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Continuous breeding of fossorial water voles in northwestern Spain: potential impact on apple orchards

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Abstract. The montane water vole, *Arvicola scherman*, can be found at low altitude in northwestern Spain, where it has become a key pest in apple orchards. Its sustainable control entails the knowledge of its reproduction pattern, which is unknown for this region. Thus, we conducted a study on more than 800 voles caught monthly over two years in apple orchards located in Asturias. Sexual characteristics, body measurements and relative age class were recorded. Intra-annual changes in body mass, testicular volume and seminal vesicle length of males did not affect significantly reproduction at a population scale, since pregnant females were detected over the whole year and their occurrence did not show significant intra-annual differences. Consequently, the recruitment of young specimens was also continuous during the study period. Mild temperatures, even in winter, and ample food all the year around presumably meets the demands of physiological cost of continuous reproduction of *A. scherman* in this area. The implications of our results for facing this vole control in this agroecosystem are discussed. Furthermore, the information here reported might be useful to accurately assess the effect of sustainable control strategies on the reproductive biology of fossorial water voles in this and in similar environments.

Key words: *Arvicola scherman cantabriae*, population structure, reproduction, rodent pest management

Introduction

The montane water vole, *Arvicola scherman* (formerly fossorial form of *Arvicola terrestris*; for details see Musser & Carleton 2005, but see also Kryštufek et al. 2015) occurs in mountainous areas of southern and central Europe (Meylan 1977, Morel 1981), living underground and constructing extensive burrow systems in grasslands, pastures and orchards (Airoldi 1976). These fossorial water voles consume both epigeic and hypogeic parts of plants (Kopp 1993), and specifically in fruit crops they may feed on tree bark and roots injuring and even killing the trees (Meylan 1977, Walther et al. 2008). In the particular case of apple orchards, *A. scherman* caused damages valued between 50 and 40000 € ha⁻¹ year⁻¹ in Germany (Walther et al. 2008). Likewise, in Asturias (northwestern Spain), where apple is cultivated in around 10000 ha for cider production, fossorial water voles are frequently responsible for noticeable economic losses (Miñarro et al. 2012, Somoano et al.

2016). In fact, *A. scherman* is considered one of the most harmful agricultural pests in several countries (e.g. Walther et al. 2008, Blant et al. 2009, Delattre & Giraudoux 2009), including Spain (Miñarro et al. 2012), where preventive actions to reduce their population densities have been recommended (BOE 2008).

The management of rodent pests requires effective, specific, environmentally benign, economically feasible and socially acceptable approaches (Jacob 2013). Thus, 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 for non-target wildlife (Rattner et al. 2014). In France, for example, anticoagulant rodenticides have been routinely applied 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).

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Ultimately, a deep knowledge of relevant aspects on the pest biology and ecology are required for the implementation and success of sustainable control methods (Delattre & Giraudoux 2009, Jacob 2013, Ranchelli et al. 2016).

Two subspecies of *A. scherman* are currently recognized in Spain (see Ventura 2007): *A. scherman monticola*, which is found in the Pyrenees, and *A. scherman cantabriae*, which extends throughout the Cantabrian region (northwestern Iberian Peninsula), from lowlands to mountains. These taxa are geographically isolated and show significant morphological differences (Ventura & Gosálbez 1990a, Ventura & Sans-Fuentes 1997). Although the reproduction pattern of the Pyrenean subspecies has been analysed in several studies (see Ventura & Gosálbez 1990b, c), that knowledge is scarce for Cantabrian populations. The breeding characteristics reported for *A. scherman monticola* correspond to populations from Pyrenean meadows located at about 900 m a.s.l., habitat very different from apple orchards below 400 m a.s.l. on the Asturian coast, where many populations of *A. scherman cantabriae* are established. Since in rodents altitude has an important moulder effect on reproduction (Bronson 1979, Murie et al. 1980, Zammuto & Millar 1985), even at small scale in the same area (Dunmire 1960, Hille & Rödel 2014), important differences in the reproduction between Pyrenean and Cantabrian *A. scherman* populations can be expected. In fact, recent results on the reproductive potential of *A. scherman* in orchards from Asturias revealed substantial differences in respect to Pyrenean populations (Somoano et al. 2016).

Arvicola scherman populations studied to date restrict their breeding to a specific favourable period (Airoldi 1978, Morel 1981, Pascal 1981, Ventura et al. 1991), in which the individuals synchronize the demands of reproduction according to favourable conditions. Temperature and rainfall determine the amount of available food which ultimately condition the reproductive physiology of rodents (Nelson et al. 1992, Demas & Nelson 1998, Bergallo & Magnusson 1999, Pierce et al. 2005, Medger et al. 2012). In this way, it is known that habitats with favourable environment allow rodent species to lengthen their reproductive period (Sicard & Fuminier 1996, Bergallo & Magnusson 1999, Trebatická et al. 2012). Thus, the length of the breeding season is defined by the seasonal variations of the environmental conditions (Smith & McGinnis 1968, Kriegsfeld et al. 2015), which might also occur in *A. scherman* populations even within temperate areas.

The main goal of this study was to generate for the first

time detailed information on the reproduction cycle of *A. scherman* in Northwest of Spain, specifically in agricultural environments located at low altitudes. We also aimed to highlight reproductive differences between Cantabrian and Pyrenean populations of this species to provide robust information, which in turn can be useful for planning and improving efficient and sustainable population control strategies and to assess their effects accurately.

