Breeding, abundance and population structure of the Bank vole *Clethrionomys glareolus* (Schreber, 1780) in the western Pyrenees

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Breeding, abundance and population structure of the Bank vole Clethrionomys glareolus *(Schreber, 1780) in the western Pyrenees.*– The reproductive cycle of a population of Bank voles *(Clethrionomys glareolus)* in the western Pyrenees was related to the population structure over a two-year period and compared to other European populations. There were marked differences in the length of the reproductive season between the two years. Breeding began at the end of the winter and reached its highest rate during the autumn of the first year. In the second year the breeding did not commence until summer. The average litter size was similar to that previously reported in the north of the Iberian peninsula and France, although it varied with time. Changes in litter size were related to the age of reproductive females.

Key words: Bank vole, *Clethrionomys glareolus*, Reproductive cycle, Breeding.

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Introduction

The Bank vole (*Clethrionomys glareolus*) exhibits marked differences in population dynamics throughout its distribution area. In northern Scandinavia it undergoes multiannual cycles lasting from 3 to 4 years (KAIKUSALO, 1972; LARSSON & HANSSON, 1977) while in central Europe it usually exhibits fluctuations from one year to another (SOUTHERN & LOWE, 1982), which may either be constant over a period of several years (BOBEK, 1973), or more variable (GURNELL, 1981). The reproductive biology of this species is affected by intrinsic variables (NYLHOM & MEURLING, 1979) and extrinsic factors (ZEJDA, 1962; WATTS, 1970; BUJALSKA, 1975) and has been studied in depth in central and northern Europe (CLARKE, 1985). There are fewer studies available on the reproduction of this species on the Iberian peninsula (REY, 1972; GOSÁLBEZ, 1976; GOSÁLBEZ & SANS-COMA, 1976).

This paper describes the reproductive cycle of a population located in the western Pyrenees and compares it to other European populations.

Material and methods

Two-hundred and sixty-one specimens of *Clethrionomys glareolus* (136 males and 125 females) were studied. They were collected between September 1984 and August 1986 in the Quinto Real Massif (western Pyrenees, north of the Iberian peninsula) at altitudes ranging between 660 m and 1,000 m. The annual rainfall average in the study area was 2,138 l/m^2. Maximum values were found in April (243 l/m^2) and November (253 l/m^2) and the minimum values in July (68 l/m^2). The lowest and highest mean temperatures occurred in January (2.9°C) and August (16.6°C) respectively. The average annual temperature was 8.8°C.

The study area was covered largely by an acidophilic beech forest (*Saxifrago hirsutae-Fagetum sylvaticae*; BRAUN-BLANQUET, 1967). The clearings in the forest due to tree felling consisted of moorlands (*Daboecio cantabricae-Ulicetum cantabrici*; BRAUN-BLANQUET, 1967). At the edge of the forest there were brambles (*Rubo ulmifolii-Tametum communis*; TÜXEN & OBERDORFER, 1958) and megaphorbia of the *Valerianetum pyrenaicae* type (RIVAS-MARTÍNEZ et al., 1984), which occurred continuously depending on the dampness of the soil and the availability of light. The vegetation on the riverbanks belonged to the *Hyperico androsaemi-Alnetum association* (BRAUN-BLANQUET, 1967).

The animals were caught using mainly snap-traps and live traps. The number of snap-traps set per month ranged between 300 and 1,000. The total number of snap-traps set during the field sampling was 15,535.

Reproductive activity was determined taking the following into account:

1. In males whether the testes were scrotal or abdominal, the length of the seminal vesicles, the two maximum orthogonal lengths of each testicle and a smear of the testicular and epididymal material. The cell content of these smears was stained with Dif-Quik (GOSÁLBEZ et al., 1979).
2. For females the following were recorded: vaginal perforation, the presence of a seminal plug, the state and development of the mammary glands, irrigation or dilation of the uterus and number of recent or old placental scars.
3. In pregnant females, the number of embryos in each branch of the uterus was recorded.

