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### Research Report

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## On the function of the greeting ceremony in social canids – exemplified by African wild dogs *Lycaon pictus*

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### Abstract

The mutual greeting ceremony is one of the most conspicuous behaviours in African wild dogs (*Lycaon pictus*). This highly ritualised pattern of behaviour is a lively, noisy and playful activity with frequent annulment of social status of all pack members through appeasement signals. Greeting behaviour also appears in other pack-living canids, and the domestic dog's greeting of the "lord and master" may be a legacy of it. The function of this behaviour must be of high adaptive value, because the animals run the risk of attracting predators. It is widely believed that the greeting ceremony serves to hold the pack together and to further cooperative behaviour. A quantitative analysis of the greeting behaviour is still missing. Pack-living and cooperative breeding is associated with successful reproduction in African wild dogs. Therefore, it would be expected that greeting behaviour should occur more often during the gestation period than at other times.

A pack of 14 African wild dogs in captivity was observed for one year. During the gestation period the amount of time spent on greeting behaviour more than doubled. Greeting appeared in the 12 yearlings with significantly longer duration and higher frequency during gestation period than out of it. For the two adult dogs the duration of the greeting was significantly longer during gestation period, but not the frequency.

In cooperatively breeding canids, specializations in behaviour have evolved to hold the group together and to reduce aggression. Synchronisation of activity and friendly relationships are mandatory, and become more important during gestation period and in the presence of pups. The function of the greeting ceremony seems to be the furtherance of cooperative and amicable behaviour, its function as a social *Zeitgeber* for the pack to synchronize daily activity is discussed, the greeting behaviour in other pack-living canids is considered.

## Introduction

Some mammals practice cooperative breeding, in which individuals help others with care of the young rather than breed themselves. Such altruistic behaviour can be found in mole rats *Heterocephalus glaber*, social mongooses such as the slender-tailed meerkat *Suricata suricatta* (Doolan and Macdonald 1999) and in several canid species. In canids the level of sociality varies, with a tendency for larger species to be more social, to have large litters and a later dispersal of young (Bekoff et al. 1981). The social system of the most cooperative canids (African wild dog *Lycaon pictus*, Ethiopian wolf *Canis simensis*, bush dog *Speothos venaticus*, grey wolf *Canis lupus* and dhole *Cuon alpinus*) requires so-called “helpers” or alloparents (Wilson 2000) that provide postnatal care to young others than their own. This implies friendly relationships among pack members and synchronisation of daily activity. The question is how this is achieved and reinforced and which specialisations in behaviour have evolved to further cooperative behaviour.

African wild dogs have taken sociality to an extreme. Relations are most of the time amicable and group cohesion is extremely strong (Frame et al. 1979; Estes 1991). Pack members seldom quarrel with one another, and serious fights are rare. African wild dogs share food even when there is not enough. Instead of quarrelling for food they show submissive behaviour patterns: mouth licking is performed together with a variety of excited whines and squeaks. These behaviours are derived from the begging solicitation of juveniles and subsequent regurgitation of food to the young. The same solicitations for food sharing are used in appeasement contexts. These patterns of behaviour occur in intraspecific interactions and they are a key component of the greeting ceremony.

### The greeting

Greeting is a behaviour found in most social canids. In African wild dogs it is a highly ritualised and stereotyped pattern of behaviour the animals show in their daily routine. Shortly after a pack becomes active after a rest or after being separated they greet each other intensively: they run together side by side or one after the other, try to lick each other's lips and

face, and they poke their nose into the corner of the other's mouth (Figure 1).



Figure 1. African wild dogs performing the greeting ceremony. The frequent use of appeasement signals regardless of social status is typical.

Every dog, regardless of status, displays appeasement signals to any other member of the pack. They crouch low with head and rump, the tail raised stiffly and there is a lot of twittering, whining, squeaking and locomotory activity in the whole pack. The behaviour is ritualised from infantile food-begging behaviour. Very often, intensive play by some dogs follows the greeting, and this can trigger a mobbing reaction in other pack members, where they “gang up” on one dog, tumble and roll it, but do not actually bite. African wild dogs observed in captivity repeated the greeting even in the night. Typically, one dog would get up and nose others until they responded. After the greeting they would settle down to sleep again, this appeared three to four times every night (unpubl. data).

