Revista de Etologia 2001, Vol.3, N°2, 129-136

Suckling Behaviour in Water Buffalo (*Bubalus bubalis*): Development and Individual Differences

ARTUR ANDRIOLO[1], MATEUS J.R. PARANHOS DA COSTA[2] AND WERNER R. SCHMIDEK[3]

[1]*Universidade de Juiz de Fora, Minas Gerais*
[2]*Universidade Estadual Paulista, Jaboticabal, São Paulo*
[3]*Faculdade de Medicina - USP, Ribeirão Preto, São Paulo*

Suckling behaviour was studied in 29 cows of Murrah-Mediterranian phenotypes and their respective calves, for 10 months. The suckling frequency and duration of females and the attempts made by calves to suck were recorded. The calves were constantly interested in the females, especially their own mothers, during the suckling period. Weaning was a gradual process: frequency and duration of suckling episodes decreased regularly during the development of the calf. Significant differences among females in their tolerance for collective filial suckling were observed and such individual differences were stable over a period of time. The calves also evidenced stable individual differences when trying to suck females other than their mothers. It can be inferred that females, being the providers of the resource, are modulators of the nursing process and that calves behave from birth, to maximize milk obtainment.

Index terms: Water buffalo. Suckling. Allosuckling. Development. Individual differences. Bubalus bubalis.

Comportamento de amamentação do Buffalo (*Bubalus bubalis*): desenvolvimento e diferenças individuais. O comportamento de amamentação em 29 fêmeas de búfalo das raças Murrah-Mediterrânia e seus respectivos filhotes foi estudado durante 10 meses. As fêmeas e seus filhotes foram observados, e seus comportamentos relacionadas à amamentação registrados. Os bezerros apresentaram um interesse constante pelas fêmeas, principalmente pelas suas próprias mães, durante o período de amamentação. A freqüência e a duração dos episódios de amamentação decresceram regulamente durante o desenvolvimento dos bezerros; o desmame ocorre portanto de maneira gradual nessa espécie. Diferenças individuais significativas foram encontradas entre as fêmeas que permitiam a amamentação coletiva, indicando a existência de graus diferentes de tolerância das fêmeas para a amamentação coletiva. Os bezerros também apresentaram diferenças individuais estáveis quando tentavam mamar em fêmeas que não suas próprias mães. Conclui-se que as fêmeas, como provedoras do recurso, modulam o processo de amamentação e que os bezerros, desde o nascimento, são ativos na tentativa de maximizar a obtenção de leite.

Descritores: Búfalo. Amamentação. Aloamamentação. Desenvolvimento. Diferenças individuais. Bubalus bubalis.

Riedman (1982) and Packer, Lewis, and Pusey (1992) listed approximately a hundred mammalian species that exhibit alloparental care. Alloparental care has been discussed in more detail by Bygott, Bertram, and Hanby (1979) in lions (*Panthera leo*); Lee (1987) in elephants (*Loxodonta africana*); Sayler and Salmon (1971) and König (1993) in mice (*Mus*

Artur Andriolo, Depto. de Zoologia, Instituto de Ciências Biológicas, UFJF, Campus Universitário, 36036-330, Juiz de Fora, MG, Brasil; andriolo@icb.ufjf.br Mateus J.R.P. Costa, ETCO – Grupo de Estudos e Pesquisas em Etologia e Ecologia Animal, Brazil. W. Schmidek, Depto. de Fisiologia da FMRP-USP, Ribeirão Preto, 14049-900, Brazil.

This study resulted from a Master Thesis. We thank the administrator José Fernando Simplício de Oliveira and all employees of the Estação Experimental de Zootecnia do Vale do Ribeira whose invaluable assistance to made this project possible. We also would like to thank Humberto Giusti and Roberto Carlos de Souza for the technical assistance. This research was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo and Fundação para o Desenvolvimento da Universidade Estadual Paulista.

