**American Journal of Primatology 56:43–56 (2002)**

# Information Content of Female Copulation Calls in Yellow Baboons

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In a wide variety of animal species, females produce vocalizations just before, during, or immediately after copulation. Observational and experimental evidence indicates that these copulation calls are sexually selected traits, functioning to promote competition between males for access to the calling female. In this paper, we present an acoustic analysis of variation in the form of copulation calls of female yellow baboons, *Papio cynocephalus cynocephalus*. In particular, we examine whether information about three factors—the calling female's reproductive state, the occurrence or absence of ejaculation, and the dominance rank of the mating male—is encoded in call structure and hence is potentially available to male receivers attending to the signal. Although several features of copulation calls were correlated with each of these factors, when all three were included in multiple regressions only reproductive state and rank of the mating male had independent effects on call form. These findings indicate that female copulation calls in this species signal information about the proximity to ovulation of the calling female and also the relative competitive strength of her mating partner. Am. J. Primatol. 56:43–56, 2002. © 2002 Wiley-Liss, Inc.

**Key words: copulation call; communication; sexual selection; baboon; *Papio cynocephalus cynocephalus***

## INTRODUCTION

Copulation calls are loud, distinctive vocalizations produced immediately before, during, or just after copulation. These calls are found in a wide range of animal species (e.g., African elephants (*Loxodonta africana*) [Poole et al., 1988], lions (*Panthera leo*) [Schaller, 1972], and elephant seals (*Mirounga angustirostris*) [Cox & LeBoeuf, 1977]). Although in some species only the male produces a copu-

Contract grant sponsor: Biotechnology and Biological Sciences Research Council; Contract grant number: Ref 94306525; Contract grant sponsor: Chicago Zoological Society; Contract grant sponsor: U.S. National Science Foundation; Contract grant number: IBN 9729586 and predecessors; Contract grant sponsor: Natural Environment Research Council; Contract grant number: GR9/1191.

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Received 21 November 2000; revision accepted 10 September 2001

**DOI 10.1002/ajp.1062**

lation call, more commonly it is the female that calls, either alone or in conjunction with the male. Female copulation calls are found in a wide variety of primate species [Hamilton & Arrowood, 1978; Hauser, 1996; Semple, 1998a]. While there is little empirical evidence relating to the function of this signal, it has been hypothesized that female copulation calls among primates are sexually selected traits, functioning to promote competition between males for access to the calling female [e.g., O'Connell & Cowlishaw, 1994; Henzi, 1996; Semple, 1998b].

Two potential benefits to females of competition incitement have been proposed. The first is that these vocalizations provide the caller with a mechanism of indirect mate choice. It has been hypothesized, for example, that copulation calls advertise the increasing probability of conception occurring and incite the dominant male to initiate his consort behavior, with the result that the female is mated only by the alpha male during the most likely period of conception [Henzi, 1996]. The second proposed benefit to females of calling is that copulation calls incite males to compete for consortships, such that the rate of consort takeover is increased around the time of ovulation, and sperm competition occurs [O'Connell & Cowlishaw, 1994]. It is important to note that these two proposed benefits to females of copulation calling—indirect mate choice and promotion of sperm competition—are not necessarily alternatives; both might occur. For example, playback experiments have shown that in Barbary macaques (*Macaca sylvanus*) females increase the number of copulations they receive by copulation calling, and, as a result of a male-rank-based difference in response to this signal, indirectly select for the strongest males as mating partners [Semple, 1998b].

It is important to ask what information, in addition to the fact that a copulation is occurring, is available to males in the structure of female copulation calls. There are three key factors of interest in this context. First, males might be expected to attend to specific information revealing the female's reproductive state (i.e., her proximity to ovulation), due to the higher probability of obtaining a successful fertilization around the time when ovulation occurs. Second, males might also attend to information revealing whether ejaculation has occurred, as this could indicate the intensity of sperm competition that they are likely to face should they later mate with the female. Finally, particularly during the time when the female is being consorted, males may be expected to look for clues as to the dominance rank of the male that is mating with the female. This information would be important when assessing the resource-holding potential of the female's current sexual partner, and hence the likelihood of a consort takeover attempt proving successful.

In order to investigate whether information on the three characters discussed above is actually available to males in female copulation calls, it is crucial to acknowledge that their effects on call form are unlikely to be independent. If, for example, calls given by females are found to be longer as ovulation approaches, this may be due to reproductive state per se, or to a difference in the proportion of ejaculatory mounts and/or a change in the dominance rank of mating males over this time. While there is evidence in the literature that the frequency of utterance and length of female primate copulation calls are related to the calling female's reproductive state, the occurrence of ejaculation, and the dominance rank of the mating male (see below), such studies have failed to control for the non-independence of these factors and hence have failed to examine whether call form is directly affected by, rather then merely correlated with, each factor.

