Applied Animal Behaviour Science 122 (2010) 127–132

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

Mother–offspring conflict in captive plains zebra (*Equus burchellii*): Suckling bout duration

Jan Pluháček [a,b,*], Luděk Bartoš [a], Jitka Bartošová [a]

[a] Department of Ethology, Institute of Animal Science, Přátelství 815, 104 00 Praha - Uhříněves, Czech Republic
[b] Ostrava Zoo, Michálkovická 197, 710 00 Ostrava, Czech Republic

ARTICLE INFO

Article history:
Accepted 11 November 2009

Keywords:
Equus burchellii
Suckling behaviour
Equid
Zebra
Parent–offspring conflict

ABSTRACT

Recently, a lack of any significant relationship between suckling bout duration and milk or energy intake has been revealed in several mammal species. However, a short suckling bout duration could be taken as an indicator of shortage of milk and lack of maternal care, and could therefore be used to test the parent–offspring conflict hypothesis. We examined suckling bout duration of 20 plains zebra (*Equus burchellii*) foals, at the Dvůr Králové Zoo, and collected data on suckling events during 19 months of observation. In total, we recorded 3252 suckling bouts during 831 h of observation. As expected, suckling bout duration decreased with increasing age of the foal. The suckling bouts differed in duration when terminated by the foal, mother or any other adult mare (foal > mother > herdmate). Thus, bouts terminated by the mother should indicate that demands of the foal were not satisfied. The shortest bouts were those terminated by a herdmate; however, herdmates terminated few suckling bouts. Moreover, since the foal was able to resume suckling after interruption, the effect of a herdmate on suckling behaviour was very limited. Finally, we found that suckling bout duration was shorter in pregnant mothers than in non-pregnant ones, suggesting higher mother–offspring conflict when the mother was pregnant. In conclusion, this study demonstrates the importance of the termination of suckling bouts and the mother's pregnancy when interpreting suckling bout duration of equids, which has received little attention in previous studies. Our study showed that environmental condition can affect the suckling behaviour of captive equids.

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1. Introduction

Lactation is a far more demanding form of maternal investment than gestation, oestrus behaviour or ovulation (Sadleir, 1984), and has important consequences for the morphology, food gathering and energy balance of the mother (Pond, 1977). In wild plains zebra (*Equus burchellii*) lactation affects social behaviour of herds as it is a key determinant of leadership and it plays an important role in herd movements (Fischhoff et al., 2007).

In studies on mammalian maternal investment, time spent suckling was often used as a predictor of the milk transferred to the infant. However, a meta-analysis of studies in mammals that have correlated measures of time spent suckling with milk intake estimates based on weight gain revealed a weak positive relationship and significant heterogeneity between studies (Cameron, 1998). Moreover, in feral horses (*Equus caballus*; Cameron et al., 1999), fallow deer (*Dama dama*; Birgersson and Ekvall, 1994), domestic mice (*Mus domesticus*; Mendl and Paul, 1989) and domestic cats (*Felis cattus*; Mendl and Paul, 1989), no significant relationship between suckle bout duration and/or suckling frequency and milk or energy intake was found.

* Corresponding author at: Department of Ethology, Institute of Animal Science, Přátelství 815, 104 00 Praha - Uhříněves, Czech Republic. Tel.: +420 267 009 765; fax: +420 267 710 797.
E-mail address: janpluhacek@seznam.cz (J. Pluháček).

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doi:10.1016/j.applanim.2009.11.009

Suckling behaviour, however, can be used to determine the degree of conflict between mother and offspring over the allocation of resources (Cameron et al., 2003). In a recent study on feral horses by Cameron et al. (2003), suckling behaviour was not used as an index of energy intake, but as an indication of conflict between the mare and foal over energy intake. Other studies have also showed that suckling bout duration is not a good indicator of milk transfer, but that "behavioural measurements of nursing and foraging are useful to assess the amount of maternal care in current offspring" (Mendl and Paul, 1989; Therrien et al., 2007).

Suckling bout duration could be used to test the hypothesis concerning parent–offspring conflict theory (Trivers, 1974). Parent–offspring conflict theory says that "An offspring attempting from the very beginning to maximize its reproductive success would presumably want more investment then the parent is selected to give" (Trivers, 1974). Plains zebra fits well the presumption of this theory as it is species in which different, unrelated males commonly father a female's successive offspring. In such a species stronger parent–offspring conflict is expected (Trivers, 1974). Conflict should be higher when a suckling bout is terminated by the mother rather than the foal. Thus if conflict occurs, bouts terminated by the mother should be shorter than those terminated by the foal.

