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Correlates of Agonistic and Competitive Interactions in Pregnant Baboons

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Maternal condition during pregnancy is known to influence fetal viability. Recently, primatologists have suggested that certain characteristics of the fetus may influence maternal condition as well. For example, among captive pigtailed macaques (*Macaca nemestrina*) mothers of female infants may be at greater risk of injury during their pregnancies than mothers of male infants. Analysis of the rates of aggression, submission, competition, and wounding among free-ranging pregnant baboons (*Papio cynocephalus*) in Amboseli National Park generally fail to support these findings, but several other factors such as maternal dominance rank, environmental conditions during pregnancy, maternal parity, and fetal age correlate with aggression, submission, competition, and injuries sustained by pregnant female baboons.

Key words: *Papio cynocephalus*, pregnancy, aggression, competition

INTRODUCTION

It is well established that maternal condition during pregnancy influences the viability of the fetus [Riopelle, 1982]. Recently, however, primatologists have begun to suspect that certain characteristics of the fetus may influence maternal condition as well. One study of captive pigtailed macaques (*Macaca nemestrina*) indicated that mothers of female infants were at greater risk of being wounded during their pregnancies than were mothers of male infants [Sackett, 1981; Sackett et al, 1975a,b]. Among pregnant females who required treatment for bite wounds in the colony, a larger fraction were carrying female fetuses than would be expected by chance alone. The effects of fetal sex emerged during the second half of pregnancy. Two lines of evidence suggested that females carrying male infants have been the principal source of aggression toward females carrying female fetuses. First, aggression among females accounted for the great majority of aggression in the colony [Erwin, 1978]. Second, females who performed more aggressive than submissive behaviors in the second half of their pregnancies were more likely to give birth to male infants than female infants [Erwin & Anderson, 1975]. Sackett [1981] speculated that females carrying male fetuses may have become more aggressive and less vulnerable to aggression themselves than females carrying female fetuses because male fetuses secrete high levels of testosterone, which are detectable in the mother's bloodstream. The fact that the effects of fetal gender emerged at the same time that sexual differentiation occurs in the fetus provided indirect support for this view.

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It has been more than a decade since a preliminary description of these data was published. In the interim, these results have figured in discussions of the reproductive strategies of Cercopithecine primate females. Some authors have argued that harassment of females carrying female fetuses may reduce the viability of their fetuses and account in part for the fact that low-ranking females produce more male infants than female infants [eg, Wasser, 1983]. In a similar vein, Silk and Boyd [1983] have argued that harassment of females carrying female fetuses may be an effective form of reproductive competition among primate females, as females attempt to reduce the number of unrelated female competitors within their groups.

Although the proximate mechanisms and ultimate implications of these results have intrigued many primatologists, there have been surprisingly few attempts to replicate these results in other primate colonies or in the field. Simpson and Simpson [1982] found that aggressivity was not consistently associated with progeny gender among ten rhesus macaque (*Macaca mulatta*) females in the Madingley colony, but no other information regarding the effect of fetal sex upon maternal behavior during pregnancy is currently available.

In this paper, the effects of fetal gender upon rates of aggression, submission, competition, and injuries among free-ranging pregnant baboons, *Papio cynocephalus*, in Amboseli National Park are described. The following predictions about the effects of fetal sex upon maternal behavior during pregnancy were evaluated:

1. Females carrying female fetuses will be wounded and harassed more often than females carrying male fetuses.
2. Females carrying male fetuses will generally be more aggressive than will females carrying female fetuses.
3. The effects of fetal sex will be most pronounced during the second half of pregnancy. Females carrying female fetuses will be harassed relatively more often during the second half of pregnancy than during the first half of pregnancy, and females carrying male fetuses will be particularly aggressive during the second half of their pregnancies.

In general, the results of the present analysis fail to support prior findings for captive pigtailed macaques that females carrying female fetuses are more susceptible to injury or are harassed more often than females carrying male fetuses. At the same time, the analysis reveals that several other factors such as maternal dominance rank, environmental conditions during pregnancy, maternal parity, and fetal age are closely associated with the rates of aggression and competition and frequencies of injuries sustained by pregnant female baboons.

MATERIALS AND METHODS

Study Population and Site

Two groups of free-ranging and unprovisioned yellow baboons, *Papio cynocephalus*, were observed in Amboseli National Park, Kenya, from December 1982 through September 1983. Ecological conditions in the study area have been described in detail by Western [1972] and Western and van Praet [1973], and the baboon population has been censused intermittently since 1964 [Altmann, 1980; Hausfater, 1975; Altmann & Altmann, 1970]. Members of one group (Alto's Group) have been habituated, individually recognized, and regularly observed since 1971 [see Altmann, 1980]. Similarly detailed observations of a second study group, Hook's Group, were initiated in 1980. The members of these two groups were the subjects of the current study. At the beginning of the study period, Alto's Group contained 52 individuals (8 adult males, 4 subadult males, 19 adult females, 10 juvenile males, 11 juvenile females), and Hook's Group contained 39 individuals (7 adult males, 1 subadult male, 14 adult females, 8 juvenile males, and 9 juvenile females). By the end of the study period, membership in Alto's Group and Hook's Group had increased to 63 and 44, respectively.

