Laterality of suckling behaviour in three zebra species

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Although side preference while suckling is an easily characterised lateralised behaviour, few studies have been conducted. We observed laterality in suckling behaviour in three captive zebra species to test two hypotheses: laterality affected by the foal (motor laterality) and laterality affected by the mother. In total we observed 35 foals of Grevy’s, plains, and mountain zebra in two zoos and recorded 5128 successful suckling bouts and 9095 unsuccessful suckling attempts. At the population level the only factor affecting side preference of suckling bouts and attempts was the identity of the individual foal. Ten foals showed individual preferences: seven foals preferred suckling from the left side of the mother, three preferred suckling from the right side of the mother. The individual preferences increased with increasing age of the foal. Only one foal was refused more often from the opposite side than the preferred side used for suckling whereas three other foals were refused from the preferred side. Foals that preferred suckling either from left or right side were refused by the mare more often than foals which showed non-preference. Thus lateral preferences in suckling behaviour of zebra foals seem to be in line with the motor laterality hypotheses.

Keywords: Laterality; Suckling behaviour; Equus; Zebra.

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The authors gratefully acknowledge the assistance of the staff of the Zoological Garden at Dvůr Králové and Ostrava, in particular Luděk Čulík, Markéta Čulíková, Aleš Kopecký, Jiří Soumar, Miroslava Kubelková, Miroslava Doležalová, Pavel Moucha, Radek Hlávka, Barbara Raková, Kristína Tomášová, Jiří Hrubý, Dana Holečková, Eva Zajoncová, Robert Kopia, Rostislav Střižík, Karin Skýbová, Lenka Málová, and Petr Čolas. We are indebted to Alois Pluháček for technical help. The manuscript was much improved by comments from Martina Komářková, Radka Šárová, Marek Špinka, and Radim Kotrba. We highly appreciated the help of Sarah R. B. King who improved the English. This work was supported by the Ministry of Agriculture of the Czech Republic (MZe0002701404).

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Interest in lateralised behaviour in animals has increased in recent years (Austin & Rogers, 2012; Sankey, Henry, Clouard, Richard-Yris, & Hausberger, 2011; Wells & Millsopp, 2009). Lateralised behaviour is thought to reflect brain asymmetries (MacNeilage, Rogers, & Vallortigara, 2009; Rogers, 2010). Research on a range of species has shown that the left hemisphere controls well-established patterns of behaviour performed in non-stressful situations, whereas the right hemisphere responds to unexpected stimuli and controls escape and other emergency responses (Rogers, 2010; Sankey et al., 2011). Perception by an eye is related to contralateral hemisphere, therefore animals (e.g., toads, chicks, or horses) exhibit fear or aggression when a stimulus comes from the left side (Austin & Rogers, 2012; Bisazza, Rogers, & Vallortigara, 1998; MacNeilage et al., 2009). Since suckling behaviour contributes to parent-offspring conflict (Pluháček, Bartošová, & Bartoš, 2010; Therrien, Côté, Festa-Bianchet, & Ouellet, 2007; Trivers, 1974), offspring should prefer to approach the female from her right side to prevent maternal aggression before starting to suckle.

Although laterality in teat or side preference while suckling is an easily characterised lateralised behaviour, few studies have been conducted in this area of research. Teat preference has been investigated in primates (Hopkins & De Lathouwers, 2006; Jaffe et al., 2006). Some researchers found a slight left bias in teat preference in certain Old World primates (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Nishida, 1993; Tomaszyczki, Cline, Griffin, Maestripieri, & Hopkins, 1998). In contrast, other researchers have found a population right teat preference (rhesus monkey Macaca mulatta; Lindburg, 1971) or no population preference whatsoever (Japanese macaques Macaca fuscata; Hiraiwa, 1981; Tanaka, 1989). On the other hand, several studies (Erwin, Anderson, & Bunger, 1975; Rogers & Kaplan, 1998; Tanaka, 1989) revealed that infants display a strong individual preference for either the left or right teat. Infant age and mother’s parity are the factors that appear to have the most influence in laterality of suckling behaviour (Jaffe et al., 2006; Nishida, 1993; Tanaka, 1997). Therefore lateral preferences should be studied on both the population as well as individual level (Damerose & Hopkins, 2002). As recently suggested by Hopkins and Lathouwers (2006), additional longitudinal studies on the interrelationship between early mother-infant asymmetries and development of the offspring should provide important data on the issue.

