Acta Theriologica 49 (3): 319–335, 2004.
PL ISSN 0001-7051

Population parameters and reproductive biology of the Iberian hare *Lepus granatensis* in southern Iberia

Miguel A. FARFÁN, Juan M. VARGAS, Raimundo REAL,
Luis J. PALOMO and Jesús DUARTE

Farfán M. A., Vargas J. M., Real R., Palomo L. J. and Duarte J. 2004. Population parameters and reproductive biology of the Iberian hare *Lepus granatensis* in southern Iberia. Acta Theriologica 49: 319–335.

To analyse the population structure and reproductive biology of the Iberian hare *Lepus granatensis* Rosenhauer, 1856, 498 hares (264 males and 234 females) were collected in monthly samples from October 1998 to September 1999. Females reached larger sizes than males, with approximately 400 g difference in body mass on reaching sexual maturity. The total sex ratio was 1:1, with a bias in favour of males in winter. Sexually active males and females appeared in every month but August, when no sexually active female was found. Births occurred in every month and were more frequent between March and July. Seasonal variation in kidney fat index (KFI) followed a similar pattern in males and females, with an increase in mid-autumn and a decline at the end of winter. Reproductive activity appeared in every month, with a maximum from February to June. Reproductively hyperactive females (simultaneously pregnant and nursing) appeared in every month except in January, with a first peak in March and a second lower peak in May–June. Litter size fluctuated between 1 and 7 leverets. The most frequent gestations involved 1 or 2 foetuses. The mean annual litter size was 2.08 and the average number of litters per productive female per year was estimated to be 3.48. The maximum productivity was recorded between March and May. The total annual production of young per adult female was estimated to be 7.21. The minimum annual survival rate of young was 27.91%. On the basis of these results we propose to maintain the limit of the hunting period between October and December. We discuss the relationship between the low young/adult ratio obtained and the hunting method used.

Departamento de Biología Animal, Universidad de Málaga, E-29071 Málaga, Spain, e-mail: mafarfanaguilar@hotmail.com, (MAF, JMV, RR, LJP); Servicios Ambientales Daidín S. L. Nuestra Señora de Gracia, 4. 29600 Marbella, Spain, e-mail: jduarte@daidin.com (JD)

Key words: *Lepus granatensis*, Iberian hare, reproduction, population structure, Iberian Peninsula

Introduction

The Iberian hare *Lepus granatensis* Rosenhauer, 1856 is endemic to the Iberian Peninsula, where it coexists in parapatry with two other hare species, *L. europaeus* and *L. castroviejoi* (Palacios 1976, Palacios and Meijide 1979, Bonhomme *et al.* 1986), and in sympatry with the wild rabbit *Oryctolagus cuniculus*. Within its range, *L. granatensis* is very common and abundant, and in some localities it is one of the most important game species. It is harmful to local crops that grow on irrigated land and to young plantations of woody crops (Duarte *et al.* 2002). In spite of this, information on the biology and population dynamics of the Iberian hare is still scarce. Only a few studies have been carried out on its reproduction (Palacios 1980, López *et al.* 1996, Alves *et al.* 2002), population size (Lazo *et al.* 1992, Batista and Carvalho de Cruz 1996, Carro *et al.* 1999), and habitat characteristics (Palacios and Ramos 1979, Calzada and Martinez 1994, Duarte and Vargas 1998, Duarte *et al.* 2002).

From the end of the 1980s onwards, *L. granatensis* has shown considerable demographic growth, especially in southern Iberia (Duarte *et al.* 2002), which was accompanied by an increase in hunting pressure. According to Vargas (2002), hunting bag records indicate a progressive increase in the number of hares captured in Spain between 1992 (695 967 individuals captured) and 1998 (1 286 860 individuals captured). This increase in hunting pressure (45.9%) is also a consequence of the decline shown by both the wild rabbit and the red-legged partridge, which are more attractive than hares to Spanish hunters (Vargas and Muñoz 1996). The current situation of *L. granatensis* is opposite to that of *L. europaeus*, whose populations have declined dramatically in western Europe during the last decades (Tapper 1992, Schneider 1997).

The length of the reproductive period, annual production of juveniles, and postnatal survival rate of juveniles are important parameters for the suitable management of the wild populations. Seasonal variation in hare reproduction is an adaptation to annual changes in the environment (Blottner *et al.* 2000), and the seasonal trend in the production of young is the result of changes in the percentage of pregnant females and litter size (Broekhuizen and Maaskamp 1981, Pépin 1989). The abundance and fluctuations in hare populations are probably primarily generated by changes in survival rates among juveniles (Keith 1981). However, information on the reproductive cycle and the population dynamics of *L. granatensis* is scarce, in contrast to information on *L. europaeus* and *L. timidus* (Raczyński 1964, Flux 1967, 1970, Lincoln 1974, Pépin 1977, Hewson and Taylor 1975, Frylestam 1980b, Martinet and Demarne 1984, Hansen 1992, Angerbjörn and Flux 1995, Bonino and Montenegro 1997).

In this paper, we analyse some aspects of the reproductive biology of *L. granatensis*, including basic reproductive characteristics and seasonal variation of male and female breeding activity, and the annual production and postnatal survival of juveniles in a large-scale farming area in southern Spain.

Material and methods

Study area and material

The study was carried out in Granada province, located in southern Iberia, between 36°37' and 38°6'N and 2°4' and 4°16'W of Greenwich. It covers an area of 12 531 km^2 and is mostly a mountainous region with high mean altitude, reaching 3479 m in the Sierra Nevada (the maximum altitude in the

Table 1. Number of hares captured each month at the "plant of Granada".