musculus); Mennella, Blumberg, McClintock, and Moltz (1990) in rats (*Rattus norvegicus*); Jacquot and Vessey (1994) in white-footed mice (*Peromyscus leucopus*); Hoogland, Tamarin, and Levy (1989) in prairie dogs (*Cynomys ludovicianus*); in several deer species by Birgersson, Ekval, and Temrin (1991) (*Dama dama*); Nixon, Brewer, and Hansen (1990) (*Odocoileus virginianus*); San Jose and Braza (1993) (*Cervus dama*); by Tiplady (1990) in muskoxen (*Ovibos moschatus*); Hudson (1977) in cows (*Bos taurus*); Tulloch (1979, 1988) and Murphey, Paranhos da Costa, Lima, and Duarte (1991); Murphey, Penedo, Paranhos da Costa, Gomes da Silva, and Souza (1993); Murphey, Paranhos da Costa, Gomes da Silva, and Souza (1995) in water buffaloes (*Bubalus bubalis*). Parental care is usually associated with the degree of relatedness of the individuals. Alloparental care has been also been documented in the water buffalo (*Bubalus bubalis*) by Murphey et al. (1993). In their study of microsatellites of DNA in water buffaloes, these authors showed that collective suckling was not related to kinship, nor was it even reciprocal, as should have been the case if the behaviour had resulted from kin selection.

In the majority of mammals, the female dedicates a high level of energy to the offspring during a period of high maternal motivation. This period of investment is followed by weaning which involves a gradual reduction of the milk quantity supplied by the mother to the calf. Weaning is associated with an increase in solid food ingestion by the calf and behavioural changes in the mother-calf relationship. The parental investment rate increases just after birth. The bigger the calf the higher the investment during this first period. After weaning starts, the parental investment is gradually reduced until it reaches null values (Martin, 1984).

There are marked individual differences in performance, in mammal species. According to Mayr (1977), such individual differences could be the result of mechanisms that tend to increase fitness. Scientists have been interested in variability among normal infants in the efficiency to suck (Blass & Teicher, 1980). Studies carried out in our laboratory investigated such differences (Negrão & Schmidek, 1987; Pinto & Schmidek, 1994; Schmidek & Schmidek, 1988). In water buffalo, Paranhos da Costa, Silva, Murphey, and Souza (1994) and Murphey et al. (1991, 1995) studied collective suckling and found significant ID among females in their acceptance of calves which were not their own. They also verified there was ID among calves when they attempted to suck either their own mother or other females.

The purpose of this study was to evaluate the long-term variation and development of suckling behavior of individual cows and calves. We were interested in obtaining information about the regulation of this process, taking especially into account the occurrence of allosuckling. Relevant questions were: does females neglect her own calf when permitting allosuckling? Do offspring participate in collective suckling? We also assessed individual differences. In contrast to Paranhos da Costa et al. (1994) and Murphey et al. (1991, 1995) who analyzed a short time span of the suckling period, we were able to follow the same animals for 10 months. It was thus possible to observe if specific females are more prone to accept collective suckling and to evaluate the temporal stability of individual differences.

Material and Method

The study began with 34 water buffalo (*Bubalus bubalis*) females and their calves. Murrah-Mediterranian phenotypes were predominant in the herd. They were raised and selected to produce milk. Four of the cows and their respective calves were sold during the study period. Another cow rejected her calf 4 days after birth. These five pairs were excluded, leaving 29 for subsequent analysis. The animals were observed at a state experimental farm (Estação Experimental de Zootecnia do Vale do Ribeira), in Registro, São Paulo State, Brazil.

Females were milked every day at approximately 06:00h and then placed in a corral with their calves until 08:00h. After that,

the entire herd was released into a pasture and retrieved again at approximately 16:30h, when it was returned to the milking area in which the females and calves spent the night separated from each other. To individually identify animals, numbers were painted with yellow ink on their haunches. Mother and offspring received the same number.

Observations began in February 1993 (with three calves already born) and ended in November of the same year. Data were collected for 10 months, 3 consecutive days every month from 10:00h to 16:00h local time. Observation periods were scheduled to be equally spaced by one month.

