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Authors: Fernandez, Alfonso, Soriguer, Ramón, Castien, Enrique, and Carro, Francisco

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Reproduction parameters of the Iberian hare *Lepus granatensis* at the edge of its range

Alfonso Fernandez, Ramón Soriguer, Enrique Castien & Francisco Carro

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In order to provide a basis for the sustainable exploitation of the heavily hunted Iberian hare *Lepus granatensis*, we compared its reproductive parameters at the northern edge of its range, where it occurs at low densities, with those reported in other studies elsewhere within the species' range. Monthly samples totalling 212 Iberian hares (104 males and 108 females) were collected in the province of Navarra during November 2001 - December 2002. Reproductive parameters varied only slightly from season to season. Sexually competent males, defined by the presence of epididymal spermatozoa, were present in all bimonthly periods. Reproductively active adult females were also present in all the bimonthly periods, although a slight seasonality was detected: the highest incidence of pregnancy and lactation (100%) occurred in March-April, while the lowest incidence of adult females that were neither pregnant nor lactating (15%) occurred in September-December. Mean annual litter size was 2.09 and the theoretical value of annual young production per female was estimated to be 16.1, which is much higher than estimates reported in studies of *L. granatensis* in Portugal and southern Spain. In Navarra, which is at the northern limit of the species' range, densities are low due to intense hunting. However, the observed reproductive potential was surprisingly high and facilitates recruitment to the population which could, to a certain extent, make up for the high hunting pressure in the area.

Key words: Lepus granatensis, litter size, Navarra, productivity, reproduction

Alfonso Fernandez & Francisco Carro, Universidad Pública de Navarra, IARN, Campus Arrosadía s/n. E-31006 Pamplona, Spain - e-mail addresses: edualf@telefonica.net (Alfonso Fernandez); pcarro@ebd.csic.es (Francisco Carro)
Ramón Soriguer, Estación Biológica de Doñana (CSIC). Av. María Luisa s/n., Sevilla, Spain - e-mail: soriguer@ebd.csic.es
Enrique Castien, Departamento de Medio Ambiente, Gobierno de Navarra. C/ Yanguas y Miranda. E-31002 Pamplona, Spain - e-mail: ecastiea@cfnavarra.es

Corresponding author: Alfonso Fernandez

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The Iberian hare *Lepus granatensis* is endemic to the Iberian Peninsula, where it mainly occupies agricultural areas and open fields (Duarte 2000). The species is widely distributed and intensively hunted throughout its range. More than one million individuals are taken annually and hunting pressure is increasing every year (Vargas 2002). Hunting thus needs to be sustainable and any application of the concepts of sustainable harvesting must take into account the demographic characteristics of the species' populations. This would be possible if local data on demography (e.g. age structure and reproductive parameters) were available, and would allow implementation of strategies for managing populations based on knowledge of the species' reproductive characteristics (Marboutin et al. 2003). Yet, through most of the Iberian hare's distribution area (including our study area), population management is often based exclusively on abundance data (Lucio 1996) and, although abundance is directly related to reproduction, it is above all related to the breeding success of females and juvenile survival rates (Marboutin et al. 2003). In contrast to the situation regarding other *Lepus* species (e.g. brown hare *L. europaeus* and mountain hare *L. timidus*), information about the reproductive biology of the Iberian hare is still scarce.

Recent studies have investigated the reproductive parameters and cycles of the Iberian hare on the Iberian Peninsula (Alves et al. 2002, Duarte et al. 2002, Alves & Rocha 2003, Farfán et al. 2004), but all these studies have been carried out in the south of the species' distribution range, where environmental conditions are optimal for the species and populations are higher than in the north (Duarte et al. 2002). Studies of other *Lepus* species have shown that the proportion of breeding females and their fecundity varies over the species' geographical range in relation to differences in environmental characteristics and densities (Hansen 1992, Hackländer et al. 2001, Kauhala et al. 2005). If reproduction in the Iberian hare were density dependent, we would expect high reproductive rates to occur in the low-density study population at the edge of the species' range. A possible hypothesis is that this low density occurs because conditions are not suitable for either a high reproductive output or juvenile survival. We therefore investigated the basic reproductive parameters of Iberian hares in Navarra by a) analysing their intra-annual variation, b) estimating the annual potential production of young and c) comparing our results with those already published for the species.