In mammals in general, greeting ceremonies are thought to be signals that serve to reunite group members after being separated (Bradbury and Vehrencamp 1998). We argue that there may be more to it in dogs since greeting behaviour also occurs when the pack is together day and night. It is widely believed that the greeting ceremony in African wild dogs serves to hold the pack together and further cooperative behaviour and amicable relationships between pack members (Kühme 1965; van Lawick-Goodall and van Lawick-Goodall 1971, Frame et al. 1979; Estes 1991; Kingdon 1997; Wilson 2000). The occurrence of the greeting ceremony after times of rest and between sleeping periods supports another pos-

sible function. It is probably a means ("Zeitgeber", *sensu* Aschoff 1957) of synchronizing the animal's internal clock by transmission of mood. It must be important for a highly social animal like *Lycaon* to be socially synchronized.

For African wild dogs cooperation is obligatory for breeding; five pack members has been suggested as critical size of a pack (Courchamp et al. 2002). Besides provisioning the young, the work of helpers includes watching the pups while the pack is hunting, and after the hunt the pups and the babysitters are provided with regurgitated food from the pack (Malcolm and Marten 1982). Without helpers, breeding success is low (Courchamp and Macdonald 2001).

We hypothesise that if the greeting is an adaptive behaviour to further cooperation within the pack, it should occur significantly more often or with longer duration during gestation period and in the presence of pups than out of gestation period. In free-ranging African wild dogs the duration of the greeting in the presence of pups was reported to be three to five minutes (Kühme 1965). Grey wolves were seen to perform a similar greeting ceremony, but only in the presence of pups (Lawrence 1997); duration was not reported. In Ethiopian wolves, social greetings were more common during the breeding season (Sillero et al. 2004).

Observation of African wild dogs in captivity offered the possibility of making continuous recordings of the greeting ceremony for a long period from the same group. In addition we knew the condition of the female, because gestation period could be calculated from the day of parturition. To the best of our knowledge there has been no prior quantitative analysis of this behaviour. In the field it is hard to observe and follow a pack without pups, due to wide-ranging movement and difficulty in assessing the female's condition.

## Methods

### Animals and study site

A group of two (one male, one female) adult African wild dogs and 12 (six male, six female) pups which became yearlings was observed from 27 August 2001 to 23 August 2002 at Frankfurt Zoo. The pups were born in No-

vember 2000 and the adults were born in November/October 1994. All animals were captive-bred, and the parents and two subadults reared the yearlings. The animals were fed once a day with chunks of raw meat on the bone or with whole, freshly killed animals. The dogs were kept in an outdoor enclosure of 360m<sup>2</sup> with free admittance to a heated shelter of 20m<sup>2</sup> day and night. In addition there was a man-made heated den below ground level with a burrowed entrance in the enclosure. This had been used by several litters in the past. Every morning, the shelter and outdoor enclosure were cleaned. From one side visitors had an open view of the enclosure, and they could stand as close as 1m. On the other side there were trees and bushes. The animals were well habituated to visitors, with only the adult female showing aggressive behaviour if people left the path and touched the fence.

Additional observations were made in the shelter where the animals slept, employing a time-lapse video tape recording system with infrared light from 11 January to 3 March 2001.

### Data collection

Observations always took place from the front of the enclosure. The animals were used to the close presence of the same observer, who studied them from November 2000, and camouflage was not necessary. After five minutes of habituation the observer was almost completely ignored. Observations were made during the animals' most active time, starting about 1h before feeding. Half of the observations included dusk or dawn. The duration of a single observation was between four and six hours, depending on the weather. During rainfall the animals remained in the shelter and were not visible. Observations totalled 182h over 31 days, with a mean duration of 5.7h. Sixteen observations were made during the gestation period, with nine of these including dusk or dawn. In hot weather conditions, twilight period was included because activity shifted to the early morning and late afternoon; this is also true in the field (Kühme 1965; Pfeffer 1972).

Data was collected with *Observer for Windows 3.0* (Noldus Information Technology B.V. Wageningen, Netherlands). With this software, durations and frequencies of the different behaviours were recorded and later analysed.

The behaviour of the two adult animals was recorded separately and the yearlings were recorded as a group. "Focal sampling" (Altmann 1974) was used and the greeting ceremony was recorded as "state" to count frequency and duration of the behaviour. For "duration" the longest of all greetings from one observational file was recorded. We scored "greeting" when the typical vocalisations starting the greeting were audible from at least two animals. The frequency of greetings was recorded.

#### **Definition of the greeting ceremony**

Energetic and noisy greetings with ritualised begging behaviour and appeasement signals were used by all the dogs (for identification of these signals see Introduction). Excitement before feeding (when the animals sometimes uttered the same high frequency vocalisations and showed locomotory activity as seen in the greeting) was not considered if no appeasement signals were used.

