



Comparing functions of copulation calls in wild olive baboons, *Papio anubis*, using multimodel inference

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ARTICLE INFO

Article history:

Received 22 December 2016

Initial acceptance 20 February 2017

Final acceptance 27 October 2017

MS. number: 16-01091R

Keywords:

copulation call
female choice
male–male competition
model ranking
multi-model inference
olive baboon
Papio anubis
sperm competition

Female copulation calls are species specific, distinct vocal signals sometimes given during or shortly after mating. Despite being common in primates and despite much empirical work, their function remains largely unclear for most species. Here, we used an information-theoretic approach to examine simultaneously three main competing hypotheses for the evolution of copulation calls. Two of the three hypotheses predict that female copulation calls function to incite competition between males, either directly (the male–male competition hypothesis) or indirectly (the sperm competition hypothesis), while the third predicts that females use calls to choose mating partners (the female choice hypothesis). We collected data on copulations of wild female olive baboons in Kibale National Park, Uganda, to compare the relative support for these hypotheses by modelling whether or not females produced copulation calls after mounts. Our analytical approach enabled us to objectively rank models corresponding to the three hypotheses according to how well our data fitted the models. Our data favoured the sperm competition hypothesis over the female choice hypothesis although much variation in calling remained unexplained. The male–male competition hypothesis seems unlikely given our data. We also discuss the possibility that copulation calls have no function, functions not included in our analysis, or that they are multifunctional, a reflection of the species' social evolution history.

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Copulation calls are loud, rhythmic vocalizations given before, during or just after mating. They occur in a wide range of species from African elephants, *Loxodonta africana* (Poole, Payne, Langbauer, & Moss, 1988) to peacocks, *Pavo cristatus* (Yorzinski & Anoop, 2013). In some species, only one sex calls during mating (males: Hauser, 1993; Hsu, Lin, Chen, & Agoramoorthy, 2002; Manno et al., 2007); (females: Semple, 1998; Semple, McComb, Alberts, & Altmann, 2002) while in others both sexes vocalize (Higham et al., 2012).

In primates, copulation calls are mostly found in females where they tend to co-occur with visual signals, that is, exaggerated anogenital swellings (Nunn, 1999). They are common in species that form multimale, multifemale groups where females mate

promiscuously (Maestriperi & Roney, 2005). Despite much interest and empirical work (e.g. Engelhardt, Fischer, Neumann, Pfeifer, & Heistermann, 2012; Pfeifferle, Brauch, Heistermann, Hodges, & Fischer, 2008; reviewed in Maestriperi & Roney, 2005; Pradhan, Engelhardt, van Schaik, & Maestriperi, 2006), the function of female copulation calls still remains debated. Several hypotheses have been proposed, from orgasm synchronization to strengthening the bonds between mating partners (Hamilton & Arrowood, 1978; Pradhan et al., 2006). Despite their function not yet being fully clarified, there is general agreement that copulation calls are vocalizations that allow the mating and surrounding males to gain information about the receptivity of the mating female, which increases her inclusive fitness (Cox & Leboeuf, 1977; Hauser, 1990; Pradhan et al., 2006), for example by inciting competition between males either directly or indirectly.

Below, we describe three major hypotheses that have been put forward in the current literature to explain female copulation calling. Our goal is to test these hypotheses with our study species, olive baboons, using a multimodel inference framework. In contrast

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to traditional null hypothesis testing, the multimodel inference approach does not seek to reject null hypotheses, but compares and ranks different, biologically informed models in terms of their relative explanatory power of the dependent variable, in our case whether or not females produce calls after copulations. Given the complexity of evolutionary processes and the long evolutionary history of primate social systems, the multimodel inference approach is likely to generate more meaningful findings than traditional statistical methods (Burnham, Anderson, & Huyvaert, 2011).

A first main hypothesis (the male–male competition hypothesis) states that copulation calling induces direct male–male competition, by attracting nonconsorting males (for consortship definition see Table 1) to physically interrupt or displace the consorting male, which will then increase the probability of the female mating with another, competitively stronger male (i.e. high-ranking or friendly male; Hamilton & Arrowood, 1978). One prediction of this hypothesis is that female calling behaviour directed towards surrounding, nonconsorting males should vary with the rank or age of the mating partner, factors that are likely to impact on male competitiveness.

Some evidence for the male–male competition hypothesis is found in Japanese macaques, *Macaca fuscata*, where males regularly interrupt copulations if the female has vocalized (Oda & Masataka, 1995). The male–male competition hypothesis is also indirectly supported by evidence that the acoustic structure of copulation calls can provide relatively rich information to other group members. For example, in yellow baboons, *Papio cynocephalus*, copulation calls convey information about the calling female's swelling size (and thus temporal proximity of ovulation), her identity and the rank of the male partner, allowing the surrounding males to make decisions about whether or not to approach and interrupt the ongoing mating event (Semple et al., 2002). In contrast, male long-tailed macaques, *Macaca fascicularis*, however, do not interrupt the mating when females utter copulation calls (Nikitopoulos, Arnheim, van Hooff, & Sterck, 2004). One well-documented exception in nonprimates is elephant seals, *Mirounga angustirostris*, where calling females are more often interrupted by high-ranking males if they are mounted by low-ranking males (Cox & Leboeuf, 1977). However, copulations in elephant seals can last for more than 60 s (Cox & Leboeuf, 1977), which gives ample opportunity for rival males to interrupt copulations. In contrast, primate copulations are typically much shorter (olive baboons 5 s, Y. Bouquet, personal observation; several primates species: <1 min, Dixson, 1987) thereby reducing the possibility of successful interruptions unless the interrupting male is in the direct vicinity of the mating pair.

