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Mechanisms of sexual selection: Sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons

Laurence R. Gesquiere[a,*], Emmanuel O. Wango[c,e], Susan C. Alberts[b,c], Jeanne Altmann[a,c,d]

[a] *Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA*
[b] *Department of Biology, Duke University, Durham, NC 27708, USA*
[c] *Institute of Primate Research, National Museums of Kenya, Nairobi, Kenya*
[d] *Department of Conservation Biology, Chicago Zoological Society, Brookfield, IL 60513, USA*
[e] *Department of Animal Physiology and Veterinary Medicine, University of Nairobi, Nairobi, Kenya*

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Abstract

Male mate-guarding episodes (‘consortships’), are taxonomically widespread, yet costly to individual males. Consequently, males should bias consortships toward females with whom the probability of conception is high. We combined data on consortships with visual scoring of sexual swellings and assays of fecal estrogen concentrations (fE) in a wild population of baboons (*Papio cynocephalus*) to test the hypotheses that sexual swellings are reliable indicators of (1) within-cycle timing of ovulation, (2) differences in conception probability among females that differ in maturational stage, and (3) conceptive versus non-conceptive cycles of parous females. We also evaluated whether adult males might rely on swellings or other estrogen-dependent signals (e.g., fE) for mate-guarding decisions. We found that sexual swellings reflected conception probability within and among cycles. Adult males limited their consortships to the turgescent phase of cycles, and consorted more with adult females than with newly cycling adolescents. The highest ranking (alpha) males discriminated more than did males of other ranks; they (1) limited their consortships to the 5-day peri-ovulatory period, (2) consorted more with adult than with adolescent females, and (3) consorted more with adult females on conceptive cycles than on non-conceptive cycles, all to a greater extent than did males of other ranks. Male mate choice based on sexual swellings and other estrogenic cues of fertility may result in sexual selection on these female traits and enhance dominance-based reproductive skew in males. Alpha males are the least constrained in their mating behavior and can best take advantage of these cues to mate selectively.

Keywords: Sexual swellings; Consortships; Mate choice; Fecal steroids; Estrogen; Baboons; *Papio*

Introduction

Both pre- and post-copulatory mate guarding are widespread across animal taxa, conferring mating and paternity advantage, but often imposing costs in terms of energetic expenditure, time, feeding opportunities, or direct survival risks (Alberts et al., 1996; Alcock, 1994; Bercovitch, 1983; Clutton-Brock et al., 1982; Ellis, 1995; Low, 2006; Packer, 1979). Among many primate species, including baboons, *Papio cynocephalus*, mate guarding takes the form of “sexual consortships”, extended periods of guarding that last from several hours to several days or even weeks. During consortships males follow, groom and maintain close proximity to an estrous female, threatening other males who approach her and monopolizing mating (e.g., Bercovitch, 1987; Hausfater, 1975; van Noordwijk, 1985; Packer, 1979; Saayman, 1970; Setchell et al., 2005; Tutin, 1979). By so doing, males experience an increased chance of fathering offspring (Alberts et al., in press; Altmann et al., 1996; Buchan et al., 2003; Setchell et al., 2005).

Because mate guarding imposes costs on male primates (Alberts et al., 1996; Packer, 1979; Rasmussen, 1985), males

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[*] Corresponding author. Fax: +1 609 258 2712.
E-mail address: lgesquie@princeton.edu (L.R. Gesquiere).

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may not have the energy to engage in mate guarding continuously without rests. This is particularly true if cycling females are continuously available for extended periods, as they are in species such as baboons, chimpanzees, and humans that are not seasonal in their mating (Bercovitch, 1988). When faced with such constraints, adult males are predicted to be discriminating in mate guarding decisions. In particular, males are predicted to discriminate among females based on fertility differences (1) within female reproductive cycles (based on the timing of the mating opportunity relative to ovulation), (2) between females in their fertility (if fertility changes with age, for instance), and (3) between cycles of a given female (if differences in fertility are a function of how old her current infant is, for instance) (Bercovitch, 2001; Domb and Pagel, 2001; Pagel, 1994; Zinner et al., 2002). However, not all males are predicted to discriminate to the same extent. In particular, in a number of primates, including baboons, male mating success is dominance rank-based, so that high ranking males achieve the highest mating success (Altmann, 1962; Bulger, 1993; Cowlishaw and Dunbar, 1991; Pope, 1990; de Ruiter and van Hooff, 1993; de Ruiter et al., 1994; Weingrill et al., 2000). When this occurs, the highest ranking male in a group (the alpha male) is predicted to be the least constrained by male–male competition, and hence the one most likely to exhibit fertility-based mate choice.

Data are available to evaluate some of these predictions in a number of primate species. First, in several species adult males were most likely to consort on days when conception was most probable (Aujard et al., 1998; Bercovitch, 1986, 1987; Bulger, 1993; Deschner et al., 2004; Engelhardt et al., 2004; Hausfater, 1975; Packer, 1979; de Ruiter et al., 1994; Setchell et al., 2005). Second, males of several primate species exhibited discrimination among females of different age classes by ignoring newly cycling adolescent females (who are unlikely to conceive in the first few cycles after menarche) even though these females solicited matings at high levels (reviewed in Anderson, 1986; see also Perry and Manson, 1995; Thierry et al., 1996). Finally, alpha males discriminated between the conceptive and non-conceptive cycles of fully adult females at least under some conditions (Alberts et al., in press; Bulger, 1993; Deschner et al., 2004; Setchell et al., 2005; Weingrill et al., 2003).

What information is available to males to make these mating decisions and how reliable is this information? Three potentially important proximate cues – behavioral, visual (specifically sexual skin swellings) and olfactory – have been proposed. In this study, we focus on fecal estrogen concentrations, which may be involved in producing such cues, and on swelling size as one potential specific cue. Estrogens not only are implicated in the development of sexual swellings (Gillman, 1937, 1942), they also have an important role in the production of olfactory cues (Goldfoot, 1981; Michael et al., 1971, 1974; Singh and Bronstad, 2001) and in female sexual behavior (Aujard et al., 1998; Engelhardt et al., 2005; O'Neill et al., 2004; Saayman, 1970; reviewed in Dixson, 1998, Chapter 12). In particular, we seek to clarify whether sexual swellings and fecal estrogen concentrations provide reliable indicators of fertility in female baboons, and to evaluate the extent to which adult males seem to rely on swelling size or on other estrogen-dependant cues to make decisions as to whether to consort with a female.