In the wild, at least half of plains zebra mares conceive when still lactating (Klingel, 1969; Smuts, 1976). Thus, mares frequently have to invest in two offspring at one time. Considering parent–offspring conflict theory (Trivers, 1974), a pregnant mare should give a lower level of maternal care to a suckling foal than a non-pregnant mare.

The effect of age of the foal on suckling bout duration differs among various studies. While in Asiatic wild ass (*Equus hemionus*), mountain zebra (*Equus zebra*), Grevy's zebra (*Equus grevyi*) and in some domestic horse populations the suckling bout duration decreases as foal age increases, especially during the foal's first month of life (Joubert, 1972; Rashek, 1976; Carson and Wood-Gush, 1983a; Crowell-Davis, 1985; Crowell-Davis and Houpt, 1986; Becker and Ginsberg, 1990; Smith-Funk and Crowell-Davis, 1992), other studies dealing with domestic horses and wild plains zebra did not find any change in duration with increasing age of the foal (Becker and Ginsberg, 1990; Barber and Crowell-Davis, 1994). In some feral horse populations, suckling bout duration decreased with increasing age of the foal until the foal reached the age of three to four months, then suckling bout duration increased (Tyler, 1972; Becker and Ginsberg, 1990).

In horses, suckling bout duration was further affected by parity (Duncan et al., 1984), and by the animal that terminated the bout (Crowell-Davis, 1985; Crowell-Davis and Houpt, 1986; but see: Tyler, 1972; Barber and Crowell-Davis, 1994). No effect of sex of the foal on suckling bout duration has been found, when this has been examined (Tyler, 1972; Crowell-Davis, 1985; Smith-Funk and Crowell-Davis, 1992; Barber and Crowell-Davis, 1994).

The suckling behaviour of equids has been studied intensively since the 1960s (Zwoliński and Siudziński, 1966; Rossdale, 1967; Tyler, 1972; Rogalski, 1973; for a review see: Carson and Wood-Gush, 1983b). However, almost all studies dealt with feral or domestic horses (Zwoliński and Siudziński, 1966; Tyler, 1972; Carson and Wood-Gush, 1983a; Duncan et al., 1984; Crowell-Davis, 1985). Reports of suckling bout duration in zebras and asses are very rare. In many cases the reports did not detail the number of animals observed suckling (Joubert, 1972; Penzhorn, 1984; Rowen, 1993), or the sample size is limited (e.g. plains zebra in Becker and Ginsberg, 1990). To date, only two reports dealing with suckling bout duration of captive (Prescott, 1981) or wild plains zebra (Becker and Ginsberg, 1990) have been published. Only one and seven foals were involved in these studies respectively. Thus, basic biological information concerning the suckling behaviour of the most common non-domesticated equid species is needed.

In our previous study (Pluháček et al., 2010) we analysed the factors affecting rejection of suckling, termination of suckling, interruptions, and suckling frequency. In the present study we looked at factors affecting the suckling bout duration of captive plains zebra. We predicted that the duration of suckling bouts (1) would be shorter when the bout is terminated by the mother than when terminated by the foal; (2) would be shorter when the mother was pregnant as compared to non-pregnant mothers; and (3) would decrease with increasing age of the foal.

2. Animals, materials and methods

2.1. Animals

We observed 20 foals of 14 mares, split into three different herds, at the Dvůr Králové Zoo, Czech Republic (see Table 1.). The herd sizes ranged from two to six breeding mares, aged from four to 19 years. All but three of the observed adult mares were multiparous. Two of these three mothers were observed as both primiparous (in 1999–2000) and multiparous (in 2001–2002). In 13 cases the suckling mother conceived. The size of the enclosures of the three herds were 800, 1200 and 1400 m^2, respectively. The yards were of 105 and 125 m^2 of size. The size of stable for each herd ranged from 62 to 120 m^2. Gravel, concrete and straw on bricks have been used as a substrate in enclosures, yards, and stables, respectively. There was almost no vegetation present in any of the enclosures. Food was provided to the zebras *ad libitum*. They were given fresh food daily, usually in the morning. From October to April zebras were stabled together (herd was not split) for night. In summer, all herds have been left in the enclosure during 24 h. As in our previous study, the dominance hierarchy among the adult females was based on observed biting and offensive kicking (Pluháček et al., 2006). Comparing the dyadic interactions between mares we expressed rank by a simple criterion of the number of mares which dominated the focal individual (further referred to as "number of dominant mares").

Each group was observed at least once a week (on Saturday or Sunday) from January 1999 to January 2000 and from September 2001 to March 2002. We performed the observations in four different sessions each week. Each

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