Month	n	Adult		Young
		Male	Female	
October 1998	46	17	22	7
November 1998	46	17	22	7
December 1998	50	27	22	1
January 1999	60	38	20	2
February 1999	60	29	31	0
March 1999	29	20	9	0
April 1999	50	31	17	2
May 1999	38	18	16	4
June 1999	30	14	14	2
July 1999	34	9	11	14
August 1999	30	19	4	7
September 1999	25	12	11	2
Total	498	251	199	48

Iberian Peninsula). The mountain ranges are separated by a series of depressions whose mean altitudes increase from the west (685 m in Granada) to the east (953 m in Huéscar). We sampled four very close areas located in the westernmost depression known as the "plain of Granada". These four areas are named Íllora, Caparacena, Loja, and Albolote. All are characterised by a smooth relief dominated mainly by olive groves. A total of 498 hares were collected in monthly samples from October 1998 to September 1999 in the four sampling areas (Table 1). The hunters shot the hares during daytime. Several hunters, with or without dogs, walked in line maintaining a certain distance between them and then flushed out the game and attempted to bring it down.

Body weight and length

The hares were weighed to the nearest 50 g using a dynamometer and the total body length (from snout, placed in line with the main axis of the body, to the beginning of the tail) was measured using a tape measure with 1 mm accuracy. The results were grouped according to season and sex. For pregnant females we calculated the lean body mass, excluding the weight of embryos. If there were no evidences against the normality of the distributions or against the homoscedasticity of the variances, then inter-sex differences for the variables were tested using ANOVA, otherwise we used the Mann-Whitney U-test (Sokal and Rohlf, 1981). Similarly, we used either ANOVA or the Kruskal-Wallis test to check the significance of the seasonal differences in body mass and length for both males and females.

Body condition

We used the body mass divided by the cubic body length (BM/BL^3) as an estimate of the body condition. By using the Mann-Whitney U-test we assessed the significance of the differences in BM/BL^3 between contiguous seasons. In addition, the abdomen of all collected individuals was opened and the left kidney and its surrounding fat were weighed on a digital balance with 0.1 g accuracy. Using the same approach as Flux (1967), we calculated the monthly average kidney fat index (KFI) for each sex by weighing the perirenal fat of the left kidney and expressing it as a percentage of mass of that kidney.

Reproduction activity

In males, the number of descended testicles was recorded. The left testicle was excised and the length, with the epididymus removed, was measured using a calliper. Males were considered reproductively active if they showed at least one descended testicle and sperm was present as revealed using the Diff-Quick dye technique (Gosalbez *et al.* 1979). Using the Mann-Whitney *U*-test we checked the differences between the testis length of reproductively active and reproductively inactive males. Seasonal variation in testis length was assessed by means of the Kruskal-Wallis test.

We recorded the monthly proportion of reproductively active females, which represents the percentage of the total number of females in a given month that were pregnant or nursing. The activity of the mammary glands was estimated by the presence of milk. Pregnant females with milk in the mammary glands were considered to be reproductively hyperactive. We recorded the percentage of the total number of females that were reproductively hyperactive in every month.

The embryos were counted, weighed on a digital balance, and preserved in 70% alcohol. The length of the ovaries and the embryos were measured with a calliper. Differences in ovary length among pregnant, nursing and sexually inactive females were established using the Mann-Whitney *U*-test. The period when each female was mating, up to two months before the shooting date, was inferred taking into account the embryos' weight and length and the activity of the mammary glands, according to the different categories shown in Table 2. When the body mass and length of the embryos did not belong to the same category, only the value of the body mass was considered for determining the time when the female mated. A reproductively hyperactive female could be estimated as mating at two different periods, according to the embryos' size and the activity of the mammary glands.

We determined the minimum size at which males and females are sexually active taking into account the body mass and length. Using the date of the hunts and the size of the embryos we estimated the potential dates of births, and calculated the percentage of potential production of young expected in every month.

Age and sex ratios

The hares shot were classified as adults or juveniles in relation to the minimum size at which males and females are sexually active. We obtained a young/adult ratio for every season and checked seasonal differences by using the Kruskal-Wallis test. The overall and seasonal sex ratio were calculated by dividing the number of adult males by the number of adult females, and differences with respect to an expected 1:1 ratio were assessed by means of the χ^2-test.

Litter size

To analyse the litter size variation throughout the study period, we calculated the monthly average litter size by dividing the number of embryos by the number of pregnant females in every month. The frequency of each litter size was determined by dividing the number of litters of a given size by the total number of litters.

Table 2. Criteria established for determining when a female hare was mating.

Parameter	Category			
	1	2	3	4
Female sexually active	15 days ago	30 days ago	45 days ago	60 days ago
Body mass of the embryo	< 30.3 g	> 30.3 < 60.5 g	> 60.5 g	Mammary gland with milk
Body length of the embryo	< 37.7 mm	> 37.7 < 75.3 mm	> 75.3 mm	

The mean annual litter size (MALS) was calculated using the formula of Pépin (1989):

$$\text{MALS} = \frac{\sum_{\text{month1}}^{\text{month12}} \%\ \text{pregnant} \times \text{mean size of letter}}{\sum_{\text{month1}}^{\text{month12}} \%\ \text{pregnant}}$$

Production and survival rate of young hares

According to Rodríguez and Palacios (1997a), the gestation period of the Iberian hare is 42 days. Therefore, a healthy adult female may have, on average, a maximum of 0.71 litters in one month. Using the method described by Pépin (1989), the production of young hares throughout the annual cycle has been calculated by multiplying the monthly average litter size by the proportion of pregnant females in the same month and by 0.71. To explain the variation of the monthly productivity, the production of leverets has been correlated with the monthly average litter size and with the proportion of pregnant females.

Using the method described by Broekhuizen and Maaskamp (1981), the average number of litters per productive female per year was estimated from the quotient between the total annual production of young and the mean annual litter size. The minimum annual survival rate of young has been calculated from the quotient between the total number of juveniles and the total number of embryos found during the study period.