A second main hypothesis (the sperm competition hypothesis) is that females use copulation calls to induce indirect competition between males because they are primarily interested in obtaining the best sperm, which will enable their sons to inherit competitive sperm (Keller & Reeve, 1995). Females should therefore mate with all available males, including subadult males, whose phenotypic potential is not yet fully displayed. Here, females call to attract and mate with as many males as possible to obtain the best or most compatible sperm for their own genotype. To select the 'best' sperm, females across different species have evolved several mechanisms, including mechanically complex genitalia, chemical and physical barriers or ova that are difficult to penetrate (Keller & Reeve, 1995). In cuis, *Galea musteloides*, females that mated with several males had higher offspring survival than those that mated with a single male (Keil & Sachser, 1998), suggesting direct reproductive consequences of sperm competition. For primates, we are not aware of strong evidence that females gain fitness benefits through sperm competition. However, a number of morphological features in both sexes suggest that sperm competition plays a role (e.g. male testis size/body weight ratio and long vaginal tracts in females, Dixson & Mundy, 1994).

The sperm competition hypothesis has been examined in chacma baboons, *Papio ursinus*, albeit with no clear conclusion. In one study, copulation call duration was longer if females mated with adult males than with subadults or juveniles and, importantly, if adult males ejaculated (O'Connell & Cowlshaw, 1994). However, in other populations (Henzi & Lycett, 1995; Ron, Henzi, & Motro, 1996; Smith, 1986) the majority of matings were with high-ranking males, which were not contested by other males despite female calls, suggesting that inciting sperm competition is not the main function of copulation calls in this species (Henzi, 1996). Instead, Henzi (1996) proposed three alternative hypotheses for the evolution of copulation calls: (1) no functional significance; (2) inciting sperm competition in ancestral populations but currently no longer evolutionarily relevant; and (3) encouraging consort behaviour in high-ranking males to increase their paternity certainty (i.e. female choice hypothesis, see below). However, sperm competition may only play a role in large multimale groups, and some of the studies cited above featured an atypically low number of males (<5), where male takeovers are difficult (Cowlshaw & O'Connell, 1996). One other complexity with the sperm competition hypothesis is that primate sperm is viable over several days, so that male mating success should be analysed over consecutive days, including the pre-oestrous period (Bercovitch, 1989). In Barbary macaques, *Macaca sylvanus*, females appear to influence male ejaculations by adjusting call onset and amplitude or suppressing

Table 1
Definitions of key terms

Term	Definition
Adult male	Individual that displays fully developed secondary sexual characteristics, such as large canines and long neck hair (Altmann, Altmann, Hausfater, & McCuskey, 1977)
Consortship	Adult male 'shows continual attention and awareness of the swelling female, and when one or both animals move so as to maintain close proximity with each other' (Hausfater, 1975, p. 18). The adult male copulates with the female, grooms her frequently and aggressively repulses the takeover attempts of the other nonconsorting males (Ransom, 1981)
Mount	Adult male 'grasps the pelvis of the female, elevates his forequarters over the hind end of the female and clasps the female's ankles with his feet' (Hausfater, 1975, p. 14). The male makes an intromission with pelvic thrusting. It can occur with or without ejaculation. For a video example, see Supplementary material
Female parity	Parous: females that have given birth to an infant (Smuts & Nicolson, 1989); nulliparous: subadult females reaching menarche that have not yet given birth but have full swellings (Smuts & Nicolson, 1989)
Full swelling	Top, middle and sides of the rumps are swollen around the day of ovulation (Higham, MacLarnon, et al., 2008)
Audience	Identities of all the individuals within 10 m of the focal animal
Friendship	Relationship between two individuals characterized by high rate of grooming, close proximity, low rate of aggression and tolerance at food resources (Silk, 2002; Silk et al., 2013)
Habitat visibility	Low: 50–100% tree cover High: 0–50% tree cover

calling behaviour altogether, suggesting a role for sperm competition (Pfefferle et al., 2008).

Another set of studies (Maestripieri, Leoni, Raza, Hirsch, & Whitham, 2005; Todt, Hammerschmidt, Ansorge, & Fischer, 1995) have argued that, in some primates, females have an element of choice in whom they mate with such that (1) females should adjust calling decisions depending on whether mounted by a preferred male or not and (2) calling should induce mate guarding by this preferred partner (the female choice hypothesis). This way, a female can increase the paternity certainty in a single male, who might consequently be more likely to provide paternal care for her offspring or at least be tolerant of them (Buchan, Alberts, Silk, & Altmann, 2003). Here, the call is primarily directed at the male consort partner and the female presumably provides information about her fertility (Maestripieri & Roney, 2005) but the fact that nonconsorting males could also hear the call forces the consort male into mate guarding. Under this hypothesis, females have some control over whose genes their offspring will inherit (Maestripieri & Roney, 2005; Todt et al., 1995). In Guinea baboons, *Papio papio*, females that copulated with the most successful males were also most active in giving copulation calls (Maestripieri et al., 2005). In eastern chimpanzees, *Pan troglodytes schweinfurthii*, females called significantly more with high-ranking than other males, possibly because being found copulating with a low-ranking male could expose the female to male aggression (Townsend, Deschner, & Zuberbühler, 2008).

