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Mother-Offspring Relationship in the Vicuña, *Vicugna vicugna* (Mammalia: Camelidae)

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Abstract

The vicuña mother-offspring bond was studied during the calves' first and third months of life. Pairs kept in field and corral conditions allowed to compare mother-offspring relationships between animals with and without management. Vicuñas belong to the "follower type" in the classic distinction among ungulate species between "followers" and "hiders". In the field, mother-offspring distances were small during the first month then increased. In the corral, mother-offspring distance was greater than in the field in the first month and did not vary with age. In the third month, in both "conditions" mothers tended to avoid their calves more than in the first month. Although calves initiated approximately 90 % of nursing bouts during both periods, the percent terminated by the mother was significantly higher in the third month than in the first (96 % to 59 %). The calves increased their grazing time from a few scans per h in the first month to half the sample period in the third month. The mother-offspring bonds showed some quantitative differences between field and corral, but in both "conditions" the mothers nursed their calves successfully.

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Introduction

The mother-offspring bond is one of the principal social associations in mammals (EISENBERG 1966; CROOK et al. 1976; GAUTHIER & BARRETTE 1985). The energetic costs of gestation and lactation are high (SADLIER 1969; POND 1977) and mammalian females allocate a large proportion of their reproductive effort to each offspring (FISHER 1930). The reproductive success of a female depends principally on "her ability to acquire resources and to transfer them to the offspring during the gestation and nursing period" (CLUTTON-BROCK et al. 1982, 1988). As present reproductive investment may affect future reproductive success (CLUTTON-BROCK et al. 1989), there is a conflict between mothers and offspring, with offspring demanding more than mothers are selected to give (TRIVERS 1974). Maternal

investment is not only related to milk transfer but also includes the care of the young and associated behaviour which can have a negative impact upon future maternal reproductive success (TRIVERS 1974).

The distance between the mother and her offspring is the basis for the classification of the ungulates' mother-offspring bond types into "followers" and "hiders" described by WALTHER (1965), reviewed by LENT (1974) and used by LEUTHOLD (1977); RALLS et al. (1986, 1987); CARL & ROBBINS (1988). These two strategies have been seen as predation avoidance in open (following) and closed (hiding) habitats (LENT 1974). The predation risk to wild ungulates during the first few months is important, as a large proportion of the young may be killed by predators in natural populations (CROOK et al. 1971; CARROL & BROWN 1977; SMITH 1986; CARL & ROBBINS 1988).

There is a lack of information on the relationship between the mother and the offspring in camelids in general and particularly in wild South American species.

The vicuña is a 45-kg South American camelid that inhabits the high grasslands and scrublands of the Puna or Altiplano (the altitudinal distribution is 3200—4900 m above sea level) region of Bolivia, Chile, Peru and Argentina (KOFORD 1957; FRANKLIN 1974). It lacks sexual dimorphism, is an obligatory drinker and is sedentary (FRANKLIN 1974, 1983).

Vicuñas form stable family groups with one male, 3—4 females and offspring, and more variable groups of bachelor animals (KOFORD 1957; FRANKLIN 1974, 1983; CAJAL 1985; VILÁ 1990; VILÁ & ROIG 1992). Males defend year round areas where females and calves live (KOFORD 1957; FRANKLIN 1974, 1983). Within one or two weeks of parturition (one calf per partum) females are in oestrus and may copulate. Females nurse while pregnant, the gestation period is 350 days and nursing period is about 6—8 months (FRANKLIN 1983). Calves weigh approximately 10—15 % of their mother's weight and there is a high frequency of abortion in animals in poor condition in winter (HOFMANN et al. 1983). During the first month of life calves are susceptible to predation by the fox or "zorro", *Dusicyon culpaeus* (KOFORD 1957; FRANKLIN 1974; HOFMANN et al. 1983).

The objectives of this report were to study the vicuñas' mother-offspring relationship including (a) a quantitative description of the interactions in relation to age, (b) evaluation of the differences between mother-calf pairs living in a big semi-enclosure ("field") and a small enclosure free from predators ("corral"), and (c) a characterization of the species in the "following-hiding" classification system of mother-offspring ungulate bonds.

