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ARTICLE

Maternal behavior and early development of pampas deer (*Ozotoceros bezoarticus*) fawns in a semi-captive environment

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Abstract Maternal–infant interaction and behaviors are adapted to reduce the risk of predation and increase the probability of survival of the species. We determined how mother–young encounters and communication change by the development of the fawn (locomotion and feeding) throughout lactation in pampas deer (*Ozotocerus bezoarticus*). We registered the behavior of mother–fawn dyads for the first 60 postnatal days. Our results revealed three main developmental stages in the fawn, *hiding* (~0–19 days), *active* (~20–39 days), and *adult-like* (~40–60 days). In the *hiding* stage, the fawn stayed hidden, closer to the mother, and spent less time active, the mothers vocalized more often than the fawn, licked the fawns intensively while nursing, and were responsible for initiating nursing. In the *active* stage, licking behavior and vocalizations of the mother decreased while the fawns ate solid food, initiated nursing bouts, and displayed bursts of running activity. Finally, in the *adult-like* stage, the fawn showed many signs of nutritional weaning, and similar patterns of activity to their mothers. However, the duration and frequency of nursing bouts were unchanged during the study. We described mother–fawn interaction in pampas deer for the first time, and found that increased running activity in fawns anticipates nutritional weaning. Our results also suggest that to adapt to the development of the fawn, mothers only modify the dynamics of interaction and encounters rather than the time invested in nursing, an activity that also plays a role in maintaining mother–young affiliation.

Keywords Activity · Cervid · Development · Grazing · Licking · Nursing · Vocalization

Introduction

Maternal behavior varies widely among mammals, even among closely related species (Ralls et al. 1986, 1987; González-Mariscal and Poindron 2002; Fisher et al. 2002; Numan et al. 2006; Olazábal and Young 2006). One aspect that varies significantly in ungulates with precocious offspring is the type of mother–young interaction. For example, ungulates spend long periods of time with their newborn during the first hours after parturition. However, after the first hours of life, there is variation in the length of time mother and young spend together, and their patterns of behavioral interactions and encounters (Lickliter 1984; Ralls et al. 1987). Ungulates are generally described as followers or hiders (Ralls et al. 1986, 1987; Schwede et al. 1994). In followers, mothers lead their offspring and are followed by them as she moves with conspecifics of their group (horse, sheep, reindeer; Nowak et al. 2007). This is hypothesized to be an adaptation to avoid predation in open habits by group vigilance and defense (Ralls et al. 1986). In other species, the pattern of behavioral interaction is adapted to protect the young from predators while the mothers are foraging (Hirth 1985; Fisher et al. 2002). That is the case of "hider" species, in which the newborn stays hidden for several days, before starting to follow her

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mother or graze with her (goat, most deer). During this hiding stage, the mother returns periodically to feed her offspring (Ralls et al. 1986).

However, hiding appears to be more extreme in some deer species than others, with significant variability in the duration of the hiding period, and with some species also behaving as followers after hiding for a few days (Gauthier and Barrette 1985). This variation may be a consequence of species-specific strategies to avoid predation that include different locomotor and feeding development of the fawn throughout lactation, and different adaptation to these changes by the mother. How these mechanisms of adaptation and regulation of encounters in 'hider' species change throughout lactation is not well understood. Unfortunately, most studies on maternal behavior in free-range, captive, or laboratory animals have focused mainly on the immediate postpartum period, while relatively few have investigated adaptation of mother–offspring interactions throughout the lactational period (Gauthier and Barrette 1985; Cramer et al. 1990; Gerrish and Alberts 1997; Daleszczyk 2004; Pereira and Morrell 2011).

In the present study, we investigated the pampas deer (*Ozotocerus bezoarticus*), a species in which mother–infant interaction was completely unknown. We made the first comprehensive investigation in ungulates that explored not only mother–infant mechanisms of interaction throughout lactation but also their relationship with the locomotor and feeding development of the fawn, which has also been hypothesized to predict the initiation of weaning (Campbell et al. 1969; Gerrish and Alberts 1997).