Material and methods

Study area

Our study was carried out in southern Navarra (northern Iberian Peninsula), between 42°10', 42° 40'N and 1°10', 2°20'W. In this region, the distribution of the Iberian hare covers a total area of ca 4,000 km^2. Samples for our study were collected in 15 hunting areas along the Ebro river, which forms a wide alluvial plain characterised by smooth relief and mean altitudes of 400-500 m a.s.l. The landscape in the sampling areas consisted mainly of wheat and barley crops, mixed with vineyards, olive groves and fruit trees. The climate of the area can be considered to be Mediterranean, with warm, dry summers and cold to mild rainy winters, and a total annual rainfall of ca 600 mm (Pejenaute 1992).

Samples and data collection

We collected samples monthly during November 2001 - December 2002 as part of a monitoring programme carried out by the regional Government. Extra samples were collected during the hunting season (November-December) and some road-killed hares were also examined. We analysed a total of 212 reproductive tracts (N = 104 males and N = 108 females; Table 1) by examining the gonads (male testes and female uterus and ovaries) and reproductive status of individuals. As a result of this

Table 1. Bimonthly distribution of the number of male and female reproductive tracts examined in the study.

	Males		Females			Total		
	Young	Adult	Young	Adult	Indeterminate	Males	Females	Total
January-February	2	10	2	10	-	12	12	24
March-April	5	10	3	4	-	15	7	22
May-June	6	2	3	8	-	8	11	19
July-August	3	6	5	5	-	9	10	19
September-October	3	5	5	4	1	8	10	18
November-December	21	31	13	38	7	52	58	110
	40	64	31	69	8	104	108	212

heterogeneous sampling, variable sample sizes for each parameter were obtained. Hares were weighed to the nearest 25 g using a dynamometer and analysed, if possible, when fresh. Otherwise, reproductive organs were frozen (-20°C) and analysed in the laboratory within 48 hours of removal from the dead animals. Individuals were classified as adult or young on the basis of the presence or absence of epiphyseal distal cartilage in the radius and ulna ('Stroh's sing'; Stroh 1931): forelegs were first palpated and then cleaned and examined with the naked eye. This has been shown to be a reliable and practical method for age classification in *Lepus* species (e.g. mountain hare), in particular when combined with eye-lens weight (Kauhala & Soveri 2001). A growth curve for the Iberian hare which determines exactly the discriminating adult-young eye-lens weight value is still lacking, although we have defined approximate values in previous studies (A. Fernandez & R. Soriguer, pers. obs.). Additional biometric parameters were measured and eye lenses were removed and handled as described in the literature for *Lepus* species (Suchentrunk et al. 1991). In the very few cases where age could not be determined from the ossification stage of the radius and ulna, the dry weight of the eye lenses was used as described previously (A. Fernandez & R. Soriguer, pers. obs.).

Reproductive activity

Males

After noting their position (intra or extra-abdominal), testes were excised, measured lengthways and weighed to the nearest 1 mg (including epididymides). To verify the presence of spermatozoa, a sample from the tail of the epididymis was taken and analysed microscopically. The presence of sperm in the testes was taken to indicate reproductive maturity. Several studies of the brown hare have already demonstrated that the presence of spermatozoids in the epididymides is a reliable indicator of reproductive activity (Blottner et al. 2000, Brodowski et al. 2001), and this criterion has also been applied to the Iberian hare (Alves et al. 2002). On the basis of this criterion, two categories of males were considered: 'active' with spermatozoa and 'inactive' without spermatozoa.

Females

The reproductive activity of females was estimated on the basis of mammary gland activity and the presence/absence of embryos in the uterus. Thus, five reproductive statuses were distinguished: 1) pregnant with embryos implanted, 2) lactating with developed mammary glands present and giving milk if squeezed, 3) pregnant and lactating, 4) inactive adult females with no sign of reproductive activity, i.e. neither pregnant nor lactating, and 5) immature young females with no development of their reproductive tracts. First, an external examination of the activity of the mammary glands was performed. Then, reproductive tracts (ovaries and uterus) were excised and analysed. If pregnant, the uterus was opened and the number of embryos and their implantation sites were noted. The length and weight of embryos were also measured. Ovaries were weighed to the nearest mg and preserved in 10% formalin for at least 30 days (Flux 1967). This parameter varies during the yearly cycle when *corpora lutea* develop as a consequence of embryo implantation in the corresponding uterus horn. In this case, the ovaries were cut by hand with a scalpel into longitudinal sections approximately 2 mm thick and the *corpora lutea*, if present, were counted using a binocular microscope.