There is evidence from two studies of chacma baboons (*Papio cynocephalus ursinus*) that the form of female copulation calls is correlated with female reproductive state. In these studies, the size of the sexual swelling has been used as an index of reproductive state. Hormonal studies and controlled mating experiments provide some evidence that the size of the sexual swelling is indeed a reasonably accurate indicator of proximity to ovulation [Dixson, 1998]. Saayman [1970] found that in chacma baboons the female copulation call occurred more frequently during inflation of the sexual swelling and the period of maximum turgesence than when the sexual swelling was undergoing deturgesence. Working with the same species, O'Connell and Cowlishaw [1994] found that female copulation calls were longer when the sex skin was fully swollen than during its inflation or detumesence.

Evidence that the occurrence of ejaculation is related to both the form of copulation calls of female primates and the frequency with which they are given comes from a number of studies. Deputte and Goustard [1980], for example, found that the copulation calls of female long-tailed macaques (*Macaca fascicularis*) were longer when ejaculation took place. In their study on chacma baboons, O'Connell and Cowlishaw [1994] found that female copulation call length for the same mating pair on a particular day tended to be greater in copulations that terminated in ejaculation; this difference was not statistically significant, however. Collins [1981] found that female yellow baboons were more likely to give a "full vocal response" during copulations in which ejaculation took place than in those not involving ejaculation.

Finally, although no study has yet investigated the effect of the rank of the mating male on copulation call type, there is some evidence that an approximate indicator of rank—the maturational stage of the mating male—is correlated with the form or frequency of utterance of female primate copulation calls. In chacma baboons, Saayman [1970] found that females called less frequently when mating with juveniles than with adults. In the same species, O'Connell and Cowlishaw [1994] found that copulation calls tended to be of greater duration for matings with adult males than with juveniles. Collins [1981] reported that female yellow baboons uttered "full" copulation calls in 63% of matings with juvenile males, but in 80% of matings with adult males.

In this paper, we present the results of an acoustic analysis of the copulation calls of free-ranging female yellow baboons studied in Amboseli National Park, Kenya. This analysis was designed to investigate what information is available to male receivers in the copulation calls of individual females. In previous analyses of this kind [e.g., Collins, 1981; O'Connell & Cowlishaw, 1994] only the length of the call was examined. Here, we analyze a range of call parameters in addition to length in order to investigate whether information is encoded in any of these characteristics. Importantly, we also examine not only the correlation between each aspect of call form on the one hand, and female reproductive state, occurrence of ejaculation, and dominance rank of the mating male on the other, but also investigate whether each of these three factors has an independent effect on call form.

## METHODS

### Study Animals

Yellow baboons live in multimale, multifemale groups, and are nonseasonal breeders. The average length of the menstrual cycle, defined as the interval between successive onsets of deturgesence of the sexual swelling, is 32.5 days [Hausfater, 1975]. Females develop prominent sexual swellings during the menstrual cycle. During the early stages of inflation of the sexual swelling, females are typically mated by juvenile and subadult males [Collins, 1981]. However, as the cycle proceeds and the sexual swelling approaches its maximum, adult males begin to form lengthy consorts (lasting from several hours up to several days) with the female, aggressively excluding the mating attempts of other males [Hausfater, 1975; Collins, 1981].

Females give copulation calls in nearly all matings; this call consists of a rhythmic succession of low-frequency grunts, and typically begins after dismount, during the postcopulation withdrawal. Previous work indicates that the copulation calls of female yellow baboons are individually distinct and retain this individuality throughout the menstrual cycle [Semple, 2001]. Playback experiments further demonstrate that males are able to discriminate between females on the basis of this interindividual variation in the form of copulatory vocalizations [Semple, 2001].

The study animals in this work belonged to two groups of yellow baboons living in Amboseli National Park, Southern Kenya. Members of the two study groups are part of a long-term study of behavior and demography, and are habituated to researchers [Altmann et al., 1996]. The groups—Joy's group and Nzige's group—were the product of a recent fission of a larger group (Lodge group). Both groups acquire a variable proportion of their daily food intake from refuse sites around tourist lodges. All cycling females, and subadult and adult males were individually recognized during this study.

### Recording of Copulation Calls

Copulation calls were recorded ad libitum throughout the menstrual cycles of seven different females, between March and June 1996. Recordings were made using a Sennheiser (High Wycombe, UK) MKH 416T directional microphone (with Sennheiser windshield and Rycote (Stroud, UK) high-wind cover) in conjunction with a Sony TCD-D7 digital audio tape recorder.