Gregariousness, formation of large herds, living in open habitats, and delayed weaning are commonly associated with following behavior as adaptations to avoid predation in ungulates (Fisher et al. 2002). Although there is scarce information on pampas deer life history, their populations have been reduced by human hunting and predators (e.g., fox, and wild dogs and boars, Pérez Carusi et al. 2009), and also displaced from their territories by agriculture activities and competition with farm animals (e.g., cattle, sheep; Demaría et al. 2003). They currently live in closed habitats and in solitary or small family or male groups (2–9) that occasionally form larger associations (Cosse 2010; García Pereira et al. 2006). According to the hypothesis of adaptation of mother–infant interaction to avoid predation, we hypothesized that pampas deer would have a classic hiding phase, followed by the quick development of nutritional independence and locomotor capabilities that would anticipate the early nutritional weaning. On the other hand, mothers would adapt to the development of the fawn by playing a passive role in nursing, but maintaining affiliative encounters until complete behavioral independence and dispersion.

Materials and methods

Animal management

The pampas deer (*Ozotocerus bezoarticus*) is a South American deer threatened with extinction (González et al. 1998; Ungerfeld et al. 2008; CITES 2012; UICN 2012). There is a small semi-captive population of 80 individuals in the Estación de Cría de Fauna Autóctona Cerro Pan de Azúcar (ECFA), Uruguay (González et al. 1998; Ungerfeld et al. 2008). They live in open grassland areas that were reduced and transformed in recent decades mainly by livestock activity and agriculture (Demaría et al. 2003).

The ECFA is located in Uruguay's SE coast (33°47′S, 54°00′W; altitude ∼200 m), 6 km from the coast. The animals are organized into 4 breeding groups composed of one adult buck and 5–10 does, which are run together throughout the year in 0.50- to 1-ha paddocks with abundant vegetation, shrubbery, and small trees. The animals graze on native pasture and also receive dairy cow rations (Molinos San José, Uruguay) ad libitum (approximately 600 g of rations/deer/day). Rations contain a minimum of 16 % protein and 2.5 % ether extract, and a maximum of 12.5 % humidity, 12 % crude fiber, 9 % total minerals, 2 % HCl insoluble ash, and 0.6 NaCl, 1.4–0.9 % calcium, 0.9–0.6 % phosphorus, and supplements. All adults were tagged before the study began, and fawns were identified with different colored chalk marks on the inside and outside of the ear 1–2 days after birth until they were permanently tagged at approximately 3 weeks of age.

Data were recorded from October to February (spring/summer, temperature range 10–33 °C), the period during which most births are usually observed (Ungerfeld et al. 2008). All pregnant females in the population were inspected for signs of delivery each morning. Animals are not manipulated in any way and parturition occurs naturally in the field. After birth, the behavior of each mother–fawn dyad was recorded during 4 h of observations during each of the first 2 days post-partum, 2 h in the morning between 0700 and 1200 hours, and 2 h in the afternoon, between 1400 and 2000 hours to cover at least two long periods of the day when behavior might change (sunrise 0600–700, sunset 1900–2000 hours). From day 3 to day 60, the behaviors of each dyad were recorded for 1 h in the morning and a second hour in the afternoon. Two observers experienced in the behavior of deer recorded a range of parameters from a distance of approximately 10 m: duration of licking, frequency of vocalizations by mother or fawn, duration and frequency of nursing (i.e., when the fawn suckled for at least 3 s.), time spent feeding (i.e., ingesting grass or rations), approximate distance between mother and fawn (duration at a distance ≤ 1, ~ 2–4, ~ 5–7 or >7 m), time spent walking (slow displacements of at least 1 m) or running, and time spent lying down or standing, respectively, were also recorded. We also analyzed the behaviors that immediately preceded or followed nursing, vocalizations, licking, and approaches (defined as walking toward the other member of the dyad from a distance >4 m to within <1 m). All behaviors were manually recorded on pre-coded sheets.

