# MALE CONSORTSHIP BEHAVIOUR IN CHACMA BABOONS: THE ROLE OF DEMOGRAPHIC FACTORS AND FEMALE CONCEPTIVE PROBABILITIES

by

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## Summary

There is evidence for a general relationship between male dominance rank and mating success in primates, although the strength of this relationship differs among species. In chacma baboons (*Papio hamadryas ursinus*) male rank is found to be of more importance than in the other savannah baboon subspecies. However, even though the priority-of-access model explains the proportion of time spent in consortship for males of different rank in chacmas, highest-ranking males usually consort less often than expected. In this study, conducted in the Drakensberg Mountains of Natal and at De Hoop in the Western Cape, we investigated why dominant males in four study troops consorted only between 50% and 75% of days that they were expected to consort according to the priority-of-access model. Consortship success

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of highest-ranking males was primarily dependant on the number of available oestrous females in a troop. This was likely due to costs involved in consorting which limit the amount of days that a male could spend in consortship. Females pass through several cycles before conceiving and highest-ranking males were observed to consort more often on the conceptive cycle compared to the nearest nonconceptive cycle, but this was only true for males that were already resident for several months. Recently immigrated males that became highest-ranking often consorted during nonconceptive female cycles, while older, lower-ranking males consorted during the conceptive cycles. We propose that males with longer residency have more information about reproductive state of females and thus higher reproductive success than recently immigrated males.

## Introduction

The priority-of-access model as originally published by Altmann (1962) argues that male reproductive success should correlate with dominance rank because highest-ranking males are expected to monopolise mating whenever at least one female is in oestrous. Low-ranking males are expected to mate only when two or more females are synchronously in oestrous. While some attempts to test this model have yielded a positive relationship between rank and mating success, others have found no relationship or only in some years but not in others (for reviews see Cowlishaw & Dunbar, 1991; Bulger, 1993). However, Cowlishaw & Dunbar (1991) have concluded that there is a general relationship between male rank and mating success in polygamous primates and Bulger (1993) found that this relationship also stands for the subset of the savannah baboon data. Although paternity tests are lacking for most studies, the reproductive priority of highest-ranking males has been confirmed by several genetic studies of free-ranging primates (Pope, 1990; de Ruiter *et al.*, 1992; Altmann *et al.*, 1996; Gerloff *et al.*, 1999; Constable *et al.*, 2001; Launhardt *et al.*, 2001; Soltis *et al.*, 2001).

For baboons, time spent in consortship rather than the number of matings is used as a measure of mating success. Mate-guarding behaviour has been studied in detail for yellow baboons (*e.g.* Hausfater, 1975; Rasmussen, 1980; Collins, 1981; Noë & Sluijter, 1990) and for olive baboons (*e.g.* Hall & DeVore, 1965; Packer, 1979; Strum, 1982; Smuts, 1985; Bercovitch, 1987). In the past, research on chacmas has focussed on troops with only few adult males (Hall & DeVore, 1965; Saayman, 1970; Seyfarth, 1978). Only more recent studies include data from troops with male numbers comparable to the other savannah baboon subspecies (Bulger, 1993; Henzi *et al.*, 1999;

Weingrill *et al.*, 2000), revealing a strong correlation between rank and consortship success. However, although this correlation was found to be stronger than in the other savannah baboon subspecies, and the priority-of-access model explained the proportion of time spent in consortship for males of different rank, highest-ranking males consorted less than expected.

This paper investigates why dominant males consort on fewer days than predicted by the priority-of-access model, using data from the highest-ranking males of four chacma baboon troops situated in the mountains of the Natal Drakensberg and the coastal fynbos vegetation of the Western Cape. Previous studies addressing determinants of mating success have mainly been concerned with the general relationship between male rank and mating success but some studies also looked into how demographic factors influence the strength of this relationship. However, the use of the correlation coefficient to determine factors that influence the relationship between rank and mating success has been controversial and conclusions may be based on statistical artefacts (Barton & Simpson, 1992; Simpson & Barton, 1992). To circumvent this problem we use the deviation in mate-guarding performance of highest-ranking males from the priority-of-access model to identify factors influencing consortship success.