### Classification of Copulation Type

**Assessment of the reproductive state of the calling female.** The size of the sexual swelling was used as the measure of female reproductive state. Swelling size of each female was assessed on each day on which recording occurred; swellings were scored according to their absolute distance of protrusion, using the scale employed in the Amboseli Baboon Research Project [for further details, see Hausfater, 1975].

**Classification of copulations according to the occurrence or absence of ejaculation.** Copulations were classified as ejaculatory if the mating male showed a characteristic ejaculatory pause and/or fresh ejaculate was seen on the female's sex skin following dismount, and non-ejaculatory if not. Although some juveniles showed a brief pause at the end of mounts, all copulations by juveniles were considered as non-ejaculatory as no fresh ejaculate was seen on the sex skin after any such mounts, and such males showed no signs of development of secondary sexual characters.

**Assessment of male dominance rank.** The dominance rank of sexually mature males was determined by examining the occurrence of submissive and aggressive behaviors in agonistic encounters between males. Patterns of wins and losses in these encounters were used to assign dominance ranks to males [Hausfater, 1975], with low rank number indicating high status, i.e., rank 1 is the highest rank.

## Acoustic Analysis of Female Copulation Calls

Although copulatory vocalizations have until now always been referred to in the literature as "copulation calls," they should in most cases more correctly be termed "copulation call bouts," comprised of individual "copulation calls." Here, however, we shall continue to employ the ubiquitously utilized term of copulation call to refer to the copulation call bout, and shall refer to the individual copulation calls as "call units," following the terminology of Deputte and Goustard [1980].

Copulation calls were analyzed using a Kay Elemetrics (Lincoln Park, USA) DSP sonograph (model 5500). Narrow band spectrograms, with a sampling rate of 8 KHz, transform size of 512 points, and filter bandwidth of 29 Hz were used for the acoustic analysis. Temporal parameters of calls and call units were measured using time cursors. The peak fundamental frequency of tonal call units was determined with frequency cursors by dividing by two the distance between three harmonics at their highest point. Call units were classified as tonal if at least three harmonics could be distinguished by eye, and atonal if not (see Fig. 1).

The following parameters were assessed for each copulation call: copulation call length, number of calls units in the call, rate of call unit delivery (number of call units uttered per second), mean call unit duration, mean peak fundamental frequency of tonal call units, and percentage of tonal call units per copulation call.

## Analyses

We employed simple linear regressions (SPSS version 7.51) to examine the extent to which female reproductive state (size of the sexual swelling) and male dominance rank predicted the form of copulation calls. We performed six of these bivariate analyses (one for each call parameter) for each female, and then combined the results across females for each parameter using Fisher's technique for combining probabilities [Sokal & Rohlf, 1995]. In this technique, the natural logarithm of the $P$ value for each comparison (i.e., for each female) is calculated, and the sum of ln $P$ determined. The quantity $-2\Sigma \ln P$, which is distributed as $\chi^2$ with $2n$ degrees of freedom, where $n$ is the number of probabilities combined [Sokal & Rohlf, 1995], is then compared with the $\chi^2$ distribution. This allows us to examine the pattern of variation across females while avoiding the problem of nonindependence of the data points from one particular individual. For the analy-

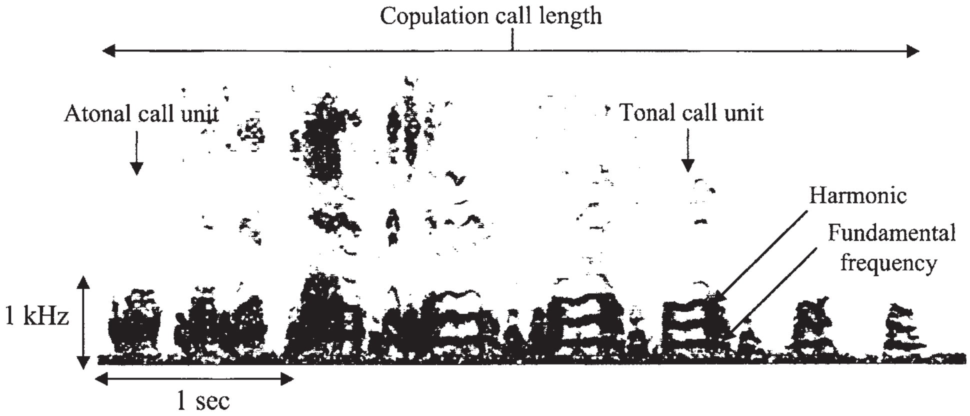

Fig. 1. Spectrogram of the copulation call of a female yellow baboon. This call was given when the female was at peak swelling.

sis of dominance rank only calls given during copulations with subadult or adult males were considered, as juvenile males were not individually recognized and hence it was not possible to assign their dominance rank. We also measured the extent to which occurrence of ejaculation predicted the form of copulation calls using analysis of variance (ANOVA) (SPSS), again employing a separate analysis for each female for the six call parameters, before combining the results across females for each parameter, as described above.