#### **Calculation of gestation period**

Mating was observed from 30 August 2001 to 2 October 2001. On 22 November 2001 the female gave birth to an unknown number of pups. Because all litters in captivity were born after a gestation of 69-73 days (Cade 1967; Dekker 1968; Wilden 1995), the beginning of gestation was considered to be 10-14 September 2001. There was a peak in mating activity around this date, although there was mating behaviour more than two weeks after it. Observations after this date were considered as "during gestation period". Because parental behaviour eliciting prolactin levels in canids is at its maximum at least two weeks after parturition (Kreeger et al. 1991), 15 days after birth

were included in the data for "during gestation period".

In order to minimise disturbance, no observations were made one week before and after parturition. Two fully developed pups were found dead in the enclosure two days after birth. All pups died or disappeared after one week.

#### **Statistics**

Using a Student's t-test we tested for differences between means of durations and frequencies for all animals ( $p=0.05$ ). A one-tailed test was used because a longer duration or higher frequency during gestation period was expected.

## **Results**

All animals spent a greater portion of time engaged in greeting behaviour while the alpha female was pregnant (Table 1). The yearlings' greeting required 1.0% of total time, but only 0.4% out of gestation period. Adult dogs required three times more time during gestation than out of it (Table 1).

In two out of 32 days of observation, neither the yearlings nor the adults performed a greeting. Both were out of gestation period (Figures 2, 3, and 4).

Greetings lasted longer for all animals during gestation period (Table 2). Yearlings' greetings lasted up to 226s during gestation period and up to 117s at other times; for adult dogs it was up to 203s and 106s respectively.

Table 1. Amount of time required for greeting ceremony for yearlings and adults, % from 100% total observed time in and out of gestation period.

	Total amount of time/yearlings (%)	Total amount of time/adult females (%)	Total amount of time/adult males (%)
During gestation period	1.0	0.6	0.6
Outside gestation period	0.4	0.2	0.2

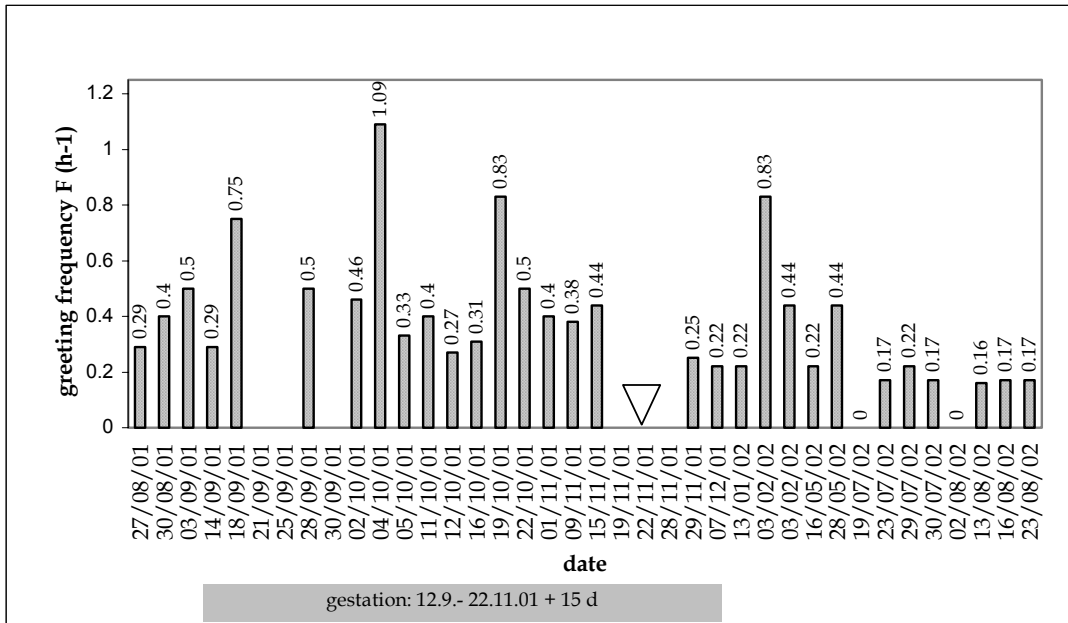


Figure 2. Frequency of greeting of the African wild dog yearlings.

