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The ecology of conception and pregnancy failure in wild baboons

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Environmental conditions are a key factor mediating reproductive success or failure. Consequently, many mammalian taxa have breeding seasons that coordinate critical reproductive stages with optimal environmental conditions. However, in contrast with most mammals, baboons (*Papio cynocephalus*) of Kenya reproduce throughout the year. Here we depart from the typical approach of evaluating seasonal effects on reproduction and engage in a more fine-grained analysis of the actual ecological conditions leading up to reproduction for females. Our aim was to determine how environmental conditions, in combination with social and demographic factors, might mediate baboon reproduction. The data set includes all female reproductive cycles from multiple baboon groups in the Amboseli basin between 1976 and 2004. Results indicate that after periods of drought or extreme heat, females were significantly less likely to cycle than expected. If females did cycle after these conditions, they were less likely to conceive; and if they did conceive after drought (heat effects were nonsignificant), they were less likely to have a successful pregnancy. Age also significantly predicted conceptive failure; conceptive probability was lowest among the youngest and oldest cycling females. There was also a trend for high ambient temperatures to contribute to fetal loss during the first trimester but not other trimesters. Finally, group size and drought conditions interacted in their effects on the probability of conception. Although females in all groups had equal conception probabilities during optimal conditions, females in large groups were less likely than those in small groups to conceive during periods of drought. These results indicate that in a highly variable environment, baboon reproductive success is mediated by the interaction between proximate ecological conditions and individual demographic factors. *Key words:* conception, ecology of reproduction, estrous cycle, fetal loss, *Papio.* *[Behav Ecol 17:741–750 (2006)]*

Breeding seasons and birth peaks are particularly salient examples of the ultimate impact of ecology on reproduction (Baker 1938; Negus and Berger 1987), and many mammalian taxa exhibit seasonal variation in their reproduction. In some species, this variation is extreme, with all mating and births taking place during a very restricted part of the year. In others, variation is less skewed or entirely absent. Whether a mammal reproduces seasonally or continuously depends primarily on ecological factors, such as temperature and availability of resources (reviewed in Bronson 1985, 1989). Large fluctuations in these factors can produce high variability in female reproductive condition because decreased food intake must be balanced by decreased energy expenditure on activities such as reproduction that are not essential for immediate survival (Bronson 1989). Moreover, reproductive physiology and behaviors are sensitive to the availability of oxidizable metabolic fuels (Wade and Schneider 1992). Therefore, environmental conditions can be a highly influential factor affecting female reproduction (reviewed in Loudon and Racey 1987).

Facultative and obligatory seasonality identify 2 broad mammalian reproductive strategies to cope with the problem of reproducing under changing environmental conditions (Negus and Berger 1987). Facultative seasonality is typically found among mammals that have short life histories and that live in unpredictable environments. Facultative seasonal breeders initiate reproduction based exclusively on immediate energetic conditions. Because the duration of the reproductive cycle is relatively short, environmental conditions at the start of reproduction are usually a good indicator of conditions throughout cycling, conception, and parturition. In contrast, obligate seasonality typically occurs in mammals that experience long gestation and lactation periods and that live in reasonably predictable environments. To time birth or weaning with optimal environmental conditions, obligate seasonal breeders must couple the start of each reproductive cycle with a cue (such as photoperiod) that predicts future energetic conditions. The advantage of obligate seasonality is that females can initiate a reproductive cycle during unfavorable ecological conditions so that a vulnerable or energetically demanding stage coincides with a more auspicious period (Negus and Berger 1987).

Although the Negus and Berger dichotomy has proved useful when applied to the majority of mammalian taxa, it does not as readily apply to several large-bodied, tropically derived mammals with reproductive cycles that last more than a single year (see examples in Bronson 1995). In environments that vary, often unpredictably, over both short and long time scales, meteorological cues may have little predictive power. Furthermore, even in predictable environments, seasonal breeding becomes progressively less adaptive as the length of the reproductive cycle extends beyond a year and as the reproductive stages become more variable. In considering these difficulties, we asked the questions: What factors trigger the onset of reproduction in large-bodied mammals that have long life histories and that are adapted for life in unpredictable environments? Is reproduction random with respect to proximate environmental and/or social and demographic factors? Is there a degree of adaptive opportunism to the onset of reproduction that coincides with conditions unique to each individual?

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To answer these questions, we use data generated over 3 decades from a population of yellow baboons (*Papio cynocephalus*) in the Amboseli basin, Kenya. Like humans and apes, baboons present a challenge to the facultative/obligate dichotomy of Negus and Berger (1987). Baboons are relatively large-bodied, semiterrestrial, cercopithecine primates that produce a single offspring approximately every other year. Although the majority of cercopithecines exhibit seasonality, baboons (*Papio* spp.) represent one of the few exceptions (Bercovitch and Harding 1993), breeding continuously throughout the year. Nevertheless, environmental factors regulate baboon reproduction to some degree; captive females routinely reproduce both more frequently and more successfully than their wild counterparts, suggesting that natural habitats provide fewer resources than that required for maximum reproduction (Dunbar 1990). Additionally, a slight degree of reproductive seasonality exists in many wild baboon populations (Rhine et al. 1988, 1989; Bercovitch and Harding 1993; Lycett et al. 1999; Beehner 2003; Cheney et al. 2004) including the Amboseli baboons (Alberts et al. 2005).