Several explanations have been given as to why the linearity of the correlation between rank and mating success can be disrupted and why highest-ranking males often have lower consortship success than expected. For example, the behaviour of females could influence the possibility of consortship establishment (Smuts, 1985; Small, 1989), particularly if females have a non-dominance based preference for males. Alternatively, the occurrence of male-male coalitions may allow some lower-ranking males to displace dominant males and this is often responsible for consortship takeovers in yellow and olive baboons (Packer, 1979; Bercovitch, 1988; Noë & Sluijter, 1990, 1995). In contrast to the other savannah baboon subspecies, chacma males were not observed to form coalitions in order to gain access to oestrous females and direct female choice seems to have little or no effect on mating success of males (Bulger, 1993; Weingrill, 2000). In principle, four other variables are likely to influence the ability of highest-ranking males to monopolise oestrous females and could thus be responsible for the observed deviations from the priority-of-access model. These include the number of males and females in a troop, costs entailed in consorting and finally the ability of males to identify conceptive probabilities. If an increase in the number of males decreases power differentials between males, consorting males will be challenged by individuals of similar resource-holding potential (Cowlishaw & Dunbar, 1991; Noë, 1994). This makes the displacement of consorting males more likely and thus leads to a negative relationship between the number of males and consortship success of highest-ranking males. Larger female cohort size is related to increased overlap of oestrous periods (Dunbar, 1988; Altmann, 1989), allowing more lower-ranking males to consort due to the increase of simultaneously cycling females. Although this reduces consortship success of highest-ranking males, it does not explain why males consort on fewer days than expected from the priority-of-access model. A lower than expected consortship success of highest-ranking males with increasing number of available oestrous females can only be expected if constraints such as decreased energy intake or increased energy expenditure during consortship limits the number of days a male can mate-guard a female during the oestrous period (Alberts *et al.*, 1996). Finally, when testing the priority-of-access model, one has to consider the assumption the model makes, specifically that all cycles are of equal quality with the same probability of conceiving. This assumption is not fulfilled since females usually pass trough several oestrus cycles before conceiving and males often do not show any interest during some cycles (*e.g.* Altmann *et al.*, 1978; Noë & Sluijter, 1990; Bulger, 1993). If dominant males are not able to consort all oestrous females due to any of the above factors, a strategy where males can efficiently identify the most fertile females and the most likely times of conception is expected to be adaptive. Data from several baboon study sites show that consorting males tend to be selective for cycle-days during which conception is most likely (Hausfater, 1975; Packer, 1979; Bercovitch, 1987; Bulger, 1993), but this pattern is not always evident (Rasmussen, 1980; Collins, 1981). Experimental findings suggest that male baboons are able to use the size of perineal swellings to determine the most likely time of ovulation (Bielert & van der Walt, 1982). However, it seems more difficult for males to tell apart fertile from non-fertile female cycles. So far, only highest-ranking chacma males from a single study site were found to consort significantly more often on fertile cycles (Bulger, 1993) and no general trend for selectivity of conceptive cycles has been reported in any other primate study. Therefore, besides analysing the effect of demographic factors on consortship success of the highest-ranking males in the four study troops, we will investigate whether these males consorted preferentially on cycles with a high probability of conception.

## Methods

### *Study troops*

Two of the study troops (FT and HT) were observed at Cathedral Peak in the Drakensberg Mountains of Natal, South Africa. Data on FT were collected between July 1991 and May 1992, data on HT between May 1994 and July 1995. Another troop (VT) was observed between April 1997 and September 1999 at the De Hoop Nature Reserve, Western Cape, a coastal reserve about 50 km east of the southern tip of Africa, Cape Agulhas. During this study demographic changes took place and as a consequence the data are divided into two periods and analysed separately:

— VT I: April 1997 - March 1998. The troop remained stable throughout this period. In April 1998 all adult and subadult males, three adult females and seven subadult females, juveniles and infants died of an infectious disease (Barrett & Henzi, 1998).

— VT II: June 1998 - September 1999. The only five surviving members (three females, two subadult males) of a neighbouring troop also affected by the disease joined VT in May 1998. Five adult males immigrated into VT between end of May and middle of June 1998. Another male immigrated in September 1998 and became highest-ranking after two females and three males emigrated in October 1998. VT II is the only of the four study troops where two different males occupied the highest-ranking position during the study period. Group size, composition and the number of observation hours for all troops are given in Table 1.

### *Sampling methods*

All troops were followed on 5-10 days per month from sunrise to sunset. Together with observations from incomplete day-follows, data on the size of the perineal swelling, the onset of detumescence and consort partners were gathered *ad libitum* (Altmann, 1974) on 12-23 days per month. Activity scan samples were collected throughout the study period only from HT and VT (period I and II). During follows, activity of all observable troop members was recorded every 30 minutes as one of four mutually exclusive categories: foraging, grooming, resting or moving. In order to calculate mating frequencies, focal animal sampling was carried out for eight cycling females in VT for a minimum of twelve minutes, but not longer than 25 minutes. The exact observation time was used to calculate mating frequencies. In HT, focal animal samples of 20 minutes duration were collected on the seven males. The main purpose of the FT study was the relationship between mothers and infants and no focal animal samples on cycling females or males were collected (Lycett *et al.*, 1998).

TABLE 1. *Troop size, composition and the number of observation hours for the study troops*

| Troop | Troop size | *N* Males | *N* Females | Observation hours |
|---|---|---|---|---|
| FT | 23-28 | 4 | 9 | 1020 |
| HT | 32-36 | 7 | 12 | 980 |
| VT I | 48-50 | 4 | 12 | 1380 |
| VT II | 40-49 | 5.3 | 12.7 | 1950 |

### *Female cycles*

Female baboons display prominent swellings which correlate with the menstrual cycle (Hendrickx & Kraemer, 1969). The day when the sexual swelling declines abruptly is called D-0 (Hausfater, 1975), and preceding days are counted backwards (D-1, D-2, *etc.*). The day of detumescence is a more reliable index for the assessment of ovulation than using the midpoint of a menstrual cycle; ovulation in baboons is most likely to occur two or three days prior to D-0 (Hendrickx & Kraemer, 1969; Shaikh *et al.*, 1982). However, matings leading to conception can occur earlier due to sperm survival in the female's reproductive tract and therefore days D-7 through D-1 are defined as the receptive period of a cycle in this study (in accordance with Smuts, 1985; Bercovitch, 1986; Bulger, 1993; Weingrill *et al.*, 2000). Maximum swelling was reached a few days before this period, with no observable size differences during the receptive period. We were able to assess the day of detumescence of 122 cycles (FT: $N = 21$, HT: $N = 28$, VT I: $N = 21$, VT II: $N = 52$). Only cycles from adult females were analysed in this study. Subadult nulliparous females were usually not consorted by males and hence have been excluded. Thirty of the above cycles were conceptive (FT: $N = 2$, HT: $N = 9$, VT I: $N = 7$, VT II, $N = 12$). The conceptive or fertile cycle was the cycle prior to the onset of pink coloration of the paracolossal skin of females, indicating pregnancy (Altmann, 1970). All conceptive cycles resulted in birth of infants.