Behaviour sampling methods (Martin & Bateson, 1986) were used to record two broad behavioral categories: *suckling attempts* (A) recorded every time a calf inserted its muzzle within approximately one head-length of a female's udder but did not get a teat into its mouth; *effective suckling* (S) recorded when the calf succeeded in getting a teat into its mouth for even a short period of time. Suckling attempts and effective suckling that occurred on a cow were subdivided into the following categories: *individual filial* (I), when a female was only sucked by her own calf or when her calf attempted to suck; *collective* (C) when a female was approached by her calf accompanied by one or more alien calves. Categories used for calf behavior were: *individual* (I) when the calf attempted or sucked its own mother *collective filial* (CF) when the calf sucked (or attempted to suck) its mother, collectively; *collective non-filial* (CNF) when the calf sucked (or attempted to suck) a non-mother, collectively. The frequency and the duration of events were calculated for each individual. Attempts and effective sucking by alien calves (whether alone or in a group) were very rare and were thus ignored as a category.

Female data were adjusted for the parturition month of each mother-offspring pair, in order to compare animals with the same nursing period. Comparisons among periods and among individuals were made by Manova with a = .05 followed by Tuckey tests whenever pertinent. The Kendall Concordance Coefficient W was performed to evaluate temporal stability of individual differences.

Results

The herd was observed for 180 hours. The calves were observed from birth to weaning. Duration of filial suckling (IS) provided by females (Fig. 1) varied significantly during the observation period ($F_{9,189} = 14.47$; $p<.001$). It was quite high in the first month but decreased in subsequent months. Maternal investment of IS was not differente for male or female calves ($F_{1,189}=2.20$; $p > .05$). Collective suckling duration also varied significantly during the 10 months of the study ($F_{9,189} = 3.72$; $p<.001$). It increased during the first four months in contrast to the decrease in filial suckling. After the fourth month of nursing, it decreased following the gradual process of weaning.

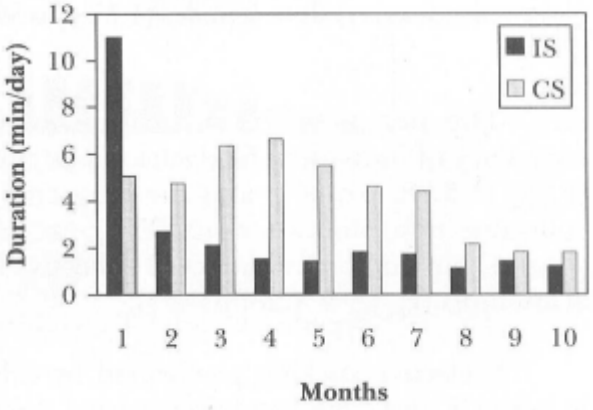

Figure 1. Mean daily duration of individual (IS) and collective suckling CS) allowed by water buffalo cows in each of the 10 postpartum months.

The frequency of sucking attempts of isolated calves on their own mother, IA, did not change significantly throughout development ($F_{9,180} = 1.22$; $p > .05$), nor did the frequency of collective attempts, CFA ($F_{9,180} = 1.74$; $p > .05$). However the frequency of collective non-filial attempts, CNFA, did show significant development changes ($F_{9,180} = 2.48$; $p < .05$), although without time dependent reduction (Fig. 2). Male and female calves did not differ significantly in the frequency of sucking attempts on their own mother. However, the

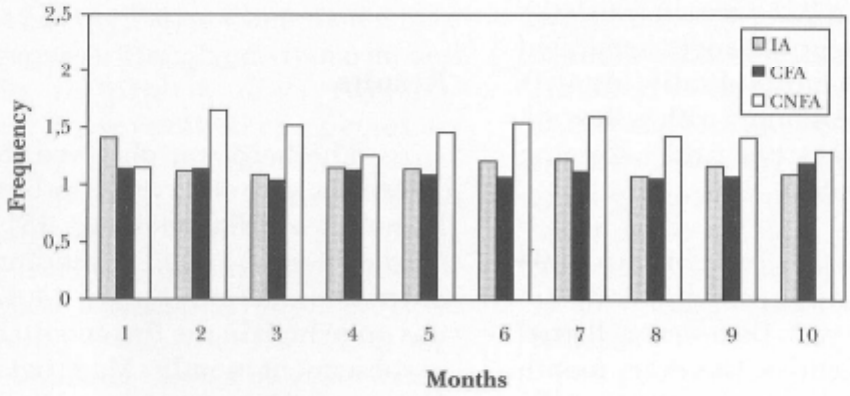

Figure 2. Mean daily frequency of individual (IA), collective filial (CFA) and non filial (CNFA) attempts performed by calves during the first 10 months of life.

frequencies of their collective non-filial attempts were significantly different ($F_{23,180}$ = 2.81; p<.001): males had a higher mean frequency (1.52 episodes/day) than females (1.37 episodes/day).

