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Flehmen and birth synchrony among female sable antelope, *Hippotragus niger*

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Abstract. The role of female flehmen behaviour in maintaining reproductive synchrony was investigated in 11 adult female sable antelope and their associated offspring maintained on a 13·2-ha pasture at the National Zoological Park's Conservation and Research Center near Front Royal, Virginia. All occurrences of aggression and flehmen by adult females were recorded during 274 h of observation over a 10-month period (1987), and the timing of births was recorded for four birth seasons (1986–1989). In each year, dominant females tended to give birth in temporal proximity to other females (birth clustering), while subordinates gave birth asynchronously. Flehmen frequency fluctuated seasonally, reaching highest levels just prior to the approximated time of conception. Adult, multiparous females were the primary targets of flehmen. There was positive assortment by reproductive state: pregnant females attended to urinations by other pregnant females and postpartum females responded to other postpartum females. Prepartum flehmen rates reliably predicted subsequent birth synchrony, and the degree of synchrony between a given pair of females was directly proportional to the frequency with which they sampled each other's urine in the preceding year. These results indicate that flehmen is a potential mechanism by which female sable antelope can manipulate the timing of both conception and parturition.
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Reproductive seasonality, a clustering of births during a limited time period, is exhibited by many mammalian species. Suggested benefits of a restricted birth season include coordinating birth with periods of optimal environmental conditions (Sadleir 1969; Rutberg 1987; Bronson 1989), minimizing predation through predator swamping or group protection of young (Estes 1966, 1976; Bergerud 1974; Sekulic 1978; Estes & Estes 1979; Murray 1982; Boinski 1987) and optimizing social development by facilitating peer interaction (Brown 1985; Pfeifer 1985).

Reproductive seasonality is especially pronounced in ungulates, and is strongly correlated with climatic variation (Rutberg 1987), with species in temperate and subarctic regions often having birth seasons restricted to several days each year (e.g. caribou, *Rangifer tarandus*: Lent 1966). Many tropical ungulate species, however,

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exhibit birth seasons more restricted than predicted based solely on climatic variation (Estes 1976), whereas others show tight birth synchrony within but not between herds in the same locality (e.g. sable antelope: Sekulic 1978). Environmental cues such as photoperiod and food quality and availability undoubtedly play a major role in determining reproductive seasonality (Bronson 1989); however, social cues may be of major importance in synchronizing reproduction within social groups (Ims 1990).

Olfactory cues are sufficient to establish reproductive synchrony among female laboratory rats (McClintock 1978), and olfaction appears to be the primary social cue responsible for reproductive synchrony in several other mammalian taxa, including golden hamsters, *Mesocricetus auratus* (Handelmann et al. 1980), opossums, *Monodelphis domestica* (Fadem 1987), bison, *Bison bison* (Berger 1992), domestic cattle (Vandenbergh & Izard 1983), squirrel monkeys, *Saimiri oerstedi* (Boinski 1987), and humans (Russell et al. 1980). Olfactory investigation in ungulates is characterized by the performance of flehmen, a retraction

of the upper lip commonly exhibited immediately following anogenital sniffing or investigating freshly voided urine (Estes 1972). Flehmen is a prominent component of male reproductive behaviour (Grau 1976) and is believed to enable males to evaluate the reproductive status of females (Ladewig & Hart 1980; Ladewig et al. 1980; Hart 1983). Although rarely displayed by females of several ungulate species (Dagg & Taub 1970; Mykytowycz 1976; Henderson et al. 1980; O'Brien 1982; Rhienhardt 1983), flehmen is reported to be common among females in both captive and free-ranging species of the bovid tribe Hippotraginae (Estes & Estes 1974; Pfeifer 1985; Thompson 1991) and thus is a potential mechanism for the precise within-herd birth synchrony in populations where reproduction is not highly seasonal (e.g. Sekulic 1978). Flehmen behaviour in female ungulates has only rarely been quantified, and no attempts have been made to examine the role of flehmen in mediating reproductive synchrony.

