

THE APPLICATION OF THE CHEETAH (*Acinonyx jubatus*) SOCIAL BEHAVIORAL FEATURES FOR OPTIMIZING HOLDING CONDITIONS IN CAPTIVITY

Elena V. Chelysheva, PhD
(Moscow, Russia)

Abstract

In two zoos (Moscow, Russia and Deit, UAE), 15 groups from 28 cheetahs of different ages and sex were formed: 1 coalition of males, 10 groups of females and 4 mixed groups. Social behavior was studied and breeding was monitored in order to identify the optimal group composition for reproduction in captivity. Two types of groups of females are described. Type I is characterized by similarities in behavioral patterns to the coalitions of males, including: the synchronization of daily activities, low level of aggression and high level of affiliative contacts. In such "coalitions of females", a high level of tactile contacts between individuals (social grooming, joint rest), synchronization of births, co-raising litters and adoptions were observed. For breeding cheetahs in captivity, a "female coalition" is the most promising type of group.

Key words: *Acinonyx jubatus*, cheetah, coalition, breeding, affiliative behaviour, sociality

Introduction

Cheetahs have been held in captivity for over 1500 years; however, breeding remains a problem and, to this day, a self-sustaining population has never been achieved in captivity. In the wild more than 90% of females reproduce, while in captivity the figure is only 20% (Terio et al., 2003). Many researchers attribute this to the poor management of cheetahs and to their behavior (Wildt et al., 1993; Lindburg et al., 1993; Caro, 1994; Brown et al., 1996; Munson et al., 2005). In particular, the question regarding optimal conditions of holding mixed- and same-sex individuals is widely debated (Wielebnowski, et al., 2002). It is recommended that cheetahs are kept according to their natural social organization: males singly or in coalitions and females singly (Caro, 1993; Laurenson, 1993). This, however, ignores information regarding the existence of groups of females in the wild (see, for example, McVittie, 1979) and positive experience of holding groups of females in captivity (CCF, 1998).

Materials and methods

Work was performed from 1983 to 2001 at the Moscow Zoo, Russia (MZ) and from August 2002 to March 2003 at the zoo in Deit, UAE (DZ). In total, 15 groups of different composition were created of 28 cheetahs: 1 male coalition, 11 female groups and 4 mixed groups. At the MZ, 12 groups were created of 21 (8.13) cheetahs between the ages of 6 months and 10 years. Of those: 1 coalition of 2 males and 7 groups of females (2 groups of 2 females; 2 groups of 3 females; 3 groups of more than 3 females) and 4 mixed groups. At the DZ, 3 groups of 2 females were formed of 7 (2.5) cheetahs between the ages of 3.5 and 4 years. All animals were individually

identified. Prior to the formation of the groups, the animals were placed in adjacent enclosures for a period of time, during which they had contact with one another through the bars. If the individuals demonstrated friendly behavior, they were put together. In each case the animals were provided an enclosure of an approximate average of 600 m² (580-625 m²) and were fed separately. The behavior of cheetahs which made up the groups, as well as the individually held animals of both sexes and the existing coalition of males, was observed.

Animal behavior was observed by continuously logging (Popov, Ilchenko, 1990) 2-4 hour sessions. The following behavioral patterns were recorded: self-grooming, grooming the companion (including mutual grooming), playing alone, playing with the companion, following the companion, tactile contact, joint rest, aggression towards the companion and marking (urine-spraying, scuffing with or without urination, rubbing an object with the head and neck, clawing objects). Touching the companion during any interaction, except during rest, play and aggression, was considered tactile contact; for example, while lying near the companion, a cheetah touches the other's head or body with its forepaws or rubs the other's head with its own (this may be followed by mutual grooming). Another example: a cheetah steps towards the either moving or idle companion, and touches or "picks" its hind legs with its paw (which can then be followed by play). When the distance between cheetahs lying down during rest was less than 1m (the range of potential physical contact) or when the animals were in direct contact—lying their head or limbs on their companion for example—it was considered joint rest.

Additionally, the reproductive activity of the animals was monitored—behavior while in heat, courting, mating, birthing, the number of cubs per litter and parental behavior.

Two types of groups of females, made up of 2-3 individuals, were defined based on these observations. The first type of group included breeding females; the second type included non-breeding females. A comparison of the different types of behavior in different groups of cheetahs was made by creating behavioral profiles of these groups (average findings for the group). Profiles were constructed as follows:

1. Since the number of times the same pattern was displayed over time varied in different observation sessions, it was necessary to take into account the heterogeneity of the observations. For this, all of the time spent observing animals has been divided into hours.

2. The number of times each pattern was displayed in one hour was counted for each animal in each group.

3. Furthermore, the total number of each pattern was totaled for all of the animals of one group and the sum was divided by the total number of hours observed for this group and then by the number of animals in the group.

4. To assess the degree of differences in the frequency of each type of behavior in different groups, the standard Excel TTEST function was used based on the criteria for calculating Student and reliability of differences between mean values in two arrays of data. Confidence intervals were constructed using the standard, built-in Excel CONFIDENCE function with a 0.05 significance level.

