

Reproductive output of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.): a comparative analysis

Mathieu Garel^{1,2*}, Jean-Marc Cugnasse², Jean-Michel Gaillard¹, Anne Loison¹, Philippe Gibert², Philippe Douvre³ and Dominique Dubray²

¹ Unité Mixte de Recherche n°5558 'Biométrie et Biologie Evolutive', Bâtiment Gregor Mendel, Université Claude Bernard Lyon 1, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France

² Office National de la Chasse et de la Faune Sauvage, Centre National d'Etude et de Recherche Appliquée Faune de Montagne, 95 rue Pierre Flourens, BP 74267, 34098 Montpellier Cedex 5, France

³ Fédération Départementale des Chasseurs de la Drôme, immeuble le sud, 497 avenue Victor Hugo, 26000 Valence, France

(Accepted 5 October 2004)

Abstract

Although many mouflon *Ovis gmelini musimon* populations have been introduced to continental southern and central Europe, little is known about their reproductive output. Based on post-mortem analysis of 344 harvested females, the variation in reproductive performance was investigated in three wild populations: two located in the French Alps and one in the south of France. Examination of tracts indicated a high pregnancy rate (> 80%) for females ≥ 1.5 years old. We found that a significant proportion of female lambs were pregnant in the Alps, c. 1 year earlier than generally reported for first reproduction in the mouflon, whereas female lambs did not conceive in the southern France population. Pregnant female lambs and yearling females always bore a single foetus. Among pregnant females ≥ 1.5 years old, twinning occurred less often in southern France (2.5%) than in the Alps (10.8% and 20.7%). The data required to relate body mass and reproductive output of ewes at individual level were lacking, but female lamb–ewe body mass ratio was used to test that the population with high reproductive output should have the highest ratio. As expected, the index was higher in the Alps than in southern France, suggesting between-population differences in the quality of the local environment. Differences in growth pattern and birth timing of lambs, or different tactics of maternal care could also have influenced the female lamb–ewe body mass ratio. Crossings between wild and domestic sheep during the recent history of these populations and differences in environmental conditions might have interplayed to shape age at first reproduction and twinning rates.

Key words: age at first reproduction, twinning rate, body mass, crossbreeding, *Ovis gmelini musimon* × *Ovis* sp.

INTRODUCTION

To understand population dynamics and fix management programmes, the modelling of demographic processes requires age- and time-specific vital rates such as fecundity, age at first reproduction and survival (Gaillard, Festa-Bianchet & Yoccoz, 1998). Reproductive parameters are easier to measure than survival, and abundant data on age- and time-related variations in fecundity of females are therefore available in many mammalian populations (see Gaillard, Festa-Bianchet, Yoccoz, Loison *et al.*, 2000).

In mouflon *Ovis gmelini musimon* (Cugnasse, 1994), ewes are commonly viewed as monotocous and sexually

mature from 1.5 years of age (Türcke & Schmincke, 1965; Pfeffer, 1967; Cugnasse, Garcia & Veyrac, 1985; Bon, Cugnasse *et al.*, 1991). Females with two lambs at heel, however, have been observed occasionally, raising the possibility of twinning (De Beaufort, 1970; Cugnasse *et al.*, 1985; but see Geist, 1971; Eccles & Shackleton, 1979). Recently, firm evidence of twinning in mouflon has been reported from post-mortem examination in enclosed populations (Briedermann, 1992), in free-living populations given supplemental feed (Nahlik, 2001), and in wild populations (Briedermann, 1992). High twinning rates may even be reached (33.8%; Boussès & Réale, 1998). Likewise some cases of early sexual maturation between 6 and 10 months of age (De Beaufort, 1970; Briedermann, 1992) have been reported.

During introductions of mouflon to continental Europe from native Corsican and Sardinian populations (Bon, Cugnasse *et al.*, 1991), some crossing occurred with

*All correspondence to: M. Garel, Unité Mixte de Recherche n°5558 'Biométrie et Biologie Evolutive', Bâtiment Grégoire Mendel, Université Claude Bernard Lyon 1, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France. E-mail: mgarel@biomserv.univ-lyon1.fr

Table 1. Characteristics of study areas and datasets

Study area	Environmental characteristics				Mouflon population origin ^a	Reproductive output	
	Coordinates	Altitude (meters)	Climate	Vegetation		Sample size	Hunting seasons
Bauges, French Alps (BG)	45°40'N 6°13'E	800–2217	Mountain	Coniferous and beech up to 1500 m; cliffs and open grasslands between 1700–2200 m	6 females and 10 males ^b (1954–55; French National Reserve of Chambord)	43	9
Caroux-espinoise, South of France (CE)	43°40'N 3°0'E	150–1124	Mediterranean, oceanic and mountain influences	Irregular mosaic of beech, chestnut, coniferous, evergreen oak with open area dominated by moorlands of heather and broom heathlands	2 females and 2 males (1956), and 2 females and 2 males (1959) (French National Reserve of Cadarache) 3 females and 3 males (1960; Chambord) 3 females and 2 males (1960; Czechoslovakia)	201 ^c	18
Vercors Drômois, French Alps (VD)	44°50'N 5°17'E	500–1706	Mountain and oceanic influences	Beech up to 800 m; mosaic of cliffs, open grasslands and forest (coniferous and beech) above	4 females and 4 males (1956; Chambord)	100	5

^a Date of introduction and origin of founder are reported in brackets.