Prenatal mortality in lagomorphs can be caused by both preimplantation mortality of ova and embryo resorption (Allen et al. 1947). Thus, the number of *corpora lutea* is used as an indicator of the number of ova which ovulated and preimplantation mortality was estimated as the difference between this number and the number of implanted embryos in the uterus (Broekhuizen & Maaskamp 1981, Hansen 1992, Bonino & Montenegro 1997, Alves et al. 2002). However, due to the difficulty in detecting recent implantations and fertilised zygotes, prenatal mortality analysis was restricted to females with implanted embryos (Alves et al. 2002). Finally, some females were considered to have just given birth, evidenced by the presence of signs of pregnancy, i.e. *corpora lutea* were still present in the ovaries, the uterus was very irrigated and enlarged, and there were recent placental scars in the uterus horns. In these few cases, placental scars were counted and taken to be implanted embryos. In order to compare our results with those published by other authors (Alves et al. 2002, Farfán et al. 2004), the annual productivity of females (number of young produced) was estimated using the following formula (Pepin 1989):

$$\Sigma(\text{bimonthly \% pregnant females} \times \text{bimonthly mean litter size}) \times 1.46.$$

Over a period of two months, a healthy adult female may have 1.46 litters (Pepin 1989), assuming that the average birth interval of the Iberian hare is similar to the length of the gestation period (41-42 days; Alves et al. 2002). We calculated bimonthly mean litter size by dividing the number of embryos by the number of pregnant females in the relevant period.

Data analysis

Values for reproductive parameters were pooled bimonthly in order to increase the sample size and to be able to compare the reproductive activity of the Iberian hare in Navarra with that of other hare species and with Iberian hares from other parts of its range (i.e. Alves et al. 2002). The normality of the data was tested using Shapiro-Wilk's tests; log x transformations were employed when data did not fit normality. Paired Z or Student t-tests were used to compare the mean values of reproductive and biometric parameters i.e. weight of right and left testes and ovaries, size and weight of testes in males with and without sperm, intra and extra-abdominal weight of testes, weight of young and adult testes, body weight of active and inactive young females, and the number of *corpora lutea* (mean litter size of pregnant females). Pearson correlation coefficients were calculated in an attempt to relate weight and testes size, and to analyse the relationship between the number of ova ovulated and prenatal mortality. A one-way analysis of variance (ANOVA) was employed to test for differences between bimonthly periods in testis and ovary weights and in mean litter size. When F was significant, Newman-Keuls tests were performed to show which groups differed most from each other. We used STATISTICA version 6 to perform all the statistical analysis.

Results

Males

Testis weight

No differences were detected between right and left testes for the parameters described; size (t=1.12, df=196, ns) and weight (t=0.34, df=196, ns). Thus, mean values were always used in the analyses. Mean testis size and weight in individuals without spermatozoids were 25.2 mm ± 8.1 and 1.97 g ± 1.79, respectively, and for active individuals the values were 42.9 mm ± 4.5 and 8.63 g ± 2.1, respectively; the differences were statistically significant for both parameters (t=17.5, df=94, P<0.01 and t=20.66, df=94, P<0.01). Furthermore, we observed a significant correlation between both parameters (r=0.89, N=101, P<0.01), which allowed us to use the weight of just one of them (testis weight) during the analyses.

Reproductive activity

A high percentage of males with spermatozoids in their epididymides were found throughout the year. Likewise, a high mean testis weight in adult males was also observed throughout the year (Fig. 1). Nevertheless, a significant variation in testis weight during the bimonthly periods was also observed (ANOVA $F_{5df}=3.59$, P<0.05), with a period of maximum values occurring in winter and spring (January-April; see Fig. 1). Males with extra-abdominal testes were present in all bimonthly periods, with percentages ranging from 58% in November-December to 100% in January-February and May-June. Of the adult males, 100% had spermatozoids in their epididymides in all periods except November-December (90%; see Fig. 1).