In this paper, we address these three hypotheses in olive baboons, a species living in multimale, multifemale troops with linear dominance hierarchies among females and males. Group size of olive baboons can range from 30 to more than 90 individuals, with between five and 16 males and seven to 30 females (Ransom, 1981; Rowell, 1966; Strum & Western, 1982). Olive baboons are nonseasonal breeders; females' oestrous cycles last between 30 and 40 days and they are fertile for 5 days (Higham, Heistermann, Ross, Semple, & MacLarnon, 2008; Higham, MacLarnon, Ross, Heistermann, & Semple, 2008; Swedell, 2011). The females develop large swellings and, around the time of ovulation, males seek consortships with them, by shadowing them from a few hours to several days and by aggressively repulsing mating attempts by other nonconsorting males (Bercovitch, 1988). Nonconsorting males follow different strategies to take over the consortship, such as (1) following and (2) harassing the consort couple or (3) forming coalitions with other nonconsorting males (Danish & Palombit, 2014). Previous studies have shown that females produce copulation calls in 10–62% of matings (Hall, 1965; F. Bercovitch, personal communication in ; Pradhan et al., 2006). Typically, females mate multiple times with different males across their cycle, generating a high consort turnover in this species (Ransom, 1981; Strum, 1982).

In olive baboons, females and males form long-lasting, durable social bonds, so-called 'friendships' (Smuts, 1985), which are manifested by high rates of grooming, close proximity and travelling together. Male friends also protect their females' infants against predators or harassment from other baboons, even if they are not necessarily the infants' fathers. Male infanticide rates are lower in olive than chacma baboons (Palombit, 2003).

Considering the ongoing debate on the function of primate copulation calls, we revisit the direct versus indirect competition and the female choice hypotheses. We analyse variables related to female and male characteristics, audience and environment. We use multimodel inference (Burnham & Anderson, 2002) with distinct models that represent the three hypotheses (direct competition, indirect competition, female choice) by investigating whether or not a female uttered a copulation call. Our approach allows us to quantify the relative support for each of the three functions we consider. The three hypotheses are biologically

relevant for olive baboons in at least two major ways. First, olive baboons form consortships between males and oestrous females, a behaviour that is directly relevant for the female choice hypothesis. Second, they live in multifemale, multimale groups, with multiple males having direct access to an oestrous female (Smuts, 1985), a behaviour directly relevant to induce both indirect sperm and direct male–male competition.

METHODS

Study Site and Subjects

We studied the Kabasinguzi troop (Johnson, Swedell, & Rothman, 2012) at the Kanyawara study site, Kibale National Park, Uganda (0.13–0.41°N; 30.19–30.32°E) from May to December 2015. The troop is fully habituated to human presence and all individuals (adults and juveniles) were individually identified. During the study period, the group included between 39 and 44 individuals (seven to eight adult females, two subadult females, 7–11 adult males, three subadult males, two juvenile females, 13 juvenile males, four infant females and one infant male). This research was approved by the Executive Director, Dr A. G Seguya, of the Uganda Wildlife Authority.

Data Collection

During each day of the study, we collected focal animal samples and 15 min scan samples (Altmann, 1974). We recorded the nearest neighbour of the focal animal, as well as all the individuals' identities within a circle of radius 10 m around the focal animal. We also recorded the identity of all the focal individual's grooming partners. We recorded these parameters because grooming and proximity are standard behavioural variables to calculate friendship indices (Silk, 2002; Silk, Alberts, & Altmann, 2003).

We began consecutive daily follows, from 0700 to 1600 hours, of females when they displayed perineal swelling signalling oestrus and when an adult male started consortship with them (see definition in Table 1), ending daily follows when females displayed detumescence (Smuts & Nicolson, 1989) and when adult males showed no more interest in them and ended the consortship. Mounts were recorded as all-occurrence samples during daily follows of tumescent individual females (Altmann, 1974; for a video example of a mount, see Supplementary material). When a mount occurred, we recorded the adult male's identity, whether the female was parous or nulliparous, whether the female gave a copulation call, the audience around the consorting pair, the female's swelling state and the habitat visibility (for definitions see Table 1). Genetic relatedness among troop members was unknown at the time of the study. It was not possible to determine with sufficient accuracy whether ejaculations occurred.

Behavioural Analyses

We calculated the dominance status of females and males separately, using decided aggressive interactions (i.e. when the outcome of the agonistic interaction was clear, with a winner and a loser; for definitions see below), displacements and unidirectional fear barks (given by subordinates to dominants only, Ransom, 1981). To assign dominance status, we calculated Elo-ratings (Albers & De Vries, 2001; Neumann et al., 2011), which is based on the following logic. For any observed agonistic interaction between two individuals, the Elo-rating increases by a certain amount for the winner (i.e. the individual who displaces or chases another one) and decreases for the loser (i.e. the individual who gives a fear bark, gets displaced or chased). If the same two individuals have

another agonistic interaction, then expected outcomes (i.e. the former winner wins again) add smaller changes in ratings than unexpected outcomes (i.e. the former winner loses). This method is useful in species with unstable dominance relations and male migration, such as olive baboons (Ransom, 1981; Smuts, 1985), owing to its dynamic properties (Neumann et al., 2011). We did not include Elo-ratings for the adult females in the analyses because one female accounted for about a third of all interaction data.

For ease of interpretation, we refer to an individual's Elo-rating as its dominance rank.