Data analysis

To examine changes in mother–fawn interactions across time, and after a previous analysis showed no significant differences among days within each interval, data were grouped into 12 4-day intervals: days 1–4, 5–9, 10–14, 15–19, 20–24, 25–29, 30–34, 35–39, 40–44, 45–49, and 55–60. Overall, data from 13 dyads (3 male and 10 female fawns) were recorded, although some of them not during all the defined periods. Behavioral records for at least 4 and as many as 13 dyads were obtained during each interval. Bad weather, and the overlap of behavioral observations corresponding to different temporal intervals, were the main reasons for variability in the numbers of dyads observed among the defined periods.

Multiple behavioral observations of one animal for that interval were averaged and data shown as percentage of time spent performing that particular behavior in 1 h of observation. Intervals with no significant differences among them were grouped for further comparisons. Data of mothers or fawns for all intervals were analyzed using ANOVA repeated measures and post hoc tests, if they passed the homogeneity of variance test (distances between mother and fawn, and time lying, standing, walking, or running), or Friedman followed by Wilcoxon non-parametric test, if not. To compare mother versus fawn within each interval we used paired *t* test or Wilcoxon Signed Ranks. A correlation matrix was used to reveal associations between all pairs of variables. Percentage of occurrence of events was compared using Chi-square. Data are expressed as mean ± SE or median (SIQR) according to the statistic test used. The significance level was $p < 0.05$.

Results

Fawn motor development

Percentage of time the fawn spent resting, standing, or active

Fawn spent significantly more time resting during the intervals 1–4, 5–19, and 20–39 ($F_3 = 5.3$, $p = 0.005$), compared to the interval 40–60 ($p = 0.001$, $p = 0.003$, $p = 0.046$, respectively). Fawns also spent less time standing (walking and running not included in this variable) during the intervals 1–4, 5–19, 20–39 ($F_3 = 6.2$, $p = 0.002$), compared to the interval 40–60 ($p = 0.001$, $p = 0.001$, $p = 0.046$, respectively, Table 1).

Table 1 Pattern of activity during the first 60 postpartum days

Postpartum days	1–4	5–19	20–39	40–60
Distance between mother (M) and fawn (F) (% of total time)				
<1 m	10 ± 3	10 ± 2	10 ± 2	11 ± 2
2–4 m	16 ± 5 a	11 ± 3	10 ± 3	7 ± 2
5–7 m	39 ± 6 b	20 ± 5	17 ± 4	13 ± 5
>7 m	35 ± 7 b	59 ± 6 a	63 ± 6	69 ± 5
Time lying, standing, walking and running (% of total time)				
Lie M	48 ± 6	48 ± 4	56 ± 7	56 ± 6
Lie F	85 ± 6*	82 ± 4*	72 ± 2*	63 ± 5 b
Stand M	24 ± 5	29 ± 4	21 ± 4	22 ± 4
Stand F	5 ± 2*	6 ± 2*	10 ± 2*	18 ± 4 b
Walk M	20 ± 3	17 ± 3	15 ± 4	20 ± 5
Walk F	7 ± 5 a*	6 ± 1 a*	11 ± 1	16 ± 2
Run M	0.2 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.1
Run F	0.1 ± 0.1	0.5 ± 0.1	2.4 ± 0.7 b*	0.9 ± 0.3

Significant difference (ANOVA repeated measures) between the group with the letter ‘a’ versus 40–60 ($p < 0.05$) tested separately (no significant difference was found among the other intervals); significant difference (ANOVA repeated measures) between the group with the letter ‘b’ and all other intervals ($p < 0.05$) tested separately (no significant difference was found among the other intervals). Data expressed as mean ± SE

* $p < 0.05$ significant difference (*t* test) between mother and fawn for that interval

