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The Many Axes of Deer Lactation

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Abstract In undomesticated animals information about the production and composition of milk over time is still scarce. In general, for most mammals it is known that milk composition changes across lactation, is different for male and female offspring, and even that marsupials, such as kangaroos, can simultaneously produce milk of different compositions for young of different ages. Such parallel milk production of differing compositions has not yet been studied in single-offspring placental mammals, but may help to explain behavioural processes like allosuckling (feeding the young of other adults) and lateralized suckling preferences. In this study we analysed the production and composition of milk in red deer throughout the lactation period and now confirm for the first time that there are axial differences present. The front teats, which are the favoured suckling positions of the deer's offspring, produce milk with a greater protein-to-fat ratio. Also, from the beginning of lactation the yield is greater on the left side, the side preferred by calves in all of the studied species, both at population and individual level. The links between milk production and calf behaviour in deer deserve further study.

Keywords Allosuckling · Laterality · Milk composition · Milk production · Udders

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Introduction

Lactation is a key process in the development of mammals [1] and the most costly phase of the reproductive cycle for females [2]. Understandably, most of the studies on lactation have been made in domestic species and to a lesser extent, humans [3]; however, only a limited amount of information about milk production and composition has been published for wild species, with very few long-term studies carried out using animal science techniques throughout the whole lactation period, due to the obvious difficulties in obtaining samples in a standardized way. Nevertheless, recent studies have shown that research in this area may help to understand different behavioural processes: as well as the changes in milk composition across lactation already reported for some species, it has been discovered that there is a greater protein content in milk for male offspring over female [4], reflecting their different ontogenetic needs. Differences in milk composition related to the sex of the offspring have been found in rhesus macaques (protein and lipids [4–7]), tammar wallabies (protein [8]), red deer (minerals [9]), and even in humans (energy [10]).

But there are still unexplored areas. Certain species of metatherians (marsupials) have been observed to simultaneously suckle young of different ages from separate teats. The glands supplying each teat produce milk of a different composition

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appropriate for the age of each offspring [11]. However, this differential production has rarely been reported in long-term studies in the other mammal clade of eutherians (placentals): mostly in domestic pigs [12] and cats [13], which are multiparous species where the young compete from birth for the most nutritious nipples. However, in other species such as dogs, there are no such differences in milk production and/or composition, and puppies do not fight for the teats [14]. Considering this, in uniparous mammals differential production could also be expected in certain circumstances, like in social species with a high occurrence of allonursing. In such species it can be hypothesized that the milk quality in the teats favoured by the maternal offspring would be better than those more frequently used by the young of other individuals. In addition, recent studies have shown lateralized preferences in the suckling behaviour of different groups of mammals. Preference for suckling from the left nipple was observed initially in chimpanzees [15], and subsequently recorded in bonobos, olive baboons and rhesus monkeys [16–18]. Thereafter it was found that sperm whales also favoured suckling from the left side [19]. The same case was seen in zebra foals [20] and horses [21] as well, but these left-side preferences have been explained as motor-related due to the fact that all nipples can be reached from both sides. Nevertheless, this repeated pattern is surprising, and deserves further study as it suggests the possibility of differential milk production being biased to a preferred side. Red deer is an adequate model for this, since they are uniparous, allosuckling is common, and easy to keep in captive conditions.

Are there asymmetries in milk production in red deer? The only study to our knowledge, that by Landete-Castillejos et al. [22], showed in a reduced sample size (14 hinds), that there was no difference between the left and right sides in production or composition, but that there was a greater milk production in the rear udders compared to the front ones. Here we analysed 28 lactations in two subspecies of captive red deer hinds (22 hinds of the subspecies *Cervus elaphus hispanicus* and 6 of the subspecies *C. e. scoticus*), assessing milk production and composition separately for each of the udder quarters.