To quantify friendships (for definition see Table 1), we used the dyadic sociality index (DSI), which assesses the strength of affiliative relationships (Silk, Alberts, & Altmann, 2006; Silk, Cheney, & Seyfarth, 2013). To obtain the DSI for all adult dyads, we considered grooming between the focal and other adult individuals, the focal individual's nearest neighbour and all adult individuals within 10 m. Then, for each female, we determined the top three male friends, defined as the three males with which a female had the largest DSI. These three males were considered as 'friends', and all remaining males as 'nonfriends'. In all analyses we used this dichotomized categorical variable (e.g. Silk et al., 2006; Young, Majolo, Schülke, & Ostner, 2014).

Model Formulation and Statistical Analysis

To address our questions, we used multimodel inference (Burnham & Anderson, 2002; Burnham et al., 2011), which is based on the principle that models (corresponding to hypotheses) can be ranked and weighted relative to each other in order to obtain 'a quantitative measure of relative support for each competing hypothesis' (Grueber, Nakagawa, Laws, & Jamieson, 2011, p. 699). We used Akaike's information criterion (AICc, corrected for small sample sizes) to rank our three models. One important aspect of this approach is that it represents a trade-off between model complexity and model fit. For example, if two models have the same fit (quantified with R^2 , for example, see below), the one with fewer parameters (less complex) will have a smaller AICc and larger weight (see below) than the model with more parameters. Another important point is that any ranking of models is relative, such that there will be always a relative 'best' model, and evaluating fit of all candidate models should be used in conjunction with model ranking to assess whether the (best) model(s) are good in an absolute sense (Anderson, 2008; Dochtermann & Jenkins, 2011).

For inference, we used model weights, which represented normalized ratios of the difference of AICc between the target model and the best model in the candidate set. These model weights can be interpreted as probabilities that a given model is the best model in our set of models (Anderson, 2008).

Note that our goal was to compare relative support for the three functional hypotheses (i.e. three models, Table 2). As such, we were not primarily interested in estimates of specific model parameters

for which we could have used techniques, such as model averaging, to account for model selection uncertainty (Grueber et al., 2011; Johnson & Omland, 2004).

We fitted generalized linear mixed models with binomial error structure and logit-link (Bolker et al., 2009). In all models, we entered whether or not the focal female uttered a copulation call as the response variable and the focal female identity and the copulating male identity as random intercepts (crossed design as any female could have mated with any male). We log transformed the number of males in the audience to achieve a more symmetric distribution (Schielzeth, 2010). We calculated the coefficient of determination for the three models (Nakagawa & Schielzeth, 2013), which represents the variance explained by the fixed effects (R^2_m) and the variance explained by fixed and random effects (R^2_c). In addition to the relative ranking of models via AICc, these measures allowed us to quantify the absolute explanatory value of our models.

In the following, we describe how we designed each model such that it reflected the corresponding hypothesis to be tested (Table 2), by considering different combinations of variables. Since our study questions are concerned with the function of copulation calls and not with the underpinning mechanisms, we refrained from making predictions about the direction of the effect, that is, increased or decreased calling probabilities (Maestripietri et al., 2005; Semple et al., 2002).

Male–Male Competition

This hypothesis states that female calling behaviour induces competition between males over consortship. We thus expected the consorting male's rank to affect the female's calling behaviour, for example, to encourage bystanders to displace the consort male (Bercovitch, 1991). Similarly, since male olive baboons sometimes form coalitions to displace consorting males, females should adjust their calling activity according to the number of male bystanders and/or the presence of high-ranking bystanders. We also included female parity because young/nulliparous females are less likely to raise offspring successfully than older females (Anderson, 1986), which may affect the male's motivation to compete for younger females. We further expected the female's swelling stage, an indicator of ovulation, to play a role, since this is likely to affect the male's motivation to challenge a consortship (Higham, Heistermann, et al., 2008). We also added whether at least one additional female in the troop was fully swollen since this is likely to influence the level of male–male competition (Muller & Wrangham, 2004). Finally, we included habitat visibility as this is likely to influence how easily mating events can be detected by other males.

Sperm Competition

Under the sperm competition hypothesis, we expected females to modify their calling behaviour to facilitate their mating with as

Table 2
Predictor variables used in the three functional models

Predictor variable	Hypothesis/Model			
	Male–male competition	Sperm competition	Female choice	Null
Habitat visibility	+	+		
Male Elo-rating	+		+	
At least one other swollen female in troop	+	+	+	
Focal female fully swollen	+	+	+	
Mating partner is friend			+	
Female parity	+			
No. of males in audience	+	+	+	
At least one high-ranking male in audience	+			

+: factor included in the model.

many males as possible. First, habitat visibility is likely to affect calling behaviour since it is more challenging for nonconsorting males to locate the mating pair in closed habitat. As in the previous model, the presence of additional receptive females is likely to affect competition, so we included whether or not there was at least one more swollen female in the troop. We expected that female calling behaviour may change depending on whether the focal female was fully swollen, which could for instance lead to higher calling probability if the female wants to advertise her receptive/fertile state. Finally, we expected that females should adjust their calling behaviour depending on the number of bystanders. For example, females may adjust their vocal behaviour with larger male audiences to attract and to copulate with as many males as possible.

Female Choice

Under this hypothesis, females should adjust their vocal behaviour to express preferences for specific males and encourage their mate guarding. In contrast to male–male competition and sperm competition, this hypothesis assumes that copulation calls are directed primarily towards the male mating partner. Hence, we expected calling to be influenced by the male's rank and friendship status (Henzi, 1996), either because he provides 'good genes' or offers protection (Buchan et al., 2003). We added whether at least one additional fully swollen female was in the troop, as this is likely to affect intrasexual competition for preferred males. We included the female's swelling stage, as calling may be affected with changing receptivity. Finally, since females may additionally communicate to nonconsorting males to encourage the mating male's mate guarding, we included the number of males in the audience in our model.

