



Individuality and male discrimination of female copulation calls in the yellow baboon

STUART SEMPLE

Institute of Zoology, London

(Received 5 January 2000; initial acceptance 17 February 2000;
final acceptance 17 January 2001; MS. number: 6453)

In a wide variety of animal species, females produce vocalizations just before, during or immediately after copulation. These calls are thought to be sexually selected traits that function to incite males to compete for access to the calling females in such a way that, by calling, females maximize the quality and/or the number of their mating partners. The signalling of individual identity within these vocalizations, in conjunction with male discrimination between females on this basis, would have important implications for their function. I analysed the copulation calls of free-ranging yellow baboons, *Papio cynocephalus cynocephalus*, to examine whether sufficient acoustic cues existed to broadcast information on the individual identity of the caller. Discriminant function analysis indicated that calls could be assigned to the correct female with a high degree of accuracy, both when considering calls given throughout the menstrual cycle and also those given only during the period of likely conception (when the sexual swelling is at its largest). A playback experiment showed that consorting male baboons were able to discriminate the copulation call of their consort female from that of another cycling female. I discuss the implications of individuality of female copulation calls and males' perception of this variability.

© 2001 The Association for the Study of Animal Behaviour

Copulation calls are loud, characteristic vocalizations given immediately prior to, during, or just after copulation and are found in a wide range of animal species. Although in some species only the male produces a copulation call, more commonly it is the female that calls, either alone or in conjunction with the male, for example elephant seals, *Mirounga angustirostris* (Cox & Le Boeuf 1977), African elephants, *Loxodonta africana* (Poole et al. 1988) and lions, *Panthera leo* (Schaller 1972). Female copulation calls are particularly common among the primates (Semple 1998a; see also review by Hauser 1996) and are thought to be sexually selected traits, functioning to alert males to the presence of a receptive female and consequently inciting competition between males in the group for the opportunity to mate with her (Hauser 1996; Semple 1998b).

Two potential benefits to females of inciting competition (i.e. consequences of calling on which sexual selection may act to favour the trait) have been proposed. The first is that, by inciting male–male competition for access to her, a female is able to effect a mechanism of indirect mate choice for the strongest male as a mating partner, as this will be the male most likely to succeed in direct

competitive interactions and thus achieve successful copulations (Oda & Masataka 1992, 1995; Henzi 1996). As a result, copulation calling should enable females to acquire 'good genes' (Andersson 1994) for their offspring. The second potential benefit to females of copulation calling is that, by promoting competition between males, females increase their number of mating partners at the time they are likely to conceive, thus creating an environment for sperm competition (O'Connell & Cowlshaw 1994). The reduced paternity certainty of males in the group resulting from sperm competition may increase male care of infants and reduce the likelihood of infanticidal attacks (O'Connell & Cowlshaw 1994).

By giving a copulation call, females may gain both of these benefits. Copulation calling in female Barbary macaques, *Macaca sylvanus*, for example, not only increases the number of copulations a female receives but also, as a result of a rank-based difference in male response, provides females with a mechanism of indirectly selecting for the strongest males as mating partners (Semple 1998b).

There would be important implications for the function of female copulation calls if females signal individual identity in these calls and males are able to recognize females on this basis. By alerting males not only to her presence and the number of copulations she has received, but also her identity (even when out of sight), a female

Correspondence: S. Semple, Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, U.K. (email: stuart.semple@ucl.ac.uk).

could maximize the benefits of inciting male–male competition, whether these occur as the result of an increase in the quality or number of mating partners, or both. This would be particularly important if a number of females are cycling simultaneously, as occurs in even nonseasonally breeding primate species (e.g. Altmann et al. 1996).

