

Research article

A comparative study of nightly allonursing behaviour in four zoo-housed groups of giraffes *Giraffa camelopardalis*

Franziska Zoelzer, Caroline Engel, Paul W. Dierkes and Anna L. Burger

Bioscience Education and Zoo Biology, Goethe University Frankfurt, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany

Correspondence: Franziska Zoelzer, email: zoelzer@bio.uni-frankfurt.de

Keywords: allosuckling, group housing, zoo animal

Article history:

Received: 23 Oct 2019

Accepted: 16 Mar 2020

Published online: 31 Jul 2020

Abstract

In the wild, giraffes *Giraffa camelopardalis* have a pronounced and complex social structure, which is characterised, for instance, by the joint rearing of calves. Allomaternal behaviour results in the formation of nursery groups and the suckling of non-filial calves. Despite externally determined group size and composition, this behaviour has also been observed in zoological institutions. It is believed that this study is the first to focus on the nocturnal allomaternal behaviour of four giraffe herds in three German and one Dutch zoos. Using video recordings of 30 individuals over 12 nights, all allonursing events were analysed using the continuous behaviour sampling method. Substantial differences were observed among the four zoos in the frequency and nightly course of allonursing behaviour. In all zoos, allonursing occurred in roughly two periods during the night, which were highly variable in length according to the zoo. A combination of the nocturnal activity, group persistency and group size seems to drive allonursing behaviour in the analysed giraffe groups. Additionally, the composition of allosuckling calves is zoo-specific and includes two to three animals. The results show that allomaternal behaviour in the observed zoos can rather be explained with the milk-theft-hypothesis than with the theories of misdirected-care or reciprocity. Overall, the study showed that nocturnal group-housing of giraffes of various ages enables allonursing and therefore complements natural behaviour by the formation of nursery groups.

Introduction

Many mammal species develop distinctive social behaviours, which offer various advantages to the individuals involved. One such behaviour that has been little researched so far is alloparenting, the suckling of non-related calves alongside the individual's own offspring. It is advantageous for the nursing mother for the high energy costs associated with lactation to be distributed among several individuals (Trivers 1971; Maniscalco et al. 2007). Despite the risks of pathogen transmission, the calves also benefit from this behaviour through an improved nutrient supply (Bartoš et al. 2001a) and through a strengthened immune system (Roulin and Heeb 1999; König 2006). Alloparental behaviour has been described in particular in ungulates such as zebras *Equus burchellii*,

guanacos *Lama guanicoe*, Pyrenean chamois *Rupicapra pyrenaica* and reindeer *Rangifer tarandus* in the wild and in zoological institutions (Zapata et al. 2009; Pluháček et al. 2011; Engelhardt et al. 2016; Scornavacca et al. 2018).

Wild giraffes *Giraffa camelopardalis* have a highly complex social structure (Bercovitch and Berry 2010, 2013; Carter et al. 2013). One characteristic of this is community parental care through the formation of nursery groups (Langman 1977; Riedman 1982). Giraffes show strong social bonds and females join other cows and their offspring a few days after birth. Often, only a few cows remain with the calf group during daily browsing, therefore allonursing has also been observed in the wild (Pratt and Anderson 1979; Estes 1992; Gloneková et al. 2017).

Table 1. Characterisation and recording period of the observed giraffe groups. The composition is given in the format 'number of male animals . number of female animals'. Age classification is based on Dagg and Foster (1982) and van der Jeugd and Prins (2000), where animals under 18 months are classified as juvenile, animals up to 4 years old as subadult and animals 4 years and older as adult.