Subjects

All females who were pregnant during the study period became subjects of observations. Six females were pregnant when the study began, 12 females conceived and gave birth during the study period, and seven conceived during the study and gave birth shortly after the study ended. Two more females who conceived during the study period miscarried during the first two months of their pregnancies. One of these females and another female whose infant died three days after birth conceived again during the study period. These females constituted a heterogeneous sample of the adult female population, varying in age, parity, dominance rank, and infant survivorship. The number of females who were simultaneously pregnant during the study period ranged from 6 to 18.

Assessment of Female Reproductive Status

To monitor the reproductive condition of females, the size of the sexual swelling, presence of menstrual blood, and the coloration of the paracolossal skin of all adult females were recorded on each occasion that the group was contacted. Alto's Group was contacted on 201 days and Hook's Group was contacted on 174 days during the 304-day study period by one of the three investigators then participating in the longitudinal study (A. Samuels, R. Mututua, and the author). Thus, the reproductive condition of females in each group was recorded on average once every two days. Observations of reproductive status were made at similar intervals by other researchers before the present study began.

The group was also censused each time it was contacted. These frequent censuses provide precise information about the dates of parturition. In most cases, the exact day of birth is known because the group was censused on successive days. In some cases, the group was not contacted on successive days, but the first time the infant was seen its coat was still wet and matted, and the mother's perineum, hands, and feet were still bloody. Since the infant dries quickly and the mother cleans herself shortly after she gives birth, this was taken as evidence that parturition had occurred on the same day. In a few cases, the day of birth can only be estimated within a range of two or three days.

Pregnancy was initially suspected when females failed to menstruate within the prescribed period after detumescence of the sex skin or when their sex skin did not begin to swell within a few days of the expected onset of the next cycle. Pregnancy was confirmed when the upper portion of the paracolossal skin started to turn pink. Regular observations were initiated as soon as a female was suspected to be pregnant (mean = 17.8 days after the onset of deturgescence, range = 3–27 days). Observations were terminated upon delivery of an infant or the resumption of cycles which indicated the occurrence of an early miscarriage.

Behavioral Data Collection Procedures

The results presented here are based mainly upon focal animal observations [terms defined by Altmann, 1974] of adult females during their pregnancies. Three focal females were observed on each day that focal data were collected. Each female was observed for four 20-minute periods distributed throughout the day. The first observation of the day began at 0740, often before the baboons had descended from their sleeping trees, and the last observation of the day ended at 1700, before the baboons entered their sleeping trees for the night. These four 20-minute samples collectively constituted a single "female day." When a female became pregnant she was immediately inserted into the list of subjects, and when a female gave birth she was dropped from the list. An effort was made to ensure that individual females did not consistently occupy the same position in the daily observation order. The length of the interval between "female days" varied as the size of the sample of pregnant females changed (average interval = 7.6 days). The observation schedule was modified to accommodate occasional absences from the field and to include additional observations of females who were approaching parturition.

The baboons were followed on foot and were usually observed from a distance of approximately 5 m. Although observation conditions were generally very good, animals sometimes moved out of sight during observations. Moreover, problems with equipment or the proximity of lions, elephants, or buffalo sometimes delayed or interrupted observations. If an observation was interrupted for any reason, an entry was recorded to this effect. If the interruption lasted for more than half of the 20-minute observation period, a new sample was begun as soon as the animal was found or conditions permitted observations to be conducted safely. If a sample could not be repeated or completed before the next sample was scheduled to begin, the sample was skipped. Out-of-sight time during completed samples accounted for approximately one-half of 1% of all focal observation time (n = 547.6 hours). Approximately 1% of all scheduled samples were skipped.

In the field, data were typed directly onto a hand-held microcomputer (Radio Shack PC2) programmed in BASIC. The program was designed to accept alphanumeric data and to associate each datum with the current time. These data provided a continuous record of activities and interactions. At the end of each day's observations, the data were transferred onto cassette tape and were also printed and manually edited. Upon return from the field, the data were transferred from cassette tape to a microcomputer for storage, editing, and analysis.

During focal observations, the activities (eg, feed, rest, travel) and social interactions (eg, groom, approach, threaten) involving the focal female were recorded on a continuous basis. For every interaction three kinds of information were noted: (1) the kind of interaction; (2) the identity of the partner(s); and (3) the identity of the individual(s) responsible for initiating the interaction. Aggressive interactions included hit, bite, push, yawn, raise-brow, and lunge. Submissive behaviors included lean away, grimace, raised tail, crouch, and cower [defined more fully by Hausfater, 1975].

Competitive encounters included two similar kinds of interactions. A "replacement" was scored when one baboon approached to within 1 m of a second baboon, the second baboon interrupted its activities, and the newcomer appropriated the resource that the original occupant of the site had been using. An "interruption" was scored when one baboon approached to within 1 m of a second baboon, the second baboon interrupted its activities, but the newcomer did not appropriate the resource that the original occupant of the site had been using. These interactions were not differentiated in this analysis, and they are collectively referred to as competitive encounters.

Supplementary Information

Each time that the group was censused observers checked for the presence of injuries, wounds, and illnesses. These were described in detail on the first day that they were observed, and information about the animals' condition was updated regularly. Agonistic interactions were recorded ad libitum in a standardized format by all investigators throughout the period of contact with the group.

