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# Maternal expenditure during lactation in mouflon (*Ovis orientalis musimon*)

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ABSTRACT. *Maternal expenditure during lactation in mouflon* (Ovis orientalis musimon).– Maternal expenditure in the mouflon during lactation was studied according to infant sex on the basis of the associated suckling and nursing behaviour. The study was conducted at the Parque Natural de Cazorla, Segura y Las Villas, in Jaén (Spain), on a captive group composed of seven mother-infant pairs. The results obtained reveal differences in maternal expenditure between the two sexes. Males suckled more frequently and for longer periods than females did. The differences remained throughout lactation. In addition, unsuccessful attempts were more frequent in female infants, so they had lower success rates.

KEY WORDS. *Ovis orientalis musimon*, Maternal expenditure, Maternal investment, Lactation.

## Introduction

Female mammals invest heavily on their offsprings during pregnancy, lactation and post-weaning nursing (Gittleman & Thompson, 1988), of which lactation is considered to be the most onerous of the above periods (Millar, 1977; Randolph et al., 1977) and accounts for up to 75% of all the energy expended by ungulates on reproduction (Oftedal, 1985).

On the other hand, paternal investment in mammals is usually limited to gamete production. Even though their cost is far from insignificant (Dewsbury, 1982), they allow males to save a substantial amount of their energy to compete with other males for oestrous females (Payne, 1979; Clutton-Brock et al., 1982). This competition results in a wide variability in reproductive success inasmuch a few dominant males can have a large number of offspring. Reproductive success in females, however, is more even since most of them accomplish their own offspring irrespective of their rank in the female group. Sexual selection thus favours phenotypical characters suited to male competition [e.g. body size (Barash, 1982)] and fosters development of polygynous mating systems (Zeveloff & Boyce, 1980; Csermely, 1984).

Insofar as lactation involves the greatest relative body growth in the offspring (Mottl, 1960, in Pfeffer, 1967; Blood et al., 1970; Hansen & Deming, 1980), mothers must spend greater amounts of energy on male infants, thereby favouring their development and increasing their reproductive success likelihood (Trivers & Willard, 1973; Maynard Smith, 1980; Clutton-Brock et al., 1982; Trivers, 1985). Differences in maternal investment on the two sexes have been observed in various mammal species such as *Cervus elaphus* (Clutton-Brock et al., 1981, 1984), *Loxodonta africana* (Lee & Moss, 1986), *Myocastor coypus* (Gosling et al., 1984) and some seal species (Reiter et al.,

1978; Kovacs & Lavigne, 1985, 1986; Trillmich, 1986; Anderson & Fedak, 1987).

The occurrence of differential maternal investment in mouflon can be predicted from various features, namely: (a) its polygynous mating system (Pfeffer, 1967; Auvray, 1983; Bon & Campan, 1989); (b) its sexual dimorphism, with larger males than females (Pfeffer, 1967); and (c) a hierarchical access to females, which is accomplished by direct or indirect aggressions and is correlated with horn and overall body size (Pfeffer, 1967; Geist, 1971; Schaffer & Reed, 1972; Schaller, 1977).

The aim of this work was to analyse maternal expenditure according to infant sex in the mouflon (*Ovis orientalis musimon*) during lactation on the basis of the associated nursing and suckling behaviour.

## Material and Methods

Observation were made at the Parque Natural de Cazorla, Segura y Las Villas in Jaén (Spain) from April to September 1987. Animals were kept in a 800 $m^2$ enclosure where they fed on externally provided food, water and salt, as well as on the natural vegetation. In order to facilitate acclimation, adult ewes were enclosed during pregnancy.

The surveyed group consisted of seven mother-young pairs (three male and four female lambs). An overall 288 hours of observation were performed from the offspring birth to five months later, in daylight hours from a hide which provided a full view of the area. In each daily observation period, two observers recorded all suckling actions in all group members. Each individual was recognized by peculiar features or by painted marks on its back.

A suckling action was considered to have taken place every time a lamb poked its head into an adult female's bosom (Le Neindre & Garel, 1977). Suckling actions were classed as suckles if they lasted 5 seconds or longer (Shackleton & Haywood, 1985), or as unsuccessful attempts otherwise. Recordings for each suckling action included the clock time (hour and minute) and duration, the identity of the individuals involved and, occasionally, whether the suckle was mother or lamb terminated.

