Annual weight variation and reproductive cycle of the wood mouse (*Apodemus sylvaticus*) in a Mediterranean environment

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ABSTRACT

This paper describes the weight variation and reproductive seasonal patterns of the wood mouse in a Mediterranean scrubland in southern Portugal. A total of 156 individuals were marked and followed up to 242 days. Summer corresponded to the non-breeding period in the study area, instead of winter, such as in other areas of central and northern Europe. As a consequence, a displacement of the annual density and weight cycles were observed. The higher densities, usually recorded before the non-reproductive period, were recorded during spring instead of summer. In addition, the typical weight depression of the non-reproductive period was reported in summer. Reproductive individuals were consistently heavier than non-reproductive, except in summer when a significant weight decrease was observed and in autumn when there were few subadults in the population. Juvenile males grew faster than juvenile females. However, there was little evidence of differences on growth of juveniles born at different times of the year.

KEY WORDS

Apodemus sylvaticus,
weight,
Mediterranean habitat,
reproduction,
density.

RÉSUMÉ

Variation annuelle du poids et cycle reproducteur du mulot sylvestre (Apodemus sylvaticus) dans un habitat méditerranéen.

L'influence des conditions d'environnement sur la croissance et la reproduction du mulot *Apodemus sylvaticus* font l'objet de cette étude. 156 individus ont été marqués et suivis pendant huit mois dans un habitat typiquement méditerranéen du Sud du Portugal. Contrairement à d'autres zones d'Europe du Nord, l'été est dans cette région, la période de non reproduction; on a constaté un déplacement du cycle annuel de densité de population et du poids des individus. Les fortes densités, habituellement observées en été, avant la période de reproduction, ont été observées au printemps; les individus reproducteurs étaient alors nettement plus lourds que les non reproducteurs. Mais en été, une diminution du poids a été constatée; en automne il n'y avait pas d'individus sub-adultes. On a observé une croissance plus rapide des mâles juvéniles, mais les juvéniles nés à des époques différentes de l'année ont montré peu de différences.

MOTS-CLÉS

Apodemus sylvaticus,
poids,
habitat Méditerranéen,
reproduction,
densité.

INTRODUCTION

Studies on small mammal's body weight have been addressed in several papers (e.g. Hansson & Jaarola 1989; Korn 1989; Hansson 1990, 1992; Zejda 1992). While short-term variations in individual body weight were usually attributed to differences in digestive tracts or female parturition (e.g. Holířov 1973; Gaisler & Zejda 1974) seasonal variations were mostly related to reproductive activity (e.g. Bengston *et al.* 1989). Breeding animals are usually heavier than non-breeding ones, especially due to gonadal or embryonic development. Individuals of the same cohort at different stages of maturity showing clear differences in body weight have been recorded (e.g. Batzli *et al.* 1977; Zejda 1992). Multiannual variations in weight are especially common in northern cyclic populations (Hansson & Henttonen 1985; Hansson 1989). In fact, weight dynamics are now known to be related to density cycles (e.g. Dawkins & Krebs 1978; Hansson & Jaarola 1989; Hansson 1992). Several studies have also addressed the geographical variation in the weight of different species (e.g. Corbet 1978; Korn 1989), in accordance with the Bergman's rule, postulating that body size in endothermic animals increases as latitude rises, as an adaptation to minimize the metabolic costs of thermoregulation in cold northern climates (Pantelejev 1985). The wood mouse (*Apodemus sylvaticus*) is an abundant and well-known species in Europe, but few studies have been undertaken in Mediterranean habitats (e.g. Moreno & Kufner 1988; Garcia 1993). The climate of this region is characterized by hot dry summers and relatively mild winters. As an adaptation to the severe summer drought some plants evolved from ligneous to herbaceous, from persistent to deciduous and from perennial to annual (Pignatti 1978). During the summer, vegetation is dominated by xerophytic shrubs and herbaceous vegetation is almost absent over large areas. These characteristics differ greatly from other European regions farther north where winters are cold and summers are relatively mild. Such differences might greatly affect habitat use and life history traits of Mediterranean populations.