The time spent running differed among the four intervals ($F_3 = 5.2$; $p < 0.01$). Fawns spent more time running in the interval 20–39 (maximum peak at days 25–29) compared to the intervals 1–4, 5–19, or 40–60 ($p < 0.\ 01$, $p < 0.01$, $p = 0.04$, Fig. 1). The time spent walking was not significantly different among the intervals ($F_3 = 2.4$; $p = 0.08$), but comparisons between two groups revealed some differences. Fawns spent more time walking during the interval 40–60 compared to the interval 1–4 and 5–19 ($p = 0.04$, $p = 0.02$, respectively). Combining walking and running as locomotor activity revealed that there was an increase in locomotor activity at the interval 20–39 that remained unchanged at the period 40–60.

Comparison of mother and fawn time spent resting, standing, or active

Fawns spent more time lying in the grass and less time standing than mothers during the intervals 1–39 days ($p < 0.05$; Table 1). Mothers walked more than fawns during the interval 1–19 ($p < 0.01$). No difference was found between mother and fawn walking in the interval

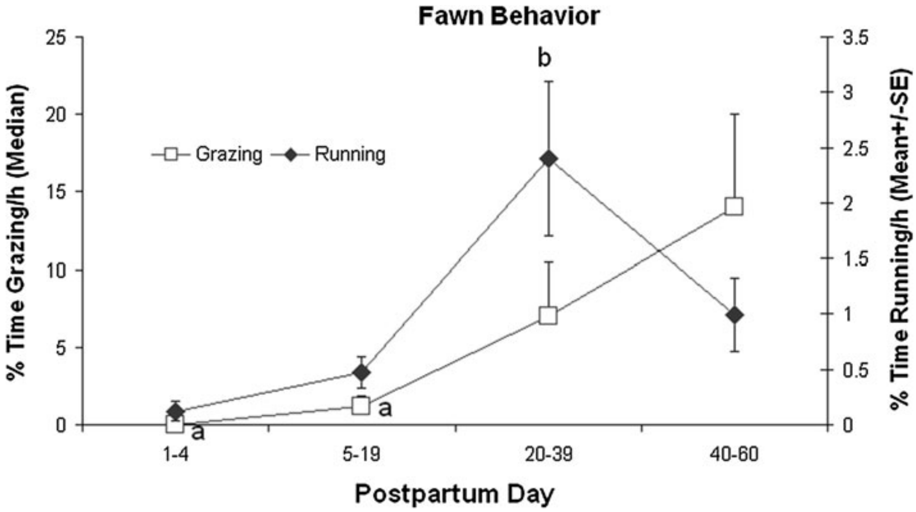

Fig. 1 Percentage of total time the fawn spent running and grazing during the first 2 months after parturition (*a* $p < 0.01$ significant difference between intervals 1–4, 5–19 vs. 20–39, 40–60; *b* $p < 0.05$ significant difference between interval 20–39 vs. 1–4, 5–19, and 40–60)

20–39 (Table 1). Fawns spent more time running than mothers in the interval 20–39 ($p < 0.01$). Before and after that interval, there was no difference in the time mothers and fawns spent running. No difference was found in the pattern of locomotor activity of mothers and fawns at the interval 40–60.

Fawn feeding development

Percentage of time the fawn spent feeding

During the intervals 1–19, fawns grazed less (Chi-square = 15, $p < 0.01$; Fig. 1) compared with the intervals 20–39 ($p < 0.01$) and 40–60 ($p < 0.01$, Table 2). Fawns also ate less rations (Chi-square = 9, $p < 0.01$; Table 2) in the intervals 1–19, compared to the intervals 20–39 ($p < 0.05$) and 40–60 ($p = 0.01$; Table 2). The time spent eating rations was also lower in the interval 20–39 compared to the interval 40–60 ($p < 0.05$).