We next performed multiple regression analyses (SPSS) on the calls of each female to examine whether reproductive state, occurrence of ejaculation, and dominance rank of the mating male each had independent effects on copulation call form. For each female, these three variables were included in a multiple regression analysis with each of the six measured call parameters in turn as dependent variables. In order to control for potentially confounding variables in the analysis, the effect of each variable on the six call parameters was assessed after taking account of the variance due to the other two. Results for each parameter were then combined across females, as detailed above. Thus, the analysis examined whether call form was directly and independently affected by reproductive state, occurrence of ejaculation, and dominance rank of the mating male.

As a large number of statistical tests were carried out in these analyses, we controlled the type-I error rate for each independent variable (reproductive state, occurrence of ejaculation, and rank of the mating male) by sequential Bonferroni tests. A Bonferroni adjustment (k) equal to 6 (the number of dependent variables in each analysis) was therefore used [see Rice, 1989, for further discussion of this technique].

## RESULTS

Recordings were made from 554 observed copulations involving seven different females: BET (190 copulations; 96 with subadult/adult males), JUH (127; 96), DOL (81; 7), JOY (78; 43), UMB (40; 39), MWE (22; 13), and JAZ (16; 9). In 537 (96.9%) of these copulations, a vocalization was uttered by the female.

### Relationship Between Copulation Call Form and Reproductive State of the Calling Female, Occurrence of Ejaculation, and Dominance Rank of the Mating Male

**Reproductive state.** When data were combined across females, the reproductive state (swelling size) of the calling female explained a significant amount of variance in five of the six call parameters measured (see Table I): copulation call length ($\chi^2_{[14]} = 80.214$, $P < 0.01$), number of calls units in the call ($\chi^2_{[14]} = 103.090$, $P < 0.01$), mean call unit duration ($\chi^2_{[14]} = 29.198$, $P < 0.05$), mean peak fundamental frequency of tonal call units ($\chi^2_{[14]} = 48.380$, $P < 0.01$), and percentage of tonal call units per copulation call ($\chi^2_{[14]} = 30.672$, $P < 0.05$). Reproductive state did not account for a significant amount of the variance in rate of call unit delivery ($\chi^2_{[14]} = 13.092$, ns). Interestingly, even in the analyses of individual females, two of the six call parameters varied consistently with swelling size. Copulation call length and number of calls units in the call both increased significantly with swelling size for all females except MWE.

**Occurrence of ejaculation.** Combining across all females, calls given during ejaculatory matings differed significantly from calls given during non-ejaculatory matings for three of the six call parameters measured (see Table II): copulation call length ($\chi^2_{[12]} = 60.783$, $P < 0.01$), number of calls units in the call

**TABLE I. Results of Regression Performed to Examine the Relationship Between Reproductive State and Copulation Call Form**

| | Copulation call length | | Number of call units per call | | Rate of call unit delivery | | Mean call unit duration | | Mean peak fundamental frequency of call units | | Percentage of tonal units per copulation call | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | P | B | P | B | P | B | P | B | P | B | P |
| BET | 0.357 | 9.3E-09 | 1.042 | 9.4E-09 | 0.028 | 0.302 | 0.002 | 0.827 | 0.118 | 0.886 | –1.683 | 0.021 |
| DOL | 0.326 | 0.009 | 0.879 | 0.010 | –0.091 | 0.144 | 0.001 | 0.764 | –6.964 | 0.025 | –0.068 | 0.981 |
| JAZ | 0.246 | 0.008 | 1.121 | 0.008 | –0.825 | 0.284 | 0.004 | 0.444 | 5.125 | 0.492 | 8.343 | 0.002 |
| JOY | 0.294 | 0.004 | 1.230 | 0.004 | 0.025 | 0.712 | –0.005 | 0.033 | 5.685 | 2.5E-04 | 0.079 | 0.967 |
| JUH | 0.109 | 0.036 | 0.724 | 5.2E-06 | 0.071 | 0.254 | –0.009 | 0.005 | –2.929 | 0.007 | –1.474 | 0.302 |
| MWE | –0.012 | 0.850 | –0.302 | 0.264 | –0.147 | 0.212 | 0.006 | 0.035 | 13.660 | 0.015 | 2.890 | 0.158 |
| UMB | 0.452 | 0.046 | 1.978 | 0.010 | –0.008 | 0.981 | –0.007 | 0.282 | 8.797 | 0.110 | –13.953 | 0.115 |

Values indicate regression coefficients (B) and significance levels (P).