^b Five males and two females died during winter following their introduction.

^c Combined with data from Cugnasse *et al.* (1985).

domestic and wild sheep (Türcke & Schmincke, 1965; Uloth, 1972; Cugnasse, 1994). Reproductive potential in domestic sheep is controlled by both genetic and environmental components (Geist, 1971; Land, 1978; Eccles & Shackleton, 1979; Berger, 1982; and see Michels, Decuyper & Onagbesan, 2000), and domestic species are known to be able to produce twins and mature earlier (at 6 months) than their wild counterparts (Schaller, 1977). Therefore, both genetic factors (see Boussès & Réale, 1998) and environmental conditions encountered in mouflon populations (see Briedermann, 1992; Nahlik, 2001) might explain the high reproductive output reported in some populations. However, despite many successful introductions and hunting of these populations, accurate data on reproductive patterns and factors related to the variations are lacking.

From data collected on harvested females in three introduced populations of mouflon *Ovis gmelini musimon* × *Ovis* sp. in France (Table 1), the twinning rate, the age at first reproduction, the pregnancy rate by age class, and the sex-ratio of foetuses was assessed. We predicted that the twinning rate would be higher in the alpine populations originating from mouflon crossbred with domestic and feral sheep (Cugnasse & Houssin, 1993; Cugnasse, 1994; Montgelard, Nguyen & Dubray, 1994), than in the southern population partially originating from native Corsican mouflon (Cugnasse & Houssin, 1993) for which there is no evidence of twinning (Pfeffer, 1967; Dubray, 1988).

Ungulate reproductive output is highly sensitive to female body size (Gaillard, Sempéré *et al.*, 1992; Bérubé, Festa-Bianchet & Jorgenson, 1999; Réale *et al.*, 2000; Hewison & Gaillard, 2001; Bonenfant *et al.*, 2002). In several ungulates, a weight threshold for breeding has

been reported (Sadleir, 1969; Sæther & Heim, 1993; Hewison, 1996; Sand, 1996; Gaillard, Festa-Bianchet, Yoccoz, Loison *et al.*, 2000). Because the reproductive status and the body weight of ewes were recorded independently, the female lamb–ewe body mass ratio was used to estimate the proportion of adult female body mass reached by lambs in each population. It was thus predicted that populations with high reproductive output should have the highest female lamb–ewe body mass ratio.

MATERIALS AND METHODS

Study areas

Data were collected in 3 free-living populations of mouflon located in France: the Bauges (French Alps, BG), Vercors Drômois (French Alps, VD) and Caroux-Espinoise, (southern France, CE) populations. These populations are contrasted according to the origin of the founder individuals and environmental characteristics (Table 1).

BG and VD were founded with mouflon from the French National Reserve of Chambord (Cugnasse & Houssin, 1993). In CE, mouflon initially originated from native Corsican mouflon (French National Reserve of Cadarache: *Ovis gmelini musimon* var *corsicana*; Cugnasse, 1994) introduced 4 years before further groups from Czechoslovakia and Chambord (Cugnasse & Houssin, 1993). Mouflon introduced from Chambord and Czechoslovakia had some ancestors that had been crossbred with other domestic or wild sheep (Türcke & Schmincke, 1965; Uloth, 1972; Cugnasse, 1994; Montgelard *et al.*, 1994; Boussès & Réale, 1998). The 3

populations are of uncertain and possibly mixed origin, so the denomination of *Ovis gmelini musimon* × *Ovis* sp. was used, following the recommendations of Cugnasse (1994). Domestic sheep were abundant ($n = 8450$ in 2003) in VD and crossbreeding may have occurred with mouflon. In BG and VD animals were located at a higher elevation and a more northern latitude than CE mouflon. They are therefore exposed to low ambient temperature, winters with deep snow and short growing seasons (especially in BG, see Loison, Jullien & Menaut, 1999). In CE, mouflon encounter hot dry summers (Garel *et al.*, 2004), wet autumns and fairly cold winters with snow cover lasting only for short periods on hill tops and plateaus (Thiebaut, 1971). None of these populations was given supplemental feed. In the 3 areas studied, hunting takes place from September to February.