Methods

Subjects were 28 red deer hinds, 6 of three years of age belonging to *Cervus elaphus scoticus* and 22 of the Iberian subspecies *C. e. hispanicus*, ranging in age from three to six. The study was conducted during years 1998 and 1999 using 14 hinds each year, but no hind entered twice in the study. Animals were kept in a 10,000 m^2 enclosure on an irrigated pasture which included tall fescue (*Festuca arundinacea*, 52.4 %), cocksfoot (*Dactylis glomerata*, 28.6 %), lucerne (*Medicago sativa*, 14.3 %), and white clover (*Trifolium repens*, 4.8 %). Hinds were fed diets based on suggestions by Brelurut et al. [23], using barley straw and hay from barley, alfalfa, oat, and sweet beetroot (16 % crude protein). All calves had the same available diet. Half of the hinds were hand-milked under anaesthesia on weeks 2, 6, 10, 14, 18, 22, 26, 30, and 34; the other half were milked in weeks 1, 2, 3, 4, 5, 6, 10, 14, 18. Prior to each milking, hinds were isolated from their calves for 6 h. Thus, daily production was considered to be four times the amount collected at each milking. Anaesthesia consisted of a low-dose combination of Xylazine (0.5 mg/kg) and ketamine (1 mg/kg) delivered by intravenous injection. Once anaesthesia was induced, 10 I.U. of oxytocin were injected into the right jugular vein 1 min before the start of milking. Each quarter was hand-milked individually with the udder completely emptied to measure milk production, and a 30 mL sample of milk from each quarter was collected for chemical analysis. Milk analyses were carried out in an automatic milk analyzer Milkoscan series 4000 (Foss Electric, Hillerød, Denmark) based on infrared spectrophotometry, which uses traditional regression equations for fat, protein, and lactose [22]. Azidiol was added as preservative (4 μL per ml of milk), and samples were stored at 4 °C and sent to the laboratory where they were analyzed within the next 24 h. Samples were also diluted by 50 % to adjust their composition to the calibration range of the analyzer (after several tests, we concluded that this dilution is the one which gives more accurate measurements and fit better to the regression equations, since frequently fat and protein values are above the detection range of the machine). Every three months the automatic milk analyzer is calibrated following the accepted standards (Röse Gottlieb/Mojonnier for fat, and Kjeldahl for protein). The caloric value of the milk samples was assessed by bomb calorimetry. A 15 mL sample was freeze dried in a Telstar Cryodos lyophilizer at −45 °C and 0.1 mbar. Samples for incineration consisted of approximately 1 g of dried milk. Incineration was carried out in a Gallenkamp Autobomb CBA–305 calorimeter. Each combustion data point was the mean of two replicate samples. If the CV was greater than 3 % the duplicates were repeated [24]. All the statistical analyses were done both on full production (daily yield, protein, fat, lactose, and energy), and relative content (percentage of dry matter, protein, fat, lactose, and protein-to-fat ratio).

Analyses were performed using IBM® SPSS® Statistics (version 20.0 for Windows, IBM, USA). Kolmogórov-Smirnov tests were performed to check the normality of the variables studied (all them were normally distributed and no transformation was necessary). General Linear Models showed the influence on milk production (daily yield, protein, fat, lactose, and energy) and composition (percentage of dry matter, protein, fat, lactose, and protein-to-fat ratio) of the longitudinal and lateral axes (both entering the model as binomial variables), together with all the variables previously known to have some effect [4, 9, 22, 24, 25]: time (week), sex, subspecies, birth date, birth weight, calf and hind weight on the milking day, and hind age. For the independent variables included in the models, multicollinearity was previously tested, but all them showed VIF < 3. Finally, Spearman's ranked correlation showed the influence of the week of lactation on the laterally biased production of milk.

RESULTS and DISCUSSION

Axial Differences in Milk Production

Table 1 shows that longitudinal and lateral axial differences in milk production and composition were found in red deer hinds, after controlling for other factors previously known to be influential, such as birth date, birth weight, weights of calf and hind on the sampling day, age of the hind, week of lactation and subspecies [22, 25].

Regarding the longitudinal axis, milk production in the rear teats was almost double that of the front ones, reflecting the well-known asymmetry in udder volume (rear teats are 2 to 4 times bigger than front ones [22, 26]. The total protein, lactose, fat and energy produced by the rear teats was higher than that of the front teats, but the percentage content of dry matter, protein, fat and lactose was the same for front and rear teats. However, the front teats produced milk with a greater protein-to-fat ratio (0.791 ± 0.007 in the front teats vs. 0.772 ± 0.007 in the rear ones; F = 4.522, p = 0.034; Fig. 1). That means better quality milk, since a higher protein-to-fat ratio is correlated with increased calf growth [25]. From 1080

Table 1 General Lineal Models performed on milk production and composition of 28 red deer hinds periodically milked along the lactation season. Results are presented to highlight axial differences, but other variables known to affect milk yield, and significant in the models, are also shown

