

Biology of twinning and origin of an unusually high twinning rate in an insular mouflon population

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*Receipt of Ms. 16. 05. 1997
Acceptance of Ms. 29. 09. 1997*

Abstract

Twins have rarely been reported from wild populations of European mouflons (*Ovis ammon musimon*), and this subspecies is commonly regarded as monotocous. During the winter of 1994, we autopsied 71 pregnant females in a population established on Île Haute, a small island of the subantarctic Kerguelen archipelago. Though pregnant yearlings always bore single fetuses, the twinning rate reached 36% among pregnant adult females. The study population was founded by two individuals, originating from the Vincennes Zoo (France). Our analysis of the birth registers revealed that multiple births were common in this zoo herd, and a founding effect may explain the high twinning rate observed during this study. Crossings with sheep (*O. ammon* f. *aries*) and oriental mouflons (*O. ammon orientalis*) during the recent history of the mouflon in continental Europe are probably responsible for the occurrence of twinning in the Kerguelen population, as well as in some captive mouflon populations.

Key words: *Ovis ammon musimon*, mouflon, reproduction, twins, Kerguelen

Introduction

Among Eurasian wild sheep (*Ovis ammon*), twinning is quite common in the Urial (i.e. *O. ammon orientalis*; VALDEZ 1976) and Argali groups (i.e. *O. ammon ammon*; SCHALLER 1977; VALDEZ 1988). In contrast, twinning is exceptional among American wild sheep (*O. nivicolla*, *O. dalli*, and *O. canadensis*; SPALDING 1966; GEIST 1971; HOEFS 1978; ECCLES and SHACKLETON 1979). Twins are also uncommon among populations of European mouflons (*O. ammon musimon* Schreber, 1782): no multiple birth has been reported from the original populations of Corsica, Sardinia, and Cyprus (PFEFFER 1967), and their occurrence in most wild populations of continental Europe is much debated (BON et al. 1991; CUGNASSE et al. 1985). Females accompanied by two lambs were observed on some occasions, leading to speculations about the twinning ability of this subspecies (CUGNASSE 1982; BON et al. 1991). However, in ungulates, two or more young may temporarily associate with a female without implying kinship, and such reports are poor evidence of twinning. Even simultaneous nursings of two young are inconclusive: allosuckling has been reported in several ungulate species (RIEDMAN 1982; PACKER et al. 1992), notably in close relatives of mouflons, such as American wild sheep (ECCLES and SHACKLETON 1979; HASS 1990) and domestic sheep (*Ovis ammon* f. *aries*; POINDRON and LE NEINDRE 1980). This usually occurs while a female is already nursing her own single offspring (MURPHEY et al. 1995), a behaviour probably responsible for many unconfirmed field observations of twin-

ning among ungulates otherwise considered to be monotocous. The aims of this study are to investigate the biology of twinning in a population of European mouflons established on a small subantarctic island, and to compare their reproductive performances with those of the mouflon herd maintained at the Vincennes Zoo (France), from which the studied population derived.

Material and methods

The study was performed on île Haute (49°24'S, 69°56'E), a small island (6.5 km²) of the Kerguelen archipelago. Details of the study area and climate have been reported elsewhere (BOUSSÈS et al. 1994). The vegetation is typically subantarctic and characterized by the absence of trees and shrubs. Rocky and eroded areas cover 70% of the island, while swards represent no more than 7%. The high population density during the study period must be considered in regard to these characteristics.

The study population was founded in 1957 by a pair of mouflons which came from the Vincennes Zoo (LÉSEL 1967). Following an initial period of rapid demographic growth, the Kerguelen population entered cyclic oscillations by the end of the 70's, with massive die-offs occurring every two to five years due to food shortages (BOUSSÈS et al. 1992). Our study was carried out from July to September 1994, during the austral winter, corresponding to the gestation period. The population density was very high, with about 100 ind./km², and a die-off occurred during the study period. Eighty females were shot and autopsied in the field. In this study, we have restricted the analysis to 71 females with embryos large enough to be detected macroscopically. The ovaries were bisected and examined for the presence of corpora lutea. Except for some ewes collected by hunters, the implantation side of embryos in the uterine horns was noted. Females were divided into yearlings and adults by the number of definite incisors (RYDER 1983).