A preliminary investigation of birth synchrony and flehmen in captive sable antelope (Thompson 1991) suggested that flehmen may be a means by which females synchronize births: both flehmen rate and a female's ability to give birth in temporal proximity to herdmates were strongly correlated with dominance rank. High-ranking females exhibited high rates of flehmen and gave birth in clusters, whereas low-ranking females rarely performed flehmen and tended to give birth much earlier or later than the rest of the herd. Differential access to urine was maintained by direct aggression. These data further suggest that small birth clusters, rather than herd-wide birth synchrony, may be the optimal reproductive strategy of dominant females. My objectives in the present study were to determine the factors influencing the performance of flehmen in females, and to investigate the relationship between flehmen and clustering of births in a captive herd of sable antelope.

METHODS

I observed a captive herd of sable antelope maintained on a 13·2-ha pasture at the National Zoological Park's Conservation and Research Center near Front Royal, Virginia, for a total of 274 h on 45 days between 9 March and 7 December 1987.

The herd initially consisted of 11 adult females, 10 of which were pregnant, and their 1986 offspring, four female and four male calves. Three female and seven male calves were born between 16 May and 7 July 1987. The yearling calves were removed from the herd on 5 August 1987, shortly before reintroduction of the herd bull on 12 August 1987. All individuals were individually recognizable by horn shape and unique colour combinations of ear tags.

For all instances of urination I recorded (1) the time of day, (2) the identity of the individual urinating, (3) the number of adult females in close proximity, defined as within five body lengths (approximately 10 m), (4) any subsequent flehmen responses, whether precipitated by sampling urine as it was being voided or by investigating urine deposited on the substrate and (5) the identities of individuals performing flehmen. I obtained the number of opportunities to perform flehmen for each female by subtracting the number of urinations by that female from the total urinations by adult females. Flehmen rates were then expressed as the number of flehmen responses by an individual female divided by the number of urinations to which she had the opportunity to respond. Instances in which a female displayed flehmen multiple times in response to a single urination were counted as a single flehmen response. The rate at which each female received flehmen was quantified by dividing the number of flehmens received by her frequency of urination.

I determined the degree to which each female was reproductively synchronous with other herd members from birth records from the 1986, 1987, 1988 and 1989 birth seasons. In each year and for each female, birth synchrony was calculated using two measures: (1) herd-wide birth synchrony (the absolute value of the number of days between a given female's day of parturition and the median birthdate) and (2) pair-wise clustering (the absolute value of the number of days between a given female's day of paturition and the nearest preceding or following birth). The first measure is more appropriate for measuring degree of synchrony in situations where the benefits of synchrony are positively related to the number of females synchronising, whereas the second measure may be more appropriate when partial synchrony is optimal. Synchrony scores were log-transformed when necessary for statistical analysis. The correspondence between urine sampling and degree of birth

clustering for all possible pair-wise combinations of females was evaluated with Mantel z, r and r_r tests (Hemelrijk 1990). I first used the r_r (ranks within rows) test to determine if a relative association existed between the two variables. The Mantel z and r tests were then used to test whether the variables were directly proportional. Probability levels for Mantel z, r and r_r tests were determined with a quadratic permutation method (Hemelrijk 1990). Null distributions of each statistic were obtained by performing 1000 permutations.

I investigated changes in flehmen frequency over the course of the reproductive cycle by calculating monthly frequencies with respect to parturition for each female. I similarly quantified hourly rates of male reproductive behaviour (anogenital sniffing, following, foreleg kicking, flehmen and mounting) directed to each female. For statistical analysis, I chose a 6-month period for which flehmen data were available for all 10 pregnant females, beginning 1 month prior to parturition and ending 5 months following parturition. To investigate age-class effects on the likelihood of receiving a flehmen response, I divided female herd members into four categories: calves (born during the course of the study), yearlings (born the previous year), primiparas (2 years of age) and multiparas (≥ 3 years of age). Because the likelihood of receiving flehmen could be influenced by the number of females nearby, data were analysed by an analysis of covariance, using age class as main effect and the mean number of females in close proximity as a covariate.

Dominance relationships between the adult females were determined by recording all interactions in which one female (designated the winner) displaced another (the loser). I constructed a sociogram based on wins and losses so as to minimize the number of entries falling below the diagonal (Lehner 1979), and assigned ordinal ranks, with the most dominant female receiving a rank of 1. The resultant hierarchy was strictly linear, with no reversals (Thompson 1991, 1993) and remained stable during the course of behavioural observations and for at least 3 years following.