In addition to random intercepts for female ID and male ID, we included random slopes to account for variation between individuals in how predictors affected the response variable, that is, whether a copulation call occurred or not (see Barr, Levy, Scheepers, & Tily, 2013; Bates, Kliegl, Vasishth, & Baayen, 2015). Since the focus of our study was to explain female copulation calling and to avoid overfitting, we only included uncorrelated random slopes for female ID (Appendix Table A1). Furthermore, we did not fit female parity as a random slope because during our study period none of the females changed her parity status.

Finally, we included a null model in our analysis. It comprised a fixed intercept and all random slopes for female ID of the three other models and a random intercept for male ID. The null model can be conceptualized as none of the three functional models explaining copulation calling. For example, if the null model had a large weight (relative to the three functional models), the conclusion was that none of the functional models is very likely to explain copulation calling. In contrast, if the null model had a small weight the conclusion was that the functional models had explanatory power for copulation calling. Also important is that, regardless of the null model's position in the ranking, there is always the possibility that some other model not included here might perform better.

We conducted all analyses in R (v.3.4.0, R Core Team, 2017), using the following packages for R: lme4 (v 1.1–12, Bates, Machler, Bolker, & Walker, 2015); MuMIn (v.1.16.6, Barton, 2016), EloRating (v. 0.43, Neumann & Kulik, 2014) and socialindices (v. 0.46–08, Neumann, 2016). Raw data used in this study are available online at figshare (<https://figshare.com/s/d7b998a4901999764582>, <https://doi.org/10.6084/m9.figshare.5383633>)

RESULTS

We observed 203 copulation events from five females mating with eight different males. Overall, the average percentage of copulation events with calls was 60.8% ($N = 5$ females; Table 3). For a presentation of the raw data for all variables and for all females separately, see Appendix Fig. A1.

Multimodel Inference

Among our models, the model representing the sperm competition hypothesis had the highest weight ($w_i = 0.55$) and therefore the highest probability of being the best model in our set. The three models representing female choice, the null model and male–male competition had lower weights (Table 4). Variance explained by our functional models ranged between 6% and 15% for the fixed effects and 54% and 62% for the combined random and fixed effects (R^2_m and R^2_c , respectively, Table 4). Detailed results of all models are in Table 5 and the random effect estimates are presented in Appendix Table A1.

DISCUSSION

We investigated three major hypotheses for the occurrence of copulation calls in female olive baboons. In doing so, we followed an information–theoretic approach, which enabled us to simultaneously evaluate relative support for three competing hypotheses that dominate the current literature on female copulation calling: the male–male competition, sperm competition and female choice hypotheses. Our results show two things. First, although no single hypothesis clearly outcompeted the others, inciting sperm competition is the best explanation for copulation calling in this study on olive baboons, at least among the alternatives we considered. The female choice hypothesis still received some support, while the male–male competition hypothesis received the least support and therefore seems very unlikely. The null model, that is, the possibility that none of the three tested functional hypotheses explained copulation calling, also received some support and as such cannot be ruled out. Second, none of the models explained large amounts of variation in our data, which raises the possibility that females might apply different or conditional tactics with which they utter copulation calls or that they serve a different or no function altogether. In the following, we discuss methodological considerations and evolutionary interpretations that seem plausible to explain our results.

Table 3
Descriptive statistics of all consort females

Female ID	Elo-rating	Observed in consortship (h)	Observed in nonoestrus (h)	No. of cycles	No. of adult partners	No. of males/cycle (mean, range)	No. of mounts	% Calling
Emā	1157	47.75	24.50	2	8	6.50 (6–7)	131	24.8
Msa	835	21.25	27.25	4	3	1.75 (1–3)	33	72.7
Spe	665	12.25	24.75	3	5	2.00 (1–4)	23	56.5
Mga	547	2.25	38.75	5	4	1.20 (1–2)	8	62.5
Ria	342	3.50	22.5	2	2	1.50 (1–2)	8	87.5

Italics: nulliparous female.

Table 4
Results from the multimodel inference

Model	K	AICc	Δ AICc	w_i	ER	R^2_m	R^2_c
Sperm competition	11	219.6	0	0.55	—	0.06	0.54
Female choice	13	220.8	1.20	0.31	1.8	0.15	0.55
Null	10	222.8	3.22	0.11	5.0	0.00	0.62
Male–male competition	16	225.1	5.50	0.04	15.7	0.11	0.57

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; Δ AICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with the lowest AICc divided by the weight of another model; R^2_m : variance explained by fixed effects; R^2_c : variance explained by fixed and random effects combined.