Reproduction is one of the biological traits that might be influenced by differences in climate and vegetation, since water and food availability are key factors on the onset of reproduction (Lee & Gorman 2000). At non-equatorial latitudes the majority of female mammals become pregnant at a time of the year ensuring that offspring will be born during a season of mild temperatures and abundant water and food to support rapid growth and maturation (Bronson 1989). In the north of Europe the wood mouse reproduces mainly in spring and became reproductively inactive in winter (e.g. Montgomery *et al.* 1991; Jamon 1994; Wilson *et al.* 1996). As the Mediterranean summer is very dry and hot, it is expected that in Mediterranean populations, contrary to those in northern Europe, the non-breeding period occurs during summer. Because reproductive activity and body weight are highly related we also anticipate changes on the annual body weight cycle.

In the present study the annual variation in individual body weight was investigated in a population of *A. sylvaticus* living in a Mediterranean scrubland in southern Portugal (Évora). Our main purpose was to relate body weight variations to the reproductive pattern and to seasonal changes in environmental conditions.

METHODS

STUDY AREA

This study was carried out at Mitra (Évora, southern Portugal, 38° 32' N; 1° 07' W), between January 1999 and January 2000, over an area of 1.1 ha, included in a field station of the University of Évora. The climate in this region is classified in the dry mesomediterranean bioclimatic zone (Rivas-Martinez 1981), characterized by hot dry summers and mild winters. In summer, precipitation is usually absent while in the wettest season the average monthly precipitation is of 50 to 150 mm (I.N.A.G. 2002). Data from a meteorological station set up at Mitra, are shown in figure 1. During the period of this study, a clear seasonal fluctuation in precipitation was observed. Two peaks occurred in spring and autumn and, as expected, a period

of drought was recorded in summer. The highest temperature was reached in July (42.6 °C). Minimum temperatures reached below 0°C values between November and March.

The study site is included in a wider and continuous area of cork oak woodland. The vegetation is typically Mediterranean, dominated by tree and shrub species such as *Quercus coccifera*, *Arbutus unedo*, *Smilax aspera*, *Quercus suber*, *Quercus rotundifolia*, *Cistus salvifolius* and *Cistus ladanifer*. Herbaceous species, such as *Plantago lanceolata*, *Scilla monophylla*, *Cardamine hirsuta*, *Anagallis arvensis* and *Sanguisorba minor* were also present.

FIELD PROCEDURES

Trapping was carried out monthly for five consecutive nights on a permanent grid of 132 Sherman live-traps, set up at 10m intervals. Traps were baited with oat and sardine and supplied with cotton for bedding. Each morning first-caught mice were marked by toe-clipping for permanent identification with a unique sequence of toe clips (e.g. Slade *et al.* 1993; Andersen 1994; Dooley & Bowers 1996). Sex, reproductive condition, body weight and measurements (with an accuracy of 0.5 g and 1 mm, respectively) were recorded individually before releasing at the point of capture. Body weight was further obtained at each recapture. Mice with a greyish pelage or weighting less than 15g were considered juveniles; all the remaining were classified as adults (e.g. Flowerdew 1974; Fernandez *et al.* 1996). Males with large and scrotal testes and females in lactation, pregnant or with perforated vagina were considered as reproductive individuals (e.g. Gibson & Delany 1984; Foster & Gaines 1991; Morris 1996).

