Reproductive potential of a vole pest (Arvicola scherman) in Spanish apple orchards

Aitor Somoano\(^1\), Marcos Miñarro\(^1\) and Jacint Ventura\(^2\)

\(^1\) Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA), Apdo. 13, 33300 Villaviciosa (Asturias), Spain  \(^2\) Universitat Autònoma de Barcelona, Facultat de Biociències, Departament de Biologia Animal, de Biologia Vegetal i d’Ecologia, 08193 Cerdanyola del Vallès (Barcelona), Spain

Abstract

Fossorial water voles, Arvicola scherman, feed on tree roots causing important damages in European apple orchards. Since the intensity of crop damage produced by rodents ultimately depends on their inherent capacity to increase their population, the main goal of this study was to determine the reproductive potential of the subspecies A. scherman cantabriae in apple orchards from Asturias (NW Spain), where voles breed over the whole year. Our results were compared with those reported for the subspecies A. scherman monticola from the Spanish Pyrenees (where reproduction ceases in winter). Sexual characteristics, body condition, relative age class and number of embryos were recorded from 422 females caught in apple orchards along two years. We found pregnant females all along the year, which were able to produce a high number of litters per year (7.30) although litter size was relatively moderate (first year: 3.87 embryos/female; second year: 3.63 embryos/females). The potential number of pups per female and year (first year: 28.25; second year: 26.50) was substantially higher than that reported for Pyrenean voles, what is probably related with differences in the length of the breeding season and in life histories between subspecies. In our population, the number of implanted embryos correlated positively with the body condition of the mother. Our results reveal that management efforts should not be seasonal as they used to be so far and invite to explore the physiological consequences of management practices.

Additional keywords: Arvicola scherman cantabriae; body condition; litter size; reproduction; rodent pest; fossorial water voles.

Abbreviations used: BCI (body condition index); CM (carcass mass); HBL (head and body length).

Authors’ contributions: MM and JV conceived and designed research. AS and MM conducted sampling. AS performed the necropsies and the study of specimens, and statistically analysed the data. AS, MM and JV wrote the manuscript.

Citation: Somoano, A.; Miñarro, M.; Ventura, J. (2016). Reproductive potential of a vole pest (Arvicola scherman) in Spanish apple orchards. Spanish Journal of Agricultural Research, Volume 14, Issue 4, e1008. http://dx.doi.org/10.5424/sjar/2016144-9870.

Received: 26 Apr 2016. Accepted: 25 Oct 2016.

Copyright © 2016 INIA. This is an open access article distributed under the terms of the Creative Commons Attribution-Non Commercial (by-nc) Spain 3.0 Licence, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Funding: Gobierno del Principado de Asturias; FEDER; Caja Rural de Gijón; CADAE; and AACOMASI (Project FICYT PC10-52). DOC-INIA Program (granted to MM); FPI-INIA Program (granted to AS).

Competing interests: The authors have declared that no competing interests exist.

Correspondence should be addressed to Aitor Somoano: aitors@serida.org, or Marcos Miñarro: mminarro@serida.org (shared corresponding authors).

Introduction

The montane water vole, Arvicola scherman (formerly fossorial form of Arvicola terrestris; for taxonomic consideration see Musser & Carleton, 2005), is one of the most harmful rodent species in the European farmlands (Walther et al., 2008; Blant et al., 2009; Delattre & Giraudoux, 2009; Miñarro et al., 2012). These voles live underground, dig extensive burrow systems and feed preferably on roots, bulbs and tubers (Airoldi, 1976). In fruit crops, fossorial water voles feed on bark and roots and may kill the trees (Meylan, 1977; Walther et al., 2008). Additionally, injuries to the root system make the trees less productive and more susceptible to falling down by winds or high fruit load due to deficient anchorage. Its occurrence in crops can cause important economic losses, being estimated in German orchards between 50 and 40,000 €/ha/year (Walther et al., 2008).

In the Iberian Peninsula two forms of this species are currently recognised (Ventura & Gosálbez, 1989; Musser & Carleton, 2005): A. scherman monticola, which occurs in the Pyrenees, and A. scherman cantabriae, distributed along the Cantabrian region (NW Spain) and in the northern tip of Portugal. These taxa are geograph-
ically isolated and show significant morphological differences, being cantabriae 40% lighter (Ventura, 1993). *Arvicola scherman* is officially considered a pest in Spain and preventive actions to reduce its population density have been recommended (BOE, 2008). In Asturias (NW Spain) this species has become one of the main causes of economical loss in apple orchards (Miñarro et al., 2012), a crop that in 2010 occupied 10,324 ha in this region (INDUROT, 2010) supposing the 32.4% of the total planted area intended to this crop in Spain (31,812 ha), whose national production, for example in 2013, reached 546,400 tons (Faostat, http://faostat.fao.org).

The effect of seasonal environmental factors, such as the decrease of temperature or food availability, can vary with altitude, which in turn affects rodent reproduction at population scale (Dunmire, 1960; Bronson, 1979; Murie et al., 1980; Zammuto & Millar, 1985; Hille & Rödel, 2014). Until now, studies about reproduction of *A. scherman* populations have been conducted above 400 m a.s.l., where all of them showed a delimited breeding season (Airoldi, 1978; Morel, 1981; Pascal, 1981; Ventura & Gosálbez, 1990a; Ventura et al., 1991). However, populations located in apple orchards below 270 m a.s.l. in Asturias breed continuously throughout the year (unpublished own data). Furthermore, it must be kept in mind that favourable habitats with plenty of food, such as crops, may allow rodents to invest their extra energy in increasing the reproductive effort (Doonan & Slade, 1995; Koskela et al., 1998; Díaz & Alonso, 2003; Eifler et al., 2003). Particularly, pregnant females of *A. scherman cantabriae* were detected over the whole year and, consequently, the recruitment of young specimens was continuous (unpublished own data). The optimal investment hypothesis predicts that litter size produced by a female should give the best reproductive success in a particular environment (Mapes et al., 1995). Therefore, reproductive potential among populations of *A. scherman* could vary through phenotypic plasticity or microevolution driven by the corresponding environmental conditions (Williams et al., 2014).