Males with extra-abdominal testes weighed on average 2,006 g ± 260 and all except one (which had a body weight of 1,615 g) had sperm in their

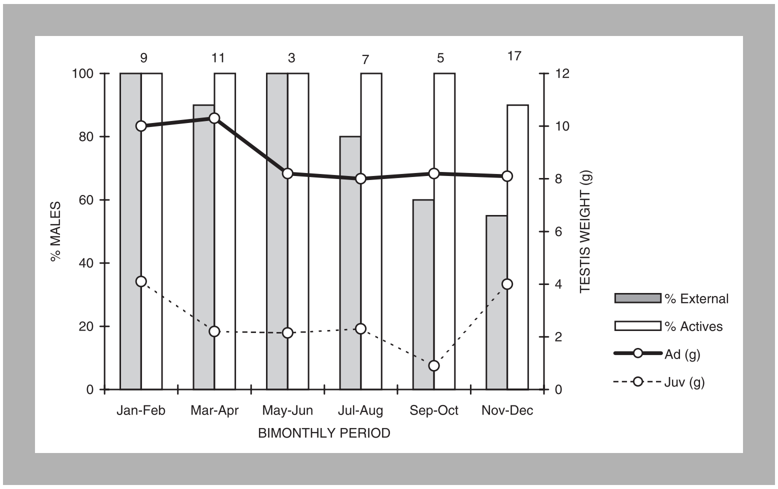

Figure 1. Bimonthly variation in mean testis weight of adult and juvenile male Iberian hares, and proportion of males with external testes and adult males with sperm in epididymidis. Figures above the bars give sample size for each period.

Table 2. Sperm presence in epididymides in relation to testicular position in adult Iberian hare males (N = 77). ** indicates P < 0.01.

Testicular position	N	With sperm (%)	Without sperm (%)
Intra-abdominal	36	14 (39%)	22 (61%)
Testis weight (g)		7.70 ± 2.43	1.42 ± 1.13
Extra-abdominal	41	40 (98%)	1 (2%)
Testis weight (g)		9.38 ± 1.84 **	3.89

epididymides. However, of the males with intra-abdominal testes, 39% were also active (Table 2). The differences in mean weight between intra (N = 14) and extra-abdominal (N = 39) active testes was significant (t-test = 3.41, P = 0.001; see Table 2).

The presence of spermatozoids was confirmed in 70 pairs of testes, all weighing >4 g and 86% of which were from individuals classified as adults (mean body weight = 1,977 g ± 232) and 14% from young hares (1,680 g ± 170). The testes of young males were significantly lighter (6.53 g ± 1.33, N = 11) than those of adults (9.14 g ± 1.80, N = 59; t = 4.56, P < 0.001). The heaviest pair of testes recorded (13.6 g) was that of an adult male with a body weight of 2,450 g; the lightest testes (2.11 g) were found in an adult male with a body weight of 1,950 g.

Females

Ovary weight

We observed no differences in the weight of right and left ovaries, neither when no *corpora lutea* were present (N = 37, Z = 0.14, ns) nor when they were present in both ovaries (N = 27, t = 0.26, ns). However, significant differences were observed when *corpora lutea* were present in only one ovary (N = 21, t = 3.59, P < 0.01). Thus, in the first two cases, the mean value of both ovaries was taken and used in the analyses, whereas in the third case, only the weight of the ovary with *corpora lutea* was used.

The mean weight of ovaries in adult and young females (N = 50) was 1.32 g ± 0.7 and 0.30 g ± 0.33 (N = 28), respectively. These results are similar to those obtained by comparing the mean weights of ovaries with (N = 38) and without (N = 48) *corpora lutea* (1.27 g ± 0.54 and 0.30 g ± 0.27, respectively). The mean ovary weight of adult females varied significantly between bimonthly periods (F_{5df} = 4.92, P = 0.001), with the highest values observed in May-June and the lowest in November-December (Fig. 2). Nevertheless, no statistically significant differences were detected between any of the bimonthly periods (Newman-Keuls test: P > 0.05). For young females, the variation in mean ovary weight was not significant (F_{5df} = 2.12, P = 0.10; see Fig. 2).