Results and discussion

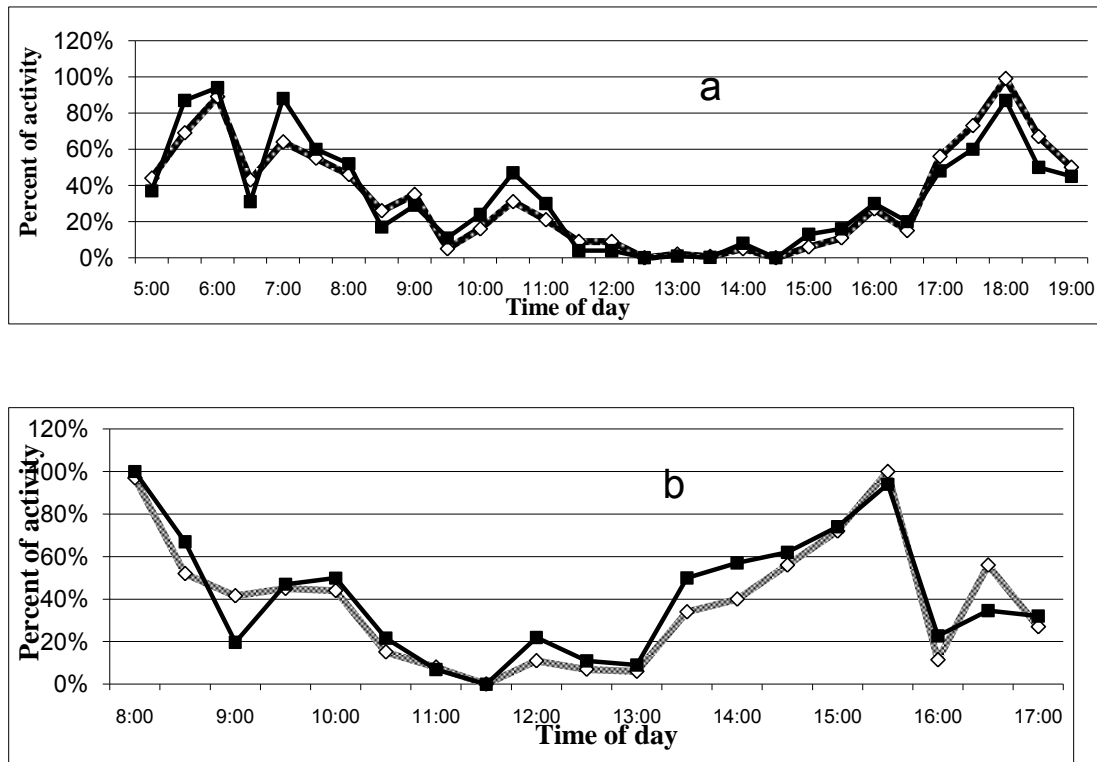
Coalitions of males. Of the 6 attempts to create coalitions of males, only one was successful, namely: one coalition of two presumably related 3 year old males, received by the MZ at the same time, was created. The five other attempts to put together four unrelated males (between the ages of 1 and 5.5 years) at the DZ and MZ in various combinations failed due to high level of aggression and a lack of affiliative contacts.

The animals' behavior in the artificially created coalition at the MZ compared with the behavior of the cheetahs in the existing coalition of two 4 year old brothers who were kept together at the DZ since birth. In the created coalition, signs of three patterns of affiliative behavior (grooming with companion, playing with companion and joint rest) were more frequent than in the animals in the existing coalition, with little to no aggression (Table 1). Additionally, the synchronization of daily activities with the companion was observed (Fig. 1). The group of males created at the MZ can be considered an authentic coalition based on the basic behavioral characteristics of male cheetah coalitions in the wild, which include: high level of affiliative interactions (rest in close proximity, grooming of a companion, and search for companions if they become separated), following the companion, low overt aggression within groups (Caro 1994) and synchronization of daily activities.

Table 1 – Male interactions in created (A) and existing (B) coalitions

	Types of behavior								
	Mark- ing	Self- groom- ing	Groom- ing with compa- nion	Foll- owing	Play- ing alone	Play- ing with compa- nion	Aggre- sion	Tactile contact	Joint rest
	A-Coalition of males MZ								
Average for 1 hour	1.60	0.51	1.08	0.27	0.00	0.20	0.00	0.00	3.44
Confidence interval	0.64	0.31	0.29	0.19	-	0.18	-	-	0.58
	B-Coalition of males DZ								
Average for 1 hour	0.84	0.42	0.39	0.48	0.09	0.16	0.12	0.05	1.17
Confidence interval	0.26	0.14	0.10	0.30	0.06	0.11	0.08	0.07	0.24
Probability of difference between A and B	0.95	0.39	1.00	0.75	0.99	0.24	0.99	0.87	1.00

Figure 1 – Synchronization of males' daily activities in the DZ (a) and MZ (b) coalitions

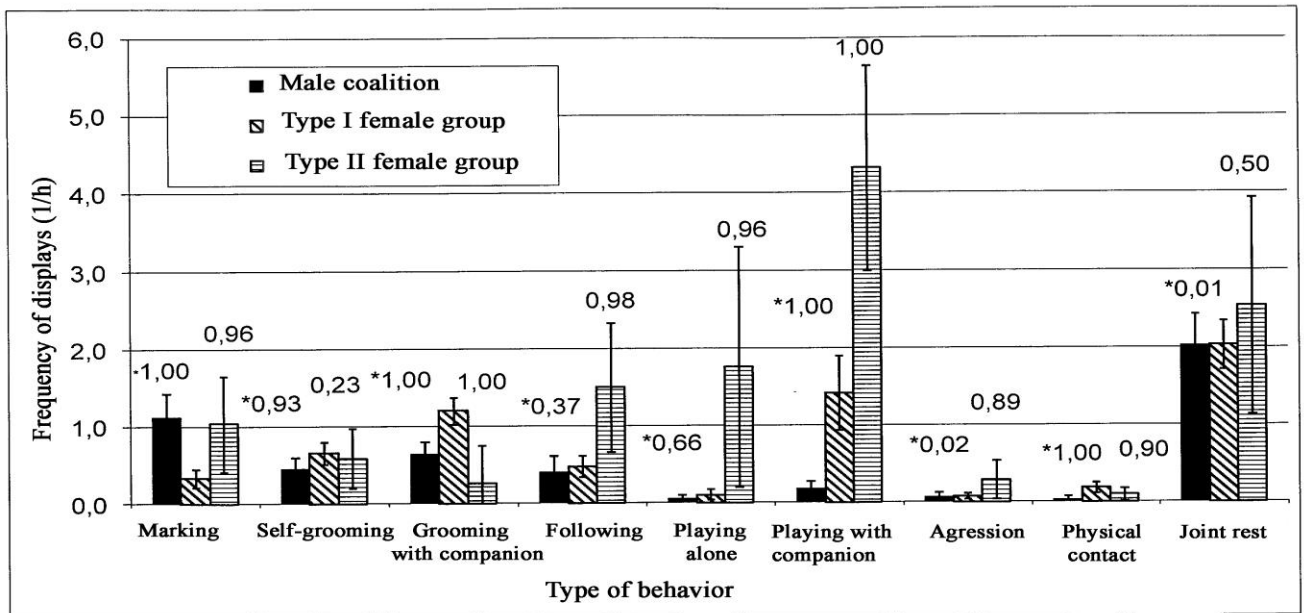


The created male coalition at the MZ was used for breeding with the females. In this case, only one male, which suppressed the sexual behavior of its coalition partner, bred. Eight litters from 3 different females were yielded in 11 years. However, an individually held male at the MZ took part in 6 breeding seasons and 12 litters were yielded in 7 years. Thus, the reproductive success of the coalition was not higher than that of an individually held male.