To the best of our knowledge, this is the first empirical study that has directly compared different functional hypotheses for the evolution of copulation calls to evaluate their relative explanatory value. Our approach, using information theory-based model ranking, illustrates some important conceptual advances with direct implications for other areas of research. Our goal was to provide a gradual interpretation of evidence, in light of a set of different functional hypotheses of copulation calling (Pradhan et al., 2006), and we suspect that this approach is likely to be useful for the study of signal evolution more generally. For instance, studies on copulation calls typically investigate and interpret individual factors that are hypothesized to reflect a functional hypothesis. However, it is crucial to realize that many, if not most, such factors are important in the context of several hypotheses (O'Connell & Cowlshaw, 1994). For example, Townsend et al. (2008) tested the effect of male rank on calling probability in female chimpanzees. They found that females were more likely to call if they mated with a high-ranking male than with a low-ranking one. As this result was counter to their predictions, the authors concluded that their study 'lent no support to the 'male–male competition' hypothesis' (p. 3). However, the study did not address other potential functions of female copulation calls for which male rank is important, for example female choice, suggesting that the conclusion was premature (because the male–male competition hypothesis may still be a better explanation than, say, female choice). In our study, out of the eight variables that were present across the three models, we considered five variables as relevant in more than one model. This highlights the benefits of using multimodel inference based on integrated models over traditional interpretation of individual factors in studies where different (functional) hypotheses compete with one other. More generally, we believe that this approach also better addresses the complexity of biological systems that often allow for several plausible explanations on the basis of evolutionary principles.

Several aspects of olive baboon sexual behaviour also support our best model that copulation calling functions to incite sperm

competition. Females are expected to copulate and obtain sperm from as many males as possible in a short period of time and female baboons typically gave copulation calls at the end of a mount, supposedly after ejaculation has taken place. By calling at the end of the mount, females allow the male to deposit his sperm before attracting other males subsequently. Furthermore, in olive baboons, females are typically consorted by several males in succession and simultaneously during their fertile period (Bercovitch, 1991; Danish & Palombit, 2014), which allows females to receive sperm from multiple males. Specifically, in our studied troop, females mated between 1.2 and 6.5 males per cycle (see Table 3), which suggests that females observed here have received sperm from on average three different males. Another relevant observation is that, at the end of the mount, females often run away from their consorting partners, up to 100 m (Smuts, 1985), which facilitates access by nonconsorting males. Male olive baboons also have large testes relative to their body size, which enable them to deposit more sperm per ejaculation, in line with the sperm competition hypothesis (Bercovitch, 1989; Harcourt, Harvey, Larson, & Short, 1981).

Although the sperm competition model ranked first in our analysis, we also found some support for the female choice model. In olive baboons, there might be potential for female choice as mate guarding is relatively inefficient, especially around the time of ovulation when consort turnover rates are high (Ransom, 1981). Furthermore, some females try to escape after mating by running towards other males or by trying to split from a consorting male with constant movement (Saayman, 1970; Smuts, 1985). Whether females are able to exert such choice of potential mates in species where females are much more strictly monopolized by males during their fertile phase, and hence the potential for female choice seems much more limited, remains to be studied (e.g. Bulger, 1993).

The male–male competition model ranked last beneath the null model and thus seems a very unlikely explanation for copulation calling in our study animals. Although harassment and aggression towards consorting males have been reported in olive baboons (Niemeyer & Anderson, 1983; Rowell, 1966), we never witnessed nonconsorting males (single or in coalition) interrupting an ongoing mating nor harassing the couple. This might be mainly due to very short mating durations (average: 5 s, Y. Bouquet, personal observation), which renders it unlikely that a nonconsorting male could disrupt copulations.

Interestingly, our results raise the possibility that copulations calls might serve multiple functions that vary with short-term changes in the ecological factors or social structure to which individual females are exposed. For instance, the degree of stability of the male dominance hierarchy has been shown to affect hormonal levels in nonhuman primates (e.g. Engh et al., 2006; Gesquiere et al., 2011). In such a scenario, if the male dominance hierarchy is unstable and females are not yet able to reliably

Table 5
Parameter estimates \pm SE for all three functional and the null models

Predictor variable	Hypothesis/Model			
	Male–male competition	Sperm competition	Female choice	Null
Intercept	−2.52 \pm 1.93	−1.65 \pm 0.83	−2.09 \pm 0.86	−0.82 \pm 0.76
Habitat visibility	0.65 \pm 0.44	0.59 \pm 0.42		
Male Elo-rating	−0.52 \pm 0.47		−0.40 \pm 0.46	
At least one other swollen female in troop	0.39 \pm 0.88	0.03 \pm 0.84	0.48 \pm 0.85	
Focal female fully swollen	1.51 \pm 1.00	1.67 \pm 0.89	1.31 \pm 0.94	
Mating partner is friend			1.38 \pm 0.64	
Female parity	0.54 \pm 1.74			
No. of males in audience	0.62 \pm 0.73	−0.20 \pm 0.60	−0.21 \pm 0.51	
At least one high-ranking male in audience	−1.32 \pm 0.58			

infer male ranks, females should adopt a strategy that incites sperm competition. In contrast, if the hierarchy is more stable and females are able to associate ranks with individual males more easily, this scenario may select for females to apply strategies such as male–male competition or female choice. In contrast to a general instability of social structure, which may have similar effects on all group members, individual attributes such as the ability to reliably keep track of social hierarchies might alternatively vary with a female's experience (e.g. age). Our results suggest a strong influence of individual identity on the preferred strategy, mainly because the variance attributable to female and male identities (R^2_{c}) is substantially higher than the variance explained by the fixed effects (R^2_{m} , Table 4). Consequently, the personal histories of females with the different males may impact on how likely they are to produce copulation calls. Similarly, individual dietary variation might influence female reproductive behaviour when plant components have direct impact on the endocrine system (for a review on primates, see Wasserman, Milton, & Chapman, 2013). For instance, in red colobus, *Procolobus rufomitratu*s, oestrogenic plant components increased aggression and copulation rates and reduced affiliative interactions (Wasserman et al., 2012). Similar results come from wild baboons, where progesterone-like compounds in a plum species prevented sexual swellings and thus decreased male consortship and rates of copulation (Higham, Ross, Warren, Heistermann, & MacLarnon, 2007). To investigate whether behavioural changes in reproductive context due to dietary intake indeed result in switching behavioural strategies and impact on calling behaviour, it would be necessary to incorporate physiological data, especially hormone levels. In primates, female copulation calls are known to vary with oestrous cycles, suggesting that they are under hormonal control (e.g. Engelhardt et al., 2012; Semple & McComb, 2000; but see ; Townsend et al., 2008).