	Opel-Zoo	Cologne Zoo	Osnabruck Zoo	Burgers' Zoo
Subspecies	<i>G. c. rothschildi</i>	<i>G. c. reticulata</i>	<i>G. c. reticulata</i>	<i>G. c. rothschildi</i>
Observed individuals	2.3	1.4	1.4	6.9
adult	0.1	0.2	0.3	0.7
subadult	1.2	0.1	1.0	4.4
juvenile	1.0	1.1	1.0	1.0
Observation days	12	12	12	12

Group composition of zoo giraffes is determined by the zoo. Even so, captive giraffes appear to form nursery groups and display the highest allonursing rate among zoo-kept mammals along with the water buffalo *Bubalus bubalis* (Gloneková et al. 2016). Nevertheless, giraffe cows are often separated from the group shortly before giving birth, in order for the birth to be monitored and to protect the calf. So far, it is unclear to what extent group size and composition influences the formation of nurseries and the associated allonursing.

This study contributes to existing research on allomaternal behaviour in the daytime, by comparing nightly allomaternal behaviour in giraffes in four zoos. The study takes a particular focus on the composition and order of allosuckling calves, as well as the nightly course of allonursing events.

Methods

Animals and keeping conditions

A total of 30 individuals from three German and one Dutch breeding groups were observed for this study (Table 1). At the time of observations, the giraffe group at Opel-Zoo in Kronberg consisted of five Rothschild giraffes *Giraffa camelopardalis rothschildi*: one nursing cow, three subadult animals and one juvenile calf. Due to sexual maturity, some subadult animals were alternately isolated from the group at night. At Cologne and Osnabruck Zoos, group size was also five animals each. During the period of observation, two cows each nursed a calf at Osnabruck Zoo, and one cow nursed a calf at Cologne Zoo. The largest group, of 15 individuals, was housed at Burgers' Zoo, in Arnhem, where four of seven adult cows nursed a calf during data collection.

All animals in all zoos had access to the outdoor enclosure for several hours during the day. Adult bulls were separated from the group at night, as well as one alternating subadult animal at Opel-Zoo. Animals isolated from the group were not included in the study.

Data collection and evaluation

Data were recorded in each zoo for 12 nights from 1700 to 0700 the following day, using video cameras. Up to five Mobotix AllRound Dual M15 cameras per zoo were installed to cover the entire indoor enclosure. The resulting 58 nights (696 hours) of video material were analysed with a behavioural observation research interactive software, BORIS Version 2.1.5 (Friard and Gamba 2016). Using the behaviour sampling method (Martin and

Bateson 2007), all allonursing events were continuously recorded throughout the night. Total numbers, duration of events and the animals involved were recorded. Successful allonursing was defined as the simultaneous suckling of at least two calves for a period of five seconds or more. If the nursing cow prematurely terminated the suckling attempt of another calf, or if the suckler was not allowed to suckle, this was categorised as attempted allonursing.

Due to the small sample size, despite a positive Kolmogorov-Smirnov test for normal distribution ($P=0.86$), a non-parametric test was used for further evaluation. In addition to calculating the percentage frequencies of the various calf compositions during allonursing, a comparison of suckling duration between the four groups was performed using Kruskal-Wallis tests. The ages of the suckling calves at Burgers' Zoo were compared to the three other zoos pooled together and tested using the Mann-Whitney U test.

Results

A total of 58 allonursing attempts occurred during the recording period. Of these, 23 were observed in Burgers' Zoo, 17 in Opel-Zoo, 11 in Cologne Zoo and seven in Osnabruck Zoo (Table 2). In general, allosuckling durations did not differ significantly between the zoos ($P=0.12$). Regarding mean suckling duration, Burgers' and Opel-Zoo were similar, whereas giraffes at Cologne Zoo exhibited a considerably lower suckling duration. The shortest occurred at Osnabruck Zoo, about half the durations seen at the other zoos. There was the least variation in allosuckling duration at Cologne Zoo, followed by Opel-Zoo and Osnabruck Zoo. The greatest variation in allosuckling duration occurred at Burgers' zoo. Considering all factors, Cologne Zoo and Opel-Zoo displayed similar allosuckling durations, whereas the allosuckling events in Osnabruck were the shortest, and those at Burgers' Zoo the most varied in length.