The period of birth influenced the frequency of individual filial sucking attempts ($F_{21,180}$ = 3.78; p<.001) and the frequency of collective non-filial attempts ($F_{21,180}$ = 2.75; p<.001) but not the frequency of collective filial attempts ($F_{21,180}$ = 1.28; p>.05).

Collective sucking performed by calves in both CF and CNF conditions varied during the lactation period (respectively: $F_{9,180}$ = 3.85, p<.001 and $F_{9,180}$ = 2.77, p<.01). Male and female calves did not differ significantly in this respect.

The effect of calf age was significant in both CFS ($F_{21,180}$ = 2.98; p<.001) and CNFS ($F_{21,180}$ = 2.28; p<.01) conditions.

There were no significant individual differences among females when they were suckling their own calves alone ($F_{23,189}$ =.80; p>.05). However, when they suckled calves collectively, significant individual differences appeared in the duration of suckling ($F_{23,189}$ = 5.26; p<.001; Figure 3). These individual differences were stable over the observation period (Kendal W, W =.37, χ^2 = 71.39, p<.001).When different cows were approached by a group of calves they reacted differently. Some showed a very intense rejection whereas others reacted only mildly. The rejection was always stronger against calves that were not their own. Thus, if a cow that suckled its own calf was approached by a group of alien calves it often tried to push away the newcomers with head blows but usually only on the side of her body opposite to that of her own suckling calf.

There was no difference in the amount of CFS allowed by cows with male or females calves ($F_{1,189}$ = 2.11; p>.05). Male and female calves showed no significant differences in individual filial sucking attempts ($F_{1,180}$ =.10; p>.05) nor were there significant individual differences in this variable ($F_{23,180}$ = 1.0; p>.05). Neither were there significant differences between male and female calves in terms of collective sucking attempts, both filial ($F_{1,180}$ = 1.35; p>.05) and non-filial ($F_{1,180}$ =.08; p>.05). There were however significant individual differences in the frequency of attempts in the CFS ($F_{23,180}$ = 1.75; p<.05) and CNFS ($F_{23,180}$ = 2.81; p<001) conditions. In fact, some animals, especially male calves (e.g. animals 6, 7 and 9) showed very high collective non-filial suckling attempt rates whereas others (as females 25, 27 and 32, but also male 33) showed a reduced tendency for such a behavioural pattern (Figure 4). Individual differences in CNFA frequency had a high and significant temporal stability for

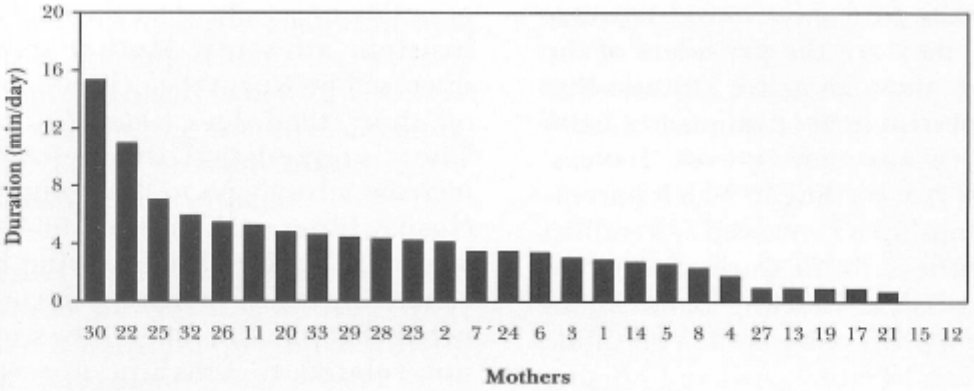

Figure 3. Mean duration of collective suckling (CS) allowed by each individual female during the observation period.