When suckling, foals most often adopt an anti-parallel position (Figure 1) from which it is able to reach both teats, although it is easier to reach the closer teat. If the foal prefers one teat over the other it should stand by one side of the mother more often to reach the preferred teat better. This type of lateralised behaviour is defined as motor laterality of the foal (McGreevy & Rogers, 2005). In contrast, the mare can prefer to nurse the foal standing along her right side rather than her left side since the left hemisphere of the
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Figure 1. When suckling the zebra foal adopts mostly an anti-parallel position.

brain (affecting the right visual hemifield) controls proactive behaviour and is responsible for positive cognitive bias (Rogers, 2010). Recognition of a mare’s own foal is important to prevent allonursing (Cameron, Linklater, Stafford, & Minot, 1999; Lloyd & Harper, 1980; Pluháček, Bartošová, & Bartoš, 2011a). In some mammalian species the female lies down to nurse (Ralls, Kranz, & Lundrigan, 1986), and is therefore responsible for laterality in nursing behaviour; for instance, we recently reported that females of common hippopotamus (Hippopotamus amphibius) preferred to nurse while lying on their left side (Pluháček & Bartošová, 2011).

Although suckling behaviour (Barber & Crowell-Davis, 1994; Becker & Ginsberg, 1990; Boyd, 1988; Carson & Wood-Gush, 1983b; Crowell-Davis, 1985; Duncan, Harvey, & Wells, 1984; Feist & McCullough, 1976; French, 1998; Heitor & Vicente, 2008; Martin-Rosset, Doreau, & Cloix, 1978; Rashek, 1976; Rowen, 1993; Smith-Funk & Crowell-Davis, 1992; Tyler, 1972; Waring, 1982) and behavioural lateral preferences (Larose, Rogers, & Ricard-Yaris, 2006; McGreevy, Landrieu, & Malou, 2007; McGreevy & Rogers, 2005; McGreevy & Thomson, 2006; Sankey et al. 2011) have been studied intensively in equids, as far as we are aware only one study refers to side preferences of suckling behaviour in the domestic horse (Equus caballus;
Carson & Wood-Gush, 1983a). The researchers reported that the only difference, which occurred when horses were stabled, was that more successful nursing bouts were made from the right side of the dam than from the left side (Carson & Wood-Gush, 1983a). No other difference was reported, including the total number of nursing bouts made from left or right side of the dam. Side preferences have not yet been studied in other equid species.

In the current study we first investigated if foals of three zebra species show any side preferences in suckling behaviour, either on the population level or on the individual basis. We tested two hypotheses: (1) laterality affected by the foal (motor laterality) and (2) laterality affected by the mother. We predicted that if side preference is due to motor laterality then there should be no difference in the side of successful suckling bouts and unsuccessful suckling attempts. On the other hand, if laterality is affected by the mother then the opposite side preference should be recorded for successful suckling bouts than for unsuccessful suckling attempts. Based on previous research in other mammalian species we also explored if side preferences were affected by the sex or the age of the foal, and the species and parity of the mother. Lastly, we tested if suckling bout duration and termination was affected by side of mother along which the foal stood while suckling.

**METHOD**

**Animals**

We observed 33 foals (19 plains zebra *Equus quagga* [formerly named *Equus burchelli*], 8 Grevy's zebra *Equus grevyi*, and 6 mountain zebra *Equus zebra*) in five different herds (including three plains zebra herds) at the Dvůr Králové Zoo, Czech Republic and 2 foals of Grevy's zebra at the Ostrava Zoo, Czech Republic (see Table 1). The herd sizes ranged from 2 to 14 breeding mares, aged from 4 to 27 years. All but five of the observed adult mares were multiparous.

In the summer all herds were in enclosures (800 to 2800 m$^2$) 24 hours a day. From October to April the zebras were stabled at night (stables were 62 to 194 m$^2$ per herd). Plains and Grevy's zebras were stabled in groups. Mountain zebra mares were stabled individually, therefore they were not observed in stables. There was almost no vegetation present in any of the enclosures. Food was provided *ad libitum* and was given fresh daily, usually in the morning.