The combination of sole nursing and allonursing events reveals that, in all zoos, allonursing attempts occur less frequently (46.4%) than nursing attempts of a filial calf alone (Figure 1). A total of 36.0% of these were successful allonursing events, whereas 10.4% were rejected. Furthermore, the proportions of allonursing and nursing events varied between zoos. The greatest proportion of allonursing occurred at Cologne Zoo, with 53.3% successful and 20.0% rejection events. Additionally, 6.7% were successful sole nursing events at this zoo, representing the lowest proportion across all zoos. Burgers' Zoo exhibited a total of 63.6% successful

Table 2. Comparison of allomaternal behaviour in the four zoos studied. The table shows the total number of allonursing attempts, mean suckling duration, the number of suckling calves and the number of giraffe cows showing allomaternal behaviour per zoo.

	Opel-Zoo	Cologne Zoo	Osnabruck Zoo	Burgers' Zoo
Total allonursing attempts	17	11	7	23
Mean allosuckling duration [sec]	33.6±12.3	29.1±8.9	14.4±13.4	33.0±19.7
Allosuckling calves	2-3	3	2	2-3
Allonursing cows	1	1	1	4

allonursing events, representing the most frequent allonursing of all zoos. Furthermore, no rejection events, while nursing filial offspring alone, were observed, and this zoo exhibited the second lowest allonursing rejection rate of all. In Opel-Zoo, allonursing attempts occurred slightly less often than sole nursing attempts. Here, the rejection rate of allonursing was only half that of filial nursing. The least frequent occurrence of allonursing, both successful events and attempts, were observed at Osnabruck Zoo. Only 12.2% of events were successful allonursing events. Therefore, this zoo exhibited the highest frequency of sole nursing events, at 70.7%, with only 12.2% rejection rate.

Composition and age of allosuckling calves

Calf-dam combinations during allonursing events are zoo specific. Overall, allonursing occurred with either two or three participating calves in different compositions (Figure 2). The most common combination (48.3%) in all zoos comprised the filial calf and one other non-related calf. Successful allonursing occurred with the filial and two non-filial calves suckling together (16.7%), or with two filial and one other non-filial offspring (13.3%). The rejection rate for all combinations was similar, at 5.0–8.3%. Just sole suckling attempts of non-related calves was rejected consequently.

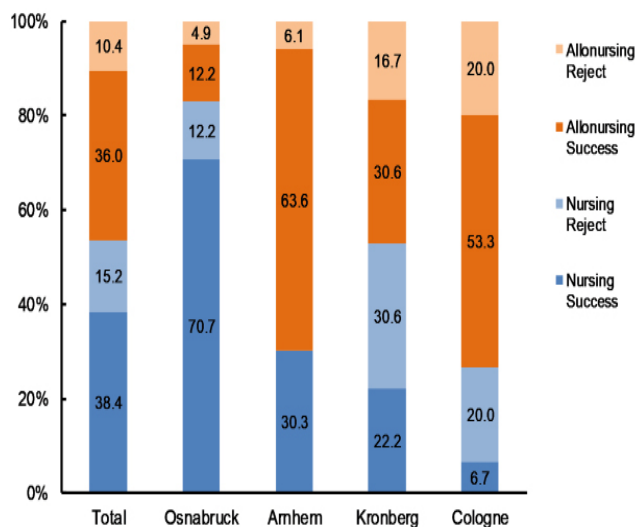


Figure 1. Proportions of suckling and allosuckling events across the four zoos. Successful and rejected allonursing events are shown in proportions for each zoo and for all zoos combined.