Notes : Out of gestation period time scale is not continuous. The arrowhead shows litter day, 22/11/01. Their frequency was significantly longer during pregnancy of the adult female as it was out of it ( $p=0.05$ , one-tailed,  $t_{crit.}=1.697$ ,  $t=2.398$ ). There was a greeting on all days observed during gestation period, but there were two days out of it with no greetings observed. On 4 October the greeting ceremony occurred more than once in an hour; this was the highest frequency observed.

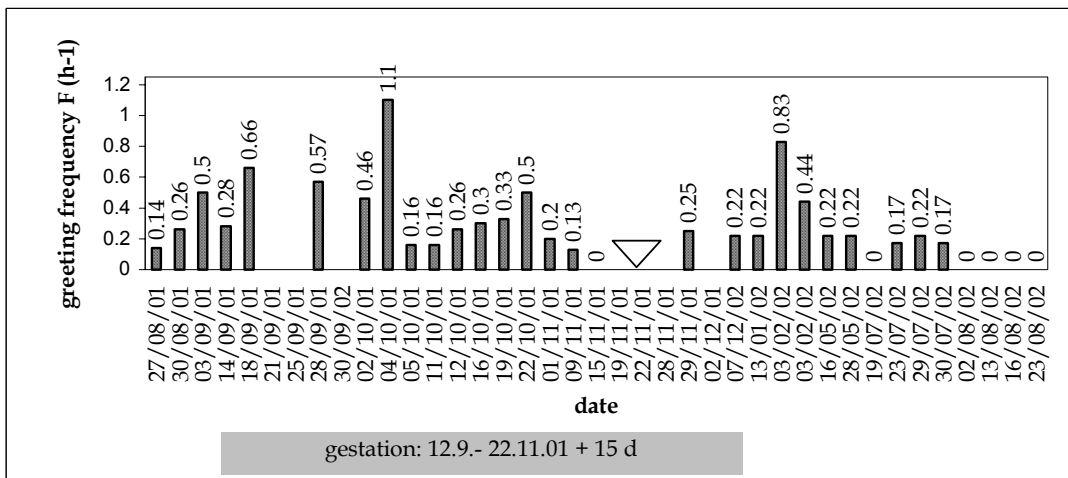


Figure 3. Frequency of greeting of the adult female African wild dog.

Notes as in Figure 2: The frequency was not significantly longer during her pregnancy ( $p=0.05$ , one-tailed,  $t_{crit.} = 1.697$ ,  $t=1.579$ ). There were five days out of gestation period without a greeting but only one during gestation period. This day, which was one week before littering, the female was sleeping and resting all day.

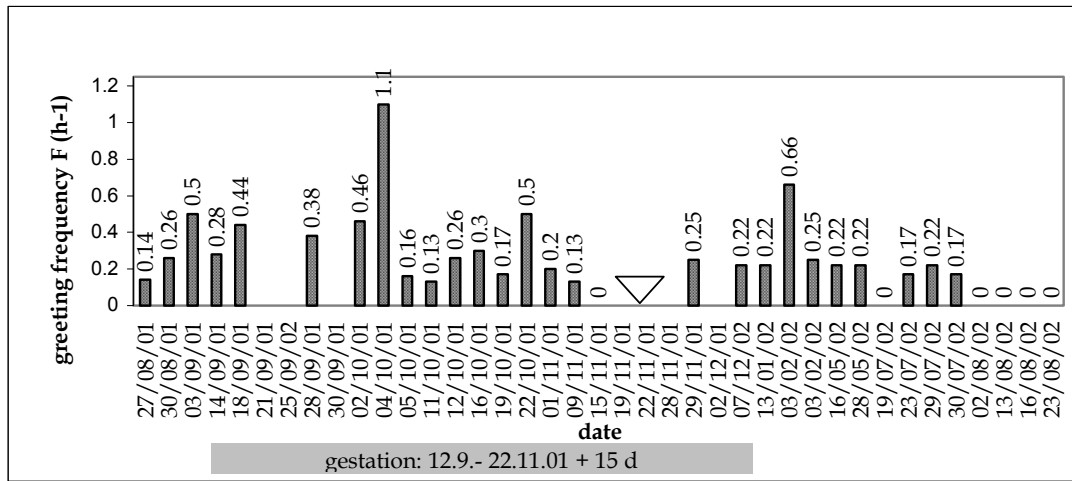


Figure 4. Frequency of greeting of the adult male African wild dog.