	R^2	Longitudinal axis [a]	Lateral axis [b]	Other significant variables in the model [c]
Dry matter (%)	76.7 %	ns	ns	Week (p < 0.001); BD (p < 0.001); Sex (p = 0.005); ssp (p = 0.008)
Protein (%)	61.3 %	ns	ns	Week (p < 0.001); CBW (p < 0.001); CW (p < 0.001); HW (p < 0.001); ssp (p < 0.001); HA (p = 0.039)
Fat (%)	75.1 %	ns	ns	Sex (p < 0.001); Week (p < 0.001); BD (p < 0.001); CBW (p = 0.001); ssp (p = 0.009); CW (p = 0.036)
Lactose (%)	35.4 %	ns	ns	Week (p < 0.001); BD (p < 0.001); CBW (p < 0.001); CW (p < 0.001); Sex (p = 0.002); HA (p = 0.006)
Protein:fat ratio	52.6 %	β = 0.019; $F_{(1905)}$ = 4.522; p = 0.034	ns	Sex (p < 0.001); ssp (p < 0.001); BD (p < 0.001); CBW (p < 0.001); CW (p < 0.001); HA (p = 0.011)
Daily yield (mL)	65.7 %	β = −181.9; $F_{(1919)}$ = 347.2; p < 0.001	β = 21.401; $F_{(1919)}$ = 4.809; p = 0.029	ssp (p < 0.001); Week (p < 0.001); BD (p < 0.001); CBW (p < 0.001); HW (p < 0.001); HA (p = 0.001); CW (p = 0.001); Sex (p= 0.004)
Daily protein (g)	62.8 %	β = −12.549; $F_{(1901)}$ = 340.4; p < 0.001	β = 1.336; $F_{(1919)}$ = 3.774; p = 0.052	ssp (p < 0.001); Week (p < 0.001); BD (p < 0.001); CBW (p < 0.001); HW (p < 0.001); HA (p = 0.001); Sex (p = 0.001); CW (p = 0.021)
Daily fat (g)	50.2 %	β = −16.799; $F_{(1900)}$ = 331.1; p < 0.001	β = 2.082; $F_{(1900)}$ = 5.087; p = 0.024	Sex (p < 0.001); Week (p < 0.001); HW (p < 0.001); HA (p < 0.001); CW (p = 0.001); BD (p = 0.006); ssp (p = 0.006)
Daily lactose (g)	67.2 %	β = −11.106; $F_{(1898)}$ = 43.513; p < 0.001	β = 1.412; $F_{(1898)}$ = 5.508; p = 0.019	ssp (p < 0.001); Week (p < 0.001); BD (p < 0.001); CBW (p < 0.001); CW (p < 0.001); HW (p < 0.001); HA (p = 0.007); Sex (p = 0.029)
Daily energy (J)	57.5 %	β = −249.2; $F_{(1897)}$ = 354.5; p < 0.001	β = 29.191; $F_{(1897)}$ = 4.868; p = 0.024	Sex (p < 0.001); ssp (p < 0.001); Week (p < 0.001); BD (p< 0.001); HW (p < 0.001); HA (p < 0.001); CBW (p = 0.003);

[a] Rear teats as reference (i.e., positive values of β means greater values for the front teats)

[b] Right teats as reference (i.e., positive values of β means greater values for the left teats)

[c] *BD* Birth date, *CBW* Birth weight, *CW* Calf weight (on the milking day), *HW* Hind weight (on the milking day), *HA* Hind age, *ssp* subspecies