Evidence that vocal signals contain sufficient information for vocal recognition, and that group members are able to discriminate between signallers as a result of variability between individuals' vocalizations, has been documented for a wide variety of primate species (see review by Cheney & Seyfarth 1990). Acoustic analysis of the female copulation calls of the chacma baboon, *Papio ursinus* (Hamilton & Arrowood 1978), sooty mangabey, *Cercocebus torquatus atys* (Gust et al. 1990), Barbary macaque (Todt et al. 1995) and longtailed macaque, *Macaca fascicularis* (Deputte & Goustard 1980) has shown that these calls do contain sufficient cues for individual identification. There is as yet, however, no experimental evidence that males can recognize individual females on the basis of their copulation calls. This discrimination may be more difficult than with other vocalizations in the repertoire, because there are significant periods of time (e.g. pregnancy, postpartum amenorrhoea) during which an individual female does not utter a copulatory vocalization.

I investigated whether the copulation calls of free-ranging yellow baboons, *Papio cynocephalus cynocephalus*, contain sufficient cues for individual identification and I conducted a playback experiment to determine whether male yellow baboons are able to discriminate between females on the basis of their copulation call.

METHODS

Study Animals

I studied two groups of yellow baboons, living in Amboseli National Park, southern Kenya, that are part of a long-term study of behaviour 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 large 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 recognizable. Yellow baboons live in multimale, multi-female groups and are nonseasonal breeders. The average length of the menstrual cycle, defined as the interval between successive onsets of deturgescence 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 to several days) with the female, aggressively excluding the mating attempts of other males (Hausfater 1975; Collins 1981). Although they are rare, extraconsort matings by females do occur, most often with juvenile or

subadult males. 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 (Semple 1998a).

Assessment of Female Reproductive State

The size of the sexual swelling of females was assessed on each day on which recording occurred; swellings were scored according to the absolute scale employed in the Amboseli Baboon Research Project (Altmann & Altmann 1970).

Recording of Copulation Calls

I recorded copulation calls ad libitum throughout the menstrual cycles of eight females, between March and June 1996. I used a Sennheiser MKH 416T directional microphone (with Sennheiser windshield and Rycote high wind cover) in conjunction with a Sony TCD-D7 Digital Audio Tape Recorder.

Assessment of Individuality of Copulation Calls

Acoustic analysis

Although copulatory vocalizations are 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, I continue to use the term copulation call to refer to the copulation call bout, and I refer to the individual copulation calls as 'call units', following the terminology of Deputte & Goustard (1980).

Copulation calls were played on a Sony TCD D10 Digital Audio Tape Recorder, and analysed with a Kay Elemetrics DSP Sonograph (Model 5500). Narrow band spectrograms, with a maximum frequency of 4 kHz and time range of 8 s, were used for the sound analysis. Temporal parameters of calls and call units were measured with time cursors. I assessed the following parameters for each copulation call: call length (s); number of call units in the call; rate of call unit delivery (number of call units/s); mean call unit duration (s); mean maximum fundamental frequency of tonal call units (Hz); and the percentage of tonal call units/copulation call. I determined the maximum fundamental frequency of tonal call units with frequency cursors by dividing by two the distance between three harmonics at their highest point; tonality of calls was assessed visually: call units were classified as tonal if at least three harmonics could be distinguished by eye, and atonal if not. Figure 1 gives an example of a yellow baboon female copulation call.

Statistical analysis

I used discriminant function analysis (SPSS) to determine whether the calls were individually distinct. I analysed calls from 554 observed copulations involving