Material and Methods

Study site

The study was conducted in ten experimental and commercial apple orchards over 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 Asturias: Villaviciosa (43°38′55″ N, 5°26′08″ W) and Nava (43°21′31″ N, 5°30′29″ W), which are separated by 15 km. 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 woodland.

The studied area has a temperate hyperoceanic 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. Relatively high rainfall and fertile soils of Asturian meadows favor the establishment of an evergreen and dense grass coverage in orchards all the year around (Díaz-González & Fernández-Prieto 2005, Miñarro 2012). Meteorological data comprising monthly rainfall as well as temperatures and day-length in hours (Fig. 1) were registered for the area of Villaviciosa throughout the study period.
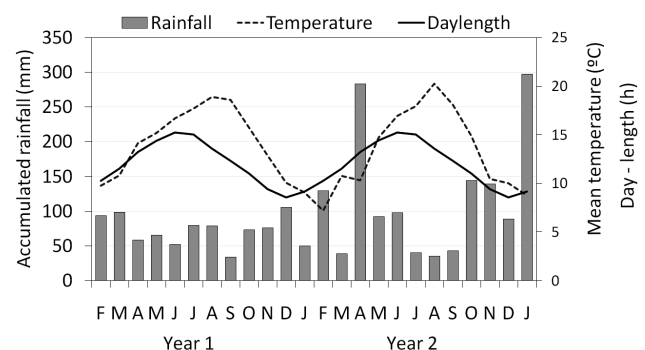

Fig. 1. Climatic conditions in the study area. Variation of monthly temperature, rainfall and day-length during the sampling period (Year 1: February 2011-January 2012; Year 2: February 2012-January 2013).

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Specimens and data collection

A total of 823 voles (401 males, 422 females) were captured. Each month, one or more orchards, depending on orchard surface area and vole density, were visited for trapping. Voles caught in a single month were grouped and analysed together. Where possible, the same orchard was not visited in two consecutive months to avoid potential alterations on population patterns due to trappings. Voles were captured with snap traps (Topcat® Andermatt Biocontrol, Switzerland) placed in galleries. Traps were activated during the day and checked twice per day for maximum of five days. Each captured specimen was assigned to a particular burrow and thus voles caught in the same trap during the same trapping session were considered as living together. Shortly after capture, body mass (BM) was registered with a precision scale to the nearest 0.5 g and voles were cryopreserved at –20 °C before necropsy. In the field work we have followed the recommendation of the Directive of the European Parliament and of the Council on the Protection of Animals Used for Scientific Purposes (Directive 2010/63/UE 2010).

Head and body length (HBL) and carcass mass (CM) of each animal were taken. In males, the position of testes (abdominal or scrotal), maximum length (TL) and maximum width (TW) of left testis, length of the left branch of seminal vesicle (SVL), and cell content of testis and epididymis tail (Gosálbez 1987) were recorded. Testicular volume (TV) was calculated as follows: $TV = 4/3 \pi (TL/2) (TW/2)^2$. Length variables were measured using a digital calliper to the nearest 0.01 mm (see Ventura 1993). From these characteristics the following sexual maturity states were established: immature males, individuals lacking spermatids or spermatozoids in the testis; submature males, voles with few spermatozoids and spermatids in the testis and without or with a very scarce number of spermatozoids in the epididymis; and mature males, specimens with a large amount of spermatozoids in both structures. Although spermatozoids were not quantified, the differences between mature and submature males was clear since, contrary to what happened in the latter, in mature individuals the presence of spermatozoids in epididymis and testis was homogeneous and high in the smears.

In females, the main criterion used to establish the maturity state was determined from the histological characteristics of the ovaries, which were removed and preserved in 70 % ethanol until the analysis was conducted. Four longitudinal histological sections (sections of 5 μm thick taken 150 μm apart) were performed on the left ovary. Sections were stained with hematoxylin-eosin. Other sexual parameters considered in females were: status of the vulva (closed or open), degree of development and vascularisation of the uterus, and the presence of placental scars and/or embryos (Ventura & Gosálbez 1990b). The following sexual maturity states were established: immature females, specimens without *corpora lutea*, closed vulva, uterus poorly developed and vascularised, without placental scars; submature females, voles without *corpora lutea* but with secondary follicles and/or Graafian follicles in the ovary, open vulva, uterus poorly vascularised, without placental scars or embryos; active mature females, individuals with *corpora lutea*, uterus completely developed and well or scarcely vascularised, showing placental scars and/or embryos, and with open vulva; inactive mature females, specimens with *corpora lutea*, uterus completely developed and well or scarcely vascularised, with or without placental scars, without embryos and with closed vulva. The mass of embryos was subtracted from BM of pregnant females to assess the general pattern of BM variation during the study period. Moreover, pregnant females were discarded in determining BM differences between sexes and relative age classes (Table 1) in order to prevent considering the mass gain associated to pregnancy (Nazarova & Evsikov 2008).

A subsample of 611 specimens was classified into six classes of relative age (0-V). This subsample was formed by all immature and submature individuals, and a random selection of mature ones to balance their high number of captures. The assignation to each class was done according to the following criteria: moulting stage, sturdiness of the mastoid and the condylar processes, the separation of the angular process from the ascending branch of the mandible, and the values of the interorbital crests index (ICI), which relates the distance between the interorbital crests and the rostral length (see Ventura 1992, Ventura & Gosálbez 1992 and references therein). The approximate age intervals corresponding to these 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, 14-30 weeks; class V, specimens older than 30 weeks. Condylobasal length (CL) and length of upper diastema (LUD) were also measured. Cranial variables were taken only on undamaged skulls.