Data collection

Data were collected on female mouflon killed during the hunting season (Table 1) and examined by PG. Each female was autopsied to estimate twinning rate, age at first reproduction, pregnancy rate by age class and sex-ratio of the foetuses. Uteri were collected and stored in a freezer at $-20\text{ }^{\circ}\text{C}$ and ovaries fixed in 10% formalin, and stored in 70% alcohol until analysis. The uterine horns were cut longitudinally and the embryos or foetuses were collected. Culled females were classified as pregnant when at least 1 foetus was present. Foetuses can be sexed only after 45 days of age (Barone, 1978). The crown-rump lengths and mass of embryos and foetus were measured in VD, and age was thus estimated from curves reported for domestic sheep (Barone, 1978).

Teeth eruption and replacement were used in BG and CE to estimate the age of ewes. When performed during the hunting season (September–February) this technique provides a reliable estimation of age until 3.5 years (Rieck, 1975; Ryder, 1983). Three age classes were used: lamb (non-permanent incisor), yearling (2 permanent incisors, 1.5 years) and ewes > 1.5 years old (more than 2 permanent incisors). Two age classes were used for VD: lamb and adult females because no distinction was made for ewes ≥ 1.5 years old. To compare adult reproductive output among the 3 populations, yearling and > 1.5 years age classes were pooled for BG and CE.

Eviscerated body mass of female lambs and adult females (≥ 1.5 years) was measured to the nearest 0.5 kg with a spring scale in each population (25, 13 and 5 years of data for BG, CE and VD, respectively). Because the reproductive status and the body weight of ewes were recorded independently, data did not allow us to relate body mass and reproductive output of ewes at the individual level.

Chronology of reproduction

(1) *CE*. Gestation time of mouflon is *c.* 148–159 days (Türcke & Schmincke, 1965; Pfeffer, 1967; Briedermann, 1992). Mating occurs from the end of October until the

beginning of January, with a median date between 7 and 26 November, and most of the matings should have occurred before 15 December (Bon, Dardaillon & Estevez, 1993). Therefore, the pregnancy rates were calculated for females culled after 15 December.

(2) *BG*. Timing of mating is unknown. Field observations reported that most of the lambing occurs from middle to late April (J.-M. Jullien, pers. comm.). We thus assumed that most of the matings also occurred before 15 December in this population.

(3) *VD*. Timing of mating is also unknown, but for most breeding females (93.8%, $n = 61$) the age of the foetus was known. Therefore, the mating period has been estimated as the number of days from first mating to the 80th percentile. This measure is not affected by the timing of a few late fertilizations and has often been used as a measure for birth season in ungulates (e.g. Rutberg, 1987; Berger, 1992; Gaillard, Delorme *et al.*, 1993; Linnell & Andersen, 1998; Coté & Festa-Bianchet, 2001). Timing of parturition was estimated by calculating the median (\pm median absolute deviation) of mating dates.

The lack of strong data on the timing of breeding could lead to underestimating the true pregnancy rate. This bias was limited in our study, however, because: (1) a late date was used for field observations of the end of rut; (2) for the BG population, for which the estimation was not based on a specific study (Bon *et al.*, 1993 for CE and current study for VD), only 2 ewes (both pregnant) were killed before 1 January (i.e. an interval of 2 weeks after the end-of-rut date used).

Statistical analysis

(1) *Reproductive output*. Between 5 and 18 years of data were pooled to increase sample size (Table 1). A log-likelihood ratio test was used to compare pregnancy and twinning rates among populations, and Fisher's exact test for 2×2 contingency table analysis (Venables & Ripley, 2002). Sex-ratio (SR) of foetuses was calculated as the number of male foetuses divided by the total number of foetuses. A bias in sex ratio was tested for using a binomial test (Conover, 1971).

(2) *Body mass*. Between 5 and 25 years of data were pooled to increase sample size (see above). The date of kill was accounted for and body mass of females (lambs and adults) killed in the 3 populations compared by using an ANCOVA. All analyses were performed using R 1.8.0 (Ihaka & Gentleman, 1996).

RESULTS

Mating period in VD

The median date of mating was estimated as 22 October (± 16 days), and 80% of matings took place between 6 July and 4 November, over 17 weeks (Fig. 1). The latest mating occurred on 7 January. Therefore, the percentage of pregnant females was calculated from ewes culled after 4 November. During the following 10 days, few females