Turgescence of the primate sexual skin is induced by increasing estrogen concentrations, whereas deturgescence is stimulated by declining estrogen and increasing progesterone concentrations (Carlisle et al., 1981; Gillman, 1937, 1940, 1942; Gillman and Gilbert, 1946; Gillman and Stein, 1941; Onouchi and Kato, 1983; Ozasa and Gould, 1982, 1984; West et al., 1990). Based on laboratory experiments, the prominent swellings of baboons are considered to be a relatively good indicator of the timing of ovulation within cycles (Shaikh et al., 1982; Wildt et al., 1977). Furthermore, male baboons become sexually aroused in response to the sight of sexual swellings (Bielert and Girolami, 1986; Bielert et al., 1989; Girolami and Bielert, 1987; reviewed in Snowdon, 2004). Males may, therefore, attend closely to swelling size and use it to choose the best time of the cycle to consort (Bercovitch, 1987, 1999; Bulger, 1993; Hausfater, 1975; Hendrickx and Kraemer, 1969; Packer, 1979). Less clear is whether differences in swelling size among cycles can indicate differences in conception probability and thereby provide a cue that males could use to make individual or cycle-to-cycle mating decisions (Bercovitch, 1987, 1999; Domb and Pagel, 2001; Emery and Whitten, 2003; Nunn et al., 2001; Scott, 1984; Setchell and Wickings, 2004; Zinner et al., 2002).

In the present investigation, we measured the frequency of male mate guarding (i.e., male consortship activity) as a function of fecal estrogen (fE) concentrations and of swelling turgescence and size in a population of wild baboons, *P. cynocephalus*. We sought to identify differences across the menstrual cycle, between cycles of adolescent and adult females, and between conceptive and non-conceptive cycles of adult females. That is, we tested both for increasingly fine differences in swelling size and estrogen concentrations and for increasingly challenging mate choice by males. In testing male mate choice, we analyzed data on mate guarding by the alpha male separately from that by other males, because of the prediction that alpha males are the least constrained in their mating decisions (see above; see also Alberts et al., in press; Bulger, 1993; Deschner et al., 2004; Setchell et al., 2005; Weingrill et al., 2003).

Methods

Field site and subjects

Subjects were the individually identified members of five social groups in the Amboseli baboon population that has been monitored for reproductive, demographic, and behavioral events on a near-daily basis over three decades (e.g., Alberts and Altmann, 1995a,b; Altmann and Alberts, 2003; Altmann et al., 1988; Hausfater, 1975; Noë and Sluijter, 1990; Shopland, 1987). Since December 1999, physiological data have been obtained through non-invasive collection of freshly deposited feces from known individuals and subsequent analysis of steroid hormones extracted from the feces.

For this study we used all data for cycling females from late 1999 through 2004. The records included swelling size and consortships for a total of 1139 ovarian cycles, corresponding to 104 females. For a subset of those females and cycles we also had fecal samples, from which we determined fE concentrations (422 cycles, 88 females). We excluded data from one sterile adult female and one very old female (26–27 years old), both of whom had abnormally small sexual swellings. Observers were with each study group 2–3 times a week, resulting in records of swelling size and consortships for an average of a little over one third of the days of each cycle (cycle length: median 39 days, mean 43 days, 617 cycles) and for an average of 1.6 days of the 5 day peri-ovulatory period of the follicular phase. For approximately 1 out of 6 observation days, i.e., on average 2 days per 39-day cycle, we also had fE samples.

Data collection

All data collection procedures adhered to the regulations of the Institutional Animal Care and Use Committee of Princeton University.

Female reproductive state and sexual swelling size

Data on each female's reproductive state were recorded on each observation day for her group. We recorded the presence of external menstrual bleeding, the color of the paracallosal skin (an indication of pregnancy or recent parturition; Altmann, 1970), and characteristics of the sexual swelling (see the Amboseli Baboon Research Project (ABRP) Monitoring Guide at www.princeton.edu/~baboon for details of data collection protocols). The observers recorded swelling state (turgescent or deturgescent) and scored the swelling size using a visual estimate of swelling volume, measured on a 10-point absolute scale. This subjective scale, used in the Amboseli studies for over three decades, is maintained by three long-term field assistants doing most of the scoring (collecting data for 25, 16, and 10 years, respectively), by intensive training and checking of the occasional new observers, and by inter-observer reliability checks each month (see Bercovitch, 1999; Hausfater, 1975; Scott, 1984). In addition, any potential biases that might be introduced by such a scale would not influence the results of the present study. In particular, observers were blind as to (could not anticipate) whether a cycle was conceptive or non-conceptive, so that the differences between conceptive and non-conceptive cycles should reflect real differences.

Dates of transition between the reproductive states, e.g., onset of turgescence and deturgescence, were subsequently estimated from the field data in our laboratories in the USA and entered into our relational database, BABASE. For the present analyses, onset of deturgescence was then used as the reference day (termed 'D0') for each cycle, and days of that cycle were expressed relative to D0. Thus, the last day of turgescent swelling was considered as $D-1$, the second to last as $D-2$ and so on, and the first day following the onset of deturgescence was $D+1$, etc. Days with negative numbers were taken as representing the follicular phase of the cycle and non-negative ones as representing the luteal phase. Ovulation was estimated to occur in the 5-day period before the onset of deturgescence (days $D-5$ through $D-1$), as shown by previous data from various laboratories (e.g., Shaikh et al., 1982; Wildt et al., 1977; see also Alberts et al., 2003; Altmann et al., 1996; Bercovitch, 1987); herein we refer to this 5-day period as the ovulatory or peri-ovulatory period, while keeping in mind that not all cycles were known to be ovulatory. Dates were referenced to the onset of deturgescence, and thereby to the approximate onset of the luteal phase, rather than to onset of the follicular phase or to known ovulation date. We used this approach because (1) the follicular phase is highly variable for baboons as for humans, thereby making it difficult to create composite cycles referenced to onset of the follicular phase (Hausfater, 1975), (2) onset of menstruation, i.e., onset of the follicular phase, is not as reliably estimated when observation on a female is not daily, and (3) in the absence of hormone samples for every day of every cycle, we could not confirm either ovulation or its exact day of occurrence. We excluded any cycle days prior to $D-22$ or subsequent to $D+12$ from analyses because most cycles did not extend beyond these days, and exclusion of these days only provided more stringent tests throughout.