Groups of 2-3 females. All of the groups were created on the first attempt of putting together unrelated 3-4 year old individuals and lasted for 2 to 10 years. Two types of groups can be distinguished by comparing the females' behavioral patterns.

The behavior of females in type I group (3 pairs and 2 groups of three) was similar to those of males in coalitions. So, along with low-aggression, the females didn't demonstrate a level of affiliative contact lower than that of males, which is shown by comparing the average data from two pairs of females to two coalitions of males (Fig. 2). Groups of three were created by splitting newly arrived females up into the type I groups of females formed a year or two earlier.

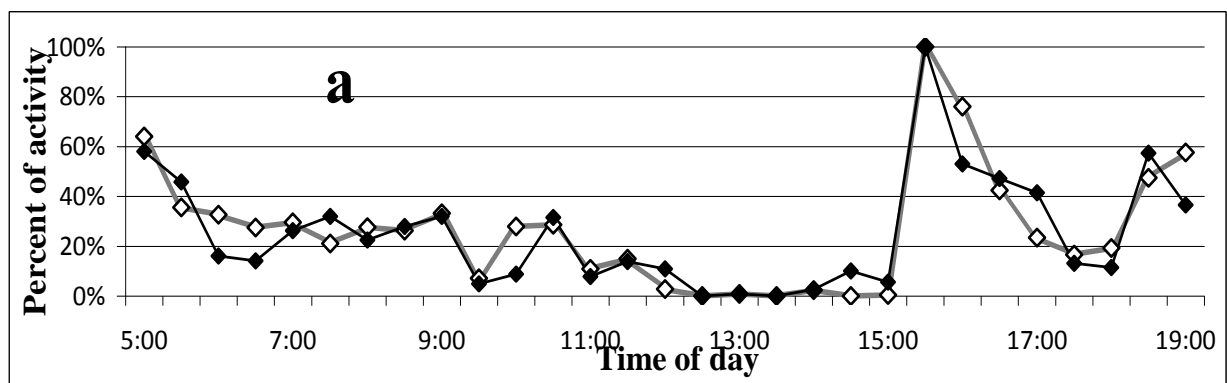
Figure 2 – Behavior of males in coalitions and females in type I and II groups (the probability of differences of: *coalitions of males to type I groups of females; type I groups of females to type II groups of females)



The behavioral profile of the type II groups (2 pairs) differs from that of the type I group of females and the coalition of males with a high level of aggression, a low level of social grooming and a very high level of playful behavior (Fig. 2). In type II groups, frequent sequences of behavior in individuals were noted: following, play, aggression. At the same time, this type of group is characterized by the asymmetry of the females' participation in this type of behavior—often only one female in a pair followed behind the other and initiated a game or grooming whereas the other showed aggression. Additionally, the frequency of marking in females in type II groups was similar to that in male coalitions (Fig.2), and often only one individual in the pair demonstrated this. This female behavior is possibly due to the individual's desire to increase their self-confidence in a state of discomfort.

In type I groups of females, the synchronization of daily activities was observed (the average percentage of activity of a 30-minute interval for all observations). This was demonstrated, for example, in pairs of females (Fig.3a) and group of three females (Fig.3b). At the same time, asynchronous activity was observed in type II groups of females (Fig.4).

Fig. 3 – Synchronization of females' activities in type 1 groups
(a – pair of females; b – group of three females)



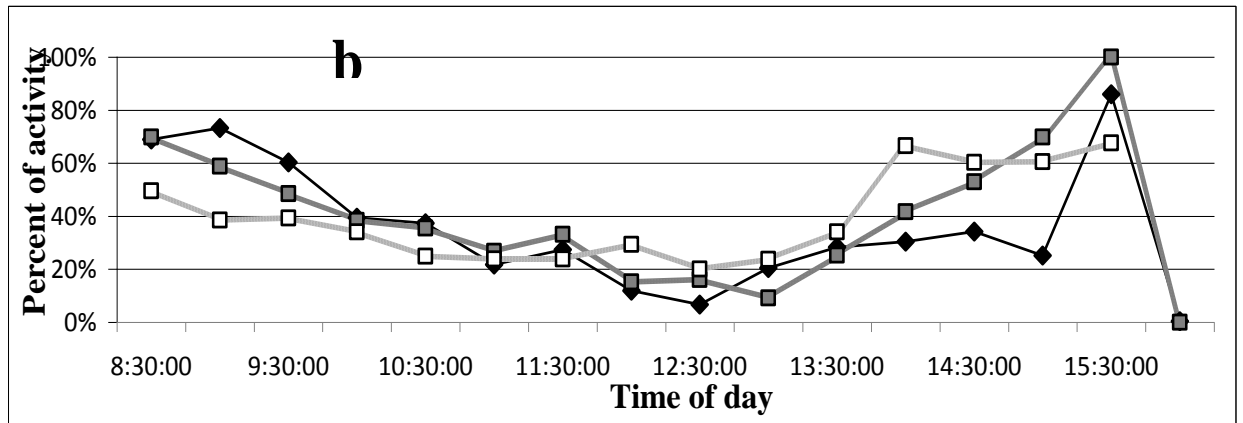
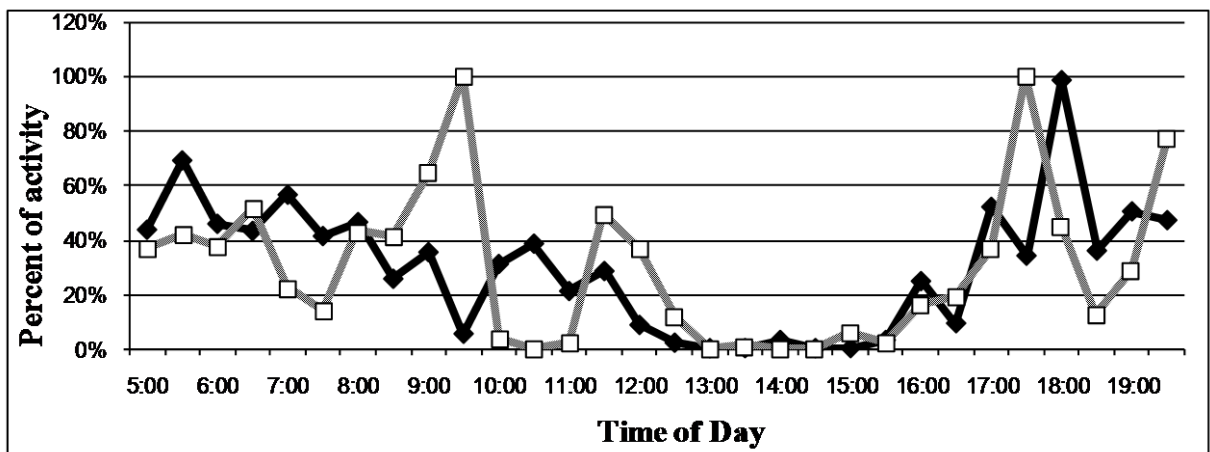