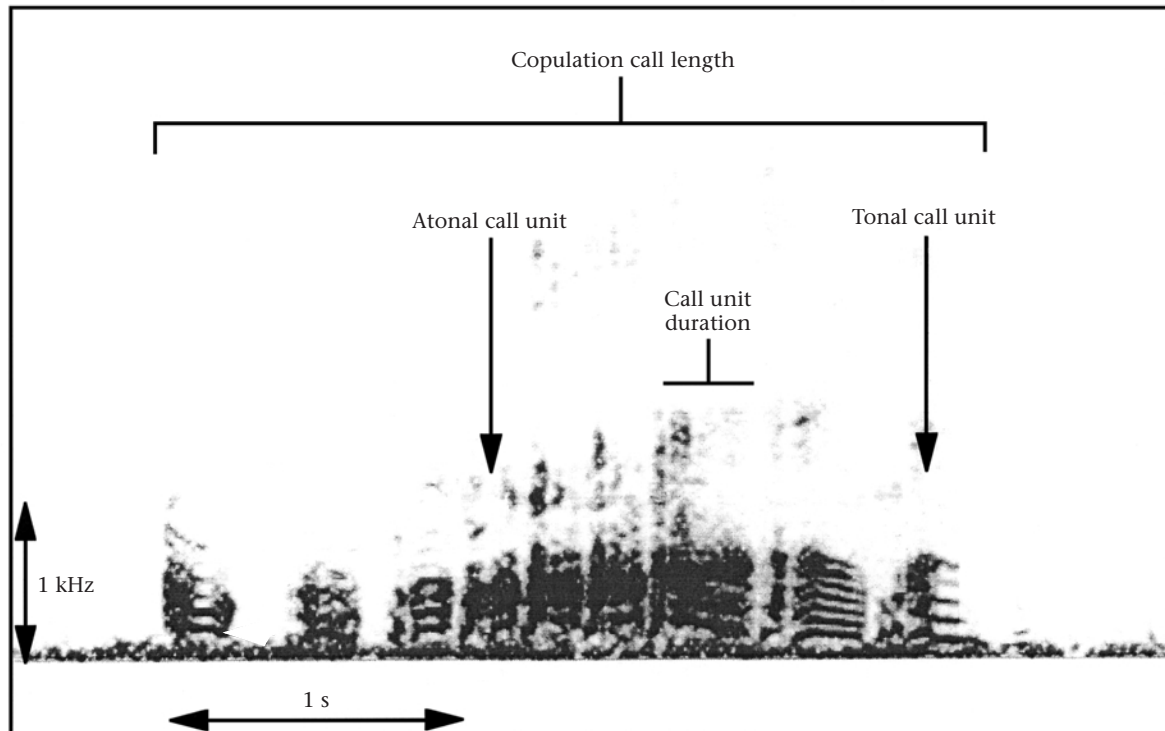


Figure 1. Spectrogram of the copulation call of a female yellow baboon; this call was given when the female was at peak swelling.

seven females: Betty (190 copulations); Juha (127); Dolphin (81); Joy (78); Umbo (40); Mwezi (22); and Jazz (16). Calls from an eighth female (Rita) were not used in the analysis as only two calls were recorded from her. Two analyses were carried out with this data set. In the first I looked for individual variation in calls, using calls given throughout the menstrual cycle (i.e. the full set of calls) and the second involved calls given only when the sexual swelling was at its largest (hereafter referred to as ‘peak swelling’). The playback experiment presented below examined male perception of interindividual variability in calls given at this time.

Playback Experiment

Selection and playback of experimental stimuli

I conducted playback experiments between March and June 1996. As stimuli, I used recordings of calls given at peak swelling during copulations with adult males, in which ejaculation occurred, and in which no other vocalizations were present. The volume of all copulation calls used as playback stimuli was equalized to reach a peak sound pressure level of 64 dB at 5 m. Copulation calls were played back with a Sony TCD-D7 Digital Audio Tape Recorder in conjunction with a NAGRA DSM amplifier-loudspeaker. During all playbacks, the loudspeaker was placed behind vegetation of sufficient height and thickness to conceal a copulating pair, at a mean distance of 9 m (range 7–12 m) from the consort male.