POPULATION SIZE AND SURVIVAL

The trapping procedure was designed according to the Pollock's robust design (Pollock 1982): the whole sampling was divided in several primary sampling periods (sessions/months) which were subdivided in several secondary sampling periods (days). It was considered that time between primary periods was sufficiently long to allow deaths, births and migration and that time between secondary periods was so short that those processes were

FIG. 1. – Mean (white squares), minimum and maximum (vertical lines) monthly temperatures and monthly precipitation (grey bars) in the study area from January 1999 to January 2000.

negligible. Data of secondary periods allowed the estimation of population size by statistical methods developed for closed populations (Pollock *et al.* 1989). Data of primary periods allowed to estimate survival with statistical methods developed for open populations. The use of this two sources of information (secondary and primary periods) makes the overall analysis more robust (Kendall 1999), which is suitable for small mammal studies (Paradis 1995). The program MARK 1.8 software (White 2000) was used in data analysis.

BODY WEIGHT ANALYSIS

For all juveniles captured more than once within a season, a relative growth rate (Fisher 1921) was calculated as:

$$RGR = (\log W_2 - \log W_1) / (t_2 - t_1)$$

where W_1 is the weight at first capture and W_2 is the weight of the first capture in the following month, t_1 is the time at first capture and t_2 is the time at first capture in the following month.

To analyse weight variation across seasons it was considered the weight at the first capture of each individual in each season. Juveniles were excluded from these analyses.

Non-parametric tests were used in comparisons among variables (Sokal & Rolf 1995).

RESULTS

REPRODUCTION, SURVIVAL AND POPULATION SIZE

The 12 trapping sessions (7920 trap-nights) resulted in the capture of 156 mice, 71 females and 85 males, of which 22 were caught as juveniles

FIG. 2. – Monthly densities and confidence intervals (lines), of total caught mice and numbers of reproductive (black bar) and non-reproductive (white bar) individuals.

TABLE 1. – Monthly survival rates (ϕ) and standard error (S.E.) of wood mice throughout an annual cycle.

Period	ϕ	S.E.
Jan-Feb	0,825	0,228055
Feb-Mar	0,811	0,000014
Mar-Apr	0,994	0,000004
Apr-May	0,983	0,000006
May-Jun	0,572	0,000012
Jun-Jul	0,373	0,000013
Jul-Aug	0,656	0,000013
Aug-Sep	0,688	0,000014
Sep-Oct	0,707	0,000014
Oct-Nov	0,412	0,127585
Nov-Dec	0,541	0,234142
Dec-Jan	0,796	0,202953

FIG. 3. – Median, minimum and maximum values of Relative Growth Rate (RGR) for juvenile males and females wood mice.

(10 females, 12 males). Reproductively active individuals were recorded throughout the year, except in June and July (Fig. 2), with peaks in March-April and in September-October. Reproductively inactive individuals were more abundant in spring months. During spring, population size reached the highest value of 60 ind/ha in May and decreased to 10 ind/ha in November-January.

Survival changed across seasons (Table 1). From March to May, survival reached the maximum value of almost 100%. On the contrary, in the beginning of summer survival decreased to values around 37%, rising up again in the beginning of autumn, although never reaching the high spring values.

BODY WEIGHT

Juveniles born in spring and winter have similar relative growth rates (Mann-Whitney U test: $Z = -0.3965$; $p = 0.6917$; $n = 16$) in spite of males growing faster than females (Fig. 3; Mann-Whitney U test: $Z = 2.2091$; $p = 0.0271$; $n = 16$) in both seasons. Overall adult males were heavier than females ($Z = -2.8831$, $p = 0.0039$, $n = 219$). Changes in mean body weight in both sexes followed a similar pattern across seasons, in agreement with their reproductive condition (Table 2). Reproductively active individuals were significantly heavier than inactive ones in spring (males $p = 0.0002$; females $p = 0.0001$) and winter (males $p = 0.0096$; females $p = 0.0036$). On the contrary, there were no differences between the mean weights of reproductive and non-reproductive individuals in summer (males $p = 0.3069$; females $p = 0.5508$) and autumn (males $p = 0.1296$; females $p = 0.6093$). In fact, the weight of reproductively active individuals in summer was the lowest of all seasons and very similar to the weight of inactive individuals, both for males and females. In autumn, the mean weights of reproductively active and inactive individuals were also similar but now due to the heavier weights achieved by inactive individuals.