Fig. 4 – Asynchronous activity of two females in type II group



Thus, because of behavioral indicators, we believe that the type I group is a formation more similar to male coalitions. Despite the fact that the synchronization of estrus was observed in all of the groups, breeding occurred only in members of the female “coalitions” (Table 2).

Table 2 – The dependence of the reproductive success of females on the structure of the group and the presence of female “coalition”

Number of females in a group	Number of female members in a “coalition”	Number of groups	Number of couplings with a male	Number of births	Coefficient of reproductive success (number of births/number of couplings with a male)
2	2	2	6	4	0.66
2	0	2	7	0	0
3	3	2	14	9	0.64

Additionally, synchronized births, co-raising litters and adoptions occurred in the female “coalitions”.

Adopting a cub took place at the MZ twice in 1986—after its birth and at the age of 5 months. In the “coalition” of 3 females, two of them gave birth one day apart, and the third 5 days later. The last female didn’t feed the cub, she was transferred to a different location and female “coalition” member was given the opportunity to take in the newborn, which she began to feed with her cubs. A week later, the two female “coalition” members were combined, along with their litters, and raised all cubs together. At 1.5 months, the adopted cub named Diana was handed over to the “Cub Grounds”. After 3.5 months, she was returned to the group consisting of the female “coalition” (Mary and Nanga) and their cubs. Of the new members, Diana was accepted by Mary first, and by the rest of the group within 3 weeks.

At the age of 4 Diana was singled out from the group of females, and after a 2 year break, at 6 years old, she was again reunited with the 14 year old Mary as a pair which lasted until Mary’s death at the age of 15. Besides the usual display of affiliative behavior (grooming the head and neck for example), Diana constantly licked the areas affected by trophic ulcers on the outside of Mary’s thighs, which contributed to their healing. This example may indicate, firstly, that an age difference (in this case, 8 years) does not interfere with high level of affiliative interactions between females, and secondly, that females are able to remember friendly contact with one another and renew it two years later. At the same time, in male coalitions, it is known that their members recognize each other after a year of separation, but there is an age limit for integrating unrelated males; according to Caro, a newcomer should not be older than 20 months old (Caro, 1994). This is most likely due to the fact of male cheetahs’ territoriality.

Co-raising litters. Our experience has shown that synchronized births in a female “coalition” allows for the females to unite with their litters; thus, the adult females raise their litters together (Fig. 5). The females Mary and Nanga were brought together for the first time in 1982 with their 7 month old cubs, and the adult cheetahs showed friendly behavior towards one another and towards each other’s cubs. The next union occurred in 1985 when Mary’s cubs were 9 days old and Nanga’s were 2 days old and invoked this behavior in both females. This will be described in further detail.

Before birth, the females were separated; each of them was placed into 2 adjacent cages, fitted with wooden nest boxes (200x100x15 cm) without roof. The females gave birth 7 days apart; Nanga gave birth on April 25 and Mary on May 2. On May 2, 1985, hearing the sound of Mary’s newborn cubs, Nanga grew concerned and tried to get to them, but Mary did not respond feeding the cubs. The next day, Nanga tried again, and Mary began to nervously drag her litter around the cage. When Mary left the dwelling for walks, Nanga was able to meet the other’s cubs and immediately began to lick them. After Mary returned, both females engaged in mutual grooming while loudly purring, after which Mary again began to drag one of her cubs around. Nanga stood up and gently pushed Mary with her head, after which she put the cub down and lied down. After some time, the two females went to Nanga’s cubs, licked them together and then lied by their side. That same evening, after a joint walk, they were separated with their respective litter, and Nanga began to grow concerned and again tried to get to Mary, who also began to worry, leaving her

cubs. The females were brought together and Nanga immediately began to feed the litter and Mary lied down next to her, both females loudly purring. At night, the females were divided, leaving each with their own litter.

On the morning of May 4, 1985, the sliding doors between the cages were opened and the two swapped places—Nanga went towards Mary's cubs and Mary towards Nanga's remaining food. After a joint walk, Nanga fed Mary's cubs and both females went to Nanga's litter. Just as Nanga lied down to feed the cubs, Mary began to drag some of them around the cage. Nanga left the cubs, allowing Mary to feed them, and lied down on the adjacent nest box, purring. After the second walk, the females licked each other's cubs, sat with them for a while, and, switching places then began feeding their own cubs. After the evening walk, Mary immediately started eating (the females were fed in separate cages), and Nanga immediately began crying for her, refusing to eat. Still, it was decided to keep the females separated for the night. On May 5, 1985, the females alternately spent time with both litters, moving from one to the other, and on May 7, 1985, they brought the cubs to one cage and fed them together in a single nest box. While the females were on a walk, the staff moved the largest nest box (210x120x0.20cm) to one of Nanga's cages and moved all of the cubs there, but the cubs immediately moved back. They were again carried back by the keepers and the females were let back in from the outside enclosure. Once the mothers lied down with the cubs, they calmed down. The females took turns feeding the young; they crawled from one mother to the other and slept in a general group. An attempt to divide the females caused anxiety in them and it was not attempted again.

On May 12, 1985, a clear difference regarding the relationship of the females to the young emerged: Mary spent more time on walks or would lie nearby while Nanga fed all the cubs or groomed them. She would go on walks, making sure the cubs were sleeping and there were no outsiders in their dwelling. Sometimes both females lied on one nest box opposite one another and fed at the same time, but more cubs were always observed around Nanga.