**TABLE II. Results of ANOVA Performed to Examine the Relationship Between Occurrence of Ejaculation and Copulation Call Form**

| | Copulation call length | | Number of call units per call | | Rate of call unit delivery | | Mean call unit duration | | Mean peak fundamental frequency of call units | | Percentage of tonal units per copulation call | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | P | F | P | F | P | F | P | F | P | F | P |
| BET | $F_{(1,188)}$=20.698 | 9.6E-06 | $F_{(1,188)}$=23.189 | 3.0E-06 | $F_{(1,188)}$=0.014 | 0.905 | $F_{(1,186)}$=1.161 | 0.283 | $F_{(1,185)}$=5.960 | 0.016 | $F_{(1,184)}$=2.632 | 0.106 |
| DOL | — | — | — | — | — | — | — | — | — | — | — | — |
| JAZ | $F_{(1,14)}$=5.032 | 0.042 | $F_{(1,14)}$=9.355 | 0.009 | $F_{(1,10)}$=1.052 | 0.329 | $F_{(1,10)}$=0.003 | 0.959 | $F_{(1,7)}$=2.714 | 0.143 | $F_{(1,8)}$=0.062 | 0.809 |
| JOY | $F_{(1,76)}$=17.092 | 9.1E-05 | $F_{(1,76)}$=23.680 | 6.0E-06 | $F_{(1,76)}$=0.007 | 0.932 | $F_{(1,76)}$=8.534 | 0.005 | $F_{(1,76)}$=5.405 | 0.023 | $F_{(1,76)}$=0.515 | 0.475 |
| JUH | $F_{(1,125)}$=0.672 | 0.414 | $F_{(1,125)}$=5.091 | 0.026 | $F_{(1,124)}$=0.350 | 0.555 | $F_{(1,123)}$=0.416 | 0.520 | $F_{(1,122)}$=7.532 | 0.007 | $F_{(1,124)}$=0.003 | 0.957 |
| MWE | $F_{(1,20}$=2.498 | 0.130 | $F_{(1,20)}$=4.348 | 0.050 | $F_{(1,20)}$=0.024 | 0.878 | $F_{(1,18)}$=0.169 | 0.686 | $F_{(1,16)}$=0.308 | 0.587 | $F_{(1,18)}$=0.276 | 0.606 |
| UMB | $F_{(1,38)}$=4.979 | 0.032 | $F_{(1,38)}$=5.595 | 0.023 | $F_{(1,37)}$=0.402 | 0.530 | $F_{(1,37)}$=0.006 | 0.940 | $F_{(1,36)}$=0.507 | 0.481 | $F_{(1,38)}$=1.122 | 0.296 |

Values indicate F-values with relevant degrees of freedom and significance levels (P).

($\chi^2_{[12]}$ = 79.723, $P < 0.01$), and mean peak fundamental frequency of tonal call units ($\chi^2_{[12]}$ = 32.158, $P < 0.01$). Calls given during ejaculatory and non-ejaculatory matings did not differ significantly for rate of call unit delivery ($\chi^2_{[12]}$ = 5.271, ns), mean call unit duration ($\chi^2_{[12]}$ = 15.390, ns) or percentage of tonal call units per copulation call ($\chi^2_{[12]}$ = 9.926, ns). For two parameters, copulation call length and number of calls units in the call, a clear pattern also emerged within females. For all six females in this analysis (female DOL had no ejaculatory copulations and was excluded from this analysis), calls were longer and contained more units in ejaculatory copulations.

**Male dominance rank.** Male rank explained a significant amount of variance in two of the six call parameters measured (see Table III): copulation call length ($\chi^2_{[12]}$ = 54.958, $P < 0.01$), and number of calls units in the call ($\chi^2_{[12]}$ = 57.975, $P < 0.01$). For all six females in this analysis (female UMB mated with only one male whose rank was known, and was therefore excluded from the analysis), calls were longer and contained more units in copulations with higher-ranked males. Male dominance rank did not explain a significant amount of variance in rate of call unit delivery ($\chi^2_{[12]}$ = 13.924, ns), mean call unit duration ($\chi^2_{[12]}$ = 13.737, ns), mean peak fundamental frequency of tonal call units ($\chi^2_{[12]}$ = 13.874, ns), or percentage of tonal call units per copulation call ($\chi^2_{[12]}$ = 5.940, ns).