The animals were divided into reproductive classes following the criteria of VENTURA & GOSÁLBEZ (1987). Three categories were established in males depending on their reproductive state: immature, individuals without either spermatids or spermatozoids in the testicle; submature, animals having very few spermatozoids and spermatids in the testicle; mature, animals having an abundance of spermatozoids in the testicle. Observations made of the epididymal material were used to help corroborate this classification.

In females, the following categories were established: immature, closed vulva, underdeveloped uterus, lack of placental scars; inactive mature, closed vulva, partially developed uterus with no signs of vascularization, there may be uterine scars but no embryos; active mature, animals having a perforated vulva, a well developed and vascularized uterus, they may have embryos or placental scars.

Age was estimated by calculating the mean length of the root of M_1 according to the ZEJDA (1960) method.

Results

The male breeding cycle

The smallest seminal vesicle found in a submature individual measured 3 mm in length. All individuals caught under this length were immature. The smallest seminal vesicle length found in a mature animal was 3.9 mm. A maximum seminal vesicle length of 10.25 mm was found in immature individuals and up to 9 mm in submature animals. The maximum seminal vesicle length found in a mature animal was 15.3 mm.

The lowest weight found in the animals caught was 14.5 gr (fig. 1); the lowest weight in subadult animals was 18.8 gr. The minimum weight in a mature individual was 22 gr, while the maximum weight in mature males was 37.8 gr.

The average testicle length decreased starting in September 1984 (fig. 2) and reached minimum values in December of the same year. There was a rapid growth starting in January-February 1985, which continued until it reached a maximum value in September of the same year. From this date on, it decreased again until the following May. In 1986, the maximum size was attained in August and September, after which time it began to drop once again.

Figure 1 shows the sharp difference in the development of maturity during the two years of study. From October 1984 to March 1985, all of the males caught were immature. March marked the appearance of the first males showing signs of sexual activity. All the animals were sexually mature between May and October 1985. Between November 1985 and October 1986, there was an almost constant presence of mature, immature and submature animals.

The female breeding cycle

The minimum weight in females corresponded to an individual caught in January, 1985 (11 gr) (fig. 3). The active female hav-

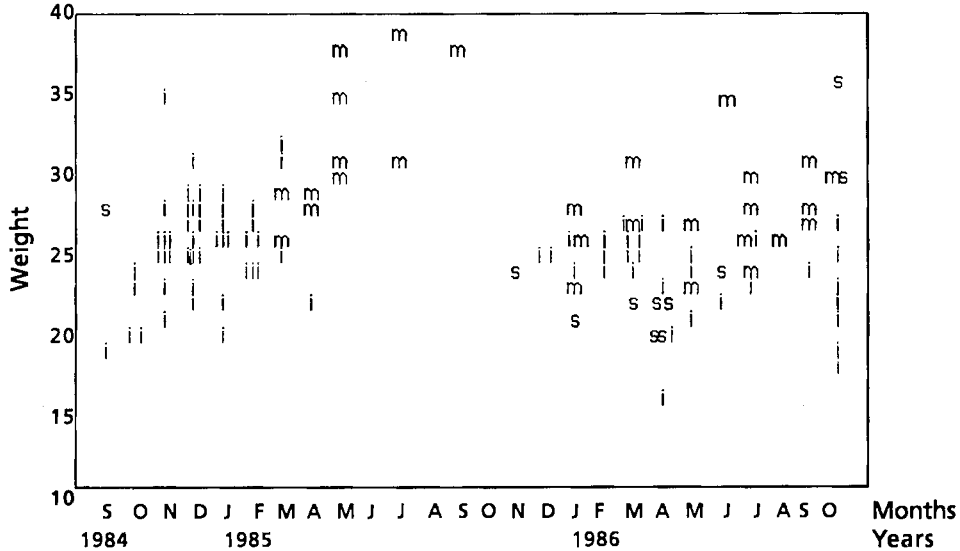

Fig. 1. State of reproductive maturity in males in terms of weight of the animal (gr) and month animal was caught: i. Immature; s. Submature; m. Mature. (n = 126.)

Estado de madurez reproductora de los machos en función del peso del animal (gr) y del mes en que fue capturado: i. Inmaduro; s. Submaduro; m. Maduro. (n = 126.)