Baboons live in a wide variety of habitats across the continent of Africa. The semiarid savannahs that they occupy, in particular, are often characterized by a high degree of environmental unpredictability. For example, annual rainfall in the Amboseli basin ranges from less than 150 mm to more than 550 mm (Altmann et al. 2002). The Amboseli baboons, therefore, combine a long reproductive cycle with high year-to-year variability, making them particularly well suited for answering questions about reproduction in long-term, unpredictable environments.

One mechanism by which environmental factors mediate reproductive timing is through reproductive failure (Lam et al. 1994). Reproductive failure is a broad term that can refer to disruptions at any of several stages in a female's reproductive cycle. The result of reproductive failure, however, is always the same—a delay in successful reproduction. In seasonally varying environments, selection acts on the energetically demanding or most vulnerable stages rather than on the reproductive cycle as a whole (Bronson 1995). As in other mammals, baboon reproduction is a multistage process, broadly including ovulation, conception, successful gestation, and infant survival to weaning. Reproductive failure can potentially occur at each stage, and baboon populations under different environmental pressures could experience greater selection on different stages. We focus specifically on reproductive failure at the conceptive and gestation stages of baboon reproduction. Although previous research in Amboseli has reported only a modest relationship between annual rainfall and baboon conceptions and births (Alberts et al. 2005), the unpredictability of the environment from year to year has prompted us to expand our analysis beyond annual (or seasonal) means to assess more specific cues that might trigger the onset of an estrous cycle.

Here, we depart from the typical approach of assessing reproduction with respect to seasons defined by calendar months or threshold rainfall values. Instead, we evaluate the specific weather conditions leading up to the fertile period of each female, in order to determine to what extent environmental conditions might predict reproductive timing and success in baboons. Rainfall affects reproduction indirectly through the productivity of food and availability of drinking water. With this in mind, we have developed an approach that asks whether each reproductive cycle was preceded by a drought, defined as a dry period longer than a normal, predictable dry season of 5-month duration. Based on the sharp plant biomass reduction during drought (Le Houérou 1989) and the importance of nutritional condition to successful female reproduction (Loudon and Racey 1987; Wade and Schneider 1992), we predicted that estrous cycles would be disproportionately absent after the drought periods, that estrous cycles after the drought periods would disproportionately fail to result in conceptions, and that those conceptions would disproportionately fail to produce live births.

Extreme temperatures, heat in the case of Amboseli, also can have a potent influence on reproductive success. Heat stress is induced when temperatures cause an animal's core temperature to exceed its normal limits (Bronson 1989). Therefore, we asked whether each reproductive cycle was preceded by extreme heat, defined in a preliminary fashion as daily ambient temperature highs over 35 °C. We then hypothesized that estrous cycles, conceptions, and live births would occur at lower rates on days preceded by extreme heat. Based on literature from farm and experimental animals that identifies the first trimester of pregnancy as the time of greatest reproductive vulnerability to heat stress (Sod-Moriah 1971; Wolfenson et al. 2000), we further hypothesized that extreme heat during the first trimester of gestation would also predict failure, in this case, fetal loss.

We also considered several social and demographic factors such as group size, age, parity, and dominance rank that might also affect reproductive failure. For example, high female status confers priority of access to important resources. Perhaps as a result, several baboon studies (including studies from the Amboseli population) have reported higher success for high-ranking females for some fitness components (Bulger and Hamilton 1987; Altmann et al. 1988; Bercovitch and Strum 1993; Packer et al. 1995; Wasser 1995; Altmann and Alberts 2003a; Johnson 2003; Cheney et al. 2004; Wasser et al. 2004). Additionally, among Amboseli females, larger groups are associated with lower reproductive rates overall (longer interbirth intervals, Altmann and Alberts 2003a). Based on these results, we predicted that a relationship between reproductive success and individual variables that mediate access to resources such as group size or dominance rank would be strengthened during drought conditions when resources may be scarce. Our goal was to assess whether individual females adjust their reproductive effort across reproductive cycles and to identify some of the proximate mechanisms involved in life-history trade-offs.

METHODS

Study site and study population

The Amboseli basin (lat 2°40′S, 1100-m altitude) is a semiarid short-grass savannah ecosystem located in an ancient lake basin at the base of Mt. Kilimanjaro in East Africa. The data for this study come from multiple groups of wild-feeding baboons in Amboseli. Individual life-history data for members of these study groups cover more than 3 decades (e.g., Shopland 1987; Altmann et al. 1988; Pereira 1988; Alberts and Altmann 1995; Alberts et al. 1996, 2003; Altmann and Alberts 2003b; see http://www.princeton.edu/~baboon for a complete bibliography and the Baboon Project Monitoring Guide, which outlines data collection protocols). Here, the subjects include all mature females (after reaching menarche at mean age of 4.5 years) from 8 different study groups that were monitored between January 1976 and December 2004. Two initial study groups fissioned, yielding 4 new study groups, and one of those fissioned again, resulting in an additional 2 study groups for a total of 8 groups. Each of the study groups defined by fission events is treated separately in this analysis because each group had unique characteristics (group composition, area of home range) that made it distinct from both its group of origin and its sister fission product.