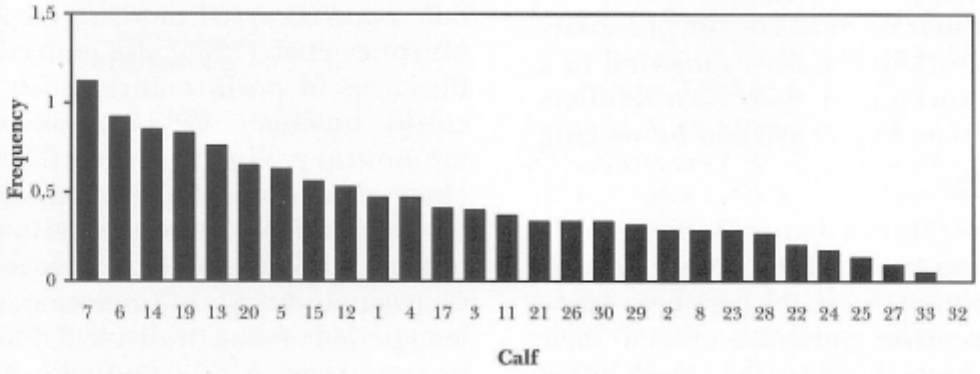

Figure 4. Mean values of the frequency of collective non filial suckling attempts (CNFA) performed by each individual calf during the observation period.

males ($W = .35$; $\chi^2 = 32.32$; $p < .01$) and females ($W = .40$, $\chi^2 = 37.05$, $p < .001$).

There was no difference between sexes in the duration of effective collective suckling episodes, both in the CFS and CNF conditions (respectively: $F_{1,180} = 2.72$; and $F_{1,180} = .57$; $p > .05$). Individual differences in this variable were however significant (CFS, $F_{5,180} = 5.30$; $p < .001$; CNF, $F_{5,180} = 3.81$; $p < .001$).

Discussion

Our results which show the occurrence of collective suckling in buffaloes under breeding conditions confirm some of the data of Murphey et al. (1991) .They also show the role of the calf both in individual as in collective nursing episodes.

Suckling behavior decreased during the period of lactation, a decrease which corresponds to the gradual process of weaning, with a reduction in milk production by the females, and a decline in maternal motivation. The frequency of calves acting in groups and attempting to get milk did not decline during the lactation period, suggesting the occurrence of social facilitation (Wilson, 1975). Biergersson et al. (1991) studying *Dama dama* verified that when a calf saw another one sucking its own mother, it ran to suck her on another teat. A similar behavior was observed in water

buffaloes. Females probably control effective suckling, since they are the providers of the resource; calves show an active attitude that reflects their persistent motivation to obtain milk. This is in agreement with Trivers' hypothesis (1974) according to which parent-offspring relationship is conceived as a conflict centered in fitness, both parts aiming to improve advantages. Suckling behavior in water buffalo is a process dependent on subtle interplay between lactating cows and nursing calves. Cows being the providers of the resource tend to gradually wean their calves by limiting access to milk. Calves, on the other hand, tend to maximize this resource extending the suckling period as much as possible and to obtain supplementary milk from non-mother females. In the water buffalo, this obtainement is favoured by the possibility of communal suckling. Calves subjected to a restriction in sucking by their own mothers partly compensate this restriction by sucking from other cows.

It was here shown that, in the first month of life, offspring suck mainly alone. Tulloch (1979) also observed that in the first three weeks of life, calves remains constantly close to their mother. This strategy allows the calves to get enough milk while sucking alone. Individual filial suckling showed a marked decline in the second month, but was substituted by the collective filial suckling which still benefited offspring. The females remained interested in their own calf till weaning. For the eldest and thus first-born calves this gradual increase in collective sucking may be the simple consequence of an increase in the number of calves in the herd. However, for the later born calves, another factor, possibly related to the cow's response to alien calves, may have a role. Cows are indeed very protective regarding the newborn, during the first period after birth; and this may exclude alien calves from collective suckling.

