Introduction

Allonursing or communal nursing, communal suckling, non-offspring nursing in mammals refers to the situation when a lactating female nurses a young which is not her own [1,2]. When an offspring sucks milk from female which is not its mother, we call this allonursing or communal sucking [3,4]. We use the term allosuckling for both behaviours together. This phenomenon can be explained as an extreme form of communal maternal care [5,6], known in various mammalian orders [1]. Nevertheless, the explanations of allosuckling occurrence are diverse across the species and situations and functions of allonursing are not well understood. Allosuckling involves tolerance by nursing females, ranging from kin directed discrimination or social affiliation of females [2,7,8], to a parasitic behaviour of young in which they steal milk without the female's acceptance [1,2]. Motivation of calves for allosuckling is often explained as a compensation of nutritional requirements of the young [9,10], using either the tolerance of females or a milk-theft strategy [9–13]. The explanation of allosuckling as an adaptive behaviour of females involves mostly the kin selection hypothesis [1,2,4,10] in which females nurse preferably the offspring of related females, or the reciprocity hypothesis, when females nurse the offspring of another group member reciprocally [14,15]. The reciprocity hypothesis in general is expected to apply in stable groups of social animals and is therefore connected with social affiliation [8]. In accordance with the compensation theory, females in better body condition may be more tolerant to non-filial calves. In some extreme cases a female actively nurses a non-filial offspring because she does not recognize that the offspring is not her own [16]. Roulin [2] calls this behaviour the misdirected parental care, connecting it with milk-theft. The milk-theft hypothesis [1] predicts that the calf tries to ‘steal’ the milk from a non-maternal female, but when the female recognizes the calf is not her own, she would refuse to nurse and to test whether it can be explained as a ‘milk-theft’ (opportunistic behaviour of calves) or alternatively as an altruistic behaviour of females. During 2005 and 2007, nine camel females and ten calves in four zoological gardens in the Czech Republic were observed. In total, 373 sucking bouts were recorded, from which 32 were non-filial (the calf sucked from the non-maternal female). Allosuckling regularly appeared in captive camel herds. As predicted for the milk-theft explanation, the non-filial calves sucked more often in the lateral position and even did not suck in the antiparallel position at all. The non-filial calves preferably joined the filial calf when sucking but in five cases (15.6% of non-filial sucking bouts) the calves sucked from non-maternal dam without the presence of filial calf. We then expected the differences in terminations of sucking bouts by females but did not find any difference in sucking terminations for filial and non-filial calves. As the calves were getting older, the incidence of allosuckling increased. This was probably because skills of the calf to outwit the non-maternal dam increased and/or the older calves might be more motivated for allosuckling due to the weaning process. Finally, duration of a sucking bout was shorter with non-filial than filial calves. The results of the study support the hypothesis of ‘milk theft’, being mostly performed by calves behaving as opportunistic parasites, but we cannot reject certain level of altruism from the allonursing females or their increased degree of tolerance to non-filial calves.
regular occurrence of allosuckling in captive farmed guanacos as behaviours that were consistent with the milk-theft hypothesis and a compensation theory [20,21].

The wild Bactrian camel (Camelus bactrianus) is now considered like a separate species [22] and is found exclusively in China and Mongolia [23]. No information about the suckling behaviour of wild camels has been published. The Bactrian camels kept in European breeding facilities belong to the domestic form (Camelus bactrianus) [24]. Camels are monotocous ungulate species, having only one offspring per litter [25,26]. A female in feral or extensively bred camels usually leaves the herd for parturition, while in captivity is often separated from the herd by keepers. The calf follows the mother for several hours after birth. Within a week the mother and the calf rejoin the herd [27,28]. According to our observations in zoo camels, females which are not separated often give birth surrounded by the other herd members. Camels are seasonal breeders and the calves are born during spring months [25]. In European breeding facilities the breeding season is prolonged and calves are born all over the year with a peak in spring months [24]. Camel calves are nursed up to two years and the female can have a calf every two years [28]. Some of the females may give birth every year [29]. According to the study of Sambraus [30], camel calves sucked 8 times in 24 h period, slightly more during the daylight. Nursing dams did not limit sucking of calves up to 3 months of age, while they frequently terminated sucking bouts of older calves [30].