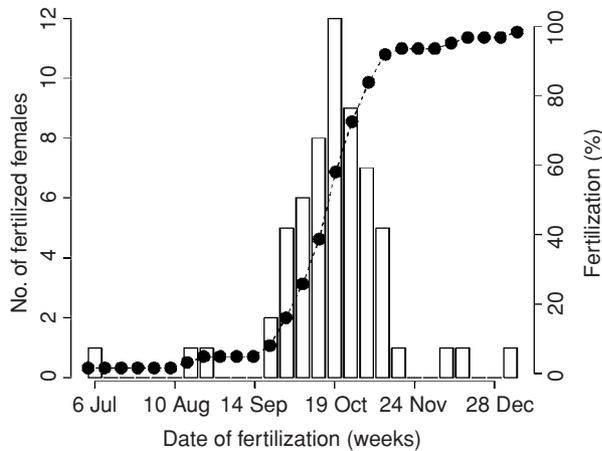


Fig. 1. Dates of fertilization estimated from the age of foetuses of 61 females killed between 1996 and 2001 in the Vercors Drôme population of mouflon, France. Dashed line, cumulative percentage of fertilization; histograms, number of fertilizations every week beginning 6 July.

were killed ($n=10$) and only one was not pregnant, allowing us to avoid including false negatives in the estimation of pregnancy rates.

Comparison of reproductive output

The sex ratio of foetuses did not differ from 0.5 in the BG (SR = 0.50; $n_{\text{females}} = 12$, $n_{\text{males}} = 12$), CE (SR = 0.44; $n_{\text{females}} = 55$, $n_{\text{males}} = 44$, $P=0.32$) or VD (SR = 0.59; $n_{\text{females}} = 18$, $n_{\text{males}} = 26$, $P=0.29$) populations.

An identical proportion of female lambs were pregnant in BG (41.7%, $n=12$) and VD (41.7%, $n=12$) whereas female lambs did not conceive in CE ($n=39$).

A high and similar proportion ($P=0.53$) of yearlings were pregnant both in BG (100%, $n=6$) and CE (81.3%, $n=16$). For these two populations, more than 90% of ewes > 1.5 years old were pregnant (BG: 95.2%, $n=21$; CE: 91.0%, $n=122$; $P=1$). The proportion of pregnant adult females did not vary significantly among populations (CE = 89.9%, $n=138$; $G=4.07$, d.f. = 2, $P=0.13$), although the estimated pregnancy rate for BG (96.3%, $n=27$) tended to be greater than for VD (83.3%, $n=72$; $P=0.11$). In contrast, the twinning rate was different among populations ($G=14.83$, d.f. = 2, $P < 0.001$). The proportion of adult females bearing twins was higher in VD (10.8%, $n=74$) than in CE (2.5%, $n=198$; $P=0.008$), but not statistically different from BG (20.7%, $n=29$; $P=0.21$). None of the female lambs autopsied in BG ($n=5$) and VD ($n=5$), and yearlings autopsied in BG ($n=7$) and CE ($n=13$), had twins. Therefore, the twinning rate in ewes > 1.5 years old was higher, and statistically different between the BG (27.3%, $n=22$) and CE populations (2.7%, $n=185$; $P < 0.001$).

Comparison of body mass

Body mass of adult (≥ 1.5 years) ewes (\pm SE) was similar in the three populations ($F=0.12$, d.f. = 2, 318, $P=0.89$; BG: 21.8 kg (± 0.3), $n=188$; CE: 21.7 kg

(± 0.3), $n=79$; VD: 22.0 kg (± 0.5), $n=55$) and did not change over the hunting season (date effect: $F=0.38$, d.f. = 1, 318, $P=0.54$). For female lambs, the best model included interactive effects of the date of kill and population ($F=3.31$, d.f. = 2, 78, $P=0.04$). Predicted values (SE) for the median date of kill (30 November) show that female lambs are heavier in the Alps (BG, VD) than in CE (population effect: $F=6.80$, d.f. = 2, 78, $P=0.002$; BG: 14.0 kg (± 0.4), $n=46$; CE: 12.2 kg (± 0.5), $n=26$; VD: 15.5 kg (± 0.8), $n=12$). Alpine lambs thus reach a larger proportion of the adult body mass than southern lambs (lamb-ewe body mass ratio: BG = 0.64; CE = 0.56; VD = 0.71).

DISCUSSION

Comparison with other populations of sheep

Age at first reproduction as early as found here (pregnant female lambs) was reported from post-mortem examination earlier in Bauges (BG) populations (De Beaufort, 1970, $n=1$) and mentioned in another population in the Alps originating from the Chambord/Bauges stock by Cugnasse *et al.* (1985). Briedermann (1992) had also reported evidence of mouflon giving birth at 1 year of age, with a pregnancy rate (45% and 60%, $n=38$ and $n=16$, respectively) similar to populations in the Alps. In other sheep populations, maturity is reached at 1.5 years of age (Valdez, 1976; Hoefs, 1978; Nichols, 1978; Berger, 1982; Hadjisterkotis & Bider, 1993; Festa-Bianchet *et al.*, 1995; Boussès & Réale, 1998) and early reproduction is generally only observed in populations bred in captivity (McCuthen, 1977; Berger, 1982) or for domestic (Land, 1978) and feral populations of sheep (Clutton-Brock *et al.*, 1991; Réale *et al.*, 2000).