### Independent Effects of Reproductive State, Occurrence of Ejaculation, and Dominance Rank of the Mating Male on Copulation Call Form

**Reproductive state.** When the effects of the occurrence of ejaculation and male dominance rank were controlled for statistically, the reproductive state of the calling female explained a significant amount of variance in three call parameters (see Table IV): number of calls units in the call ($\chi^2_{[14]}$ = 45.413, $P < 0.01$), rate of call unit delivery ($\chi^2_{[14]}$ = 43.009, $P < 0.01$) and mean call unit duration ($\chi^2_{[14]}$ = 49.390, $P < 0.01$). Reproductive state did not account for a significant amount of the variance in copulation call length ($\chi^2_{[14]}$ = 18.944, ns), mean peak fundamental frequency of tonal call units ($\chi^2_{[14]}$ = 23.349, ns), or percentage of tonal call units per copulation call ($\chi^2_{[14]}$ = 19.410, ns).

**Occurrence of ejaculation.** When the effects of the other independent variables were controlled for, none of the call parameters measured differed significantly between ejaculatory and non-ejaculatory mounts (see Table IV): copulation call length ($\chi^2_{[12]}$ = 14.745, ns), number of calls units in the call ($\chi^2_{[12]}$ = 13.168, ns), rate of call unit delivery ($\chi^2_{[12]}$ = 16.317, ns), mean call unit duration ($\chi^2_{[12]}$ = 16.382, ns), mean peak fundamental frequency of tonal call units ($\chi^2_{[12]}$ = 22.279, ns), percentage of tonal call units per copulation call ($\chi^2_{[12]}$ = 13.447, ns).

**Male dominance rank.** Male dominance rank explained a significant amount of variance in two of the six call parameters measured when the effects of the other two independent variables were controlled for (see Table IV): copulation call length ($\chi^2_{[12]}$ = 45.528, $P < 0.01$) and number of calls units in the call ($\chi^2_{[12]}$ = 52.458, $P < 0.01$). Male dominance rank did not explain a significant amount of variance in rate of call unit delivery ($\chi^2_{[12]}$ = 9.290, ns), mean call unit duration ($\chi^2_{[12]}$ = 20.036, ns), mean peak fundamental frequency of tonal call units ($\chi^2_{[12]}$ = 11.460, ns), or the percentage of tonal call units per copulation call ($\chi^2_{[12]}$ = 15.362, ns).

## DISCUSSION

This analysis of variation in the copulation calls of female yellow baboons demonstrated that reproductive state, occurrence of ejaculation, and dominance

**TABLE III. Results of Regression Performed to Examine the Relationship Between Male Dominance Rank and Copulation Call Form**

| | Copulation call length | | Number of call units per call | | Rate of call unit delivery | | Mean call unit duration | | Mean peak fundamental frequency of call units | | Percentage of tonal units per copulation call | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | P | B | P | B | P | B | P | B | P | B | P |
| BET | –0.258 | 4.1E-10 | –0.113 | 6.1E-10 | 0.003 | 0.754 | 0.002 | 0.071 | –0.235 | 0.606 | –0.002 | 0.995 |
| DOL | –0.135 | 0.523 | –0.003 | 0.718 | 0.106 | 0.064 | –0.003 | 0.381 | 2.897 | 0.133 | 1.348 | 0.658 |
| JAZ | –0.130 | 0.045 | –0.195 | 0.013 | 0.109 | 0.372 | –0.002 | 0.528 | –0.885 | 0.237 | –0.929 | 0.501 |
| JOY | –0.003 | 0.945 | –0.008 | 0.746 | –0.013 | 0.676 | –0.000 | 0.594 | –0.505 | 0.492 | –1.091 | 0.203 |
| JUH | –0.000 | 0.994 | –0.017 | 0.296 | –0.028 | 0.088 | 0.002 | 0.204 | 0.511 | 0.321 | 0.052 | 0.934 |
| MWE | –0.101 | 0.130 | –0.007 | 0.204 | –0.014 | 0.887 | 0.002 | 0.601 | –6.146 | 0.322 | 0.395 | 0.825 |
| UMB | — | — | — | — | — | — | — | — | — | — | — | — |

Values indicate regression coefficients (B) and significance levels (P).

**TABLE IV. Results of Regression Performed to Examine the Effect of (a) Female Reproductive State, (b) Occurrence of Ejaculation, and (c) Male Rank on Copulation Call Form**