Data analyses

To obtain values for BM and HBL to set sexual maturity at a population level, BM_{50} and HBL_{50} were
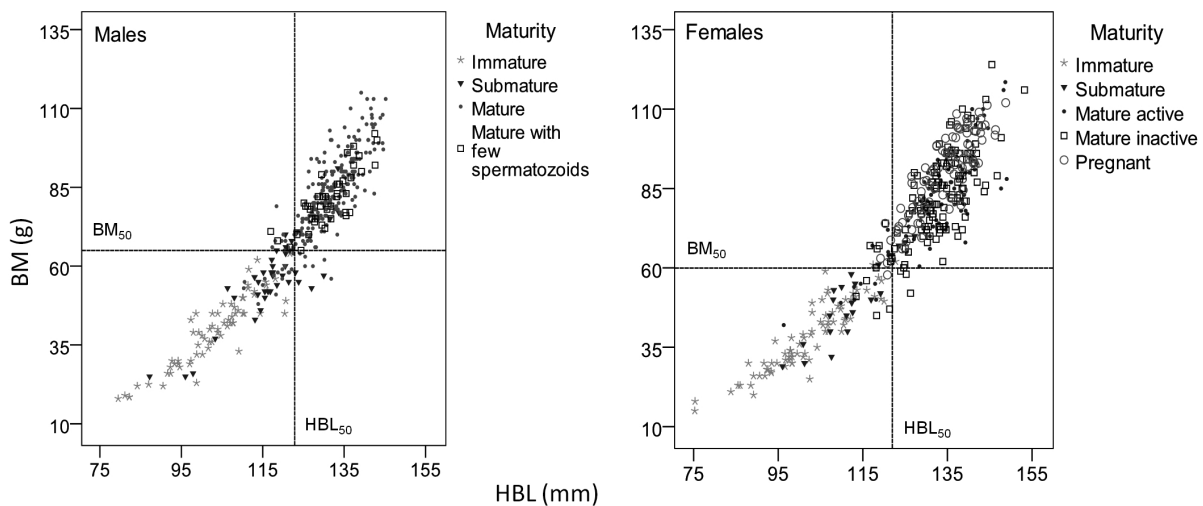
Fig. 2. Relationship between head and body length (HBL) and body mass (BM) according to sexual state in *A. scherman cantabriae*. BM_{50} and HBL_{50} are the BM and HBL hypothetical values at which 50 % of specimens of the population are matures and mark the limit above which individuals can be considered as adults.

calculated. This approach provides the values of BM and HBL at which 50 % of specimens of the population are mature, and marks a cut-off value above which all individuals can be considered as adults (Pelikán 1972). BM_{50} and HBL_{50} were calculated using a probit regression model, which relates a binomial response variable (mature – non-mature) with an independent variable (BM or HBL) (Finney 1952, Pelikán 1972, Ventura & Gosálbez 1990b).

Significant differences in body and cranial measurements due to age class and sex were tested by a 2-way ANOVA test, followed by a Tukey's test to establish differences between age classes. Sexual differences in body and cranial measurements in each class were assessed by Student's t-tests. To determine the significance of intra-annual and inter-annual variations in BM and CM a 2-way ANOVA test was used. Intra-annual and inter-annual variation in SVL and TV were analysed by a 2-way ANCOVA test using BM as covariate. The relationships between SVL and TV, and BM and CM were determined by Pearson correlations. Partial correlations controlling for BM were used to assess the effect of temperature, rainfall and day-length on TV and SVL. Relationships between the monthly percentages of both pregnant and active mature females respect to the mean values of rainfall, temperature and day length were determined by Pearson correlations. The significance of intra- and inter-annual variations in the number of pregnant females was evaluated using Kruskal-Wallis test. Mann-Whitney U test and Bonferroni adjustment for multiple tests (α = 0.05/number of pair-wise comparisons (6) = 0.0083) were used to determine differences between maturity classes. Differences in sex ratio were assessed by chi-

square test. Statistical analyses were performed using SPSS 22.0 (IBM Corp. 2013).

Results

Body and skull size variation

In general, mean HBL and BM were similar for males and females, and increased progressively with relative age class (HBL: $F_{5, 605} = 548.01$, $p < 0.001$; BM: $F_{5, 494} = 370.91$, $p < 0.001$; Table 1). Only HBL was affected by the interaction of sex and age classes ($F_{5, 605} = 3.12$, $p < 0.01$): class I, males (mean = 100.9 mm), females (97.3 mm); class V, males (134.9 mm), females (137.6 mm). Cranial dimensions also varied significantly with age class (CL: $F_{5, 511} = 566.32$, $p < 0.001$; LUD: $F_{5, 539} = 573.22$, $p < 0.001$; ICI: $F_{5, 536} = 529.63$, $p <$
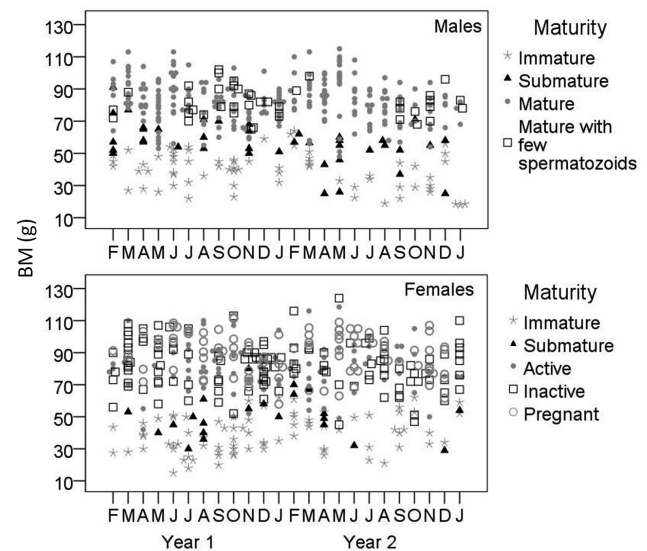