Table 1

Sample sizes for reproductive variables under different ecological conditions

Ecological condition	Number of study days	Cycles	Conceptive cycles	Nonconceptive cycles	Live births	Fetal losses
Drought	2895	634	122	512	98	23
Nondrought	7670	1849	540	1309	461	64
Heat	2366	469	106	363	91	11
Nonheat	8258	2014	556	1458	468	76

Demographic and reproductive data

Demographic and reproductive data were drawn from the long-term database of the Amboseli Baboon Project, BABASE. Age (rounded up to nearest whole year), parity (number of pregnancies), dominance rank (ordinal rank number), group, and the number of mature females in the group were determined for each estrous cycle. Female reproductive stages were assigned post hoc based on external signs recorded in the field notes. Ovarian cycle phase is signaled by highly visible sexual swellings and menstruation. Pregnancy is indicated by failure of menstruation and sexual swelling after the usual duration of the luteal phase. In the absence of fetal loss, after approximately 2 months, the female's paracollosal skin also changes from black to pink (Altmann SA and Altmann J 1970; Beehner et al. 2006). Estrous cycles that resulted in pregnancy were recorded as a conception, and the first day of swelling deturgescence (d-date) was taken as the conception day. In the Amboseli population, mean gestation is 177 days ($N = 590$ successful pregnancies, outliers removed). Assigned pregnancies that did not result in live birth were recorded as fetal losses. In a study of fecal ovarian hormone profiles across Amboseli female baboons, we demonstrated that our long-standing external basis for early detection of pregnancies identifies 97% of pregnancies (Beehner et al. 2006). Nevertheless, neither fecal hormone sampling nor visual detection reliably identifies pregnancies terminated within the first 3 weeks. Therefore, a fetal loss prior to the third week of gestation would be recorded as a conceptive failure in our data set. Data collected during the protracted fission of one group (Alto's) were not included in the current study because sampling was less frequent during this period compared with other periods in BABASE.

Ecological data

Temperature (°C) and precipitation (mm) were measured daily from a central location within the Amboseli basin, our base camp, using a maximum–minimum thermometer and a rain gauge. We assessed monthly precipitation to determine whether each day was preceded by "drought" or "nondrought." In Amboseli, the long dry season predictably lasts 5 months (Altmann et al. 2002; Alberts et al. 2005). Consequently, a period of more than 5 dry months was classified as drought. We defined dry months according to the criterion suggested by Le Houérou (1989) as a month with rainfall less than twice the mean annual temperature, a statistic that has been successfully used by many ecologists and agronomists throughout the world in distinguishing dry seasons from growing seasons (Le Houérou 1989). For Amboseli, this value is approximately 50 mm (see also Dunbar 1992; Bronikowski and Altmann 1996).

To measure the probability of cycling during droughts compared with nondrought conditions, we measured the number of cycles per day after each ecological condition; each cycle was counted only once with the day of deturgescence being used as the marker (hence, we measured the number of deturgescences per day). To measure the probability of conception given that a female was cycling, we measured the number of conceptions per cycle after droughts compared with nondrought conditions, where the ecological condition was determined on the day of deturgescence. To measure the probability of fetal loss in drought versus nondrought conditions, we examined conditions preceding the conceptive cycle as well as conditions during gestation. That is, based on the 5 months of rainfall prior to each conceptive cycle, we assigned each conception as either drought or nondrought, and then, based on the 5 months of rainfall prior to the fetal loss or live birth, we assigned the loss/birth as drought or nondrought. Sample sizes for all reproductive variables during each ecological condition are listed in Table 1. Drought days (as defined in this study) occurred primarily during the 3 months after the June–October "dry season" (Altmann et al. 2002). In particular, 75% of drought days occurred during October–December, which is the period during which the yearly "short rains" generally begin in nondrought years (Altmann et al. 2002).

Similarly, temperature was analyzed as a dichotomous variable to assess whether the months preceding each cycle, conception, and loss were characterized by extreme heat. We used the same approach as described for drought versus nondrought conditions. Because the effects of high temperatures on reproduction are more direct (via elevated core body temperature), we restricted the temperature analysis to the 2 months prior to the event in question. If the mean maximum temperature for those 2 months was at least 35 °C, the cycle was categorized as having occurred after extreme heat. A laboratory study demonstrated that captive yellow baboons exposed to 40 °C for 2 h exhibit a rise in core body temperature, respiratory frequency, and cutaneous moisture loss (Hiley 1976). We chose 35 °C as our threshold for 2 reasons. 1) Air temperature measurements in Amboseli were taken in the shade, and thus, the temperatures that the baboons experience are probably much higher. 2) A preliminary study on physiological stress and daily maximum temperature for male baboons in Amboseli found that males exhibited a physiological stress response (i.e., elevated "stress" hormones or glucocorticoids) at temperatures over 34 °C (J Altmann and L Shek, unpublished data).

Data analysis

First, we used chi-square analyses to determine if observed probabilities of the 3 major reproductive events—cycling, conception, and fetal loss—were different from expected during extreme conditions (drought and heat). Specifically, because all study days could be scored as drought or nondrought as described above, we calculated the expected number of "drought cycles" (i.e., female cycles for which drought preceded its onset) based on the proportion of drought days to total study days. We calculated the expected proportion of "drought conceptions" based on the proportion of conceptive cycles to all cycles recorded. We calculated the expected

Table 2

Variables included in the logistic regression analyses for conceptions and fetal losses