### *Male rank and consortship*

Approach/avoid interactions and agonistic interactions were gathered *ad libitum* and used to establish a dominance hierarchy among adult males. All adult males had fully developed shoulder musculature, large testes and long canine teeth. Subadult males were only observed to consort for a few days in VT I and VT II and were not included in this study. Males usually consorted throughout the day. Overall, only seven cases were observed where females had two consort partners in one day (2% of all observed consortships during full day follows). The average consortship duration for highest-ranking males during cycles where the first and last days of a consortship could be determined was 6.3 days for the Drakensberg troops ($N = 19$ cycles) and 7.2 days at De Hoop ($N = 14$ cycles). Because males are able to monopolise access to females for extended periods we used days spent in consortship rather than the number of copulations as a measure of mating success. Although no paternity tests were carried out, the long consortship duration throughout the receptive period allowed us to identify putative fathers of infants.

The correlations between male rank and the number of days spent in consortship for the Drakensberg troops have been published elsewhere (Weingrill *et al.*, 2000). This data, together with data from the De Hoop troops, are given in Table 2. With the exception of VT I, all correlation coefficients are 0.9 or higher, indicating a strong correlation. The relatively low correlation coefficient of 0.63 in VT I can be attributed to a higher consortship success of the third-ranking male compared to the second ranking male. In VT II, data from two highest-ranking males were combined. If the time period is split and analysed during tenure of each male, the correlation between rank and consortship remains similar for both males ($r_S = 0.9$, $N = 5$ and $r_S = 0.9$, $N = 6$).

Due to overlapping receptive periods of females, highest-ranking males were unable to consort each female on every receptive day. The maximum expected number of consorted

TABLE 2. *Spearman rank correlation between male rank and number of consorted days during the receptive period of oestrous females*

| Troop | *N* males | $r_S$ | *p* |
|---|---|---|---|
| FT | 4 | 0.95 | ns |
| HT | 7 | 0.96 | <0.01 |
| VT I | 4 | 0.63 | ns |
| VT II | 5.3 | 0.9 | <0.05 |

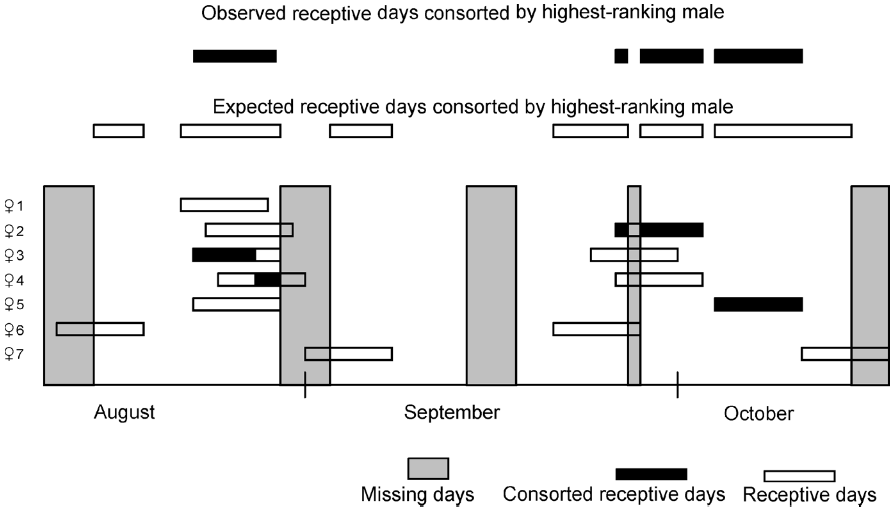

Fig. 1. Distribution of receptive days of cycling females during a three month period for VT II and the expected number of consorted days calculated for the highest-ranking male according to the priority-of-access model, together with the observed number of consorted days during receptive periods.

days for highest-ranking males was calculated according to the priority of access model: all receptive days (D-7 through D-1) minus overlapping receptive days. Figure 1 shows the observed distribution of receptive days during three months of the VT II study and the number of days that the highest-ranking male was expected to consort during this period, together with the observed number of consorted days. For this paper, consortship success of males is defined as the number of observed days spent in consortship divided by the expected number of consorted days. All data were analysed using nonparametric tests. Significance levels were set at 0.05 and all tests were two-tailed.

## Results

### *Consortship success of highest-ranking males*

The four highest-ranking males of the four study troops consorted only between 50.3% and 75.4% of the possible receptive days they were expected to consort (Table 3). The number of males and females per troop was not significantly correlated with consortship success (males $r_s = -0.74$, NS; females $r_s = -0.63$, NS, Fig. 2a, b). We calculated the average number of receptive days that highest-ranking males were expected to consort per study month according to the priority-of-access model. In contrast to the number of females in a troop, this number was strongly correlated with consortship success ($r_s = -1$, $p < 0.05$, Fig. 2c). Highest-ranking males in troops with less available receptive females days per month consorted a higher percentage of days than males in troops with more receptive days. The number of receptive days that a male was expected to consort was not significantly correlated with the female cohort size ($r_s = 0.63$, NS). This implies that the number of cycling females was independent from the total number of females in a troop.