Reproductive activity

As expected, reproductive activity was significantly higher in adult than in young females (85 and 16%, respectively; P < 0.001). Adult females with signs of reproductive activity were found in different proportions in all the bimonthly samples (Fig. 3). Of the total active females, 69% were pregnant (29% were also lactating at the same time) and 16% were

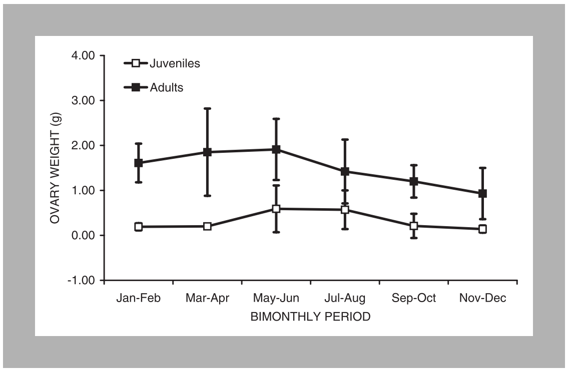

Figure 2. Bimonthly variation in mean ovary weight (±SD) of adult and juvenile female Iberian hares.

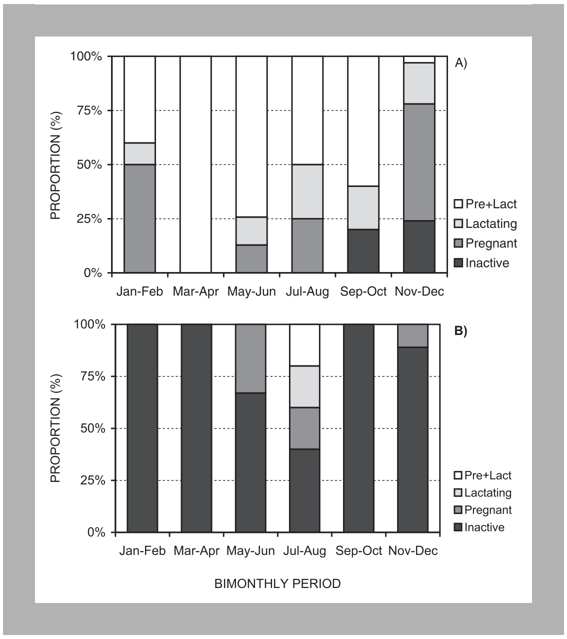

Figure 3. Annual variation in proportions of considered reproductive status of adult and young female Iberian hares.

lactating. The lowest percentage corresponded to inactive adult females (15%), which were detected only in the last two bimonthly periods of the year, i.e. September-October and November-December (20 and 24%, respectively; see Fig. 3). We also found some young females showing signs of reproductive activity. In the period July-August, three females classified as young, due to the presence of unossified distal epiphysis in the radius-ulna, were active (two were pregnant and one lactating). In May-June, one young female was found to be pregnant and another was found in November-December (see Fig. 3). The mean body weight of these young active females was 1,910 g ± 285 (N = 5), which was significantly higher ($t = 2.20$, $P = 0.03$) than the mean body weight of inactive young females (1,535 g ± 305, N = 23).

Reproductive efficiency

Litter size

Litter size ranged between one and a maximum of four embryos. A total of 107 embryos were counted and the estimated overall mean litter size was 2.09 (N = 51 pregnant females). The most frequent litter sizes were two (51%) or one (24%) embryo (Fig. 4). Mean bimonthly litter sizes varied significantly throughout the year ($F_{5df} = 2.95$, $P < 0.05$; Fig. 5). The highest litter-size value, observed in March-April (3.00 ± 0.82), was significantly higher than those observed in November-December (1.83 ± 0.79) and January-February (1.89 ± 0.78; Newman Keuls test: $P < 0.05$).

Prenatal mortality

Almost 33% of females with *corpora lutea* (N = 49) had suffered reproductive losses, and overall prenatal mortality was 18% (N = 124 *corpora lutea* observed as compared to N = 102 embryos implanted). The majority of this mortality was due to non-implantation (86%), and resorption (partially resorbed embryo) accounted for 14% (N = 3 cases). Preimplantation mortality was evenly distributed throughout the bimonthly periods ($\chi^2_{5df} = 3.42$, $P = 0.6$; ns) and resorption was observed only in January-February and March-April (see Fig. 5). The maximum difference between ovulation and implantation levels was observed in May-June and July-August (23.8 and 18.3%, respectively) and the maximum percentages of mortality (preimplantation plus resorption) were observed in January-February and September-October (see Fig. 5). Thus, the mean number of *corpora lutea* per female (2.52 ± 1.13) differed significantly ($Z = 2.59$, $N = 51$, $P < 0.01$) from the mean litter size (2.19 ± 0.85). In addition, a significant tendency towards a loss in reproductive efficiency as the ovulation level rose was observed in monthly samples ($r_{10df} = 0.71$, $P < 0.05$). Super-foetation (embryos in different developmental stages) was not observed and seems to be very infrequent in this species (Vargas et al. 1999, Alves et al. 2002). One case of possible blastocystis migration was detected (Broekhuizen & Maaskamp 1981).