On May 23, 1985, the cubs obeyed the two females, responding to their calls; however, not all of the cubs obeyed Mary's inviting calls trying to bring the cubs outside—the 2 week old cubs did not move as confidently as Nanga's. Since the last ten days of May, Nanga fed more often, but on June 10, 1985, the cubs, after trying Mary's nipples, went to Nanga and only went to her from that point on. Starting on June 1, 1985, the cubs ate meat on the bone and walked with the females in open enclosures.

Figure 5 – The females Mary and Nanga with their cubs in 1985 (left) and with their cubs (background) and adopted cub (foreground) in 1986 (right).



In some cases though, behavior indicative of anxiety was observed in females in a “coalition” at birth. At the MZ for example, a pair of 3 year old females was combined in the first week after arriving. That pair had demonstrated a high degree of affiliative interactions, based on what we define that pair of females as a “coalition”. Both females went into heat and mated with the males within a week and a half. Before giving birth, the females were separated from the males into different cages of the dwelling during feeding time and at night. Three months after their arrival, on the night of the birth, one female broke through the bars on the window and gave birth in a remote part of the enclosure. The other one, left alone at the dwelling with 2 males in the opposite cages, gave birth and committed infanticide.

Females with cubs mating. Our experience shows that females mating before completely being separated from their litter can result in pregnancy. For example, while two females were with their 10 month old cubs, synchronous estrus was not observed: the difference in the onset of estrus in this coalition was 4 months. At mating time, the females took turns being separated with males in an adjacent enclosure, while the second female stayed with her group and the adopted cubs. Only the second mating female gave birth. It is possible that the presence of cubs that haven’t reached the age of independence does not contribute to the synchronization of estrus in mothers.

Mutual relationships in groups of females after birth. In female “coalitions”, the female who has no cubs may be aggressive towards the females carrying a litter. At the MZ, this behavior was observed twice in different females. In one instance, a female who had not given birth was aggressive towards a female with whom she had previously co-raised a litter. In another instance, a female who had given birth, but was not nursing her cub, after its weaning became aggressive towards females adopting cubs.

If births in the female “coalition” occurred within one day, but one of the females lost her cubs, she would not become aggressive, and moreover, if kept separately, would tend towards the other “coalition” members in case of keeping visual contact with them. We observed this behavior at the MZ. The females were brought together when the cubs of one of them were 4 months old and both were raising a litter together.

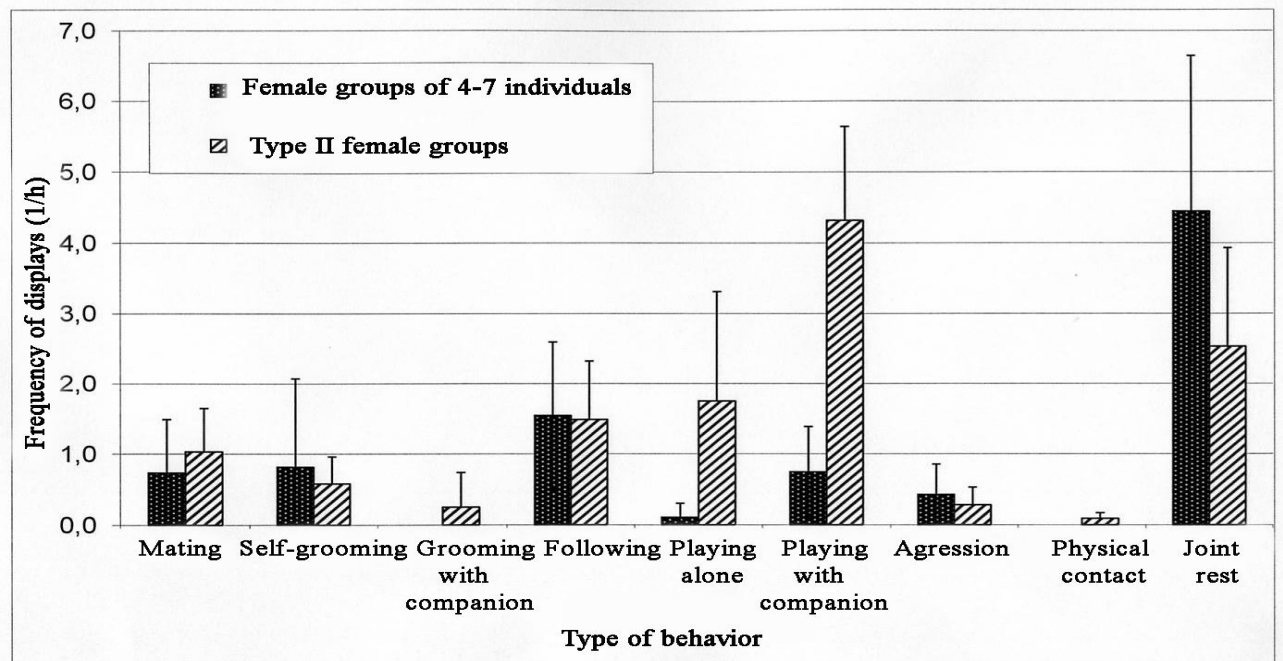
The formation of the female “coalition”. The possibility of forming a "coalition" of individuals not bound by familiar ties can be illustrated by the example of bringing together two females at the DZ.

Two superficially similar females were brought to the zoo at the age of 1.5 to 2 months with a number of other cubs, were hand-raised and then were kept separate from one another for the next 4 years prior to the formation of the pair. On the first day after moving to adjacent enclosures, the females began to show signs of affiliative behavior: they played and often engaged in mutual grooming through the bars, loudly purring during this time. When they were put together in an exercise enclosure after a week, they demonstrated behavior more characteristic of family members who had been separated for a while. From the first minutes they performed grooming of each other and playing together. Subsequently, the females consistently showed affiliative behavior and, even during joint feedings, there had never been conflicts between them. In general, this pair was characterized by the displays of all types of social behavior we have focused on.

The nature of the relationship of this pair of females could indicate that either the females were relatives who preserved the memory of each other from childhood, or that even at 4 years of age unrelated females may have a relationship characteristic of a coalition of male littermates. In addition, this example may indicate that while in captivity, females respond more calmly to an unfamiliar cheetah of the same sex intruding onto their territory than males.