RESULTS

Temporal Characteristics of Urination

Urinations were clumped in time. When observation time was divided into 15-min time blocks,
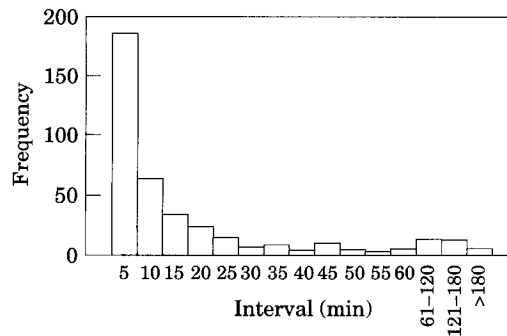

Figure 1. Time interval between successive urinations in a herd of 11 female sable antelope ($N=487$ urinations).

the frequency distribution of urinations was significantly different from that expected by chance under a Poisson distribution ($\chi^2=404\cdot9$, $df=4$, $P<0\cdot001$). There were more time blocks with no urinations and more time blocks with three or more urinations than expected by chance. Forty-four per cent of urinations occurred within 5 min of another urination, and 67% occurred within 15 min of another urination (Fig. 1). The timing of urination also appeared to be highly predictable. The activity cycles of females within herds were highly synchronous, and females within the study herd generally urinated within several minutes of the transition from rest to activity.

Spatial Characteristics of Urination

During urination, there was a high probability that other individuals were in close proximity (defined here as within five body lengths). At least one adult female was within five body lengths of a urinating individual 74% of the time. There were significant individual differences in the distribution of females around a given urinating female ($\chi^2=46\cdot31$, $df=30$, $P=0\cdot029$), but the mean number of females in close proximity was not correlated with the dominance rank of the urinating individual (Spearman rank correlation: $r_S= -0\cdot337$, $N=11$, $P>0\cdot05$). No significant seasonal fluctuations were found in the number of females in close proximity to each female when she was urinating ($\chi^2=26\cdot26$, $df=18$, $P>0\cdot05$).

Although the likelihood of a urination eliciting at least one flehmen response and the probability that a urination would elicit flehmen responses by multiple females were significantly and positively
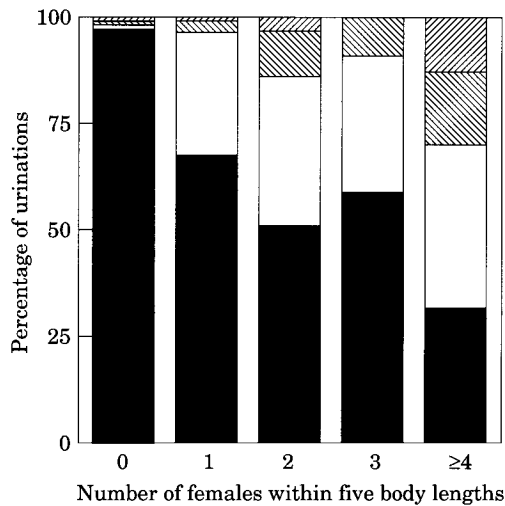
Figure 2. Per cent of urinations ($N=487$) by 11 adult female sable antelope eliciting flehmen responses from zero (■), one (□), two (▨) and three or more (▨) adult females when differing numbers of females were within five body lengths (approximately 10 m) of the urinating individual.

Figure 3. Mean (± SE) flehmen responses received by four age classes of female sable antelope. Sample sizes are shown.

influenced by the number of females in close proximity (Fig. 2; MANOVA: $F_{3,8}=43.68$, $P<0.001$ and $\chi^2=31.06$, $df=3$, $P<0.001$, respectively), proximity patterns alone did not explain individual differences in the frequency with which flehmen was received. The number of flehmen responses received by a given female was unrelated to the mean number of females in close proximity when she urinated ($r_S= -0.337$, $N=11$, $P>0.05$).