| | | Copulation call length | | Number of call unit per call | | Rate of call unit delivery | | Mean call unit duration | | Mean peak fundamental frequency of call units | | Percentage of tonal units per copulation call | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | B | P | B | P | B | P | B | P | B | P | B | P |
| a) | BET | –0.134 | 0.276 | –0.085 | 0.119 | –0.022 | 0.446 | 0.007 | 0.010 | 1.353 | 0.351 | –0.282 | 0.841 |
| | DOL | 1.359 | 0.125 | 0.710 | 0.060 | 0.005 | 0.972 | –0.020 | 0.028 | –12.000 | 0.102 | –19.764 | 0.215 |
| | JAZ | 0.265 | 0.932 | –3.561 | 0.325 | 1.840 | 0.015 | –0.037 | 0.025 | –0.167 | 0.397 | –19.382 | 0.048 |
| | JOY | 0.364 | 0.039 | 0.265 | 0.007 | 0.090 | 0.493 | –0.006 | 0.177 | –0.534 | 0.858 | 2.912 | 0.401 |
| | JUH | 0.078 | 0.260 | 0.163 | 3.9E-04 | 0.198 | 3.0E-05 | –0.014 | 0.004 | –4.160 | 0.006 | –1.293 | 0.511 |
| | MWE | –0.016 | 0.908 | –0.166 | 0.137 | –0.452 | 0.007 | 0.019 | 0.021 | 17.878 | 0.122 | 3.945 | 0.281 |
| | UMB | –0.307 | 0.260 | 0.348 | 0.157 | –0.189 | 0.676 | 0.011 | 0.181 | 0.340 | 0.953 | 16.956 | 0.122 |
| b) | BET | –0.078 | 0.845 | 0.005 | 0.978 | 0.024 | 0.797 | –0.002 | 0.840 | –13.210 | 0.006 | –2.465 | 0.592 |
| | DOL | — | — | — | — | — | — | — | — | — | — | — | — |
| | JAZ | –0.838 | 0.286 | –0.116 | 0.888 | 1.840 | 0.015 | –0.037 | 0.017 | –0.167 | 0.978 | –19.382 | 0.039 |
| | JOY | 0.565 | 0.051 | 0.323 | 0.041 | –0.158 | 0.462 | –0.006 | 0.404 | 4.063 | 0.412 | –3.086 | 0.588 |
| | JUH | 0.155 | 0.403 | 0.175 | 0.145 | 0.101 | 0.388 | –0.008 | 0.509 | –9.772 | 0.012 | 2.928 | 0.563 |
| | MWE | 0.186 | 0.744 | –0.076 | 0.861 | –0.626 | 0.283 | –0.040 | 0.193 | 13.233 | 0.774 | 20.210 | 0.193 |
| | UMB | 0.464 | 0.170 | 0.305 | 0.311 | –0.404 | 0.472 | –0.007 | 0.489 | –3.269 | 0.647 | –3.118 | 0.815 |
| c) | BET | –0.288 | 1.9E-08 | –0.131 | 9.2E-09 | –0.001 | 0.921 | –0.003 | 0.005 | –0.347 | 0.531 | –0.134 | 0.804 |
| | DOL | –0.220 | 0.308 | –0.095 | 0.233 | 0.052 | 0.342 | –0.002 | 0.111 | 4.000 | 0.088 | 3.125 | 0.452 |
| | JAZ | –0.177 | 0.588 | –0.577 | 0.15 | –0.216 | 0.376 | –0.003 | 0.977 | –0.167 | 0.538 | –11.111 | 0.015 |
| | JOY | –0.049 | 0.292 | –0.025 | 0.324 | –0.015 | 0.663 | –0.000 | 0.929 | –0.341 | 0.670 | –1.049 | 0.259 |
| | JUH | 0.021 | 0.45 | 0.018 | 0.316 | 0.006 | 0.720 | –0.004 | 0.835 | –0.617 | 0.286 | 0.042 | 0.956 |
| | MWE | –0.093 | 0.284 | –0.107 | 0.123 | –0.121 | 0.170 | 0.008 | 0.106 | –2.893 | 0.674 | 2.135 | 0.342 |
| | UMB | — | — | — | — | — | — | — | — | — | — | — | — |
| | | $R^2$ | P | $R^2$ | P | $R^2$ | P | $R^2$ | P | $R^2$ | P | $R^2$ | P |
| d) | BET | 0.350 | 1.1E-08 | 0.337 | 2.7E-08 | 0.008 | 0.855 | 0.103 | 0.018 | 0.092 | 0.030 | 0.003 | 0.957 |
| | DOL | 0.768 | 0.232 | 0.888 | 0.112 | 0.559 | 0.441 | 0.946 | 0.054 | 0.850 | 0.150 | 0.620 | 0.380 |
| | JAZ | 0.581 | 0.193 | 0.694 | 0.093 | 0.761 | 0.052 | 0.780 | 0.042 | 0.510 | 0.275 | 0.894 | 0.007 |
| | JOY | 0.207 | 0.027 | 0.278 | 0.005 | 0.027 | 0.786 | 0.079 | 0.355 | 0.029 | 0.764 | 0.061 | 0.480 |
| | JUH | 0.021 | 0.594 | 0.154 | 0.002 | 0.204 | 1.2E-04 | 0.104 | 0.019 | 0.139 | 0.004 | 0.009 | 0.838 |
| | MWE | 0.225 | 0.492 | 0.417 | 0.165 | 0.617 | 0.029 | 0.490 | 0.095 | 0.410 | 0.215 | 0.189 | 0.576 |
| | UMB | 0.145 | 0.060 | 0.138 | 0.068 | 0.015 | 0.766 | 0.051 | 0.402 | 0.009 | 0.858 | 0.094 | 0.170 |