Fig. 3. Relationship between body mass (BM) and sexual maturity state in both sexes in *A. scherman cantabriae* throughout the study period.

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Table 1. Body and cranial measurements according to relative age classes in *A. scherman cantabriae*. (HBL: head and body length, BM: body mass, CL: condylobasal length, LUD: length of upper diastema, ICI: interorbital crests index, M: male, F: female. $*p < 0.05$; $**p < 0.01$; n.s.: not significant).

Variable	Age class	n males	n females	Mean ± SD	Range	Sex
HBL	0	8	9	88.7 ± 7.26	75.27-102.44	n.s.
	I	39	40	99.1 ± 8.13	75.33-120.67	$* M > F$
	II	50	44	110.8 ± 7.01	87.20-127.00	n.s.
	III	47	51	121.4 ± 6.41	96.00-138.22	n.s.
	IV	58	92	130.6 ± 5.88	115.87-144.48	n.s.
	V	75	92	136.4 ± 6.02	116.68-157.00	$** M < F$
BM	0	7	9	23.4 ± 4.39	15.00-30.00	n.s.
	I	37	39	35.9 ± 8.83	18.00-56.50	n.s.
	II	50	43	48.1 ± 9.41	22.00-73.00	n.s.
	III	46	47	62.4 ± 9.69	29.00-91.00	n.s.
	IV	58	46	76.3 ± 10.61	45.00-108.00	n.s.
	V	75	50	89.5 ± 12.84	47.00-124.00	n.s.
CL	0	4	5	24.2 ± 1.13	22.27-26.22	n.s.
	I	28	30	26.5 ± 1.01	24.05-28.39	n.s.
	II	35	37	28.8 ± 1.03	26.57-32.02	n.s.
	III	37	40	30.7 ± 1.04	28.09-33.06	n.s.
	IV	57	79	32.3 ± 0.99	29.65-34.82	$* M > F$
	V	73	86	33.3 ± 1.08	30.14-35.88	$** M > F$
LUD	0	6	8	8.1 ± 0.38	7.40-8.63	n.s.
	I	35	33	9.0 ± 0.51	7.63-10.05	n.s.
	II	39	40	10.1 ± 0.49	8.76-11.81	n.s.
	III	36	43	10.9 ± 0.51	9.72-12.15	n.s.
	IV	57	81	11.7 ± 0.48	10.53-12.90	$** M > F$
	V	75	86	12.1 ± 0.53	10.53-13.55	$** M > F$
ICI	0	6	8	0.2207 ± 0.0484	0.3161-0.1679	n.s.
	I	35	32	0.1753 ± 0.0412	0.2863-0.0929	n.s.
	II	37	41	0.1293 ± 0.0485	0.2781-0.0086	n.s.
	III	37	43	0.0674 ± 0.0309	0.1573-0.0089	n.s.
	IV	57	79	0.0248 ± 0.0221	0.2222-0.0000	n.s.
	V	74	87	0.0017 ± 0.0053	0.0342-0.0000	n.s.

Table 2. Number of captured specimens of *A. scherman cantabriae* according to sex, sexual maturity state and age class. For each sex and age class, the percentage of individuals corresponding to each sexual state is indicated in brackets.

Sex	Maturity	N	0	I	II	III	IV	V
					Age class			
Males	Immature	75	9 (100)	37 (90.2)	27 (54.0)	2 (4.3)		
	Submature	41		4 (9.8)	18 (36.0)	19 (40.4)		
	Mature	285			5 (10.0)	26 (55.3)	254 (100)	
Females	Immature	83	9 (100)	35 (87.5)	30 (68.2)	9 (17.6)		
	Submature	23		5 (12.5)	8 (18.2)	10 (19.6)		
	Mature	316			7 (13.6)	32 (62.7)	277 (100)	
Total		823	18	81	95	98	531	

0.001; Table 1). Significant differences between sexes were detected for CL ($F_{5, 511}$ = 8.00, $p < 0.01$) and LUD ($F_{5, 539}$ = 11.61, $p < 0.01$), with males showing significantly higher values than females in classes IV (CL: males = 32.5 mm, females = 32.1 mm; LUD: males = 11.8 mm, females = 11.6 mm) and V (CL: males = 33.6 mm, females = 33.1 mm; LUD: males = 12.2 mm, females = 11.9 mm). Body mass and CM were correlated significantly in both sexes (males: r = 0.967, $p < 0.001$; females: r = 0.957, $p < 0.001$); since mean values for both variables showed similar inter-annual and intra-annual variation patterns (results concerning CM are not shown).