It is worth noting that in both, semiaquatic (*A. amphibius*; see Musser & Carleton, 2005) and fossorial water voles, the number of implanted embryos is positively correlated with the body dimensions of the mother (van Wijngaarden, 1954; Pelikán, 1972; Wie- land, 1973; Ventura & Gosálbez, 1990b). In that sense, the reproductive potential is closely related to the body condition in semiaquatic water vole populations, which reflects energy provisions (Evsikov et al., 2008). Likewise, a good body condition in pregnant females leads to a higher number of ovulated oocytes and implanted embryos, and decreases the risk of pregnancy failure (Evsikov et al., 2008; Nazarova & Evsikov, 2008; Yu-zhik et al., 2015). Furthermore, mother body condition in *A. amphibius* has also effects on the reproductive success, life span, body mass (Nazarova & Evsikov, 2008) and maturation of young (Yakovleva et al., 1997). Conversely, a worsening of the body condition might lead to lower fitness in females (Evsikov et al., 2008).

Management of rodent pests requires effective, specific, environmentally benign, economically feasible and socially acceptable approaches (Jacob, 2013). Thus, and especially in organic farming, there is a need for environmentally sustainable strategies, avoiding the use of rodenticides which generate genetic resistance in target species and are a risk to non-target wildlife (Rattner et al., 2014). Anticoagulant rodenticides have been routinely applied in France to control fossorial water vole populations since the 1990s (Defaut et al., 2009) with negative effects on predators (Coeurdassier et al., 2014) and scavengers (Montaz et al., 2014). Enhancing the implementation and success of sustainable control methods entail a deep knowledge of relevant aspects of the pest biology and ecology (Delattre & Giraudoux, 2009; Jacob, 2013; Ranchelli et al., 2016).

The reproductive characteristics of fossorial water voles in the Iberian Peninsula are known exclusively from studies on a population from the Aran Valley placed at about 900 m a.s.l. in the Spanish Pyrenees (Ventura & Gosálbez, 1990a, b). Thus, regarding the lack of information on this subject on *A. scherman* from NW Spain and given the pest condition of the species in this geographic area, the main aim of this study was to determine the reproductive potential of fossorial water voles in the Cantabrian region (*A. scherman cantabriae*), specifically in apple orchards located at low altitude in Asturias. Since body size and the length of the breeding season differ substantially between Pyrenean and Asturian populations (Ventura & Gosálbez, 1989, 1990a; unpublished own data), differences in the reproduction potential between those populations can be expected. Thus, a further goal of the present research was to elucidate this question by comparing our results on *A. scherman cantabriae* with those previously reported for *A. scherman monticolola*. The information obtained in this study could be useful to design effective control plans for fossorial water vole populations both in our study area and in others with similar environmental characteristics.

**Material and methods**

**Study site**

The study was conducted in ten experimental and commercial apple orchards throughout two years (first
year: February 2011-January 2012; second year: February 2012-January 2013). These orchards are separated from each other by 20.5 km as maximum and are located in two municipalities of the autonomous community of Asturias (NW Spain): Villaviciosa (43° 38’ 55” N, 5° 26’ 08” W) and Nava (43° 21’ 31” N, 5° 30’ 29” W). Their surface ranged from 1 to 6 ha and their altitude from 3 to 270 m a.s.l. Apples in Asturias are mainly produced in an area characterized by an irregular topography of smooth hills and valleys and distributed in a mosaic landscape of small agricultural plots separated by hedgerows and woodlands. The studied area has a temperate oceanic climate (Rivas-Martínez & Rivas-Sáenz, 2015) with abundant rainfall spread evenly along the year, and mild temperatures even in winter with low risk of frost and snowfall. The relatively high rainfall and fertile soils of Asturian meadows favor the establishment of evergreen and dense grass coverage in orchards all the year around (Díaz-González & Fernández-Prieto, 2005; Miñarro, 2012).

Specimen and data collection

A total of 422 female water voles were analysed. Each month, one or more orchards, depending on orchard surface and vole density, were visited for trapping. Individuals were captured with snap traps (Top-cat® Andermatt Biocontrol, Switzerland) placed in galleries. Traps were activated during the day and checked twice per day for five days maximum. Shortly after capture the specimens were cryopreserved to -20°C until the necropsy. The recommendation of the Directive of the European Parliament and of the Council on the Protection of Animals Used for Scientific Purposes (EU, 2010) was followed during the field work.

For each specimen, head and body length (HBL) and carcass mass (CM; body mass of the animal without neither the skin nor the thoracic and abdominal organs) were recorded using a digital calliper to the nearest 0.01 mm and a precision scale to the nearest 0.5 g, respectively. The body length of each embryo and the uterus of implantation were also registered. Litter size was evaluated according to the number of embryos implanted in uteri, discarding those showing macroscopic sign of resorption. Considering HBL range (1.4 - 38.1 mm) and mean value (12.5 mm) obtained in all embryos analysed, pregnant females whose embryos showed a HBL average lower than 6 mm were considered females in an early pregnancy state. The number of placental scars in each uterus was recorded.

The main criterion used to establish the sexual maturity state was the presence/absence of corpora lutea. Ovaries were extirpated and preserved in 70% ethanol until the analysis was conducted. Four longitudinal histological sections (sections of 5 μm thick separated between them 150 μm) were performed in the left ovary to obtain a whole representation of this organ. Sections were stained with hematoxylin-eosin. Other sexual parameters considered in each specimen were the following: development and vascularisation degree of the uteri, and presence and number of placental scars and/or embryos (Ventura & Gosálbez, 1990b). The sexual maturity states were the following: immature, specimens without corpora lutea, uteri poorly developed and vascularised, without placental scars; mature, individuals with corpora lutea, uteri completely developed and well or scarcely vascularised, and showing placental scars and/or embryos.

Specimens were distributed into six classes of relative age (0-V) according to the following criteria (for details see Ventura & Gosálbez, 1992): moulting stage, sturdiness of the mastoid process and the condylar process, the separation of angular process from the ascending branch of the mandible, and the values of the interorbital crest index, which relates the breadth of interorbital crests and the rostral length. The approximate age intervals corresponding to these relative age classes are the following (see Ventura & Gosálbez, 1992, and references therein): class 0, 0-3 weeks; class I, 3-6 weeks; class II, 6-10 weeks; class III, 10-14 weeks; class IV; specimens older than 14 weeks that have not overwintered; class V, specimens that have overwintered at least once. To assess differences on CM and body condition index (see below) between relative age classes, a random selection of non-pregnant females from relative age classes IV and V was used in an attempt to balance the number of analysed specimens in each age class.