The aim of this study was to provide the first description of allosuckling occurrence in camels and to test possible hypotheses explaining this behaviour. The kin selection hypothesis did not seem to be a major factor in this study, as the females were not related to each other. Based on the findings of Zapata et al. [19,20] on another camelid, the guanaco, we predicted the milk-theft hypothesis be the main cause why the camel calves sucked from non-maternal females. If this was valid we predicted that (i) a calf would suck from the non-maternally standing in other than antiparallel sucking position so that it was more difficult for the dam to distinguish the calf's identity or to threat the non-filial calf. (ii) A calf should preferably join the filial calf during sucking non-maternal dam. (iii) If the position served as a tactic not to be recognized or threatened, one would expect termination of a sucking bout involving a non-filial calf in an antiparallel position (if any) by the dam more frequent than if the non-filial calf was sucking in a lateral position. We also predicted that (iv) the incidence of allosuckling will increase with age of the allosucking camel as skills of the calf to outwit the non-maternal dam would increase or the calf will be more motivated for allosuckling. Finally, we predicted (v) duration of a sucking bout will take shorter time with non-filial than filial calves. Alternatively, if the result will not correspond with the milk-theft hypothesis, an altruistic behaviour of females should be taken in account, either in the form of reciprocal help or compensation.

Materials and Methods

Ethic statement

Observations of camels were carried out in zoos mostly from the visitors’ area or from the background yards when needed. The observer did not enter animal enclosure and did not affect the behaviour, husbandry, and management of studied animals. The zoo managers were informed and agreed with the research activities.

Animals and husbandry

From 2005 to 2007, we have studied maternal behaviour of Bactrian camels kept in four zoological gardens in the Czech Republic (Praha, Brno, Ostrava, Zlín–Lešná). Nine females (one of them reproduced two times within the observation period) and ten calves (4 males, 6 females), were included in the study. The size of herds ranged between 5 and 11 individuals; including 2 to 3 calves (Table 1). All calves in each herd were sired by the same bull, making them half-siblings to one another. Females were not related to one another, but have lived together most of their lives. All except one female were multiparous. Additional data on calves are presented in Table 2. Each animal was identified individually, according to the shape of humps, hair and facial traits. Age, origin, kinship, and other attributes of females were available according to Animal Record Keeping System (ARKS) records of every zoo (see Table 3 for details).

Camels in all facilities were fed once or twice a day by hay and grasses ad libitum, supplemented with grains and vegetables, and ad libitum water supply. The animals were kept outdoors, mostly with the access to unheated stables or shelters. The outdoor enclosures of camels in the zoos had mostly grassy or sandy surface with a similar space allowance in all cases. Even in larger enclosures camels spent most of the time close to each other and were not dispersed. The daily maintenance of herd was done by the keepers either entering the herd directly or moving animals from the stable to enclosure and back to clean all the space without the direct contact with animals. Females were separated before parturition and joined the rest of the herd after two to 30 days of the calves’ life.

Recorded variables

We recorded all occurrences of sucking by ad libitum sampling method [31]. Selected activities were directly observed by one observer (Karolina Brandlová). The observations were performed monthly in all studied calves during 7–10 hours a day (0800–1800, 0800–1700, 0900–1800, 0800–1600), depending on locality and season, starting as soon as possible after birth of the second calf in the respective herd and continuing at least 3 months.

For each sucking bout we recorded the identity of the animals, duration of sucking bout, position of sucking calf, which animal terminated the sucking bout (mother, calf, or other). The position of the sucking calf was classified into two classes - antiparallel, when the hind part of the calf was directed toward a cow’s head, and lateral, when the calf stands at least in the right angle to the cow’s body axis. As the gap between the start of sucking and milk let-down is not documented in camels, we consider all bouts longer than 5 seconds as successful as in other studied species e.g. [4,32,33]. Sucking bout was considered to terminate when it was interrupted for at least 10 seconds.

Assessment and statistics

The data were analysed using Statistical Analysis Systems (SAS) version 9.2. Frequency counts for prediction (i) were analysed by computing chi-square test (PROC FREQ). The output contained cell or cells counts less than 5, hence Pearson exact chi-square was used. For other data we used Generalised Linear Mixed Model (GLMM) for analysing numeric variables (PROC MIXED) or categorical variables (PROC GLIMMIX for binary distribution). To account for repeated measures, all mixed model analyses but one were performed using individual camel ‘call’ nested within the ‘herd’ as a random effect. In unbalanced designs with more than one effect, the arithmetic mean for a group may not accurately reflect response for that group, because it does not take other effects into account. Therefore, we used least-squares-means (LSMEANS) instead. LSMEANS are, in effect, within-group means appropriately adjusted for other effects in the model. LSMEANS were computed for each class and differences between classes were
Sucking position

Filial calves sucked from their mothers mostly standing in the antiparallel position (62.17% of cases), while non-filial calves sucked exclusively in the lateral position (n = 32, difference Pearson exact chi-square test p = 3.04 * 10^{-13}, Figure 1).