Data on the reproductive characteristics of the founding stock were collected from the registers of births and deaths of the Vincennes Zoo. Although the zoo was created in 1934, complete registers are only available for the periods 1947–1965 and 1978–1988, and the origin of this collection is not reported. Unfortunately, mouflon multiple births were explicitly noted in very few cases. Two or more births were often recorded at a particular date, and multiple births were obviously much more frequent than those explicitly reported. However, the frequency of multiple reports provides only a crude estimate of multiple births since, for example, a double report might correspond to one set of twins or to two single-lamb births. Moreover, up to nine lambs were sometimes recorded the same day, and in several cases we suspect that the registration corresponds to a grouping of births for the preceding few days. To circumvent this problem, we examined for each year the ratio of the number of lamb births recorded to the number of potentially reproductive females present in the herd. Females were considered potentially reproductive at one year of age and able to give birth when 17 months old.

Results

In the Kerguelen population, twins were present in 33.8% of pregnant females ($n = 71$). The five yearling females sampled carried a single fetus, while 24 out of 66 (36.4%) pregnant adult females carried twins. There were 38 (53.5%) fetuses implanted in the right uterine horn and 33 in the left one, a proportion that did not differ significantly from a 50:50 distribution ($\chi^2_1 = 0.553$, $P = 0.55$). The proportion of right-implanted embryos was similar for females with single fetus (51.5%, $n = 33$ fetuses) and those with twins (55.3%, $n = 38$; $\chi^2_1 = 0.1$, $P = 0.75$). Among females with twins, the fetuses were always located in separate uterine horns when each ovary produced one egg ($n = 6$). In contrast, when the eggs were released by the same ovary, embryos shared the same uterine horn in only four out of 12 cases, a distribution explained by the trans-uterine migration of 33.3% of the eggs.

At the Vincennes Zoo, two pairs of twins and one set of triplets were explicitly recorded for 316 lambs born. However, only 57% of the reports referred unambiguously to

Table 1. Distribution of birth reports at Vincennes zoo, according to the number of lambs noted on a particular date (periods 1947–1965, 1978–1988).

	Number of lambs per report									total
	1	2	3	4	5	6	7	8	9	
Number of reports	106	55	15	6	3	0	1	0	1	182
Proportion (%)	56.7	29.4	8	3.2	1.7	0	0.5	0	0.5	
Number of lambs	106	110	45	24	15	0	7	0	9	316
Proportion (%)	32.9	34.8	14.5	7.7	4.8	0	2.3	0	2.9	

Table 2. Reproductive characteristics of mouflons at Vincennes zoo, France, between 1949 and 1957. Though the potential number of reproductive females was known, the number of females failing to reproduce in any particular year was unknown, leading to minimal estimates of the number and proportion of twin-births

Year	Females	Lambs	Lambs/female	Min. number of twin births	Min. twinning rate
1949	13	15	1.15	2	0.15
1950	8	10	1.25	2	0.25
1951	15	17	1.13	2	0.13
1952	14	15	1.07	1	0.07
1953	12	18	1.50	6	0.50
1954	14	20	1.43	6	0.43
1955	15	23	1.53	8	0.53
1956	15	16	1.07	1	0.07
1957	18	16	0.89	0	0
total	124	150		28	
mean			1.23		0.23

single births (only one lamb recorded on a particular day), while double (29%) and triple daily reports of births (8%) were also frequent (Tab. 1). For a more precise analysis, we established the number of potentially reproductive females present each year from an analysis of the registers. Since we were interested in the characteristics of the herd before the founding of the Kerguelen population, we considered only the period 1949–1957. During this period, a mean number of 1.23 ± 0.22 (s.d., $n = 9$) lambs per potentially reproductive female was produced, and more than one lamb per female was evidently born in eight out of nine years (Tab. 2). Assuming that each potentially reproductive female reproduced, a minimum of 28 twin pairs is required to account for the excess of lambs produced. Thus, the twinning rate was at least 23% for the period considered, but exceeded 50% some years. These values are obviously underestimated, since some females could have failed to reproduce in a given year.