Methods

Study Area

The study was conducted in the Abrapampa Experimental Station of the National Institute of Agricultural Technology (INTA) in 1987. The station is located in a high altitude dry grassland 3475 m above sea level in the puna region of Jujuy Province, NW Argentina. Precipitation occurs during summer, between Dec. and Apr., with a mean annual precipitation of 280 mm. In the dry

winter season, cooler and windy conditions prevail with minimum temperature of −25 °C. Night temperatures are almost always below freezing. Temperature fluctuation is greater daily than seasonally. The vegetation is dominated by *Festuca* sp. and *Distichlis humilis* tall perennial bunchgrasses. Some perennial rhizomatous grasses and several ephemeral forbs occur between bunchgrasses (BERTONI, pers. comm.). The vicuña population comprised approx. 600 animals, held in 4 semi-enclosures (each approx. 100 ha) bordered by a sheep fence (not a barrier for vicuñas). The pasture was natural and a narrow river flowed through the field. One family group was enclosed in a corral of approx. 1.5 ha. This corral had the same ecological structure as the semi-enclosures but it was free from predation risks because it is nearer the station. In the corral, the animals were not provided with artificial food, but were provided with water. As habitat was constant, I will refer to the two types of enclosures as "conditions". The field work was carried out during Feb. and Mar. (during the calves' first month of life, 137 1-h samples) and at the end of Apr. (calves 3 months old, 46 1-h samples).

Observations were made for 8 h each day in the field and in the corral (4 h each). The order in which the sites were visited was alternated in order to control the effect of time of day. Mother-offspring pairs for observation were selected at random.

In the field, observations were made from a wooden observatory hut (6.5 m above ground) with the aid of binoculars 8×30, a telescope Bushnell 20×40, a Camera Canon AE1 with a 500-mm Zikkor lens, and a Casio watch-chronometer. In the corral, observations were carried out from the roof of a nearby house with the same apparatus. Exactly the same sampling methods were used to permit comparison of the data.

A total of 5 mother-offspring pairs were observed. Two pairs belonged to the "corral" family composed of a male, 5 females and 2 offspring, one 8 d old (pair Co-1W) and the other 13 d old (pair Co-2W) at the start of observation. The other 3 pairs belonged to 2 families in the field population. Observations of pair Fi-1W began when the calf was approx. 1 wk old. This pair belonged to a family composed of a male, 3 females and 2 offspring, Fi-NB belonged to the same family and this calf was born during the study. The pair Fi-2W was approx. 2 wk old when observations commenced and belonged to a family composed of a male, 3 females, 1 yearling and an offspring. All the calves and their mothers could be individually recognized using plastic neck collars with an individual number in the corral pairs and natural marks in the field. Thereafter pairs/calves that were 1 or 2 weeks old at the start of observation are referred to either as 1-wk or 2-wk pairs/calves.

Sampling Methods

Scan sampling (ALTMANN 1974) using 1-min intervals for a 1-h sample period, were used to sample:

(a) *Mother-infant distance:* estimated in "vicuñas length" units (V.U.), that is the mean length of a female (approx. 1 m). Five distance categories were used: contact, 1, 2, 3, > 4 V.U.

(b) *Calf-grazing:* calves biting and chewing grass.

Focal-animal sampling (ALTMANN 1974) was used to record the occurrences in 1-h sample of the following interactions between mother and calf: (c) *Suckling:* when the calf's mouth was in contact with the udder of the mother (its duration was measured ± 1 min); (d) *following:* when the mother started to move and the calf moved in the same direction less than 5 s later; (e) *approaches by the mother:* when the movement of the mother resulted in a decrease in the distance from its calf; (f) *rejections of suckling attempts:* when the mother prevented the calf reaching her nipple by stepping or shifted position.

For each suckling bout, a note was made of which member of the pair "initiated" the bout according to which member approached the other in either the min when suckling began or the preceding min. The member of the pair which "finished" each suckling bout was also noted with the criterion that a suckling bout was ended when it was followed by other activities for 20 s.

To characterize the vicuñas' mother-offspring bonds, 3 of the mother-offspring association measures that RALLS et al. (1986) took in various ungulates were used with the Fi-NB pair using data recorded during the calf's first week of life (11 1-h samples): (a) Contact (percentage of 1-min intervals mother and young in contact), (b) < 1ML (percentage of 1-min intervals mother and young were less than 1 mother-length apart), and (c) Walther's measure (number of min mother and young both lying within 1 mother length/total min both mother and young lying × 100).

I made two types of time-dependent comparisons: one between the first and third month ("monthly") in the 5 mother-offspring pairs and another between weeks for 3 wks in Feb. ("weekly") for the 4 pairs that were studied for 3 wks (Fi-1W, Fi-2W, Co-1W, Co-2W). The data consist of counts of events in 1-h periods. Because of the small sample size, each pair was treated individually. Examination showed no obvious relationship between mean and variance, and no transformation of the data was considered necessary. An unbalanced one-way ANOVA (general linear model, SAS) was performed for each behavioral variable and pair, and the "time" was treated as the independent variable.

Results

The mother-offspring interactions were analysed for each pair and the results of the monthly comparison are shown in Fig. 1.