Notes as in Figure 2: Frequency was not significantly longer during gestation period of the adult female as it was out of it ( $p=0.05$ , 1 tailed,  $t_{crit.} = 1.697$ ,  $t= 1.569$ ). There were five days out of gestation period without a greeting but only one during gestation period. His highest frequency ( $1,1h^{-1}$ ) was on 4 October, as for the others.

Table 2. Range of duration of the greeting ceremony for yearlings and adults in and out of gestation period.

	Duration/yearlings (s)	Duration/adult females (s)	Duration/adult males (s)
During gestation period	44-226	18-193	17-203
Outside gestation period	10-117	21-102	27-106

The mean duration and frequency of the greeting ceremony is shown in Table 3. These do not seem to be dependent upon each other. Days with long durations do not show high frequencies (Figures 2-7). The greater amount of time spent on the greeting ceremony is

achieved either by a longer duration or by a higher frequency, because these two parameters appeared almost always independently from another.

Table 3. Duration and frequency of the greeting ceremony during gestation period and out of it (n=16 for each). Tested for significance with Student's t-test for duration  $p= 0,01$ ,  $t_{crit.}=2,457$  and for frequency  $p =0,05$ ,  $t_{crit.} = 1,697$ .

	Duration/yearling (s)	Duration/female (s)	Duration/male	Frequency/yearling (h <sup>-1</sup> )	Frequency/female (h <sup>-1</sup> )	Frequency/male (h <sup>-1</sup> )
During gestation period	118.9 S.D. 57.8	73.1 S.D. 48.6	79.8 S.D. 57.2	0.46 S.D. 0.24	0.35 S.D. 0.26	0.31 S.D. 0.25
Outside gesta-	57.3	36.9	38.0	0.28	0.21	0.19

tion period	S.D. 37.1	S.D. 33.4	S.D 34.1	S.D. 0.21	S.D. 0.22	S.D. 0.18
Significant difference	t=3.586 p < 0.01	t=2.462 p < 0.01	t=2.511 p < 0.01	t=2.398 p < 0.05	t=1.579 p > 0.05	t=1.569 p > 0.05

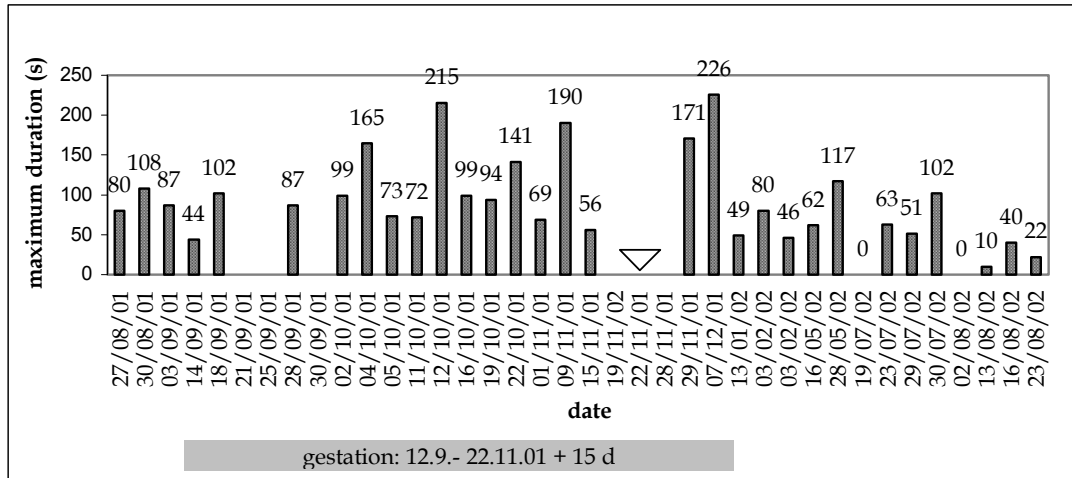


Figure 5. Longest greeting duration of the African wild dog yearlings.

Notes: Out of gestation period time scale is not continuous. The longest greeting duration of each observation was taken into account. The arrowhead shows litter day, 22/11/01. The greeting duration of the yearlings was significantly longer during gestation period of the adult female than out of it ( $p=0.0$ , 1 tailed,  $t_{crit.} = 2.457$ ,  $t = 3.586$ ). The longest duration observed was 7 December, one week after the death of the pups.