The average operational sex ratio (OSR) was calculated for each troop (number of cycling females per month / number of males). We found no significant correlation between OSR (FT: 0.49, HT: 0.33, VT I: 0.46, VT II: 0.68) and consortship success of highest-ranking males ($r_s = -0.4$, NS), indicating that male competition did not increase with decreasing OSR. If the number of males influences competition for females, then we might expect to find higher levels of agonistic interactions during consortship in troops with greater male numbers. However, the number of males in a troop was not found to have an effect on the rate of agonistic interactions during

TABLE 3. *Expected number of receptive days that a highest-ranking male could possibly consort and the observed number of days consorted by highest-ranking males*

| Troop | Expected consorted receptive days | Observed consorted receptive days | % Consorted |
|---|---|---|---|
| FT | 142 | 94 | 66.2% |
| HT | 88 | 46 | 52.3% |
| VT I | 65 | 49 | 75.4% |
| VT II | 175 | 88 | 50.3% |

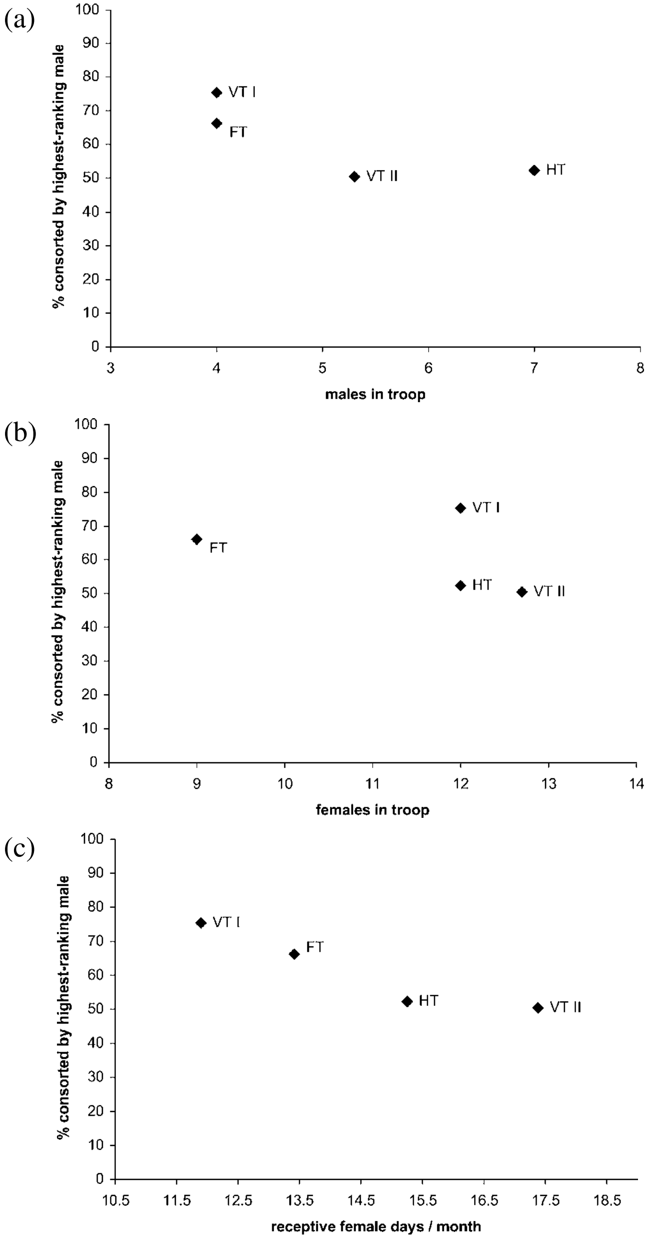

Fig. 2. Correlation between the percentage of consorted days by highest-ranking males (in relation to the expected number of days) and the number of males in a troop (a), the number of females in a troop (b) and the average number of available receptive female days per month (c).

consortship; no agonistic encounters were observed in the Drakensberg or in the De Hoop troops during consortship focal animal samples (total of 38 and 45 hours, respectively). During day-follows, we only observed four incidents where higher-ranking males challenged lower-ranking consorting males.

### *Costs of consortship*

For the following analysis we compared the expected number of consorted days per month with the observed number of consorted days per month for the highest-ranking males from each troop (Fig. 3). As reported above, all highest-ranking males consorted less than expected. Interestingly, all highest-ranking males consorted a similar number of days per month (between 8 and 9 days) regardless of the number of available receptive days. Although males consorted primarily during the receptive period (78.4% of all observed consorted days), they often started to consort a few days prior to the receptive period. If those consorted days are included males of the four troops consorted on average a few days more per month (HT: 11.3 days, FT: 9.5 days, VT I: 12.3 days, VT II: 11.7 days).

Costs involved in consorting may represent an explanation why males do not consort during more days. Maintaining a consortship can be assumed to be disruptive of time and energy budgets. To assess if costs were reflected

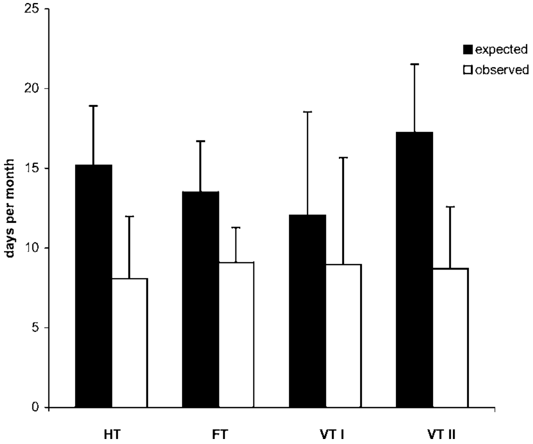

Fig. 3. The expected and observed number of consorted days per month (±SD) during the receptive period (D-7 through D-1) by the highest-ranking male of each troop.