Results

Body mass and length

Seasonal mean values of body mass and body length obtained for males and females are shown in Fig. 1. Females reached bigger size than males, both in body mass (Mann-Whitney *U*-test: $U_{450} = 9375$, $p < 0.001$) and length (ANOVA $F = 100.133$, $n = 435$, $p < 0.001$). There were seasonal differences in mass for females (Kruskal-Wallis test: $H = 43.11$, df = 3, $p < 0.001$), which were heavier in spring and lighter in autumn, but not for males ($H = 4.38$, df = 3, not significant). Conversely, there were seasonal differences in body length for males ($F = 7.80$, $n = 4$, $p < 0.001$), whose average size decreased from autumn to summer, but not for females ($F = 1.32$, $n = 4$, not significant).

Body condition

In females, BM/BL^3 increased from autumn to winter (Mann-Whitney *U*-test: $U_{126} = 1{,}131.5$, $p < 0.001$), increased again in spring ($U_{107} = 698$, $p < 0.001$) and then decreased in summer ($U_{73} = 395$, $p < 0.05$) to the same levels as in winter. In males the only significant trend in BM/BL^3 was to be lower in autumn than in winter ($U_{147} = 1460$, $p < 0.001$), and then the body condition stabilised until summer. The seasonal variation in Kidney Fat Index (KFI) is similar for females and males. There is a steep increase in fat deposits at the end of autumn followed by a decline to normal levels at the end of winter.

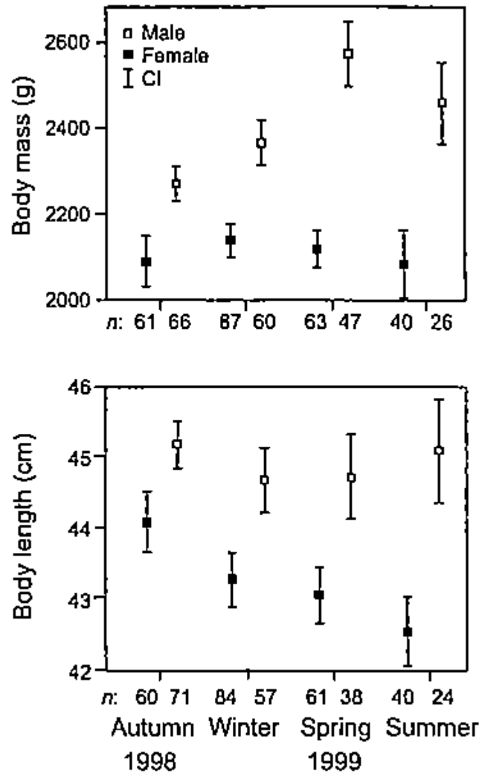

Fig. 1. Seasonal variation of the mean (and confidence intervals – CI) body mass (top) and length (bottom) of adult male and female Iberian hares from the "plant of Granada", S Spain. *n* – number of individual analysed in each season.

Reproduction activity

We detected reproductively active males and females in every month (Fig. 2). The proportion of reproductively active males is highest between January and May, reaching a maximum in March, and then again in August and September. The highest values for females appeared between February and June with a new peak in September, that is, with a lag of one month with respect to the activity of males. Reproductively hyperactive females occurred in every month except January, with a maximum in March, when 55.6% of females were reproductively hyperactive, and a lower second peak in May–June, with 38.9% and 46.7% of hyperactive females.

The monthly proportion of females that were estimated to mate before the shooting date is shown in Table 3. Only in January, all reproductively active females had mated in the month of capture. However, in March and June, for example, a high proportion of reproductively active females had mated two months before.

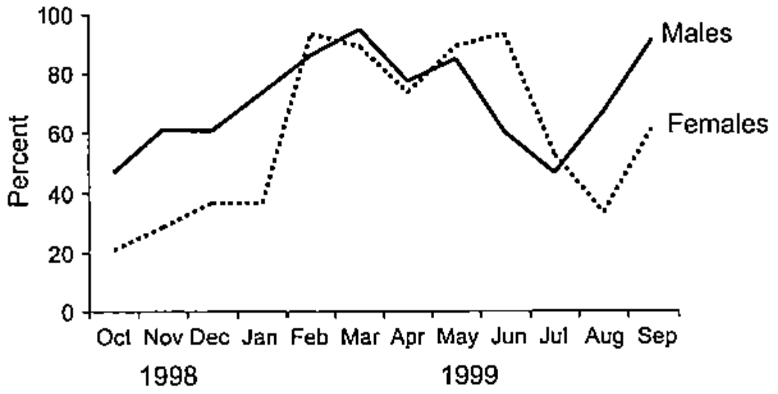

Fig. 2. Monthly variation in the percentage of reproductively active male and female Iberian hares in southern Spain.

The testis length was similar for males with descended testes and with abdominal testes (Mann-Whitney U-test: $U_{241} = 4461$, not significant). Seasonal differences in testes length were found significant (Kruskal-Wallis test: $H = 29.6$, df = 3, $p < 0.001$) with highest values recorded in spring and winter and lowest values obtained in summer.

The mean ovary length was longer in reproductively active females than in inactive females (Mann-Whitney U-test: $U_{192} = 1568.5$, $p < 0.001$), and pregnant females had longer ovaries than nursing females ($U_{125} = 1156.5$, $p < 0.05$). Seasonal variation in ovary length was significant for nursing females (Kruskal-Wallis

Table 3. Monthly proportion of female Iberian hares that mated in the same month (category 1) or in previous months (categories 2, 3 and 4, see Table 2). n – number of females captured in each month.