Additional fertility-related data were then associated with each of the daily cycle records because this information might indicate to a male the potential 'value' of a consortship and perhaps be used by him in consortship decisions. Using the demographic and reproductive records for each female and cycle, our analyses included the female's parity (starting with adolescence as zero, first pregnancy as 1, etc.), the cycle number (starting with the first cycle of adolescence as cycle 1), whether that cycle resulted in a pregnancy or not (termed a 'conceptive' or 'non-conceptive' cycle respectively), and whether the cycle was the first cycle following a pregnancy (a 'resume' cycle), which could be either a conceptive or non-conceptive cycle.

Consortship and male rank

All instances of sexual consortships between cycling females and adult males were recorded whenever observers were with each group (Alberts and Altmann, 1995a,b; see also ABRP Monitoring Guide at www.princeton.edu/~baboon for details). Independent of the present investigations, monthly dominance ranks were routinely assigned for each male by using the field data on wins and losses in dyadic agonistic encounters between males, as described in Hausfater (1975) and Alberts et al. (2003); these ranks were then incorporated into BABASE for use in this study as well as in a range of others.

We treated consortships with the alpha male separately from those with all other males. Therefore, for each female cycle day, the female received a score based on whether she consorted with the alpha male (1 for consortship, 0 for not), and similarly she also received a separate score based on whether she consorted with males of other ranks (again, 1 or 0).

Collection, preparation, and assay of fecal samples

Fecal sample collection, storage, and extraction were as described previously (Khan et al., 2002; Lynch et al., 2003). The samples were then assayed for estrogen (fE) by radioimmunoassay (Altmann et al., 2004; Beehner et al., 2006; Gesquiere et al., 2005; full laboratory protocols also available at www.princeton.edu/~baboon). The primary antibody in the Total Estrogen kit (ICN Diagnostics, Costa Mesa, CA) cross-reacts 100% with estradiol-17β and estrone, 9% with estriol, 7% with estradiol-17α, and 2.5% with equilin. Inter-assay coefficients of variation ($n=21$) were 11% and 8% for a low and high control, respectively. Intra-assay coefficients of variation were below 5% for both the low and high control (any duplicate above 15% was re-assayed). All hormone values are expressed as nanogram per gram of dry feces.

Data analysis

Although we could use neither a within-subjects design nor include just a single value per subject, within any analysis subjects contributed few, and relatively equal numbers of, data points (almost always only 1 or 2 after averaging as indicated below). The various questions required analysis of different subsets of the data, to test for increasingly fine discrimination, as follows.

Variation across the menstrual cycle

For the general profile of changes in swelling size, consortship behavior, and estrogen concentrations across the menstrual cycle, we used the subset of swelling data and consortship data collected only on days for which we also had a fecal estrogen value (898 cycle days for 88 females). These pooled data constituted a mixed longitudinal/cross-sectional set. For each cycle day (indexed from D0), we calculated a mean value (across females and cycles) of swelling size and fE concentrations. The probability of consortship by males (alpha or other) on any given day of the cycle, e.g., on $D-7$, was estimated simply by dividing the number of cycles on which the female was consorted on $D-7$ (by alpha male or others) by the total number of cycles for which we had data on $D-7$ (both consorted and non-consorted).

We next used linear regression analysis to test whether swelling size or fE concentrations predicted consortship probability for females on any cycle day, and to test whether fE concentrations predicted swelling size. Here we restricted the data set to the follicular phase of the cycle (479 cycle days for 86 females) because the previous analysis found no consortships during the luteal phase. We thereby tested for greater discrimination than if we had included the luteal as well as the follicular phase.

Differences between adolescent and adult females during the peri-ovulatory period

To test for differences solely within the 5-day peri-ovulatory phase among females of different age categories, we next classified the females based on differences in fertility at different maturational stages. These stages were defined by major differences in the percentage of cycles that resulted in conception: newly cycling adolescents with very low fertility (cycles 1–4), later stage adolescents with markedly higher fertility (cycles ≥ 5) and adult females (parity ≥ 1). By including only the peri-ovulatory period of the cycle, we again conducted a more stringent test than if we had included the whole cycle or even the whole follicular phase. We sometimes had data for more than 1 day of the peri-ovulatory period of a given cycle; in these cases we reduced the data for each cycle from multiple days to a single value by using the mean across these days within any given cycle. We then calculated the mean of these means for each class of female.

Because we restricted our analysis of the peri-ovulatory phase to days for which we had complete swelling size, consortship and fE data, data were available only for 18 cycles for newly cycling females, 23 cycles for later adolescents and 50 cycles for adults. Therefore, in order to increase the power of our analysis for variables other than fE, we next conducted an analysis using the full peri-ovulatory data set of 1139 cycles, i.e., including even those days for which no fE data were available. This allowed us to calculate the consortship probability and the average swelling size for days in the peri-ovulatory phase with sample size of 213 cycles of newly cycling females, 269 cycles of later adolescents and 657 cycles of adults.

We used the non-parametric Kruskal–Wallis test to compare the probability of consortships by males (alpha and others), swelling size, and fE concentrations among the three female maturation categories. When there were significant differences, we then further compared the maturation categories two by two using the Mann–Whitney *U* test.

Differences between conceptive and non-conceptive cycles of adult females

To next test the hypothesis that peri-ovulatory periods of conceptive and non-conceptive cycles were distinguishable and discriminated by males, we categorized cycles based on whether they resulted in pregnancy. We restricted this analysis to adult females, again to provide a more stringent test than if we had included categories of females for which we had already demonstrated major differences. As in the previous analysis, we used the full set of data, regardless of whether fE samples were available, to calculate consortship probabilities and swelling size for a total of 459 non-conceptive cycles and 198 conceptive cycles. For calculation of average fE concentrations for adults in these two conditions, data were available from a total of 27 non-conceptive cycles and 23 conceptive cycles.

For conceptive and non-conceptive cycles, we used the non-parametric Mann–Whitney *U* test to compare the probability of consortships by males (alpha and others), swelling size, and fE concentrations.