Each female appears to have a different tolerance for collective suckling. Birgersson *et al.* (1991) observed that females *Dama dama* tried to push away alien calves when they were suckling their own calves. Sometimes, however, one of them permitted an alien calf to suck after insistent attempts. Mother tolerance was discussed by Nixon *et al.* (1990), in their study of white-tailed does (*Odocoileus virginianus*). They inferred that this behaviour might increase advantages to the group through inclusive fitness (Hamilton,1964). However, Murphey et al. (1991) studying buffaloes in conditions similar to those of the present study, noted that allowing alien calves to nurse was not related to kinship, nor was it even reciprocal, results that are not easely accounted for by the assumptions of kin selection

Females did not differ in performance when feeding only their own calf. When, however, they suckled collectively, even when their own calf participated, marked individual differences occurred. Studying the same species, Murphey et al. (1995) also noticed marked differences in performance. Such differences could however be the consequence of momentary, contextual influences, once observations were done at a short-term basis. Our results show that proneness to allomaternal nursing is a feature of individual animals, since the magnitude of performance was stable for a long period of time. Individual differences may be considered as contributing to the plasticity of the species, providing variability for selection to act upon (Mayr, 1977). Individual differences may be related to differential experience and motivational states of each animal. Schmidek and Negrão (1987), Pinto and Schmidek (1994) studying rats and mice, suggested that behavioral individualization could provide the group with individuals having specific community roles, based on a particular motivational setup. Individual differences in the degrees of tolerance towards alien calves, among females, could be an instance of this hypothesis. According to Wilson (1975), avoiding the death of infant orphans is one of the advantages of collective suckling. Some cows, being more tolerant, may eventually provide milk to orphan calves. Individual differences in filial behavior of calves cannot be thus accounted for. The calves that sucked more were probably only increasing their own fitness, without any clear benefit to the group. Paranhos da Costa et al. (2000) discussed the advantages obtained by

oldest calves in terms of weight gain. Individual differences among calves expressed themselves more explicity when calves were competing to suck during collective attempts. A situation of conflict probably makes individual characteristics more evident.

The cows do not neglect their own offspring when permitting allosuckling, offspring are a constant presence during collective suckling. Some females seem to be more tolerant to the allosuckling than others, an individual characteristic which is maintained throughout the lactation period. The existence of individual differences in female tolerance for communal suckling, reinforces the persistence of suckling attempts among calves.

References

Blass, E, & Teicher, M. H. (1980). Suckling. *Science, 210* (3), 15-22.

Birgersson, B., Ekval, K., & Temrin, H. (1991) Allosuckling in fallow deer, *Dama dama*. *Animal Behaviour, 42*, 326-327.

Bygott, J. D., Bertram, B. C. R., & Hanby, J. P. (1979). Male lions in large gain reproductive advantages. *Nature, 282*, 839-41.

Hamilton, W. D. (1964). The genetical theory of social behaviour, I, II. *Journal of Theoretical Biology, 7* (1), 1-52.

Hoogland, J. L., Tamarin, R. H., & Levy, C. K. (1989). Communal nursing in prairie dogs. *Behaviour Ecology and Sociobiology, 24*, 91-95.

Hudson, S. J. (1977). Multiple fostering of calves onto nurse cows at birth. *Applied Animal Ethology, 3*, 57-63.

Jacquot, J. J., & Vessey, S. H. (1994). Non-offspring nursing in the white-footed mouse, Peromyscus leucopus. *Animal Behaviour, 48*, 1238-1240.

König, B. (1993). Maternal investment of communally nursing female house mice Mus musculus domesticus. *Behavioural Processes, 30*, 61-74.

Lee, P. C. (1987). Allomothering among african elephants. *Animal Behaviour, 35*, 278-291.

Martin, P. (1984). The meaning of weaning. *Animal Behaviour, 32* (4), 1257-1259.

Martin, P.; & Bateson, P. (1986). Recording methods. In: *Measuring behaviour: An introductory guide* (pp.48-69). Cambridge: Cambridge University Press.