Discussion

In the île Haute population, females with twins always had two corpora lutea and the fetuses were located in separate embryonic membranes, indicating dizygotic twins. However, a female found dead in 1992 had two fetuses sharing the same embryonic membranes, a pattern that reveals the occasional occurrence of monozygotic twins (RENFREE

1982). The predominance of dizygotic twins agrees with data on other ungulate species (BAZER et al. 1993).

As in most ungulates (HAFEZ 1993), eggs are produced equally by the two ovaries in mouflons. Twins tended to be implanted in separate uterine horns, even when the two eggs were produced by the same ovary. A trans-uterine migration of one egg occurred in these cases. We suggest that there is a selective advantage favoring this implantation pattern, which might result in reduced competition for resources between sibs. Indeed, it has been shown in several species that when the number of multiple fetuses differs between horns, those in the horn with a lower number tend to be heavier (BARR et al. 1970; PAGE et al. 1994).

All the yearling females autopsied in the Kerguelen population were pregnant but none had twins. Though based on a small sample (five individuals), this result agrees with those obtained for oriental mouflons in which reproductive yearling ewes always produce single lambs (VALDEZ 1976). It also conforms to most results for polytocous ungulates showing that primiparous females usually have a smaller litter size than older ones (e.g. PIMLOTT 1959 in moose *Alces alces*; FOLK and KLIMSTRA 1991 in white-tailed deer *Odocoileus virginianus*; HEWINSON 1996 in roe deer *Capreolus capreolus*; MILNER-GULLAND 1994 in saiga *Saiga tatarica*; CLUTTON-BROCK et al. 1991 in feralized domestic Soay sheep; CASINELLO and GOMENDIO 1996 in Saharan arrui *Ammotragus lervia sahariensis*).

The twinning rate observed in the Kerguelen population is by far the highest reported for any mouflon population, with about 36% of the pregnant adult females bearing twins. One set of three male fetuses was even recorded for an adult female found dead during a winter die-off. In contrast, twinning is unknown in most free-living populations of continental Europe. For instance, all 51 pregnant females shot in the Caroux-Espinouse Massif, France, bore a single fetus (CUGNASSE et al. 1985). When twinning occurs, it rarely exceeds a few percent of the births (1 to 3% in three populations studied by BRIEDERMANN 1992).

Multiple births have, however, been observed in several captive mouflon populations (CUGNASSE et al. 1985). Twins represented 14% of births in an enclosed population in Germany (BRIEDERMANN 1992), approximately 10% of births at the London zoo (ZUCKERMAN 1953) and at the New York Zoological Park (CRANDAL LEE 1964), and 5% at the National Zoo of South Africa (BRAND 1963). The maintenance of a good food supply all year round may have contributed to the relatively high frequency of multiple births in captive populations. Ungulate fecundity is known to be very sensitive to diet quality (SADLEIR 1969). For example, 22% of births involved twins in a captive population of Spanish ibex (*Capra pyrenaica*) with supplemented food, whereas no multiple births or females bearing two fetuses were observed in the founding population (FANDOS 1989).

Improved food resources cannot, however, explain the twinning phenomenon observed in the Kerguelen population. During the study period, the population was at very high density and was obviously suffering from food shortage, as shown by the death of more than 50% of the individuals between June and November.