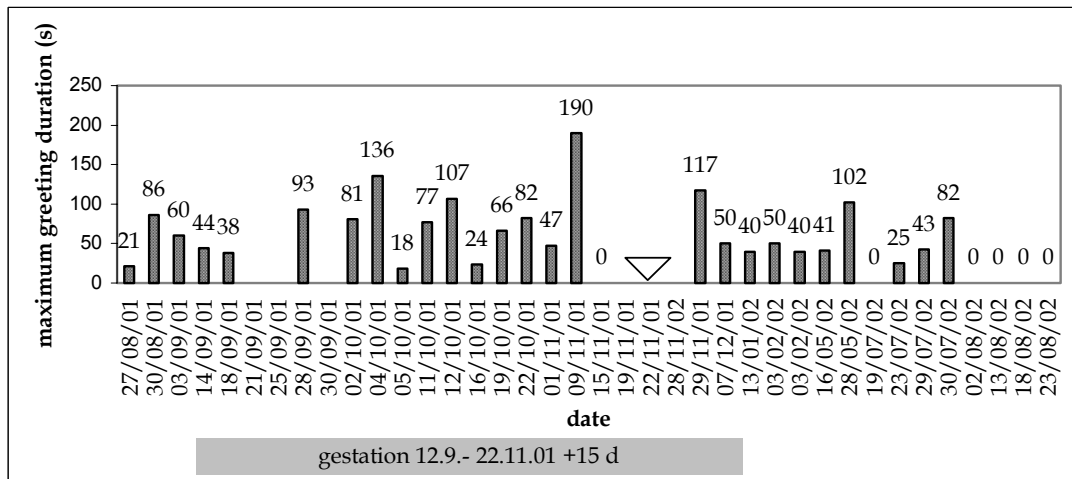


Figure 6. Longest greeting duration of the adult female African wild dog

Notes: Notes as in Figure 5. The greeting duration was significantly longer during her pregnancy ( $p=0.1$ , 1 tailed,  $t_{crit.} = 2.457$ ,  $t = 2.462$ ). Her longest greeting was 190s and was observed 13 days before littering. One week before littering she slept a lot, and on the day of littering she did not participate in the greeting of the yearlings.

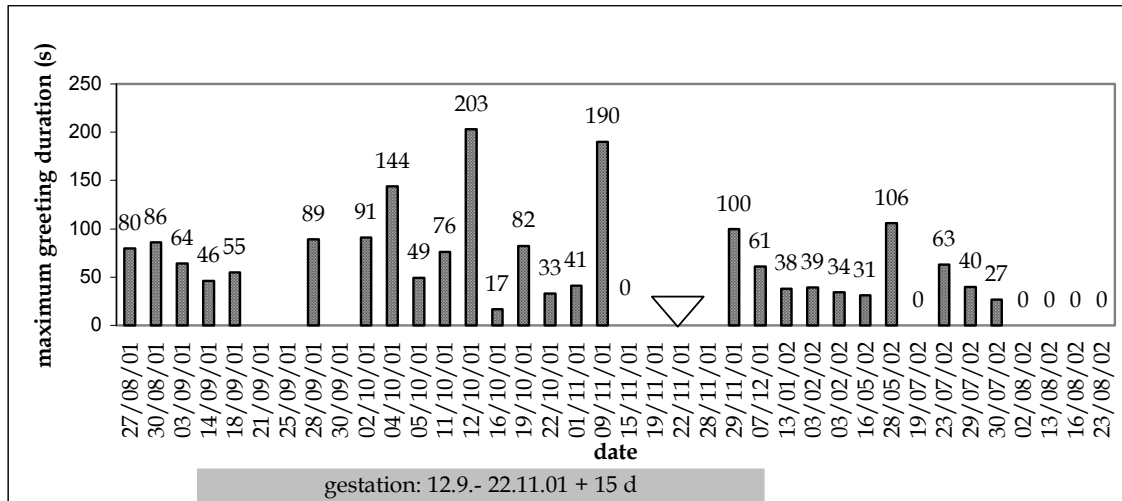


Figure 7. Longest greeting duration of the adult male African wild dog.

Notes: Notes as in Figure 5. His greeting duration was significantly longer during pregnancy of the female than out of it ( $p=0.1$ , 1 tailed,  $t_{crit.}=2.457$ ,  $t=2.511$ ). His longest greeting observed was on 12 October; this was similar to the yearlings' duration on this day. Most of the time his greeting duration was similar to the female's, but slightly shorter because he always followed her.

### The yearlings

Yearlings performed the greeting together most of the time, but four times one or two animals did not join in, and towards the end of the study the young males and females performed two separate greetings.