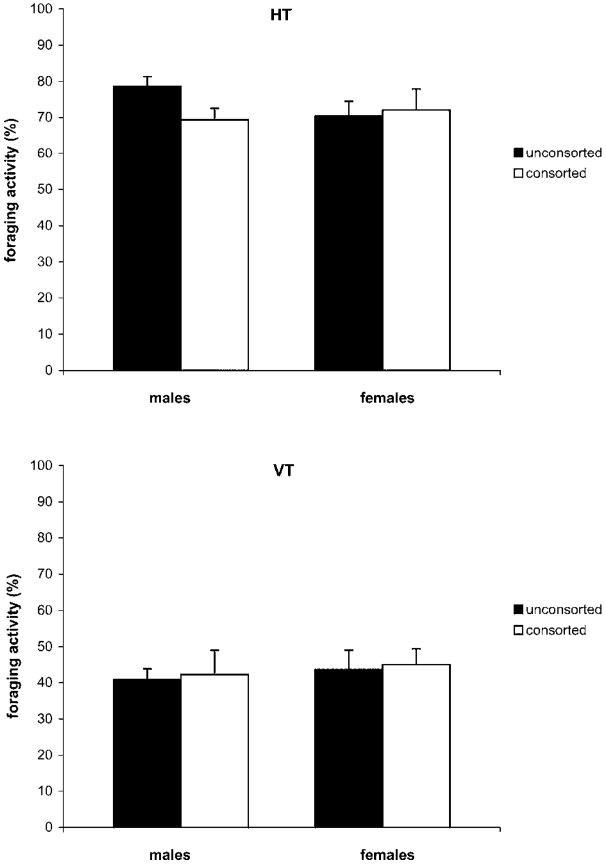

Fig. 4. Comparison of the proportion of foraging activity (±SD) during consorted and unconsorted periods for males and females in HT (4 males, 8 females), and VT (6 males, 9 females).

in activity budgets we compared the percentage of foraging activity for cycling females and males during consorted and unconsorted time periods for the Drakensberg troop HT and the combined De Hoop troops (Fig. 4). Drakensberg males reduced foraging activity towards the level of females during consortship, indicating that costs were involved. However, the number of consorting males in HT was small and permitted statistical analysis only for the highest-ranking male who was found to spend less time foraging during consortship compared to the previously unconsorted days (Wilcoxon signed-ranks test, $z = -2.69$, $N = 9$ time periods, $p < 0.01$). The four consorting males showed a decrease in time spent foraging between 5% and 11%

(mean 9.2%). In contrast, De Hoop males did not show a significant change in foraging activity between consorted and unconsorted periods (Wilcoxon signed-ranks test, $z = -0.73$, $N = 6$ males, NS) and no significant differences between males and females was found (Mann-Whitney $U$-test: consorted $U = 21$, NS; unconsorted $U = 17.5$, NS). No significant changes in female foraging activity were found between consorted and unconsorted time periods for the females in both troops (Wilcoxon signed-ranks test, HT: $z = -0.71$, $N = 8$, NS; VT: $z = -0.71$, $N = 9$, NS).

### *Distributions of consorted days among female cycles*

The mean number of cycles before conceiving was 4.1 in HT (range 1-7) and 4.9 in VT (range 1-9). Figure 5 shows the percentage of consorted days during the fertile cycles and the preceding cycles for the highest-ranking males of the four study troops. Also included are consorted days of females that did not conceive during the study periods. If the number of days that highest-ranking males can consort is limited by the costs of consortship, how do they distribute these days among the cycling females? The highest-ranking males in HT and VT I consorted a higher proportion of days during the conceptive cycles compared to the foregoing nonconceptive cycles, although this was statistically significant only in VT I ($\chi^2 = 14.6$, $p < 0.01$). The highest-ranking males in the other two troops were not found to consort conceptive cycles selectively. In FT, the only two conceptive cycles were observed during the first few study months. Two other females cycled throughout the study and conceived only in the following year. Because of this the highest-ranking male in this troop was able to consort a large proportion of receptive days of nonconceptive cycles without risking neglecting potentially conceptive cycles (Fig. 5).

The highest-ranking males in FT and VT I were already resident in the troop for several months before the study began. The effect of residence length can be analysed for HT and VT II, where the start of the study period coincided with the immigration of new highest-ranking males. The study periods were split and the percentages of consorted cycles from the first half compared with the second half (Fig. 6). It is evident that newly immigrated males often consorted infertile cycles during the first few months of the study period. Due to the relatively low number of conceptive cycles in the split time periods the differences were only significant in VT II (HT $\chi^2 = 2.5$,