Observations of dyadic agonistic interactions with clearly decided outcomes were used to establish the dominance hierarchy among adult females. The methods that have been used to assess dominance among the Amboseli baboons have been described in detail by Hausfater [1975] and Walters [1980]. Briefly, decided agonistic bouts are those in which one individual, the "loser," performs only submissive behaviors (eg, grimace, tail up, lean aside, crouch) in response to aggressive (eg, bite, hit, lunge) or neutral behaviors by the "winner." Interactions were entered in a square matrix in which females were ordered so as to minimize the number of entries below the diagonal.

Normally, individuals are assigned ordinal dominance ranks that correspond to the number of individuals they dominate. In a group of size n, the highest-ranking individual is assigned rank 1 and the lowest-ranking individual is assigned to rank n. Such measures are problematic when individuals from groups of different sizes are compared. Hence, dominance rank is expressed here as the percent of females dominated [after Cheney et al, 1981]. This measure is calculated as $(n-m)/(n-1)$, where n is the total number of females in the group and m equals the female's ordinal rank. One is subtracted from the denominator because the individual itself is excluded from the potential number of females dominated. Thus, in a group of size 10, the second-ranking individual dominates 89% of the other females in her group $[(10-2)/(10-1) = 0.89]$. The highest- and lowest-ranking females dominate 100% and 0% of the other females in the group, respectively.

Data Analysis

In the analyses that follow, three kinds of social interactions were considered: aggression, submission, and competition. The frequency with which pregnant females were wounded or injured was also evaluated. This analysis included a broader range of interactions than did the macaque research described above. This is largely due to the fact that overt acts of aggression were rare events among adult females. Pregnant females threatened and attacked other members of their groups only 0.14 times per hour of focal observation and received only 0.27 acts of aggression from others per hour of observation. It is possible that the small size of the sample of aggressive events would make it difficult to detect underlying patterns in these data. One way to remedy this problem is to analyze the pattern of other events that are functionally related to aggression but occur more often.

If females carrying female fetuses are more vulnerable to aggression than females carrying male fetuses, it is reasonable to suppose that females carrying female fetuses would also show more evidence of submission than females carrying male fetuses. This follows from the fact that females often react submissively to aggression, creating a direct association between aggression and submission. However, females also behave submissively toward others in the absence of overt aggression from them. If spontaneous submission occurs when females perceive potential threats from others, the frequency and pattern of submission may provide a useful index of a female's potential vulnerability to aggression.

Competitive encounters often occur without any obvious evidence of aggression or submission. Nonetheless, the outcomes of aggressive encounters between pairs of baboons are highly consistent with the outcomes of competitive encounters between the same pairs of individuals. Moreover, it is generally assumed that competitive encounters have negative effects upon individuals who are displaced from resources and can, therefore, be considered a form of harassment.

In this analysis, rates of aggressive, submissive, and competitive interactions involving females carrying male and female fetuses are compared. The rates of interactions for each female were calculated separately by dividing the number of events in which each female was involved by the total number of minutes that she was observed. Thus, the rate of aggression initiated by female Spot is equal to the number of aggressive acts that she directed toward others divided by the number of minutes that she was observed. Rates of interactions were available for 25 pregnancies.

For 22 pregnant females, the total number of wounds and injuries sustained between conception and parturition was known. Hence, the absolute frequency of injuries and wounds during pregnancy was the unit of analysis.

T-tests were performed to determine whether the mean rates of interactions or frequencies of injuries involving females carrying male and female fetuses differed significantly. Pearson correlation coefficients were performed to determine whether the rates of interactions and frequencies of injuries varied in relationship to continuous variables such as dominance rank, maternal parity, and cumulative rainfall. In the analyses of the effects of fetal age, the unit of analysis was a single female day (defined above).

Analyses of the effects of fetal sex upon maternal behavior are complicated by the fact that fetal sex is associated with maternal rank in this population [Altmann, 1980; Altmann et al, in press]. During the study period in Amboseli, high-ranking females produced 11 daughters and 1 son while low-ranking females produced 6 daughters and 7 sons (Fisher exact test, $P = .0095$). Thus, it is important to determine whether effects of fetal sex are independent of the effects of maternal rank. If maternal rank is unrelated to the rate of any of these interactions, it is reasonable to conclude that fetal sex has an independent effect upon the rate of that behavior. However, if both maternal rank and fetal sex are related to the rate of interactions, it is difficult to distinguish the relative importance of these variables.

Standard multiple regression procedures cannot be used to tease apart the effects of maternal rank and fetal sex because the two independent variables are correlated with one another [Wannacott & Wannacott, 1977]. Hence, a more conservative procedure must be adopted. For each kind of interaction in which the effects of fetal sex appear to be significant, a one-dimensional linear regression was computed between maternal rank and the rate of the interaction. By using the slopes and y-intercepts of the resultant regression equation, it is possible to calculate the expected rate of interaction for each female, given her rank. Residuals from these expected values are obtained by subtracting the observed values for each female from the expected values. A positive residual indicates that the rate of interaction was higher than expected based upon that female's rank, while a negative residual indicates that the rate of interaction was lower than expected based upon her rank. Finally, t-tests were performed on these residuals. If the results of a t-test are significant, then it is reasonable to conclude that fetal sex has an independent effect upon the rate of interaction.

RESULTS

Did Fetal Gender Influence Maternal Behavior?

Females carrying male and female fetuses were wounded or injured with equal frequency, received similar amounts of aggression, gave similar amounts of submission, and were the targets of similar amounts of competition during their pregnancies (Table I). Thus, there was no support for the prediction that females carrying female fetuses would be harassed more often than females carrying male fetuses.