Factors predicting consortships in the face of multiple sources of information

Finally, we sought to identify which cues males might use when they had multiple sources of information (proximate hormonal cues as well as other demographic or reproductive information). For this analysis we excluded cycle stages and classes of females for which consortships were rare or absent; that is, we analyzed decisions to consort or not only for consortship decisions that involved late adolescent or adult females in the turgescent phase of a cycle. With this dataset, we performed a binary logistic regression using SPSS 12.0 (SPSS Inc., 2003) in which the binary dependent variable was ‘consorting’ versus ‘not consorting’. We did this analysis twice, once for the alpha males and once for males of other rank. The independent variables were swelling size, fE concentrations, cycle number, maturation stage (later adolescent or adult), follicular phase of the cycle (divided into early follicular (EF) or ovulatory (O) portions), whether the cycle was ‘conceptive’ (yes or no), and whether the cycle was a ‘resume’ cycle (yes or no, where a resume cycle was the first postpartum cycle).

Results

Consortships, swelling size and fE levels across the menstrual cycle: general patterns

Adult males (alpha males and males of other ranks) consorted with females only during the follicular phase of the cycle; no consortships were observed during the luteal phase (Figs. 1a and b). For both alpha males and males of other ranks, consorting was more likely on days that fell within the ovulatory period ($D-5$ through $D-1$) than during the early follicular phase ($D-22$ through $D-6$; Mann–Whitney test: $Z=-3.223$, $p=0.001$ for alpha males and $Z=-2.295$, $p=0.022$ for males of other ranks). In particular, consortships by alpha males occurred on 33% of cycle days in the ovulatory period, and consortships by other males occurred on 29% of cycle days in the ovulatory period. In contrast, consortships by alpha males occurred on only 3.5% of days in the early follicular phase, and consortships by other males occurred on 11% of days in the early follicular phase. Examining cycle days in more detail revealed that alpha males slightly ‘anticipated’ the ovulatory period by consorting more during days $D-7$ and $D-6$ than on days earlier than $D-7$ (average of 19% on days $D-7$ and $D-6$ compared with an average of 1.5% on days earlier than $D-7$; Mann–Whitney test: $Z=-2.616$, $p=0.009$). Further, within the ovulatory period alpha males primarily limited their consortships to days $D-5$ through $D-2$, during which they consorted on an average of 40% of all female cycles, and they only very rarely consorted on the last day of the ovulatory period (4.5% on $D-1$) (Fig. 1a). Adult males of lower ranks, in contrast, extended their consortships more broadly across the last 2 weeks of the follicular phase, consorting on an average of 21% across all cycle days from $D-13$ through $D-6$ (Fig. 1b).

Swelling size (Fig. 1c) increased linearly throughout the early follicular phase of the cycle and reached a plateau at an average size of 6 during the ovulatory period. At the onset of the luteal phase, swelling size then decreased much more rapidly than it had increased. In contrast to the several weeks of gradual increase in swelling size during the follicular phase, residual swelling remained beyond the first week of the luteal phase in only a few cycles.

Fecal estrogen concentrations (Fig. 1d) increased slowly during the early follicular phase, then increased rapidly at the onset of the peri-ovulatory period, and remained high but variable during the rest of the ovulatory period. At the onset of the luteal phase (D0), fE levels dropped precipitously to nearly baseline levels (55 ng/g).

Predicting consort probabilities during turgescence for all females

Swelling size during turgescence was a good predictor of the probability that a female would consort with the alpha male ($r^2=0.557$, $df=21$, $p<0.001$) or with males of lower ranks ($r^2=0.808$, $df=21$, $p<0.001$). An examination of the full data set (479 values for 86 females) revealed that adult males did not consort when sex skin size was below 3. Alpha males were even more selective of their consort partners than males of other ranks; they never consorted when sex skin size was below 4; this more narrow range explains the lower r^2 value for alpha males than for other males.

As the follicular phase progressed, fE increased and so did consortships (alpha males: $r^2=0.674$ between fE and consortship