Targets of Flehmen

The likelihood that a urinating female would attract a flehmen response by an adult female was influenced by age class (ANCOVA: $F_{3,13}=9.065$, $P=0.002$) and was independent of the mean number of adult females in close proximity ($F_{1,13}=0.001$, $P>0.50$). A linear contrast revealed that flehmen was directed significantly more often to multiparous females than to primiparas, female yearlings or female calves (Fig. 3; $F_{1,13}=21.987$, $P<0.001$).

During the birth season, when both pregnant and postpartum females were available as targets of flehmen, there was positive assortment by reproductive state in flehmen responses (Fig. 4).
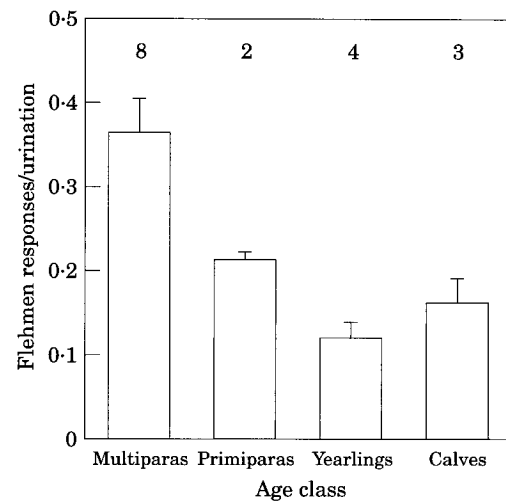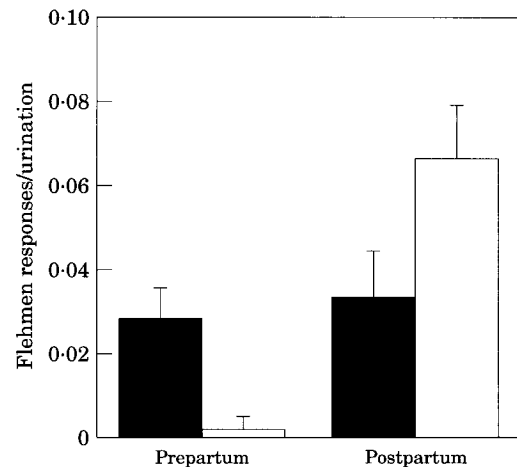
Figure 4. Mean (± SE) frequencies of flehmen towards pregnant (■) and non-pregnant (□) target females in the 3 months preceding and following parturition in female sable antelope ($N=10$).

In the 3 months prior to giving birth, females were significantly more likely to perform flehmen in response to the urination of another pregnant female than to a female who was not pregnant (Wilcoxon signed-rank test: $T^+=34$, $N=8$, $P=0.012$; sample size does not equal the number of pregnant females because this paired-sample test uses non-tied values only). Females in the 3

months following parturition were more likely to respond to a postpartum female ($T^+=38$, $N=9$, $P=0\cdot037$). It is possible that this apparent selectivity is an artefact of spatial clustering of females of similar reproductive state. This possibility could not be examined with the present data because the identities and reproductive states of females close to urinating individuals were not recorded.

The likelihood that a postpartum female would respond to a urination by another postpartum female increased with time following the onset of the birth season ($r_S=1\cdot00$, $N=6$, $P<0\cdot001$), showing a monotonic increase through each month of the breeding season. This increased responsiveness was very specific: urination by yearlings did not have a higher likelihood of eliciting a flehmen response with time ($r_S=0\cdot377$, $N=6$, $P>0\cdot05$). The increase in responsiveness could not be attributed to increases in the number of females in close proximity, because mean proximity scores did not change over this time ($r_S=-0\cdot086$, $N=6$, $P>0\cdot05$).

Changes in Flehmen Frequency with Reproductive State

Changes in flehmen frequency during the reproductive cycle were evident in the 10 females who gave birth during the course of the study (repeated-measures ANOVA: $F_{5,4}=11\cdot04$, $P<0\cdot02$). A quadratic model best described the variation in flehmen frequency ($F_{1,8}=9\cdot15$, $P<0\cdot02$), with mean flehmen frequencies reaching peak values 2–3 months following parturition and then declining (Fig. 5). This peak in flehmen frequency shortly preceded the peak of male reproductive behaviour. For six out of 10 females, male courtship behaviour was most frequent 4 months postpartum. The peak of male reproductive interest occurred 5 months postpartum for three females and 6 months postpartum for one female. Only two copulations were observed. Both occurred 4 months postpartum, coinciding with the highest rates of other male reproductive behaviour patterns. The timing of male reproductive interest was unrelated to female dominance rank, birth synchrony or the timing of the male's reintroduction to the herd.