Data analyses

The pregnancy frequency (F) gives information about how many times a female may become pregnant and was evaluated according to the method described by Emlen & Davis (1948): \( F = \frac{(T/V)}{R} \); where \( T \) = duration of the study (days), \( V \) = number of days in which pregnancy is visible (16 days: see Ventura & Gosálbez, 1989 and references therein) and \( R \) = ratio of visible pregnant females in relation to the total number of matures ones.

Mann-Whitney U-tests were used to assess interannual differences in litter size and differences in embryo implantation in each uterus. Differences in litter size and the number of placental scars among relative age classes were assessed by Kruskal-Wallis
tests. Then, Mann-Whitney U-tests with Bonferroni adjustment for multiple tests ($\alpha = 0.05/\text{number of pairwise comparisons}$) were used to establish differences among relative age classes.

The individual body condition index (BCI) was calculated as the difference between measured CM and the theoretically expected CM, which was obtained from the corresponding regressions against HBL after logarithmic transformation of the data of both variables (Evsikov et al., 2008). Females with visible signs of gestation were not taken into account to construct the regression equations. One-way ANOVA tests was used to assess differences in CM among relative age classes. This same test was also used to assess differences between years in BCI of mature non-pregnant and pregnant females. General linear models (GLM) were used to assess differences in BCI between years and relative age classes of non-pregnant and pregnant females. Tukey HSD tests were used to establish differences in BCI and CM among relative age classes. Changes in BCI of mature non-pregnant females along time were assessed by a Spearman correlation. This method was also used to determine relationships between pairs of the following variables: CM, BCI, litter size, number of placental scars and age class. Statistical analyses were performed with SPSS v22.0 (IBM Corp., Armonk, NY, 2013).

## Results

### Pregnant females

Out of the 422 females analysed, 101 females (32.0% of total mature females; $n = 316$) were pregnant; 55 of them were obtained during the first year and 46 during the second one (Table 1). Pregnant females were found in all months excepting January 2013. The youngest pregnant females corresponded to age class III and were detected in all seasons (Table 1).

### Litter size

The total number of implanted embryos was 380, distributed in litters formed by 1-9 embryos (Table 2). The most frequent litter size was formed by four (35.6%, $n = 36$) and three (33.7%, $n = 34$) embryos, and the less frequent by nine (0.9%, $n = 1$). The mean ($\pm$ SE) litter size was 3.7 ($\pm$ 0.2).

### Table 1. Number and percentage of pregnant females respect to the total number of mature females according to the relative age class and the month of capture in *Arvicola scherman cantabriae*.

| Year | Month | Age class | Total | N matures | % pregnant |
|------|-------|-----------|-------|-----------|------------|
|      |       | III  | IV  | V  |   |               |
| 1st 2011 | Feb  | 1    | 1   | 2   | 9 | 22.2          |
|        | Mar  | 1    | 1   | 2   | 19| 10.5          |
|        | Apr  | 1    | 2   | 1   | 4 | 44.4          |
|        | May  | 3    | 4   | 2   | 9 | 45.0          |
|        | Jun  | 1    | 1   | 4   | 6 | 50.0          |
|        | Jul  | 1    | 2   | 3   | 13| 23.1          |
|        | Aug  | 2    | 2   | 6   | 12| 50.0          |
|        | Sep  | 3    | 1   | 4   | 16| 25.0          |
|        | Oct  | 3    | 3   | 6   | 14| 42.9          |
|        | Nov  | 3    | 2   | 1   | 6 | 40.0          |
|        | Dec  | 1    | 2   | 2   | 22| 9.1           |
|        | Jan  | 2    | 2   | 5   | 12| 41.7          |
| 2nd 2012 | Feb  | 1    | 1   | 1   | 11| 9.1           |
|        | Mar  | 1    | 2   | 2   | 5 | 38.5          |
|        | Apr  | 1    | 1   | 2   | 12| 16.7          |
|        | May  | 4    | 4   | 8   | 14| 57.1          |
|        | Jun  | 1    | 1   | 6   | 8 | 53.3          |
|        | Jul  | 1    | 2   | 2   | 11| 18.2          |
|        | Aug  | 1    | 3   | 4   | 13| 30.8          |
|        | Sep  | 1    | 1   | 10  | 10.0       |
|        | Oct  | 2    | 2   | 1   | 11| 18.2          |
|        | Nov  | 1    | 5   | 2   | 8 | 57.1          |
|        | Dec  | 2    | 2   | 1   | 5 | 55.6          |
| 2013   | Jan  | 0    | 9   | 0   | 0   |
| Total  | 17   | 43   | 41  | 101| 315| 32.1         |
Reproductive potential of *Arvicola scherman* in orchards

The number of implanted embryos per female was 3.76 (± 0.12). There were no inter-annual significant differences in the litter size (Fig. 1) (first year: 3.87 ± 0.18 (SE); second year: 3.63 ± 0.14 (SE); U = 1165.0; p = 0.475).

The mean number of embryos in the right uterus (2.11 ± 0.11) was significantly higher than the number in the left one (1.66 ± 0.10) (U = 3031.5; p < 0.01). Considering pregnancy states, females in early pregnancy state (n = 27) did not show significant differences in the average of embryos implanted in each uterus (right uterus: 1.92 ± 0.21; left uterus: 1.48 ± 0.11 (SE); U = 1260.0; p < 0.001).

Macroscopic signs of embryonic resorption were observed in 11 females in advanced pregnancy (10.9%) (Table 2). Some resorption signs were observed in 12 embryos (3.1%), in litter sizes of three (n = 4), four (n = 4) or five embryos (n = 4). Moreover, there were 14 litters with unilateral implantations (14.1%); 9 of these litters were found in the right uterus (R: right, L: left; 4R-0L, n = 2; 3R-0L, n = 3; 2R-0L, n = 2; 1R-0L, n = 2) and 5 in the left one (0R-3L, n = 4; 0R-1L, n = 1).

Litter size correlated positively with CM (r = 0.294; p < 0.01) (Fig. 2a) and increased with age (r = 0.217; p < 0.05), although it was not possible to establish differences among classes (H’ = 4.881, p = 0.087).