There was no evidence that females carrying male fetuses threatened and attacked other members of their groups more often than did females carrying female fetuses (Table I). However, females carrying female fetuses elicited more submission from others, particularly adult females, than did females carrying male fetuses. Moreover, females carrying female fetuses initiated significantly more competitive encounters than did females carrying male fetuses (Table I). Thus, it was females

TABLE I. Effects of Fetal Sex on Rates of Interaction†

	Male fetus (n = 8)		Female fetus (n = 17)			
	Mean	sd	Mean	sd	t	*P*
Aggression toward focal females from						
All others	0.2667	0.234	0.2700	0.196	−0.04	.973
Adult males	0.0865	0.069	0.0806	0.066	0.20	.843
Adult females	0.0625	0.114	0.0921	0.108	−0.62	.549
Juveniles	0.1013	0.110	0.0918	0.118	0.20	.847
Aggression by focal females toward						
All others	0.0862	0.126	0.1828	0.145	−1.70	.109
Adult males	nd	nd	nd	nd	nd	nd
Adult females	0.0457	0.044	0.0757	0.075	−1.26	.221
Juveniles	0.0519	0.097	0.0917	0.095	−0.96	.352
Submission toward focal females from						
All others	0.3364	0.440	0.9393	0.713	−2.59	.017*
Adult males	nd	nd	nd	nd	nd	nd
Adult females	0.2737	0.319	0.7869	0.577	−2.85	.009*
Juveniles	0.0628	0.130	0.1445	0.158	−1.36	.191
Submission by focal females toward						
All others	1.1866	0.557	1.3920	0.653	−0.81	.428
Adult males	0.5353	0.295	0.6639	0.191	−1.13	.286
Adult females	0.5232	0.304	0.5127	0.492	0.06	.949
Juveniles	0.1282	0.090	0.2039	0.136	−1.65	.115
Competition toward focal females from						
All others	1.2061	0.478	0.3921	0.391	−0.96	.357
Adult males	0.3598	0.208	0.5548	0.092	−1.77	.092
Adult females	0.3909	0.347	0.3656	0.857	0.18	.857
Juveniles	0.4617	0.351	0.4599	0.198	0.01	.989
Competition by focal females toward						
All others	0.2217	0.293	0.6494	0.344	−3.22	.005*
Adult males	nd	nd	nd	nd	nd	nd
Adult females	0.1699	0.182	0.5156	0.320	−3.43	.002*
Juveniles	0.0574	0.125	0.1760	0.151	−2.07	.055
Wounds and injuries sustained by focal females						
	2.5714[a]	2.992[a]	1.0000[b]	1.134[b]	1.35	.222

†The rates of aggressive, submissive, and competitive interactions and frequencies of injuries are compared for females carrying male and female fetuses. The means and standard deviations of the rates of interactions for females carrying male and female fetuses are given in columns 1–4. The values (t) and significance (*P*) of the t-test statistics are listed in columns 5 and 6. * indicates that differences are significant at the .05 level.
[a]n = 7.
[b]n = 15.

carrying female fetuses, not females carrying male fetuses, who appeared to elicit the most fear from other members of their groups and to compete most actively for resources.

Patterns of aggression, submission, and competition generally appeared to be very similar in the first and second half of gestation (Table II). The effects of fetal sex upon the rates of aggression and competition received by pregnant females and upon the rates of submission given by pregnant females toward others did not approach significance in either the first or second halves of pregnancy. Thus, there was little evidence that females carrying female fetuses were more vulnerable to harassment than females carrying male fetuses during either the first or the second half of pregnancy.

TABLE II. Effects of Fetal Sex During the First and Second Halves of Pregnancy on Rates of Interaction†