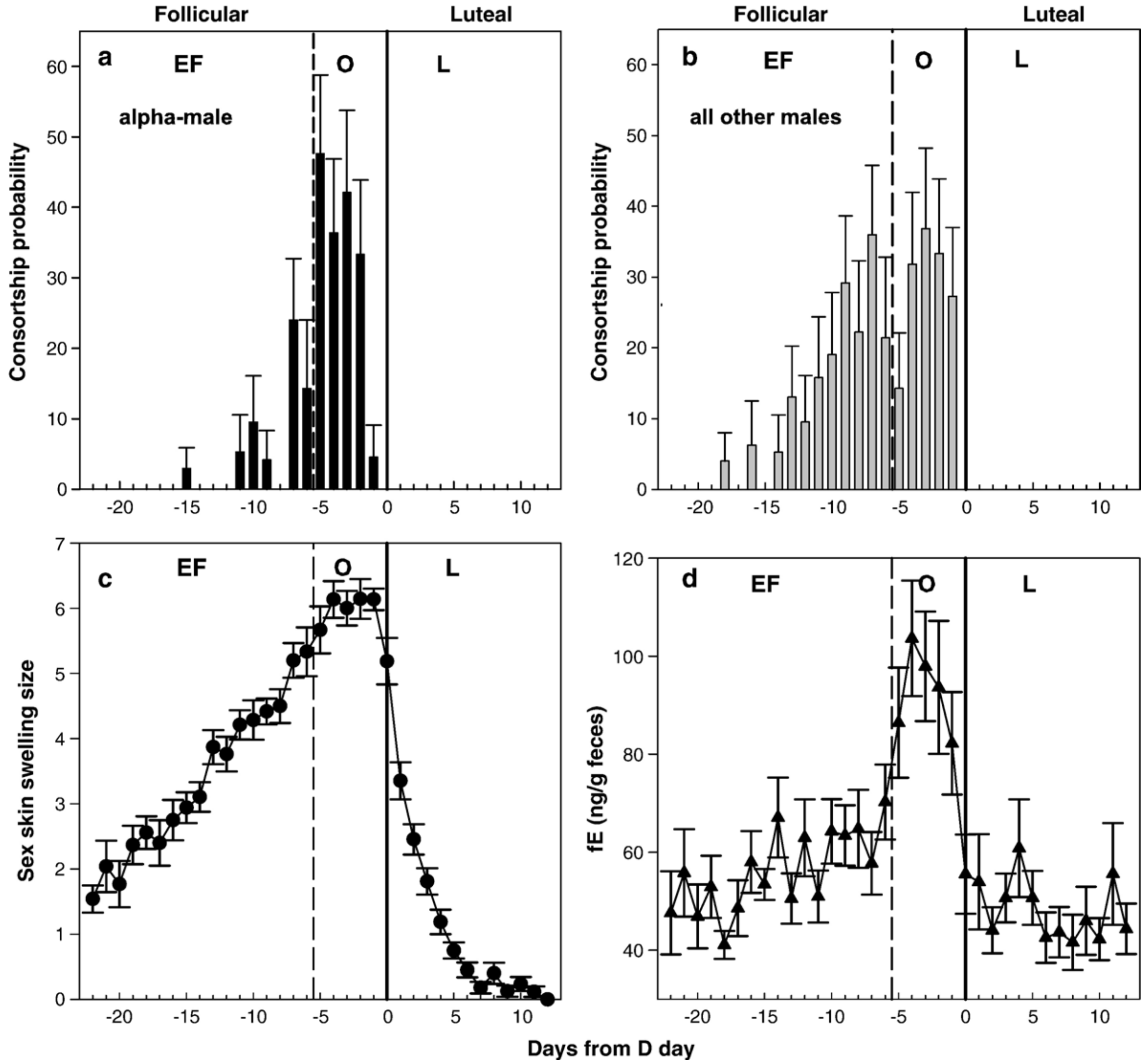

Fig. 1. Profile across the menstrual cycle (mixed longitudinal and cross-sectional samples) of (a) consortship probability with alpha males or (b) with adult males of other ranks, (c) sex skin swelling size, and (d) fE concentration. Each value represents the mean ± SE across females' cycles, for each cycle day indexed from the onset of deturgescence (D0). EF = early follicular part of the follicular phase, O = peri-ovulatory part of the follicular phase, L = luteal phase.

probability across days, *df* = 21, $p < 0.001$; lower ranking males: $r^2 = 0.492$, *df* = 21, $p < 0.001$). In addition, average daily fE concentrations for a cycle day predicted swelling size during turgescence ($r^2 = 0.731$, *df* = 21, $p < 0.001$) but not during deturgescence ($r^2 = 0.216$, *df* = 11, $p = 0.11$).

Differences between adolescent and adult females

Newly cycling adolescents (cycles 1–4) conceived on less than 1% of their cycles. In contrast, later stage adolescents (cycles ≥ 5) conceived on 16%, and adult females (those who had experienced at least one pregnancy) on 30% of their cycles (Fig. 2a).

The proportion of cycles on which males and females consorted differed for females across the three different maturational stages (Kruskal–Wallis test: $\chi^2 = 53.027$, *df* = 2, $p < 0.001$ for alpha males and $\chi^2 = 156.982$, *df* = 2, $p < 0.001$ for males of other ranks; Fig. 2b). Alpha males consorted with adult females on 21.99 ± 1.46% of the females' cycles (*n* = 657); with later stage adolescents on 15.36 ± 1.95% (*n* = 269); and with newly cycling adolescents on 3.76 ± 1.22% (*n* = 213). In terms of odds ratios, adult females were 5.8 times more likely (Mann–Whitney test: $Z = -7.172$, $p < 0.001$), and later stage adolescents 4 times more likely ($Z = -5.131$, $p < 0.001$) to have consortships with the alpha male than were newly cycling adolescents. Lower ranking males also favored adult and later stage adolescents as consort partners; non-alpha males consorted with adult females on 54.99 ± 1.73% of cycles (*n* = 657); with later stage adolescents on 50.43 ± 2.80% (*n* = 269); and with newly cycling adolescents on 11.11 ± 1.99% (*n* = 213) (Fig. 2b). Adult females were 5 times more likely ($Z = -12.478$, $p < 0.001$) and later stage adolescents 4.5 times more likely ($Z = -9.925$, $p < 0.001$) to consort with non-alpha males than were newly cycling adolescents. However, whereas adult females and alpha males consorted significantly more than late adolescents did ($Z = -2.479$, $p = 0.013$), the comparable difference was not significant for consortships with males of other ranks ($Z = -1.345$, $p = 0.179$; Fig. 2b).