The time spent ruminating was not significantly different among the intervals (Chi-square = 6.6; $p = 0.08$), but comparisons between two intervals also revealed some differences. Time spent ruminating was lower in the intervals 1–4 (0 [0], median [SIQR]), 5–19 (0 [0]), and 20–39 (0.9 [0.6]) compared to interval 40–60 (2.6 [1]; $p = 0.03$; $p = 0.03$, $p = 0.03$, respectively). There was no difference in the time ruminating among the intervals 1–4, 5–19, or 20–39. Seven of 13 fawns were grazing by day 7 while none of them was observed eating rations ($p < 0.5$). A fawn was first observed eating cattle rations by day 15.

During the first 2 months of life, fawns were nursed with a frequency of 0 [0.5] times per hour, and brief nursing bouts (16 [20] s, median [SIQR]). The time the fawn suckled in an hour of observation varied from 0 to 7 min. No difference was found in the time the mother spent nursing, among the intervals 1–19 (0.89 [0.5], median [SIQR]), 20–39 (0.6 [0.35]), and 40–60 (0.8 [0.3]) (Fig. 2). Frequency of nursing bouts was not different among the four intervals (data not shown).

Table 2 Pattern of feeding during the first 60 postpartum days

Postpartum days	1–19	20–39	40–60
% of time spent by mother (M) and fawn (F) feeding solid			
Graze M	18 [5]	19 [6]	23 [9]
Graze F	0.9 [0.5] a*	7 [3.5]*	14 [6]
Ration M	3.2 [2.5]	8 [4]	8 [6]
Ration F	0 [0] a*	0 [0.3] b*	2.5 [2.5]

Significant difference between group with the letter 'a' and the intervals 20–39 and 40–60 ($p < 0.05$) tested separately; significant difference between group with the letter 'b' and the interval 40–60 ($p < 0.05$). Data expressed as median [SIQR]

* $p < 0.05$ significant difference (Mann–Whitney) between mother and fawn for that interval

Comparison of feeding behavior of mother and fawn

Mothers spent more time grazing, eating rations, and ruminating (data not shown) than fawns during the intervals 1–19 and 20–39 ($p < 0.03$; Table 2). The pattern of solid feeding in mothers and fawns was not significantly different at the interval 40–60. Mothers and fawns spent longer foraging on grass than on cattle rations during all intervals (Table 2).

Changes in mother–fawn behavioral interactions

Distances and reunions between mother and fawn

During the first 4 days post-partum, mothers and fawns were closer than during subsequent days, staying within a distance <7 m (Table 1; $p < 0.005$). During the interval

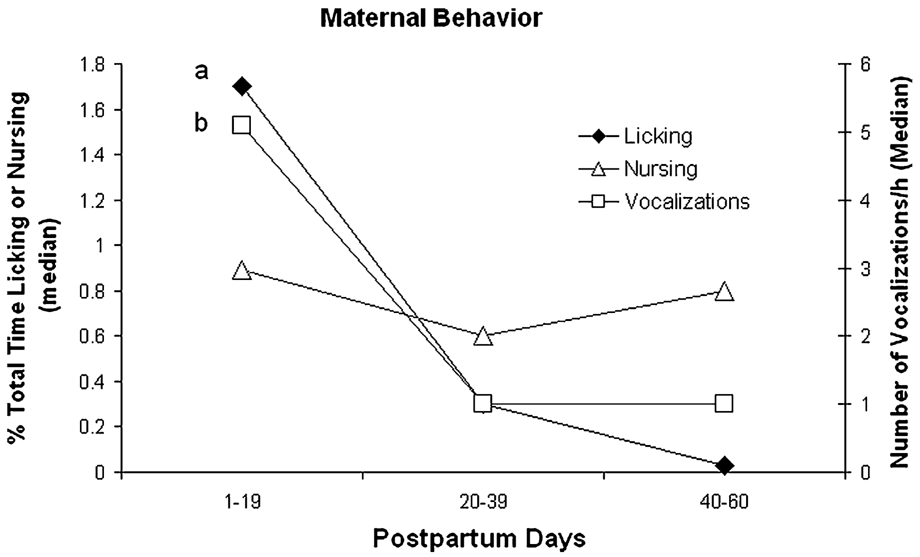

Fig. 2 Number of vocalizations and percentage of total time (1 h) the mother licked and nursed the fawn during the first 2 months after parturition (*a* $p < 0.05$ significantly different compared to interval 40–60; *b* significantly different to interval 20–39)