Our analysis of the Vincennes Zoo records revealed that twinning was very frequent in this herd. Thus, a founding effect is certainly responsible for the propensity of females to produce twins in the Kerguelen population. However, because twins are absent, or at least extremely rare, in the mouflon populations of the Mediterranean islands (PFEFFER 1967), the origin of this capability is probably linked to the recent history of the species. The introduction of mouflons in continental Europe can be traced back to the 18th century, and it is well established that some crossing occurred subsequently with domestic sheep and oriental mouflons (PFEFFER 1967; ULOTH 1972). Some mouflon populations inherited the twinning capability from these crosses and the alleles responsible for this trait were surely introduced by chance into the Vincennes stock.

Inbreeding commonly results in substantial reduction in young survival, body size, and fecundity (RALLS et al. 1979; FALCONNER 1989). Since the Kerguelen population traces its

ancestry to only two individuals, we might have expected a reduced fecundity instead of the particularly high one observed. However, a history of forced inbreeding, as occurred in the Vincennes herd, may have purged the population of deleterious recessive alleles (SMITH 1978; LANDE and BARROWCLOUGH 1987). Indeed, there has been no external acquisition to the Vincennes Zoo population since 1947 at least, while the female population size varied between 8 and 19 individuals, and male number between only 4 and 9, such that the effective population size was extremely reduced.

Finally, our results bring a new insight into the population dynamics of the Kerguelen mouflon. LÉSEL (1969) first noticed that the population was characterized by a very high growth rate (46.3%) during the colonization period, a value much higher than those reported for other introduced mouflon populations. LÉSEL and DERENNE (1975) suggested that a highly-biased sex-ratio (i.e. 35 females for a total adult population estimated at 42 individuals in 1968) could account for the population growth rate. Present knowledge of the mechanisms controlling birth sex-ratio in ungulates is unable to explain such a huge excess of females (CLUTTON-BROCK and IASON 1986). The high fecundity revealed by this study offers a simpler explanation for the unusual growth rate observed.

Acknowledgements

We are grateful to Professors RENVOISÉ and N'GUYEN TU-LINH for providing access to the Vincennes Zoo registers. We are particularly indebted to OLIVIER COMBES and GILLES SALÜN for performing the field autopsies, and to MARK JUDSON for improving the English. This research was supported by the Institut Français pour la Recherche et la Technologie Polaires, the CNRS (U.M.R. 6553) and the Office National de la Chasse. D. RÉALE received grants from the Ministère de l'Enseignement supérieur et de la Recherche.

Zusammenfassung

Die Biologie von Zwillingsgeburten und mögliche Ursachen für eine ungewöhnlich hohe Rate von Zwillingsgeburten in einer inselbewohnenden Mufflonpopulation

Bisher wurde in freilebenden Mufflonpopulationen (*Ovis ammon musimon*) nur selten das Auftreten von Zwillingen beobachtet. Während des Winters von 1994 wurden in einer Population auf Île Haute, einer kleinen Insel des subantarktischen Kerguelen-Archipels, 71 trächtige Weibchen autopsiert. Obwohl trächtige einjährige Weibchen stets nur einen Fötus aufwiesen, erreichte die Rate von Zwillingen bei den adulten Weibchen 36%. Die untersuchte Population geht auf zwei Gründerindividuen zurück, die aus dem Zoo von Vincennes (Frankreich) stammten. Eine Analyse des Geburtenbuches ergab, daß Zwillingsgeburten in diesem Zoobestand häufig auftraten, und die hohe Rate von Zwillingsgeburten in der Île Haute-population könnte daher auf einen Gründereffekt zurückgehen. Kreuzungen mit Schafen (*O. ammon f. aries*) und orientalischen Mufflons (*O. ammon orientalis*) während der jüngeren Geschichte des Mufflons auf dem europäischen Festland sind möglicherweise für das Auftreten von Zwillingsgeburten in Zoos und in der Kerguelen-Population verantwortlich.

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Réale, Denis. 1998. "Biology of twinning and origin of an unusually high twinning rate in an insular mouflon population." *Zeitschrift für Säugetierkunde : im Auftrage der Deutschen Gesellschaft für Säugetierkunde e.V* 63, 147–153.

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