DISCUSSION

In this study the influence of the Mediterranean-type climate of southern Portugal on reproduction,

TABLE 2. – Seasonal variation in mean body weight (g) of reproductive and non-reproductive males and females wood mice. p-value (p) for the Mann-Whitney U test statistics.

Season	Females								Males							
	Sexually inactive			Sexually active					Sexually inactive			Sexually active				
	mean	SD	n	mean	SD	n	Z	p	mean	SD	n	mean	SD	n	Z	p
Spring	18.963	2.825	41	27.500	2.302	6	-3.841	0.0001	21.082	3.4828	45	30.500	6.103	9	-3.749	0.0002
Summer	21.667	5.871	6	21.350	2.973	10	-0.597	0.5508	24.125	3.2923	8	22.700	3.967	10	1.021	0.3069
Autumn	26.000	6.538	7	25.643	4.679	7	0.511	0.6093	24.875	8.2601	4	31.708	3.454	12	-1.516	0.1296
Winter	18.083	2.060	6	25.094	5.302	16	-2.912	0.0036	21.026	2.9034	19	27.154	7.075	13	-2.590	0.0096

density and weight was assessed on a seasonal basis in the wood mouse. In comparison with other European populations a displacement of the annual reproductive cycle was observed. Contrary to the north of Europe, where winter is the non-reproductive season for the wood mouse (e.g. Bengtson *et al.* 1989; Montgomery *et al.* 1991; Jamon 1994; Wilson *et al.* 1996), in southern Portugal reproductive activity decreased in late spring and summer. In such months, when precipitation was almost absent, reproduction ceased. In fact, mice became reproductively active only in September, when temperatures were declining and after the first rains. At this time, species such as *Quercus coccifera*, *Arbutus unedo*, *Smilax aspera* and *Myrtus communis*, occurring at the study area, started to ripen their large and fleshy fruits (Blondel & Aronson 1999). As water and food availability are two of the major factors regulating the onset of reproduction (Lee & Gorman 2000) it was not unexpected that mice reproduce on this season. Similar findings have been already recorded in other Mediterranean populations (e.g. Moreno & Kufner 1988, Garcia 1993). In Doñana National Park (south of Spain), Moreno and Kufner (1988) had also recorded an absence of reproductive activity during summer which was attributed to the summer drought. They also justified the reproductive activity recorded in the autumn by a higher availability of food resources. Due to the displacement of the reproductive cycle a corresponding displacement of the annual density cycle was also recorded. The highest densities, normally recorded before the non-reproductive period (e.g. Gibson & Delany 1984;

Bengtson *et al.* 1989; Fernandez *et al.* 1996), have occurred in spring instead of autumn and the highest mortality rate, usually occurring during the non-reproductive period (e.g. Fernandez *et al.* 1996), was transferred to the summer. In the study area, mean population density lay between the limits usually reported for this species in European woodlands (Corbet & Harris 1991). Yet, spring values exceeded those reported by Moreno & Kufner (1988) in the south of Spain. Climate in the south of Spain is also typically Mediterranean, but the above study referred to was carried out in a scrubland of *Cistaceae*, while the present study was carried out over an area of more diverse and complex vegetation. This fact might be responsible for the higher numbers of *Apodemus* found during spring, when most of the perennial and annual plants germinate. Although in the studied mice mean body weights were similar to those found in other European populations (Gonsálbez & Claramunt 1982; Gibson & Delany 1984; Alcántara 1986, 1991), the displacement of both the non-reproductive period and the dynamic cycle has originated differences in the annual weight pattern. Mean body weights are usually higher during the reproductive period (e.g. Gibson & Delany 1984) and lower weights may be recorded when subadults are included in the population (e.g. Bengtson *et al.* 1989). The higher weight values during the reproductive period are due to high numbers of individuals that are reproducing. In active individuals weight increase results from testes and accessory glands growth, in males, and from embryos, foetuses and milk glands growth, in