Except for the native Corsican mouflon in which the lamb-ewe ratio is low (36–59%, $n=54$ –205, Dubray, 1988), the reproductive rate of other mouflon populations is consistently high (enclosed populations: 87.5%, $n=75$, Briedermann, 1992; free-living populations: 91.3%, $n=396$, Briedermann, 1992; population given supplemental feed: 99%, $n=158$, Nahlik, 2001).

Multiple births are rare in North American bighorn sheep (Spalding, 1966; Geist, 1971; Eccles & Shackleton, 1979), although relatively high twinning rates have been reported for California bighorn sheep *Ovis canadensis californiana* (Spalding, 1966; Eccles & Shackleton, 1979) in both wild (36.2%, $n=11$) and captive populations (12.5%, $n=16$). On the other hand, multiple births are frequent in Asiatic sheep (*Ovis orientalis* 40% and one case of triplets, $n=120$, Valdez, 1976; *Ovis gmelini anatolica* 70% from visual observations in a captive population, Arihan & Bilgin, 2001). Twinning rates recorded in the BG and VD populations were among the highest reported for wild and captive populations of mouflon (1–14%, $n=286$, Briedermann, 1992; 8.2%, $n=158$, Nahlik, 2001). Only the wild population of the Kerguelen Archipelago had a greater rate of twinning

(33.8%, $n=71$) with one case of triplets (Boussès & Réale, 1998).

None of the female lambs and yearling females autopsied in the three populations had twins. Though based on a small sample, our results are consistent with those obtained in other mouflon (Briedermann, 1992; Boussès & Réale, 1998; Nahlik, 2001) and sheep (Valdez, 1976; Eccles & Shackleton, 1979; Clutton-Brock *et al.*, 1991) populations. Sheep thereby fit the general patterns reported for polytocous ungulates with primiparous females usually having a smaller litter size than older ones (e.g. Sæther *et al.*, 1996; Hewison & Gaillard, 2001).

Reproductive output: environmental and genetic effects

Populations in the Alps matured earlier and had higher twinning rates than in southern France. Sexual development and fecundity are known to be strongly influenced by the level and quality of diet in ungulates (Sadleir, 1969; Land, 1978). Puberty and the reproductive performance of females depend closely on weight thresholds (Sæther & Heim, 1993; Hewison, 1996; Sand, 1996) and could be related to body mass (Gaillard, Sempéré *et al.*, 1992; Festa-Bianchet *et al.*, 1995; Bérubé *et al.*, 1999; Réale *et al.*, 2000; Hewison & Gaillard, 2001; Bonenfant *et al.*, 2002) rather than to age. During the hunting/rutting season, the body mass of female lambs reached a larger proportion of the adult female body mass in the Alps than in the CE population, which is consistent with the differences in reproductive output observed between these populations (see Sand & Cederlund, 1996). Such a difference could involve between-population differences in environmental conditions. The reproductive output of female ungulates is known to be highly variable according to environmental conditions (Gaillard, Festa-Bianchet, Yoccoz, Loison *et al.*, 2000). Under harsh conditions, females decrease their reproductive effort to avoid jeopardizing their own survival (Festa-Bianchet & Jorgenson, 1998; Gaillard & Yoccoz, 2003). Female lamb-ewe body mass ratio could thus be positively related to the quality of the local environment. The possible effect of differences in growth patterns and birth timing of lambs, and in tactics of maternal care on variation in female lamb-ewe body mass ratio cannot, however, be disregarded.

The earlier age at maturity in the Alps (VE, BG) compared to CE was in contradiction with the first assessment of habitat suitability for mouflon in France (Gindre, 1979), which assumed that Mediterranean habitats, such as the Caroux-Espinouse massif, were more suitable for mouflon than Alpine habitats, where snow cover may be limiting for this species. Indeed, snow cover may have a negative impact on mouflon condition, because mouflon do not scrape through deep snow to obtain food as do other mountain ungulates (Pfeffer, 1967; Heroldova, 1988; Nahlik, 2001). The relationship between habitat suitability and abundance of snow cover during winter, however, may not be so simple. For example, the CE population faces annual summer droughts that limit food availability

and quality (Baudière, 1970; Garel *et al.*, 2004), during the period of lamb and yearling growth, while no such drought occurs at higher altitudes in the Alps (Loison *et al.*, 1999). This summer difference may partly account for the accelerated maturation rates in Alpine populations.