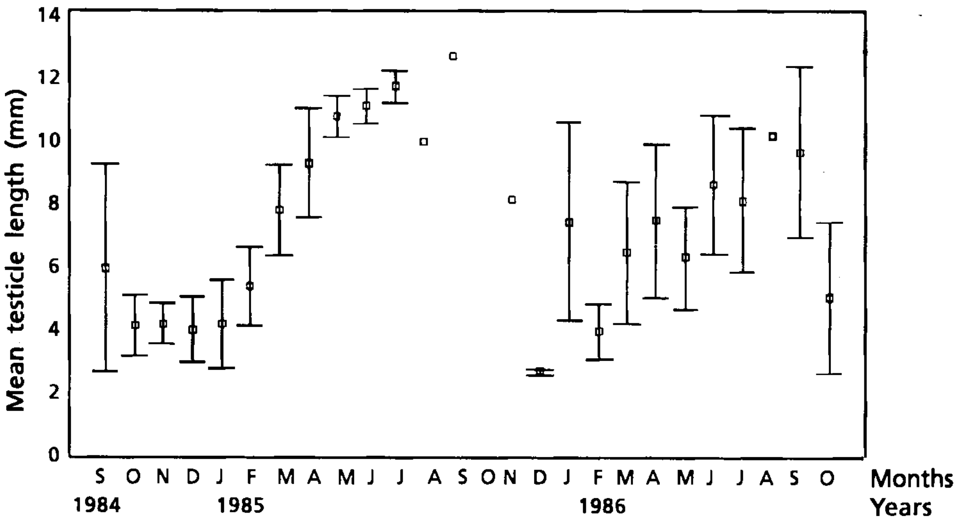

Fig. 2. Variation in mean testicle length (mm) with standard deviation over the period studied. (n = 136.)

Variación de la longitud media del testículo (mm) y desviación estándar a lo largo del periodo de estudio. (n = 136.)

ing the lowest weight was found in July, 1985 (20 gr) and of the non-pregnant active females the animal having the greatest weight was caught in October, 1985 (41 gr). Active females, including pregnant animals, were found in all the age classes.

The reproductive season did not coincide in the two years under study. The first reproductive period started during the winter of the first year (1984), after an inactive autumn. The ratio of active females gradually increased in the following seasons until reaching a maximum in the autumn of 1985. During the following winter and spring, no active animals were found and the next reproductive cycle started in the summer of 1986.

The proportion of pregnant females varied considerably throughout the season. During the spring of 1985, it was 23% (n = 13), in the summer of the same year it went up to 43% (n = 7) and in the autumn it reached 54% (n = 13). In the spring of 1986 no pregnant females were caught. The ratios found in the summer and autumn of 1986 were 33% (n = 9) and 30% (n = 10) respectively.

The mean litter size found based on the embryo count was 3.9 (n = 18; s.d. = 1.57; 2-7) (table 1). An estimation based on the presence of placental scars was 3.8 (n = 17; s.d. = 1.24; 2-6).

There was no significant correlation ($P > 0.1$) between litter size and head + body length ($r_s = 0.3738$; n = 17), or between the litter size and animal weight ($r_s = 0.374$; n = 16). Nor did we find a significant correlation between litter size and the body condition coefficient (weight/head+body^3) ($r_s = 0.296$; n = 15).

The mean size of the litter was greatest in the first two age classes (table 1), and decreased substantially after that. The mean value of classes I and II together was significantly higher than classes III, IV and V using the Student t test ($t = 4.093$; d.f. = 1; $P < 0.001$; $\bar{x}_{1,2} = 4.909$; $\bar{x}_{3,4,5} = 3.167$) which indicates that there is a highly significant difference.