Comparison of the duration of the greeting showed a non-random distribution during gestation period and out of it. Yearlings' greetings were significantly longer ( $t=3.5866$ ,  $t_{crit}=2.457$ ,  $p=0.01$ ) when the adult female was pregnant. The longest greetings were observed during gestation period, for six out of 16 days the greetings were longer than two minutes. The longest greeting (almost four minutes) was ten days after the death of the pups. Out of gestation period there was no observed greeting longer than 117s (Figure 5). The mean greeting duration was 118.9s (S.D. 57.8s) during gestation and 57.3s (S.D. 37.1s) out of gestation (see Table 3). Yearlings' greetings occurred more frequently during gestation ( $t=2.398$ ,  $t_{crit}=1.697$ ,  $p=0.05$ ). Their highest frequency ( $1.1h^{-1}$ ) occurred three weeks into the female's pregnancy (Figure 2). The mean frequency during gestation period was  $0.46h^{-1}$  (S.D.  $0.24h^{-1}$ ) and out of it  $0.28h^{-1}$  (S.D.  $0.21h^{-1}$ ) (see Table 3).

### The adults

For the two adult dogs the duration/frequency of greeting results were very similar most of the time. The alpha male's behaviour always followed the female's, so his durations were similar (or slightly shorter). There were two exceptions to this (Figures 6 and 7). On 30 July 2002 the female's greeting was much longer than the male's. On 12 October 2001 the female's greeting was shorter than the male's, but this time due to disturbance from visitors.

The female performed significantly longer greetings during her pregnancy ( $t=2.4615$ ,  $t_{crit}=2.457$ ,  $p=0.01$ ) compared to out of gestation period (Table 3 and Figure 6). The longest greeting was 190s; this was two weeks before she gave birth. Mean greeting during gestation was 73.1s (S.D. 48.6) and 36.9s (S.D. 33.4) out of it. After the first month of gestation the female always started the greeting and the other dogs followed, whereas out of gestation one of the yearlings would start the greeting. Only once, one week before she gave birth, the female did not join in the greeting started by one of the yearlings. Out of gestation she did not perform a greeting for five days. The frequency of her greetings during gestation was not signifi-



cantly higher ( $t=1.5793$ ,  $t_{crit.}=1.697$ ,  $p=0.05$ ) than out of it. The day with most frequent greetings was 4 October (Figure 3), when they greeted every hour; it was three weeks after the female became pregnant.

Out of gestation period the male did not perform a greeting during the same five days as the female. The frequency of his greetings was not significantly higher during gestation ( $t=1.569$ ,  $t_{crit.}=1.697$ ,  $p=0.05$ ) than out of it. The day with the highest frequency of greetings was also 4 October (Figure 4). There was a non-random distribution of the duration of the male's greeting (Figure 7). Duration was highly significant during gestation ( $t=2.511$ ,  $t_{crit.}=2.457$ ,  $p=0.01$ ).

There was a change in behaviour at the beginning of August 2002. From 23 July 2002 the male's greeting durations dropped from 63s, 40s and 27s to zero (Figure 7), possibly reflecting a loss in rank. The male yearling "Chapati" appeared to have taken the dominant male's position, indicated by his behaviour (including mating) towards the alpha female. In contrast to this, the female's greetings initially became longer (25, 43, 82s) but then dropped to zero (Figure 6).

### Greeting behaviour in the night

All animals became very active three to five times every night, engaging in greeting behaviour. Pack members remained in close proximity to one another while resting and sleeping. In a single observation, yearlings remained in body contact with their same-sex siblings for up to 97% of observed time.

## Discussion

The effect of outside temperature on behaviour was not considered, due to the small number of observations. We tried to minimize temperature effects by choosing the animals' most active time for observations. Days with severe human interference (general cleaning, veterinary involvement, New Year celebration) were excluded. The animals did not usually perform greetings on days with high disturbance, and the female seemed most affected by this. On 12 October her greeting was shorter; she attacked a visitor close to the fence. Although the ani-

mals became habituated to the presence of the observer over time, such observer effect cannot be ruled out.

For all animals observed, the duration of the greeting ceremony during gestation period was significantly longer compared to out of gestation period. We found the total time spent on the greeting was doubled to tripled during gestation period.