Habitat characteristics may not be sufficient to explain the high twinning rate in the two populations in the Alps. In Dall sheep *Ovis dalli dalli* (Hoefs, 1978), supplemental feeding during ovulation did not result in twinning. Soay sheep (*Ovis aries* Clutton-Brock *et al.*, 1991) and mouflon in the Kerguelen Archipelago (Boussès & Réale, 1998) have a high twinning rate (23% and 33.8%, respectively) despite periodic food shortages, as shown by the death of > 50% of the individuals. Because reproductive potential in domestic sheep is controlled by both environmental and genetic components (Geist, 1971; Land, 1978; Eccles & Shackleton, 1979; Berger, 1982), animals could have inherited their twinning capability from ancestors crossbred from domestic and wild sheep (see Boussès & Réale, 1998).

Because twins are extremely rare in the native mouflon populations of Corsica, Cyprus and Sardinia (Pfeffer, 1967; Dubray, 1988), the twinning capability of our populations could thus be linked to the mixed origin of mouflon introduced from the French National Reserve of Chambord and Czechoslovakia (Türcke & Schmincke, 1965; Pfeffer, 1967; Uloth, 1972; Cugnasse, 1994; Montgelard *et al.*, 1994; Table 1). The alleles responsible for twinning may have been introduced from the Chambord and/or Czechoslovakia stocks (Boussès & Réale, 1998) and therefore, some mouflon may have inherited the twinning capability from these crosses. The CE population grew initially from native Corsican mouflon introduced 4 years before crossbred animals (Chambord and Czechoslovakia stocks). Thus, mouflon in CE could have maintained their twinning capability at a relatively low frequency, in contrast to the mouflon of BG and VD native only from Chambord stock.

Genetic origin and environmental conditions are not independent and particular attention should be given to the interactions between these factors (Land, 1978; Berger, 1982; Harvey & Zammuto, 1985). In Soay sheep, ewes first lamb at 1 year of age despite periodic die-offs resulting from a shortage of food when the population density is high. The rate of twinning and the proportion of females breeding as lambs declined, however, with rising population size, i.e. owing to reduced food availability (Clutton-Brock *et al.*, 1991). Thus, sexual maturation at an early age may not be restricted by intrinsic capability, but could rather be the result of the interaction of genetic origins and environmental characteristics (Berger, 1982; Harvey & Zammuto, 1985). Genetic and environmental factors could interplay to shape the age at first reproduction and twinning rates of mouflon ewes: genetic origin confers phenotypical reproductive plasticity, and environmental conditions influence its expression. This plasticity of mouflon is reported elsewhere, especially in relation to diet (Homolka, 1991; Cransac *et al.*, 1997; Chapuis *et al.*, 2001) and allows an exceptional adaptation of the species to several habitats (Weller, 2001).

Acknowledgements

For the Caroux-Espinouse population, we thank the Groupement d'Intérêt environmental et Cynégétique and the Office National des Forêts for collecting uteri and ovaries, and C. Vuiton and L. Calatayud for their participation in the field. For the Bauges population, we thank H. Houssin and J.-M. Jullien, co-managers of Bauges Wildlife Reserve. For the Bauges and Vercors Drômois populations, we thank hunters for collecting uteri and ovaries. We acknowledge M. R. Frisina and an anonymous referee for their useful comments on a previous draft.