**Table 2.** Litter size and number of individuals with resorbed embryos along the sampling period in *Arvicola scherman cantabriae*.

| Year | Month | N | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | Mean | SE | Cases of resorbed embryos |
|------|-------|---|---|---|---|---|---|---|---|---|---|------|----|--------------------------|
| 1st  | Feb   | 2 | 1 | 1 |   |   |   |   |   |   |   | 2.50 | 0.50 | 1 |                  |
|      | Mar   | 2 |   | 2 |   |   |   |   |   |   |   | 5.00 |     |   |                  |
|      | Apr   | 4 | 1 | 1 | 2 |   |   |   |   |   |   | 4.75 | 0.75 |   |                  |
|      | May   | 9 | 1 | 1 | 4 | 2 |   |   | 1 |   |   | 4.44 | 0.65 | 1 |                  |
|      | Jun   | 6 | 1 | 3 | 1 | 1 |   |   |   |   |   | 3.33 | 0.42 | 1 |                  |
|      | Jul   | 3 | 1 | 1 | 1 |   |   |   |   |   |   | 4.33 | 0.88 |   |                  |
|      | Aug   | 6 | 3 | 2 | 1 |   |   |   |   |   |   | 3.67 | 0.33 | 1 |                  |
|      | Sep   | 4 | 1 |   | 1 | 1 |   |   |   |   |   | 4.00 | 1.08 |   |                  |
|      | Oct   | 6 | 1 | 3 | 2 |   |   |   |   |   |   | 4.17 | 0.31 | 1 |                  |
|      | Nov   | 6 | 1 | 4 | 1 |   |   |   |   |   |   | 3.00 | 0.52 | 1 |                  |
|      | Dec   | 2 | 1 |   |   |   |   |   |   |   |   | 4.50 | 0.50 | 1 |                  |
|      | Jan   | 5 | 4 |   | 1 |   |   |   |   |   |   | 3.20 | 0.20 | 1 |                  |
| 2nd  | Feb   | 1 | 1 |   |   |   |   |   |   |   |   | 3.00 |     |   |                  |
|      | Mar   | 5 | 1 | 1 | 3 |   |   |   |   |   |   | 4.40 | 0.40 | 1 |                  |
|      | Apr   | 2 | 2 |   |   |   |   |   |   |   |   | 4.00 |     |   |                  |
|      | May   | 8 | 1 | 4 | 2 | 1 |   |   |   |   |   | 4.38 | 0.32 |   |                  |
|      | Jun   | 8 | 1 | 3 | 4 |   |   |   |   |   |   | 3.38 | 0.26 | 2 |                  |
|      | Jul   | 2 | 2 |   |   |   |   |   |   |   |   | 4.00 |     |   |                  |
|      | Aug   | 4 | 2 | 2 |   |   |   |   |   |   |   | 3.50 | 0.29 |   |                  |
|      | Sep   | 1 | 1 |   |   |   |   |   |   |   |   | 3.00 |     |   |                  |
|      | Oct   | 2 | 1 | 1 |   |   |   |   |   |   |   | 3.50 | 0.50 |   |                  |
|      | Nov   | 8 | 1 | 1 | 2 | 4 |   |   |   |   |   | 3.13 | 0.40 |   |                  |
|      | Dec   | 5 | 1 | 3 | 1 |   |   |   |   |   |   | 3.00 | 0.32 | 1 |                  |
|      | Jan   | 0 |   |   |   |   |   |   |   |   |   | 3.00 |     |   |                  |
| Total |      | 101 | 3 | 6 | 34 | 36 | 16 | 5 |   | 1 | 3.76 | 0.12 | 11 |                  |

| %    | 100 | 3.0 | 5.9 | 33.7 | 35.6 | 15.8 | 5.0 |   | 0.9 | 10.9 |       |     |               |

**Figure 1.** Frequency of litter size per year in the sample of *Arvicola scherman cantabriae* analysed.
It is worth mentioning that the only pregnant female with 9 embryos showed an extremely low CM value (-0.0294). So, we considered this individual as outlier and therefore it was discarded in the regression analysis. The number of placental scars per female ranged from 1 to 15, being four (13.8%) and three (12.0%) the most frequent values; this variable increased significantly with both relative age (rs = 0.439; p < 0.001) (Table 3) and CM (r_s = 0.218; p < 0.05) (Fig. 2b).

### Potential fecundity

The ratio of visible pregnant females for the first year of the study was 0.32 (55 out of 173 mature females). Accordingly, the potential number of litters per mature female during the breeding season was 7.30 (F = (365/16)-0.32). The average litter size was 3.87 and the potential number of offspring by female was 28.25 (3.87-7.30). For the second year, the ratio of visible pregnant females was also 0.32 (46/142) and the potential number of litters was also 7.30. However, the average litter size was 3.63, and hence the potential number of offspring by female was slightly lower (26.50).

### Body condition index

The BCI of non-pregnant females did not vary significantly with the relative age (F_{5, 214} = 1.661; p = 0.145) neither between years (F_{1, 214} = 0.057; p = 0.811). The result of the interaction of both factors showed that differences in BCI among age classes depend on the year (F_{5, 214} = 2.364; p < 0.05) (Table 4). Moreover, in pregnant females there were no significant differences in BCI among relative age classes (F_{2, 94} = 2.582; p = 0.081) neither between years (F_{1, 94} = 0.193; p = 0.662). Nevertheless, the interaction between relative age class and year in pregnant females showed that differences in BCI among age classes do not depend on the year (F_{2, 94} = 0.444; p = 0.643) (Table 4). A significant positive correlation between BCI and litter size was observed (r_s = 0.230; p < 0.05) (Fig. 3).

Considering only mature specimens, mean values of BCI of non-pregnant females were significantly higher in the first year than in the second one (F_{1, 211} = 6.257; p < 0.05); no significant inter-annual differences were found for pregnant females (F_{1, 94} = 0.006; p = 0.938) (Table 4). Moreover, BCI was significantly higher in pregnant females respect to non-pregnant ones in the second year (F_{1, 137} = 9.726; p < 0.01); whereas no significant differences between these groups were found.
Reproductive potential of *Arvicola scherman* in orchards

in the first year (F1, 172 = 1.380; *p* = 0.242) (Table 4). In mature non-pregnant females BCI diminished along the sampling period (r = -0.197; *p* < 0.05) (Fig. 4).