Table 1. The classification of males’ response to playback

Response	Definition
No reaction	Male made no visible reaction to the playback stimulus
Look	Male oriented his head towards the loudspeaker during playback
Approach (walk)	During, or within 5 s of the end of, the playback stimulus, the male stood and walked at least one step towards the loudspeaker
Approach (run)	During, or within 5 s of the end of, the playback stimulus, the male stood and ran towards the loudspeaker
Vocalize	During, or within 5 s of the end of, the playback stimulus, the male produced an audible vocalization

Experimental protocol

I played calls to consorting adult males, when their consort female, and the other female whose call was used as a control stimulus (see below), were out of their sight. This situation arose most often during foraging, particularly in the dense vegetation of palm groves, when the consort pair became separated. During a playback presentation, a female copulation call was played from a loudspeaker concealed in vegetation in the general area in which the consort female was last seen. Playbacks were made ca. 1–3 min after she was last in view. Two calls

Table 2. The mean values for each of the six call parameters for each female for calls given throughout the menstrual cycle and for calls given at peak swelling

Female	Copulation call length (s)	Number of call units	Rate of call unit delivery (No./s)	Mean call unit duration (s)	Mean maximum fundamental frequency of tonal call units (Hz)	Percentage of tonal call units/copulation call
Whole cycle						
Betty	3.08±1.89	8.72±5.52	2.88±0.81	0.23±0.05	194.06±23.65	72.66±21.00
Dolphin	2.27±0.92	6.46±2.53	2.90±0.46	0.23±0.04	113.26±22.79	82.38±17.21
Jazz	0.81±0.80	3.88±3.74	6.11±3.54	0.12±0.02	89.56±6.46	40.56±9.18
Joy	2.82±0.99	8.53±3.38	3.00±0.63	0.19±0.02	148.33±15.28	74.22±17.93
Juha	2.15±0.81	7.06±2.57	3.42±0.95	0.18±0.05	126.05±16.59	57.56±21.67
Mwezi	1.66±0.75	6.36±3.20	4.07±1.40	0.15±0.04	138.94±60.10	44.63±20.67
Umbo	1.71±0.69	6.50±2.38	4.01±1.07	0.15±0.02	168.11±16.53	78.12±26.65
Peak swelling						
Betty	5.79±2.01	16.13±5.59	2.81±0.27	0.22±0.02	200.07±15.07	70.53±17.20
Dolphin	2.36±0.88	6.76±2.57	2.86±0.30	0.23±0.03	111.12±15.43	81.60±13.63
Jazz	1.45±0.67	6.86±3.29	4.80±0.82	0.13±0.02	91.82±4.88	40.29±9.34
Joy	3.67±0.93	11.50±3.12	3.14±0.35	0.19±0.02	147.67±16.43	72.00±16.72
Juha	2.65±0.74	9.23±2.39	3.55±0.50	0.16±0.02	122.23±13.22	58.00±23.00
Mwezi	2.18±0.45	7.20±2.39	3.31±0.95	0.15±0.03	210.60±25.53	45.20±20.83
Umbo	1.70±0.64	6.38±1.97	4.03±1.22	0.15±0.02	166.14±12.00	87.31±16.15

Values are $\bar{X} \pm SD$.

Table 3. Percentage of copulation calls correctly assigned to individual females by discriminant functions

Female	Whole cycle	Peak swelling
Betty	74.7	86.7
Dolphin	84.0	92.0
Jazz	88.9	100.0
Joy	64.1	66.7
Juha	54.0	84.6
Mwezi	11.1	100.0
Umba	84.2	96.6
Calls correctly assigned (%)	65.7	89.6

Analyses were carried out on calls given throughout the menstrual cycle, and the subset of calls given at peak swelling.

were played to each male: one the call of the consort female, the other the call of another cycling female in the group, although the latter did not necessarily show maximal swelling (i.e. this female was not necessarily close to the time of ovulation). The call of the other cycling female served as a control for the call of the consort female and the copulation calls of four females were used at least once in both roles (i.e. as 'consort female' copulation call and 'other female' copulation call) in the experiment. Playbacks of the two calls to a particular male were separated by 1–2 days, and the order of their presentation was randomized. Playbacks were made during eight consortships involving six females and seven males. Where possible, I recorded males' reactions to playbacks with a Sony CCD-TR550E 8 mm video camera. When environmental conditions (e.g. thick vegetation) made video recording impractical, I monitored reactions by eye and with a stopwatch, and noted them in a field notebook. Table 1 gives the classification of males' reactions.