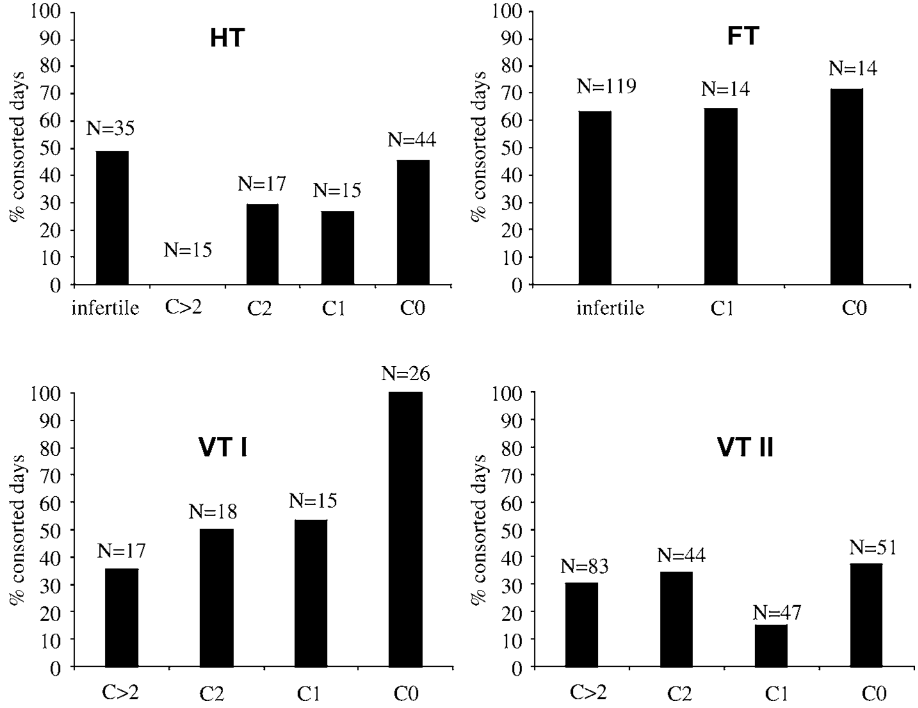

Fig. 5. Distribution of observed consorted days among receptive days (D-7 through D-1) in relation to the fertile cycle. C0 = fertile, conceptive cycle, C1 and C2 = first and second cycle before conceiving, $C > 2$ = average of all cycles preceding C2. One infertile female cycled in HT and did not give birth for at least another three years, and two females in FT cycled throughout the study period but only became pregnant during the following year. $N$ = total number of observation days during receptive period.

$p < 0.14$, VT II $\chi^2 = 16.1$, $p < 0.01$). During the first months of residency the highest-ranking male in HT consorted preferably an older female with large swelling which did not become pregnant for at least another three years. During this period he putatively sired only one out of four possible infants (Fig. 7). Throughout the second half of the study he monopolized three out of four conceptive cycles. Data from VT II, where data from two males are combined, shows a similar picture (Fig. 6). One highest-ranking male left the troop after five months. He putatively sired one out of four possible infants in the last month of his residency. The following highest-ranking male monopolised mating only on one out of five conceptive cycles during the first five months of residence while consorting two out of three conceptive cycles during later months. Combining the data from HT and VT II, conceptive

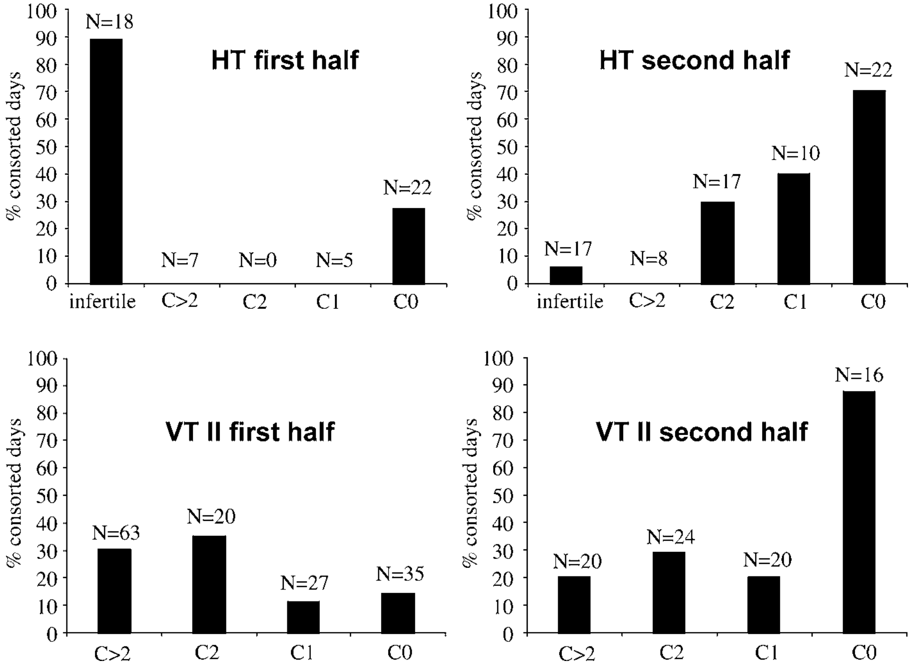

Fig. 6. Distribution of consorted days during the receptive period in relation to the fertile cycle for HT and VT II. In both troops the highest-ranking male immigrated at the start of the study period and the first and second half of the study period are analysed separately (x axis as in Fig. 5).

cycles throughout the first four months of tenure were consorted less often by the highest-ranking male (two out of eleven consorted by highest-ranking male) than during later stages of their residency (six out of nine consorted by highest-ranking male, $\chi^2 = 4.85$, $p = 0.07$).

Two issues still need to be addressed. Firstly, dominant males could find it easier to consort selectively if fewer females are simultaneously in *oestrous* during conceptive cycles. Therefore we compared the observed number of overlapping receptive days during conceptive and nonconceptive cycles. Fewer overlapping days during conceptive cycles were only found in VT I (conceptive: 19% overlap, nonconceptive: 40%; $\chi^2 = 2.5$, NS). In the other troops conceptive cycles were found to have more synchronous receptive days compared to nonconceptive cycles, but this was only significant for the second half of the study period of VT II ($\chi^2 = 6.0$, $p < 0.05$). Secondly, it is possible that females are more likely to conceive during a cycle in which a male shows extended consortship. For this reason it is difficult to

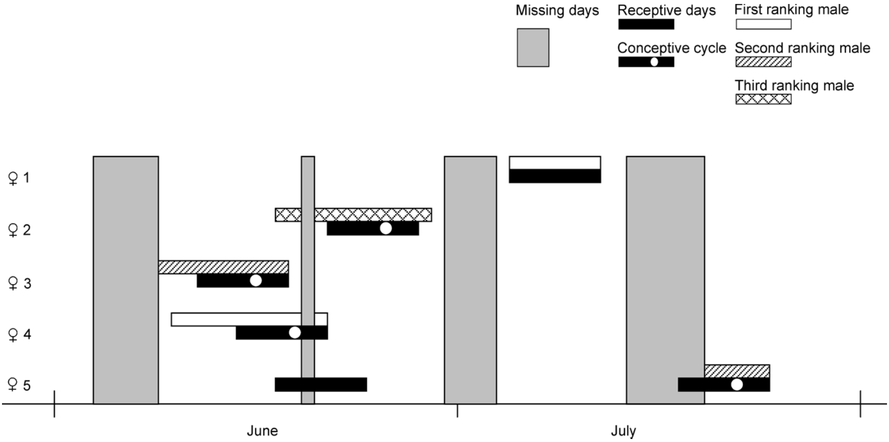

Fig. 7. Distribution of the receptive days of female cycles for HT during a two month period shortly after immigration of the highest-ranking male, together with consortship activity of males.