**Table 4.** Body condition index (BCI) of non-pregnant and pregnant females for each age class and for mature females in *Arvicola scherman cantabriae*. Significant differences in BCI among relative age classes for pregnant and non-pregnant females are indicated by different lower case letters. Significant differences in BCI between years in mature non-pregnant and pregnant females are indicated by different capital letters.

| Age class | Year | Non-pregnant females | Pregnant females |
|-----------|------|----------------------|------------------|
|           |      | N | Mean | SE | Min  | Max  | N | Mean | SE | Min  | Max  |
| 0         | 1    | 7 | -0.0584 | 0.0258 | -0.1909 | 0.0251 | a |
| I         | 33   | -0.0004 | 0.0120 | -0.2124 | 0.1177 | ab |
| II        | 16   | -0.0141 | 0.0113 | -0.1181 | 0.0422 | ab |
| III       | 19   | 0.0157 | 0.0140 | -0.1138 | 0.1367 | b |
| IV        | 20   | 0.0123 | 0.0099 | -0.0546 | 0.0920 | b |
| V         | 20   | 0.0194 | 0.0115 | -0.0995 | 0.1079 | b |
| 0         | 2    | 2 | 0.0644 | 0.0133 | 0.0511 | 0.0776 | a |
| I         | 7    | -0.0337 | 0.0133 | -0.0995 | 0.0007 | a |
| II        | 28   | -0.0222 | 0.0081 | -0.1277 | 0.0945 | a |
| III       | 15   | -0.0041 | 0.0099 | -0.0922 | 0.0631 | a |
| IV        | 28   | -0.0141 | 0.0098 | -0.1245 | 0.1568 | a |
| V         | 31   | -0.0015 | 0.0103 | -0.1577 | 0.0935 | a |
| Matures   | 1    | 118 | 0.0106 | 0.0047 | -0.1803 | 0.1615 | A |
| 2         | 96   | -0.0068 | 0.0051 | -0.1577 | 0.1568 | B |

**Figure 3.** Correlation between body condition index (BCI) and litter size in *Arvicola scherman cantabriae*.

Discussion

General results of this study reveal that *A. scherman cantabriae* inhabiting Asturian apple orchards shows higher reproductive potential than Pyrenean fossorial water voles. Specifically, during the study period each female was able to produce 7.3 litters in a year, a value that to our knowledge is the highest one reported for *A. scherman* and also in the closely related species *A. amphibius* (2.0 - 7.1 litters/year) (van Wijngaarden, 1954; Tupikova & Švecov, 1956; Hamar & Marin, 1962; Kminiak, 1968; Pelikán, 1972; Wieland, 1973; Ventura & Gosálbez, 1990b). On the contrary, the average litter size we found in *A. scherman cantabriae* (3.76 embryos per female) was among the smallest values reported for *A. scherman* and also for *A. amphibius* (Perry, 1943; Van Wijngaarden, 1954; Maksimov, 1959; Kminiak, 1968; Panteleyev, 1968; Stoddart, 1971; Pelikán, 1972; Wieland, 1973; Kratochvíl, 1974; Blake, 1982; Evsikov et al., 1989; Ventura & Gosálbez, 1990b). As a result of these values, the potential number of offspring per female and year reached 28.25 in Cantabrian voles, which is higher than the value indicated for *A. scherman monticola* (23.5) (Ventura & Gosálbez, 1990b). Therefore, populations of *A. scherman* can show different reproductive potential in the Iberian Peninsula depending, at least partially, on the habitat, which might ultimately determine their role as agricultural pest.

The length of the breeding season is a critical factor in determining litter size in small mammals: reproduction can be extended throughout the year at lower elevations, whereas in higher elevations larger litters are needed to sustain an equal level of reproduction during a shorter breeding season (Dunmire, 1960; Smith & McGinnis, 1968; Spencer & Steinhoff, 1968; Innes, 1978; Tkadlec & Zejda, 1998). Specifically in *Arvicola*, this pattern was found in semiaquatic water voles (Kratochvíl, 1974). In that sense, apple orchards in Asturias are located in a temperate hyperoceanic climate (Rivas-Martínez & Rivas-Sáenz, 2015), which implies benign weather condition that allows fossorial water voles to breed continuously along the year (unpublished own data), whereas the breeding season of *A. scherman* is limited to the period March-November.
in the Pyrenees (Ventura & Gosálbez, 1990a). These differences between Spanish populations can be explained by an adaptation to seasonal changes of each geographic zone, as occur in other rodent species (Hansen et al., 1999; Solonen, 2006). Although differences in litter size between the Cantabrian and Pyrenean populations can be related with an altitudinal effect, intrinsic factors could also be involved. For example, differences in ovulation rate between wild populations of the house mouse (Mus musculus) are mainly determined by body size, whereas the influence of extrinsic factors is low (Jacob et al., 2007). Therefore, a smaller litter size in the small-sized A. scherman cantabriae (Ventura & Gosálbez, 1989; Ventura, 1993) cannot be discarded as an own characteristic of the subspecies. Additionally, we found in our sample that the body size of the mother was significantly correlated with the number of implanted embryos, result that is concordant with that reported for A. scherman monticola (Ventura & Gosálbez, 1990b). Thus, an intrapopulation effect of the relationship between body size and litter size can be added to that found between these variables in an evolutionary context.

As expected and also as observed in A. scherman monticola (Ventura & Gosálbez, 1990b), the number of placental scars increased with age in our population. Differences in the range of this variable between Cantabrian (1-15) and Pyrenean (2-20; Ventura & Gosálbez, 1990b) A. scherman are probably due to differences, at a population level, in the relationship between the number of reproductive events and litter size, and also to differences in the persistence of placental scars. Pregnant females with macroscopic signs of resorption were also found in other populations of both A. scherman and A. amphibius (van Wijngaarden, 1954; Pelikán, 1972; Wieland, 1973; Ventura & Gosálbez, 1990b). In our sample, females in early pregnancy had similar embryonic implantation in each uterus, which suggests a balanced ovulation in both ovaries. Nevertheless, a significantly larger number of embryos implanted in the right uterus was observed for the total pregnant females, which might be due to embryo resorption. Indeed, an unequal uteri-functioning has been well described formerly in mouse and rat (Wiebold & Becker, 1987 and references therein). Moreover, Isakov et al. (2012) found in A. amphibius that an important percentage of embryos suffer a resorption in the uteri (16.7%) caused probably by mutation processes.