The litter size of pregnant females found

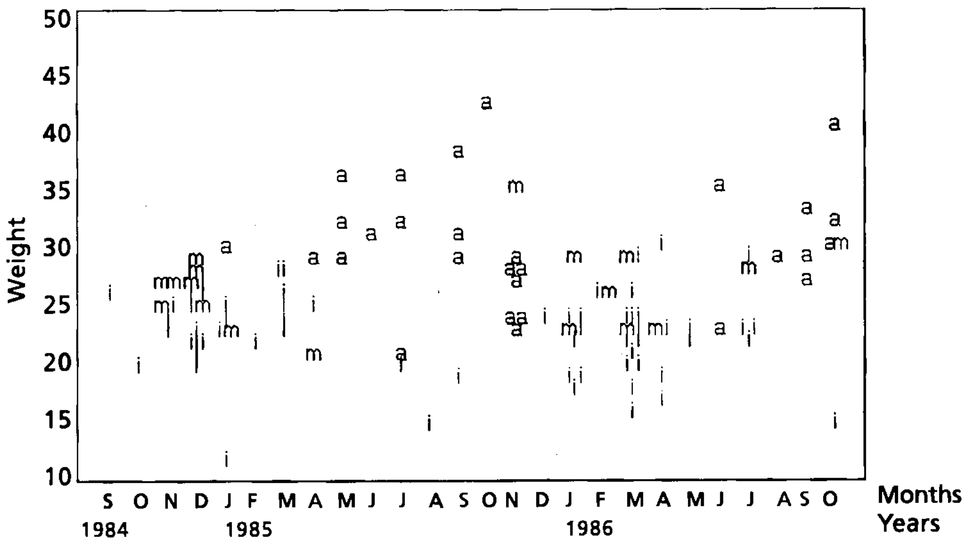

Fig. 3. State of reproductive maturity in females in terms of weight (gr) and month caught: i. Immature; m. Inactive mature females; a. Active mature females. (n = 115.)

Estado de madurez reproductora en hembras en función del peso (gr) y mes de captura: i. Inmadura; m. Hembras maduras inactivas; a. Hembras maduras activas. (n = 115.)

in October 1985 was substantially greater than in the other seasons (table 2). However, the ages of the sample of reproductive females varied from season to season.

Population structure and dynamics

The age structure of the population proved to be different in the same seasons of the different years studied (fig. 4). In the autumn of 1984, 95% of the individuals caught (n = 20) belonged to age classes III and IV. If we consider, in a broad sense, the monthly growth averages of the root of M_1 determined by ZEJDA (1960), they would correspond to individuals born between November, 1983 and July, 1984. Only one individual (5%) pertained to the summer of 1984. A similar situation was found in the winter of the same year (n = 51), where we may point to the presence of 2 class I individuals whose ages may be estimated at under 2.5 months, which would therefore mean that they were born in autumn. During the spring (n = 22) and summer (n = 11) the presence of the oldest age class (V) gradually increased, while age class III declined. Class I was also seen to increase during the spring (5%) and summer (8%). In the autumn of 1985 the individuals belonging to class I reached their maximum value (67%, n = 12), totalling 97% of the individuals belonging to classes I and II. The older animals, represented by class V, were present in low proportions (8%). Starting in this season, the population gradually began to age again during the winter of 1985-86 and the spring and summer of 1986, at which time the population was made up of 17% of class II individuals, 56% from class III, 22% from class IV and 5.6% from class V. The samplings taken in autumn 1996 point to the appearance once again of the younger age classes (class I: 26%) while at the same time there was a progressive ageing of the rest of the members (the disappearance of class II, diminished presence of class III (40%) and an increase in class IV (30%), whereas class V maintained values similar to those reported during the previous season (5%).

Table 1. Litter size for each age class.

Tamaño de las camadas segun clases de edad.

	Age classes				
	I	II	III	IV	V
Embryos					
n	5	2	4	2	2
$\bar{x}$	4.8	6.0	3.0	2.5	2.5
s.d.	1.79	0.00	0.00	0.71	0.71
range	3-7	6-6	3-3	2-3	2-3
Placental scars					
n	-	4	5	2	3
$\bar{x}$	-	4.5	4.0	3.0	3.0
s.d.	-	1.29	0.45	0.00	1.00
range	-	3-6	3-5	3-3	2-4

Table 2. Litter size for each season during which pregnant females were caught: Spr. Spring; Sum. Summer; Aut. Autumn.

Tamaño de las camadas para cada estación en las que se capturaron hembras gestantes: Spr. Primavera; Sum. Verano; Aut. Otoño.