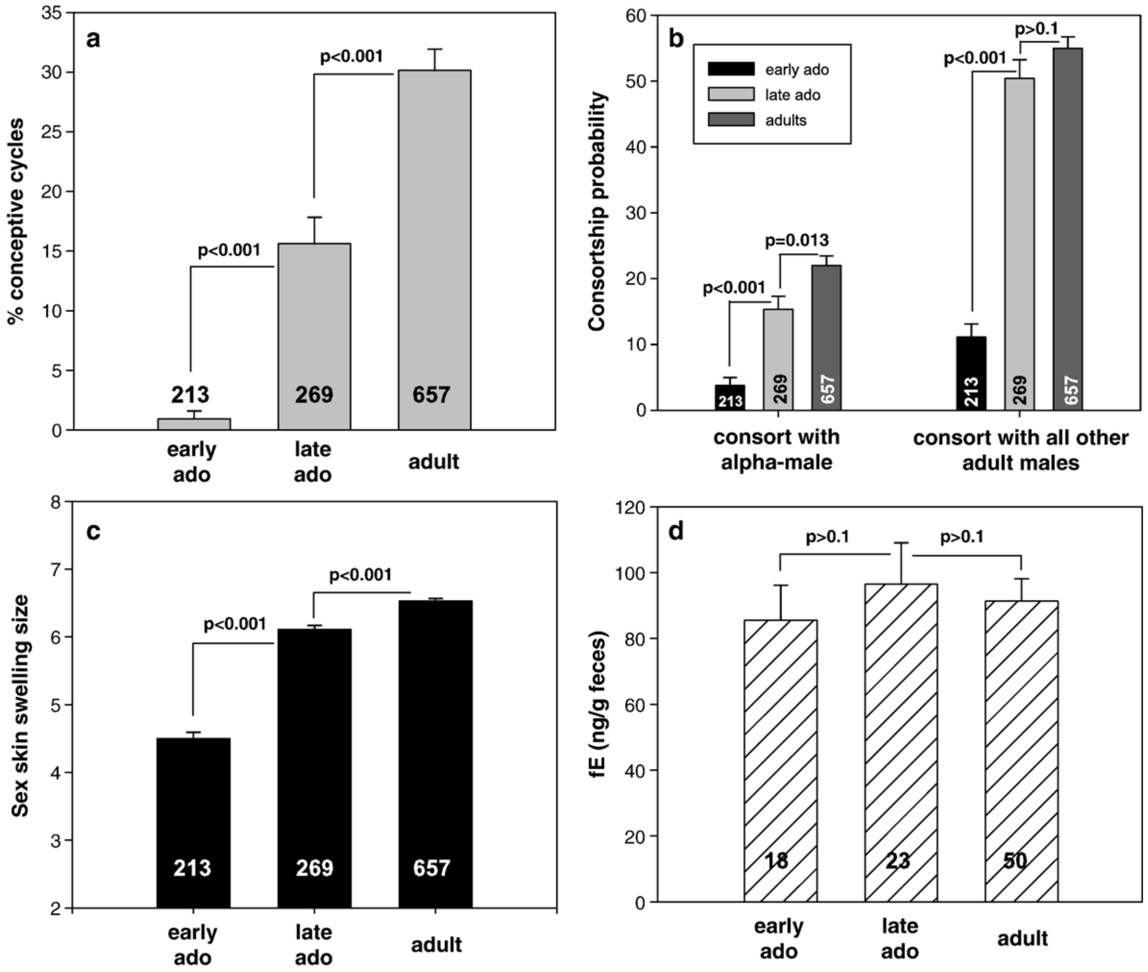

Fig. 2. Comparison between females of different maturational stages—early adolescents, later stage adolescents, and adult females (see text for details)—for (a) percentage of conceptive cycles, (b) consortship probability, (c) sex skin swelling size, and (d) fE concentration during the ovulatory period. Each value represents the mean ± SE across females' cycles, for each age stage. Numbers represent the number of cycles for each maturational stage.

Swelling size also differed among maturation categories (Kruskal–Wallis test: $\chi^2=353.213$, $df=2$, $p<0.001$; Fig. 2c). Newly cycling adolescents had smaller sexual swellings than later stage adolescents (Mann–Whitney test: $Z=-12.932$, $p<0.001$) or adults ($Z=-18.057$, $p<0.001$) and later stage adolescents had smaller swellings than adults ($Z=-6.466$, $p<0.001$). Fecal estrogen concentrations did not differ across these three female age categories (Kruskal–Wallis test: $\chi^2=0.249$, $df=2$, $p=0.883$; Fig. 2d).

Differences between the conceptive and non-conceptive cycles of adult females

Alpha males tended to consort with adult females on a higher proportion of these females' conceptive than non-conceptive cycles (Mann–Whitney test: $Z=-1.925$, $p=0.054$). In contrast, no such tendency was present with males of other ranks ($Z=-0.281$, $p=0.778$) (Fig. 3a). Females had larger swellings on conceptive than non-conceptive cycles ($Z=-2.432$, $p=0.015$) (Fig. 3b), and they exhibited a non-significant tendency to have higher fE concentrations on conceptive than non-conceptive cycles ($Z=-1.684$, $p=0.092$) (Fig. 3c).

Multiple simultaneous factors predicting consortship for late adolescents and adult females: logistic regression

Alpha males discriminated among cycles, even considering just adult and late adolescent females that were in the follicular phase of the cycle. In particular, alpha males were biased towards consorting with females in the ovulatory phase of their cycle and with females that had larger swellings ($\chi^2=91$, $df=7$, $p<0.001$) (Table 1). When holding all other variables constant, the alpha male was 2.6 times more likely to consort with females during the ovulatory phase than during the early follicular phase ($p=0.040$). Similarly, on average for a one point increase, e.g., from sizes 5 to 6, on the 10-point scale of swelling size, the odds of a consortship with the alpha male doubled ($p<0.001$).

Males of other ranks also behaved differently depending on female swelling size and on timing within the follicular phase (Table 2; $\chi^2=124$, $df=7$, $p<0.001$). However, the relationship within the follicular phase was the opposite of that for alpha males. When holding all other variables constant, lower ranking males were 3.3 times less likely to consort with females in the peri-ovulatory phase than with females in the early follicular

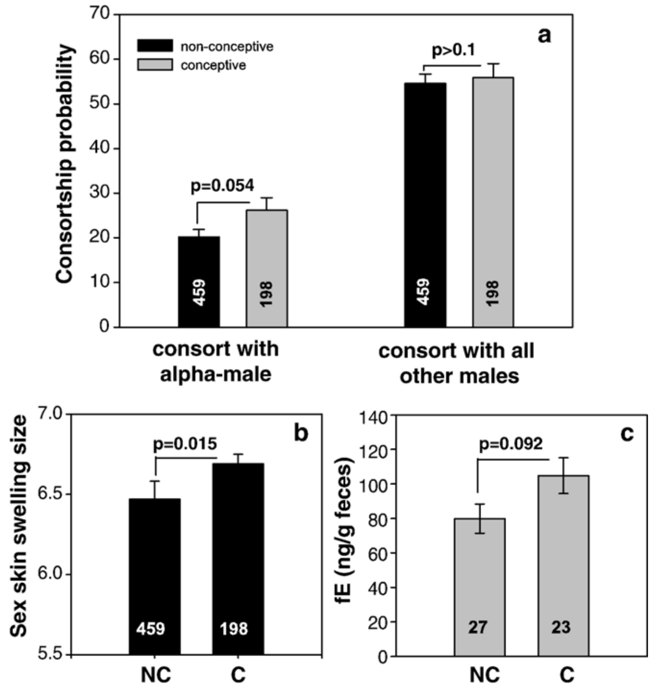

Fig. 3. Comparison of adult females' conceptive (C) and non-conceptive (NC) cycles during the ovulatory period for (a) consortship probability, (b) sex skin swelling size, and (c) fE concentration. Note that females are more likely to mate with non-alpha males as a class because each group has only a single alpha male and on average 3.6 other adult males. Each value represents the mean ± SE across adult females' cycles, for conceptive or non-conceptive cycles. Numbers represent the number of cycles for each cycle category.

phase ($p=0.008$). Holding all other variables constant, however, for each one-point increase on the 10-point scale of swelling size the odds of consortship were 3.1 greater ($p<0.001$).