In general, these findings support our hypothesis that the greeting ceremony is an adaptive pattern of behaviour which functions to further cooperative behaviour. The duration of the greeting ceremony shows how this behaviour is influenced by the condition of the alpha female: during her pregnancy, the greeting duration of all animals was extended ( $p = 0.01$ ). It may be an inert response to the female's condition, clearly visible in the alpha male's behaviour: his greetings were of similar duration and frequency as the female's. But ten months later, when he lost his rank to the yearling Chapati in August 2002, his greetings became shorter and stopped completely. In contrast, the female's greetings towards him became longer and then stopped, too. It is possible that this occurred due to the change in status of the yearling male. No successful matings were observed between him and the female.

The greeting behaviour may be influenced by the hormone prolactin, which is thought to elicit parental behaviour. In a pack of captive grey wolves, all pack members had similar prolactin levels and synchronised prolactin cycles during gestation period (Kreeger et al. 1991). In this study, it was not possible to measure prolactin levels as blood samples were not taken. The high greeting frequency for all animals on 4 October could be explained by a rise in hormone levels at the beginning of gestation period. The adaptive value of the greeting ceremony must be higher when cooperation is most needed: for this reason the total amount of time spent in greeting was extended during gestation period (Table 1). This is further supported by the fact that the longest greeting duration of the alpha female occurred two weeks before parturition, and she did not greet in 31% (5 out of 16) of all observations out of gestation period but only in 6% (1 out of 16) during gestation period. She used the greeting more when pack cooperation was more important for her. We would expect an even higher

duration or frequency of the greeting in the presence of pups, especially during the first weeks. This was not tested due to the early death of the neonatal pups.

The missing significance for the occurrence of greeting behaviour of the female may be explained by her age (8 years) and poor condition in the last weeks of gestation. On occasion, she did not take part in the greetings. This explains the lower frequency of the male's greeting too, because he followed her. During the last four observations, the yearlings alone performed greetings. At 20 months of age they began to split into separate male and female groups. They slept at different times and locations and the males/females were sometimes observed performing a greeting on their own. Under natural conditions, young dogs split into same-sex dispersal groups. The young females leave the pack to look for mates and usually first breed at approximately two years of age (Bekoff et al. 1981).

The rhythmical occurrence of the greeting ceremony during the night when disturbance was low may indicate Zeitgeber, in order to synchronize the pack members. However, in this study synchronization could be a result of zoo conditions, for example illumination or noise of the town. G. Rasmussen (pers. comm.) found no such night activity in free-ranging *Lycaon*.

It is also interesting to note the animal initiating the greeting ceremony. Normally, out of gestation period, it was a yearling. But during gestation period and shortly after birth, the alpha female initiated the greeting. This period coincides with the highest level of cooperative behaviour in the pack.

The same was true for a pack of captive Indian dholes observed by Ludwig and Ludwig (2001). Here too, the mother of the pups started the greeting. Greeting duration was only 20-40s, and aggressive behaviour was occasionally seen during greetings. However, aggressive behaviour was not observed between the dogs in this study, and most greetings had durations lasting more than one minute (Figures 5, 6 and 7). The difference in the degree of African wild dog and Indian dhole sociality may be reflected here.

In Ethiopian wolves which breed cooperatively but forage and feed alone, social gatherings

were reported to be more common during the breeding season (Sillero et al. 2004). In grey wolves the "greeting" involves two animals, and resembles food begging in pups: a subordinate wolf thrusts its snout to the muzzle of a dominant one. Active submission is part of the "group ceremony" in which all wolves surround the leader, nose-push and lick his face or tenderly seize his muzzle, which takes place spontaneously or after wolves have separated and regrouped (Mech 1970). In contrast to African wild dogs, there is no annulment of social status of dominant animals during the greeting. In a pack of wolves there is pressure to keep the society stable; a wolf must constantly assert his position to preserve status (Mech 1970). This is not the case with African wild dogs. With the exception of Kühme (1965), no greeting durations for *Lycaon* have been reported. Kühme (1965) reported a greeting duration of 3-5 minutes. In our study the longest observed greeting (3min 46s) was two weeks after parturition, a time when cooperation would have been very important.

It is thought that the greeting ceremony evolved in cooperative canids to reinforce amicable relationships and synchronize activity patterns; it is apparent in all social canids. The duration and frequency of the greeting may reflect the level of sociality of the species. The difference in behaviour is of degree rather than of kind. Comparisons of the greeting behaviour in different canid species could underline this.

Other behaviours that could reinforce cooperative behaviour in canids are play (Bekoff 1984), grooming (Lamprecht 1979) or the maintenance of body contact (McCreery 2000). Further studies focusing on such quantitative data are required (Bekoff and Allen 1998).

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