Body condition (relationship between the carcass mass and body length) indicates energy provision and plays an important role in the reproductive potential. Specifically, in A. amphibius it has been indicated that a good body condition in pregnant females leads to higher number of ovulated oocytes and implanted embryos, and decreases the risk of pregnancy failure (Evskov et al., 2008; Nazarova & Evskov, 2008; Yuzhik et al., 2015). This seems to agree with our results in A. scherman cantabriae regarding the increase of litter size with the BCI of the mother. Although a clear correlation between the number of implanted embryos and the body mass of the mother has also been reported in both A. scherman and A. amphibius (Ventura & Gosálbez, 1990b and references therein), our data suggest ultimately that the BCI is the key. Therefore, the body condition of the mother seems to be one of the main factors involved in the variation of the reproductive potential in Cantabrian voles.

The succession of monthly samplings during our two-year study involved a population control by removing specimens of both sexes from the burrow. Since the burrow system of fossorial water voles is generally
inhabited by a breeding couple with their offspring (Airoldi, 1976, 1978; Morel, 1981; unpublished own data) and its maintenance and the storage of food are performed by the couple (Airoldi, 1976), the removal of the male mate might suppose a handicap for the female. In this situation, the female might face the maintenance of the burrow and the acquisition of food by its own until de arrival of a new partner which in turns can induce a decrease of the body condition, as we observed in mature non-pregnant females along this study period. Ultimately, this fact might have negative consequences on the reproductive success as it has been reported for several arvicoline species (Ostfeld, 1985).

As conclusions, the reproductive potential of *A. scherman cantabriae* in areas of NW Spain located at low altitude and with a temperate hyperoceanic climate is relatively high in comparison with that of fossorial water voles from the Pyrenees. Specifically, mild temperatures and enough resource availability along the whole year in our study area allow fossorial water voles to breed continuously and to perform a greater number of reproductive events per year than *A. scherman moniticola*. Conversely, the favourable environmental conditions in the Pyrenean meadows are restricted to a part of the year, what leads voles to concentrate its energy in fewer but larger litters. Therefore, the smaller litter size in *A. scherman cantabriae* seems to fit with a different reproductive pattern, in which the variation in this parameter within the population may be due, at least in part, to the body condition of the mother.

Our results show that a female can produce almost 30 new specimens distributed along the whole year, what means a continuous and considerably high recruitment of juvenile specimens to the population. Such a situation suggests that management efforts should not be seasonal as they used to be so far, as it was generally assumed that reproduction stopped in winter. The recommended strategy was to increase control activity in winter in order to remove adults before the hypothetical breeding season, which was expected to start in spring. However, our results showing a continuous breeding season suggest extending these practices along the whole year. We do not mean to increase the effort (especially in the case of rodenticides given the associated environmental issues) but just that control practices could have a similar effect with independence of the time of the year. Also important to avoid secondary effects on non-target animals, surface signs of activity of *A. scherman* should be distinguished from those of *Talpa occidentalis*, an innocuous species inhabiting also apple orchards (Miñarro et al., 2012). For the same reason, alternative strategies, such as fences to avoid invasions from dispersal juvenile specimens from nearby source demes (Saucy & Schneider, 1998; Saucy, 2002; Walther & Fuelling, 2010) should be also maintained all the year. The effectiveness of other sustainable control management strategies, such as frequent mowing (Morilhat et al., 2007; Jacob, 2008), livestock grazing (Defaut et al., 2009) or the use of repellents (Fischer et al., 2013) should be explored in our particular case. As mentioned for *A. amphibius*, mother body condition might also have other physiological consequences in the offspring, affecting the reproductive success, life span, body mass and maturation of young (Yakovleva et al., 1997; Nazarova & Evsikov, 2008). Since population density and the subsequent damage to crops could be ultimately proportional to the population growth, which in turn depends on the reproductive effort (Ostfeld, 1985; Cerqueira et al., 2006), further studies focused on the physiological consequences of management practices (those creating a more disadvantageous environment; Morilhat et al., 2007; Jacob, 2008; Defaut et al., 2009) will be welcome to unravel their effect on the reproductive fitness in *A. scherman*, and to evaluate their feasibility as alternative control strategies.

**Acknowledgements**

The authors are grateful to growers who allowed access to their orchards for obtaining voles analysed in this study.

**References**

Airoldi JP, 1976. Le terrier de la forme fouisseuse du campagnol terrestre, *Arvicola terrestris scherman* Shaw (Mammalia, Rodentia). Zeitschrift für Säugetierkunde 41: 23-42.

Airoldi JP, 1978. Etude par capture et recapture d’une population de campagnols terrestres *Arvicola terrestris scherman* Shaw. Terre et Vie 32: 3-45.

Blake BH, 1982. Reproduction in captive water voles, *Arvicola terrestris*. J Zool 198: 524-529.

Blant M, Ducommun A, Beuret B, Poitry R, Joseph E, 2009. Influence du paysage et du sol sur les pullulations du campagnol terrestre dans le Jura suisse. Revue Suisse d’Agriculture 41: 301-307.

BOE, 2008. Royal decree 409/2008, of 28 March, that established national program for controlling pests of field voles. Boletín Oficial del Estado (Spain) No. 86: 19217-19219.

Bronson MT, 1979. Altitudinal variation in the life history of the golden-mantled ground squirrel (*Spermophilus lateralis*). Ecology 60: 272-279. http://dx.doi.org/10.2307/1937655.

Cerqueira D, De Sousa B, Gabrion C, Giraudoux P, Quéré JP, Delattre P, 2006. Cyclic changes in the population structure and reproductive pattern of the water vole, *Ar-
vicola terrestris Linnaeus, 1758. Mammalian Biology / Zeitschrift für Säugetierkunde 71: 193-202.

Coeurdassier M, Riols R, Decors A, Mionnet A, David F, Quintaine T, Truchetet D, Scheifler R, Giraudoux P. 2014. Unintentional wildlife poisoning and proposals for sustainable management of rodents. Conserv Biol 28: 315-321. http://dx.doi.org/10.1111/cobi.12230.

Defaut R, Note P, Chabalier C, Couval G, Truchetet D, Giraudoux P. 2009. Le campagnol terrestre. Éditions Que, Versailles Cedex.

Delattre P, Giraudoux P. 2009. Le campagnol terrestre. Prévention et contrôle des populations. Éditions Que, Versailles Cedex. 263 pp.

Díaz M, Alonso CL. 2003. Wood mouse Apodemus sylvaticus. Delattre P, Giraudoux P (eds.). pp: 143-153. Éditions Que, Versailles Cedex.