Month	n	Category			
		1 (15 days ago)	2 (30 days ago)	3 (45 days ago)	4 (60 days ago)
October 1998	29	3.45	0.00	3.45	13.79
November 1998	28	7.14	0.00	0.00	25.00
December 1998	22	9.09	0.00	0.00	31.82
January 1099	22	36.36	0.00	0.00	0.00
February 1999	31	70.97	12.90	3.23	9.68
March 1999	9	33.33	11.11	11.11	88.89
April 1999	19	52.63	0.00	5.26	26.32
May1999	18	44.44	11.11	5.56	66.67
June 1999	15	20.00	13.33	26.67	80.00
July 1999	19	10.53	5.26	21.05	36.84
August 1999	9	0.00	0.00	22.22	22.22
September 1999	13	15.38	15.38	15.38	23.08

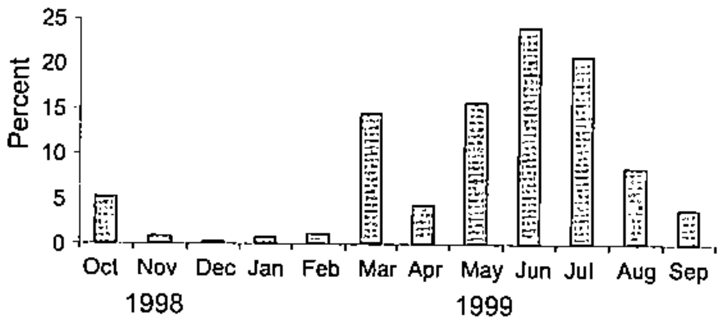

Fig. 3. Annual distribution of the production of young expected on the basis of the number and size of the embryos found in each sample and the date of shooting.

test: H = 8.99, df = 3, $p < 0.05$), with longest ovaries recorded in summer and shortest ovaries found in autumn, and for reproductively inactive individuals (H = 9.31, df = 3, $p < 0.05$) with longest ovaries recorded in spring.

The minimum size at which males and females were reproductively active is different. On reaching sexual maturity, females were approximately 400 g heavier than males. The smallest reproductively active female weighed 2 kg and measured 42.2 cm, while the smallest reproductively active male weighed 1.6 kg and measured 40 cm. The monthly variation in the distribution of potential number of young born is shown in Fig. 3. Births were expected in every month, but nearly 90% of embryos were to be born between March and August.

Age and sex ratios

The number of young and adults captured each month are shown in Table 1. The young/adult ratio was lower than one in every month. The proportion of young hares reached a peak at the beginning of summer. However, seasonal differences in young/adult ratio were not significant (Kruskal-Wallis test: H = 7.049, df = 3, not significant). The overall adult sex ratio was 264 males/234 females, which was not significantly different from 1:1 (χ^2 = 1.81, n = 2, not significant), but there was a significant deviation form the 1:1 ratio in winter, when it was biased in favour of males (χ^2 = 4.96, n = 2, $p < 0.05$).

Litter size

The litter size fluctuated between 1 and 7 leverets. The most frequent gestations were those of 1 foetus, and second of 2 foetuses (Fig. 4). The mean annual litter size was 2.08 (Table 4). From March to July the average number of embryos/pregnant females was ≥ 2, but only in April and May the average number of embryos/ pregnant females was > 3.

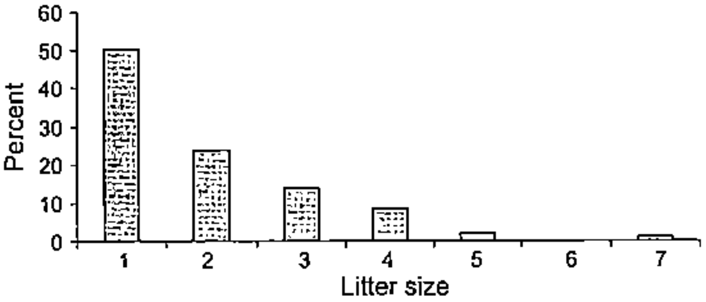

Fig. 4. Relative frequency of each litter size of Iberian hare in southern Spain.

Production and survival rate of young hares

The maximum productivity of leverets per female was recorded between March and May (>1), while the lowest values were obtained in autumn (Table 4). This parameter has a higher correlation with the monthly average size of litter (r = 0.932) than with the monthly proportion of pregnant females (r = 0.791). The annual production of young per female was 7.21. The average number of litters per female per year was estimated to be 3.48, after dividing the annual production of young per female by the mean annual litter size (see Table 4). The minimum annual survival rate of young was 27.91% (Table 4).

Table 4. Monthly pregnancy rate, mean litter size and production of young Iberian hares per female and survival rate of young hares. The number of litters per month was 0.71. Mean annual litter size: 10.17/4.9 = 2.07. Minimum annual survival rate of young hares was calculated: (48 × 100)/172 = 27.91%.

Month	Proportion of pregnant females (A)	Mean litter size (B)	A × B	Production of young per female	Juveniles shot	Number of embryos
October 1998	0.10	1.00	0.10	0.07	7	3
November 1998	0.07	1.00	0.07	0.05	7	2
December 1998	0.09	1.00	0.09	0.06	1	2
January 1999	0.36	1.00	0.36	0.26	2	8
February 1999	0.87	1.19	1.04	0.73	0	32
March 1999	0.56	2.60	1.46	1.03	0	13
April 1999	0.58	3.36	1.95	1.38	2	37
May 1999	0.61	3.27	1.99	1.42	4	36
June 1999	0.60	2.11	1.27	0.90	2	19
July 1999	0.37	2.00	0.74	0.52	14	14
August 1999	0.22	1.50	0.33	0.24	7	3
September 1999	0.46	1.67	0.77	0.55	2	3
Total	4.9		10.17	7.21	48	172

Discussion

Size and body condition

Both body mass and length values show that in wild populations of *Lepus granatensis* females reach a larger size than males. This is in concordance with Alves *et al.* (2002), who affirmed that in all hare species females are larger than males. Two studies of *L. granatensis* carried out in Zamora and Valladolid (Rodríguez and Palacios 1997b) and Évora (Batista and Meixa de Almeida 1996), near the North and West limits of its distribution area (see Palacios and Meijide 1979), reported a similar sexual dimorphism in body mass. In at least four other species of *Lepus*, females have been found to be heavier than males: *L. europaeus* (Flux 1967, Frylestam 1980a), *L. timidus* (Flux 1962), *L. californicus* (Bronson 1958, Lechleitner 1959), and *L. americanus* (Newson and de Vos 1964). Females were also longer than males, which agrees with the results obtained by Rodríguez and Palacios (1997b) and Batista and Meixa de Almeida (1996).