	First half of pregnancy						Second Half of Pregnancy					
	Male fetus (n = 8)		Female fetus (n = 16)				Male fetus (n = 8)		Female fetus (n = 17)			
	Mean	sd	Mean	sd	t	P	Mean	sd	Mean	sd	t	P
Aggression toward focal females from												
All others	0.1725	0.185	0.2439	0.238	−0.81	.430	0.3342	0.315	0.2550	0.228	0.64	.537
Adult males	0.0666	0.083	0.0773	0.071	−0.31	.760	0.0910	0.082	0.0950	0.124	−0.09	.926
Adult females	0.0352	0.099	0.0795	0.121	−0.96	.353	0.0857	0.137	0.0722	0.098	0.25	.806
Juveniles	0.0344	0.068	0.0751	0.145	−0.94	.360	0.1574	0.193	0.0879	0.126	0.93	.375
Aggression by focal females toward												
All others	0.1690	0.348	0.1721	0.186	−0.02	.982	0.1120	0.216	0.1634	0.151	−0.61	.557
Adult males	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Adult females	0.1852	0.340	0.0704	0.093	0.94	.377	0.0117	0.033	0.0718	0.088	−2.46	.022*
Juveniles	0.0080	0.023	0.0819	0.121	−2.36	.031*	0.1003	0.189	0.0916	0.098	0.12	.906
Submission toward focal females from												
All others	0.3692	0.427	1.0008	0.901	−2.33	.029*	0.4015	0.606	0.8692	0.639	−1.77	.098
Adult males	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Adult females	0.3453	0.389	0.8512	0.751	−2.17	.041*	0.2935	0.403	0.7306	0.518	−2.30	.034*
Juveniles	0.0239	0.068	0.1391	0.189	−2.18	.041*	0.1081	0.216	0.1320	0.169	−0.28	.787
Submission by focal females toward												
All others	1.8844	1.133	1.2904	0.752	1.34	.209	1.1317	0.670	1.3810	0.727	−0.84	.412
Adult males	0.6729	0.406	0.5801	0.385	0.54	.601	0.4728	0.328	0.6764	0.286	−1.51	.157
Adult females	1.1643	1.191	0.5783	0.535	1.33	.219	0.4708	0.231	0.4047	0.540	0.38	.710
Juveniles	0.0473	0.072	0.1190	0.111	−1.91	.071	0.1881	0.157	0.2878	0.225	−1.28	.215
Competition toward focal females from												
All others	1.4135	1.922	1.6818	1.248	−0.36	.727	1.2118	0.410	1.3796	0.406	−0.85	.406
Adult males	0.0666	0.083	0.0773	0.071	−0.31	.760	0.0910	0.082	0.0950	0.124	−0.09	.926
Adult females	0.0352	0.099	0.0795	0.121	−0.96	.353	0.0857	0.137	0.0722	0.098	0.25	.806
Juveniles	0.0344	0.068	0.0751	0.145	−0.94	.360	0.1574	0.193	0.0879	0.126	0.93	.375
Competition by focal females toward												
All others	0.3500	0.323	0.8541	1.042	−1.77	.092	0.1868	0.274	0.7709	0.491	−3.81	.001*
Adult males	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Adult females	0.1852	0.340	0.0704	0.093	0.94	.377	0.0117	0.033	0.0718	0.088	−2.46	.022*
Juveniles	0.0080	0.023	0.0819	0.121	−2.36	.031*	0.1003	0.189	0.0916	0.098	0.12	.906*

†The rates of aggressive, submissive, and competitive interactions are compared for females carrying male and female fetuses during the first and second halves of their pregnancies. Other conventions as in Table I.

TABLE III. Effects of Maternal Rank on Rates of Interaction†

	Relationship to rank		Male fetus (n = 8)		Female fetus (n = 17)		Residual rate	
	r	*P*	Mean	sd	Mean	sd	t	*P*
Submission by all others toward focal females	.8190	.001	−0.1044	.197	0.0491	0.460	1.17	.255
Submission by adult females toward focal females	.8097	.001	0.0495	0.378	−0.1051	0.154	−1.45	.160
Competition by focal females toward all others	.6787	.001	−0.1513	0.146	0.0712	0.302	−2.48	.021*
Competition by focal females toward adult females	.7833	.001	0.0544	0.259	−0.1156	0.128	−2.20	.039*
Competition by focal females toward juveniles	.4406	.014	0.0210	0.153	−0.0446	0.081	−1.40	.175

†For cases in which fetal sex was significantly associated with rates of interactions, the values of the correlations between maternal rank and rates of interaction are given. The mean values of residuals from the linear regression between maternal rank and rates of interaction for females carrying male and female fetuses are given in columns 3 and 5. Results of t-tests that assess the significance of these residual differences are given in columns 7 and 8. * indicates that differences are significant at the .05 level.

In contrast, the strength of the effects of fetal sex upon rates of aggression and competition initiated by pregnant females toward others and rates of submission elicited by pregnant females from others did vary to some extent over the course of pregnancy. In three cases, the effect of fetal sex achieved significance during the first half of pregnancy but not during the second half of pregnancy, and in three cases the opposite pattern held. Thus, there was no consistent evidence that the effects of fetal sex upon rates of harassment toward others were more pronounced during the second half of pregnancy than during the first half of pregnancy.

In summary, none of the three predictions about the effects of fetal sex upon maternal behavior derived from observations of captive pigtailed macaques were supported by observations of pregnant baboons in Amboseli. Fetal sex was generally unrelated to the rate at which pregnant females were wounded and harassed. Fetal sex did influence the rate at which pregnant females initiated competitive encounters and elicited submission from other members of their groups. However, it was females carrying female fetuses, not females carrying male fetuses, who were responsible for the highest rates of these interactions. Finally, there was no evidence that the effects of fetal sex were more pronounced during the second half of pregnancy than during the first half of pregnancy. There were several cases in which the effects of fetal sex were significant during one-half of pregnancy and not the other. However, there was no consistent tendency for the effects of fetal sex to be more pronounced during the second half of pregnancy than during the first half of pregnancy.

Are the Effects of Fetal Sex Independent of the Effects of Other Variables?

There were several cases in which females carrying female fetuses behaved differently than females carrying male fetuses. For each case in which fetal sex was significantly associated with the rate of interactions, the correlation between maternal rank and the rate of interaction was also significant (Table III). High-ranking females elicited submission from other members of their groups, particularly from other adult females, at higher rates than did lower-ranking females. High-ranking females also directed more competitive encounters toward other adult females and juveniles than did lower-ranking females.

Analyses of the residuals from the regressions between maternal rank and the rates of interactions revealed that fetal sex did not have an independent effect upon the rate of submission received from all others, the rate of submission received from adult females, or the rate of competition directed toward juveniles (Table III). However, females carrying female fetuses initiated significantly more competitive encounters than expected toward all others, and toward adult females, than did females carrying male fetuses. Put another way, the effects of fetal sex upon the rate of competitive encounters among adult females appeared to be independent of variation in maternal rank. Note again, however, that it was females carrying female fetuses, not females carrying male fetuses, who were the most active competitors.