Values indicate partial regression coefficients (B) and significance levels (P). Table (d) shows the R-squared and significance values for the whole models.

rank of the mating male correlated with a number of specific temporal and acoustic parameters of copulation calls. When the effects of confounding variables were controlled for, however, it was found that only reproductive state and male rank independently had significant effects on call form. These findings indicate that female copulation calls in this species have the potential to provide males with information about the proximity to ovulation of the calling female, and also the relative competitive strength of her mating partner.

The finding that the form of copulation calls was directly affected by female reproductive state suggests that the copulation calls of female yellow baboons provide cues to indicate the proximity of ovulation. Previous work with Barbary macaques, a species in which females give copulation calls but do not form lengthy consortships, demonstrated that males are able to detect variation in the form of female copulation calls given at different stages in the menstrual cycle [Semple & McComb, 2000]. Furthermore, the experimental design utilized in this study ensured that the variation perceived by males was attributable to female reproductive state itself, rather than other potentially confounding factors. The results of the acoustic analysis presented here suggest that in the yellow baboon, also, there is variation in call form over the menstrual cycle which is attributable to female reproductive state and not to other potentially confounding variables.

The finding that the occurrence of ejaculation did not have an effect on call form once the effects of female reproductive state and rank of the mating male were taken into account indicates that ejaculation itself does not lead to a change in the form of the call a female gives, and hence that this information is not available to attending males. This suggests that the correlation between call form and the occurrence of ejaculation found in this study is therefore most likely attributable to the covariance of the occurrence of ejaculation with female reproductive state and/or rank of the mating male. This may well have been the case in previous studies [e.g., Collins, 1981] of female copulation calls, where confounding variables were not controlled for in the analysis.

Finally, this analysis demonstrated for the first time that the dominance rank of the mating male has a direct effect on the nature of female copulation calls of yellow baboons. It was found that after the effects of female reproductive state and the occurrence of ejaculation were taken into account, calls were longer and contained more units during matings with higher-ranked males. This greater investment of energy in calls by females when mated by higher-ranked males is an interesting contrast to the findings of studies on elephant seals [Cox & LeBoeuf, 1977] and feral fowl [Pizzari, 2001] in which females are less, rather than more, likely to give calls during copulations with high-ranking males. While it is unclear why this should be the case, the fact remains that male yellow baboons can gain useful information about the rank of mating competitors from the structure of copulation calls given by females.

The finding that information on reproductive state and dominance rank of the mating male is accurately coded in female copulation calls may be attributable to a simple physical mechanism, in which call form is related to a female's level of stimulation. The stimulation of the anogenital region may be greater when the swelling is larger around the time of ovulation because of an increase in sensitivity of the region at this time. Furthermore, this region may also be more stimulated when the female mates with large-bodied, high-ranked males. This proximate explanation would also account for the observation that female copulation calls have been noted to occur in situations where the anogenital region is stimulated other than during mating, such as when urinating or defecating [e.g., Collins, 1981].

Having established that females do advertise their reproductive state and the dominance rank of the male with whom they are mating in their copulation calls, it is clearly now crucial to investigate the extent to which males can perceive this variation. Playback experiments to investigate this, and to identify the particular cues (or combinations of cues) on which males focus, are now required. More generally, our study should prompt a reexamination of the assumption that females should copulation call more when being mated by low-ranking males; in yellow baboons they actually put more energy into calls when their mating partner is of higher rank.

## ACKNOWLEDGMENTS

We thank Raphael Mututua, Serah Saiyalel, and particularly Kinyua Waterere, who helped with behavioral scoring for dominance determination, and helped S.S. with recognition of individual baboons. Financial support for this study was provided by a studentship to S.S. from the Biotechnology and Biological Sciences Research Council (Ref 94306525), and research grants to J.A. by the Chicago Zoological Society and the U.S. National Science Foundation (IBN 9729586 and its predecessors). The sound analysis was carried out on equipment purchased on a Natural Environment Research Council small project grant to K.McC. (GR9/1191). The Republic of Kenya and the Kenya Wildlife Service kindly provided permission and permits for the Amboseli Baboon Research Project codirected by J.A. and S.C.A.

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