Groups of more than 3 females. Each of these groups was composed of 4 to 7 individuals and included: females of “coalition”, their adolescent cubs (including adopted ones), and unrelated females. These groups lasted 1-2 years while maintaining their female “coalition” composition. Observations showed that all forms of affiliative interaction were noticed between members within the “coalition” but very rarely between “coalition” members and the remaining females in the group. As is the case with type II groups (Fig. 6), a low level of affiliative interactions and a high level of aggression in these groups indicate a low reproductive potential for the females kept in this type of group. In these groups, suppressed estrus in all of the individuals, except the “coalition” members, who demonstrated synchronized estrus, was observed; however, none of the females in this group reproduced (Table 1).

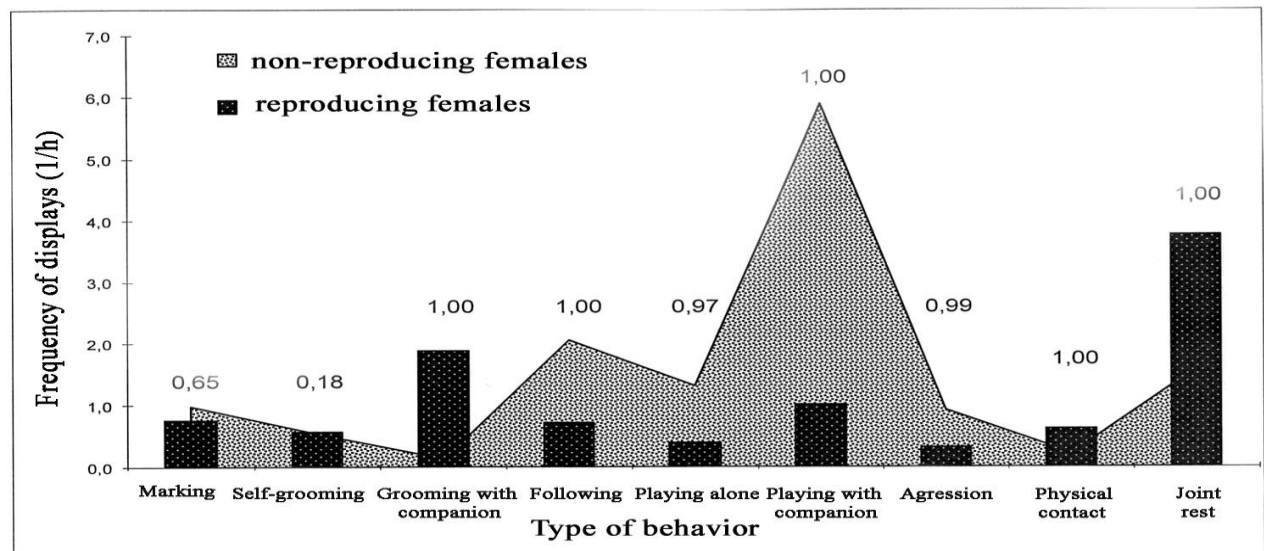
Figure 6 - Behavior of females in type II groups and in groups of 4-7 individuals



Mixed groups. Of the 4 created groups, 3 were composed of pairs of individuals of the opposite sex and characterized by a low level of aggression and high level of affiliative contacts. During their existence (5 months-5 years) there was no reproduction. One group consisted of a 2-male coalition and 3-4 females not forming a “coalition”. In the 9 years of this group’s existence, synchronized estrus among females was not observed and there was only one instance of reproduction.

Individual reproductive success of females. At different times, one female was able to be in a group where reproduction occurred and in a group where no female reproduced. A behavioral comparison of 12 females during the time when they made up non-reproducing groups (n=8) with the behavior during the time when they reproduced in a group (n=8) shows significant differences in most types of behavior (Fig. 7). Being members of groups where there was no reproduction, the females demonstrated: a high level of aggression, following and playful behavior, along with a low level of social grooming, physical contact and joint rest.

Figure 7 – The behavior of females in reproducing and non-reproducing groups (figures show the probability of differences)



In total, at the MZ, reproduction occurred 20 times in 7 females. In 25% of these instances (n=5 births), an individually held female gave birth, and in 5% (n=1), the female gave birth in a mixed group. In 70% of the instances (n=14), female “coalition” members reproduced. Of these 14 instances of reproduction, 35.7% (n=5) occurred in “coalitions” of 2 females and 64.2% (n=9) in “coalitions” of 3 females.

In total, the synchronization of births occurred in 5 out of 7 breeding seasons (71.4%). The synchronization of births in all members of “coalitions” of 2 females occurred in two out of 3 instances (i.e. 66.6%). In the last instance, the “coalition” was formed of two 11 year old females, of which only one came into estrus and gave birth to her last litter. In “coalitions” of 3 females, out of 4 instances of reproduction, 3 females synchronously gave birth two times (50%), 2 females synchronously gave birth 1 time (25%), and in one instance (25%), only one of the three gave birth.

General discussion

Analysis of holding methods of individuals of the opposite sex from the position of successful cheetah reproduction

Male coalitions. In artificially created coalitions, when coupling with one or two females, competition arose between males, and often only one of them managed to mate. Thus, the successful reproduction of an individually held male occurred more often than with males in a coalition. These results are consistent with those obtained in the wild (Durant et al., 2004) showing that living alone doesn’t reduce the chances for a male to survive and reproduce.

Groups of 2-3 females. An analysis of the behavioral characteristics of a female “coalition” revealed their similarities to coalitions of males, namely: 1) synchronization of behavioral activity; 2) the ability to accept new unrelated members; and, 3) a low level of aggression and high level of affiliative interactions (social grooming, physical contact and joint rest). At the same time, there are some differences, mainly: 1) a male coalition is always based on littermates, while a female “coalition” can be composed of unrelated females; 2) unlike males, the reproductive success of females’ increases in a “coalition”. It’s obvious that female siblings

(littermates), held together from birth, will demonstrate a high level of affiliative contacts and demonstrate all of the characteristics of a full-fledged coalition.