Reproduction in males
In our sample, males with a BM below 48 g were immature or submature, and above 77 g all males were mature (Fig. 2). Males with a HBL below 111 mm were immature or submature, and above 134 mm all males were mature. Submature specimens were detected above 25 g BM and 87 mm HBL. Males could be considered as mature with a BM (BM_{50}) over 64.9 g and a HBL (HBL_{50}) over 122.8 mm (Fig. 2).
All males belonging to class 0 were immature, and males of class I immature or, in a lower percentage, submature (Table 2). Most submature individuals corresponded to classes II (43.9 %) and III (46.3 %), although the youngest mature male corresponded to age class II. All class IV and V males were mature, although some specimens (16.5 %) had few spermatozoids in testis and epididymis.
Testicular volume was positively correlated with SVL (r = 0.805, $p < 0.001$). Mean values of TV and SVL for mature specimens with few spermatozoids did not differ significantly from the values corresponding to mature males in any month of both years (Mann-Whitney U test with Bonferroni adjustment; $p > 0.0083$, in all cases). Mature males with few spermatozoids were not detected in spring of the first year, and spring and summer of the second year (Fig. 3).
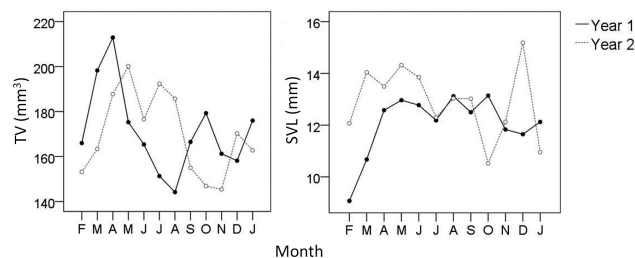

Fig. 4. Estimated marginal means of the testis volume (TV) and seminal vesicle length (SVL) using body mass as covariate in mature specimens of *A. scherman cantabriae* throughout the study period.
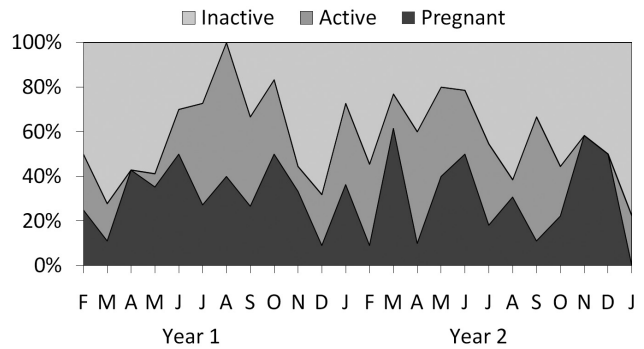

Fig. 5. Variation of the population structure of mature females belonging to age classes IV and V according to sexual activity state in *A. scherman cantabriae* during the study period.
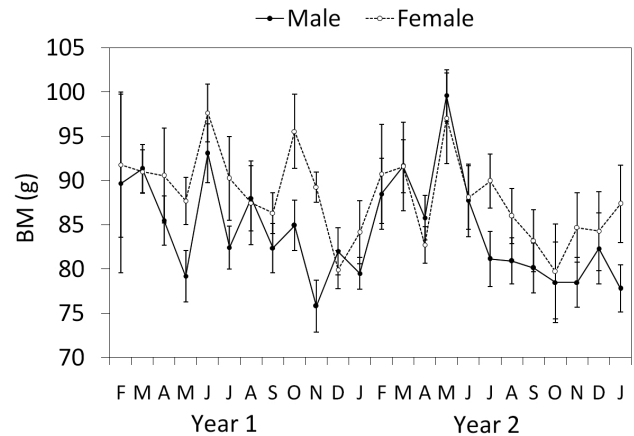

Fig. 6. Monthly variation (mean ± SE) of male and female body mass (BM) in mature specimens belonging to age classes IV and V in *A. scherman cantabriae* during the study period.

Using BM as a covariate, TV and SVL in mature males showed significant intra-annual variations (TV: $F_{11, 283}$ = 3.19, $p < 0.001$; SVL: $F_{11, 284}$ = 4.03, $p < 0.001$; Fig. 4). Significant inter-annual differences were found in SVL ($F_{1, 284}$ = 11.71, $p < 0.01$) but not in TV ($F_{1, 283}$ = 0.07, p = 0.787; Fig. 4). A significant interaction was detected between month and year both in TV and SVL (TV: $F_{11, 283}$ = 3.08, $p < 0.01$; SVL: $F_{11, 284}$ = 3.85, $p < 0.001$). Estimated marginal means of TV in mature males (Fig. 4) showed maximum values in spring of both years, and decreased till August (first year) or November (second year). Estimated marginal means of SVL (Fig. 4) did not show a clear inter-annual variation pattern. Partial correlations controlled by BM were significant between TV and day-length (r = 0.126, $p < 0.05$), whereas temperature (r = 0.006, p = 0.920) and rainfall (r = –0.003, p = 0.955) did not show a significant relationship with TV. Partial correlation between SVL and day-length, and between the former variable and temperature were significant (r = 0.190, $p < 0.01$; r = 0.144, $p < 0.05$; respectively). Rainfall did not correlate significantly with SVL (r = –0.051, p = 0.390).