In sum, individual variation in female copulation calling might be due to short-term physiological differences or long-term differences in personality traits or ontogenetic experiences. As such, copulation calls could indeed serve different functions across females, which could account for the variation observed in the present results.

Another way to interpret the current findings is to investigate whether calling itself is not functional but remaining silent is (Townsend et al., 2008). If copulation calls can be reliably used to infer mating events, it might be beneficial to conceal some ongoing copulations to prevent potential postcopulatory aggression and punishment (le Roux, Snyder-Mackler, Roberts, Beehner, & Bergman, 2013). This point has also been applied to the visual audience awareness (Gygax, 1995), including third-party inferences on bystander rank (Overduin-de Vries, Olesen, de Vries, Spruijt, & Sterck, 2013). In our data, females called in 60% of copulation events, which raises the possibility that they tactically suppressed their vocal behaviour in the remaining cases. Predictor variable candidates for a model addressing the 'tactical deception' hypothesis are whether the mating male is the normally associated male, his consorting distance, the local visibility of the habitat, the receptive state of the female and her location relative to the other males.

Yet another potential function for copulation calls that has been suggested is paternity confusion (O'Connell & Cowlshaw, 1994; Pradhan et al., 2006). However, it is difficult to disentangle paternity confusion from sperm competition because with both strategies females are expected to mate with as many males as possible, although for different purposes: either to obtain the best genes with the former strategy or to induce paternity confusion with the latter. Raising offspring can be costly for females living in multimale societies due to male infanticidal

tendencies (Engh et al., 2006; Palombit et al., 2000) and one way to reduce this is to ensure that the probability of paternity for each male is larger than zero. Promising objectives for future studies would be to take the female's visual perspective into account (i.e. by first studying a female baboon's visual range), to distinguish between sperm competition and paternity confusion. In particular, sperm competition predicts that females should mate promiscuously in full view of other males whereas paternity confusion predicts the opposite. Another relevant issue to address in this context is whether females 'keep track' of males they have mated with and allocate their copulation efforts accordingly.

It is also possible that copulation calls no longer have a biological function but are evolutionary remnants of an earlier socio-ecological environment. This somewhat counterintuitive possibility is in line with evolutionary principles, provided call production is currently not costly for callers but had been adaptive in the previous evolutionary history of the species. This 'behavioural fossil' hypothesis has been proposed by Henzi (1996). However, we consider it unlikely that copulation calls are mere remnants of past evolutionary states, mainly because copulation calling can hardly be cost free, but increases the risk of attracting predators and hostile conspecifics.

We also want to address some more points related to the methodological and conceptual approach we chose for this study. First, it is important to reiterate that the validity of any conclusions we derive from model ranking depends on the correct specification of the models we use to translate biological hypotheses into statistical models. It is possible that other researchers would add or remove specific variables or add interactions between variables. For example, one such variable might be female reproductive hormone levels, which are likely to play a role in signalling related to reproduction (e.g. Engelhardt et al., 2012; Semple & McComb, 2000). Whether their inclusion in the analysis would change the model order or the model weights is unknown at this point.

Second, our models explain small to intermediate amounts of variation, at least concerning the fixed effects, according to Cohen (1988): (small effect: $R^2 = 0.01$; intermediate effect: $R^2 = 0.09$) However, our values are well within the usual range of observational studies in ecology and evolution (mean R^2 : 5.4%; median R^2 : 2.2%; Møller & Jennions, 2002, p. 495).

Finally, it is worth considering that copulation calls potentially carry information on two interrelated levels. First, in species such as olive baboons, where a substantial proportion of copulations are silent (Aujard, Heistermann, Thierry, & Hodges, 1998; Fallon, Neumann, Byrne, & Zuberbühler, 2016; Oda & Masataka, 1992), the function may be inherent in the female's decision to call or to remain silent. Second, the function may be conveyed by the acoustic structure in species in which virtually all copulations are accompanied by vocalizations (Engelhardt et al., 2012; O'Connell & Cowlshaw, 1994; Oi, 1996; Semple, 2001; Semple et al., 2002). An interesting perspective for future studies across a broader range of species is to investigate whether the acoustic structure (given that a call is produced) relates to the same function as the calling/remaining silent distinction, or whether it carries different information.

To conclude, in our study we compared the relative merit of three main hypotheses regarding the function of copulation calls in female olive baboons. Our results do not clearly support one exclusive function, although sperm competition seems to be a more potent evolutionary force than female choice in promoting the utterance of copulation calls in this species, while male–male competition does not to appear to play any role. Another interpretation of our results suggests that copulation calls might be multifunctional with individual females applying different behavioural tactics to maximize their benefits from

calling on the basis of their respective social experiences or situation. This would be in line with the usual complexity of biological systems and further highlights the flexibility with which communicative signals might be applied, taking contextual information into account and adjusting individual calling behaviour accordingly. We also raised the possibility that copulation calls could have lost their function over evolutionary time, or have a function different from those tested in this study. We further highlight the advantages of using model ranking to present relative evidence on a gradual scale. Future research is encouraged to build on our model set, and adapt or amend the model set to gain further insights into the function of copulation in olive baboons and other species.