Number of sucking calves

Four non-filial calves were involved in a sucking bout without the presence of filial calves five times (15.6% of cases), standing in a lateral position (Figure 2). In all 27 cases when non-filial calves were allosuckling with other calf or calves present, they invariably joined already sucking filial calf.

Termination of sucking by the dam

Termination of sucking by the dam was not affected by any of the tested factors either when they entered the model alone or in any combination with other factors. Non-filial calves never sucked in anti-parallel position, so we could not test the effect of position to termination. Of the non-filial calves which sucked without a presence of filial calf, sucking was terminated by the calf three times, once by the dam and in one case we did not see who terminated the bout.

Sucking probability

The GLMM model revealed that the probability for a calf to suck from non-maternal dam was affected by ‘age’ of the calf (F(1,358) = 3.96, p = 0.047, Figure 3), and ‘number of calves’ taking part in the sucking bout (F(1,358) = 27.50, p<0.0001). In particular, allosuckling was more likely in older calves and with increasing number of sucking calves. ‘Nursing females’ and ‘sex of the calf’ were not significant predictors and were dropped from the model.

Sucking duration

The mean (± SE) sucking duration was 42.93±2.22 s (range 5–270), the mean duration of filial sucking bout 43.50±2.37 s (range 5–270) and the non-filial sucking bout 36.78±5.47 s (range 5–121).

The GLMM model showed that duration of sucking bouts was dependent on the ‘number of calves’ taking part in the sucking bout (F(1,191) = 17.19, p<0.0001), so the sucking bouts involving more than one calf were longer than those involving just one calf, either filial or non-filial (Figure 4). Duration of sucking bouts was also dependent on a relatedness by position interaction (F(1,367) = 11.05, p = 0.001), meaning that calves in the antipar-
### Table 2. Camel calves included in the study with the number of observed hours.

| Zoo       | Year | Name  | Date of birth | Sex | Mother | Age of calf (months) | Observed hours | No. of sucking bouts | Allo-sucking extent (%) | Allo-sucker | Mean duration ± SE of filial sucking (sec.) | Mean duration ± SE of allosucking (sec.) |
|-----------|------|-------|---------------|-----|--------|----------------------|----------------|----------------------|-------------------------|-------------|------------------------------------------|------------------------------------------|
| Brno      | 2006 | April | 24.2.2006     | F   | Isis   | 2–5                  | 32             | 75                   | 0,00                    | NO          | 22.48 ± 2.38                             |                                            |
| Brno      | 2006 | Gaja  | 18.4.2005     | F   | Sulika | 13–16                | 32             | 6                    | 0,00                    | NO          | 50.40 ± 2.41                             |                                            |
| Brno      | 2007 | April | 24.2.2006     | F   | Isis   | 14–17                | 24             | 3                    | 100,00                  | YES         | 37.33 ± 16.83                            |                                            |
| Brno      | 2007 | Polednice | 10.3.2007 | F   | Sulika | 2–5                  | 24             | 23                   | 0,00                    | NO          | 33.87 ± 6.58                             |                                            |
| Zlín-Lešná  | 2005 | Marek | 17.5.2005     | M   | Jade   | 0–3                  | 22             | 34                   | 0,00                    | NO          | 55.15 ± 10.41                            |                                            |
| Zlín-Lešná  | 2005 | Alžběta | 14.3.2005   | M   | Klaudiva | 3–6                  | 22             | 24                   | 8,33                    | YES         | 75.91 ± 15.66                            | 10.00 ± 0.00                             |
| Ostrava   | 2006 | 2sameček | 31.3.2006   | M   | Vendula | 2–6                  | 42,5           | 30                   | 3,33                    | YES         | 62.90 ± 9.03                             | 5.00 ± 0.00                              |
| Ostrava   | 2006 | 1samička | 23.3.2006   | F   | Čora   | 2–6                  | 42,5           | 55                   | 27,27                   | YES         | 41.23 ± 5.36                             | 36.30 ± 7.39                            |
| Ostrava   | 2007 | 2sameček | 31.3.2006   | M   | Vendula | 14–16                | 16             | 8                    | 50,0                    | YES         | 41.25 ± 15.20                            | 58.50 ± 24.15                            |
| Ostrava   | 2007 | 1samička | 23.3.2006   | F   | Čora   | 14–16                | 16             | 11                   | 45,45                   | YES         | 32.50 ± 7.06                             | 43.80 ± 14.45                            |
| Ostrava   | 2007 | Kobi   | 2.3.2007     | F   | Fatima  | 2–4                  | 16             | 17                   | 0,00                    | NO          | 46.06 ± 10.05                            |                                            |
| Praha     | 2006 | Vanda  | 18.12.2006   | F   | Lee    | 6–8                  | 29             | 43                   | 4,65                    | YES         | 37.15 ± 4.96                             | 17.50 ± 5.50                             |
| Praha     | 2006 | Věra   | 21.7.2006    | M   | Rona   | 0–3                  | 29             | 44                   | 0,00                    | NO          | 54.16 ± 6.63                             |                                            |