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Reproduction in females

Females with a BM below 42 g were immature or submature, and all individuals above 80 g were mature (Fig. 2). Specimens with a HBL below 96 mm were immature or submature, and above 127.5 mm all individuals were mature. The submature specimens were detected with BMs above 29 g and HBLs of 96 mm. Females with BMs and HBLs higher than 59.9 g and above 121.9 mm, respectively, could be considered mature (BM_{50} and HBL_{50} respectively) (Fig. 2). In classes 0, I and II most females were immature (Table 2). The youngest mature female corresponded to class II. Submature females corresponded mostly to classes II and III, and all females of classes IV and V were mature.

Active mature females and/or pregnant females were found in all months of the study period (Fig. 5). No significant inter-annual (Kruskal-Wallis H′ = 0.104, $p = 0.748$) and intra-annual (Kruskal-Wallis H′ = 18.341, $p = 0.074$) differences in the number of pregnant females were found. These females appeared in all months except January 2013 (mature females: n = 8). Between April and November of the first year, pregnant females constituted more than 25 % of mature females. However, the occurrence of pregnant females in second year was more irregular (Fig. 5), with maximums in March (61.5 %) and November (58.3 %). Monthly percentages of both pregnant and mature active females were not significantly correlated with the monthly mean values of rainfall (r = –0.380, $p = 0.067$; r = –0.326, $p = 0.120$; respectively), temperature (r = 0.215, $p = 0.314$; r = 0.322, $p = 0.125$; respectively) or day length (r = 0.207, $p = 0.331$; r = 0.343, $p = 0.101$; respectively); likewise, there were neither significant correlations when the month before the month of capture was considered: rainfall (r = 0.220, $p = 0.313$; r = 0.415, $p = 0.062$; respectively), temperature (r = 0.160, $p = 0.467$; r = 0.012, $p = 0.958$; respectively), day length (r = 0.374, $p = 0.079$; r = 0.231, $p = 0.288$; respectively).

Body mass variation

Mean variation of BM in mature male specimens belonging to classes IV and V (Fig. 6) showed significant intra- ($F_{11,253} = 4.64$, $p < 0.001$) and inter-annual differences ($F_{11,253} = 3.17$, $p < 0.01$). The BM means of these males were also affected by the month-year interaction ($F_{11,253} = 3.17$, $p < 0.01$). Conversely, mean variations in BM of adult females (classes IV and V, Fig. 6) were not significant neither intra- ($F_{11,266} = 1.67$, $p = 0.081$) nor inter-annually ($F_{1,266} = 1.07$, $p = 0.302$). Mean BM of classes IV and V did
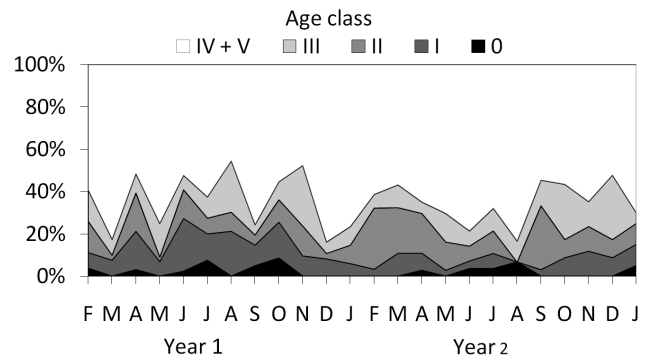

Fig. 7. Variation of the population structure according to relative age classes in *A. scherman cantabriae* throughout the study period.
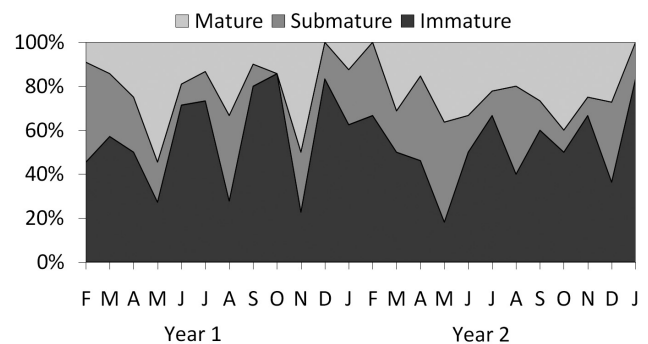

Fig. 8. Variation of population structure of immature, submature and mature specimens belonging to age classes 0-III in *A. scherman cantabriae* during the study period.

not differ significantly between sexes (t = –1 .85, df = 517, $p = 0.064$). Mean BM values of both sexes showed relative higher values in June of the first year and May of the second year (Fig. 6).

Population structure

Total sex ratio (401 males, 423 females) was not significantly different from 0.5 ($\chi^2 = 0.43$, $p = 0.512$). For each age class (class I: 0.97, class II: 1.14, class III: 0.88, classes IV-V: 0.93) the sex ratio was also not significantly different from that value (χ^2 test, $p > 0.05$ in all cases). The presence in all months of specimens from class 0 or I revealed that births occurred steadily (Fig. 7), whereby, immature specimens of both sexes were captured continuously during both years (Fig. 8). Submature or mature specimens belonging to classes I, II and/or III were detected in all months, with maximums in May (72.7 %), August (72.2 %) and November (77.3 %) of the first year and with a more regular presence between February and December of the second year (Fig. 8). The percentage of captured mature individuals of classes II and III decreased in winter of both years (Fig. 8). At least 45 % of captured voles in each month belonged to classes IV and V (Fig. 7).