In captivity, holding social animals in a group or in pairs is an important factor for environmental enrichment (Mellen et al., 1998). Additionally, the cheetah's well-being is closely related to the composition of the group and the type of relationships within it. Although some authors consider the grouping method for holding females inappropriate, hormonal studies of females in groups held in captivity have shown that when affiliative behavior is present between females, there is no suppression of estrus (Brown et al. 1996; Wielebnowski, & Brown, 1998; Laurenson et al., 1992; Wielebnowski, et al., 2002; Terio et al., 2003 and others). Of all the types of groups we created, the female "coalitions" were the most reproductively successful.

It appears that in captivity it is possible to create the conditions under which females form stable, successful reproductive "coalitions." A part of these conditions was the cheetah servicing system, in which the keeper learned to behave predictably, understand the needs and intentions of the animals based on their behavior on a personal level, and respond to it. For example, the keeper released a cheetah waiting by the exit from inside the dwelling to the external enclosure. The keepers became flexible and manageable part of the constructed environment for the animals (Neprintseva, 2004), which provided more opportunities for the cheetahs to display more natural forms of behavior. For example, the females calmly left their cubs to go on a walk for a few hours just as they would leave their litter to go hunting in the wild. On the other hand, the keepers could perform not only routine procedures in the presence of the females and cubs without disturbing them, but could observe, for example, the females co-feeding the litters and adopting a cub (Fig. 5).

Females co-raising litters is likely to happen, because: firstly, the relationship between females was affiliative; secondly, the synchronization of births in females occurred; and, thirdly, a long-term, trusting relationship was established between the keepers and the females.

At the same time, the existence of affiliative interactions between females - "coalition" members, does not guarantee a successful birthing period if the animals have not adapted to the conditions of captivity, as is evident in the case at the MZ, when females from the "coalition" tried to break out of the inside premises just before giving birth. This behavior in the females was obviously due to their discomfort during isolation in the dwelling for the following reasons: 1) the period of adapting to the conditions of captivity was probably insufficient and the changes in the females' physiological status was complicated; 2) there was not a trusting relationship between the keepers and the females; 3) males were in the neighboring cages within the dwelling at the time of birth; and, 4) the females' affiliative relationship implied their need for contact with one another. It is more than likely that the attempt at infanticide was caused by the loss of contact with the companion—a member of the "coalition".

Our observations suggest that the presence of affiliative behavior in a female group is enough for the synchronization of estrus, but not enough for successful reproduction. For the formation of a "coalition", a high level of tactile, affiliative interactions (including social grooming and joint rest) is important, along with a low

level of aggression. The behavior of females in a type II group (reproductively unsuccessful) differed from that of the females in the “coalitions” by demonstrating a typical sequence of behavioral elements (following-play-aggression), which indicated a fairly unsuccessful attempt to establish mutual female affiliative relationships, unlike females in a “coalition”.

Groups of more than three females. Despite the females’ display of affiliative behavior, in these groups, the suppression of the estrous cycle was observed in all individuals, except for “coalition” members. This is consistent with the results of hormonal studies that, in some cases, mixing females can create stress in the individuals (Laule, Desmond, 1998), causing the reproductive function to shut down (Terio and Munson, 2000; Wielebnowski et al., 2002) and consequently, reduce their chances to reproduce.

Mixed groups. In captivity, different groups can be created, including those that don’t exist in the wild and consist of individuals of different sexes and ages. However, in terms of breeding, it is irrational since reproduction did not occur in them.

Implications from the wild. As was shown in other predatory mammals, the ability of animals to form long-term, positive, social relationships among individuals not bound by familiar ties, a long-term memory of social connections and the ability to preserve them, and the expressed need for social orientation and support, indicate the presence of a kind of sociality (Ovsianikov, 2005). In our opinion, these characteristics are fully applicable to cheetahs of both sexes. In the wild, cheetahs are characterized by temporary structures (groups of siblings of the opposite sex) and permanent structures (male coalitions), and these social structures show a positive impact on the cheetahs’ survival in their natural habitat (Durant et al., 2004).

For successfully breeding rare species in captivity, including cheetahs, it is necessary to take data on the natural formation of their social organization into account (Caro, 1993; von Schmatz-Peixoto, 2003). In literature, there is information on groups of females gathering in different parts of Africa. In Namibia, for example, out of 102 adult females, 16% met in groups of two or more and 28% of litters were accompanied by more than one adult cheetah (McVittie, 1979); in Kenya, 21% of litters were accompanied by two, and 16% by three or more adult individuals (Graham, 1966); and in Tanzania (Serengeti), the largest group consisted of 9 individuals: 2 females and their cubs (Frame, 1980).

Moreover, observations in Botswana (Vandermeij, 2005) suggest the possibility for reproduction in females living together. In one territory, four females were observed: one with cubs approximately 6 month old and a group of three 4-5 year old females. Ultrasound examination revealed that two of them were in different stages of pregnancy (Vandermeij, 2005) and the genetic results confirmed that they were all related and most likely sisters (Boast L., personal communication). It is possible that they were all previously members of one group, which they left as they approached birth. This phenomenon may reflect the fact that, firstly, favorable conditions were created in Botswana to fully meet cheetah female needs regarding social contacts, and, secondly, the fact of reproduction in living together females.

Thus, we can conclude that certain natural conditions provide males leading a solitary lifestyle as well as females living in a group no less a chance of survival or reproductive success than males living in a coalition and females leading a solitary lifestyle. This principle may be taken as the basis for modeling the conditions for cheetahs in captivity.

Although there are presently no standing opinions about the sociality of cheetahs, our observations suggest that the female cheetahs' need for social contact is higher in captivity than in the wild, where environmental conditions are likely to limit the possibility for it. In captivity, where many restrictions are absent (animals regularly receive food, they are provided with shelter and are protected from natural enemies) females will demonstrate higher levels of sociality. A comparison of artificially created female "coalitions" with male coalitions revealed, firstly, a high level of affiliative interactions in all of these groups (see Fig. 2) and, secondly, displays of those relationships, which were not always observed in the wild.

To summarize, we should say that in terms of female cheetahs breeding, it is irrational to hold them in mixed groups and in groups of more than three females. At the same time, holding females in "coalitions" permits the synchronization of birth and, as a result, avoids the need to hand-rearing cubs in the event that one of the females is unable to feed the litter, which allows for the repopulating of cheetahs in captivity by the individuals of full value species-specific behavior.