	1985			1986	
	Spr	Sum	Aut	Sum	Aut
n	2	3	7	3	3
$\bar{x}$	2.5	2.7	5.6	3.0	3.3
s.d.	0.71	0.58	1.27	0.00	0.58
range	2-3	2-3	3-7	3-3	3-4

Table 3 shows the sex ratio in the sample studied corresponding to each season of the year during the study period. The chi-square values indicate that, with the exception of the autumns of 1984 and 1985, the sex ratio did not vary significantly from 1:1.

Discussion

The animals examined showed two different cycles in the years studied:

In the autumn of 1984 there was a relatively large number of non-reproductive individuals from the older age classes. In the autumn of 1985 the population consisted primarily of the first two age classes and females were found to have their maximum reproductive activity.

The first breeding period began in late winter and reached its maximum during the autumn 1985. In the second breeding period, activity did not start until the summer.

Some studies (WATTS, 1970; BUJALSKA, 1975) state that the supply of food accelerates the onset of the reproductive season by several weeks. In the study area there was practically no beech crop during the autumn of 1984. In the autumn of 1985 there was a large forestry crop. We may infer that the beech crop did not have any effect, in this respect, since the reproductive season following the autumn with the forest crop did not begin until the summer. This can be attributed to the fact that the diet of the population studied is basically folivore (CASTIÉN & GOSÁLBEZ, 1996).

The litter size is considerably higher in the northern part of the distribution area than in central and southern Europe: an average of 5.9 in Sweden (HANSSON, 1969); 5.2 in southern Norway (WIGER, 1979); 5.2 in Poland (RIZSKOVSKI, 1971); 4.1 y 5.0 in Czechoslovakia (ZEJDA, 1966); 4.1 in England (BRANBELL & ROWLANDS, 1936); 3.5 (ALIBHAI, 1976). In France it is 3.9 (SAINT-GIRONS, 1972); in Switzerland, 4.1 (CLAUDE, 1970); in the North of Spain, 4.1 (REY, 1972); 4.2 in Montseny, North-east of Spain (GOSÁLBEZ & SANS-COMA, 1976); 3.8 in the Catalonian Pyrenees (GOSÁLBEZ, 1976) and 3.9 in this study. Based on all the data obtained in this study, the mean litter size agrees with the previous reports from the North of the Iberian peninsula and France.

The breeding period varies widely (CORBET & SOUTHERN, 1964). Generally speak-

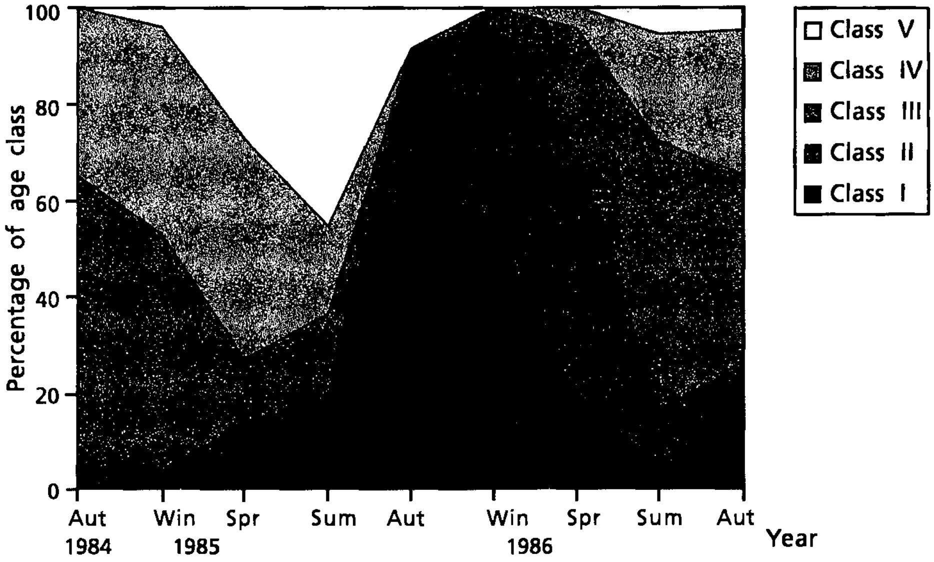

Fig. 4. The ratio of each age class found during the different seasons.
Proporción de cada clase de edad en cada estación.

ing, these authors state that it begins anytime from April to the end of September-October, although reproduction may continue throughout the winter in some years. This has been linked to the size of the tree seed crop (FLOWERDEW, 1973) or to mild temperatures in some years (ZEJDA, 1962). In the north-east of the Iberian Peninsula,

Table 3. Males and females in each season of the year: Aut. Autumn; Win. Winter; Spr. Spring; Sum. Summer.
Machos y hembras en cada estación del año: Aut. Otoño; Win. Invierno; Spr. Primavera; Sum. Verano.