REFERENCES

- Arihan, O. & Bilgin, C. C. (2001). Population biology and conservation of the Turkish mouflon (*Ovis gmelini anatolica* Valenciennes, 1856). In *Proceedings of the Third International Symposium on Mouflon*: 31–36. Nahlik, A. & Uloth, W. (Eds). Sopron, Hungary: Institute of Wildlife Management.
- Barone, R. (1978). *Anatomie comparée des mammifères domestiques III*. Lyon: Ecole National Vétérinaire de Lyon.
- Baudière, A. (1970). *Recherches phytogéographiques sur la bordure méridionale du Massif Central français (Les Monts de l'Espinouse)*. PhD Thesis, Université de Montpellier, France.
- Berger, J. (1982). Female breeding age and lamb survival in desert bighorn sheep (*Ovis canadensis*). *Mammalia* **46**: 183–190.
- Berger, J. (1992). Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. *Ecology* **73**: 323–329.
- Bérubé, C. H., Festa-Bianchet, M. & Jorgenson, J. T. (1999). Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* **80**: 2255–2565.
- Bon, R., Cugnasse, J.-M., Dubray, D., Gibert, P., Houard, T. & Rigaud, P. (1991). Le mouflon de Corse. *Rev. Ecol.* **6**(Suppl.): 67–110.
- Bon, R., Dardaillon, M. & Estevez, I. (1993). Mating and lambing periods as related to age of female mouflon. *J. Mammal.* **74**: 752–757.
- Bonenfant, C., Gaillard, J. M., Klein, F. & Loison, A. (2002). Sex- and age-dependent effects of population density on life-history traits of red deer *Cervus elphus* in a temperate forest. *Ecography* **25**: 446–458.
- Boussès, P. & Réale, D. (1998). Biology of twinning and origin of an unusually high twinning rate in an insular mouflon population. *Z. Säugetierkd.* **63**: 147–153.
- Briedermann, L. (1992). Ergebnisse von Untersuchungen zur Reproduktion des Mufflons (*Ovis amon musimon*). *Z. Jagdwiss.* **38**: 16–25.
- Chapuis, J.-L., Boussès, P., Pisanu, B. & Réale, D. (2001). Comparative rumen and fecal diet microhistological determinations of European mouflon. *J. Range Manage.* **54**: 239–242.
- Clutton-Brock, T. H., Price, O. F., Albon, S. D. & Jewell, P. A. (1991). Persistent instability and population regulation in Soay sheep. *J. Anim. Ecol.* **60**: 593–608.
- Conover, W. J. (1971). *Practical nonparametric statistics*. New York: Wiley.
- Coté, S. D. & Festa-Bianchet, M. (2001). Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia (Berl.)* **127**: 230–248.
- Cransac, N., Valet, G., Cugnasse, J.-M. & Rech, J. (1997). Seasonal diet of mouflon (*Ovis gmelini*): comparison of populations sub-units and sex-age classes. *Rev. Ecol. Terre Vie* **52**: 21–36.
- Cugnasse, J.-M. (1994). Révision taxonomique des mouflons des îles méditerranéennes. *Mammalia* **3**: 507–512.
- Cugnasse, J.-M., Garcia, M. & Veyrac, T. (1985). Contribution à l'étude de la biologie de la reproduction du mouflon (*Ovis amon musimon*), par examen post-mortem, dans le massif du Caroux-Espinouse. *Bull. Mens. Off. Nat. Chass.* **89**: 33–35.
- Cugnasse, J.-M. & Houssin, H. (1993). Acclimatation du mouflon en France: la contribution des réserves de l'Office national de la chasse. *Bull. Mens. Off. Nat. Chass.* **183**: 26–37.
- De Beaufort, F. (1970). Le mouflon des Bauges. Etude de la population. *Bull. Spec. Cons. Sup. Chass.* **14**: 37–59.
- Dubray, D. (1988). Abondance, structure et dynamique de la population de mouflons de Corse (*Ovis amon musimon* S.) du secteur est du massif du Cinto (Haute-Corse), et analyse du rôle de protection de la réserve de l'Office National de la Chasse d'Asco. *Bull. Ecol. Soc. Am.* **19**: 439–450.
- Eccles, T. R. & Shackleton, D. M. (1979). Recent records of twinning in North American mountain sheep. *J. Wildl. Manage.* **43**: 974–976.
- Festa-Bianchet, M., Jorgenson, J. T., Lucherini, M. & Wishart, W. D. (1995). Life history consequences of variation in age of primiparity in bighorn ewes. *Ecology* **76**: 871–881.
- Festa-Bianchet, M. & Jorgenson, J. T. (1998). Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behav. Ecol.* **9**: 144–150.
- Gaillard, J.-M., Delorme, D., Boutin, J.-M., Laere, G. V., Boisauvert, B. & Pradel, R. (1993). Roe deer survival patterns: a comparative analysis of contrasting populations. *J. Anim. Ecol.* **62**: 778–791.
- Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trend. Ecol. Evol.* **13**: 58–63.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**: 367–393.
- Gaillard, J.-M., Sempéré, A. J., Boutin, J.-M., Laere, G. V. & Boisauvert, B. (1992). Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Can. J. Zool.* **70**: 1541–1545.
- Gaillard, J.-M. & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* **84**: 3294–3306.
- Garel, M., Loison, A., Gaillard, J.-M., Cugnasse, J.-M. & Maillard, D. (2004). The effects of a severe drought on mouflon lamb survival. *Proc. R. Soc. Lond. B (Suppl.)* **271**: 5471–5473.
- Geist, V. (1971). *Mountain sheep*. Chicago: Chicago University Press.
- Gindre, R. (1979). Le mouflon en France. *Bull. Mens. Off. Nat. Chass.* **27**: 21–23.
- Hadjisterkotis, E. S. & Bider, J. R. (1993). Reproduction of Cyprus mouflon *Ovis gmelini ophion* in captivity and in the wild. *Int. Zoo Yearb.* **32**: 125–131.
- Harvey, P. H. & Zammuto, R. M. (1985). Patterns of mortality and age at first reproduction in natural populations of mammals. *Science* **315**: 319–320.
- Heroldova, M. (1988). Method of mouflon (*Ovis musimon*) diet research. *Folia Zool.* **37**: 113–120.
- Hewison, A. J. M. (1996). Variation in the fecundity of roe deer in Britain: effects of age and body weight. *Acta Theriol.* **41**: 187–198.
- Hewison, A. J. M. & Gaillard, J.-M. (2001). Phenotypic quality and senescence affect different components of reproductive output in roe deer. *J. Anim. Ecol.* **70**: 600–608.
- Hoefs, M. (1978). Twinning in Dall sheep. *Can. Field-Nat.* **92**: 292–293.
- Homolka, M. (1991). The diet of mouflon (*Ovis musimon*) in the mixed forest habitat of the Dražanska Vrcjovina highland. *Folia Zool.* **40**: 193–201.
- Ihaka, R. & Gentleman, R. (1996). R: a language for data analysis and graphics. *J. Comp. Graph. Stat.* **5**: 299–314.