**Note:**
- Allo-suckling is defined as an instance where the calf is suckling the mother’s milk other than from their own mother.
- Allonursing is defined as an instance where the calf is nursing its mother’s milk other than from their own mother.

### Table 3. Camel females included in the study.

| Zoo       | Female name | Birthdate | Arrival to present zoo | Parity till 2005 | Number of calves till 2005 | Parity till 2006 | Number of calves till 2006 | Parity till 2007 | Number of calves till 2007 | Allonursing extent (%) | Allonurser |
|-----------|-------------|-----------|------------------------|------------------|----------------------------|------------------|----------------------------|------------------|----------------------------|-------------------------|------------|
| Brno      | Isis        | 26.1.1998 | 24.6.1999             | 2                | 1                          | 3                | 2                          | 3                | 2                          | 0.00                    | NO         |
| Brno      | Sulíka      | 6.3.1992  | 63.1992               | 7                | 5                          | 7                | 5                          | 8                | 6                          | 9.38                    | YES        |
| Zlín-Lešná | Jade        | 24.2.1997 | 3.9.1998              | 4                | 4                          | 4                | 4                          | 5                | 4                          | 5.56                    | YES        |
| Zlín-Lešná | Klaudiva    | 3.5.1999  | 3.5.1999              | 2                | 1                          | 2                | 1                          | 3                | 2                          | 0.00                    | NO         |
| Ostrava   | Vendula     | 03.04.2000| 30.5.2001             | 1                | 0                          | 2                | 1                          | 2                | 1                          | 35.29                   | YES        |
| Ostrava   | Čora        | 02.03.2002| 30.5.2003             | 0                | 0                          | 1                | 1                          | 1                | 1                          | 2.13                    | YES        |
| Ostrava   | Fatima      | 17.05.1990| 27.6.2003             | 2                | 0                          | 2                | 0                          | 3                | 1                          | 26.09                   | YES        |
| Praha     | Lee         | 02.06.1998| 24.6.1999             | 2                | 1                          | 3                | 2                          | 4                | 3                          | 0.00                    | NO         |
| Praha     | Rona        | 15.03.1995| 26.4.1992             | 4                | 1                          | 5                | 2                          | 5                | 2                          | 4.35                    | YES        |

**Note:**
- Parity is the number of pregnancies a female has had at the time of the study.
- Number of calves is the total number of calves born to the female during the study period.

**References:**
- doi:10.1371/journal.pone.0053052.t002
- doi:10.1371/journal.pone.0053052.t003
allel position (only filial ones) sucked longer than those in the lateral position (either filial or non-filial) (Figure 5 left). Sucking duration depended also on a relatedness by sex interaction ($F(2,20.7) = 3.49$, $p = 0.049$), showing that the sucking bouts of filial males were longer than those of females, both filial and non-filial. Non-filial males did not differ from non-filial females (Figure 5 right). ‘Age of the calf’ and ‘age of the dam’ were not significant predictors and were removed from the final model. For non-filial calves only, duration of allosuckling was much shorter when the non-filial calves were sucking alone ($9.1 \pm 12.54$ seconds).

![Figure 1. Sucking positions chosen by filial and non-filial camel calves.](image1)

![Figure 2. Suckling bout occurrence for filial and non-filial calves according to the number of sucking calves and position during sucking.](image2)
compared when there were one or two other calves (41.92 ± 5.40 seconds, F(1,32) = 5.82, p = 0.02).

Comparison between allonursing and non-allonursing dams

Comparison between allonursing and non-allonursing dams is shown in Table 3. The numbers of the animals are low for statistical comparison. Nevertheless, none of the characteristics available (age, parity, number of calves reared) seems to play any significant role in whether or not the dam allows non-filial calf to suck.