Plains zebra at the Dvůr Králové Zoo were observed from September 2001 to March 2002 and from November 2004 to December 2004 (Pluháček, Bartošová, et al. 2010; Pluháček, Bartoš, & Bartošová, 2010; Pluháček,
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Individual side preferences when suckling and attempting to suckle in observed foals of three zebra species. Only statistically significant \((p < .05)\) preferences are labelled. Preference affected by the age of the foal is italicised.

* Statistically significant also on the level \(p < .01\).
Bartošová, & Bartoš, 2011a). All three species were observed at the Dvůr Králové Zoo from September 2008 to July 2010. In Ostrava Zoo Grevy’s zebra foals were observed from September 2010 to August 2011. We performed the observations in four different sessions each week. Each session lasted 180 minutes, either from 08h00 to 11h00 or from 14h00 to 17h00 on Saturday or Sunday. This timing includes peaks of suckling activity found in wild and feral equid populations (Joubert, 1972a). For detailed observation methods see Pluháček, Bartoš, Doležalová, and Bartošová-Víchová, 2007, and Pluháček, Bartoš, Bartošová, and Kotrba, 2010. In total we carried out 1254 hours of observation (357 sessions over 196 days). The respective herds were observed for 339 (herd 1 of plains zebra), 330 (herd 2 of plains zebra), 66 (herd 3 of plains zebra), 270 (Grevy’s zebra at Dvůr Králové Zoo), 129 (Grevy’s zebra at Ostrava Zoo), and 120 (mountain zebra) hours.

In each observational session we collected all data concerning any suckling event. We used the same definitions of suckling bout, suckling attempt, and interruption of suckling bouts as described in previous studies on equids (Becker & Ginsberg, 1990; Cameron, Stafford, Linklater, & Veltman, 1999; Pluháček, Bartošová, et al., 2010). The suckling bout was regarded as successful when it lasted longer than 5 seconds and was not interrupted for longer than 60 seconds. If the interruption of a suckling bout was longer than 60 seconds it was considered as two suckling bouts. Suckling attempts were defined as suckling lasting less than 5 seconds, or cases in which foals approached their mothers and the mothers walked away or did not allow the foals to make contact with the teats using her legs. We recorded the following data for each suckling bout or suckling attempt that was observed: the foal’s and mother’s identity; the animal that initiated (foal or mother), terminated, or interrupted (foal, mother, other herdmate or disturbance by people [further referred as “disturbance” only]) a suckling bout; the place (stable, yard, enclosure); the duration of the bout (in seconds); and the length of interruption within a suckling bout (from 5 to 60 seconds). The initiator of suckling bout was determined as described by Crowell-Davis (1985). Foals initiated the bout by making intention movement towards the flank of the mother. The mother was initiator when she approached either the resting foal (staying or laying) or the foal engaging in other activity (e.g., playing) and she woke up the foal or stopped its activity. The foal started to suckle immediately. The dominance hierarchy among the adult females was determined by scoring bites and offensive kicking (Pluháček, Bartoš, & Čulík 2006). In each suckling attempt and bout we recorded the side of the mother where the foal stood to suckle.

All observational data were collected using a tape recorder. All other data concerning the animals (i.e., date of birth of the foals and parents, number of previous foals of the mother, etc.) were obtained from curators of the Dvůr Králové Zoo and Ostrava Zoo. We have excluded from all the analyses the
following data: suckling bouts \((n = 113)\) and attempts \((n = 242)\) involving mares other than the mother, suckling attempts terminated due to disturbance or by a herdmate other than a given mother or foal, and successful suckling bouts performed from both sides of the mare.

Statistics

All data were analysed using the SAS System, Version 9.2. First we tested if there was any side preference and factors affecting side preferences. We carried out the analyses in three steps. In the first step we analysed all bouts to see if there was any side preference at the population level. We applied an analysis of categorical repeated measurements based on the generalised estimating equation approach (Liang & Zeger, 1986) using logistical regression (the GENMOD procedure). The explanatory variables were: the foal’s age (in days) and sex, the number of dominant mares (at the date of suckling bout or attempt), season (2001/2002, 2004, 2008/2009, 2010/2011), species, mother’s pregnancy (yes, no), place where suckling bout or attempt occurred (enclosure, yard, stable), and their first-order interaction terms.

In the second step we focused on side preferences at the individual level using chi-squared tests. If we found that the foal preferred either the left or right side we tested the effect of the age of the foal on side preference using the GENMOD procedure, using the date of observation as a repeated statement.