Discussion

Sexual swellings as reliable indicators of female conception probability

Sexual swelling size predicted female fertility even under conditions that tested for increasingly fine differences. Further, as expected, fE levels predicted swelling size. The peri-ovulatory period ($D-5$ to $D-1$) was marked by the largest sexual swellings and the highest fE concentrations, suggesting that sexual swellings serve as a reliable visual indicator of the ovulatory period in this wild population as for captive baboons (Shaikh et al., 1982; Wildt et al., 1977). Whether sexual swellings can reliably pinpoint the actual day of ovulation remains an open question. The duration of maximum swelling size appears to be four days prior to onset of deturgescence. However, the time between the actual ovulation day and D0 may vary from cycle to cycle. Swelling size might then track this variability in ovulation timing, but this variance might only be detectable by human observers when swelling size is assessed with a high-resolution scale repeatedly within days and during each successive day; less intense sampling may obscure a precise signal and that could be used by males (Bercovitch, 1987, 1999; Deschner et al., 2003; Nunn, 1999; Nunn et al., 2001; Zinner et al., 2004). To date, however, most studies of swelling size have employed measurement scales with much lower resolution than our 10-point scale (only 4 or 5 size categories have usually been used; e.g., Deschner et al., 2003; Engelhardt et al., 2005; Nadler et al., 1985; Shaikh et al., 1982; Wildt et al., 1977). Use of low-resolution scales probably accounts for some reports of low discrimination of cycle stage from records of swelling categories (review by Nunn, 1999 in Table 1, see also Deschner et al., 2003; Engelhardt et al., 2005; Reichert et al., 2002).

Table 1
Results of logistic regression model predicting consortships with the alpha male

Predictor	B	Wald χ^2	P	Odds ratio
Swelling size	0.750	20.371	**<0.001**	2.117
fE	0.03	0.394	0.530	1.003
Cycle number	−0.010	0.171	0.680	0.990
Maturation stage[a]	0.298	0.225	0.635	1.347
Follicular phase (EF/O)[b]	0.969	4.210	**0.040**	2.635
Conceptive[c]	−0.240	0.355	0.552	0.787
Resume[d]	−0.828	3.038	0.081	0.437

Significant results appear in bold typeface.

[a] Later adolescent versus adult females.

[b] Follicular phase of the cycle divided into early follicular (EF) versus ovulatory (O) portions.

[c] Whether the cycle was 'conceptive' (yes or no).

[d] Whether the cycle was a 'resume' cycle (yes or no, where a resume cycle was the first postpartum cycle).

Table 2
Results of logistic regression model predicting consortships with males other than the alpha male

Predictor	B	Wald χ^2	P	Odds ratio
Swelling size	1.129	53.786	**<0.001**	3.093
fE	0.006	1.780	0.182	1.006
Cycle number	0.032	2.273	0.132	1.032
Maturation stage[a]	−0.287	0.293	0.588	0.751
Follicular phase (EF/O)[b]	−1.184	6.971	**0.008**	0.306
Conceptive[c]	0.340	0.816	0.366	1.405
Resume[d]	0.177	0.209	0.647	1.193

Significant results appear in bold typeface.

[a] Later adolescent versus adult females.

[b] Follicular phase of the cycle divided into early follicular (EF) versus ovulatory (O) portions.

[c] Whether the cycle was 'conceptive' (yes or no).

[d] Whether the cycle was a 'resume' cycle (yes or no, where a resume cycle was the first postpartum cycle).

A few authors have attempted to avoid the problem of visual estimates of swelling size by videotaping and subsequently quantitatively measuring swelling dimensions (Deschner et al., 2004; Domb and Pagel, 2001; Emery and Whitten, 2003). The utility of this approach remains unclear; in addition to obtaining only a small proportion of adequate images and high intra-individual variability (Domb and Pagel, 2001; reviewed in Zinner et al., 2002), the authors of those studies found differences in their results depending on the swelling measure that was considered (length, width, depth, volume, area) (Domb and Pagel, 2001; Emery and Whitten, 2003). Interestingly, Deschner et al. (2004), studying 12 chimpanzees and measuring the area covered by the swelling on daily photographic images, found that swelling size continued to increase until the day of ovulation, a change that the authors' could not detect using their 4-point visual field estimation method.

In the Amboseli baboon population, maximum swelling size during the ovulatory period broadly conveyed the 'quality' (fertility) of a given female. Newly cycling adolescents had the lowest conception rate (<1%) and the smallest sexual swellings (average swelling size = 4.5), followed by the later stage adolescents (conception rate = 16%, average swelling size = 6.1), and finally the adult females, with the highest conception rate (30%) and the largest swellings (average size = 6.5). In contrast to swelling size, fE concentrations did not differ among the three female maturation classes in Amboseli and therefore was not a reliable indicator of maturation stage fertility differences. However, the absence of differences in fE among females despite differences in swelling size probably resulted from low statistical power with the smaller sample size available for this analysis: with a comparably small sample, the differences in swelling size are not significant either. Alternatively, fE concentrations may actually be the same across female age categories, and the threshold for estrogenic stimulation of the sexual skin may differ among the different categories of females. Dissociation between estrogen levels and sexual swelling size was also found by Dahl et al. (1991) but in the opposite direction than ours, with young females chimpanzees having low estrogen levels while still exhibiting large sexual swellings.

Even among adult females in the ovulatory period, swellings were significantly larger for conceptive than non-conceptive cycles, suggesting that swelling size provided fine resolution information about the fertility of a given cycle. Similarly, fE concentrations tended to be greater ($p<0.10$) for conceptive than for non-conceptive cycles among mature females. These findings are consistent with data for women: estradiol levels (during both follicular and luteal phase) were higher in conceptive versus non-conceptive cycles when women served as their own controls (Lipson and Ellison, 1996).

Our data do not answer the question of whether consistent and enduring swelling size differences exist between adult females of the same age class, or whether such differences might signal persistent fertility differences among females. This question has been addressed only by one study (Domb and Pagel, 2001), but the methodological difficulties faced by that study (reviewed in Zinner et al., 2002) call into question their conclusion that some females had consistently larger swellings than others, and that females with larger swellings had higher lifetime reproductive success. The present study and other recent work on the function of sexual swellings provide support for the hypothesis that females experience sexual selection by male mate choice (e.g., Bercovitch, 2001), but the key question of whether sexual swellings represent a sexually selected signal of enduring individual-level differences remains an important unanswered question (see discussions in Domb and Pagel, 2001; Pagel, 1994; Zinner et al., 2002).

Female conception probabilities as predictors of male mate-guarding tendencies

Male baboons at Amboseli discriminated within cycles, between cycles of females of different maturity classes, and between cycles of adult females that differed in conception probability. When we accounted for cycle stage and sexual swellings size in the present study, fE concentrations were the primary predictor of males' mate guarding. Therefore, although swelling size (a cue that is visible at appreciable distances) seems to be a primary cue baboon males rely on for mate-guarding decisions, at close range males may use other estrogen-dependant cues, such as olfactory (Goldfoot, 1981; Michael et al., 1971, 1974; Singh and Bronstad, 2001) or behavioral (Aujard et al., 1998; Engelhardt et al., 2005; O'Neill et al., 2004; Saayman, 1970).