females (Zejda 1992). Our results confirmed that mature mice were significantly heavier than immature. However, exceptions occurred in summer and autumn when the body weights of reproductively mature individuals and non-reproductive ones were similar. During summer, environmental conditions were probably very stressful and did not allow mice to reach the highest body weights found in other seasons. The weight depression in the summer, typical of the non-reproductive period in seasonal environments, has already been documented by Korn (1989). The low summer survival rate (0.373 from June to July) and the low summer reproductive rate corroborate the hypothesis that summer is a stressful period for the wood mouse in Mediterranean environments. During autumn, individuals that began reproducing have gained weight and reached the weights of the reproductively active individuals. However, mice that were not reproducing during this season had unusually high weights and attained similar weights of the reproductive ones. Contrary to the other seasons, in autumn, few subadults were recorded, probably due to the summer reproductive inactivity. Thus, inactive individuals caught during autumn were older than those captured in other seasons and were consequently heavier. In spring and winter, weights of reproductively inactive individuals were significantly lower than those of the reproductive ones. In these seasons many juveniles and subadults were present in the population and there was consequently a drop in the mean weights of the non-reproductive individuals (e.g. Bengtson *et al.* 1989).

In other small mammals populations it has been recorded that juveniles born immediately before the unfavourable season grew faster than juveniles born on other periods, as a way to reach sexual maturity and breed before this stressful period (e.g. Zejda 1992). However, our results did not corroborate the hypothesis that juveniles born before (spring juveniles) or after (autumn or winter juveniles) the unfavourable season grew in a different way. Out of the seven juveniles caught, born in spring, only four were recaptured several times. Out of these, two were captured during

summer and never reached sexual maturity. The remaining two were recaptured until autumn and became active in this season. Moreover, out of the fifteen juveniles caught, born in winter, only one was recaptured in breeding condition, still during winter. Out of the remaining individuals, six were recaptured during winter and eight until spring and none of these reached maturity. Although the results were not very robust, it seems that most of mice did not attain sexual maturity in the year of their birth. However, differences in growth rate of juvenile males and females were found. As previously referred to, males grew significantly faster than females (e.g. Quéré & Vincent 1987).

Hansson (1992) has suggested that smaller and lighter individuals should have a more pronounced weight depression in the non-reproductive season. Accordingly, this might justify why juveniles had not attained sexual maturity before summer. As for adults, in spite of their high numbers in spring, only few individuals, the heaviest, had reproduced. The heaviest mice probably dominate lighter mice when competing for mates and thus, only the heaviest breed. Competitive success in dense populations is usually related to body size (Dawkins & Krebs 1978), since large individuals are generally associated with dominance at intraspecific encounters in several animal species (Turner *et al.* 1969; Wauters & Dhondt 1992; Schoener & Schoener 1981; Dawkins & Krebs 1978; Lidicker & Ostfeld 1991). In fact, in May, when density attains the highest value of 60 ind/ha, only the heaviest older mice reproduce. Besides, this may represent for older mice their last opportunity to breed (Lee & Gorman 2000).