5–19, mothers and fawns were also closer compared to the distance at the interval 40–60 ($p = 0.02$). There was no difference in the distance between mother and fawn in the intervals 20–39 and 40–60. At these two intervals, mothers and fawns spent most time more than 7 m apart. When fawns approached mothers, nursing was the most common behavior that followed (44.4 % of behavioral events). In contrast, when the mother approached the fawn, the behaviors that most commonly followed were vocalizations of the mother (21.9 %), approaches of the fawn (12.5 %), nursing (15.6 %), and licking (18.8 %).

Time the fawn spent licking the mother and frequency of vocalizations

There was no difference in the time the fawn spent licking the mother, or in the number of vocalizations among the four intervals (data not shown). The fawn licked mostly the head (69 %), the body (26 %), and the anogenital region (5 %) of the mother.

Time the mother spent licking the fawn and frequency of vocalizations

The time the mother spent licking revealed a significant difference among the intervals 1–19 (1–4 and 5–19 combined), 20–39, and 40–60 days. Mothers licked the fawn for longer periods of time (Chi-square = 6, $p = 0.04$) during the interval 1–19 (1.7 [1.1]) compared to 40–60 (0.03 [0.3], $z = -2.2$, $p = 0.03$). The comparison between intervals 1–19 and 20–39 (0.3 [0.6]) did not reach significance level ($z = -1.9$, $p = 0.06$). No difference was observed between the interval 20–39 and 40–60 ($z = -0.65$, $p = 0.52$; Fig. 2). The mothers licked mostly the anogenital region (62 %), although they also licked the head (19 %), body (18 %) and limbs (1 %) of the fawns.

The time the mother nursed the fawn was correlated with the time she licked it (rho = 0.66, $p < 0.05$). The mother and fawn licked each other during all 4 intervals. The mother licked the fawn more often than the fawn licked the mother during the intervals 1–19 and 20–39 ($p < 0.05$). Licking behavior received by both mothers and fawns was correlated with the frequency of vocalizations of fawns (rho 0.58 and 0.56, respectively, $p < 0.05$). The duration of licking by fawns also correlated with the duration of licking by its mother (rho 0.60, $p < 0.05$). The most common behaviors observed immediately after licking behavior by either member of each dyad was nursing (49 % of total behavioral events when mother licked the fawn and 54.6 % when the fawn licked the mother). This behavioral association changed significantly between days 1–10 and 20–60 ($p < 0.05$, Chi-square). Nursing followed licking by the mother in 68.8 % of observations 1–10 days postpartum but this association declined to 33.3 % during the interval 20–60. When the fawn licked the mother, nursing occurred during 100 % of observations during the interval 1–10 days but declined to 37.5 % of observations 20–60 days post-partum ($p < 0.05$).

There was a decline ($z = -2.43$, $p = 0.02$) in the frequency of vocalization of the mother in the interval 1–19 (5.1 [4]) and 20–39 (1 [1.3]). The other groups were not significantly different from each other (1–19 vs. 40–60 (1 [0.7]), $z = -1.5$, $p = 0.13$; 20–39 vs. 40–60 $z = 0.08$, $p = 0.92$; Fig. 2). Mothers vocalized more frequently (5.1 [4]/h low-pitched) than the fawn (0.2 [0.3]/h high-pitched) during the period 1–19 days ($p < 0.02$), but not in the interval 20–39 ($z = -1.8$, $p = 0.06$; 1 [1.3], 0.3 [0.2], respectively) or 40–60 ($z = -0.65$, $p = 0.52$; 1 [0.7], 0

[0.7], respectively). The most common behaviors observed immediately after the vocalization of the mother were the fawn standing (18 % of total behavioral events), the fawn approached her (11 %), nursed (11 %), and the mother approached the fawn (10 %). The most common behaviors observed immediately after the vocalization of the fawn were the approach of the mother to the fawn (29 %) and the approach of the fawn to the mother (21 %).