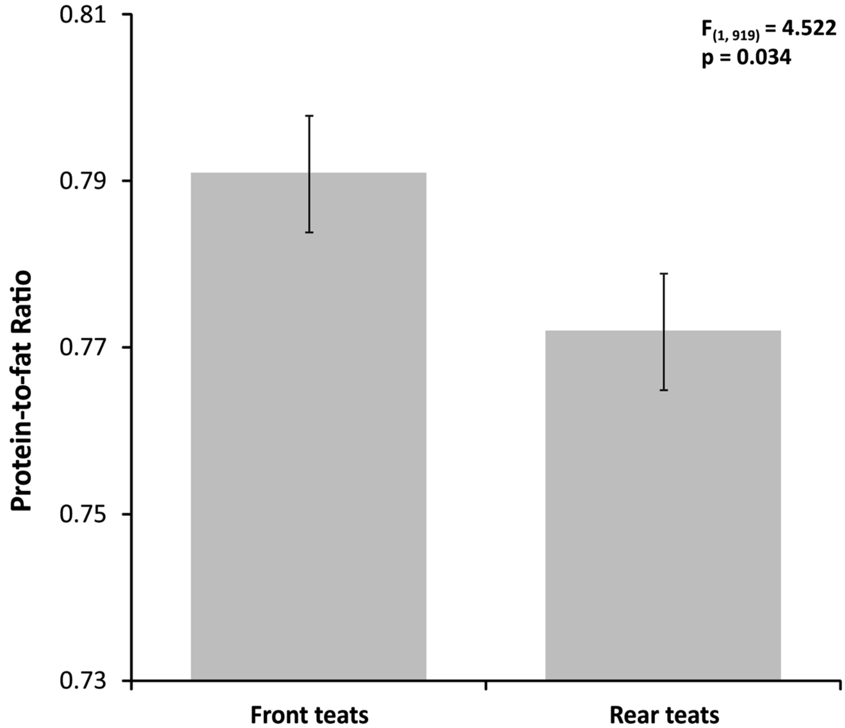

Fig. 1 Overall differences (front vs. rear teats) in protein-to-fat ratio in 970 milk samples from red deer hinds collected throughout the entire lactation period

observations of suckling attempts collected in a long term study recently carried out at the same facilities (unpublished data), the maternal calves attempted to suckle from the front position with an 89.4 % frequency, while allocalves attempted this position with a 76.7 % frequency. However, maternal calves were successful (allowed to suckle for longer than 5 s [27]) in 82.7 % of these attempts, whereas allocalves had only a 43.2 % success rate. Previous studies or preliminary results from our own [28, 29] and other groups [27–30] show similar percentages. Even though the use of teats should also be considered along with the position of the calf during suckling, these results suggest that hinds may produce a certain amount of high-quality milk in the front teats intended for the maternal calf. Since the protein content is almost exactly the same in the front and rear teats (in %: 7.187 ± 0.043 vs. 7.190 ± 0.043, respectively; F = 0.518, p = 0.472), differences in the protein-to-fat ratio seem to result from the greater (but not significant) fat content in the rear teats (in %: 9.761 ± 0.129 vs. 9.969 ± 0.124 respectively; F = 1.419, p = 0.234). One the one hand, it may seems an overall greater nutrient content for the calf suckling from the rear teats; but on the other hand, protein-to-fat ratio has been proposed in this species as the main factor explaining calf growth [25]. It may be thus speculated that quality is better than quantity for calf growth. These differences in the longitudinal axis have previously only been reported in domestic pigs (higher protein in front teats [12]) and cats (higher lactose in rear teats [13]), and in both species the young compete for preferential access to the more nutritious teats. Our results show a similar pattern in a uniparous mammal for the first time, suggesting that milk quality is a major driver of teat preference in offspring. These results also suggest that differential milk production among teats may play an important role in the resolution of parent-offspring conflicts [31, 32], especially in those species where external players (allocalves) are involved.

With respect to the lateral axis, differences were again found for daily yield, being greater in the left teats than in the right ones (in mL: 369.9 ± 7.2 vs. 348.5 ± 7.2; F = 4.809, p = 0.029; Fig. 2), and accordingly, the total protein, lactose, fat and energy were also higher in the left teats. Percentages of dry matter, protein, fat, lactose, and protein-to-fat ratio were not different for each side. Considering the repeated samples collected from each hind throughout the entire lactation period, 20 hinds (71.4 %) showed a consistent lateralized bias of greater milk production by the left teats, while only 8 (28.6 %) showed a greater production by the right teats (Fig. 3). This greater milk production by the left teats seems consistent both at the individual and population level, and agree with the preferential suckling from the left side previously observed in monkeys, whales and equids [16–21], suggesting a possible connection. However, these side preferences cannot be directly linked to nipple preference since it can also be related to motor lateralization [20, 21].