	Variable type	Description (at d-date)
Dependent variables		
Conception	Categorical (yes/no)	Did ovulation result in a conception?
Fetal loss	Categorical (yes/no)	Did pregnancy result in a fetal loss?
Independent variables		
Fetal loss		
Conception		
Demographic		
Group	Categorical (1–8)	1 of 8 Amboseli baboon groups
Age	Integer (4–22)	Age of female (rounded to nearest year)
Age^2	Integer (16–484)	$(\text{Age of female})^2$
Parity	Integer (−3.0 to 3.0)	Relative number of pregnancies (controlled for age)
Dominance rank	Ordinal (1–25)	Rank based on dominance ranks of mature females (rank 1 is highest)
Number of females	Integer (6–25)	Number of females in the group
Ecological[a]		
Drought preceding cycle	Categorical (yes/no)	Less than 50 mm precipitation/month in the 5 months before cycle
Heat preceding cycle	Categorical (yes/no)	Was mean maximum temperature 2 months before cycle >35 °C?
Drought during gestation	Categorical (yes/no)	Less than 50 mm precipitation/month in the 5 months before birth/loss
Heat during gestation	Categorical (yes/no)	Was mean maximum temperature 2 months before birth/loss >35 °C?
Interactions		
Conception		
Dominance rank × drought preceding cycle		
Number of females × drought preceding cycle		
Dominance rank × number of females		

[a] Fetal loss logistic analysis includes conceptive cycles only.

number of "drought fetal losses" based on the proportion of fetal losses to all pregnancies recorded. The same methodology was used to calculate expected numbers for cycles, conceptions, and fetal losses during conditions of extreme heat.

Second, to test the hypothesis that the probability of conception for cycling females was related to the demographic and ecological predictor variables listed in Table 2, we conducted a logistic regression with maximum likelihood estimators (SPSS, version 11.0). We used a block design for the logistic regression analysis. The first block was the main-effects model using forced entry of all predictor variables; the second block employed a forward-selection method to find interaction terms that significantly reduced the residual χ^2 (Table 2). Because age and parity were significantly correlated ($r = 0.95$, $P < 0.001$), we first generated residuals for parity controlling for age (generated from least-squares linear regression, hereafter, "relative parity") before entering it into the logistic analysis. Studies of fertility in several primate species indicate that conception rates are lowest early and late in life (Packer et al. 1998; Nishida et al. 2003), suggesting a curvilinear relationship between age and probability of conception. Therefore, we also included age^2 in the logistic regression.

The data set included all estrous cycles from mature females between January 1976 and December 2004 with the following exceptions. Because young females experience several months of "adolescent subfertility" after menarche (Altmann 1980; Scott 1984), we excluded the first 4 cycles after menarche for each female. We also excluded cycles from 2 females that repeatedly failed to conceive over many years of data collection (KAT and LUL) and from 2 other females after they ceased regular cycling (NUB and DOT, at ages 20 and 22, respectively).

Third, we conducted another logistic regression to test the hypothesis that the probability of fetal loss was also related to the predictor variables listed in Table 2. In addition to including the ecological conditions leading up to the conception cycle, we included the ecological conditions during gestation, using the methodology explained above (see "Ecological Data"). All predictor variables were entered simultaneously in the main-effects model. This data set included all pregnancies between January 1976 and December 2004. We excluded data from females that died before the outcome of the pregnancy was known. In contrast with the conceptions analysis, we did not have the power in the fetal loss analysis to adequately assess an interactions model.

Finally, because the first trimester of mammalian pregnancy is generally more susceptible than mid- and late gestation to perturbations in the external environment (Nepomnaschy 2005), we tested the hypothesis that heat stress contributes to fetal loss specifically in the first trimester. Because our sample of first-trimester losses was small ($N = 18$), we used resampling procedures for our analysis. We calculated the mean maximum temperature (°C) for the first trimester of each pregnancy. Using the Excel add-in (version 3.0), we randomly drew N samples (where $N =$ the number of first-trimester fetal losses) with replacement from the data set and calculated the mean for this randomly drawn group. This process was repeated 10 000 times to generate a frequency distribution against which the mean maximum temperature for first-trimester losses was tested (Adams and Anthony 1996). Using this procedure, some values were sampled more than once, whereas others were not sampled at all.

RESULTS

Ecology of reproductive failure

For days preceded by drought conditions, we found significant differences between observed and expected number of estrous cycles per day ($\chi^2 = 4.36$, $P < 0.05$), number of conceptions per cycle ($\chi^2 = 23.96$, $P < 0.001$), and number of fetal losses per conception ($\chi^2 = 3.92$, $P < 0.05$; Figure 1). After drought conditions, females were less likely to cycle, less likely to conceive if they did cycle, and more likely to experience fetal loss if they did conceive. Similarly, when days were preceded by conditions of heat, we found significant

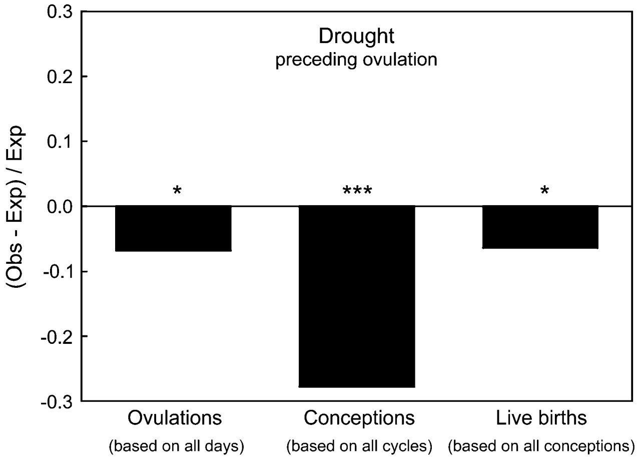

Figure 1
Relative difference between observed (Obs) and expected (Exp) number of estrous cycles, conceptions, and live births when drought conditions (see Methods) preceded each day, cycle, or conception. One estrous cycle was counted for each deturgescence (see Methods). One asterisk indicates significance at the 0.05 level, and 3 asterisks indicate significance at the 0.001 level. For calculation of expected values see text.