Body mass shows a seasonal variation only in females, which are heavier in spring. This seasonal variation was found by Flux (1967) for *L. europaeus*. However, the tendency to be lighter in autumn is shared by males and females, although in males it is only apparent when the body condition is taken into account. In autumn, male poorer body condition does not result in a lighter average mass because it is compensated by a higher average body length. The smaller average length in winter may be consequence of the shooting season (October to December), when an important proportion of the predominant large hares is captured. As females need to reach a longer length than males to obtain sexual maturity, their adult average length does not decrease in winter, because the lost in larger individuals is hardly compensated by the recruitment of younger, and thus smaller, females. The effect of the shooting season in females is reflected in the adult sex ratio instead, which is clearly in favour of males in winter.

Perirenal fat deposits showed a marked seasonal variation. The fat starts to accumulate in mid-autumn, reaching a peak at the beginning of winter. Iberian hares are fatter in January (mid-winter), immediately before the main reproduction period, which starts in February. Similar results were obtained by Flux (1971) for *L. europaeus* in New Zealand, who inferred that an important function of fat deposits is to provide energy for breeding. He argued that any fat deposits imply a physiological purpose and do not simply accumulate because of food abundance. Our results are in agreement with these observations, since the biggest fat deposits occur during a short period of the annual cycle, before the onset of the main breeding period.

Reproduction activity

The proportion of reproductively active males and females were lowest in autumn, which coincides in part with the results of Alves *et al.* (2002), who found that the proportion of reproductively active male Iberian hares in Portugal is lower in autumn. Our results are also in accordance with those obtained by Flux (1967) for *L. europaeus*, who found that males captured from the end of summer to the start of autumn were reproductively inactive.

The comparison between the seasonal trends in testis length and ovary length reveals that gonad activity of males precedes that of females. Broekhuizen and Maaskamp (1981) found that in *L. europaeus* the beginning of the reproductive season for females was mate-induced. The lowest values of ovary length for *L. granatensis* occurred in autumn-winter. These results are similar to those obtained by Flux (1967) working with *L. europaeus*, who found that the lowest values of ovary length appeared in autumn and the beginning of winter. The lightest reproductively active male and female had a lower body mass in our study area than those observed by Alves *et al.* (2002) for the same species in Portugal.

We found that the seasonal variation in the expected production of young in *L. granatensis* was similar to that reported for *L. europaeus* in Sweden (Frylestam 1980b), Denmark (Hansen 1992), and France (Pépin 1989). We found reproductively active females in every month, which is in concordance with Palacios (1980), Rodríguez and Palacios (1997a), and Alves *et al.* (2002), who affirmed that *L. granatensis* shows reproductive activity throughout the year. In contrast, indigenous and introduced populations of *L. europaeus* do not show reproductive activity in the coldest months of the year (Reynolds and Stinson 1959, Flux 1965, Hewson and Taylor 1975, Möller 1976, Palacios 1980, Frylestam 1980b, Pielowski 1981, Hansen 1992).

Rodríguez and Palacios (1997a) stated that in Spain there is a maximum period of activity from February to April, and Alves *et al.* (2002) found that the reproductive activity in Portugal is higher in January–February and then again in July–August. However, in the present study, the period of maximum reproductive activity occurs between February and June, when the highest proportion of reproductively hyperactive female hares was also found. The percentages of reproductively active and hyperactive female hares were lowest in autumn.

Superfoetation, defined as the simultaneous occurrence of distinctly developed embryos of different ages, occurs frequently in captive hares (Hediger 1948, Raczyński 1964, Jacobs 1966, Martinet 1977). However, it seems most unusual in wild hares. In the present study, embryos of two ages were never found. These results are in accordance with those obtained by Alves *et al.* (2002) for *L. granatensis*, and by Flux (1967) and Broekhuizen and Maaskamp (1981) for *L. europaeus*, since in all cases they did not observe superfoetation.

Taking into account the reproductive activity of *L. granatensis*, the hunting season in Andalusia, which occurs from October to December, seems to be appropriate, since in this period the percentage of females that were reproductively active and hyperactive was lower than during the remaining months of the year. In the same way, the results obtained by Alves *et al.* (2002) showed that *L. granatensis* breeds continuously, but with lower intensity between September and December. Nevertheless, Palacios (1980) considered that the former hunting season in Spain, which used to last from October to February, was inappropriate, because in this period the reproductive activity was very high. However, the proportion of reproductively active females obtained by Palacios (1980) was very high only in January and February, two months that now are outside of the hunting period in Andalusia.

Age and sex ratios

The overall young/adult ratio was much lower than those reported for *L. europaeus* by Pépin (1989) in France (0.12 vs 1.32–2.44), and by Pielowski (1981) in Poland (9.6 vs 50% of young). Similarly, seasonal young/adult ratios were lower than those reported for *L. europaeus* in autumn (11.8 vs 20–70.9%; Flux 1967, Abildgård *et al.* 1972, Pegel 1986, Wasilewski 1991, Hansen 1992) or in summer (39.4 vs 56%; Flux 1967).

López *et al.* (1996) analysed the ratio between juveniles and adult females during the shooting season (October–December) in a wild population of *L. granatensis* in nothern Spain, and found that it fluctuated between 0.50 and 3.16, which are higher values than our equivalent observations in souther Spain (0.05–0.32). According to Pépin (1978, 1987), hunting methods using beaters, which was the method used in our study, are non-selective and, thus, a higher proportion of small hares should be present in our samples. Flux's (1967) values, for example, were obtained after shooting hares during the night from cars equipped with spotlights (Williams *et al.* 1964), which under-represents small leverets; notwithstanding this, his proportion of young was higher than ours. However, as our hunters acted as beaters, we think that the recruitment of young animals by shooting was lower than expected because hunters preferred to shoot big hares and, as no dog was used, the leverets were able to escape.