These axial differences in milk production and composition may be mediated by the effect of prolactin [33] and

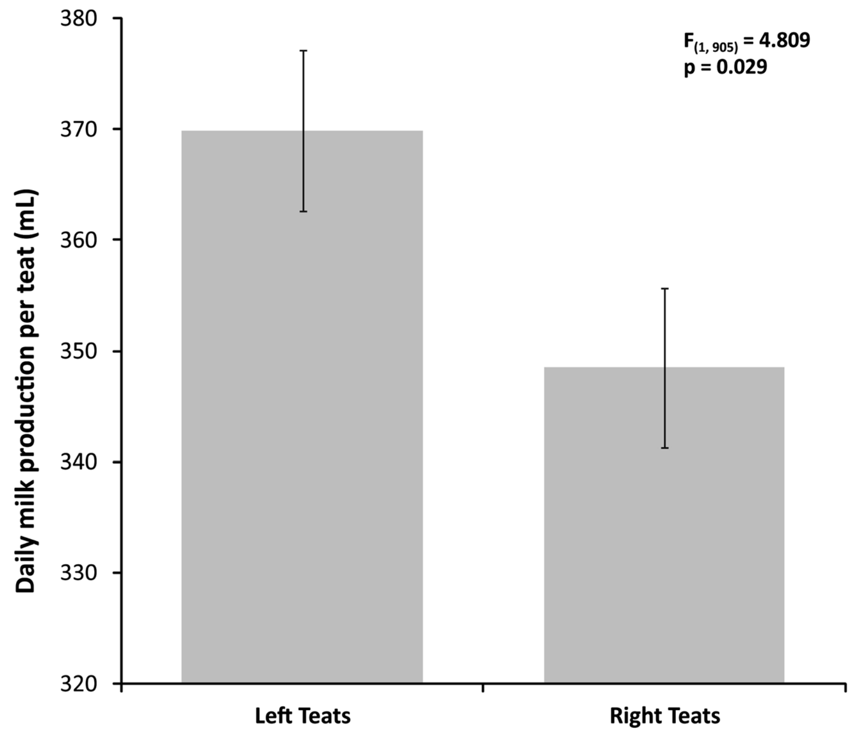

Fig. 2 Overall differences (left vs. right teats) in daily milk production per teat in 984 milk samples from red deer hinds collected throughout the entire lactation period

FIL (Feedback Inhibitor of Lactation [34]). The suckling process may induce milk production through neuronal stimulation of the pituitary gland and the secretion of prolactin, presumably having the same amount of effect on the productivity of all teats. However, the most stimulated teats also show higher production due to the local secretion of prolactin by the teat's own mammary tissue [35, 36]. Contrastingly, when a teat is not emptied periodically, the accumulation of FIL induces the decrease, and finally the cessation, of milk production [37], as happens in non-suckled teats in pigs and metatherians. Similar results on lateral asymmetries in milk production have been only observed in dairy cattle [38], although other equivalent studies failed to find the same greater production by the left side [39, 40]. In humans differential milk yield has been observed linked to the breasting preferences of the mother [41], and probably also mediated by asymmetries in breast volume (left bigger [42, 43]). Future research should be conducted to investigate these matters further. Better models like deer, a wild species which can be easily handled in captivity, should thereby be used for studying asymmetries in milk production, as humans and breeds of cattle selected for greater milk production do not represent the "natural state" of wild species.

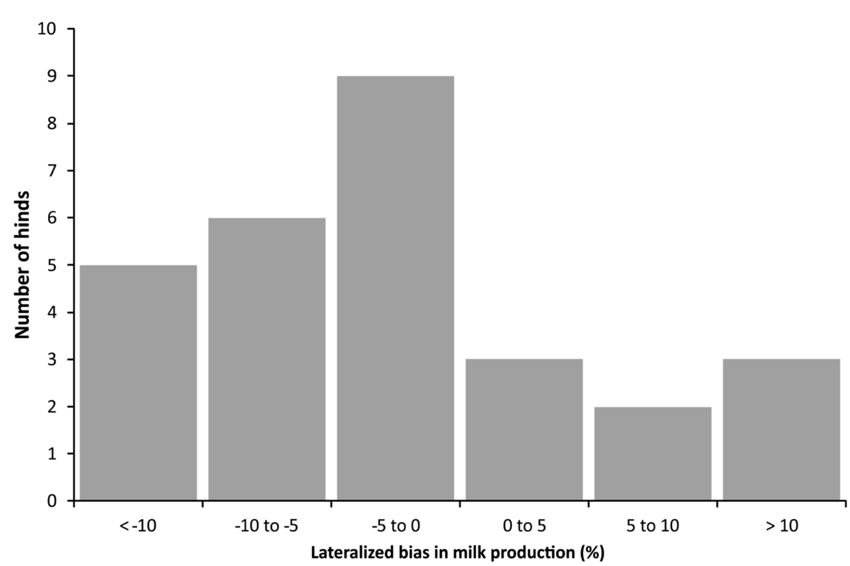

Fig. 3 Histogram of the lateral asymmetry biases in milk production in red deer hinds throughout the entire lactation period. For each hind, bias to the right (positive values) or left (negative values) was calculated as the mean of the 9 milkings conducted throughout the lactation period

