd</sup> period. Only significant (at  $\alpha$ = 0.05) results are shown (except for ZW of females, p= 0.051). Notation: *HBL*, head-body length, *CTL*, cranial total length; *CBL*, condyle-basal length; *ZW*, zygomatic width; *DL*, diastema length; *EL*, ear length; *FL*, foot length; *TL*, tail length. Modified from Jubete (2007).



Fig. 1



Fig. 2



Fig. 3

**Table 1 -** Sample sizes for the different analyses. The response variables are shown in the left column. The top of the table refers to analyses of temporal trends and the bottom of the table to analyses of sexual dimorphism. Notation: *Sex*, sex of specimens (F, females - M, males); n, number of specimens used for the analyses; *Years*, years from which collected samples proceed; *P1* and *P2*, respectively period 1 (1978, 1979, 1980, 1981) and period 2 (2006-2007).

Temporal trend			
	Sex	n	Years
Body mass	F	<b>P1</b> :345; <b>P2</b> :16	<b>P1</b> :1978,1979,1980; <b>P2</b> :1981,2006,2007
	Μ	P1:505;P2:21	P1: 1978,1979,1980,1981; P2: 2006,2007
Body length (HBL)	F	P1:377; P2:16	P1: 1978,1979,1980,1981; P2: 2006,2007
	Μ	P1:550; P2:21	P1: 1978,1979,1980,1981; P2: 2006,2007
Cranial measurements	F	<b>P1:</b> 269; <b>P2</b> :16	P1: 1978,1979,1980,1981; P2: 2006,2007
	Μ	<b>P1</b> :382; <b>P2</b> :19	P1: 1978,1979,1980,1981; P2: 2006,2007
Extremities	F	<b>P1</b> :277; <b>P2</b> :16	P1: 1978,1979,1980,1981; P2: 2006,2007
measurements	Μ	<b>P1</b> :407; <b>P2</b> :21	P1: 1978,1979,1980,1981; P2: 2006,2007
Allometry	F	<b>P1:</b> 205; <b>P2:</b> 14	P1:1978,1979,1980,1981; P2: 2006,2007
	Μ	<b>P1:</b> 323; <b>P2:</b> 20	P1: 1978,1979,1980,1981; P2: 2006,2007
		Sexual dim	orphism
	Sex	n	Years
Size dimorphism	F-M	532	1978,1979,1980,1981
Allometric dimorphism	F-M	532	1978,1979,1980,1981