Flehmen and Birth Clustering

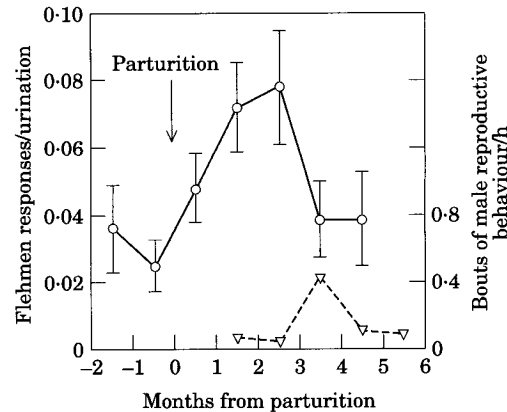The extent to which each female synchronized with the entire herd as a whole (herd-wide birth

Figure 5. Mean ($\pm$ SE) monthly flehmen rates ($\bigcirc$) for female sable antelope from 1 month prior to parturition until 5 months postpartum ($N=10$), and mean monthly rates of male reproductive behaviour directed towards each female ($\triangledown$).

synchrony) was not correlated with dominance rank in each of four birth seasons (Table I), but clustering of births was clearly evident. In 1986, 1987, 1988 and 1989, pair-wise birth clustering for each female was highly correlated with her dominance rank (Table I). In 1987, the year in which flehmen data were collected, five of the 10 pregnant females gave birth during an 8-day period (16–23 May). The two highest-ranking females gave birth on the same day, and the third-ranking female 2 days later. Remarkably, the most dominant female gave birth within 24 h of another female in each of 4 successive years.

In both 1986 and 1987, births were clustered near the onset of the birth season, shortly following the first birth. In 1988 births were most clustered near the end of the birth season. In 1989, two distinct clusters of births occurred, one at the onset of the birth season and one approximately 1 month later. The order of births during a given birth season was not related to dominance rank in any consistent way (Table I). Significant correlations between rank and birth order were obtained in 1987 and 1988, but the sign of the correlation was not consistent between years. In 1987, high-ranking females gave birth early in the season, whereas in 1988 they gave birth late in the season. The apparent correlation between rank and birth order in those years is thus likely to be an artefact of the correlation between rank and birth clustering.

Table I. Spearman rank correlations between female dominance rank and two measures of birth synchrony (herd-wide birth synchrony and pair-wise birth clustering) and birth order for a herd of 11 captive female sable antelope during four successive breeding seasons

	Year				
Variable†	1986 ($N=8$)	1987 ($N=10$)	1988 ($N=10$)	1989 ($N=9$)	$\bar{X}$
Rank versus herd-wide birth synchrony‡	0·554	− 0·409	− 0·024	0·000	− 0·027
Rank versus pair-wise birth clustering§	0·731*	0·848***	0·558*	0·490	0·765**
Rank versus birth order††	0·204	0·802***	− 0·632*	0·159	0·418

N is the number of females giving birth.
†For each variable, a single, summary measure was obtained for each female by taking the mean of all available data for that female.
‡Absolute value of the number of days between female parturition date and herd median birthdate.
§Absolute value of the number of days between female parturition date and the nearest preceding or following birth.
††Day of birth relative to the first birth of the season.
*$P<0.05$; **$P<0.01$; ***$P<0.005$.

Flehmen frequency during the month prior to parturition was strongly correlated with the degree of birth clustering (linear regression: $F_{1,8}=15.50$, $P<0.004$). Females with high rates of flehmen were more likely to give birth close in time to another female than those with low prepartum flehmen rates. Prepartum flehmen frequency explained 66% of the variation in birth clustering. Furthermore, analysis of data for all possible pair-wise combinations of females indicated that the more a given pair of females sampled each other's urine and performed flehmen in 1987, the closer in time they gave birth in 1988 ($r_r= − 71$, $P=0.01$; $z=164,210.5$, $P=0.001$; $r=614$, $P=0.003$).