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A total of 120 family groups were captured. Couples formed by adults individuals were observed in 42 cases (35 %), 33.3 % of them with pregnant females (n = 14). The number of captured couples with offspring was 59 (49.2 %), formed by one to five juveniles. The immature voles captured in each burrow mostly belonged to the same relative age class. Indeed, most immature specimens (93.6 %) corresponded to age class 0, I, and II, although some specimen of age class III were captured occasionally with mature couples (6.4 %). Occasionally, groups of more than two adults belonging to class IV and/or V were detected, mostly in May (42.1 %): one male-two females (n = 8), two males-one female (n = 6), two males-two females (n = 5). Of these associations, a pregnant female was observed in a group formed by two males-one female and in five groups of one male-two females. Furthermore, both females were pregnant in a group of one male-two females and in three groups of two males-two females.

Discussion

Rodents should organize their activity and energy budgets according mainly to food availability for balancing the competing demands of reproduction (Hansen et al. 1999, Lima et al. 2001, Merritt et al. 2001, Solonen 2006). Thus, only when primary demands, such as thermoregulation and food obtaining, have been satisfied, energy remains can be used to cope reproduction (Bronson 1985, Trebatická et al. 2012), which is often limited to a part of the year in temperate areas (Hansen et al. 1999, Lima et al. 2001, Merritt et al. 2001, Solonen 2006). In this way, most studies on both semiaquatic and fossorial water vole populations have shown that reproduction activity ceases or significantly decreases in winter, which determines a lack or a scarce number of young specimens in early spring (van Wijngaarden 1954, Kminiak 1968, Pelikán 1972, Wieland 1973, Airoldi 1978, Morel 1981, Pascal 1981, Evsikov et al. 1989, Ventura et al. 1991). However, our results show that *A. scherman* can breed continuously along the whole year in agricultural environments located at low altitudes in northwestern Spain. Winter reproduction has been previously reported in a population of *A. scherman* form the Jura mountains (Switzerland), but in a particular case of unusual benign temperatures during this season (Meylan & Airoldi 1975). Our study area has a temperate hyperoceanic climate (Rivas-Martínez & Rivas-Sáenz 2015), which entails favourable environmental conditions the whole year. Interestingly, our results are concordant with those obtained in the Lusitanian pine vole (*Microtus*

lusitanicus), another arvicoline apple pest that cohabits with fossorial water voles (Miñarro et al. 2012) and also breeds along the whole year in the study area (Miñarro et al. 2017). In fact, it has been found that environments with favourable conditions allow many populations of rodents to increase their reproductive effort (Murphy 1992, Koskela et al. 1998, Díaz & Alonso 2003) or even lengthen their reproduction throughout the whole year (Sicard & Fuminier 1996, Bergallo & Magnusson 1999).

Physiological receptors receive environmental signals and then interact with the neuroendocrine system to dictate reproductive behaviour throughout the secretion of sexual hormones, which control spermatogenesis and the ovarian cycle (Maeda et al. 1997). In this way, many rodent species may rely upon the photoperiod as a predictive cue in order to anticipate the onset and offset of optimal conditions for breeding (Nelson 1985, Bronson 1988, Steinlechner & Niklowitz 1992, Kerbeshian et al. 1994, Nelson et al. 1998, Gottreich et al. 2000). Thus, it has been found that in many species, males suffer a significant intra-annual fluctuation of the testis, epididymis and seminal vesicle masses associated with the day-length variation (e.g. Maeda et al. 1997, Gottreich et al. 2000, Pyter et al. 2005, Medger et al. 2012). Likewise, in *A. scherman monticola*, testis and seminal vesicle lengths correlated significantly with day-length (TL: r = 0.798, SVL: r = 0.920) and temperature (TL: r = 0.639, SVL: r = 0.527) (Ventura 1988). However, although photoperiod can be used as the main predictive cue for seasonal breeding, temperature and rainfall affect thermoregulatory costs and thus determine the amount of available food, which in turns can condition the reproductive physiology of rodents (Nelson et al. 1992, Demas & Nelson 1998, Bergallo & Magnusson 1999, Pierce et al. 2005, Medger et al. 2012). So, in our study area, mild temperatures and abundant rainfall allow fossorial water voles to overcome primary demands and also cope physiological costs of reproduction during the year. Whereby, although mature males of our population showed maximum mean values of the testis volume in spring, minimum averages of this variable appeared in different seasons in each studied year. Likewise, the variation of the mean of the seminal vesicle length showed a very irregular pattern during the study period, with few coincidences between years. Furthermore, in comparison with the results obtained for Pyrenean water voles, correlations between seminal vesicle and testis lengths with day-length, although significant, were clearly lower in our

population. Overall, the lack of synchrony of the size variation of both sexual organs with seasonality in the Asturian population is probably the result of the continuous breeding along the whole year.

Body mass in both semiaquatic (Pelikán 1972, Evsikov et al. 1989, Zejda 1991) and fossorial water vole populations (Ventura 1988) can increase when sexual activity starts. Whereas our analyses revealed significant intra-annual variation in body mass in males of classes IV and V, the variation detected in females was not significant. The accumulation of reserve tissues before and, especially, after mating is an important adaptation for breeding in female water voles (Nazarova & Evsikov 2008). Thus, the continuous presence in our population of pregnant females along the study period could have masked a potential intra-annual variation of the body mass in adult females.