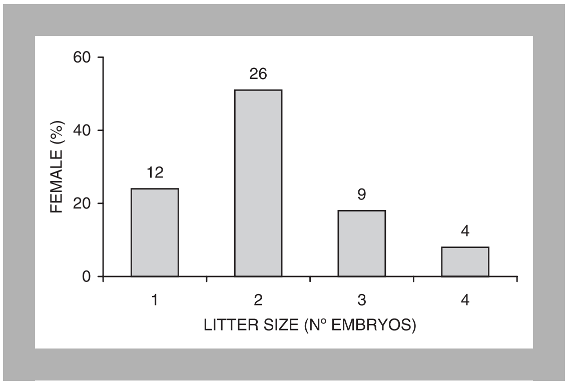

Figure 4. Distribution of litter size among pregnant adult female Iberian hares. Figures above the bars give the sample size for each litter size.

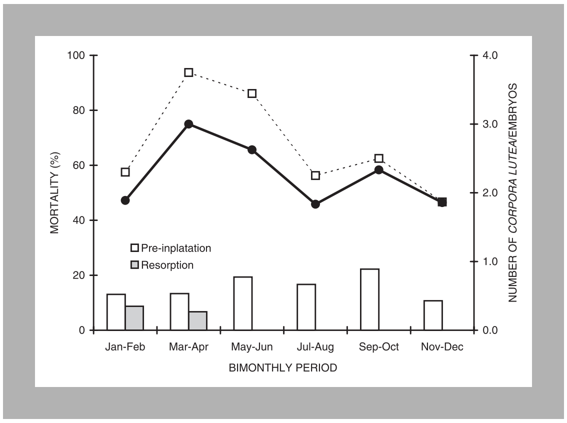

Figure 5. Bimonthly variation in ovulation (i.e. number of *corpora lutea*; ☐) and implantation (i.e. litter size; ●), and proportions of prenatal mortality in female adult Iberian hares.

Production of young

The theoretical value of the total annual production of young per female was estimated at 16.1 (Table 3). The maximum productivity of leverets per female was observed in March-April, while minimum values were observed in November-December (see Table 3).

Table 3. Bimonthly contribution and overall production of young in adult Iberian hares in Navarra.

	N	Number of embryos	Mean litter size	Pregnancy (%)	Mean production of young
January-February	9	17	1.89	0.88	2.42
March-April	4	12	3.00	1.00	4.38
May-June	8	21	2.63	0.88	3.37
July-August	6	11	1.83	0.71	1.89
September-October	3	7	2.33	0.75	2.55
November-December	21	39	1.86	0.58	1.57
Total	51	107			16.10

Discussion

Based on our data, we conclude that male and female Iberian hares in Navarra are reproductively active throughout the year. Nevertheless, the yearly breeding activity curve shows a decrease in late autumn and winter, which agrees well with the yearly cycle described for this species in the literature (Alves et al. 2002, Duarte et al. 2002, Farfán et al. 2004). Unlike other *Lepus* species (e.g. *L. europaeus* and *L. timidus*; Raczynski 1964, Flux 1970, Frylestam 1980, Broekhuizen & Maaskamp 1981, Hansen 1992, Bonino & Montenegro 1997), no period of testis involution was observed in males, and pregnant or lactating females were observed in all the bimonthly periods.