In the third step we divided all foals into three groups (“left-side-preferring”, “right-side-preferring”, and “non-preferring”) based on previous analyses. We tested if side preference was affected by the species, sex of the foal, or mother’s parity using the GENMOD procedure.

All the above analyses were performed separately for successful suckling bouts, for suckling attempts refused by the mother, and for suckling attempts abandoned by the foal.

Additionally we tested if side while suckling or side preference affected suckling bout termination and duration. Suckling bouts terminated by disturbance or herdmate (see Pluháček, Bartošová, et al., 2010) were excluded from these analyses. To test the effect of side or side preference on suckling bout termination we used the GENMOD procedure; the dependent variable was the animal terminating the bout (mother or foal). The explanatory variables were: side position during the bout (left, right), preference of the individual foal (left-side-preferring, right-side-preferring, non-preferring), age and sex of the foal, gravidity and age of the mother, species, season, and place where suckling bout occurred (for details see Pluháček, Bartošová, et al., 2010). To account for repeated measures of the same individuals across the observation period, the analysis was performed with the individual foal as a SUBJECT in the REPEATED statement.
Factors influencing the suckling bout duration were tested using a multi-variate general linear mixed model (GLMM, PROC MIXED, SAS; for details see Pluháček, Bartoš, & Bartošová, 2010). We included all the factors tested in our previous studies (Pluháček, Bartoš, & Bartošová, 2010; Pluháček, Bartoš, Bartošová, & Kotrba, 2010), the side position during the bout, and the side preference.

RESULTS

Lateral preferences in suckling bouts and attempts

In total we recorded 5128 suckling bouts (range 45–275 bouts per foal; plains zebra: 2416, Grevy’s zebra: 1912, mountain zebra: 800). The mother refused 3143 suckling attempts (range 30–227 attempts per foal; plains zebra: 1944, Grevy’s zebra: 906, mountain zebra: 293), and 5939 suckling attempts were abandoned by the foal (range 5–860 attempts per foal; plains zebra: 986, Grevy’s zebra: 4433, mountain zebra: 520). The foal stood along the right side of the mother in 2581 (50.3%) suckling bouts, in 1473 (46.9%) suckling attempts refused by the mother and 2764 (46.4%) suckling attempts it abandoned. Almost all suckling bouts were initiated by the foal (n = 5095; 99.36%).

On the population level the logistic regression revealed that the only significant factor affecting side preference of all suckling events (bouts and attempts) was the identity of the individual foal, \( \chi^2(34) = 126.44, p < .0001 \). The same factor (individual foal) affected side preference when only successful suckling bouts, \( \chi^2(34) = 173.59, p < .0001 \), suckling attempts refused by the mother, \( \chi^2(34) = 53.26, p = .0189 \), and suckling attempts abandoned by the foal itself, \( \chi^2(34) = 58.32, p = .0058 \) were considered.

When all suckling events were involved we found that 10 out of 35 foals showed a preference for standing either on the left or right side of the mare (Table 1). Seven foals preferred to suckle more often when standing along the left side of the mother, three foals from the right side. In 3 of these 10 foals the side preference grew stronger with increasing age of the foal—Brenda: \( \chi^2(1) = 14.48, p = .0001 \); Musarah: \( \chi^2(1) = 12.88, p = .0003 \); Ptolemaios: \( \chi^2(1) = 13.91, p = .0002 \) (Figure 2).

When considering only successful suckling bouts, seven foals suckled more often when standing along the left side than when standing along the right side of the mother, while for eight foals the opposite was true (Table 1). Four mares were observed in two different (but not subsequent) seasons, each rearing one foal per season. We did not find the same or opposite preference of two foals reared by the same mother (Table 1).

In five foals we recorded more suckling attempts refused by the mother from the left side than from the right; one foal was refused more often when
Figure 2. Probability that suckling bout and attempt will occur when standing along the right side of the mother according to the age of the foal in three individual zebra foals: (a) Brenda (mountain zebra, female), (b) Musarah (plains zebra, male), and (c) Ptolemaios (plains zebra, male).
attempting to suckle from the right side. However, only one foal (Alf) was refused more often when attempting to suckle from the side opposite to that where most suckling bouts were recorded (Table 1).