Discussion

The present study shows how mother–fawn interaction and communication qualitatively and quantitatively change as the pampas deer fawns develop locomotor and nutritional maturity. To our knowledge, this is the first comprehensive study that has investigated the relationship of locomotor and feeding development of the young with mother–offspring interaction throughout lactation in ungulates. In particular, mother–fawn interaction in pampas deer was completely unknown. We show for the first time that this species is a strong hider with clear developmental hallmarks that modify mother–fawn interactions, likely adapted to maintain affiliative relationships while reducing the risk of predation. The observed behavioral changes can be summarized in three developmental stages that we termed hiding, active-dependent, and adult-like. During the initial, approximately 19, post-partum days, pampas deer fawns exhibited classic "hiding" behavior (Lickliter 1984; Gauthier and Barrette 1985; Ralls et al. 1987; Dwyer and Lawrence 2000; Daleszczyk 2005), spent more time hiding and resting, displayed lower locomotor activity, fed mostly by nursing, received intense anogenital licking, and remained in close proximity to their mothers who vocalized, calling them for reunions. The period 20–39 days of age, the "active-dependent" stage, was characterized by increased mobility, feeding on solid food, active initiation of nursing by fawns, reduced proximity to mothers, and less vocalization by mothers. From 40 to 60 days, the "adult-like stage" anticipated weaning and was characterized by the fawns gradually exhibiting patterns of mobility and feeding similar to their mothers. Boundaries between these developmental stages are not absolute but we found them useful for describing the major changes presented in mother–fawn interaction and encounters during the first 2 months post-partum.

During the first week of the hiding stage, hypothesized to be an adaptation to avoid predation (Ozoga and Verme 1986; Schwede et al. 1994), the mother also maintained a short distance to the fawn which may represent a period of guarding. The very low frequency of vocalizations shown by the fawns is also likely an adaptation to reduce detection by predators during that vulnerable period. The higher frequency of vocalizations by the mother during the hiding stage probably reflects the main mechanism of starting the encounters. As in goats and sheep (Lickliter 1984; Searby and Jouventin 2003; Sèbe et al. 2008), fawns may recognize their mothers based on vocal cues. Whether the pampas deer mother can also recognize the vocalization of her fawn, as in other ungulates (reindeer and sheep; Espmark 1971; Nowak et al. 2007; Sèbe et al. 2008); is unknown. The most commonly observed sequence of events during the hiding period was that the mother vocalized, the fawn stood up, mother and fawn approached and licked each other; and then nursing occurred. This sequence was repeated several times in a day during the hiding phase. Therefore, during the first days, Pampas deer mothers establish the frequency of nursing bouts by actively looking for the fawn (Gauthier and Barrette 1985). The decline in the frequency of vocalizations of the mothers, increased mobility of fawns, and increased grazing suggested that the hiding phase ends after 2 weeks, as in reindeer (*Rangifer tarandus*), and somewhat longer than in axis (*Axis axis*, ~10 days) and red deer (*Cervus elaphus*, ~4 days) as reviewed by Van Mourik (1986). These differences might be due to many factors such as the different pattern of locomotor or feeding development in each species, or differences in the time taken by fawns of different species to be incorporated into the herd in more gregarious species.