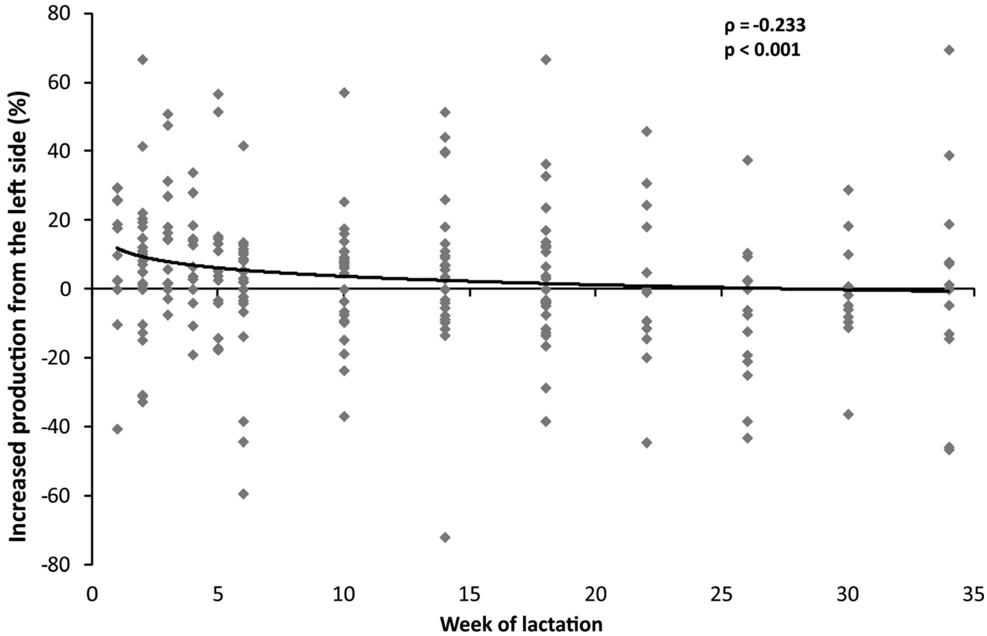

Fig. 4 Lateral asymmetries bias in milk production throughout the lactation period in red deer hinds

Laterality along the Lactation Season

This discovery of lateralized milk production being greater in left side teats, which has not been previously confirmed in any other wild mammal, raises a new question: Is the production itself lateralized, and this drives the suckling preference for the left side previously reported in most of the studies? Or is it the suckling preference of the calf which determines the final overall higher production by the left teats (mediated by prolactin and FIL)? If the latter is correct, we would expect to see no differences at the beginning of the lactation but a bias at the end driven by calf preference. Figure 4 shows that during the first two weeks of lactation, production is 7.5 % higher in the left teats than in the right ones ($n = 42$). Thereafter, there is a continuous and significant decline in the bias to the left side (Spearman's ranked correlation: $\rho = -0.233$; $p < 0.001$), in such a way that production reaches parity around the 25th week of lactation. This suggests that it is the production itself that seems lateralized to the left side. However, the cognitive preferences of the calf for one side or another during the very first days of life are unknown and behavioural observations would be necessary to determine how much this would influence lateralization. The only known similar result to ours is that from Johansson & Korkman [39], who showed a constant decline in the relative contribution of left teats to total milk yield in dairy cattle. As previously mentioned, some species compete for preferential access to the most nutritious teats, but those without such differences in milk production and/or composition do not fight for the access to the teats. In red deer, sibling rivalry does not exist, but there is competition with other young herdmates, suggesting a more widespread link between competition for milk and differences in milk production and/or compostition.

Conclusions

Axial differences in milk production and composition for a uniparous wild species such as red deer are documented here for the first time. We also suggest a link between these differences and certain calf behaviours which are of great importance in understanding their basic biology, and for gaining more insight into allosuckling and side preferences in lactation. Thus, even when axial differences in milk production and composition do exist, further experimental designs are necessary in order to study the effect on calf behaviour; and the subsequent feedback-influence of calf behaviour on milk production and composition.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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