The adult sex ratio in this study is roughly 1:1, which is similar to the results found by Frylestam (1979) and Pépin (1987) with *L. europaeus*. The predominance of adult males of Iberian hares in winter differs from the results obtained by Pielowski (1969) and Abildgård *et al.* (1972) for *L. europaeus*. This difference in winter sex ratio could be caused by the quicker recruitment of adult males, as compared to females, after the shooting season, since males need to reach a smaller size than females to attain sexual maturity (Peroux 1995).

According to Flux (1967), the sex ratio of hares probably varies with the method of capture and with the behaviour of the animals. In his study, the hares were shot at night and no seasonal variation of sex ratio was obtained. In contrast, in the present study, and in Raczyński (1964), the hares were shot in daylight, and in both of them a seasonal variation of the sex ratio is described. The results of our study show that the period when females are more abundant (autumn) coincides with the period when the proportion of reproductively active females is lowest.

Litter size

The most frequently observed gestations included 1 fetus and then 2 fetuses, which is in accordance with the results obtained by Alves *et al.* (2002). However, López *et al.* (1996) obtained different results, since litters with 2 leverets (73.33%) were more frequent than those with 1 leveret (26.66%). Palacios (1980) found that the litter size of 1 and 2 fetuses had the same frequency (50%). Nevertheless, in these comparisons it should be taken into account that the samples analysed by López *et al.* (1996) and Palacios (1980) were very small (15 and 20 individuals, respectively). Hewson and Taylor (1975) showed that the litter size of *L. europaeus* is bigger than that of *L. granatensis*. The litter sizes found by Hewson and Taylor (1975) were, in decreasing order of frequency: 3, 2, 4, 1, and 5 leverets. Some authors have related the smaller litter size in *L. granatensis* to its smaller body size (Tuomi 1980, Iason 1990, Alves *et al.* 2002).

The largest litter found in the present study held 7 embryos, although this litter size can be considered exceptional in Spain. The largest litter found by Alves *et al.* (2002) in Portugal consisted of 4 embryos. For *L. europaeus* the literature also provides few data about litters larger than 7: Jacob (1956) found 9 embryos and Broekhuizen and de Wit (1972) found a female hare with 10. However, the largest litters found by Hewson and Taylor (1975) in Scotland, Broekhuizen and Maaskamp (1981) in the Netherlands, and Hansen (1992) in Denmark all contained 5 embryos. The mean litter size showed a marked seasonal variation with maximum values in March–July. These results are similar to those obtained by Alves *et al.* (2002) in Portugal and by Frylestam (1980b) for *L. europaeus* in Sweden.

The mean annual litter size obtained in the present study was higher than that obtained by Alves *et al.* (2002). However, it was slightly lower than those obtained for *L. europaeus* (see the review in Pépin 1989, Alves *et al.* 2002). Flux (1967) found a negative correlation between the mean litter size and the mean annual temperature, and a positive correlation between the mean litter size and latitude. Such a relationship with latitude has been found in several mammals (Sadleir 1969). The general explanation for latitudinal differences in litter size is that, because of shorter breeding season in the north, fewer litters are born, and this might be compensated for by larger litters (Sadleir 1969). In accordance with this hypothesis, the average number of litters per productive female per year in Spain might be higher than in other countries located at higher latitudes. However, our results suggest that this hypothesis might be only correct in the countries located at higher latitude.

Production and survival rate of young hares

The seasonal variation observed in the production of young is the result of changes in the percentage of pregnant females and the litter size, and the maximum productivity was obtained in the middle of the period of higher reproduction activity. This result is similar to those found by Alves *et al.* (2002) for

L. granatensis, and Raczyński (1964), Flux (1967), Hewson and Taylor (1975), Amaya *et al.* (1979), Broekhuizen and Maaskamp (1981), and Pépin (1989) working with *L. europaeus*. The total annual production of young per female of this study is large compared to that obtained by López *et al.* (1996) for the same species. Nevertheless, the sample analysed by López *et al.* (1996) was very small and they used a different method for determining this parameter. However, the annual production of young is low in relation to the values found by Alves *et al.* (2002) for *L. granatensis* and other studies realised with *L. europaeus* (see the review in Pépin 1989, Alves *et al.* 2002). The low annual production of young hares (4.6) found in Argentina by Amaya *et al.* (1979) could be a consequence of a short reproductive period, imposed by the arid conditions in their study area. The high value for annual production found by Broekhuizen and Maaskamp (1981) probably was partly due to their data only referring to adult and healthy females. When considering only adult females with normal reproductive tracts, Pépin (1989) obtained an annual production of young hares lower than that found by Broekhuizen and Maaskamp (1981).

The mortality rate of young found in this study (72.1%) is similar to that obtained by López *et al.* (1996) for the same species in an area of extensive dry farming. However, it is higher than that found by López *et al.* (1996) in an area of intensive dry farming. When the results obtained in the present study are compared with other studies carried out with *L. europaeus*, the mortality rate found for *L. granatensis* is similar or lower (Pielowski and Raczyński 1976, Frylestam 1979, Pielowski 1981, Wasilewski 1991, Hansen 1992). Pépin (1989) found that the mortality rate for *L. europaeus* in different farmland areas in the Paris basin ranged between 52 and 75%. However, some variation in mortality rate may be due to differences in the quality of habitats. Möller (1971, 1977), for example, found that in Germany the postnatal mortality of *L. europaeus* was 85–95% in an unfavourable habitat, compared with 63–88% in a more favourable one, whereas the postnatal losses found by Frylestam (1980b) for this species in southern Sweden were on average 30–35% higher in a mainland population than in an island population.

References

Abildgård F., Andersen J. and Barndorff-Nielsen O. 1972. The hare population (*Lepus europaeus* Pallas) of Illumø Island, Denmark. A report on analysis of data from 1957–1970. Danish Review of Game Biology 6(5): 1–32.

Angerbjörn A. and Flux J. 1995. *Lepus timidus*. Mammalian species 495: 1–11.

Alves P. C., Gonçalves H., Santos M. and Rocha A. 2002. Reproductive biology of the Iberian hare, *Lepus granatensis*, in Portugal. Mammalian Biology 67: 258–371.