Discussion

Allosuckling in camels

In this study we brought the first description of allosuckling occurrence in camels. The results have shown that allosuckling occurred in 5 out of 10 calves from 4 camel herds containing more
than one calf in different zoos and different seasons. The allosuckling calves were in all cases the older ones in the herd, while the youngest calf from the herd never allosucked. The only herd in the study without allosuckling occurrence was the Brno Zoo in 2006, where two female calves from different mothers were kept together. Although the data were not included in the study, one author (Karolina Brandlová) observed the allosuckling occurrence there out of the range of the recording time (Gaja allosucked from Isis). These data further imply that allosuckling is common in the captive camels, comparable to captive guanaco [20], red deer [4,9], cattle [10], and captive fallow deer [11,12].

Up to three calves (always one filial and one or two non-filials, there were no more calves in the herd than three) were involved together in a sucking bout. The herd with the highest incidence of allonursing (25%) was the only herd with 3 calves providing the largest number of allonursing possibilities. The earliest allosuckling was reported in 50-days-old calf. The youngest calves in the herd were never seen allosucking, despite of the fact that they had the possibility to do it just after joining the herd where other nursing female was present. In other ungulates, except in zebra [33], allosuckling was reported from the first day [4] or the first weeks [11,20] of the calves’ lives. Even calves with the large percentage extent of allosuckling (up to 100%, Table 2) allosucked only occasionally, being weaned by their mothers and using the opportunity to get surplus milk. Generally, the sucking bouts in this study were on average much shorter than those reported by Sambraus in dromedaries [30] (43 sec and 210 sec, respectively). We found tendency for longer duration of sucking bout for filial males than for filial females [similar to Paranhos da Costa et al. [13]]. This may be caused by biased investment of females in good condition (with unlimited food supply in captivity) towards male offspring, as shown by Trivers & Willard [34] or simply by higher energetic demands by the larger sex. We did not find this difference for allosuckling bouts.

Evidence for milk-theft hypothesis

Regarding the behaviour of calves, our results widely correspond with the milk-theft hypothesis. We confirmed that (i) allosuckling calves sucked only in the lateral (other than antiparallel) position. That may have helped the calf to remain undetected by the nursing female or decrease the probability of being threatened by her. Higher incidence of allosuckling in lateral position was confirmed also by Zapata et al. [20] in guanacos. In contrast, the filial calves sucked mostly in the antiparallel position. There was no indication for changing the antiparallel to lateral positions with increasing age.

As predicted (ii), in all cases when more calves were sucking together, the non-filial calves joined filial calf during sucking non-maternal dam and the probability of allosuckling was higher when there were more calves involved in a sucking bout as reported by Ekvall [11], Zapata et al. [20] and Pluhaček et al. [7]. In connection with the lateral position this reflects the obvious tactic not to be seen or threatened by the non-maternal nursing female, characteristic for the parasitisation for the surplus milk described by Packer et al. [1].

We failed to find any support for the prediction (iii). We did not record any case of non-filial calf sucking in anti-parallel position, so we could not assess any influence of sucking position on the termination by females. This could mean that calves which tried to allosuck close to the females head were not successful. Females might have refused to nurse them and calves then learned how to approach the non-maternal dam safely and successfully as reported by Zapata [20].
In agreement with our prediction (iv), the incidence of allosuckling increased with age of the allosuckling calf as skills of the calf to outwit the non-maternal dam increased or as increased the motivation of a calf due to the weaning process of weaning. At least one of the allosuckling calves was already weaned. It corresponds with the findings of Ekvall [11] and Landette-Castillejos et al. [35], where the allosuckling occurrence increased with the length of lactation.

The suckling bouts generally lasted longer in filial calves in antiparallel position than in non-filial ones in lateral position as we expected (v). Although the sucking duration itself should not be used as a predictor of milk intake, it can reveal the level of maternal investment [36]. The sucking duration for non-filial calves which sucked alone was considerably shorter than in case when they joined already sucking filial calf. Sucking duration was longer for sucking bouts involving more than one calf. This may simply reflect the fact that in longer sucking bouts performed by a filial calf the non-filial calf got greater possibility to notice that the female is nursing, moved close to her and joined the sucking calf. The differences in sucking bout durations are also consistent with milk-theft hypothesis [1].

**Evidence for altruistic behaviour**

On five occasions a non-filial calf was allosuckling with no other calf present (ii). This could be simply a mistake from the dam, considering the fact that mentioned allosuckling bouts were considerably shorter than those including also the filial calf. On the other hand, however, we cannot reject entirely the possibility that in some cases the dams tolerated certain individuals in need as an altruistic act as was reported for red deer [4,9] and cattle [10]. Even when the non-filial calf sucked in the lateral position and together with filial calf, we cannot rule out the possibility that the females were able to recognize that they were nursing more than one calf at a time, because the size of allosuckling calves did not allow them to be completely hidden from the sight of the female even in the lateral position.