TABLE 4. *Observation hours, number of matings and matings per hour for consorted and unconsorted females of VT. Data was collected between D-10 and D-1 using the focal sampling method*

| Female | Consorted | | | Unconsorted | | |
|---|---|---|---|---|---|---|
| | Hours | Matings | Matings/Hour | Hours | Matings | Matings/Hour |
| AC | 10.36 | 23 | 2.2 | 5.71 | 15 | 2.6 |
| AL | 5.86 | 6 | 1.0 | 4.23 | 4 | 1.0 |
| DE | 4.84 | 5 | 1.0 | 12.83 | 44 | 3.4 |
| EM | 1.46 | 1 | 0.7 | 1.78 | 8 | 4.5 |
| GI | 2.93 | 7 | 2.4 | 4.48 | 15 | 3.3 |
| JU | 3.60 | 5 | 1.4 | 3.13 | 7 | 2.2 |
| NA | 5.42 | 5 | 0.9 | 3.07 | 10 | 3.3 |
| SA | 4.1 | 3 | 0.7 | 3.41 | 9 | 2.6 |
| Total | 38.58 | 55 | 1.4 | 38.64 | 112 | 2.9 |

distinguish between cause and effect in this study. Copulation rates of consorted and unconsorted females for the troops are given in Table 4 for females of VT. Females mated at a higher rate outside consortship than when they were consorted by males (Wilcoxon signed-ranks test, $N = 8$, $z = -2.37$, $p < 0.05$). For HT, only data from consorted females are available, with females showing a similar rate of matings compared to VT (HT: 1.33 matings/hour, VT: 1.42 matings/hour). In addition, some conceptive receptive periods were not fully consorted and two females conceived without being consorted in VT. Although almost all receptive days of conceptive cycles were consorted (91%, $N = 135$ observed receptive days), this demonstrates that long-lasting consortship by highest-ranking males is not a prerequisite for conception.

## Discussion

In this study, all highest-ranking males consorted on fewer days than expected by the priority-of-access model. Consortship success was correlated with the average number of receptive days per month that a male was expected to consort: highest-ranking males in troops with higher numbers of available receptive females experienced more problems consorting all females. Cowlishaw & Dunbar (1991) have found that in highly dimorphic primate species, which include savannah baboons, the strength of the correlation between rank and reproductive performance diminishes with increasing number of males in a troop. Using only data from savannah baboon field studies, Bulger (1993) showed that the number of males has an effect on the correlation between rank and days spent in consortship. In both analyses, the ability of dominant males to monopolise females also decreased with the number of females in a troop. In contrast to these studies, the number of males and females in our study troops was poorly correlated with consortship success of highest-ranking males. Furthermore, we found no significant correlation between the number of females in a troop and the average number of available receptive days per month. However, the number of study troops was small and there was little variance in the number of males and females in each troop. It is likely that a greater sample size would strengthen the relationship between the female cohort size and the number of available receptive days.

Although consortship success tended to be higher in troops with fewer males, it is unlikely that male number had an effect, since lower-ranking males never challenged highest-ranking males while consorting a female. As mentioned above, the relationship between female cohort size and the number of available receptive females can be weak for the duration of an alpha male tenure period, during which males are expected to sire most offspring

(Altmann *et al.*, 1988). Accordingly, young males with a potential to become highest-ranking should not only decide whether to migrate into a troop based on the total number of females, but also on the current and expected future number of oestrous females in a troop (Andelmann, 1986). Males do spend considerable time observing troops (Byrne *et al.*, 1987) and it seems plausible that they can assess the number of future cycling females based on their reproductive state, *e.g.* pregnant or lactating. In contrast, the operational sex ratio, the ratio of fertilizable females available to the number of males in a troop (Emlen & Oring, 1977), should only be of importance to lower-ranking males with little chance to achieve high rank. As expected, the operational sex ratio was not correlated with consortship success of dominant males in this study. To summarize, we believe that consortship success of highest-ranking chacmas males, and probably also the strength of the relationship between rank and mating success, is not determined by the number of males in a troop, but by the number of receptive days that males encountered.

How does the average number of receptive days determine mating success of males? On average highest-ranking males consorted between 9 and 12 days per month, leaving some oestrous females unconsorted, especially during time periods when the number of cycling females was high. Consorting females is likely to involve costs and may limit the number of days a male is able to consort. Chacma males are about 80% heavier than females (Barrett & Henzi, 1997) and therefore need to forage for a longer period of time and eat food of higher quality compared to females. Accordingly, most baboon studies have found males to spend more time feeding than females (*e.g.* Davidge, 1978; Cowlishaw, 1993; Gaynor 1994, but see Post *et al.*, 1980; Barton, 1989). Activity data from the Drakensberg troop (HT) provide evidence that males spent more time foraging than females. During consortship, foraging time decreased by approximately 9%, declining towards the proportion of time females spent foraging. In contrast, males from the De Hoop troop (VT) were found to forage a similar proportion of time compared to females, and this did not change during consortship. Although feeding time during consorted and unconsorted periods at De Hoop remained unchanged, this does not necessarily imply that no costs were involved. Investigating mate-guarding constraints in yellow baboons, Alberts *et al.* (1996) found little evidence that time spent feeding decreased during consortship. Instead, travel distances of consorting males decreased to the level of distances travelled by females and consorting males had shorter feeding bouts. They concluded that consorting males had a lower quality and rate of food intake, resulting in decreased energy intake. These parameters were not collected in our study. The comparison of foraging activity suggests that foraging costs are easier to detect in the Drakensberg baboons because they had to forage for longer hours than the De Hoop baboons. The food in the Drakensberg is evenly distributed and of low quality (Henzi *et al.*, 1992), such that mountain baboons cannot compensate lost feeding time through intake of high-quality food and energy intake is likely to be reflected by time spent foraging. In addition to energetic costs, males that mate-guard a single female for several days will necessarily be limited in the amount of time they are able to spend maintaining relationships with other group members. This may also represent a cost to consortship that is not apparent from activity budgets.