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REFERENCES

- ALCÂNTARA M. 1986. — *Preferências de habitat del ratón de campo (Apodemus sylvaticus L.) en medios agrícolas*. Graduate thesis, Complutense University, Madrid.
- ALCÂNTARA M. 1991. — Geographical variation in body size of the wood mouse *Apodemus sylvaticus* L. *Mammal Review* 21 (3): 143-150.
- ANDERSEN D. C. 1994. — Demographics of small mammals using anthropogenic riparian habitat in Arizona. *Journal of Wildlife Management* 58 (3): 445-454.
- BATZLI G. O., GETZ L. L. & HURLEY S. S. 1977. — Suppression of growth and reproduction of Microtine rodents by social factors. *Journal of Mammalogy* 58: 583-591.
- BENGTSON S., NILSSON A. & RUNDGREN S. 1989. — Population structure and dynamics of wood mouse *Apodemus sylvaticus* in Iceland. *Holarctic Ecology* 12: 351-368.
- BLONDEL J. & ARONSON J. 1999. — *Biology and Wildlife of Mediterranean Region*. Oxford University Press, Oxford.
- BRONSON F. H. 1989. — *Mammalian reproductive biology*. University of Chicago Press, Chicago.
- CORBET G. B. 1978. — *The mammals of the Palaearctic region: a taxonomic review*. Cornell University Press, London.
- CORBET G. B. & HARRIS S. (eds) 1991. — *The handbook of british mammals, third edition*. Blackwell scientific publication, Oxford.
- DAWKINS R. & KREBS J. R. 1978. — Animal signs: information or manipulation, in KREBS J. R. & DAVIES N. B. (eds.), *Behavioural ecology*. Blackwell, Oxford, pp. 282-309.
- DOOLEY J. L. & BOWERS M. A. 1996. — Influences of patch size and microhabitat on the demography of two old-field rodents. *Oikos* 75: 453-462.
- FERNANDEZ F.A.S., EVANS P.R. & DUNSTONE N. 1996. — Population dynamics of the wood mouse *Apodemus sylvaticus* (Rodentia: Muridae) in a Sitka spruce successional mosaic. *Journal of Zoology* 239: 717-730.
- FICHER A. R. 1921. — Some remarks on the methods formulated in a recent article on "The quantitative analysis of plant growth." *Annals of Applied Biology* 7: 367-372.
- FOSTER J. & GAINES M. S. 1991. — The effects of a successional habitat mosaic on a small mammal community. *Ecology* 72 (4): 1358-1373.
- FLOWERDEW J. R. 1974. — Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse *Apodemus sylvaticus*. *Journal of Animal Ecology* 43: 499-510.
- GAISLER J. & ZEDJA J. 1974. — Notes on a population of the water vole (*Arvicola terrestris* Linn.) on a pond. *Zoologické Listy* 23 (1): 19-33.
- GARCIA D. G. 1993. — Uso de microhabitat del ratón de campo (*Apodemus sylvaticus* L.) en robledales y áreas ecotonaes del Pirineo. *Doñana, Acta vertebrata* 20: 125-143.
- GIBSON D. ST C. & DELANY M. J. 1984. The population ecology of small rodents in Pennine woodlands. *Journal of Zoology* 203: 63-85.
- GONSÁLBES J. & CLARAMUNT T. 1982. — Sobre los roedores del Pirineo Catalán. *Pirineos* 117: 59-77.
- HANSSON L. 1989. — Ultimate factors in the winter weight depression of small mammals. *Holarctic Ecology* 12: 345-350.
- HANSSON L. 1990. — Ultimate factors in the winter weight depression of small mammals. *Mammalia* 54: 397-404.
- HANSSON L. 1992. — Fitness and life history correlates of weight variations in small mammals. *Oikos* 64: 479-484.
- HANSSON L. & HENTTONEN H. 1985. — Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* 67: 394-402.
- HANSSON L. & JAAROLA M. 1989. — Body size related to cyclicity in microtines: dominance behaviour or digestive efficiency? *Oikos* 55: 356-364.
- HOLIÖOV V. 1973. — Variation in weight of gastrointestinal tract with contents in *Clethrionomys glareolus* captured in snap-traps. *Zoologické Listy* 22 (4): 297-309.
- I.N.A.G. 2002. — Dados de base — Sistema Nacional de Informação de Recursos Hídricos. Instituto Nacional da Água. Available on line: http://snirh.inag.pt/snirh/dados_base/main_nav_fr.html
- JAMON M. 1994. — An analysis of trail-following behaviour in the wood mouse. *Apodemus sylvaticus*. *Animal behaviour* 47: 1127-1134.
- KENDALL W. L. 1999. — The Robust Design for Capture-Recapture Studies: Analysis Using Program MARK. <http://www.cnr.colostate.edu/gwhite/mark/Hungary/RobustDn/index.html>.
- KORN H. 1989. — The annual cycle in body weight of small mammals from the Transvaal, South Africa, as an adaptation to a subtropical seasonal environment. *Journal of Zoology* 218: 223-231.
- LEE T. M. & GORMAN M. R. 2000. — Timing of reproduction by the integration of photoperiod with other seasonal signals, in WALLIN K. &