Termination of sucking bouts by the females did not differ during sucking events involving filial and non-filial calves. We could not test termination of a sucking bout involving a non-filial calf in an antiparallel position (iii) in comparison with a filial calf in the same position, because none of the non-filial calves has ever been seen in the antiparallel position. Taking into account that non-filial calves were sucking more often in the presence of the filial calf and that the non-filial calf was located more distant to the head of the dam, one could presume that the female would terminate equally sucking of filial and non-filial calves when trying to terminate the non-filial sucking. This may explain generally low level of terminations of non-filial sucking bouts and the tolerance of females.

The increasing incidence of allosuckling in older calves (iv) may also imply higher tolerance of nursing females to calves that are more familiar to them as they had lived longer in the same herd than the newborn calves.

The fact that some dams allonursed while others did not, and the fact that at least some of the calves sucked regularly and very successfully suggests a possible strategy of compensation of nutritional requirements by the young as seen in red deer and cattle [9,10]. Our data was not adequate for testing this possibility, however. On the other hand, body condition of females did not affect the probability of nursing non-filial calves in guanaco [37].

Age differences among calves in herds were larger in the zoos in this study (the first calf born in January while the last in July, see Tab. 2) than expected in the wild or in semi-captive conditions (several weeks in spring) [25]. This difference may be due to the prolonged breeding season in Europe, which may also increase the possibilities for allosuckling. Similar to Murphy et al. [38] and Cassinello [39] at the moment, we may exclude the kinship selection, as the females in the herd were not closely related to one another.

Our results correspond with those of Zapata et al. [20,21] for captive and wild guanacos, where the ‘milk theft’ is most likely explanation of allosuckling. As both camels and llamas are adapted to the extreme conditions, the allosuckling occurrence in captive animals could have two possible explanations. First, as camel females live probably in the kin groups [40], allosuckling could have developed as an adaptation for the harsh climatic conditions and can work on the principles of kin selection [1,4,9,12] which should be the objective of further testing proposed also by Zapata et al. [20]. Second, females which are kept in less extreme conditions in captivity should have lost the care about what calf is suckling them, and the calves would exploit those possibilities. Moreover, the milk production of captive domesticated camels could be higher than the normal consumption of the calf because of the domestication changes and ad libitum food intake in females. Then the females may suffer from the milk overproduction, corresponding with the milk evacuation hypothesis postulated by Roulin [2].

**Conclusions**

The results of the study support the hypothesis of ‘milk theft’, being mostly performed by calves behaving as opportunistic parasites. Nevertheless, tolerance of the camel females to non-filial calves may also suggest that at least in part allosuckling in camels might be adaptive trait, despite the fact it is mostly performed by calves which have the occasion to get surplus milk from a non-maternal female as opportunistic parasites.

**Acknowledgments**

The first and most important acknowledgement is for all zoological gardens, Zoo Praha, Zoo Ostrava, Zoo Zlín-Lešná, and Zoo Brno, with their keepers and curators which provide us the best working conditions for camel observations. We are deeply grateful to Jaroslav Šimek, Jan Pňuhaček, Luis Ehensperger, and two anonymous reviewers for their useful comments and suggestions.

**Author Contributions**

Conceived and designed the experiments: KB LB. Performed the experiments: KB. Analyzed the data: KB LB TH. Contributed reagents/materials/analysis tools: KB. Wrote the paper: KB LB TH.

**References**

1. Packer C, Lewis S, Pusey A (1992) A comparative analysis of nonoffspring nursing. Animal Behaviour 43: 263–281.

2. Roulin A (2002) Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. Animal Behaviour 63: 201–208.

3. Murphy RM, Paradisis da Costa MJR, Lima LOS, Duarte FAM (1991) Communal suckling in water-buffalo (Bubalus bubalis). Applied Animal Behaviour Science 28: 341–352.

4. Bartoš L, Vaťková D, Šíler J, Ilmmann G (2001) Adoption, allonursing and allosuckling in farmed red deer (Cervus elaphus). Animal Science 72: 483–492.

5. Hayes LD (2000) To nest communally or not to nest communally: a review of rodent communal nesting and nursing. Animal Behaviour 59: 677–688.

6. Riedman ML (1982) The Evolution of Alloparental Care and Adoption in Mammals and Birds. The Quarterly Review of Biology 57: 405–453.