Although there is little or no evidence for direct female choice in baboons (Bulger, 1993; Weingrill, 2000), females may restrict chances of mating for certain males indirectly by advertising reproductive state with sexual swellings as well as synchronising receptive periods (Paul, 2002). Besides increasing male competition this also promotes promiscuous mating in order to prevent infanticide by males, which has profound consequences for social systems (van Schaik & Kappeler, 1997). Infanticide by males is more common among chacma baboons (Palombit, 1999; Weingrill, 2000) than in the other baboon subspecies. As a counterstrategy, females may increase the number of infertile cycles prior to conception (Zinner & Deschner, 2000) or extend the period of maximum swelling to confuse paternity in order to recruit several males for aid if the possibility of infanticide arises. If this is the case, then chacma males possibly experience more problems in deciding when to start a consortship.

Chacma males may have countered this female strategy by increasing the time spent in consortship during cycles with high conceptive probabilities. Reproductive success of these males is therefore likely to be higher than their consortship success suggests. However, a residency time of several months was needed before males were apparently able to detect conceptive cycles. In two troops, highest-ranking males immigrated at the start of the study. Even though these males did not consort less often, during the first few months of residency they repeatedly spent time in consortship with females that did not conceive, while lower-ranking males were observed to consort conceptive cycles. During later stages of residence, the same males consorted preferentially on cycles with higher probabilities of conception. Our result is consistent with another chacma baboon study where highest-ranking males consorted more often during conceptive cycles (Bulger, 1993), while selectivity for conceptive cycles has not been reported from the other savannah baboon subspecies. Although it has been noted that males do not consort females during some cycles, usually the first cycle after amenorrhea and the first cycles of nulliparous females (*e.g.* Altmann *et al.*, 1978; Noë & Sluijter, 1990), males have not been found to consort more during conceptive cycles than during the preceding cycles. Yet, there is anecdotal evidence from at least one study that, when an older lower-ranking male did consort a female, this usually resulted in conception (Smuts, 1985), indicating that males with more experience are able to assess fertility of females in the other baboons subspecies. Furthermore, it has been noted that newly immigrated males initially have poor consortship success (*e.g.* Hausfater, 1975; Smuts, 1985; Noë & Sluijter, 1990), which could also be due to better knowledge of older males about the reproductive state of females.

The mechanism involved in consortship selectivity remains unclear and the following explanations are speculative. For instance, there is evidence that females communicate information to discern the proximity of ovulation via vocalisations (*e.g.* Semple & McComb, 2000; Semple *et al.*, 2002). Callitrichid males can detect changes in olfactory cues emitted by females, allowing them to detect the reproductive status of females (*e.g.* Ziegler *et al.*, 1993; de Vleeschouwer *et al.*, 2000). Similar to the callitrichids, male baboons also sniff at the anogenital region of females and it therefore seems possible that they are able to use olfactory cues to evaluate the timing of ovulation (unpubl. data). However, it is not known if these mechanisms can also be used to assess conceptive probabilities in species where females pass through several cycles before conceiving. Males could also use parameters such as body fat or general appearance and consort only females in optimal condition, since fertility is expected to be correlated with body condition (Bercovitch & Harding, 1994). Living in close proximity with females over relatively large periods of time could provide long-term resident males with information about the reproductive history of females. For example, in this study a female cycled regularly but did not conceive throughout the study period. Although the female had a large swelling she was only consorted by newly immigrated males.

The sexual swelling may also be a possible indicator for conceptive probabilities baboons. It is generally accepted that males use the size of the sexual skin to determine the most likely time of ovulation (Bielert & van der

Walt, 1982). Nevertheless, little is known about differences in size, shape and colour of the female sexual swelling from cycle to cycle. In a recent study Domb & Pagel (2001) claimed that the size of swellings was correlated with indices of female fitness. Males apparently used the size of the swelling to determine their mating effort, but the size was not correlated with the current probability of conception. However, the authors only compared conceptive cycles with the nearest non-conceptive cycles and it is possible that an inclusion of more cycles will demonstrate that the swelling size is correlated with conceptive probabilities. Males should try to reproduce with as many females as possible during their alpha-male tenure period. If female behaviour or the size or shape of a female's swelling changes towards the conceptive cycle, then males should be able to detect this and consort the females that are most likely to conceive, regardless of lifetime fitness parameters. Choosing the female with highest lifetime fitness is therefore only important if conceptive cycles overlap or succeed one another too closely. Because information on swelling sizes from cycle to cycle would only be available to males that have spent several months in close proximity with the females, new males can be expected to consort less selectively, as was observed in this study. Clearly more field studies are required to clarify if selectivity for conceptive cycles exists only in chacma baboons and detailed measurements during several successive cycles are needed to investigate the ability of males to make choices based on the sexual swelling.

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