differences between observed and expected number of estrous cycles ($\chi^2 = 16.41$, $P < 0.001$) and conceptions ($\chi^2 = 4.87$, $P < 0.05$) but not fetal losses ($\chi^2 = 0.75$, $P = 0.39$; Figure 2). Under conditions of unusually high maximum temperatures, females were less likely to cycle and conceive, but overall fetal loss rate was unaffected.

Probability of conception

We recorded 2483 cycles (from 166 females) with 662 conceptions for an overall conception rate per cycle of 0.27. With the probability of conception as the dependent variable, logistic regression models including main effects (Table 3; model $\chi^2 = 91.61$, degrees of freedom [df] = 14, $P < 0.001$, -2 log likelihood = 2787.98, Cox and Snell $R^2 = 0.04$) and main effects plus interaction terms (Table 3; model $\chi^2 = 102.32$, df = 15, $P < 0.001$, -2 log likelihood = 2777.27, Cox and Snell $R^2 = 0.04$) were significantly different from a model with only the intercept. Both logistic regression models revealed a significant quadratic relationship between the probability of conception and age (Figure 3). With other variables taken into account, young cycling females had the lowest probability of conception, rising linearly until about 11 years of age and then leveling off. The probability of conception for cycling females remained level until about age 18 after which a sharp decline occurred. Significant main effects also included partial effects of drought and heat; a cycling female was 41% less likely to conceive if drought conditions led up to her estrous cycle and 29% less likely to conceive if hot conditions preceded it. By contrast, in the interactions model, drought alone failed to predict conceptive failure, but an interaction between drought and the number of females in the group emerged as significant (Table 3). Although females in large and small groups had equal probabilities of conception after nondrought conditions, after periods of drought females in large groups were significantly less likely than those in small groups to conceive (Figure 4).

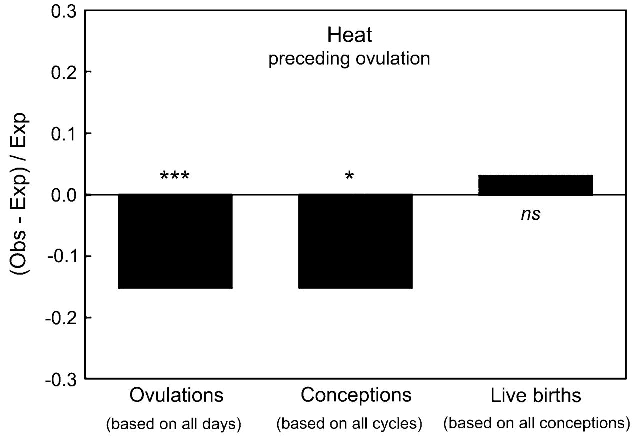

Figure 2
Relative difference between observed (Obs) and expected (Exp) number of estrous cycles, conceptions, and live births when heat (see Methods) preceded each day, cycle, or conception. One estrous cycle was counted for each deturgescence (see Methods). One asterisk indicates significance at the 0.05 level, and 3 asterisks indicate significance at the 0.001 level. For calculation of expected values see text.

Probability of fetal loss

We recorded a total of 656 pregnancies (from 146 females) with 91 cases of fetal loss for an overall loss rate of 13.9%. The current data set included ecological variables for 646 of these pregnancies (including 87 losses, Table 1). With the probability of fetal loss as the dependent variable, the logistic regression model including main effects was significantly different from a model with only the intercept (Table 4; model $\chi^2 = 25.27$, df = 15, $P < 0.05$, -2 log likelihood = 481.50, Cox and Snell $R^2 = 0.04$). The only significant variable was drought conditions preceding the conceptive cycle. On average, females were more than twice as likely to miscarry if they conceived after a period of drought.

Ecological conditions during gestation (as opposed to leading up to conception) failed to predict the probability of fetal loss in the logistic regression model (Table 4). However, pregnancies that resulted in first-trimester fetal losses were characterized by higher temperatures during gestation compared with other pregnancies. The frequency distribution of mean maximum temperatures during all first trimesters ranged from 30.9 °C to 35.3 °C. The mean maximum temperatures for pregnancies resulting in losses (34.2 °C) were higher than 9646 of the randomly calculated maximum temperature means, a result that approached significance ($P = 0.07$, 2-tailed test).