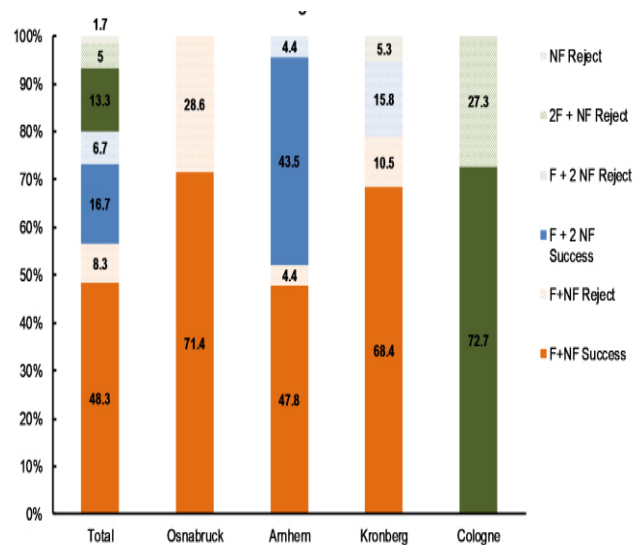


Figure 2. Calf-dam pairings during allonursing in the four zoos. The x-axis shows the zoos, the y-axis the occurrence of a combination in percent. The calf combinations are displayed in different colours, with dark colours representing successful attempts and light colours representing rejections. A distinction is also made between filial (F) and non-filial (NF) calves.

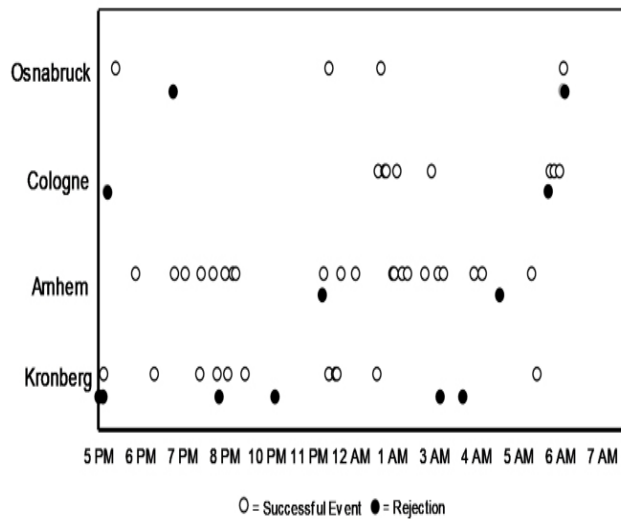


Figure 3. Nocturnal course of allonursing events. The x-axis shows the observation period between 1700 and 0700, the y-axis depicts the four zoos. Successful allonursing events are coloured in black and rejected attempts are coloured in grey.

In Osnabruck and Cologne Zoos, only one combination was observed and the same calves were constantly involved in allosuckling events, whereas the other two zoos exhibited allonursing attempts in changing calf combinations. Osnabruck and Cologne Zoos both showed a similar rate of successful allonursing and rejections. The only difference was that the cow nursed her juvenile calf together with an unrelated subadult in Osnabruck Zoo, whereas two filial calves were nursed together with a non-filial calf in Cologne Zoo. In contrast, various calf combinations were observed in Opel-Zoo and Burgers' Zoo. However, successful allonursing in Opel-Zoo only occurred in the same combination as in Osnabruck Zoo, involving the juvenile calf of the nursing cow and an unrelated subadult. In contrast, allonursing attempts with three involved calves (15.8%) or sole suckling attempts of non-filial calves (5.3%) were consistently rejected. Only in Burgers' Zoo did different calf combinations lead to successful allonursing events. Here, a filial calf was nursed in combination with one or two non-related ones to the same extent. The rejection rate of 4.4% was lower than in the other zoos.

It is noticeable that in all zoos, allomaternal behaviour was predominantly triggered by the filial calf. Only if the cow's own calf was already suckling, did the cow allow non-filial calves to approach and participate in the suckling process. Additionally, only the cow with the youngest offspring were observed to tolerate allonursing, even if there is another nursing cow in the group. An exception was observed at Burgers' Zoo, where four giraffe cows showed allomaternal behaviour. Nevertheless, the cow with the youngest calf was most frequently (52.2%) involved in the allosuckling events. Interestingly, this cow was involved in the longest suckling bouts, with an average duration of 47.7±13.4 seconds. In comparison, the average suckling time for the remaining cows was considerably shorter, at 20.7±15.9, 18.8±13.4 and 10.0±0 sec.