DISCUSSION

Female sable antelope showed clustering of births during all four birth seasons examined. Temporal proximity of parturition to other births in the herd was not random, but instead was strongly related to a female's social dominance rank. Flehmen, like birth clustering, is highly correlated with rank, and may be the mechanism through which differential birth clustering is mediated (Thompson 1991). Individuals of high rank had more opportunities to investigate freshly voided urine, performed flehmen with greater frequency and consistently gave birth in temporal proximity to herdmates. Subordinate females, with much more restricted access to the olfactory cues used

by dominant herdmates, typically gave birth several weeks before or after the modal birth date, and the resulting calves were potentially at a great disadvantage. In the wild, ungulate calves born early or late in the season experience increased predation risks due to the absence of age-mates to serve a social cover (Bergerud 1974; Estes 1976). Calves born outside of a birth cluster may also experience a reduced opportunity for beneficial peer interaction, such as social play (Pfeifer 1985). Dominance rank in adult females is strongly influenced by age (Thompson 1993), suggesting that dominant females might attempt to give birth early in the season to assure their daughters of high rank within their cohort. There are at least two potential explanations for the lack of a consistent association between female dominance rank and birth order. First, giving birth early in the season might require shortening gestation, thereby increasing the risk of giving birth to infants of low viability (Berger 1992). Second, the correlation between rank and age may not hold for male calves. The overall advantages of giving birth in clusters may outweigh the benefits of higher dominance rank for daughters born early in the birth season.

Is flehmen the mechanism by which sable antelope synchronize reproduction? Females had ample opportunities to investigate urine and perform flehmen. Urinations within the herd occurred in clusters at predictable times and with other females in close proximity. Sable antelope females were highly selective in the urinations they

attended to, in precisely the ways expected if flehmen serves to synchronize reproduction. Females preferentially directed flehmen at reproductive, multiparous females rather than non-reproductive or inexperienced females, most frequently at the approximate time when oestrous cycling typically resumes following parturition in free-ranging sable (Estes & Estes 1974; Wilson & Hirst 1977). In addition, females were increasingly likely to perform flehmen in response to urination by other females, but not yearlings, as the mating season approached. Rates of flehmen peaked shortly before male reproductive behaviour reached greatest frequencies, suggesting that females attempt to coordinate reproductive cycling prior to conception.

Evidence suggested that females synchronized parturition. Although peak frequencies were not reached until the approximate time of oestrus, flehmen occurred at appreciable rates prior to parturition. Furthermore, pregnant females showed a strong tendency to perform flehmen in response to urinations by other pregnant herdmates, while ignoring urinations by postpartum females. The strong association between prepartum flehmen frequencies and timing of births relative to herdmates provided the strongest evidence that females were able to synchronize parturition as a result of olfactory information received through flehmen. Birth synchrony in squirrel monkeys is also apparently achieved through olfactory cues (Boinski 1987). In the weeks prior to parturition, pregnant squirrel monkeys engage in intense bouts of olfactory investigation of other pregnant females.

Physiological evidence indicates that flehmen is a plausible mechanism for achieving reproductive synchrony. The act of flehmen is thought to facilitate the transfer of urine from the oral cavity to the vomeronasal organ (Estes 1972; Hart 1983), a component of the accessory olfactory system. The vomeronasal organ impinges upon areas of the brain associated with the neuroendocrine regulation of reproduction (de Olmos & Ingram 1972), and appears to mediate a variety of reproductive phenomena in rodents, including the acceleration of puberty in females, induction of ovulation, and synchronization of oestrus (Keverne 1983). Although the role of the vomeronasal system in modulating reproduction in ungulates has not been studied, ungulates do possess a well-developed vomeronasal system (Signoret

1990). Furthermore, the concentrations of steroid hormones and their metabolites vary dramatically and predictably during the oestrous cycle (Loskutoff et al. 1983; Monfort et al. 1990, 1993; Kirkpatrick et al. 1992). Thus, female sable antelope may use flehmen to alter their own ovarian activity in response to fluctuations in the urinary hormone metabolites of conspecifics.