What Other Factors Contribute to Variation in Rates of Aggression, Submission, Competition, and Injuries?

Fetal sex accounted for little of the variation in the rates of aggression, submission, and competition and in the frequency of injuries among pregnant females in Amboseli. The analysis described above suggests that there may be other variables, such as dominance rank, which may influence the behavior of pregnant females and the frequency with which they are injured and wounded. Below, five potentially important variables are evaluated. These variables are female rank, rainfall, group membership, female age or parity, and fetal age.

Female rank. The analysis presented above indicates that dominance rank of pregnant females strongly influenced the rate of submission and competition among pregnant females. A more complete analysis of the effects of maternal rank indicates that it had a pervasive impact upon aggression, submission, competition, and susceptibility to injuries.

High-ranking females tended to be more aggressive, less submissive, and more competitive toward others than did lower-ranking females (Table IV). High-ranking females also elicited more submissive gestures from other adult females than did lower-ranking females. A pregnant female's dominance rank did not consistently influence the rate at which she received aggression or competition from others. In fact, high-ranking females were more likely to be the targets of competitive encounters initiated by adult males and less likely to be the targets of competitive encounters initiated by adult females than were lower-ranking females. Finally, high-ranking females were wounded and injured significantly less often than their lower-ranking peers.

Rainfall. Cumulative rainfall, the total amount of rainfall recorded during the months in which each pregnant female was observed, was highly correlated with the rates of submissive gestures directed by pregnant females toward adult males, adult females, juveniles, and all other group members combined (Table V). That is, females whose pregnancies spanned the driest periods performed submissive gestures at the highest rates. However, cumulative rainfall had no consistent impact upon the rates of aggression or competition given or received by pregnant females or upon the rate at which others directed submissive gestures toward pregnant females. Cumulative rainfall was also unrelated to the frequency with which females were injured and wounded.

Fetal age. The rate at which aggression was received from others significantly increased with increasing fetal age (number of days since the onset of deturgescence), while the rate of submission directed toward others increased with increasing fetal age (Table VI). The correlation between fetal age and the rate of submission directed toward pregnant females also approached significance. Thus, as their fetuses matured, pregnant females were harassed more often and were more submissive to others.

TABLE IV. Effects of Female Rank on Rates of Interaction†

	n = 25	
	r	*P*
Aggression toward focal females from		
All others	−.2111	.155
Adult males	.1291	.269
Adult females	−.2710	.095
Juveniles	−.1323	.264
Aggression by focal females toward		
All others	.6978	.001*
Adult males	nd	nd
Adult females	.4776	.008*
Juveniles	.6274	.001*
Submission toward focal females from		
All others	.8190	.001*
Adult males	nd	nd
Adult females	.8097	.001*
Juveniles	.7434	.001*
Submission by focal females toward		
All others	−.2823	.086
Adult males	.2891	.081
Adult females	−.5693	.001*
Juveniles	.0631	.382
Competition toward focal females from		
All others	.1375	.256
Adult males	.6706	.001*
Adult females	−.5789	.001*
Juveniles	.1212	.282
Competition by focal females toward		
All others	.6787	.001*
Adult males	−.0811	.350
Adult females	.6833	.001*
Juveniles	.4406	.014*
Wounds and injuries sustained by focal females	−.3830[a]	.039*[,a]

†The values (r) and significance (*P*) of the correlations between maternal dominance rank and the rates of aggression, submission, and competition to and from pregnant females and the frequency of injuries sustained by pregnant females are given. * indicates that differences are significant at the .05 level.
[a]n = 22.

Group membership. Group membership has a limited effect upon rates of aggression and competition (Table VII). Pregnant females in Hook's Group received more aggression from adult females than did pregnant females in Alto's Group. The rate of aggression initiated by pregnant females in Hook's Group, particularly toward juvenile females, was also higher than the rate of aggression initiated by pregnant females in Alto's Group. In contrast, juveniles directed higher rates of competitive encounters toward pregnant females in Alto's Group than toward pregnant females in Hook's Group. The members of Alto's Group were wounded and injured significantly more often than were the members of Hook's Group.

Female age and parity. In this population, female age and parity are closely related ($r = .9203$, $P < .001$). The strength of this relationship makes it impossible to distinguish the effects of parity from the effects of maternal age. Variables that are correlated with maternal age are bound to be correlated with maternal parity as well. To avoid redundancy, only the effects of maternal parity are reported below.

TABLE V. Effects of Cumulative Rainfall on Rates of Interaction†

	n = 25		
	r		P
Aggression toward focal females from			
All others	−.2332		.131
Adult males	.2749		.092
Adult females	−.2410		.123
Juveniles	−.3257		.056
Aggression by focal females toward			
All others	−.0839		.345
Adult males	nd		nd
Adult females	−.0121		.477
Juveniles	.0290		.445
Submission toward focal females from			
All others	−.0125		.476
Adult males	nd		nd
Adult females	−.0093		.482
Juveniles	−.0399		.425
Submission by focal females toward			
All others	−.5157		.004*
Adult males	−.4548		.011*
Adult females	−.3663		.036*
Juveniles	−.4421		.013*
Competition toward focal females from			
All others	−.2318		.132
Adult males	.0238		.455
Adult females	−.1535		.232
Juveniles	−.2549		.109
Competition by focal females toward			
All others	.0536		.400
Adult males	.2623		.103
Adult females	−.0131		.475
Juveniles	.0893		.336
		(n = 22)	
Wounds and injuries sustained by focal females	−.1822		.209

†The values (r) and significance (*P*) of the correlations between the amount of cumulative rainfall and the rates of aggression, submission, and competition to and from pregnant females and the frequency of injuries sustained by pregnant females are given. * indicates that differences are significant at the .05 level.