The giraffes involved in allonursing in Osnabruck Zoo and Opel-Zoo were all younger than 20 months old. Although attempts by

a 36-month-old subadult cow occurred in Opel-Zoo, they were immediately rejected. In contrast, the ages allonursing giraffes in Cologne and Burgers' Zoos were higher. Besides the two juvenile calves, a 27-month-old cow was involved in the allonursing events at Cologne Zoo. In Burgers' Zoo, the mean age of the nine suckling giraffes was 24.5 months. In addition, successful allonursing involving two adult cows was also observed. Therefore, the allosuckling giraffes at Burgers' Zoo were significantly older ($P=0.02$) compared to the three other zoos.

Alloparenting throughout the night

Regarding the nightly occurrence of allonursing events, the four zoos revealed different timings. In Osnabruck and Cologne Zoos, allonursing events only occasionally took place during the night, and in roughly two time spans (Figure 3). The first period occurred earlier in Osnabruck, between midnight and 0130, compared to Cologne Zoo, when it occurred between 0115 and 0300. The second period of successful allonursing events occurred in the early morning hours between 0630 and 0700 in both zoos. In comparison, allonursing in Burgers' Zoo and Opel-Zoo occurred in the early evening. The first allonursing period starts at 1700 in Opel-Zoo and 1800 in Burgers' Zoo, continuing until 2130. Similarly to the other zoos, the next phase in Opel-Zoo occurred around midnight. Although there were some events in Burgers' Zoo, the highest peak in this zoo occurred a bit later, between 0145 and 0315, similar to in Cologne Zoo. In both Burgers' Zoo and Opel-Zoo, the last allonursing event was observed in the morning, at around 0600.

In general, most allonursing events took place in Burgers' Zoo. Here, the time spans during which allonursing events were observed were the longest. Furthermore, some successful allonursing occurred in between of those phases. Therefore, allonursing was more or less spread over the whole night in this zoo. Aside from the first allonursing phase in Opel-Zoo, which lasted for about 4 hours, the remaining time phases in the other three zoos were much shorter than at Burgers' Zoo (Figure 3).

Discussion

Allosuckling duration and nightly course across different zoos

Successful allonursing occurred in 36.0% of all nursing attempts. This is slightly higher than that reported in other ungulate studies, where proportions of allonursing events ranged from 23.7 to 30.5% for captive giraffes (Gloneková et al. 2017), 32.0% for red deer (Bartoš et al. 2001b) and about 20% for water buffaloes (Murphey et al. 1995) and cattle (Víchová and Bartoš 2005). Among the four observed zoos, the most frequent allonursing took place in Burgers' Zoo, which is the zoo with the largest giraffe group. Additionally, this was the only zoo where more than one cow allowed allonursing, thus leading to a higher frequency of nursing of non-related offspring. As the group contained nine potentially suckling calves, the allonursing rejection rate was quite low and sole filial nursing was never rejected. In contrast, only three calves were observed to allosuckle in Cologne Zoo and Opel-Zoo. Here, allosuckling events occurred less often than in Burgers' Zoo, and with slightly higher rejection rates. Furthermore, sole filial suckling attempts were more often rejected than accepted by the participating cow. In contrast, at Osnabruck Zoo, the nursing of one filial calf alone made up for more than three-quarters of all nursing attempts, whereas allonursing occurred in only 12.2% of events. A possible reason for the low incidence of allonursing in Osnabruck Zoo is the young age of the participating cow. At 6 years old, this cow may be inexperienced in raising offspring. According to the residual reproductive value hypothesis, this may lead to less allomaternal behaviour compared to older and more experienced cows (Gadgil and Bossert 1970; Green 1990;

Cameron 2000). Therefore, the present data support the results from Gloneková et al. (2019a) in which they describe the influence of parity on allomaternal behaviour in giraffes.

