of the year (Andrewartha & Barker, 1969). In comparison, the Bennett's wallaby in Tasmania (present study) appears to show no less synchrony but with births occurring about two weeks later. In both species, births during the period of seasonal quiescence are uncommon (Andrewartha & Barker, 1969; Catt, 1977; Merchant & Calaby, 1981) but can occur in a very low proportion of animals (tammar: Hinds & den Ottolander, 1983; Bennett's wallaby: present study). Survival of such young may be poor as peak lactation and pouch emergence would occur during the winter.

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Reproductive strategies in female Spanish ibex (*Capra pyrenaica*)

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The reproductive performance of two populations of the Spanish ibex (*Capra pyrenaica*) has been analysed by direct observations. One population was living in natural conditions, the other in semi-captivity where a daily food supplement was given. The most important differences were in quantitative aspects of reproduction, such as the age of sexual maturity and the litter size. This difference in the reproductive strategy can be explained either by the availability of food or the severity of winter.

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Introduction

The anticipation of changes in environmental conditions may be considered as one of the principal mechanisms which explain adaptations of reproductive strategies (Baharav, 1983). The relation between environmental factors and the regulatory mechanisms of the reproductive cycle have been studied by different authors, both for animals in general (Lack, 1954; Gadil & Bossert, 1970; Schaffer, 1974) and ungulates in particular (Jarman, 1974; Leuthold & Leuthold, 1975; Nichols, 1978; Anderson, 1979; Baharav, 1983).

Little is known about reproduction in the Spanish ibex (*Capra pyrenaica*) (Couturier, 1962; Fandos, 1986). Asdell (1964) described some patterns of the genus *Capra*, but not of *pyrenaica*. The long gestation period of the Spanish ibex, the unpredictable variations of climate and availability of food, which are a consequence of the mediterranean climate, involve a high risk of mortality as much for the female goat as for the kid, especially if the latter is born when there is little food available or the weather conditions are adverse (Geist, 1971).

In the present work, the seasonality of reproduction, age of sexual maturity, length of gestation and litter size of the Spanish ibex are examined in different environmental and biological conditions.

Methodology

This study compares the reproduction of two populations of the Spanish ibex in the south-east of the Iberian Peninsula. The main population lives in natural conditions occupying an area of 43,000 ha with a density of 6·2 ibex km^{-2}. The second population occupies an area of 64 ha in conditions of semi-captivity and is comprised of 92 ibex receiving a daily food supplement.

Direct observations for several days on female ibex were made monthly from October 1983 to September 1984, except during the times of birth and rut when sampling was carried out daily. Since individuals were not marked, results were based on the frequency of births (Caughley, 1977). The August sub-sample was chosen as the more representative, because by that month females have already given birth and mortality was still minimal. In the semi-captive population, the majority of the ibex gathered daily to take food so that mothers with offspring could be identified.

The age of the animals was determined by the number of segments and shape of horn, as described by Fandos (1986, In press) and Fandos *et al.*, (In press).

TABLE I

*Mean reproductive patterns of females of the two popula-
tions of Spanish ibex*

Item	Free-roaming	Semi-captivity
	Sector of population of *C. pyre-naica*	
Conception date	December	December
Gestation period	155 days	155 days
Parturition date	May	May
Age of 1st conception	30 months	18 months
Max. fawns at birth	1	2
Natality rate	0·48	0·66

Natality rate was defined as the product of the number of offspring and the number of two-year-old females in both free-roaming and semi-captive populations. The number of kids per female ibex was determined by which kids a female suckled.

The times of the year for copulation and parturition were determined in both populations from the first and last observations of their occurrence.

A known age sample of 15 foetuses was used for comparison of the time of parturition (Fandos, 1987).

Results

The reproductive patterns of the female Spanish ibex are given in Table I. The timing of parturition in both populations is fairly restricted, towards the end of spring to early summer. In semi-captivity this has been determined from the numbers of births taking place daily. In the case of free-roaming ibex, a 15-foetus sample has been used (Fig. 1). Rut occurs at the beginning of winter.