- Land, R. B. (1978). Reproduction in young sheep: some genetic and environmental sources of variation. *J. Reprod. Fertil.* **52**: 427–436.
- Linnell, J. D. C. & Andersen, R. (1998). Timing and synchrony of birth in a hider species, the roe deer *Capreolus capreolus*. *J. Zool. (Lond.)* **244**: 497–504.
- Loison, A., Jullien, J.-M. & Menaut, P. (1999). Relationship between chamois and isard survival and variation in global and local climate regimes: contrasting examples from the Alps and Pyrenees. *Ecol. Bull.* **47**: 126–136.
- McCuthen, H. E. (1977). A minimum breeding age for a desert bighorn ewe. *Southwest. Nat.* **22**: 153–155.
- Michels, H., Decuyper, E. & Onagbesan, O. (2000). Litter size, ovulation rate and prenatal survival in relation to ewe body weight: genetic review. *Small Ruminant Res.* **38**: 199–209.
- Montgelard, C., Nguyen, T. C. & Dubray, D. (1994). Genetic variability in French populations of the Corsican mouflon (*Ovis ammon musimon*): analysis of 2 blood proteins and red-cell blood groups. *Genet. Sel. Evol.* **26**: 303–315.
- Nahlik, A. (2001). Fecundity and survival of mouflon and factors affecting them. In *Proceedings of the Third International Symposium on Mouflon*: 22–30. Nahlik, A. & Uloth, W. (Eds). Sopron, Hungary: Institute of Wildlife Management.
- Nichols, L. (1978). Dall sheep reproduction. *J. Wildl. Manage.* **42**: 570–580.
- Pfeffer, P. (1967). Le mouflon de Corse (*Ovis ammon musimon* Schreber, 1782). Position systématique, écologie et éthologie comparées. *Mammalia* **31**(Suppl.): 1–262.
- Réale, D., Boussès, P., Pisanu, B. & Chapuis, J.-L. (2000). Biannual reproductive cycle in the Kerguelen feral sheep population. *J. Mammal.* **81**: 169–178.
- Rieck, W. (1975). *Muffelwildalter*. In *Brochure de l'association des chasseurs d'Allemagne Fédérale*: 1–10. Bonn: Deutscher Jagdschutz.
- Rutberg, A. T. (1987). Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *Am. Nat.* **130**: 692–710.
- Ryder, M. L. (1983). *Sheep and man*. London: Duckworth.
- Sadleir, R. M. F. S. (1969). The role of nutrition in the reproduction of wild mammals. *J. Reprod. Fertil. Suppl.* **6**: 39–48.
- Sæther, B.-E. & Heim, M. (1993). Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *J. Anim. Ecol.* **62**: 482–489.
- Sæther, B.-E., Andersen, R., Hjeljord, O. & Heim, M. (1996). Ecological correlates of regional variation in life history of the moose *Alces alces*. *Ecology* **77**: 1493–1500.
- Sand, H. (1996). Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia (Berl.)* **106**: 212–220.
- Sand, H. & Cederlund, G. (1996). Individual and geographical variation in age at maturity in female moose (*Alces alces*). *Can. J. Zool.* **74**: 954–964.
- Schaller, G. B. (1977). *Mountain monarchs. Wild sheep and goats of the Himalaya*. Chicago: Chicago University Press.
- Spalding, D. J. (1966). Twinning in bighorn sheep. *J. Wildl. Manage.* **30**: 207.
- Thiebaut, B. (1971). La transition climatique dans le massif de l'Agoût. *Vie Milieu* **22**: 167–206.
- Türcke, F. & Schmincke, S. (1965). *Das Muffelwild. Naturgeschichte*. Hamburg: Paul Parey.
- Uloth, W. (1972). To the history of the distribution, introduction and crossbreeding on the tyrrhenis mouflon in Europe and overseas. *Acta Theriol.* **17**: 412–413.
- Valdez, R. (1976). Fecundity of wild sheep (*Ovis orientalis*) in Iran. *J. Mammal.* **57**: 762–763.
- Venables, W. N. & Ripley, B. D. (2002). *Modern applied statistics with S*. 4th edn. New York: Springer.
- Weller, K. E. (2001). The status of mouflon (*Ovis musimon*) in Europe. In *Proceedings of the Third International Symposium on Mouflon*: 114–140. Nahlik, A. & Uloth, W. (Eds). Sopron, Hungary: Institute of Wildlife Management.