7. Pňuhaček J, Bartošová J, Bartoš L (2011) A case of adoption and allonursing in captive plains zebra (Equus burchelli). Behavioural Processes 86: 174–177.

8. Kacina-Cassinello [38] at the moment, we may exclude the kinship selection, as the females in the herd were not closely related to one another. Our results correspond with those of Zapata et al. [20,21] for captive and wild guanacos, where the ‘milk theft’ is most likely explanation of allosuckling. As both camels and llamas are adapted to the extreme conditions, the allosuckling occurrence in captive animals could have two possible explanations. First, as camel females live probably in the kin groups [40], allosuckling could have developed as an adaptation for the harsh climatic conditions and can work on the principles of kin selection [1,4,9,12] which should be the objective of further testing proposed also by Zapata et al. [20]. Second, females which are kept in less extreme conditions in captivity should have lost the care about what calf is suckling them, and the calves would exploit those possibilities. Moreover, the milk production of captive domesticated camels could be higher than the normal consumption of the calf because of the domestication changes and ad libitum food intake in females. Then the females may suffer from the milk overproduction, corresponding with the milk evacuation hypothesis postulated by Roulin [2].

**Conclusions**

The results of the study support the hypothesis of ‘milk theft’, being mostly performed by calves behaving as opportunistic parasites. Nevertheless, tolerance of the camel females to non-filial calves may also suggest that at least in part allosuckling in camels might be adaptive trait, despite the fact it is mostly performed by calves which have the occasion to get surplus milk from a non-maternal female as opportunistic parasites.

**Acknowledgments**

The first and most important acknowledgement is for all zoological gardens, Zoo Praha, Zoo Ostrava, Zoo Zlín-Lešná, and Zoo Brno, with their keepers and curators which provide us the best working conditions for camel observations. We are deeply grateful to Jaroslav Šimek, Jan Pňuhaček, Luis Ehensperger, and two anonymous reviewers for their useful comments and suggestions.

**Author Contributions**

Conceived and designed the experiments: KB LB. Performed the experiments: KB. Analyzed the data: KB LB TH. Contributed reagents/materials/analysis tools: KB. Wrote the paper: KB LB TH.

**References**

1. Packer C, Lewis S, Pusey A (1992) A comparative analysis of nonoffspring nursing. Animal Behaviour 43: 263–281.

2. Roulin A (2002) Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. Animal Behaviour 63: 201–208.

3. Murphy RM, Paradisis da Costa MJR, Lima LOS, Duarte FAM (1991) Communal suckling in water-buffalo (Bubalus bubalis). Applied Animal Behaviour Science 28: 341–352.

4. Bartoš L, Vaťková D, Šíler J, Ilmmann G (2001) Adoption, allonursing and allosuckling in farmed red deer (Cervus elaphus). Animal Science 72: 483–492.

5. Hayes LD (2000) To nest communally or not to nest communally: a review of rodent communal nesting and nursing. Animal Behaviour 59: 677–688.

6. Riedman ML (1982) The Evolution of Alloparental Care and Adoption in Mammals and Birds. The Quarterly Review of Biology 57: 405–453.

7. Pňuhaček J, Bartošová J, Bartoš L (2011) A case of adoption and allonursing in captive plains zebra (Equus burchelli). Behavioural Processes 86: 174–177.
10. Víchová J, Bartoš L (2005) Allosuckling in cattle: Gain or compensation? Applied Animal Behaviour Science 94: 223–235.

11. Ekvall K (1998) Effects of social organization, age and aggressive behaviour on allosuckling in wild fallow deer. Animal Behaviour 56: 695–703.

12. Birgersson B, Ekvall K, Temrin H (1991) Allosuckling in fallow deer, Dama-dama.

13. Paranhos da Costa MJR, Andriolo A, de Oliveira JFS, Schmidek WR (2000) Allosuckling and allosucking in captive common hippopotamus. Mammalian Biology 76: 380–383.

14. Pusey AE, Packer C (1994) Non-offspring nursing in social carnivores - minimizing the costs. Behavioral Ecology 5: 362–374.

15. Wilkinson GS (1992) Communal nursing in the evening bat, Nycticeius humeralis. Behavioral Ecology and Sociobiology 31: 225–235.

16. Boneas DJ, Craig MP, Honigman L, Austin S (1998) Fostering behavior and the effect of female density in Hawaiian monk seals, Monachus schauinslandi. Journal of Mammalogy 79: 1060–1069.

17. Reiter J, Simson N, Bocaf B (1978) Northern elephant seal: The transition from weaning to nutritional independence. Behavioral Ecology and Sociobiology 3: 337–367.