Eight foals showed side preferences in unsuccessful suckling attempts performed and abandoned by the foal itself (Table 1). There was no difference in the foal abandoning attempts from the opposite side than were refused by the mother, or resulted in successful suckling bouts.

What affects lateral preferences of individual foals?

The individual lateral preference was affected by the species (GENMOD), $\chi^2(2) = 6.57$, $p = .038$. We found that mountain zebra foals prefer to stand along one side while suckling more often than Grevy’s zebra foals (GENMOD), $\chi^2(1) = 4.92$, $p = .027$. On the other hand, neither the sex of the foal, nor the parity affected side preference of individual foals while suckling. Similarly no effect of species, sex or parity to side preference was found in unsuccessful suckling attempts.

Effect of laterality on rejection, duration and termination of suckling bout

The rejection of suckling bout by the mother was affected by preference shown by individual foals, $\chi^2(2) = 7.16$, $p = .0279$. The non-preferring foals were refused by the mother less often (36%, $n = 5360$ solicitations) than left-side-preferring foals (42%, $n = 1585$ solicitations); $\chi^2(1) = 7.74$, $p = .0054$, and right-side-preferring foals (46%, $n = 849$ solicitations); $\chi^2(1) = 9.47$, $p = .0021$. The interaction between the preference of individual foals and the side where the foal stood when attempting to suckle tended to reach the level of significance, $\chi^2(2) = 7.75$, $p = .0514$. The foals that preferred to stand on the right side were more often refused when they stood by the left side of the mother (55%, $n = 309$ solicitations) than by her right side (42%, $n = 540$ solicitations); $\chi^2(2) = 7.75$, $p = .0001$. No such difference was recorded in left-side-preferring and non-preferring foals.

The suckling bout duration lasted longer when the foal stood along the right side of the mother than when it was along the left side, $F(1, 4682) = 10.16$, $p = .0014$; LS means $\pm SE$: left $55.3 \pm 2.12$, right $57.2 \pm 2.11$. Preference of individual foals did not affect the suckling bout duration.

We found that the side affected probability of termination of the suckling bout by the mother, $\chi^2(1) = 4.76$, $p = .0292$. When a foal suckled along the right side, the mother terminated the bout more often (31.1%, $n = 2396$ bouts) than when a foal suckled along her left side (26.6%, $n = 2343$ bouts). Preference of individual foals did not affect the suckling bout termination.
DISCUSSION

We have found that almost one third of observed foals showed individual lateral preference for suckling from one side; 15 foals successfully suckled predominantly from one side; 13 foals showed lateral preference when performing an ultimately unsuccessful suckling attempt. Thus, unlike some studies in primates (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Nishida, 1993; Tomaszyci et al., 1998) and in line with other primate studies (Jaffe et al., 2006; Rogers & Kaplan, 1998; Tanaka, 1989) the lateral preferences were observed only on the individual level and not on the population level. Therefore our results show that when studying laterality it is important to distinguish individuals (some studies consider population level only, e.g., McGreevy et al., 2007). The main difference between our study and those on primates is that when standing along one side of the mother, a foal can potentially reach both teats (Carson & Wood-Gush, 1983a; Crowell-Davis, 1985).

We observed that only one foal (Alf; Table 1) was refused more often from the opposite side than the preferred side used for suckling, while three other foals (Brenda, Linda, Ptolemaios; Table 1) were refused from the same side as preferred for suckling. When the same mare nursed two foals in two different seasons we did not see the same lateral preferences in these foals. We found that the rejection of suckling attempts was affected by lateral preferences of individual foals. Mares were more restrictive to foals that tried to suckle more often from one (preferred) side. When a foal approaches from one side more frequently, nursing could be more painful for mares. Thus mares “preferred non-preference of their foals”. All these results showing preference either in suckling bouts or suckling attempts are in agreement with the motor hypothesis.