DISCUSSION

The results of our analyses, based on the daily meteorological data (temperature and rainfall) preceding each reproductive event, parallel those from traditional analyses of ecological effects on reproduction that use seasons (defined by calendar months or threshold levels of rain) as proxies for ecological variables. Just as seasonal breeders limit or cease reproduction during poor ecological conditions, baboons also time reproductive events with favorable ecological factors. However, by examining the environmental conditions for each individual female cycle, we were able to evaluate the relationship between weather variables and baboon reproduction in much greater detail. First, we were able to distinguish between the separate effects of high temperatures and low rainfall on reproduction in the Amboseli female baboons. Second, we were

Table 3

Logistic regression analysis of main effects and interactions for probability of conception including coefficient (B), standard error (SE), Wald score, df, significance (*P*), and odds ratio (Exp (B)) for each variable

	Main-effects model						Main-effects plus interactions model					
	B	SE	Wald	df	*P*	Exp (B)	B	SE	Wald	df	*P*	Exp (B)
Independent variables												
Group			5.04	7	0.66				5.56	7	0.59	
Age	0.39	0.07	37.00	1	0.00**	1.48	0.39	0.07	35.94	1	0.00**	1.48
Age^2	−0.01	0.00	28.64	1	0.00**	0.99	−0.01	0.00	27.48	1	0.00**	0.99
Parity	0.03	0.06	0.36	1	0.55	1.03	0.04	0.06	0.49	1	0.48	1.04
Dominance rank	0.00	0.01	0.13	1	0.72	1.00	0.00	0.01	0.17	1	0.68	1.00
Number of females	−0.03	0.02	2.44	1	0.12	0.98	−0.01	0.02	0.36	1	0.55	0.99
Drought preceding cycle	−0.52	0.12	20.50	1	0.00**	0.59	0.79	0.41	3.66	1	0.06	2.21
Heat preceding cycle	−0.35	0.13	7.36	1	0.01*	0.71	−0.39	0.13	8.93	1	0.01*	0.68
Interactions												
Dominance rank × drought preceding cycle							—	—	—	—	—	—
Number of females × drought preceding cycle							−0.08	0.03	10.52	1	0.00**	0.92
Dominance rank × number of females							—	—	—	—	—	—
Intercept												
Constant	−2.77	0.45	38.31	1	0.00**	0.06	−2.98	0.45	43.26	1	0.00**	0.05

$^{**}P < 0.001$, $^{*}P < 0.01$.

able to quantify the temporal relationship between ecological variables and reproductive failure, demonstrating that the success of each reproductive event (cycling, conception, and live birth) depends primarily on optimal temperature and rainfall conditions preceding each stage. Specifically, after both periods of drought and heat, females were significantly less likely to cycle than expected. Furthermore, if females did cycle after these conditions, they were significantly less likely to conceive. If they did conceive after conditions of drought (conditions of heat were nonsignificant), they were less likely to have a successful pregnancy. Furthermore, when additional social and demographic factors were considered in the logistic analyses, drought conditions remained a significant predictor of both conceptive failure and fetal loss among the Amboseli females.

The consistent relationship between drought conditions and female reproductive failure suggests that adequate maternal body condition may act as the primary cue for the onset of reproductive cycles among the Amboseli females. Furthermore, females experienced no increase in fetal losses when drought conditions occurred during gestation (i.e., once successful conception had taken place), suggesting that female body condition leading up to reproduction may be a better indicator of success than body condition during gestation (see also Koenig et al. 1997). If the usual dry season of 5 months duration was extended (i.e., if the rains failed) even by a month, females exhibited fewer cycles and conceptions and more fetal losses than expected. As with many herbivores, baboons depend on grassland productivity for a large portion of their diet. Consequently, when primary productivity is reduced as the result of a drought, female nutritional condition

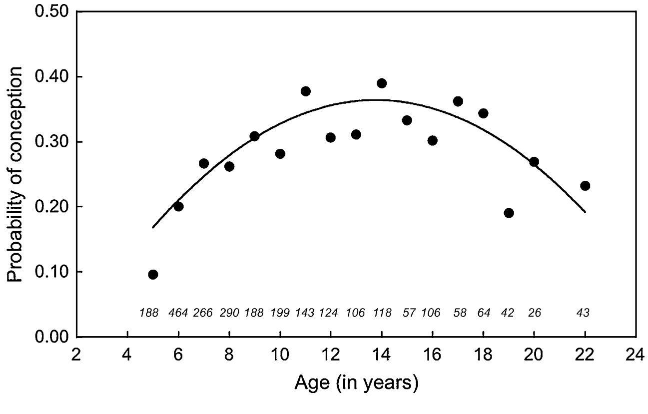

Figure 3
Probability of conception as a function of age as determined by the predicted values from the logistic regression (solid line) and the actual data (solid circles). For the actual data points, the number of cycles used to determine the probability of conception at each age is listed in italics above each age.

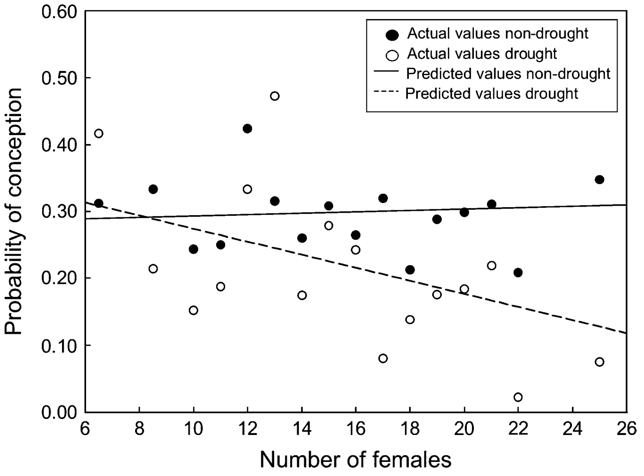

Figure 4
Probability of conception as a function of number of females in the group generated from the predicted values of the logistic regression during conditions of nondrought (solid line) and drought (dashed line). Actual values (conceptive/total cycles) for group sizes are plotted for nondrought (solid circles) and drought (open circles). In the calculation of the actual values, data from the largest groups (21+ females) were pooled and weighted appropriately to provide an adequate sample size for calculating probability of conception.