Conclusions

1. Female cheetahs in captivity demonstrate higher degrees of social flexibility than the traditional model of the cheetah social organization suggests – in pairs/groups of three, they are able to form alliances, characteristically similar to male coalitions.
2. "Coalition" members can be unrelated females. For the formation of a "coalition", a high level of tactile, affiliative interactions between individuals (including social grooming and joint rest) is important, along with a low level of aggression. This "coalition" is conducive to the successful reproduction of all members.

Acknowledgments

The author conveys his gratitude to the administration of the zoo in Deit (UAE) for the possibility to work with the animals. Sincere thanks for the many years of cooperation and support goes to the staff of the Moscow Zoo (Russia): E. Davidov, I. Igorov and Dr. E. Neprintseva, and also A.V. Kuznetsov and E.A. Nazarenko for their help in processing data.

References

- Boast Lorraine.** Cheetah Conservation Botswana, Mokolodi Nature Reserve. - (Private Bag 0457, Gaborone, Botswana; email: research@cheetahbotswana.com)
- Brown, J.L., Wildt, D.E., Wielebnowski, N., Goodrowe, K.L., Graham, L.H., Wells, S.E. & Howard, J.G.** Reproductive activity in captive female cheetahs (*Acinonyx jubatus*) assessed by fecal steroids // J.Reprod., Fert. – 1996. – No 106. – P. 337-346.

- Caro, T.M.** Behavioral Solutions to Breeding Cheetahs in Captivity: Insights From the Wild // Zoo Biology. – 1993. – No 12. – P. 19-30
- Caro, T.M.** Cheetahs of the Serengeti Plains: Group living in an asocial species. – Chicago: University of Chicago Press, 1994. – P. 478
- Cheetah Conservation Fund.** Cheetah Husbandry Manual: For the Pan African Association of Zoos, Aquarium and Botanical Gardens (PAAZAB) / Compiled by: Cheetah Conservation Fund. – 1998.
- Durant S.M., Kelly M., Caro T.M.** Factors affecting life and death in Serengeti cheetahs: Environment, age and sociality// Behavioral Ecology. – 2004. – No 15(1). – P. 11-22.
- Frame, G.W.** Cheetah social organization in the Serengeti ecosystem, Tanzania: invited paper, Animal Behavior Society annual meeting. – 1980.
- Graham, A.** East African Wild Life Society Cheetah Survey: Extracts From The Report By Wildlife Services // East African Wildlife Journal. – 1966. – Vol.4, August. – P. 50-55.
- Laule, G., Desmond, T.** Positive Reinforcement Training as an Enrichment Strategy // Second nature. Environmental Enrichment for Captive Animals / edited by David J. Shepherdson, Jill D. Mellen, and Michael Hutchins. - Washington and London: Smithsonian Institution Press, 1998. – P. 302-313.
- Laurenson, K.M.** Early Maternal Behavior of Wild Cheetahs: Implications for Captive Husbandry // Zoo Biology. – 1993. – No 12. – P. 31-43.
- Laurenson, K.M., Caro, T.M., Borner, M.** Female Cheetah Reproduction // National Geographic Research and Exploration. - 1992. – No 8(1). – P. 64-75.
- Lindburg, D., Durrant, B.S., Millard, S.E., and Oosterhuis, J.E.** Fertility assessment of cheetah males with poor quality semen // Zoo Biol. – 1993. - No 12. – P. 97-103.
- McVittie, R.** Changes in the social behavior of South West African cheetah. // Madoqua. – 1979. – No 2(3). – P. 171-184.
- Mellen, J.D., Hayes, M. P., Shepherdson, D.J.** Captive environments for small felids // Second Nature: Environmental enrichment for captive animals / Shepherdson, D.J., Mellen, J.D., Hutchins, M., (eds.). – Washington: Smithsonian Institution Press, 1998. – P. 184-201.
- Munson, L., Terio, K.A., Worley, M., Jago, M., Bagot-Smith, A. and Marker, L.** Extrinsic factors significantly affect patterns of disease in free-ranging and captive cheetah (*Acinonyx jubatus*) populations // Journal of Wildlife Disease, . – 2005. – No 41(3). - P. 542-548.
- Nepriņtseva E.** Zoo keepers as environmental-constructing factor for primates in captivity // Questions on applied primatology / Ostapenko V. (Ed.): Moscow zoo. – Moscow, 2004 – P. 47-63 (*in Russian*).
- Ovsjanikov, N.** The behavior of polar bears in the seashore congregations // Zoological magazine. – 2005. – Vol. 84, №1. – P. 94-103 (*in Russian*).
- Popov S., Ilchenko O.** Methodological recommendations for ethological observations of animals in captivity – Moscow, 1990 (*in Russian*).

- Terio K.A., Munson L.** Gastritis in cheetahs and relatedness to adrenal function // Pukazhenthi, B., Wildt, D., Mellen, J. (eds.) – Felid taxon advisory group action plan. Report.- Columbia, SC: American Zoo and Aquarium Association.-2000.-№ 36.
- Terio, K.A., Marker, L., Overstrom, E.W. & Brown, J.L.** Analysis of ovarian and adrenal activity in Namibian cheetahs // South African Journal of Wildlife Research. – October, 2003. – No 33(2). – P. 71-78.
- Vandermey N.** “Cheetah Conservation Botswana“// Animal Keepers’ Forum, Special Dedicated Issue on Cheetah. – 2005. – Vol. 32. Nos.7/8. – P. 371-374.
- von Schmatz-Peixoto, K. E.** Factors Affecting Breeding in Captive Carnivora: PhD Thesis / Wolfson College, University of Oxford, Trinity Term. – 2003.
- Wielebnowski, N. & Brown, J.L.** Behavioral Correlates of Physiological Estrus in Cheetahs // Zoo Biology. - 1998. – No 17. – P. 193-209.
- Wielebnowski, N.C., K. Ziegler, D.E. Wildt, J. Lukas, Brown, J.L.** The impact of social housing reproductive hormones, adrenal activity and behavior in female cheetahs // Cons. Biol. - 2002b. – No 5. – P. 291-301.
- Wildt, D.E., Brown, J.L., Bush, M., Barone, M.A., Cooper, K.A., Grisham, J., and Howard, J.G.** Reproductive status of cheetahs (*Acinonyx jubatus*) in North American zoos: The benefits of physiological surveys for strategic planning // Zoo. Biol. – 1993. – No 12. – P. 45-80.