Anogenetical licking by mother deer is thought to stimulate defecation by newborn fawns and also reduce odors, which could attract predators (Gauthier and Barrette 1985). However, our results (e.g., high correlation of mother and fawn licking) also suggested that mutual licking (fawn to mother and mother to fawn) of body and head, and probably also olfaction and vocalizations (as in other ungulates; Lévy et al. 2004), may contribute to mutual recognition and bond of mother and fawn during the first post-partum weeks.

After the third week, the frequency of licking exchanges while nursing declined as shown by previous studies in ungulates (Daleszczyk 2004; Gauthier and Barrette 1985). As the duration or the frequency of nursing bouts did not change, perhaps licking was less needed during nursing at the end of the first month because the mother–offspring bond was strongly established by this time and the risk of predation controlled differently.

By the third week post-partum, vocalizations of the fawn were often followed by approaches of the mother. At this time, the fawn spent more time standing and actively walking longer distances, perhaps reflecting the maturation of a new strategy to avoid predation, alertness and escaping. This is similar to the age at which fawns of white-tailed (*Odocoileus virginianus*) and fallow deer (*Dama dama*) exhibited increased mobility and actively solicited nursing opportunities from their mothers (Jackson et al. 1972; Gauthier and Barrette 1985). Jackson et al. (1972) also found a peak of running activity around age 25 days that resembled the bursts of running activity observed in our study. The increased running behavior in our study was sustained for more than 10 days, was not associated with changes in activity of the mother, and appeared to reflect a characteristic developmental hallmark of many ungulates (Muller-Schwarze 1968; Jackson et al. 1972). Jackson et al. (1972) and Muller-Schwarze (1968), studying white-tailed and black-tailed deer (*Odocoileus hemionus columbianus*), respectively, characterized bursts of activity at this stage of development (starting at 20–30 days of age) as play behavior. In our study, this burst of running activity resembled play behavior but did not include interactions with other fawns. As in other solitary deer species, fawn social interaction was restricted initially mostly to the mother. The biological implications of these bursts of running activity of fawns warrants further study, especially given its importance for understanding space and social needs of pampas deer fawns. However, the sequence of events observed in our study did not support the earlier hypothesis of Gerrish and Alberts (1997) who proposed that bursts of play or running activity in rodents occurred more often after suckling, as a natural mechanism to increase exploration and likelihood to consume solid food prior to weaning. In our study, there was already significant consumption of solid food before bursts of activity began, and running was not associated with the end of a nursing bout.

Our interpretation is that there is a developmental process characterized by increased play and running activity associated with, and anticipating, weaning and nutritional independence from the mother. However, complete behavioral weaning might occur long after fawns can clearly survive without milk (L'Heureux et al. 1995), as suggested by occasional observation of 5- to 6-month-old pampas deer fawns suckling from their mothers. Nursing after 2 months seems to have more of an affiliative than a nutritional function.

We found no significant difference in mobility or any other variables of mothers and fawns at 40–60 days, which suggests that fawns reached adult pattern of mobility and feeding near that age, and earlier than 4 months, the hypothesized age of locomotor maturation for white-tailed deer and bison (Jackson et al. 1972; Daleszczyk 2004). However, those studies did not compare or record walking/running activity of young and adults. Considering the early age of weaning (1 month) proposed by Gauthier and Barrette (1985) for white-tailed deer, we think it is unlikely that locomotor maturation occurred 3 months after weaning.

This study shows how maternal behavior and mother–fawn interaction change dynamically adapting to the growing fawn. This adaptation is not costly for the mother and optimally reduces the risk of predation and permits the frequent mother–fawn encounters that maintain nursing and bond. Future studies should be focused on describing in more detail how and when changes in the timing and frequency of nursing occur, and the dynamic of the dyad in terms of the recognition and response to mother and fawn calls. Finally, the information presented in the current paper is also very valuable for the optimal breeding and maintenance of this species at risk of extinction in semi-captive environments or protected areas. Current management in zoos and reservations (i.e. artificial rearing of abandoned fawns) is based on information provided by studies in other ungulates or cervids.

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