Opel-Zoo, Cologne and Burgers' Zoos all exhibited similar allosuckling durations, with higher deviations observed in Burgers' Zoo. This can be explained due to the overall high frequency of allonursing events. In contrast, allonursing occurred less in Osnabruck, but the observations support those recorded by Gloneková et al. (2017). Furthermore, non-filial calves approached shortly after the filial calf had started suckling and were mostly not rejected by the cow. Therefore, the suckling duration of filial and non-filial offspring was similar, as recently shown by Gloneková et al. (2019b).

For the first time, this study focused on nocturnal allonursing behaviour in zoo-housed giraffes. Over all zoos, allonursing occurred in roughly two time periods, which varied in length and event frequency. Thus, the four study zoos can be divided into two groups. Firstly, in Osnabruck and Cologne Zoos, allomaternal behaviour during the evening hours was low to non-existent. Allonursing events only occasionally took place during the night, especially around midnight and in the early morning. Secondly, in contrast, the giraffe groups in Burgers' Zoo and Opel-Zoo were characterised by a higher frequency of allonursing in longer phases all through the night. The differences between zoos can be explained by the group structure and different sleeping and resting behaviours. The giraffe groups in Osnabruck and Cologne Zoos each consisted of five individuals, plus one adult bull who was isolated at night. The video recordings revealed those giraffes to be very calm at night and to have distinctive resting and sleeping periods. Accordingly, the allonursing events occurred only in short, active-browsing intervals.

The group composition at Opel-Zoo underwent daily changes during the observation period. As the subadult animals were sexually mature, they were alternately separated into individual boxes at night. As a result, the group showed higher levels of nocturnal activity, especially in the evening, leading to a higher frequency of allonursing events during this period. In Burgers' Zoo, the giraffes showed a similar night activity budget, but the group composition remained constant. The increased activity in this zoo can probably be explained by the large group size, of 15 animals. Though the animals rested calmly together, movement of one individual often affected the others in the group, thus resulting in an increased overall level of activity. This combination of increased nocturnal activity, a high number of suckling calves and several nursing cows, fostered the highest occurrence of allonursing events and in the longest periods, of all study zoos.

Composition and age comparison of allosuckling calves

This study observed zoo-specific calf-dam combinations, with two or three participating calves during allonursing. The most common combination comprised the filial calf plus one other unrelated calf. This combination was observed in three of the four zoos, even in cases where there were more potential suckling calves in the group. Suckling of three calves was often observed in Burgers' Zoo and exclusively seen in Cologne Zoo, with two filial and one unrelated calf involved in the latter. The observed calf combinations are consistent with studies on other even-toed ungulates, such as reindeer and guanacos (Zapata et al. 2009; Engelhardt et al. 2014), where the most allonursing events included one filial and one non-filial offspring, followed by a combination of one filial and two unrelated calves. In contrast, sole allosuckling attempts of giraffe calves with non-related cows seldom occurred and were consistently rejected. Additionally, the allosuckling rejection rate was much higher for the giraffes in the present study, compared to those on guanacos and reindeers.

Additionally, this study found that the filial calf suckles first,

and that this acts as a trigger for the allosuckling attempt by other calves. This behaviour can be explained by the milk-theft hypothesis (Packer et al. 1992; Maniscalco et al. 2007; Zapata et al. 2009), which focuses on the opportunistic behaviour of the calves. For giraffes, this theory has been proven in various zoos, as well as in the field (Gloneková et al. 2016; Saito and Idani 2018). In both environments, successful allonursing only occurs if the non-filial calf approaches while the cow's own young is already suckling. Sole suckling attempts of unrelated calves are rarely seen and mostly not permitted. Additionally, Saito and Idani (2018) observed that only one cow in the wild tolerates allonursing, which is in line with the present results.