TABLE VI. Effects of Fetal Age on Rates of Interaction†

	n = 419	
	r	P
Aggression toward focal females from all others	.1252	.005*
Aggression by focal females toward all others	.0142	.386
Submission toward focal females from all others	.0782	.055
Submission by focal females toward all others	.2476	.001*
Competition toward focal females to all others	.0479	.164
Competition by focal females toward all others	−.0026	.479

†The vales (r) and significance (*P*) of the correlations between fetal age and the rates of aggression, submission, and competition to and from pregnant females and the frequency of injuries sustained by pregnant females are given. * indicates that differences are significant at the .05 level.

TABLE VII. Effects of Group Membership on Rates of Interaction†

	Alto's Group (n = 16)		Hook's Group (n = 9)			
	Mean	sd	Mean	sd	t	*P*
Aggression toward focal females from						
All others	0.2087	0.132	0.3760	0.268	−1.76	.109
Adult males	0.0873	0.071	0.0740	0.058	0.51	.616
Adult females	0.0374	0.050	0.1631	0.138	−2.63	.027*
Juveniles	0.0734	0.075	0.1330	0.159	−1.06	.314
Aggression by focal females toward						
All others	0.1030	0.143	0.2387	0.103	−2.73	.012*
Adult males	nd	nd	nd	nd	nd	nd
Adult females	0.0577	0.072	0.0812	0.058	−0.89	.385
Juveniles	0.0510	0.089	0.1285	0.090	−2.08	.054*
Submission toward focal females from						
All others	0.5744	0.556	1.0521	0.831	−1.54	.149
Adult males	nd	nd	nd	nd	nd	nd
Adult females	0.4945	0.464	0.8505	0.663	−1.43	.178
Juveniles	0.0715	0.101	0.2016	0.195	−1.86	.091
Submission by focal females toward						
All others	1.2564	0.493	1.4506	0.819	−0.65	.530
Adult males	0.5672	0.230	0.7215	0.211	−1.70	.106
Adult females	0.4908	0.314	0.5610	0.613	−0.32	.755
Juveniles	0.1928	0.115	0.1564	0.149	0.63	.537
Competition toward focal females from						
All others	1.3527	0.427	1.2968	0.430	0.31	.758
Adult males	0.4414	0.072	0.5830	0.116	−1.03	.318
Adult females	0.3834	0.294	0.3565	0.265	0.23	.817
Juveniles	0.5258	0.274	0.3444	0.148	2.15	.043*
Competition by focal females toward						
All others	0.4253	0.364	0.6676	0.380	−1.55	.140
Adult males	nd	nd	nd	nd	nd	nd
Adult females	0.3698	0.346	0.4676	0.288	−0.76	.459
Juveniles	0.0990	0.105	0.2075	0.199	−1.52	.158
Wounds and injuries sustained by focal females	2.0714[a]	2.303[a]	0.5000[b]	0.535[b]	2.44	.027*

†The rates of aggressive, submissive, and competitive interactions and frequencies of injuries are compared for members of Alto's Group and Hook's Group. Other conventions as in Table I. * indicates that differences are significant at the .05 level.
[a]n = 14.
[b]n = 8.

Maternal parity had a limited impact upon the rates of aggression, submission, and competition involving pregnant females. Multiparous females initiated less aggression toward females and competition toward juveniles and received less competition from adult females and juveniles than did females of lower parities (Table VIII). Maternal parity was uncorrelated with the number of injuries sustained by pregnant females.

DISCUSSION

Analysis of patterns of injury, aggression, submission, and competition among pregnant yellow baboons in Amboseli National Park reveals little evidence that fetal gender influenced maternal aggressivity or maternal susceptibility to injury and harassment. There is no consistent evidence that the effects of fetal gender were

TABLE VIII. Effects of Maternal Parity on Rates of Interaction†

	n = 25	
	r	*P*
Aggression toward focal females from		
All others	.0363	.432
Adult males	.1719	.206
Adult females	−.1319	.265
Juveniles	.1382	.255
Aggression by focal females toward		
All others	−.2047	.163
Adult males	nd	nd
Adult females	−.3227	.058
Juveniles	−.1625	.219
Submission toward focal females from		
All others	−.0912	.332
Adult males	nd	nd
Adult females	−.0777	.356
Juveniles	−.1678	.211
Submission by focal females toward		
All others	−.0756	.360
Adult males	−.1446	.245
Adult females	−.0157	.470
Juveniles	−.0542	.398
Competition toward focal females from		
All others	−.7120	.001*
Adult males	−.1748	.202
Adult females	−.3566	.040*
Juveniles	−.5678	.002*
Competition by focal females toward		
All others	−.2942	.077
Adult males	nd	nd
Adult females	−.2171	.149
Juveniles	−.4169	.019*
Wounds and injuries sustained by focal females	.2880[a]	.097[a]

†The values (r) and significance (*P*) of the correlations between maternal parity and the rates of aggression, submission, and competition to and from pregnant females and the frequency of injuries sustained by pregnant females are given. * indicates that differences are significant at the .05 level.
[a]n = 22.

more pronounced during the second half of pregnancy than during the first half of pregnancy. While fetal gender does appear to influence rates of competition among pregnant baboon females, it was females carrying female fetuses who appeared to initiate competitive encounters at the highest rates, not females carrying male fetuses. Thus, these data are not consistent with evidence that captive pigtailed macaques carrying female fetuses are more vulnerable to harassment than females carrying male fetuses [Sackett, 1981; Sackett et al, 1975a,b].