Males

Testicular weight and position are normally considered as valid criteria for sexual activity in lagomorphs. Testis weight has been demonstrated to be directly related to sperm production and extragonadal sperm reserves in lagomorphs such as rabbits *Oryctolagus cuniculus* (Gonçalves et al. 2002), brown hares (Blottner et al. 2000) and Iberian hares (Alves et al. 2002). The extra-abdominal position of testis has been taken as a sign of sperm maturity and sexual activity (Simeunovic et al. 2000, Alves et al. 2002). Nevertheless, males with intra-abdominal testes are sometimes spermatogenetically active (Simeunovic et al. 2000), and Alves et al. (2002) have demonstrated that there is no difference in testis and epididymidis weight or sperm and testosterone production between intra and extra-abdominal testes in Portuguese Iberian hares. Our results confirm the presence of spermatozoa in a large number of intra-abdominal testes, whose weight differs significantly from those of extra-abdominal active testes. Nevertheless, weights were in both cases >7 g which is well over the five g that has been given as a threshold for sexual activity for larger species of this genus (Hansen 1992). This leads us to believe that testis position is not a decisive criterion for sexual activity in the Iberian hare. Indeed, although the biological significance of this phenomenon has yet to be determined (Alves et al. 2002), a lower proportion of males with external testes was observed between September and December, as was also reported by Alves et al. (2002) and Farfán et al. (2004), suggesting that this is a period of lower sexual activity.

Maximum testis weight was observed in March-April, coinciding with the period of maximum sexual activity in females. Possibly, the bimonthly time scale used as a result of the small sample sizes is too coarse to reveal differences/coincidences in both sexes. Alves et al. (2002) used similar sample sizes and obtained similar results whereas Farfán et al. (2004), using larger sample sizes and a monthly time scale, observed that the pattern of reproductive activity (measured indirectly as testis and ovary weights) ran in parallel. These results allow us to conclude that male reproduction patterns are similar throughout the species' distribution area despite regional differences in climate, vegetation and habitat structure. Alves & Rocha (2003) reported that environmental factors have little influence on the reproductive activity of this species. They showed that, despite seasonal environmental variations in southern Portugal, the reproductive characteristics of Iberian hares did not vary significantly between seasons. Consequently, we should not expect to find significant differences in hare reproductive behaviour between regions with environmental differences.

High reproductive activity was observed in adult males throughout the yearly cycle, and in all bimonthly periods except November-December the percentage of adult males with sperm was 100%. Small sample sizes in some bimonthly periods may play a part in explaining this finding, although we can conclude that, as in most mammals, male Iberian hares are unlikely to be a limiting factor in population reproductive performance.

Females

The percentage of reproductively active (pregnant and/or lactating) adult females found shows that the breeding season extends throughout the year; only in the period September-December did we find some inactive adult females. However, significant differences in mean ovary weights were detected, a finding that confirms that a certain degree of seasonality in female activity exists, with maximum values occurring in spring when implantation levels also reached their highest values. This pattern was also observed by Alves et al. (2002) and Farfán et al. (2004). Overall, almost 30% of reproductively active females were both pregnant and lactating and, between March and June, >80% of the females were pregnant and lactating; an ability that enables them to reduce the period between litters and provides the species with great reproductive potential. Nevertheless, it is unlikely that a female could reproduce continuously throughout the year because many other factors such as size/age (Iason 1990), weather/food availability (Kauhala et al. 2005) and/or physical condition (Ims 1987) also affect reproduction. For example, in mountain hare (Hewson 1970) and brown hare (Frylestam 1980), only a very small proportion of females were able to realise their maximum potential number of litters. Some young females were also reproductively active; these females were heavier than young inactive females and had a mean body weight near to the 2,000 g that is considered to be the lowest possible weight of an adult (A. Fernandez & R. Soriguer, pers. obs.). This implies that, to some extent, reproductive activity may start before adult age is reached, although the lack of more reliable age data for the species prevents us from saying exactly when hares are able to start breeding. We must also be aware that although larger individuals are more likely to be reproductively active (Iason 1990), weight also increases with pregnancy, and for this reason we employed the ossification stage of the foreleg distal cartilage to determine ages. Kauhala & Soveri (2001) also employed this criterion for age classification and obtained a higher proportion of young hares when bones were examined using radiography rather than the naked eye. However, these authors consider this result to be an overestimation of the proportion of young individuals (in some adults ossification lines can still be seen) and believe that the examination of bones using the naked eye is the best method for age determination in mountain hare.

Litter size and productivity

Reported litter size in Navarra (2.09 leverets/pregnant female) is higher than that observed in the south of the Iberian Peninsula (Alves et al. 2002, Duarte et al. 2002, Farfán et al. 2004). Our results differ significantly from those reported in Portugal by Alves et al. (2002; 1.56), who analysed the same number of pregnant females. Farfán et al. (2004) used mean annual litter size, calculated as the mean of all sampled periods (2.08), instead of reported litter size. This value was also higher in our study (2.25) and lower in Alves et al. (2002; 1.67).