Males consorted more during time periods of higher fertility within female cycles. Specifically, they consorted with females only during the follicular phase, i.e., the fertile phase, as found in other studies of wild baboon populations (Bercovitch, 1987, 1999; Bulger, 1993; DeVore and Hall, 1965; Hausfater, 1975; Noë and Sluijter, 1990; Packer, 1979) and other primate species (Aujard et al., 1998; Engelhardt et al., 2004; Graham, 1981; McArthur et al., 1981; Michael and Zumpe, 1993; Tutin, 1979; Zumpe and Michael, 1996) although not in all species (Andelman, 1987; Whitten, 1982; see also Table 3 in Andelman, 1987).

Male baboons also discriminated among female maturation classes in their mate guarding. Adult males were least likely to mate with newly cycling adolescent females, the class of females least likely to conceive. Low sexual interest in nulliparous females compared to mature females has been reported for a number of primate species (reviewed in Anderson, 1986; see also Anderson and Bielert, 1994; Bielert et al., 1986; van Noordwijk, 1985; Perry and Manson, 1995; Rasmussen, 1983; Saayman, 1973; Scott, 1984; Thierry et al., 1996; Wolfe, 1978), including for the one baboon population in which adolescents are reported to have larger swellings than those of adults. The low level of interest in adolescent females may reflect both these females' lower fertility (reviewed in Anderson, 1986, see also Altmann, 1980; Dunbar, 1986) and perhaps also the lower rate of survival for firstborn infants (reviewed in Anderson, 1986; Nicolson, 1986, see also Cheney et al., 2004, Parga and Lessnau, 2005).

Fertility differences better predicted consortship bias by alpha males than by males of other ranks, as predicted for males whose behavior is least constrained by male–male competition. First, in simple bivariate analyses within the follicular phase, alpha males consorted at higher rates during the highest fertility period, the peri-ovulatory phase, than earlier in the follicular phase. In contrast, rates for males of other ranks were similar across almost two weeks prior to deturgescence, *i.e.* including cycle days prior to the most fertile period. Furthermore, when we controlled for all other variables in the multivariate analysis, non-alpha males were even less likely to consort during the ovulatory period than earlier in the follicular phase. Of the few studies that examined rank differences, similar results were found by some (Hausfater, 1975: for yellow; Packer, 1979: for olive; Bulger, 1993: for chacma) but not all (Noë and Sluijter, 1990: for yellow; Bercovitch, 1986: for olive; Saayman, 1971: for chacma) baboon populations.

Second, alpha males were also more discriminating in mate guarding with respect to females' maturity-based fertility differences. Whereas males of other ranks did not bias consortships against later stage adolescents, alpha males did (for macaques: van Noordwijk, 1985; Perry and Manson, 1995; Wolfe, 1978).

Finally, our data suggest that, even among ovulatory periods of fully adult females, alpha males but not males of other ranks may bias their consortships toward conceptive cycles, similar to findings for chimpanzees (Deschner et al., 2004), long-tailed macaques (Engelhardt et al., 2004) and two populations of wild chacma baboons (Bulger, 1993; Weingrill et al., 2003). Interestingly, Weingrill et al. (2003) found that only those alpha males that were resident in the group for several months displayed a consortship bias in favor of conceptive cycles, whereas alpha males that were recent immigrants often consorted during non-conceptive cycles, suggesting that ability to assess conceptive versus non-conceptive cycles improves with familiarity.

We do not suggest that conceptive cycles are somehow different in kind from non-conceptive cycles, and that adult males perceive this qualitative difference. In particular, the latest several adolescent and pre-conception cycles are probably of higher fertility than earlier ones, and the penultimate cycle is likely to be very similar to the conceptive cycle, perhaps even indistinguishable without very large sample sizes that can reveal very subtle differences (e.g., see data and discussion in Bercovitch, 1987; Wasser, 1996). Any ovulatory cycle should in theory be a potential conceptive cycle, with the probability of conception changing gradually from one cycle to the next; the relevant cues are probably graded as well and result in a probabilistic, not a deterministic, signal (Bercovitch, 1987; Emery and Whitten, 2003; Deschner et al., 2004; however, cf., Dahl et al. (1991) for an alternative perspective). Indeed, cycles of adult females may be non-conceptive partially because females receive less mate guarding, or receive only mate guarding by lower quality males (although this is less likely to explain fertility differences across the cycle or between adolescent and adult females). Both males and females of most species influence and control reproduction by the other sex in subtle as well as more dramatic ways, most of which are yet to be elucidated (e.g., Gowaty, 2004; Hrdy, 1997).

Behavioral differences between alpha males and those of other ranks probably do not represent differences in baboon's discriminative ability or proclivity. Rather, they are almost surely the consequence of greater constraints on non-alpha males than on alpha males. That is, the observed differences between alpha males and other males in their consort behavior probably reflect the fact that alpha males can choose most freely, whereas males of other ranks are more conditional in their mating behavior; they must adapt to opportunities that remain after the alpha males' mating decisions. Lower ranking males may also choose to consort with lower fertility females rather than forego mate guarding entirely. This strategy might either allow males to make the best of a bad situation, or it might allow them to create special bonds with females that will enhance their ability to obtain a consortship when those females are more fertile. The latter possibility would reduce alpha male advantage during high fertility times. Indeed, an affinitive bond may have a positive effect on the female's cooperation during subsequent fertile period; males in some studies were less likely to contest access to a female if she was with a preferred male (Kummer et al., 1974; Packer, 1979; Smuts, 1985; Strum, 1987). Similarly, lower ranking males may choose to consort with older adolescent females, or with adult females on their non-conceptive cycles in order to increase their opportunities for consortship on more fertile cycles.

Males of non-seasonally breeding species that live in relatively large multimale–multifemale groups face particularly great challenges with respect to mating decisions. In no season can males forgo mate guarding entirely to focus exclusively on foraging and perhaps 'fatten up'. Fertile females and sexual competitors are available throughout the year, and fertility variability among females is higher at any time of the year than in seasonally breeding species. On any given day, males may be faced with females that differ in fertility or simply with a single female with whom they decide to consort or forgo mate guarding for other activities such as foraging or caring for offspring. Species such as baboons and chimpanzees are ones for which sexual selection by male mate choice and development of reliable visual cues by females may have experienced particularly fine-tuned co-evolution.

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