On the other hand, in the case of right-side-preferring foals the preference could be caused by a higher frequency of refusal by the mare when attempting to suckle from the left side. This could support the hypothesis that laterality in suckling is affected by the mother. However, the sample size was limited (only three foals preferred suckling from the right side) and side did not affect the rejection rate in left-side-preferring foals. Thus our results do not to seem favour the hypothesis that laterality in suckling is affected by the mother as revealed in primates (Nishida, 1993). It should be noted that young of primates are altricial and a lot of suckling bouts are initiated by the mother (rhesus monkey: Berman, Rasmussen, & Suomi, 1993; great apes: Manning & Chamberlain, 1990; chimpanzee Pan troglodytes: Nishida, 1993), as opposed to the precocial young of zebras and horses where almost all suckling bouts and attempts are initiated by the foal (Crowell-Davis, 1985; Tyler, 1972; this study).
In 3 out of 10 foals the lateral preference increased significantly with increasing age of the foal. The strengthening preference over time has been reported in some primates (e.g., macaques: Jaffe et al., 2006) but not all (Hopkins & De Lathouwers, 2006). Our finding is supported by the suggestion that lateral preferences in suckling are a result of visual identification by young as part of the learning process (Jaffe et al., 2006; McGreevy & Rogers, 2005). It should also be noted that it is not clear that lateralised processes, rather than habits acquired at the individual level, are involved in zebra suckling.

Laterality in suckling of zebra foals was not affected by the sex of the foal. Absence of the effect of sex on behavioural laterality has been recorded in neonatal lambs (Ovis aries: Lane & Phillips, 2004) as well as in horses (Austin & Rogers, 2012; McGreevy & Rogers, 2005). However, sex differences in suckling behaviour have been reported in plains zebra and in other studies of the domestic horse (Berger, 1986; Duncan et al., 1984; Pluháček, Bartošová, et al., 2010; Pluháček, Bartošová, & Bartoš, 2011b). Sex also did not affect lateral teat preferences in other mammal studies (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Jaffe et al., 2006; Nishida, 1993; Tomaszycki et al., 1998).

Various equid species differ in their pattern of suckling behaviour (Becker & Ginsberg, 1990; Pluháček et al., unpublished data) and horse breeds showed differences in motor laterality (McGreevy & Thomson, 2006; Williams & Norris, 2007). In this study most of the mountain zebra foals showed a lateral preference in suckling, while most Grevy’s and plains zebra foals did not show any preference. Within the herd, mountain zebra females are very intolerant towards each other as well as towards unrelated offspring compared to the two other zebra species (Fischhoff et al., 2010; Joubert, 1972b; Lloyd & Rasa, 1989; Penzhorn, 1984; Skalka, 1986). Therefore in mountain zebra the suckling attempt could be more motivated by receiving the mother’s protection than in other zebra species. Thus we suppose that a higher lateral preference in suckling behaviour recorded in mountain zebra could be caused by a more intensive learning process of suckling.

Jaffe et al. (2006) found that infant macaques from a primiparous mother had weaker teat preferences than infants of multiparous mothers, and that infants from a primiparous mother developed a side preference earlier than infants of multiparous. In contrast to this study, and in line with others (Hopkins & De Lathouwers, 2006), we did not find any effect of parity on lateral preferences in suckling as well as on development of these preferences over the time.

Mares terminated more suckling bouts performed from their right side than those from their left. This finding is in contrast to our prediction based
on the presumption that stimuli coming from the left side induce fear or aggression more than stimuli coming from the right side. Nevertheless it should be noted that horses under experimental conditions showed quick habituation to the repeated stimulus (Austin & Rogers, 2007). Therefore we suppose that bout lateral preference does not play a role after successful start of suckling bout. On the other hand it is necessary to mention that termination is caused by the mare. Mares could use their right limbs better than their left ones to terminate a suckling bout, however we do not know lateral preferences of the observed mares.

Carson and Wood-Gush (1983a) reported no significant difference between mean sucking bout duration on the right or left teat during a successful nursing bout. Our analysis revealed that suckling bouts lasted longer when the foal stood along the mother’s right side, however the difference was very small. Therefore we suppose that such a difference has no biological meaning. It should be also noted that suckling bout duration does not reflect milk intake (Cameron, 1998; Cameron, Stafford, et al., 1999). Also we did not find any effect on suckling bout duration of interaction between side, side preference, and the animal that terminated the bout.

Our study is the first report to reveal lateral preference in suckling behaviour among ungulates. Since knowledge of laterality has particular relevance for handling, training, and welfare of animals (Austin & Rogers, 2012; Rogers, 2010), and as lateral preference displays are easily characterised during suckling behaviour (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Jaffe et al., 2006), further studies on laterality in suckling behaviour of other ungulate species are needed.

REFERENCES