18. Špíinka M, Illmann G (1992) Suckling behaviour of young dairy calves with their own and alien mothers. Applied Animal Behaviour Science 33: 165–173.

19. Zapata B, Gaete G, González B, Ebensperger L (2009) A case of allosuckling in wild guanacos (Lama guanicoe). Journal of Ethology 27: 295–297.

20. Zapata B, Gonzalez BA, Ebensperger LA (2009) Allonursing in captive guanacos. Lama guanicoe: Milk theft or misdirected parental care? Ethology 115: 731–737.

21. Zapata B, Ebensperger L, Latorre E, González B, Fernández F, et al. (2006) Amamantamiento de crías ajenas en guanacos (Lama guanicoe) en cautiverio: ¿cuidado maternal mal dirigido o robo de leche? In: D O, M M, S P, editors. Recientes Avances en Camelid Reproduction: International Conference, Dubai, 2nd–6th February 1992. pp. 317–318.

22. Al Eknah MM (2000) Reproduction in Old World camels. Animal Reproduction Science 65: 301–306.

23. Hare J (2008) Camelus ferus. IUCN Red List of Threatened Species Version 2009 2 Available: www.iucnredlist.org. Accessed 6 January 2010.

24. ISIS (2010) International Species Information System. Available: http://www. iis.org. Accessed 14 January 2010.

25. Al Ennah M (2000) Reproduction in Old World camels. Animal Reproduction Science 60: 583–592.

26. Eklund D (1986) Parturition in the camel (Camelus dromedarius) and some behavioural aspects of their newborn. Comparative Biochemistry and Physiology a-Physiology 84: 413–419.

27. Dorges B, Hureck J, Klingel H. Behaviour and social organization of feral camels in central Australia. In: Allen WR, Higgins AJ, Mayhew IG, Snow DH, Wade JF, editors; 1992. Proceedings of the First International Camel Conference, Dubai, 2nd–6th February 1992. pp. 317–318.

28. Tibary A, Anouassi A (2001) Neonatal care in Camélids. In: Skidmore I, Adams GP, editors. Recent Advances in Camelid Reproduction: International Veterinary Information Service.

29. Degen AA, Eklum M (1987) A preliminary report on the energy intake and growth rate of early weaned camel (Camelus dromedarius) calves. Animal Production 40: 301–306.

30. Sambras HJ (1995) Quantitative data on the suckling of dromedaries. Journal of Animal Breeding and Genetics-Zeitschrift Fur Tierzuchtung Und Zuchtungsbiologie 112: 469–479.

31. Altmann J (1974) Observational study of behavior - sampling methods. Behaviour 49: 227–267.

32. Drábiková J, Bartošová J, Bartoš L, Kotrba R, Pluhaček J, et al. (2008) Suckling and allosuckling duration in farmed red deer (Cervus elaphus). Applied Animal Behaviour Science 113: 215–223.

33. Olleova M, Pluhacek J, King SRB (2012) Effect of social system on allosuckling and adoption in zebras. Journal of Zoology 288: 127–134.

34. Trivers RL, Willard DE (1973) Natural selection of parental ability to vary sex ratio of offspring. Science 179: 90–92.

35. Landete-Castillejos T, García A, Garde J, Gallego L (2000) Milk intake and production curves and allosuckling in captive Iberian red deer, Cervus elaphus hispanicus. Animal Behaviour 60: 679–687.

36. Cameron E, Lankater W, Stafford K, Minot E (2003) Social grouping and maternal behaviour in feral horses (Equus caballus): the influence of males on maternal protectiveness. Behavioral Ecology and Sociobiology 55: 92–101.

37. Zapata B, Correa I, Soto-Gameba M, Latorre E, González BA, et al. (2010) Allosuckling allows growing offspring to compensate for insufficient maternal milk in farmed guanacos (Lama guanicoe). Applied Animal Behaviour Science 122: 119–126.

38. Murphy RM, Paranhos da Costa MJR, Gomes da Silva R, de Souza RC (1995) Allonursing in River buffalo, Bubalus bubalis - nepotism, incompetence, or thievery. Animal Behaviour 49: 1611–1616.

39. Cassinello J (1999) Allosuckling behaviour in the domesticated guanaco (Lama guanicoe) en cautiverio: the influence of males on maternal protectiveness. Behavioral Ecology and Sociobiology 53: 92–101.

40. Schaller GB (1986) Wildlife of the Tibetan Steppe: University of Chicago Press. 373 p.