I also followed consort males for 30 min after playback and I used the 'all-occurrence' sampling method (Altmann 1974) to note any aggressive behaviour (as defined in Hausfater 1975, page 21) directed to the consort female.

Statistical analysis

I classified responses of males in the following ascending order of strength: no reaction, look, approach (walk), approach (run), and approach (run) with vocalize. I then compared the strength of response of each subject male for the matched pair of experimental stimuli with a two-tailed sign test.

RESULTS

Acoustic Analysis

Table 2 gives the mean values for each of the six call parameters for each female. Stepwise discriminant function analysis produced six significant functions that discriminated between the calls given throughout the cycle and four for those given at peak swelling. The success rate of classification of calls to a particular individual differed between females (Table 3; Fig. 2).

Playback Experiment

The reaction of males to hearing the playback of the copulation call of their consort female was similar in all eight trials (Table 4): the male looked towards the loudspeaker, then ran towards the source of the vocalization; during this approach, he uttered one or more grunts. Having approached the loudspeaker, he then began scanning or entered the vegetation. The reaction to the

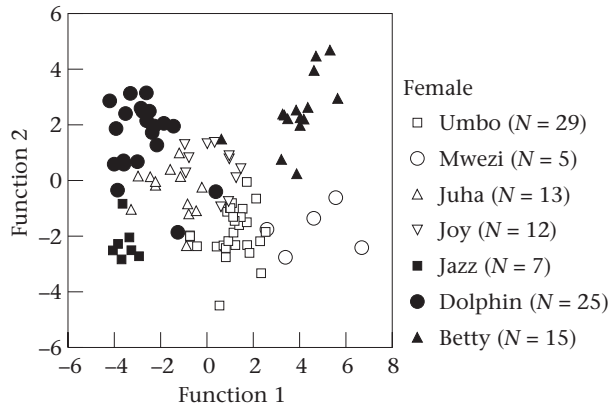


Figure 2. Scatterplot showing separation produced by the first two discriminant functions of the copulation calls given at peak swelling of seven female yellow baboons.

playback of the copulation call of another cycling female was much less marked: only one male approached the source of the vocalization, walking and without vocalizing; of the other seven trials, in six the male looked towards the loudspeaker but did not move, while in one trial there was no noticeable reaction to playback. The reaction of males was therefore stronger after playback of the copulation call of the consort female than after that of another cycling female in all eight matched pairs (sign test, two-tailed: $x=0$, $N=8$, $P<0.01$). On locating the consort female, males sat, stood or walked close to her. No aggression was directed towards the consort female by the consort male during the 30 min after any of the playback presentations.

DISCUSSION

This acoustic analysis indicates that the copulation calls of female yellow baboons vary sufficiently to allow individual recognition. The analysis of calls given both throughout the menstrual cycle and at peak swelling suggested that these calls could be assigned to the correct female with a high degree of accuracy. In addition, the results of the playback experiment showed for the first time that males are able to discriminate between females

as a result of interindividual variability in the form of calls given at peak swelling.

In the playback experiment, males may have responded more strongly to the call of their consort female than to the call of the control female because the former were their consorts per se, or because these females had maximal swellings at the time of playback while the control females did not (although the calls from these control females were recorded at maximal swelling). If the latter explanation is true, it would indicate that the males' response to the vocal signal is tempered by their knowledge of the female's reproductive state, as signalled by the visual cue of the sexual swelling. Whichever is the case, however, the conclusion is the same: consort males are able to discriminate the copulation call of their consort female from that of another female in the group. This recognition ability indicates that males can potentially identify calling females even when the latter are out of sight.