	1984	1985				1986				
	Aut	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	Total
Males	16	35	13	7	2	14	25	10	14	136
	73%	58%	50%	50%	13%	47%	49%	53%	58%	52%
Females	6	25	13	7	13	16	26	9	10	125
	27%	42%	50%	50%	87%	53%	51%	47%	42%	48%
χ^2	4,545	1,667	0,00	0,00	8,067	0,133	0,019	0,053	0,667	0,464
P	0,03	0,197	1,00	1,00	0,004	0,715	0,889	0,818	0,414	0,496

there is evidence of reproductive activity in winter (GOSÁLBEZ & SANS-COMA, 1976) although no such winter activity has been found in the population of the Pyrenees and Iberian Mountains (GOSÁLBEZ, 1976; REY, 1972). In our study, of the 25 females caught in the winter 1984-85, only one showed signs of reproductive activity. With the exception of this case, the period of sexual activity in females in 1985 started in April and ended in November. In 1986 the onset of this activity took place in June.

According to the literature, litter size varies depending on the season (SAINT-GIRONS, 1972) and is greater in the spring (ZEJDA, 1966). In a study of a laboratory population, SAINT-GIRONS (1972) found that the number of juveniles per litter reached a maximum in the third parturition and decreased after that. NYLHOM & MEURLING (1979) showed that litter size also depends on the phase in which the cyclic population is found, reporting larger litters during the growth phase than in the phase of maximum density. BRAMBELL & ROWLANDS (1936) and ZEJDA (1966) also indicate that heavier females tend to have more numerous litters.

In contrast to this information, the data from this study does not appear to substantiate a relation between weight, head + body or condition coefficient and litter size, probably because in the literature this relationship has been established between different populations and not between individuals belonging to the same population. However, a substantially larger litter size was found in the two younger size classes as compared to the older ones (4.9 for classes I and II as opposed to 3.2 for classes III, IV and V).

A direct interpretation of the results led us to infer that the younger age classes are more productive than the older ones. This would justify the fluctuations in interannual densities. However, according to the literature, other different, intra and inter-specific factors, have been seen to contribute to the cyclic or fluctuating variations in the populations of *Clethrionomys glareolus*. Therefore the variations in the litter size of this species must be considered to have several causes, one of which may, in our opinion, be the age of the reproductive females.

This corroborates the opinion that *Clethrionomys glareolus* is a species with great ecological plasticity limited or regulated by a wide variety of intrinsic and external factors which give rise to different responses in the populations and to varying situations of equilibrium.

Resumen

Reproducción, abundancia y estructura de población del topillo rojo Clethrionomys glareolus *(Schreber, 1780) en los Pirineos occidentales*

Se describe el ciclo reproductor del topillo rojo (*Clethrionomys glareolus*) en el Pirineo occidental durante un período de dos años (figs. 1-3). Se relaciona con la estructura de la población (fig. 4) y se compara con otras poblaciones europeas. Existen diferencias marcadas en la duración del período reproductor entre los dos años estudiados (fig. 3). En el primer año la reproducción comienza a finales del invierno y alcanza su mayor intensidad en el otoño siguiente. En el segundo año la reproducción no comienza hasta el verano. El tamaño medio de camada es similar al descrito para Francia y el norte de la península ibérica, pero varía con el tiempo (tabla 2). Los cambios en el tamaño de camada están relacionados con la edad de las hembras reproductoras (tabla 1). Las clases de edad más jóven (I y II) presentan tamaños de camada mayores que las clases de más edad (III, IV y V). Ello puede influir en las fluctuaciones interanuales.

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