There are a number of reasons why patterns observed among the Amboseli baboons might differ from patterns observed in the pigtailed macaque colony. First, there may be species-specific differences between baboons and pigtailed macaques in the ability to discriminate fetal gender. Moreover, differences may arise because these populations live under radically different demographic and environmental conditions. The pigtailed macaques are maintained in 25–50-square-foot enclosures that house one adult male and six to twelve females. The Amboseli baboons live in large, multimale multifemale groups and range freely over large areas. These disparate ecological and demographic conditions may somehow influence the magnitude of the impact of fetal gender upon pregnant females' susceptibility to harassment. It is also possible that the smaller size of the sample of pregnant females may obscure the underlying pattern of results. This seems unlikely because the sample was large enough to reveal significant relationships between other variables and rates of harassment and competition and the frequency of injuries.

Finally, the relationship between maternal rank and infant gender observed among Amboseli baboons may obscure the relationship between fetal gender and susceptibility to harassment and injury. Since the majority (11/17) of the mothers of females were high ranking, their status might be expected to protect them from aggression. However, maternal dominance rank is not correlated with the rate of aggression directed toward pregnant females by other members of their groups. Furthermore, low-ranking females carrying male fetuses sustained more injuries than did low-ranking females carrying female fetuses. Four low-ranking mothers of females were wounded a total of four times while seven low-ranking mothers of males were wounded a total of 17 times.

Several interesting results emerge from the investigation of variables other than fetal gender that influence patterns of aggression, submission, competition, and injuries among pregnant females. It is not surprising that female dominance rank has a pervasive impact upon these kinds of behaviors. High-ranking females are able to dominate a larger number of other individuals than are lower-ranking females and may, therefore, have more opportunities to harass, intimidate, and displace others.

Amboseli is a highly seasonal environment in which rainfall is concentrated during the "short rains," which typically begin in November or December and end in January, and the "long rains," which normally fall between March and May [Altmann, 1980]. In general, rainfall appears to create more favorable conditions for pregnant females. This is reflected in the facts that during the wet season pregnant females spent less time feeding and more time resting, that the diversity of their diet increased, and that they spent more time in proximity to other individuals [Silk, unpublished manuscript].

Available evidence suggests that the intensity of competition over resources is generally more intense during the dry season than during the wet season [Post, 1982]. Thus, it is somewhat surprising that rainfall influenced the rates of submissive gestures initiated by pregnant females toward others but did not affect the rates of aggression and competition to or from pregnant females. Perhaps females avoided harassment during the dry season by spending more time alone or forestalled aggressive and competitive acts from others by initiating submissive interactions toward them.

It is notable that pregnant females in Hook's Group initiated more aggressive interactions than did pregnant females in Alto's Group although females in Hook's Group sustained fewer wounds than females in Alto's Group. The relatively high frequency of aggression in Hook's Group may be related to the fact that females in Hook's Group spent significantly more time in proximity to other members of their groups than did females in Alto's Group [Silk, unpublished data]. The relatively high frequency of injuries sustained by pregnant females in Alto's Group may be related to substantial changes in female dominance rank that occurred during the study group. Instability in female rank relationships was associated with periods of intense fighting among females. Many females were wounded during these encounters [Samuels et al, 1987].

As their pregnancies progressed, females received more aggression and directed more submissive gestures toward others. This occurs despite the fact that females spent progressively less time in proximity to others as their fetuses matured [Silk, unpublished data]. Harassment during pregnancy might be an effective form of reproductive competition if it reduces the viability of the fetus or the mothers' ability to provide care after parturition. The increase in aggression during the late stages of pregnancy observed here is inconsistent with Wasser's [1983] contention that aggression was likely to be focused upon females in the early stages of their pregnancies when "reproductions are most easily inhibited" (p 379). However, it is also possible that the impact of harassment upon females or their fetuses is greater during late stages of pregnancy than during early stages of pregnancy. The relationship between harassment, fetal age, and subsequent reproductive outcome deserves further investigation.

CONCLUSIONS

1. The gender of the fetus did not influence (a) the rates of aggression, or competition received by pregnant baboon females, (b) the rate at which pregnant females submitted to others, or (c) the frequency with which pregnant females were injured.
2. Females carrying female fetuses elicited more submission and initiated more competition than did females carrying male fetuses.
3. The strength of the effects of fetal gender upon rates of aggression, submission, or competition were not consistently more pronounced during the second half of pregnancy than during the first half of pregnancy.
4. High-ranking pregnant females were generally more aggressive and competitive, and less submissive than were lower-ranking pregnant females.
5. Cumulative rainfall during pregnancy did not consistently influence rates of aggression or competition, but females whose pregnancies spanned the driest periods performed submissive gestures at the highest rates.
6. As their fetuses became older, pregnant females received progressively more aggression from other members of their groups and initiated progressively more submission toward others.

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