Both the percentages of pregnant females and mean litter sizes were higher in all the bimonthly periods in our study than in other studies. In all the bimonthly periods except November-December, >75% of the females were pregnant in Navarra. In Portugal (Alves et al. 2002), percentages >75% were only observed in two bimonthly periods and in southern Spain only in February (Farfán et al. 2004). In Navarra, mean litter sizes were >1.5 in all the periods. On the other hand, Alves et al. (2002) and Farfán et al. (2004) found that this value was only reached in six and five months of the year, respectively. Alves et al. (2002) did not find any differences in mean litter sizes between bimonthly periods. We, however, observed significantly higher litter sizes in March-April and May-June. These results ultimately determine important differences in the estimated productivity per female: 16.1 in our case vs 9.6 in Portugal and 7.21 in southern Spain. For a comparison with productivity values in other *Lepus* species, see the review in Alves et al. (2002). In Navarra, maximum productivity was obtained in March-April and May-June. Farfán et al. (2004) obtained similar results, whilst Alves et al. (2002) found that the highest productivity occurred in January-February and then again in July-August, the two periods in which the percentage of pregnant females was at its highest. It is possible that our sampling methodology contained a bias towards larger individuals. Many of the hares were captured in non-hunting reserves within hunting areas, where individuals live longer and the capture of young hares is avoided. Although some young hares were analysed, shot mainly during the hunting season, only adult individuals were included when we calculated productivity. This bias could be one of the explanations for the higher values in our study when compared to those in other studies. Nevertheless, reference weights and size values are lacking from these other studies and only the weights of the smallest reproductively active individuals (supposedly the youngest) are given: 2,000 g for females and 1,600 g for males in Farfán et al. (2004), and 2,150 g for females and 1,811 g for males in Alves et al. (2002). We obtained minimum weights of 2,005 g for females and 1,765 for males.

The largest litter we found had four embryos, the same as was found by Alves et al. (2002) in Portugal. Farfán et al. (2004) found a pregnant female with seven embryos, although this was taken to be exceptional; they also found two females with five embryos. Nevertheless, >50% of litters had only one embryo. Both these studies reported that the most frequently observed gestations included one and then two leverets. Contrasting this, we observed two as the most frequent value (51%), followed by one (23.5%). The reproductive strategy of the Iberian hare and the brown hare, which also reproduces continuously (Alves & Rocha 2003), is concordant with the hypothesis that lagomorph litters are smaller where breeding seasons are longer, and that larger litters occur when breeding seasons are shorter (Swihart 1984). Whether a mammal reproduces seasonally or continuously depends mostly on its environment (Bronson 1989). It has also been shown that in several mammals there is a relationship between productivity and latitude that implies that latitudinal differences in litter sizes are caused by differences in the length of the breeding season, with bigger litters compensating for shorter breeding seasons (Sadleir 1969). Along these lines, survival rates and productivity in the mountain hare have been demonstrated to differ between areas in Finland (Kauhala et al. 2005), and unfavourable climatic conditions associated with certain habitats have been related to differences in demography and body condition in the brown hare (Jennings et al. 2006).

In terms of prenatal mortality, our 18% is very similar to the 21% obtained by Alves et al. (2002). Nevertheless, these authors suggest that calculating prenatal mortality as the difference between the number of *corpora lutea* and the number of embryos may lead to errors. In both cases the number of *corpora lutea* and embryos differed statistically.

In conclusion, the reproductive output of Iberian hares is very high in Navarra, a fact that is somewhat surprising for a species at the edge of its range, where densities are low. We obtained density values of 5.8 hares/km^2 (A. Fernandez, R. Soriguer, F. Carro & E. Castien, pers. obs.) in contrast to densities of >10 hares/km^2 reported from more suitable areas in southern Spain (Calzada & Martinez 1994, Rodriguez et al. 1997). This contradiction may be due to factors such as hunting (practised intensively throughout the study area as an analysis of hares shot in the hunting season has demonstrated; A. Fernandez, F. Carro & R. Soriguer, pers. obs.) which cause great postnatal mortality. Other aspects of reproduction in Iberian hares, such as the relationship between age and reproduction, still need to be studied in more depth.

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