Amaya J. N., Alsina M. G. and Brandani A. A. 1979. Ecología de la liebre europea *Lepus europaeus* P. Parte 2. Reproducción y peso corporal de una población del área de San Carlos de Bariloche. Ecología y Control de la Fauna Silvestre. Technical Report no. 9.

Batista T. and Carvalho de Cruz E. 1996. [Dynamics of a hare population]. Revista Florestal 9: 175–188. [In Portuguese]

Batista T. and Meixa de Almeida L. 1996. [Results of measurements and other observations in hares taken from contests and hunting from 1992 to 1995]. Revista Florestal 9: 123–135. [In Portuguese]
Blottner S., Faber D. and Roelants H. 2000. Seasonal variation of testicular activity in European brown hare *Lepus europaeus*. Acta Theriologica 45: 385–394.
Bonhomme F., Fernández J., Palacios F., Catalan L. and Machordon A. 1986. Caractérisation biochimique du comples d'espéces du genre *Lepus* en Espagne. Mammalia 50: 495–506.
Bonino N. and Montenegro A. 1997. Reproduction of the European hare in Patagonia, Argentina. Acta Theriologica 42: 47–54.
Broekhuizen S. and Maaskamp F. 1981. Annual production of young in European hare (*Lepus europaeus*) in the Netherlands. Journal of Zoology, London 193: 499–516.
Broekhuizen S. and de Wit J. 1972. [A case of extrauterine pregnancy in European hare (*Lepus europaeus*)]. Nederland Jager 77: 619. [In Dutch]
Bronson F. H. 1958. Notes on body size of black-tailed jack rabbits. Transactions of the Kansas of the Academic of Science 61: 109.
Calzada E. and de la Martínez F. J. 1994. Requerimientos y selección de hábitat de la liebre mediterránea (*Lepus granatensis*) en un paisaje agrícola mesetario. Ecología 8: 381–394.
Carro F., Beltrán J. F., Pérez J. M., Márquez F. J., Iborra O. and Soriguer R. C. 1999. Dinámica poblacional de la liebre ibérica (*Lepus granatensis*) en el Parque Nacional de Doñana. Resúmenes IV Jornadas SECEM, Segovia: 1–20.
Duarte J. and Vargas J. M. 1998. La perdrix rouge et le lièvre ibérique dans les oliveraies du sud de l'Espagne. Perspectives de gestion de ce type d'habitat. Bulletin Mensuel de l'Office National de la Chasse 236: 14–23.
Duarte J., Vargas J. M. and Farfán M. A. 2002. Biología de la liebre ibérica (*Lepus granatensis*). Bases técnicas para la gestión cinegética. [In: Aportaciones a la gestión sostenible de la caza. A. Lucio and M. Sáenz de Buruaga, eds]. FEDENCA – Federación Española de Caza: 29–59.
Flux J. E. C. 1962. The ecology of the Scottish mountain hare *Lepus timidus scoticus* Hilzheimer. PhD thesis, University of Aberdeen, Aberdeen: 1–209.
Flux J. E. C. 1965. Timing of the breeding season in the hare, *Lepus europaeus* Pallas, and rabbit, *Oryctolagus cuniculus* L. Mammalia 29: 557–562.
Flux J. E. C. 1967. Reproduction and body weights of the hare *Lepus europaeus* Pallas, in New Zealand. New Zealand Journal of Science 10: 357–401.
Flux J. E. C. 1970. Life history of the mountain hare (*Lepus timidus*) in north-east Scotland. Journal of Zoology, London 161: 75–123.
Flux J. E. C. 1971. Validity of the kidney fat index for estimating the condition of hares: a discussion. New Zealand Journal of Science 14: 238–244.
Frylestam B. 1979. Structure, size and dynamics of three European hare populations in Southern Sweden. Acta Theriologica 24: 449–464.
Frylestam B. 1980a. Growth and body weight of European hares in southern Sweden. Holarctic Ecology 3: 81–86.
Frylestam B. 1980b. Reproduction in the European hare in southern Sweden. Holarctic Ecology 3: 74–80.
Gosalbez J., López-Fuster M. J. and Durfort M. 1979. Ein neues Färbungs-verfahren für Hodenzellen von Kleinsäugetieren. Säugetierkunde Mitteilungen 27: 303–305.
Hansen K. 1992. Reproduction in European hare in a Danish farmland. Acta Theriologica 37: 27–40.
Hediger H. 1948. Die Zucht des Feldhasen (*Lepus europaeus* Pallas) in Gefangenschaft. Physiology Compared 1: 46–62.
Hewson R. and Taylor M. 1975. Embryo counts and length of the breeding season in European hares in Scotland from 1960–1972. Acta Theriologica 20: 247–254.
Iason G. 1990. The effects of size, age and cost of early breeding on reproduction in females mountain hares. Holartic Ecology 13: 81–89.
Jacob A. 1956. Häsin mit 9 Junghasen. Deutsche Jäger 73: 458.

Jacobs W. 1966. Nachgewiesene Superfotation beim Feldhasen (*Lepus europaeus*). Zeitschrift für Jagdwissenschaft 12: 138.

Keith L. B. 1981. Population dynamics of hares. [In: Proceedings of the World Lagomorph Conference, Guelph, Ontario, August 1979. K. Myers and C. D. MacInnes, eds]. University of Guelph, Guelph, Ontario: 395–440.

Lazo A., de le Court C. and Soriguer R. C. 1992. Evaluation of hare abundance allowed by their use of attraction point. Zeitshrift für Säugetierkunde 7: 373–379.

Lechleitner R. R. 1959. Sex-ratio, age classes and reproduction of the black-tailed jack rabbit. Journal of Mammalogy 40: 63–81.

Lincoln G. 1974. Reproduction and "March madness" in the brown hare, *Lepus europaeus*. Journal of Zoology, London 174: 1–14.