Table 4

Logistic regression analysis of main effects for probability of fetal loss including coefficient (B), standard error (SE), Wald score, df, significance (*P*), and odds ratio (Exp (B)) for each variable

	Main-effects model					
	B	SE	Wald	df	*P*	Exp (B)
Independent variables						
Group			12.57	7	0.08	
Age	−0.03	0.03	0.68	1	0.41	0.73
Parity	−0.07	0.13	0.26	1	0.61	0.94
Dominance rank	0.01	0.02	0.13	1	0.72	1.01
Number of females	0.03	0.04	0.59	1	0.44	1.03
Drought preceding cycle	0.70	0.30	5.38	1	0.02*	2.02
Heat preceding cycle	−0.62	0.39	2.57	1	0.11	0.54
Drought during gestation	−0.28	0.28	0.96	1	0.33	0.76
Heat during gestation	0.37	0.33	1.24	1	0.27	1.45
Intercept						
Constant	−1.66	0.70	5.64	1	0.02*	0.19

* $P < 0.05$.

is poor. In particular, inadequate food intake or increased energy expenditure to obtain food (or both) are critical factors contributing to the nutritional condition of a female initiating reproduction (Wade and Schneider 1992). Females must first meet basic metabolic requirements before allocating energy to reproduction in order to avoid a negative energy balance, and female body mass and condition across many mammalian taxa have been linked to reproductive output (Roe deer, *Capreolus capreolus*: Hewison and Gaillard 2001; European badgers, *Meles meles*: Woodroffe and MacDonald 1995). Taking a more indirect approach, conceptive peaks have been linked to rainfall in several *Papio* species and their close relatives (*Papio anubis*: Bercovitch and Harding 1993; *Papio ursinus*: Lycett et al. 1999; *Theropithecus gelada*: Dunbar 1980). If baboons have adopted an opportunistic (i.e., facultative) strategy of reproduction as our results suggest, then it is easy to imagine how a progressively less variable environment might produce the moderate birth peaks reported from other baboon studies (Rhine et al. 1988, 1989; Bercovitch and Harding 1993; Lycett et al. 1999; Beehner 2003; Cheney et al. 2004) as well as the obligate seasonality of other primate species (e.g., Goldizen et al. 1988; Brockman 1999; Borries 2000). Even in Amboseli, we might expect to see stronger birth peaks during less variable periods.

Extreme heat during the 2 months preceding any given estrous cycle significantly predicted conceptive failure. Although little studied in wild populations, unusually high temperatures have been shown to affect several aspects of reproduction in laboratory and domestic animals and in humans. First, because males of most mammalian species rely on external testes for temperature control (Freeman 1990; Setchell 1998), seasonally high temperatures can suppress spermatogenesis in mature males enough to reduce the number of fertilizations in hotter months (Kandeel and Swerdloff 1988; Mendis-Handagama et al. 1990; Bedford 1991). Second, heat stress can suppress ovulation and conception in mature females (Herrenkohl 1979; Baumgartner and Chrisman 1987; Bronson 1989). In several domesticated mammals, heat stress has been linked to reduced conception rates (reviewed in Marai et al. 2002; De Rensis and Scaramuzzi 2003), and considerable research has focused on the reproductive impairment of domestic livestock due to heat stress. Nearly all components of the reproductive system of livestock were found to be susceptible to heat stress, including the oocyte, the theca cells within the preovulatory follicle, and the embryo during early stages of development (reviewed in Wolfenson et al. 2000). Fetal loss rates increase when the mother is exposed to heat stress during gestation (Wilmut et al. 1986; Bronson 1989), and the greatest impact on embryo survival occurs prior to implantation (Sod-Moriah 1971).

Nevertheless, extreme heat preceding reproductive cycles in the Amboseli females was not a significant predictor of fetal loss. In other words, although a female's prior exposure to heat stress increased the chances that she would not conceive, if she did manage to conceive, she did not experience higher probability of loss. However, because we were unable to detect pregnancies prior to the third week of gestation, a very early pregnancy termination (embryonic loss, in this case) may have been missed. Undetected embryonic losses would have been scored as conceptive failures and not pregnancies, possibly contributing to the significant relationship between high temperatures and conceptive failure. High temperatures during a female's first trimester of pregnancy affected her chance of fetal loss, but only during that first trimester. Therefore, heat stress was a critical factor affecting baboon reproduction during cycling, conception, and gestation through the first trimester. However, heat stress during mid- or late gestation did not have a significant effect on the outcome of the pregnancy. Although very little is known about the effect of heat stress on the reproduction of wild mammals, our results suggest that heat stress may affect early embryo survival in a natural baboon population. Recent results on humans have shown that maternal stress during the period prior to physiological maturation of the placenta is most likely to result in miscarriage (Nepomnaschy 2005). Given global and local climate change in the direction of increasing temperatures, the effects of heat stress on reproductive failure may be a growing concern for wildlife populations. For Amboseli mammalian populations, in particular, a dramatic local warming trend has been documented (Altmann et al. 2002).