Acknowledgments

We thank Cecily Pulver, Moses Araali Kugonza, Godfrey Adyari and Edward Akiiki for their valuable help and friendship in the field. We also thank Pawel Fedurek for comments on the manuscript and Roger Mundry for discussions about multimodel inference. We are grateful to the Ugandan Wildlife Authority and the Uganda Council for Science and Technology for giving us the permission to conduct this research. The research has been funded by the Swiss National Science Foundation (310030_143359) and the European Research Council (PRILANG GA283871).

Supplementary material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2017.11.019>.

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Appendix

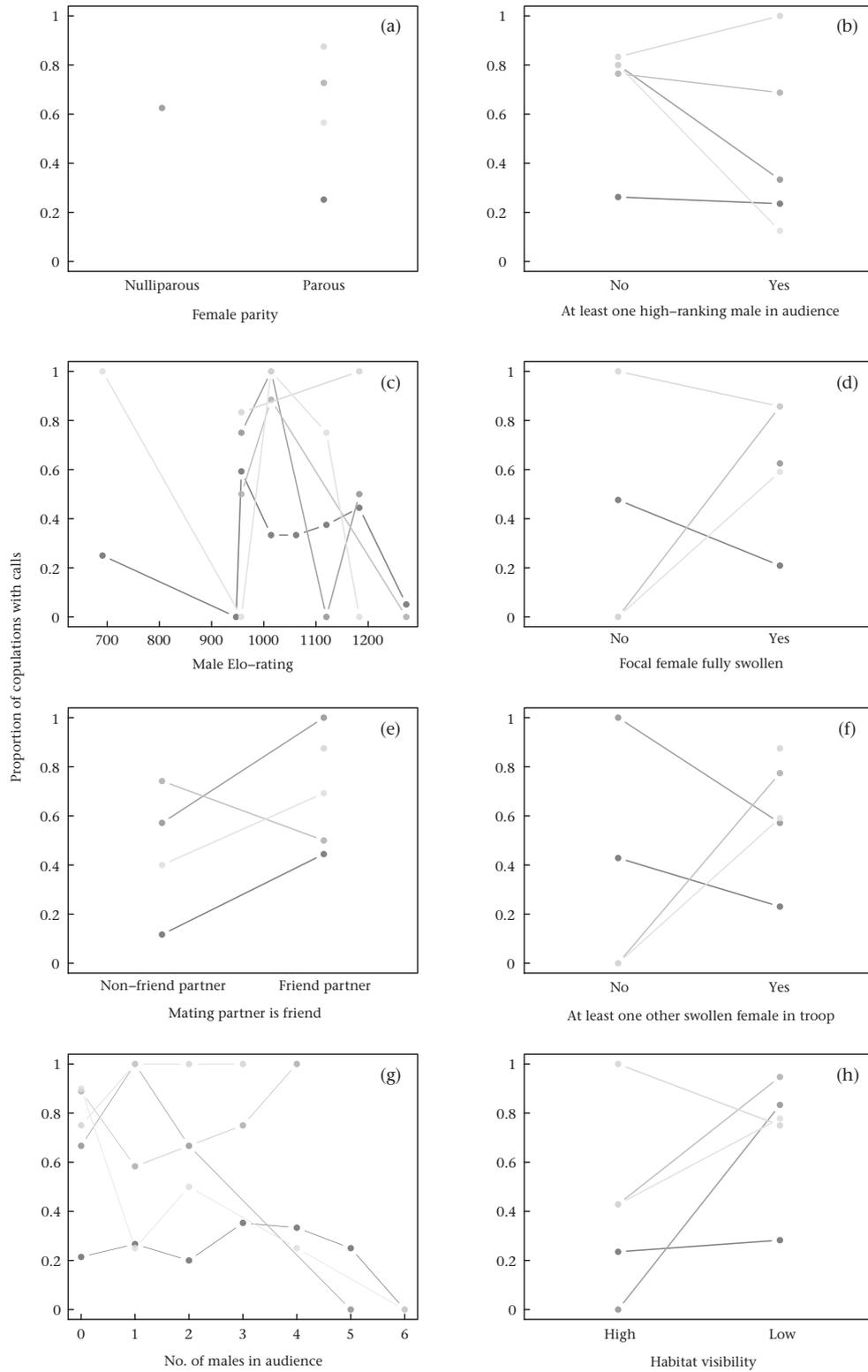


Figure A1. Proportion of copulations with calls for each predictor, separated by female. Predictors are (a) female parity, (b) if there was at least one high-ranking male in the audience, (c) male Elo-rating, (d) if the focal female was fully swollen, (e) if the mating partner is a friend, (f) if there was at least one other swollen female in the troop, (g) the number of males in the audience and (h) habitat visibility.

Table A1
Random effects of the four functional models

Random term	Hypothesis/Model			
	Male–male competition	Sperm competition	Female choice	Null
Male ID				
Intercept	1.23	1.38	1.22	1.32
Female ID				
Intercept	0.00	0.00	0.00	0.00
Habitat visibility	0.00	0.00		0.00
Male Elo-rating	0.00		0.00	0.00
At least one other swollen female in troop	0.00	0.00	0.00	0.00
Focal female fully swollen	1.19	1.02	1.16	1.70
Mating partner is friend			0.00	0.00
Female parity				
No. of males in audience	0.96	0.86	0.62	0.62
At least one high-ranking male in audience	0.00			1.55

Values are standard deviations.