Collected data were grouped by individual and day, and used to determine the following variables:

– Suckling frequency, viz. the mean number of suckles per hour of observation.

– Mean duration of suckle, namely the average of all recorded durations.

– Overall suckling time per hour of observation, which was obtained by multiplying the mean duration of suckle by the suckling frequency. It was expressed as the average number of seconds each infant spent suckling per hour of observation.

– Unsuccessful attempt frequency, i.e. the number of unsuccessful attempts recorded per hour of observation.

– Success rate, viz. the proportion of successful suckling actions.

Lamb age was divided into two-week periods and a mean value was obtained for each variable per individual per period. For the purpose of parametric tests, frequency data were log-transformed. The success rate was subjected to the arcsine transformation of Freeman & Tukey (Zar, 1984).

## Results

The suckling frequency was found to decrease with lamb age, the changes being similar for both sexes (fig. 1a). The suckling rate was quite high in the first few days of both male and female lambs, after which it decreased continuously. The decrease was more marked between periods 1 and 3, and became more gradual afterwards. However, male infants suckled more frequently than female infants did throughout the whole age range (two-

way ANOVA, Sex: F=10.21, df=1, p<0.01, Age: F=20.76, df=11, p<0.001). The mean suckle duration also decreased significantly with age, but did not differ significantly between sexes (fig. 1b, two-way ANOVA, Sex: F=0.07, df=1, p>0.05, Age: F=7.19, df=1, p<0.001). As far as the identity of the lactating ewe is concerned, no lamb of either sex obtained any suckles at a mother other than its own during the observation period.

A suckle sample from the first week (included in period 1) revealed mothers of male infants to have terminated 38.6±12.1 ($\overline{X}$±S.E.) per cent of suckles, and mothers of females to have done so in 75.0±25.0% of instances (Mann-Whitney U-test, T=0.92, p>0.05). The proportion of mother-terminated suckles increased sharply (to 100%) for both sexes by the end of the second week, and remained so until weaning.

The overall suckling time per hour of observation also decreased with age for both sexes; males spent more time suckling than females did (fig. 1c, two-way ANOVA, Sex: F=8.24, df=1, p<0.01, Age: F=25.95, df=11, p<0.001) mainly by suckling more frequently.

Conversely, female infants performed more unsuccessful attempts than males throughout the study (fig. 2a, two-way ANOVA, Sex: F=9.26, df=1, p<0.01, Age: F=3.16, df=11, p<0.01). The high frequency of unsuccessful attempts in the first five periods is related to a more marked decline in the overall suckling time. After that it decreased gradually to the end of the observation period, with the sole disruption of a peak at period 9 in female lambs that may have arisen from the small number of individuals involved.