The probability of conception for cycling females was a curvilinear function of female age, with the lowest probabilities among the youngest and oldest females and a relatively long, stable period in between (Figure 1). Although we eliminated the first few cycles for each female after menarche, at least part of this relationship can be explained by an extended period of adolescent subfertility for some young females (Altmann 1980). However, among young females, the probability of conception continued to increase well past the period of adolescent subfertility until approximately age 11. Females from age 11 to 18 had equal conception rates, and then rates dropped precipitously by age 19. Illustrating this point, one female cycled irregularly after age 22 and did not conceive for the next 4 years until she died at age 26. Although reproductive senescence has been reported in many captive nonhuman primates (reviewed in Kavanagh et al. 2005), it usually occurs at ages when senescence of most major organ systems occurs, and it is relatively rare in wild populations (but see Nishida et al. 2003 for exceptions; Packer et al, 1998). In studies on both captive and wild mammals, many old females exhibit less regular cycles, higher rates of conceptive failure, and significantly different hormone profiles than younger females (reviewed in Caro et al. 1995; baboons, *Papio* spp.: Chen et al. 1998; Packer et al. 1998; Burger et al. 2002; Altmann and Alberts 2003b; roe deer, *C. capreolus*: Hewison and Gaillard 2001; humans, *Homo sapiens*: Judd 1976; lions, *Panthera leo*: Packer et al. 1998; rhesus macaques, *Macaca mulatta*: Walker 1995; tamarins, *Saguinus* spp.: Tardif and Ziegler 1992). The overall decline in conceptions among the older Amboseli females probably represents the first stages of reproductive senescence. In contrast to humans, this pattern of reproductive senescence seems to be relatively congruous with senescence of other systems, whereas reproductive senescence in humans considerably precedes senescence of other systems (Hawkes et al. 1997).

Many mammalian studies have documented the costs of high density on female reproduction (voles, *Microtus* spp.: Agrell et al. 1995; European badgers, *M. meles*: Cresswell et al. 1992; Woodroffe and MacDonald 1995; deer mice, *Peromyscus maniculatus*: Eleftheriou et al. 1962; African mole rats, *Cryptomys hottentotus*: Jarvis 1969; house mice, *Mus musculus*: Ryan and Schwartz 1977). Additionally, previous work in Amboseli has shown that females living in larger groups had longer interbirth intervals (after a surviving offspring) than females in smaller groups (Altmann and Alberts 2003a). Consistent with these previous results, the current study revealed that conception rates were significantly altered by an interaction between the number of females in each group and periods of drought. Following "good" conditions (i.e., adequate rainfall for high primary plant productivity), large and small groups had almost identical rates of conception. In contrast, following "bad" conditions (i.e., drought), rates of conceptive failure increased for females in large groups (Figure 4). These results suggest that the costs of poor ecological conditions may be borne disproportionately by females living in large groups. The detrimental impact of large group size on reproduction, particularly during drought conditions, probably results from reduced foraging efficiency from scramble competition (Bronikowski and Altmann 1996; Altmann and Alberts 2003a), as found in several other cercopithecine populations (van Schaik and van Noordwijk 1988; Dunbar 1996). Increased within-group feeding competition is widely recognized as one of the main costs of group living among social mammals (Terborgh and Janson 1986; Wrangham et al. 1993; Janson and Goldsmith 1995). The ecological constraints model suggests that scramble competition limits group size because larger groups must forage further or more often to meet the energetic requirements of their members (Milton 1984; Janson 1988; Wrangham et al. 1993; Chapman et al. 1995), and previous studies on Amboseli groups have found that dry periods are associated with increased time spent foraging (Bronikowski and Altmann 1996).

We found no effect of female dominance rank on the probability of cycling, conception, or fetal loss. However, previous analyses indicate that high-ranking females experience shorter interbirth intervals than low-ranking females in this population (Altmann and Alberts 2003a). Taken together, these results suggest that high dominance rank affects interbirth intervals by shortening the period of postpartum amenorrhea and not by increasing the probability of conception for a given cycle. That is, high-ranking females resume cycling sooner after giving birth than low-ranking females, but they tend to experience the same number of cycles before each conception as low-ranking females. This pattern would result in higher fertility for higher ranking females but not higher rates of cycling or conception.

Our results from the Amboseli baboons suggest that reproductive failure in some large-bodied, tropically derived mammals may represent a physiological response that limits investment in reproduction after poor ecological conditions and that the mechanism for doing so may be the same for each of several reproductive stages. Rather than an obligate response to predictable weather cues, baboon females respond to their current physiological state—a state that reflects previous ecological conditions. If females are not overheated and have adequate body reserves, they cycle and conceive. If favorable conditions continue, they successfully give birth. As such, baboon females have adopted a facultative reproduction strategy that "aborts" at any of the several stages if conditions deteriorate. Because early stages of the reproductive cycle (cycling and conception) are certainly less costly to mothers than later stages (gestation and lactation), in an unpredictable environment such a strategy may represent the trade-off between current and future reproduction.

In summary, the chances for Amboseli females of cycling, conceiving, and successfully giving birth were a function of resource availability and heat stress. Droughts resulted in reduced rates of reproduction. Furthermore, females in large groups were more affected by drought conditions than females in small groups, suggesting some degree of within-group feeding competition. Unusually high temperatures immediately preceding a cycle further reduced conception rates, and high temperatures during early gestation increased the chances of early fetal loss. These results indicate that in a highly variable environment, such as Amboseli, female reproductive events are mediated by a trade-off between individual demographic factors and proximate ecological conditions.

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