The possibility remains that coordination of reproduction is mediated by a social cue other than sampling urine, and that the apparent correlation between flehmen and reproduction exists simply because both variables are correlated with a third variable, such as proximity. A stronger test of the role of flehmen would require measurement of reproductive synchrony in the absence of physical proximity, for example by providing socially isolated females with conspecific urine. In this study, it was not possible to obtain the identities of individuals surrounding a given urinating female, and therefore it was not possible to examine fully the effects of proximity on flehmen. Several lines of evidence, however, suggest that the observed differences in selectivity and responsiveness to urine from females of differing age and reproductive status are not merely the result of differences in proximity. First, the likelihood that urinations would induce flehmen changed seasonally, whereas proximity patterns did not. Second, the number of flehmen responses received was strongly dependent on female age class and previous reproductive history, even though the mean number females in close proximity did not vary among age classes or among females of differing social rank. Anecdotal evidence further supported the interpretation of flehmen as a nonrandom act. Females frequently stared at, but did not sample urine from, urinating individuals that were within one body length's proximity. Conversely, females occasionally approached at a gallop to sample the urine of females 8–10 body lengths (ca 15–20 m) away.

This is the first report of systematic differences in degree of birth synchrony among females of differing social rank, although birth synchrony is known to be affected by reproductive history. Primiparous lion-tailed macaques, *Macaca silenus*, are more likely than multiparous females to give birth asynchronously (Clarke et al. 1992). Imperfect birth synchrony in female sable antelope appears to be maintained by aggression: the highest frequencies of both aggression (Thompson

1993) and flehmen coincided with the termination of lactational anoestrus, and dominant females actively competed for access to urine (Thompson 1991).

Why should sable antelope females compete to give birth synchronously? The advantages of synchronous births are related to specific anti-predator strategies. Extreme birth synchrony is found in species where infants depend on their peers for social cover (Estes 1976) or where co-operative vigilance by mothers is necessary to minimize infant predation (Boinski 1987). In these situations, all females benefit from allowing others to synchronize with them. Precise birth synchrony has been reported in a variety of ungulates (Estes 1966; Dauphine & McClure 1974; Sinclair 1977), primates (Jolly 1966; Richard 1978; Boinski 1987) and birds (Emlen & Demong 1975).

Sable antelope, like most bovids, conceal their infants in vegetation (Grobler 1974; Lent 1974; Hnida 1985). Infants remain hidden throughout the day except for brief reunion periods during which they suckle and socialize with other members of their social group (Hnida 1985). For the first few days following birth sable antelope calves hide alone, but shortly thereafter they hide in small groups with calves of similar age. This crèche may function as social cover (Hamilton 1971) in much the same way as the herd acts as protection for adults. The selfish herd benefits of crèching, however, are counter-balanced by an increased risk that the crèche will be detected by a predator. Female sable are better able to locate crèches of calves than single calves in hiding (Thompson, in press), so it is reasonable to assume that predators could also. If so, the optimal strategy for a female sable antelope would be to synchronize parturition with a small number of other females, rather than with all females in her social group, so that crèches would contain only a small number of calves. Wissel & Brandel (1988), however, have shown that synchronization in natural breeding groups is often imperfect, and that this partial reproductive synchrony may itself be an adaptation against predation. The advantages of imperfect synchrony may explain why subordinate female sable antelope fail to form their own reproductive subgroups.

For ungulates that exhibit the follower developmental strategy, remaining inconspicuous is less vital and having other calves for social cover greatly increases each calf's chance of survival

(Estes 1966). In these species all females benefit from birth synchrony. As predicted, species with following young show more precise birth synchrony than those with young that hide (Rutberg 1987). High rates of flehmen among females of follower species would be predicted, with no overt aggression associated with flehmen and no relationship of dominance rank to flehmen rate.

Flehmen in female sable antelope occurred in highly specific contexts associated with reproduction, and appeared to influence directly the ability of females to synchronize parturition with herd-mates. Flehmen appears to be a heretofore unreported manifestation of reproductive competition, in which females attempt to optimize the timing of parturition relative to other females while simultaneously excluding some females from similar opportunities. Through its effects on reproductive synchrony, flehmen plays a significant role in determining the social environment into which calves are born and thus has a potentially profound impact on female reproductive success.

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