López J. M., Hernández A., Purroy F. and Robles J. L. 1996. Datos sobre la biología de la reproducción de la liebre ibérica (*Lepus granatensis* Rosenhauer, 1856) en agrosistemas cerealistas de la provincia de León (NW de España). Revista Florestal 9: 49–60.

Martinet L. 1977. Reproduction et fertilité du lièvre en captivité. Ecologie du petit gibier et amenagement des chasses. Gauthier-Villars, París: 265–272.

Martinet L. and Demarne Y. 1984. Nursing behaviour in the brown hare (*Lepus europaeus*) raised in captivity. Acta Zoologica Fennica 171: 187–190.

Möller D. 1971. Beitrag zur Reproduktion des Feldhasen (*Lepus europaeus* Pall.) in der Deutschen Demokratischen Republik. Beitrage zur Jagd- und Wildforschung VII, Tag.-Ver, der Deutschen Akademie der Landwirschaftswissenschaften zu Berlin 113: 191–202.

Möller D. 1976. Die Fertilität der Feldhasenpopulationen. [In: Ecology and management of European hare populations. Z. Pielowski and Z. Pucek, eds]. Polish Hunting Association, Warszawa: 69–74.

Möller D. 1977. Zur postnatalen Mortaliät des Feldhasen in der Deutschen Demokratischen Republik. Beitrage zur Jagd- und Wildforschung 10: 247–254.

Newson R. and de Vos A. 1964. Population structure and body weights of snowshoe hares on Manitoulin Island, Ontario. Canadian Journal of Zoology 42: 975–986.

Palacios F. 1976. Descripción de una nueva especie de liebre (*Lepus castroviejoi*), endémica de la Cordillera Cantábrica. Doñana, Acta Vertebrata 3: 205–223.

Palacios F. 1980. Notas sobre la reproducción en libertad de las especies del género *Lepus* Linne, 1758, en España. Actas II Reunión Iberoamericana de Conservación y Zoología de Vertebrados: 350–358.

Palacios F. and Meijide M. 1979. Distribución geográfica y hábitat de las liebres en la Península Ibérica. Naturalia Hispánica 19: 1–40.

Palacios F. and Ramos B. 1979. Situación actual de las liebres en España y medidas para su conservación. Boletín de la Estación Central de Ecología 8: 69–75.

Pegel M. 1986. Der Feldhase (*Lepus europaeus* Pallas) im Beziehungsgefüge seiner Um- und Mitweltfaktoren. Arbeitskreis Wildbiologie und Jagdwissenschaft, an der Justus-Liebig-Universität Giessen 16: 1–124.

Pépin D. 1977. Phase finale du cycle de reproduction du lièvre, *Lepus europaeus*. Mammalia 41: 221–230.

Pépin D. 1978. Structures de populations de lièvres en automne dans différents agrosystèmes. Annales de Zoologie et d'Ecologie Animale 10: 97–112.

Pépin D. 1987. Dynamics of a heavily exploited population of brown hare in a large-scale farming area. Journal of Applied Ecology 24: 725–734.

Pépin D. 1989. Variation in survival of brown hare (*Lepus europaeus*) leverets from different farmland areas in the Paris basin. Journal of Applied Ecology 26: 13–23.

Peroux R. 1995. Le lièvre d'Europe. Le Bulletin Mensuel de L'Office National de la Chasse, Spécial 204: 1–96.

Pielowski Z. 1969. Sex ratio and weights of hares in Poland. Acta Theriologica 14: 119–131.

Pielowski Z. 1981. Yearly balance of European hare population. [In: Proceedings of the World Lagomorph Conference, Canada, 1981. K. Myers and C. D. MacInnes, eds]. University of Guelph, Guelph, Ontario: 536–540.

Pielowski Z. and Raczyński J. 1976. Ecological conditions and rational management of hare populations. [In: Ecology and management of European hare populations. Z. Pielowski and Z. Pucek, eds]. Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa: 269–286.

Raczyński J. 1964. Studies on the European hare. V. Reproduction. Acta Theriologica 9: 305–352.

Reynolds J. K. and Stinson R. H. 1959. Reproduction of the European hare in southern Ontario. Canadian Journal of Zoology 37: 627–632.

Rodríguez M. and Palacios J. 1997a. Biología de la liebre. [In: La liebre. M. Rodríguez, I. Palacios, T. Yanes and P. Martin, eds]. Mundiprensa, Madrid: 33–55.

Rodríguez M. and Palacios J. 1997b. La liebre en España. [In: La liebre. M. Rodríguez, I. Palacios, T. Yanes and P. Martin, eds]. Mundiprensa, Madrid: 23–31.

Sadleir R. M. F. S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen, London: 1–231.

Schneider E. 1997. Brown hare (*Lepus europaeus*) towards the 21st century. Gibier Faune Sauvage 14: 533–534.

Sokal R. R. and Rohlf F. J. 1981. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Company, New York: 1–859.

Tapper S. 1992. Game heritage: an ecological review from shooting and gamekeeping records. Game Conservancy, Fordingbridge, Hampshire: 1–140.

Tuomi J. 1980. Mammalian reproductive strategies: a generalized relation of litter size to body size. Oecologia 45: 39–44.

Vargas J. M. 2002. Alerta cinegética. Reflexiones sobre el futuro de la caza en España. Tero, Madrid: 1–399.

Vargas J. M. and Muñoz A. R. 1996. Panorámica de la caza menor en Andalucía. [In: La caza en Andalucía y su problemática]. Federación Andaluza de Caza, Archidona, Málaga: 1–19.

Wasilewski M. 1991. Population dynamics of the European hare *Lepus europaeus* Pallas, 1778 in central Poland. Acta Theriologica 36: 267–274.

Williams R. M., Darwin J. H. and Wodzicki K. 1964. Effectiveness of rabbit and hare control by night-shooting. New Zealand Journal of Science 7: 367–86.

Received 12 June 2003, accepted 11 June 2004.

Editors were Zdzisław Pucek and Andrzej Zalewski.