The onset of reproductive activity may be important to assess the rate at which population grows by recruitment. Sexual maturity in water voles starts when a male induces by mating the onset of oestrus in a preovulatory female (Yakovleva et al. 1997). Nevertheless, populations of arvicoline rodents in seasonal environments can perform a precocious reproduction if young are born at the beginning of the breeding period, whereas individuals born at other times can delay their sexual maturation (Zejda 1991 and references therein, Lambin & Yoccoz 2001). In this way, the range of the onset of sexual maturity in *A. scherman cantabriae* appears between classes II and III, which is concordant with the results obtained in *A. scherman monticola* (Ventura & Gosálbez 1990b). According to the body size differences between Pyrenean and Cantabrian fossorial water voles (see Ventura & Gosálbez 1990a, Ventura 1993), body mass at which each sex reach sexual maturity is comparatively smaller in *A. scherman cantabriae*.

Intersexual differences in skull dimensions of adult individuals (classes IV and V) of *A. scherman cantabriae* suggest a male-biased dimorphism, which has been reported in other arvicoline rodents, even among populations of the same species (Schulte-Hostedde 2007 and references therein). Nevertheless, the degree of sexual dimorphism in the body size and the relative size of testes are the key metric issues to predict the mating system in arvicoline species (Boonstra et al. 1993, Ostfeld & Heske 1993). In our sample, no significant differences neither in body mass nor in head and body length were found between adult males and females (classes IV and V). Moreover, in comparison with other arvicolines

(see Heske & Ostfeld 1990), the mean value of the index between testis length and head and body length in adult individuals during the periods of maximal testis size was low (mean = 0.066, SD = 0.005). Furthermore, the sex ratio in our sample was balanced and our surveys in the field suggest that *A. scherman cantabriae* lives mainly in familiar burrow systems, which are independent from each other and are occupied by a couple of adults with their offspring. Overall, results obtained in the present study allow us to suggest that in our population monogamy is the rule, main mating system that has been reported for other fossorial water vole populations (Airoldi 1978, Morel 1981). Although the mating system in arvicolines can vary with population density (Waterman 2007 and references therein) and complex associations among individuals have been reported in other *A. scherman* populations (Airoldi 1978, Morel 1981), the scarce number of unusual associations found in the present study and the lack of parental assignments by genetic tests prevent us to report an alternative mating system for our population.

Implications for management

Apple orchards in Asturias are located in relatively small plots (70 % are smaller than 2 ha) immersed in a mosaic landscape with high densities of semi-natural habitat (hedgerows and woodlands) and a topography with smooth hills and valleys, leading to a closed landscape. It has been hypothesized that such setting might modulate multiannual fluctuations in abundance of fossorial water voles directly by slowing dispersion and indirectly by the presence of specialist and generalist predators (Giraudoux et al. 1997, Fichet-Calvet et al. 2000, Foltête et al. 2009, Berthier et al. 2013). Anyway, although no studies on population dynamics has been conducted and thus there is not periodic data on vole density, some population outbreaks have been observed at a local scale in Asturias (Miñarro, pers. observ.). In such situations of tree-damage threat vole control is faced without coordinate actions among farmers and according to their perception of risk.

Population control of this species in Asturias has so far mainly been achieved by manually placing rodenticide baits or snap-traps at burrow entrances. Until now, farmers increase control activity in winter in order to eliminate adults before the hypothetical breeding season, which was expected to start in spring. Thus, farmers would reduce population increase. However, our results show a continuous breeding regardless of season which suggests that population

control could be performed along the whole year. This does not mean extending the use of rodenticides throughout the year but that control effort does not need to be seasonal as it used to be. It is well known that increasing the poison input in the agroecosystem enhances the risk for wildlife (Coeurdassier et al. 2014, Montaz et al. 2014). For that reason, sustainable control management strategies should preferably be taken into account instead of poisoning practices which are maintained over time.

As control measures of direct application, trapping beyond the death of the mature couple might lead to increase control effectiveness since some offspring could remain in the burrow. It is worthwhile to keep in mind that we found up to seven specimens in a burrow. Furthermore, a continuous trapping might suppose a decrease of the body condition in females remaining in the burrow, which in turn might have negative consequences on her reproductive success (Somoano et al. 2016). On the other hand, dispersion in fossorial water voles is done aboveground by juvenile specimens (Saucy & Schneiter 1998, Saucy 2002). Installing fences can be useful to avoid invasions by dispersal specimens (see details in Walther & Fuelling 2010). Farmers should maintain these fences surrounding apple orchards continuously as young mature specimens appear throughout the year and could thus disperse at any time. Uncoordinated control actions by farmers involve potential colonization movements of juveniles from source demes (without or scarce control) to nearby sink plots (with continuous removal of voles).

The enforcement 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) can be suitable strategies to maintain fossorial water voles under physiological stress, which in turns might induce a decline in their population densities (Charbonnel et al. 2008). However, the effectiveness of these control strategies is frequently assessed by the relative abundance of voles (e.g. Morilhat et al. 2007, Jacob 2008, Delattre & Giraudoux 2009), without going into the underlying cause. The information obtained for this population can be used to assess direct consequences of control strategies on the reproductive biology of fossorial water voles, such as changes in population structure (Cerqueira et al. 2006), growth delaying (Stoddart 1971, Zejda 1991, Moorhouse et al. 2008) or delays in the onset of reproduction (Yakovleva et al. 1997).

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