Although this study only showed discrimination of female copulation calls by consort males, it seems likely that other males in the group would also be able to discriminate between group females in this way, owing to the loud volume and individually distinct nature of copulation calls (Hamilton & Arrowood 1978; Collins 1981), and the high frequency of mating by females during the menstrual cycle (Hausfater 1975). This ability would be of importance if, as has been suggested, the copulation calls of female baboons are sexually selected traits, inciting males to compete for access to the calling female. Female signalling of individual identity and perception of this variation by males should result in females maximizing the benefits of effecting indirect mate choice (Oda & Masataka 1992 1995; Henzi 1996; Semple 1998b) and/or promoting sperm competition (O'Connell & Cowlshaw 1994; Semple 1998b). In particular, females would benefit from signalling their identity when other females in the group are cycling simultaneously, as occurs in this species (Altmann et al. 1996; S. Semple, unpublished data).

Although the copulation calls of yellow baboons vary in form over the menstrual cycle (Semple 1998a), my analysis indicates that they still retain their individuality. Discrimination between females should therefore be

Table 4. Reaction of consort males to playback of the copulation call of the consort or another cycling female in the troop (only the strongest reaction is shown in each case)

Consort male	Consort female	Other female	Playback stimulus	
			Consort female	Other female
Nuru	Betty	Joy	Approach (run) and vocalize	No response
Bwana	Umbo	Meta	Approach (run) and vocalize	Look
Mito	Juha	Betty	Approach (run) and vocalize	Look
Nachos	Rita	Juha	Approach (run) and vocalize	Look
Nova	Joy	Juha	Approach (run) and vocalize	Look
Duka	Mwezi	Umbo	Approach (run) and vocalize	Look
Nuru	Juha	Joy	Approach (run) and vocalize	Look
Dacron	Mwezi	Umbo	Approach (run) and vocalize	Approach (walk)

possible throughout the menstrual cycle. Males' ability to distinguish between copulation calls given by a particular female at different stages of the cycle has been shown for Barbary macaques (Semple & McComb 2000) and if male yellow baboons also show this ability, they could use individuality of calls, in conjunction with temporal variation in call form, to assess both the identity and the reproductive state of a particular female.

However, male yellow baboons may also use other signals to assess the proximity of ovulation. One such potential signal is the sexual swelling. Bielert & van der Walt (1982), for example, found that the masturbatory behaviour and serum testosterone concentration of male chacma baboons, *Papio ursinus*, exposed to visual contact with females were linked to sexual swelling size, being greatest when the swelling was at its peak. Vocally signalling individual identity in conjunction with information about reproductive state may serve, however, to amplify the visual signal provided by the sexual swelling. Furthermore, individually identifiable copulation calls will provide males with information about the number of copulations a female has received from other males in the group, information not conveyed by the visual signal.

Although my playback experiment has shown discrimination by males of females from their copulation calls, it did not indicate which aspects of interindividual variability in call form males were using to achieve this. Discrimination could be based on variability in one call parameter; it is perhaps more likely, however, that it relies on a combination of, and interaction between, a number of different call characteristics (Epsmark 1975; Reby et al. 1998). Further playbacks involving artificially modified calls would be necessary to investigate the mechanism of discrimination.

Acknowledgments

This work was carried out as part of my D.Phil. at the University of Sussex. I thank my supervisor, Dr Karen McComb, for advice and support throughout the study and Professor Jeanne Altmann for allowing me to work with the baboons which form part of her long-term study in Amboseli. I am very grateful to Dr Susan Alberts, Raphael Mututua, Serah Saiyalel and particularly Kinyua Waterere, who helped me recognize individual baboons. Dr Karen McComb, Professor Jeanne Altmann and two anonymous referees gave invaluable comments on this manuscript. Financial support for this study was provided by the Biotechnology and Biological Sciences Research Council, U.K. and the University of Sussex. I also acknowledge Amboseli Baboon Project support to Professor Jeanne Altmann by the Chicago Zoological Society and the U.S. National Science Foundation (grants IBN 9422013 & IBN 9729586). The sound analysis was carried out on equipment purchased on a Natural Environment Research Council Small Project Grant to Dr Karen McComb (GR9/1191).