1) Distance between Mother and Calf

In the field, the distance between the mother and the calf was significantly greater in the third month than in the first month and the time they spent within 1 m was correspondingly less. In the corral, the mean distance between mothers and their offspring was approx. 3 V.U. in both months. The calves in the two corral pairs were at a distance of 1 m or less from their mothers and these values were similar in Apr.

In summary, pairs stayed closer together in the field than in the corral in the first month and showed age-dependent variability in the field, but not in the corral.

In the weekly analysis, the only differences that were significant were those between weeks of the 2 pairs that were 1-wk old at the start of observations (calves Fi-1W and Co-1W) (ANOVA calf Fi-1W: df 2, 20; $F = 9.24$; $p < 0.002$; calf 26: df 2, 31; $F = 5.18$; $p < 0.01$) and the number of scans in 1 h the mother-offspring pair were 1 m or less apart decreased (ANOVA calf Fi-1W: df 2, 20; $F = 4.15$; $p < 0.03$ and calf 26: df 2, 31; $F = 3.65$; $p < 0.03$). The mother-calf distance for the corral pairs was always greater than for the field pairs.

2) Mother-calf Interactions

The mother of Fi-NB and both "corral mothers" decreased the frequency of approaches to their calves. The other pairs showed no differences in the "approach by the mother" variable. The behaviour of the one-week corral calf was similar to the 1-wk calf in the field in showing a decrease in the following response in the weekly analysis (ANOVA df 2, 31; $F = 4.42$; $p < 0.0205$). In the Co-2W pair, the mother again played an active role by decreasing the weekly frequency of approaches to the calf (df 2, 30; $F = 3.91$; $p < 0.031$).

3) Lactation

The time spent nursing (min of suckling/h) either remained approx. constant or decreased from Feb. to Apr. Nevertheless, there was a significant difference in nursing time on a weekly basis when comparing the field and corral calves at 1 wk (calf Fi-1W: df 2, 20; $F = 5.06$; $p < 0.02$ and calf Co-1W: df 2, 31; $F = 3.33$; $p <$

0.05). Of these calves, the field calf (Fi-1W) spent approx. twice the time nursing as the corral calf. Two predictions based in the parent-offspring conflict model were tested (1) the mother will reject more suckling attempts in Apr. than in Feb.