Further theories have been developed to explain alloparental behaviour. For example, the reciprocity theory states that two giraffe cows increase the fitness of their calves by nursing the other's offspring (Pusey and Packer 1994). This mutual behaviour has been observed particularly in ungulates living in groups with a pronounced social structure (Jones and Treanor 2008; Engelhardt et al. 2015). However, the giraffes in this study revealed no such reciprocal behaviour. In Cologne Zoo, Osnabruck Zoo and Opel-Zoo, only the cow with the youngest calf allowed allonursing, even when there were other nursing cows in the group. In Burgers' Zoo, where four adult cows tolerated allonursing, the cow with the youngest offspring was more often involved in allomaternal behaviour, followed by the mother of the second youngest calf. There are two possible explanations for the observation of only giraffe cows with a juvenile calf showing allomaternal behaviour. First, juvenile calves are nursed very frequently. In the context of the milk-theft hypothesis, this increases the number of opportunities for allonursing. Second, it is possible that cows with juvenile offspring are in general more tolerant of allosuckling, because a rejection may interrupt the lactation process of their own calf. As younger calves have a higher demand for milk, the cow may not intervene for the benefit of its own offspring.

Similar to the theory of reciprocity, the misdirected-care hypothesis (Boness 1990; Cassinello 1999; Nuñez et al. 2013), which states that cows are unable to distinguish between their own and non-related offspring, cannot be confirmed by this study. No cows nursed an unrelated calf without simultaneous suckling of their own offspring. Therefore, it seems possible for a cow to distinguish between its own and an unrelated offspring.

Giraffe calves are normally nursed until the age of 13–17 months (Hall-Martin et al. 1977; Pratt and Anderson 1979; Rennoisé and Girin 2005). Calves as old as 20 months in Opel-Zoo and Osnabruck and 27 months in Cologne Zoo were regularly involved in allonursing. In contrast, some adult giraffes in the herd in Burgers' Zoo participated in allosuckling. This comparatively high tolerance of the cows can be explained by the group size of 15 individuals. It may be more energy-intensive for the cows to fend off many suckling giraffes than it is beneficial for the own calf to suckle alone. This would explain why the rejection rate in Burgers' Zoo (9%) is almost three times lower than in the other zoos.

Regarding zoo management, the knowledge gained in this study provides insights into the social structure of giraffes in nocturnal community housing. The structure of allomaternal behaviour is similar to that observed in free-living giraffes, for example in the formation of nursery groups. Since one of the main concerns in zoo animal husbandry is to promote natural behaviours, allonursing might represent an easy to implement step along these lines. Therefore, juvenile offspring could be returned to the rest of the group in a timely manner after birth, in compliance with veterinary guidelines. Furthermore, it has been shown that allonursing has a positive effect on reproductive success in various species (Macdonald 1979; Moehlman 1979; Wells 2003). As the preservation of genetic diversity is another main concern

of zoos, nightly group-housing of giraffes of different age groups might contribute to this. Nevertheless, differences were observed regarding allonursing frequencies among the four zoos. Further studies on calf growth and physical development would be necessary to further understand the effects of frequent or absent allosuckling.

Conclusion

In general, the high tolerance towards non-filial calves by giraffe cows can be attributed to the natural formation of nursery groups in the wild. Although allomaternal behaviour has been less studied in zoos, the general structure appears similar to that observed in wild giraffes. Examples include the unsuccessful attempts by calves to suckle unrelated cows when on their own, and the fact that usually only one giraffe cow tolerated allonursing. Furthermore, the findings support the milk-theft hypothesis and provide no support for the reciprocal theory or the misdirected-care hypothesis. In addition, substantial differences were found in the frequency and nightly course of allonursing among zoos, which might be founded in giraffe group composition and thereby associated nightly activity.

Acknowledgements

The authors heartily thank Dr. Martin Becker and Jörg Beckmann at Opel-Zoo in Kronberg, Constanze Mager at Burgers' Zoo in Arnhem, Andreas Wulfange at Osnabruck Zoo and Dr. Alexander Sliwa at Cologne Zoo as well as all keepers in the respective zoo for their help and support with the camera equipment. The authors are very grateful to the "von Opel Hessische Zoostiftung" for financing this study within the framework of the Opel-Zoo foundation professorship zoo biology.

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