Sexual maturation of the females

The age of sexual maturity of the female ibex was different in the two populations. In semi-captivity there is a tendency to mature sexually at 18 months. Two of the nine females that reached two years of age in the 1984 sample each gave birth to a kid. In the free-roaming population, no two-year-old females were observed with offspring. This would suggest that, under normal conditions, the females tend to delay the age of maturity to at least 30 months.

Litter size

The number of offspring per pregnancy is dependent on genetic and environmental factors, the latter generally being the limiting one. In semi-captivity, 18 births were observed, of which four
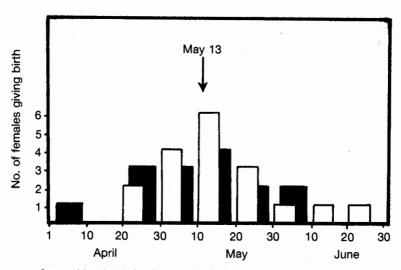

FIG. 1. Frequency of parturition in 10-day intervals in free-roaming, ■; and semi-captive, □ ibex. The median parturition date is arrowed.

TABLE II

Numbers of females (fx) and young (Bx) in known age-classes
of the two populations of Spanish ibex

Age-class	Free-roaming			Semi-captivity		
	fx	Bx	Bx/fx	fx	Bx	Bx/fx
2 years old	6	0	0	9	2	0·22
3 years old	5	2	0·4	5	4	0·80
4–6 years old	13	10	0·76	5	5	1
7–11 years old	13	7	0·52	6	6	1
12–14 years old	2	1	0·5	6	4	0·66
14 years and older	2	0	0	2	1	0·50

were twins (Table II). In this population, there was no scarcity of food since daily nourishment was provided. However, in the free-roaming population, 236 females were counted with one offspring and none with two. Similarly, in the survey of females shot during gestation period, none was observed with more than one foetus.

Discussion

The two study populations of ibex were separated more than 16 years ago. Both can be said to follow the k-strategy (low rate of population increase, advanced age of first reproduction, small litter size, repetition of the reproductive cycle, large body weight) (MacArthur & Wilson, 1967; Pianka, 1970).

Although the semi-captive population has an unlimited food supply throughout the year, the seasonality of reproduction is unaffected. The severity of winter, with the risk of births taking place in temperatures colder than $-10\ °C$, could be the factor determining seasonality instead of the quality and quantity of food. No significant difference was observed between the two samples in respect of the combined median dates of birth (May 13) ($\chi^2 = 2·1$; F.L. = 1; $P > 0·1$) (Fig. 1).

The greater availability of food is reflected in the increased birth rate in the semi-captive population (larger litter size and earlier age of sexual maturity). The same effect has been observed in the population of duiker (*Silvicapra*) in Zambia when density and the intraspecific competition are diminished (Wilson & Roth in Delany, 1982).

To approach parturition with a shortage of food and without sufficient fat reserves in habitats subject to great variation involves a high risk to females owing to the energy demand of the young. Sexual maturity generally occurs in Spanish ibex after 30 months of age when their weight exceeds 24 kg. (Fandos, 1986). This relationship between the mother's weight and the onset of reproduction has been studied by several authors (Mitchell & Brown, 1974; Ellenberg, 1978; Saether & Haagenrud, 1983) who considered nutrition as one of the factors determining body size in ungulates (Verme, 1969; Kein, 1970). In the semi-captive population, food cannot be considered as a limiting factor and the critical weight of 24 kg will be reached before about 18 months, explaining births by two-year-old mothers. Woodgerd (1964) and Berger (1982) have also found a relationship between the mother's body weight and the age of first reproduction.

Litter size depends on genetic and environmental factors (Land, 1978); so the principal adaptation of Spanish ibex relates to the capacity of certain females, who are capable genetically of producing twins, to do so only when they have, or foresee the availability of, food in quantity and

quality. Thus the observed differences in reproductive performance can be explained either by the availability of food or the severity of winter.

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