References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–265.
- Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mututua, R. S., Saiyalel, S. N., Wayne, R. K., Lacy, R. C. & Bruford, M. W. 1996. Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences U.S.A.*, **93**, 5797–5801.
- Altmann, S. A. & Altmann, J. 1970. *Baboon Ecology: African Field Research*. Chicago: University of Chicago Press.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Bielert, C. & van der Walt, L. A. 1982. Male chacma baboon (*Papio ursinus*) sexual arousal: mediation by visual cues from female conspecifics. *Psychoneuroendocrinology*, **7**, 31–48.
- Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.
- Collins, D. A. 1981. Behaviour and patterns of mating among adult yellow baboons (*Papio c. cynocephalus* L. 1766). Ph.D. thesis, University of Edinburgh.
- Cox, C. R. & LeBoeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *American Naturalist*, **111**, 317–335.
- Deputte, B. L. & Goustard, M. 1980. Copulatory vocalisations of female macaques (*Macaca fascicularis*): variability factors analysis. *Primates*, **21**, 83–99.
- Epsmark, Y. 1975. Individual characteristics in the calls of reindeer calves. *Behaviour*, **40**, 295–301.
- Gust, D. A., St Andre, E., Minter, C., Gordon, T. & Gouzoules, H. 1990. Female copulatory vocalisations in a captive group of sooty mangabeys (*Cercocebus torquatus atys*). *American Journal of Primatology*, **20**, 196.
- Hamilton, W. J. & Arrowood, P. C. 1978. Copulatory vocalisations of chacma baboons (*Papio ursinus*), gibbons (*Hylobates hoolock*), and humans. *Science*, **200**, 1405–1409.
- Hauser, M. D. 1996. *The Evolution of Communication*. Cambridge, Massachusetts: MIT Press.
- Hausfater, G. 1975. *Dominance and Reproduction in Baboons* (*Papio cynocephalus*): *Contributions to Primatology*, **7**. Basel: Karger.
- Henzi, S. P. 1996. Copulation calls and paternity in chacma baboons. *Animal Behaviour*, **51**, 233–234.
- O'Connell, S. M. & Cowlshaw, G. 1994. Infanticide avoidance, sperm competition and mate choice: the function of copulation calls in female baboons. *Animal Behaviour*, **48**, 687–694.
- Oda, R. & Masataka, N. 1992. Functional significance of female Japanese macaque copulatory calls. *Folia Primatologica*, **58**, 146–149.
- Oda, R. & Masataka, N. 1995. Function of copulatory vocalizations in mate choice by females of Japanese macaques (*Macaca fuscata*). *Folia Primatologica*, **64**, 132–139.
- Poole, J. H., Payne, K., Langbauer, W. R. & Moss, C. J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology*, **22**, 385–392.
- Reby, D., Joacim, J., Lauga, J., Lek, S. & Aulagnier, S. 1998. Individuality in the groans of fallow deer (*Dama dama*) bucks. *Journal of Zoology*, **245**, 79–84.
- Schaller, G. 1972. *The Serengeti Lion: a Study of Predator-Prey Relationships*. Chicago: University of Chicago Press.
- Semple, S. 1998a. Female copulation calls in primates. Ph.D. thesis, University of Sussex.
- Semple, S. 1998b. The function of Barbary macaque copulation calls. *Proceedings of the Royal Society of London, Series B*, **265**, 287–291.
- Semple, S. & McComb, K. 2000. Perception of female reproductive state from vocal cues in a mammal species. *Proceedings of the Royal Society of London, Series B*, **267**, 707–712.
- Todt, D., Hammerschmidt, K., Ansorge, V. & Fischer, J. 1995. The vocal behaviour of Barbary macaques (*Macaca sylvanus*): call features and their performance in infants and adults. In: *Current Topics in Primate Vocal Communication* (Ed. by E. Zimmerman, J. D. Newman & U. Jurgens), pp. 141–160. New York: Plenum.