Díaz-González TE, Fernández-Prieto JA. 2005. Prados y pastos cantábricos: origen y diversidad. In: Producciones agropanaderas: Gestión eficiente y conservación del medio natural, De la Roza B, Martínez A, Carballal A (eds.). pp: 699-730. Vol. II. XLV Reunión Científica de la SEEP, SERIDA, Gijón.

Doonan TJ, Slade NA, Doonan TJ. 2003. Effects of supplemental food on population dynamics of cotton rats, Sigmodon hispidus. Ecology 84: 2680-2691. http://dx.doi.org/10.1890/02-0534.

Díaz-González TE, Fernandez-Prieto JA. 2005. Prados y pastos cantábricos: origen y diversidad. In: Producciones agropanaderas: Gestión eficiente y conservación del medio natural, De la Roza B, Martínez A, Carballal A (eds.). pp: 699-730. Vol. II. XLV Reunión Científica de la SEEP, SERIDA, Gijón.

Dunmire WW. 1960. An altitudinal survey of reproduction and adult cotton rats (Sigmodon hispidus) in Kansas, USA. Acta Oecologica 24: 187-193. http://dx.doi.org/10.1016/S1146-609X(03)00084-5.

Eifler MA, Slade NA, Doonan TJ. 1995. Effects of supplemental food on the growth rates of neonatal, young, and adult cotton rats (Sigmodon hispidus) in north eastern Kansas, USA. Acta Oecologica 24: 187-193. http://dx.doi.org/10.1016/S1146-609X(03)00084-5.

Emlen JT, Davis DE. 1948. Determination of reproductive rates in rat populations by examination of carcasses. Physiol Zool 21: 59-65. http://dx.doi.org/10.1086/physzool.21.1.30151981.

EU. 2010. Directive 2010/63/EU Horizontal Legislation on the Protection of European Animal Used for Scientific Purposes. Official Journal of European Union L 276/33-276/79.

Evsikov VI, Skorova SV, Nazarova GG, Moshkin MP. 1989. Photoperiod effect on growth and reproductive functions in water vole (Arvicola terrestris L.). Ekologiya 6: 58-63.

Evsikov VI, Nazarova GG, Muzyka VY. 2008. Body condition and reproductive characteristics of female water voles (Arvicola terrestris L.). Russ J Ecol 39: 414-417. http://dx.doi.org/10.1111/j.1439-0426.2008.01005.x.

Fischer D, Imholt C, Pelz HJ, Wink M, Prokop A, Jacob J. 2013. The repelling effect of plant secondary metabolites on water voles, Arvicola amphibius. Pest Manage Sci 69: 437-443. http://dx.doi.org/10.1002/ps.3438.

Fischer D, Imholt C, Pelz HJ, Wink M, Prokop A, Jacob J. 2013. The repelling effect of plant secondary metabolites on water voles, Arvicola amphibius. Pest Manage Sci 69: 437-443. http://dx.doi.org/10.1002/ps.3438.

Hamar M, Marin D. 1962. Zur Biologie von Arvicola terrestris scherman Shaw 1801 in Rumänien. Travaux du Muséum d’Histoire Naturelle “Grigore Antipa” 3: 401-421.

Hansen TF, Stenseth NC, Henttonen H. 1999. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. The American Naturalist 154: 129-139. http://dx.doi.org/10.1086/303229.

Hille SM, Rödel HG. 2014. Small-scale altitudinal effects on reproduction in bank voles. Mammalian Biology 79: 90-95. http://dx.doi.org/10.1016/j.mambio.2013.09.001.

INDUROT, 2010. Cartografía del manzano en el Principado de Asturias. Consejería de Medio Rural y Pesca. Gobierno del Principado de Asturias, Mieres, Spain.

Innes DG. 1978. A reexamination of litter size in some North American microtines. Can J Zool 56: 1488-1496. http://dx.doi.org/10.1139/z78-206.

Isaková GK, Nazarova GG, Evsikov VI. 2012. Early embryonic mortality in the water vole (Arvicola terrestris L.). Russ J Develop Biol 43: 244-247. http://dx.doi.org/10.1134/S1063260412040042.

Jacob J. 2008. Response of small rodents to manipulations of vegetation height in agro-ecosystems. Integrative Zoology 3: 10.1016/j.ijizo.2008.01.002. http://dx.doi.org/10.1016/j.ijizo.2008.01.002.

Jacob J, Hinds LA, Singleton GR, Sutherland DR, Ylönen H. 2007. Is the reproductive potential of wild house mice regulated by extrinsic or intrinsic factors? Austr Ecol 32: 202-209. http://dx.doi.org/10.1111/j.1442-9970.2007.01680.x.

Kminiak M. 1968. Einige Bermerkungen zur Population dynamik der Grossen Wühlmaus (Arvicola terrestris L., 1758) in der Jahren 1965 und 1966 in der Sudwestliche Slowakei. Biologica 23: 894-900.

Koskela E, Jonsson P, Hartikainen T, Mappes T. 1998. Limitation of reproductive success by food availability and litter size in the bank vole, Clethrionomys glareolus. Proc R Soc Lond B: Biol Sci 265: 1129-1134. http://dx.doi.org/10.1098/rspb.1998.0408.

Kratochvil J. 1974. Vermehrungsfähigkeit der Art Arvicola terrestris (L.) in der CSSR (Mamm. Microtidae). Zeologické Listy 23: 3-17.

Maksimov AA. 1959. Reproduction and fluctuation of the water vole in landscapes of Western Siberia. Vodni krysa i borba s něj Z Sib Novosibirsk 71-120.

Mappes T, Koskela E, Ylönen H. 1995. Reproductive costs and litter size in the bank vole, Clethrionomys glareolus. Proc R Soc Lond B: Biol Sci 265: 1129-1134. http://dx.doi.org/10.1098/rspb.1998.0408.

Montaz J, Jacquot M, Coerdassier M. 2014. Scavenging of rodent carcasses following simulated mortality due to field applications of anticoagulant rodenticide. Ecotoxicology 23: 1671-1680. http://dx.doi.org/10.1007/s10646-014-1306-7.
Morel J, 1981. Le campagnol terrestre, Arvicola terrestris (L.) en Suisse: biologie et systématique (Mammalia, Rodentia). Thèse de Doctorat, Univ. Lausanne, Lausanne, Switzerland.