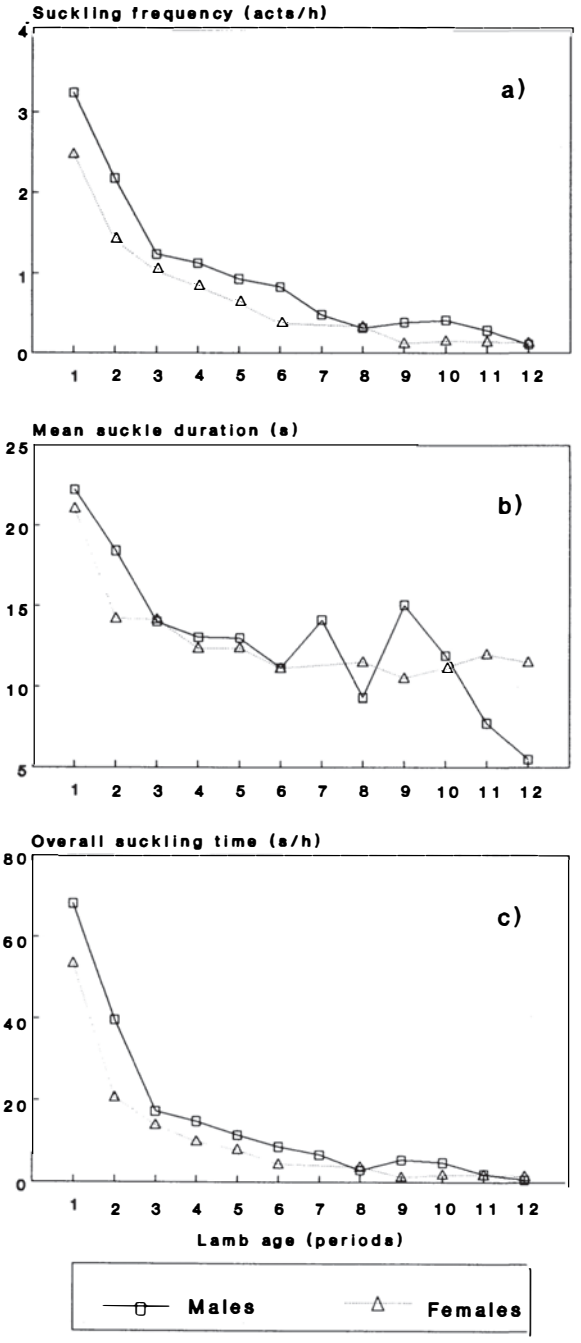


FIGURE 1. Variation with age (two-week periods) of the suckling frequency (a), mean suckle duration (b) and overall suckling time per hour of observation (c) with infant sex. Values are means.

[Variación con la edad de la frecuencia de mamada (a), duración media de la mamada (b) y tiempo total de lactancia por hora de observación (c) según el sexo de las crías.]

## Resumen

*Gasto maternal del muflón (*Ovis orientalis musimon*) durante la lactancia.*

El muflón de Córcega posee un sistema de apareamiento polígamo en el que los machos de mayor tamaño tienen prioridad de acceso a las hembras. La mayor varianza en el éxito reproductor de los machos favorece una estrategia en la que la madre destina una mayor cantidad de energía, durante el periodo de lactancia, a la cría de este sexo, para contribuir a su mejor desarrollo.

En un recinto situado en el Parque Natural de Cazorla, Segura y Las Villas, Jaén (España), donde los animales disponían de alimento ad libitum, se ha estudiado un grupo de siete parejas madre-cría, desde el nacimiento hasta los 160 días de edad, registrándose en cada sesión todas las ocurrencias de los comportamientos en todos los miembros del grupo. Para cada sexo se obtuvieron las siguientes variables: frecuencia de mamada, duración media de la mamada, tiempo total de lactancia, frecuencia de intentos no exitosos y tasa de éxito.

En ambos sexos la frecuencia de mamada es elevada en los primeros días (fig. 1a), tras los cuales desciende progresivamente. Los machos maman más veces a lo largo de todo el periodo y ninguno de los sexos obtiene leche de hembras adultas diferentes de la madre. La duración media de la mamada disminuye con la edad y no presenta diferencias significativas entre sexos (fig. 1b). El tiempo total de lactancia, variable que es una combinación de las dos anteriores, también desciende con la edad en ambos sexos (fig. 1c), mamando los machos más tiempo por hora de observación. Por tanto, las madres de crías machos suministran más energía en forma de leche, en consonancia con la teoría de inversión maternal diferenciada según el sexo de la cría.

La frecuencia de intentos sin éxito (fig. 2a) es alta en los cinco primeros periodos de edad, lo que parece reflejar una resistencia comportamental de la cría al descenso en la cantidad de leche recibida, y supondría la manifestación del conflicto materno-filial. En general, a la cría hembra le cuesta más trabajo conseguir una mamada a lo largo de toda la lactancia. Por último, la tasa de éxito (fig. 2b) desciende en ambos sexos desde el primer periodo hasta el quinto, a partir del cual se mantiene con ciertas oscilaciones, aunque siempre es mayor en las crias machos.

En cuanto al final del periodo de lactancia, éste se sitúa en nuestro estudio alrededor de los 160 días de edad para ambos sexos, aunque el alimento ad libitum, que permite un buen estado nutricional de la madre, ha podido influir prolongando la lactancia y enmascarando así la posible diferencia en las fechas del destete definitivo para cada sexo.


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