- SCHNEIDER J. E. (eds), *Reproduction in context: Social and environmental influences on reproduction*. A Bradford book. The MIT press, pp. 191-218.
- LIDICKER W. Z. JR. & OSTFELD R. S. 1991. — Extra-large body size in California voles: causes and fitness consequences. *Oikos* 61: 108-121.
- MONTGOMERY W. I., WILSON W. L., HAMILTON R. & MCCARTNEY P. 1991. — Dispersion in the wood mouse, *Apodemus sylvaticus*: variable resources in time and space. *Journal of Animal Ecology* 60: 179-192.
- MORENO S. & KUFNER M. B. 1988. — Seasonal Patterns in the Wood Mouse Population in Mediterranean Scrubland. *Acta Theriologica* 33: 79-85.
- MORRIS D. W. 1996. — Temporal and spatial population dynamics among patches connected by habitat selection. *Oikos* 75: 207-219.
- PARADIS E. 1995. — Survival, immigration and habitat quality in the Mediterranean pine vole. *Journal of Animal Ecology* 64: 579-591.
- PANTELEJEV P. A. 1985. — On the character of geographical variation of Rodents in Central Europe. *Folia Zoologica* 37 (3): 175-185.
- PIGNATTI S. 1978. — Evolutionary trends in Mediterranean Flora and Vegetation. *Vegetation* 37 (3): 175-185.
- POLLOCK K. H. 1982. — A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46: 757-760.
- POLLOCK K. H., NICHOLS J. D. & HINES J. E. 1989. — Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1-97.
- QUÉRÉ J. P. & VINCENT J. P. 1987. — Données sur la prolificité et la croissance du mulot gris (*Apodemus sylvaticus* L., 1958) en élevage. *Mammalia* 51 (4): 605-611.
- RIVAS-MARTINEZ S. 1981. — Les étages bioclimatiques de la végétation de la péninsule ibérique. *Actas III Congr. Optima. Anales Jard. Bot. Madrid* 37: 251-268.
- SCHOENER T. W. & SCHOENER A. 1981. — Intraspecific variation in home range size in some Anolis lizards. *Ecology* 63: 809-823.
- SLADE N. A., EIFLER M. A., GRUENHAGEN N. M. & DALEVOS A. L. 1993. — Differential effectiveness of standard and long Sherman live-traps in capturing small mammals. *Journal of Mammalogy* 63: 809-823.
- SOKAL R. & ROFF F. 1995. — *Biometry*, 3rd ed. W. H. Freeman and Company, New York.
- TURNER F. B., JENNRICH R. I. & WEINTRAUB J. D. 1969. — Home ranges and body size of lizards. *Ecology* 50: 1076-1081.
- WAUTERS L. & DHONT A. A. 1992. — Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. *Animal behaviour* 43: 297-311.
- WHITE G. C. 2000. — *Program Mark 1.8. Mark and Recapture Survival rate estimation*. Department of Fishery and Wildlife. Colorado State University.
- WILSON W. L., MONTGOMERY W. I. & ELWOOD R. W. 1996. — The effects of experimental removal of male wood mice (*Apodemus sylvaticus*) on both male and female numbers. *Journal of Zoology* 239: 379-382.
- ZEJDA J. 1992. — The weight growth of the water vole (*Arvicola terrestris*) under natural conditions. *Folia Zoologica* 41: 213-219.

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