Morilhat C, Bernard N, Bournais C, Meyer C, Lambole C, Giraudoux P, 2007. Responses of Arvicola terrestris scherman populations to agricultural practices, and to Talpa europaea abundance in eastern France. Agr Ecosyst Environ 122: 392-398. http://dx.doi.org/10.1016/j.agee.2007.02.005.

Murie JO, Boag DA, Kivett VK, 1980. Litter size in Columbian ground squirrels (Spermophilus columbianus). J Mammal 61: 237-244. http://dx.doi.org/10.2307/1380044.

Musser GG, Carleton MC, 2005. Arvicola Lacépède, 1799; Arvicola amphibius (Linnaeus, 1758); Arvicola scherman (Shaw, 1801). In: Mammal species of the world. A taxonomic and geographic reference, 3rd edn; Wilson DE, Reeder DM (eds.). pp: 963-966. Johns Hopkins University Press, Baltimore.

Nazarova GG, Evsikov VI, 2008. Effect of mother's physical condition during pregnancy and lactation on postnatal growth and reproductive success of offspring in water vole Arvicola terrestris. Russ J Develop Biol 39: 100-107. http://dx.doi.org/10.1134/S1062360408020069.

Ostfeld RS, 1985. Limiting resources and territoriality in Arvicola terrestris (Rodentia, Arvicolidae). Ecology 66: 2241-2252. http://dx.doi.org/10.2307/1939252.

Panteleyev PA, 1968. Population ecology of the water vole (Arvicola terrestris L.) indexes of reproduction. J Mammal 49: 281-286. http://dx.doi.org/10.1093/jmammal/49.2.281.

Pascal M, 1981. Resultats preliminaires de l’etude de la biologie du campagnol terrestre (Arvicola terrestris) dans le Doubs. Defense des Vegetaux 208: 121-134.

Pelikán J, 1972. Arvicola terrestris (L.) indexes of reproduction in Czechoslovakia. Acta Sci Nat Brno 11: 1-50.

Perry JS, 1943. Reproduction in the water-vole, Arvicola amphibius Linn. Proc Zool Soc Lond 112: 118-130. http://dx.doi.org/10.1111/j.1469-7998.1943.tb0075x.

Ranichelli E, Barfknecht R, Capizzi D, Rigamato M, Descola F. 2014. From biology to management of Savi’s pine vole (Microtus savii, Arvicolidae) in the Aran Valley, Spain. Zeitschrift für Säugetierkunde 84: 333-345. http://dx.doi.org/10.1023/A:1006583713042.

Rattner BA, Lazarus RS, Elliott JE, Shore RF, van den Brink N, 2014. Adverse outcome pathway and risks of anticoagulant rodenticides to predatory wildlife. Environ Sci Technol 48: 8433-8445. http://dx.doi.org/10.1021/es501740n.

Rivas-Martinez S, Rivas-Sáenz S, 2015. Worldwide bioclimatic classification system. Phytosociological Research Centre. http://www.globalbioclimatics.org/default.htm. Accessed 4 March 2016.

Rojas M, 1977. Breeding and survival in a population of water voles. J Anim Ecol 40: 487-494. http://dx.doi.org/10.2307/32307/3257.

Rostom DD, 1971. Breeding and survival in a population of water voles in the Volga-Akhtubinsk area. Zoologicheskii Zhurnal 35: 130-140.

Ventura J, 1993. Crecimiento relativo de Arvicola terrestris monticola (Rodentia, Arvicolidae). Miscellania Zool. 17: 237-248.

Ventura J, Gosálbez J, 1980. Taxonomic review of Arvicola terrestris (Rodentia, Arvicolidae) in the Iberian Peninsula. Boomer Zoologische Beiträge 40: 227-242.

Ventura J, Gosálbez J, 1990a. Reproduction cycle of Arvicola terrestris (Rodentia, Arvicolidae) in the Aran Valley, Spain. Zeitschrift für Säugetierkunde 55: 383-391.

Ventura J, Gosálbez J, 1990b. Reproduction potential of Arvicola terrestris (Mammalia, Rodentia) in the North-east of the Iberian Peninsula. Zoologischer Anzeiger 225: 45-54.

Ventura J, Gosálbez J, 1992. Criterios para la determinación de la edad relativa en Arvicola terrestris monticola (Rodentia, Arvicolidae). Miscelánea Zoológica 16: 197-206.

Walthier B, Fuelling O, 2010. Vole trapping fences—a new approach to migration barriers. Proc 14th Int Conf on Cultivation Technique and Phytopathological Problems in Organic Fruit-Growing. pp: 341-345. Hohenheim, Germany.

Walthier B, Fuelling O, Malevez J, Pelz JH, 2008. How expensive is vole damage? Proc 13th Int Conf on Cultivation Technique and Phytopathological Problems in Organic Fruit-Growing. pp: 330-334. Weinsberg, Germany.

Wiebold JL, Becker WC, 1987. Inequality in function of the right and left ovaries and uterine horns of the mouse. J Reprod Fertil 79: 125-134. http://dx.doi.org/10.1530/jrf.0.0790125.

Wieland H, 1973. Beitrag zur Biologie und zum Massenwechsel der Grossen Wühlmaus (Arvicola terrestris L.). Zoologisches Jahrbuch, Systematik 100: 351-428.

Wijngaarden A van, 1954. Biologie en bestrijding von der Grossen Wühlmaus (Arvicola terrestris L.) in Nederland. Med Nr 123 Plantenziektenkundige Dienst Wageningen.
Williams CT, Barnes BM, Kenagy GJ, Buck CL, 2014. Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming. J Zool 292: 112-124. http://dx.doi.org/10.1111/jzo.12103.

Yakovleva TV, Bazhan NM, Makarova EN, 1997. Effects of food deprivation in early pregnancy on the development of ovaries and adrenals in female progeny of the water vole (Arvicola terrestris). Comp Biochem Phys C 116: 103-109. http://dx.doi.org/10.1016/s0742-8413(96)00132-6.

Yuzhik EI, Proskurnyak LP, Nazarova GG, 2015. Correlations of reproductive indices of water vole females (Arvicola amphibius) with morphometric and hormonal characteristics. J Evol Biochem Physiol 51: 139-144. http://dx.doi.org/10.1134/S0022093015020076.

Zammuto RM, Millar JS, 1985. Environmental predictability, variability, and Spermophilus columbianus life history over an elevational gradient. Ecology 66: 1784-1794. http://dx.doi.org/10.2307/2937374.