Mayr, E. (1977). Populações, espécies e evolução. São Paulo: Nacional.

Mennella, J. A., Blumberg, M. S., McClintock, M. K., & Moltz, H. (1990). Inter-litter competition and communal nursing among Norway rats: Advantages of birth synchrony. *Behavioral Ecology and Sociobiology, 27*, 183-190.

Murphey, R. M., Paranhos da Costa, M. J. R., Gomes da Silva, R., & Souza, R. C. (1995). Allonursing in river buffalo Bubalus bubalis: Nepotism, incompetence, or thievery? *Animal Behaviour, 49*, 1611-1616.

Murphey, R. M., Paranhos da Costa, M. J. R., Lima, L. O. S., & Duarte, F. A. M. (1991). Communal suckling in water buffalo (*Bubalus bubalis*). *Applied Animal Behaviour Science, 28*, 341-352.

Murphey, R. M., Penedo, M. C. T., Paranhos da Costa, M. J. R., Gomes da Silva, R., & Souza, R. C. (1993). Microsatellite DNA analysis in testing relationships between kinship and communal nursing in water buffalo (*Bubalus bubalis*). *Behavior Genetics, 23* (6), 559.

Negrão, N., & Schmidek, W. R. (1987). Individual differences in the behavior of rats (*Ratus norvergicus*). *Journal of Comparative Psychology, 101* (2), 107-111.

Nixon, C. M., Brewer, P. A., & Hansen, L. P. (1990). White-Tailed doe tolerates nursing by non-offspring. *Trans. of the Illinois State Academy of Science, 83* (1-2), 104-106.

Packer, C., Lewis, S., & Pusey, A. (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour, 43*, 265-281.

Paranhos da Costa, M. J. R., Andriolo, A, Oliveira, J. F. S., Schmidek,W. R. (2000). Suckling and allosuckling in river buffalo calves and its relation with weight gain. *Applied Animal Behaviour, 66*, 1-10.

Paranhos da Costa, M. J. R., Silva, R. G., Murphey, R. M., & Souza, R. C. (1994). Individual differences and behavioural factors affecting the suckling time in buffalo calves on range. In Proceedings, *IVth Buffalo Congress*. (Vol. 2, pp. 33-35). São Paulo, Brazil.

Pinto, C. M. H., & Schmidek, W. R. (1994). Individual differences in the behavior of albino and wild house mice (*Mus musculus*). *International Journal of Comparative Psychology, 7* (2), 61-75.

Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quartely Review of Biology, 57* (4), 405-435.

San José, C., & Braza, F. (1993) Adoptive behaviour in Fallow Deer (*Cervus dama*). *Zeitschrift fuer. Säugetierkunde, 58*, 122-123.

Sayler, A., & Salmon, M. (1971). An ethological analysis of communal nursing by the house mouse (Mus musculus). *Behaviour, 40*, 61-62.

Schmidek, W. R., & Negrão, N. (1987). Individual differences in the behavior of rats (*Rattus norvergicus*). *Journal of Comparative Psychology, 101* (2), 107-111.

Schmidek, M., & Schmidek, W. R. (1988). Differences in individual rat preference for light levels. *Brazilian Journal of Medical and Biological Research, 21*, 663-665.

Tiplady, B. A. (1990). Multiple nursing in free-living Muskoxen, *Ovibos moschatus*. *The Canadian Field-Naturalist, 104* (3), 450-454.

Trivers, R. L. (1974). Parent offspring conflict. *Amer. Zool., 14*, 249-264.

Tulloch, D. G. (1979). The water buffalo, *Bubalus bubalis*, in Australia: Reproductive and parent-offspring behaviour. *Australian Wildlife Research, 6*, 265-287.

Tulloch, D. G. (1988). Parent-offspring behaviour in feral water buffaloes in Australia. In Proceedings, *II World Buffalo Congress* (Vol. 2, pt. 1, pp. 165-171). New Delhi, India.

Wilson, E. O. (1975). Parental care. In *Sociobiology, The new synthesis* (pp. 336-352). Cambridge: Harvard University Press.

Received August 15, 2001
Revision received June 24, 2002
Accepted July 18, 2002