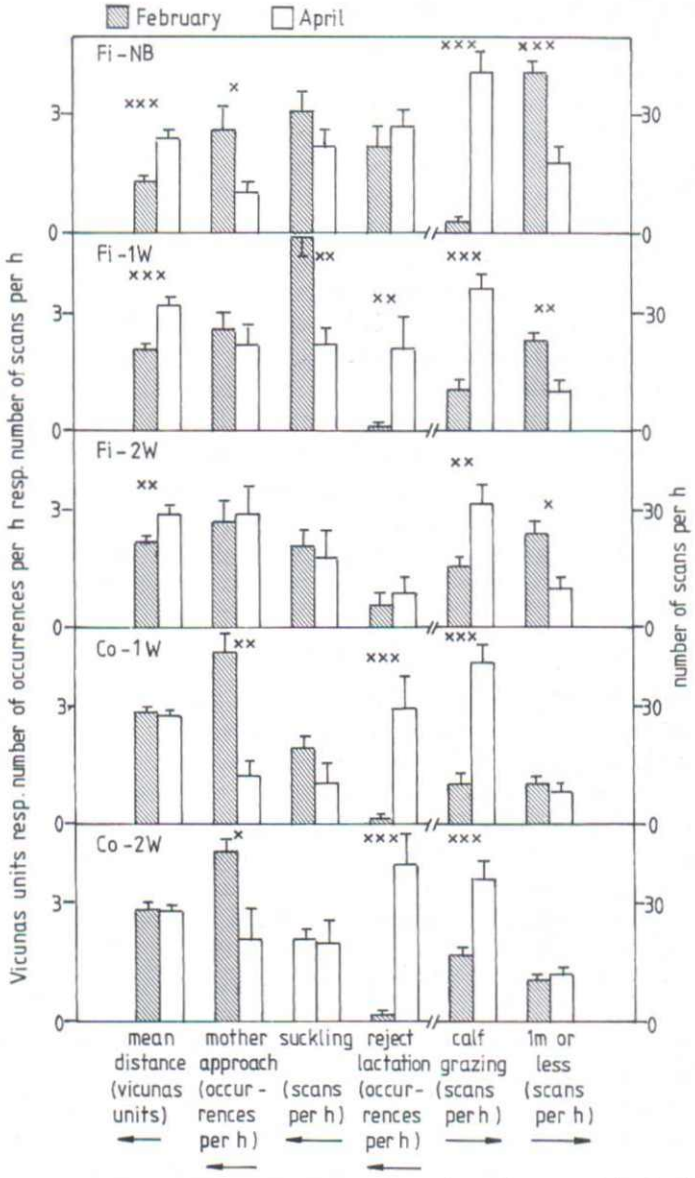

Fig. 1: $\bar{x}$ and SE of some variables analysed, in each mother-offspring pair in the first and third month: Mean distance in 1-h sample, number of scans in which mother and offspring were 1 m or less apart, the calf was grazing or suckling, number of occurrences of mother approaches to the calf and reject lactation in 1-h sample. For "1 m or less" and "calf grazing" right scale, for other variables left scale (arrows). Statistical comparison with a general linear model, unbalanced one-way ANOVA. $^{\times}: p < 0.05$, $^{\times\times}: p < 0.005$, $^{\times\times\times}: p < 0.0005$

and (2) the mother will tend to end the suckling bouts more frequently in Apr. than in Feb. The mothers behaved as expected according to the first prediction by increasing the frequency of rejections of suckling attempts from Feb. to Apr. This was especially marked in both the corral and one calf in the field.

The mean percentage of suckling bouts initiated by the calves/total bouts was 84.7 (SD = 7.6) in Feb. and 93.5 (SD = 8.3) in Apr. with no differences between months, in either the corral or the field (1st month vs. 3rd month $X(1) = 2.52$; $p > 0.05$ and corral vs. field $X(1) = 1.34$; $p > 0.05$). The percentage of bouts terminated by mothers was significantly lower in Feb. (58.8 %; s = 4.6) than in Apr. (95.5 %; s = 8.9). [$X(1) = 14.77$; $p < 0.001$]. There were no differences between field and corral [$X(1) = 0.13$; $p > 0.05$].

In all the pairs the number of scans in which the calves were grazing in 1 h increased sharply in the third month. Calves also showed this change on a weekly basis in the field (calf Fi-1W: df 2, 20; $F = 5.78$; $p < 0.010$, and calf Fi-1W: df 2, 20; $F = 3.61$; $p < 0.05$) but not in the corral where they maintained a high level of grazing from the beginning.

4) Characterization of Vicuña Mother-offspring Pair

The results of the RALLS et al. (1986) measurements in this vicuñas' study were: (a) Contact: 7.7 %. (b) < 1ML: 82 % and (c) Walther's measure: 99.2 %. These results show that vicuñas belong to the "follower" type.

Discussion

The distance between the mother and the calf plays an important role in their relationship because the vicuña mother mobs predators in the breeding season (FRANKLIN 1983), and during the first month of life, when calves are susceptible to predation by *Dusicyon culpaeus* (KOFORD 1957; FRANKLIN 1974; HOFMANN et al. 1983). Two calves killed by *Dusicyon* were found during this study in the field.

Vicuñas belong to the follower type. The follower pattern was shown by calves not having a hiding place and by a gradual increase in the distance between mother and calf. A similar pattern was described in another camelid, the camel (*Camelus bactrianus:* GAUTHIER-PILTERS & DAGG 1981 cited by RALLS et al. 1986). As was expected for this follower-type strategy, following was observed only in the 1-wk calves and gradually decreased with age. The degree of association between mothers and calves during the calves' first week of life was used by RALLS and collaborators to characterize 22 species of ungulates on a scale from "strong following-type" to "strong hiding-type". They showed that mother-offspring associations were species specific. In the present study, Walther's measure and < 1ML (Lent's index) strongly indicate that vicuñas belong to the follower type. Although time mother-offspring were in contact was low, the time mother and offspring were near was very high.

The changes in the frequency and duration of the interactions between mothers and calves followed the mother-offspring conflict model expectations, with mothers approaching less to their calves as the calf matured. By actively

allowing or preventing suckling mothers affected the rate (rejecting suckling attempts) and the duration (terminating 95.5 % of the bouts in Apr.) of suckling. This change in the behaviour of the mother has been observed in other ungulate studies. BYERS & MOODIE (1990) found that pronghorn mothers terminated 91 % of the suckling bouts in the week 7 and GAUTHIER & BARRETTE (1985) found a similar pattern with mothers terminating 100 % of the bouts in the 2-month old calves in white tailed deer and fallow deer.

There are some difficulties in measuring milk transfer because suckling rate and duration are not always proportional to intake of milk by the calf (MENDL & PAUL 1989; BABBITT & PACKARD 1990). This problem is important when comparing different mother-offspring pairs of the same age but can be minimized by observing changes in lactation with time in individual mother-offspring pairs (MENDL & PAUL 1989).

The activity cost of follower-type neonates may be greater in free ranging than in captive animals (CARL & ROBBINS 1988) and this may explain the differences in total amount of lactation in the 1-wk old calves in the field and in the corral. These differences could also be attributed to differences between individuals (MENDL & PAUL 1989).

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