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Confrontational assessment in the roving male promiscuity mating system of the Bornean orangutan

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Abstract

In many solitary mammalian species, females live alone in relatively small home ranges whereas males roam widely and converge around, and compete for matings with fertile females. In primates, orangutans are the only diurnal semi solitary species showing this roving male promiscuity mating system. Here, we develop and test hypotheses about the nature of male-male competition in Bornean orangutans by examining its sexually selected long-distance calls to disentangle the mechanisms through which males compete over mating access. This study uses a novel approach to disentangle the mechanisms of male-male competition. We established an acoustic localization system (ALS) comprising 20 recorders installed in a grid that allowed accurate localization in an area of 450 ha. With this procedure, we triangulated 1615 long calls over 109 days spread over 10 months to examine the males' ranging and calling decisions. A male's choice of area was determined mainly by local fruit availability. Once there, however, his calling behavior depended primarily on the number of sexually attractive females and the number of other flanged males present. Both these variables also predicted the proportion of calls to which individual males responded, and the proportion of males present that responded to long

calls of other males. We conclude that intra-sexual competition among Bornean flanged males comprises a combination of contest and scramble competition best summarized as confrontational assessment.

Significance statement

Where males range widely in search of scattered fertile females and these females do not broadcast their reproductive state, males could pursue a variety of strategies. Flanged male Bornean orangutans emit long calls serving to attract females and repel male rivals. In order to disentangle whether the competitive tactics of flanged males correspond to scramble or contest competition in their long-distance communication system, we used an acoustic localization approach with a grid of recorders installed in the research area. We found that flanged males go to areas with much food and then engage in vocal, and subsequently, physical battles with rivals, probably because their relative strength fluctuates rapidly. We call this unusual form of contest competition confrontational assessment.

Keywords Acoustic localization system · Mating system · Contest · Scramble · Long-distance communication · Orangutan

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Introduction

According to socioecological theory (Emlen and Oring 1977; Kappeler and van Schaik 2002), the social strategies of females (resulting in a particular spatial distribution and social relationships) serve to maximize access to resources and safety, whereas those of males serve to maximize access to mates. Hence, males should distribute themselves according to female dispersion and compete over access to receptive females.

The intensity and nature of this competition depend on details of intra-sexual selection (Emlen and Oring 1977; Clutton-Brock and Parker 1992; Arnold and Duvall 1994; Andersson and Iwasa 1996). The aim of the present study is to examine the nature of male-male competition in a species with dispersed solitary females who experience rare and rather unpredictable receptivity and roaming males: the Bornean orangutan (*Pongo pygmaeus wurmbii*).

van Schaik and Dunbar (1990) suggested that where females are solitary and widely spaced, males can opt for pair-bonded association or roving over large areas in search of receptive females, with the optimal solution depending on mobility relative to female territory size. If multiple females cannot effectively be defended against rival males, we expect a mating system with roving males that locate scattered receptive females. Such systems are indeed found in a variety of mammalian species (Fisher and Lara 1999; Andr  s and Solignac 2003; Derocher et al. 2010).

Where males rove, one can discern a spectrum of male-male competition from scramble to contest. Scramble competition is expected when males try to find scarce, widely dispersed receptive females before rivals do, or cannot afford to remain in association with receptive females for long. In such a situation, the ability to localize females and high sperm production are crucial for a male's reproductive success (Schwagmeyer and Woontner 1986; Sigg and Goldizen 2006). Scramble competition is often reflected in a low-skew polygynandrous mating system where reproduction is not monopolized by a dominant male. In contrast, contest competition is expected when combat pays off because prolonged association is possible and guarding males can monopolize mating access. In situations in which males are familiar to each other, we expect clear-cut dominance hierarchies that mediate access to receptive females. Such absolute monopolization, accompanied by polygyny and elaborate sexual dimorphism, is known for pinnipeds (Lindenfors et al. 2002). Most commonly, however, some intermediate situation will prevail because both sexes generally range alone and have insufficient information about each other's whereabouts and reproductive status. The resulting mating system is a form of high-skew polygynandry, where access is not fully monopolized by the top male because he is not necessarily the first male to locate the female (Dunbar 1988). Roving male mating systems usually are of this sort (Clutton-Brock 1989). The extent of male reproductive skew depends primarily on male mobility and density in relation to the density of receptive females (Dunbar 1988, 2000), but also on the interplay between male and female mating strategies, which may include female advertising of their reproductive status and male sexual coercion, in the form of forced copulations (Smuts and Smuts 1993), and post-copulatory mate guarding.

Orangutans are diurnal and semi-solitary, whereas most diurnal primates are permanently gregarious and all other

solitary primate species are nocturnal (Kappeler and van Schaik 2002). Orangutans are highly sexually dimorphic with flanged males about twice as big as females (Rodman and Mitani 1987), and almost uniquely among mammals, they show extreme male bimaturism with two sexually mature morphs, the smaller unflanged and the larger flanged males. Only the latter have irreversible secondary sexual characteristics such as cheek flanges, big laryngeal sacs, and a vocalization, the long call (Utami et al. 2002). Orangutans show a roving male polygynandrous mating system, but because females show pronounced preferences for mating with (particular) flanged males (Utami et al. 2009a), in this study, we concentrated on flanged males only.

Orangutan females are philopatric, with young females settling in home ranges overlapping with those of their mother, which enables them to maintain social relationships with their female maternal kin (Goossens et al. 2006; Arora et al. 2012; van Noordwijk et al. 2012). The size of female home ranges varies considerably across sites (Singleton et al. 2009; Utami et al. 2009b). Those of males are much harder to document, but the two available studies both report that flanged male home ranges exceed those of females in size by at least a factor 3–6 (Singleton and van Schaik 2001; Buckley 2014). Because of this and because female home ranges often show extensive overlap, each flanged male's home range overlaps with those of a considerable number of females. In addition, flanged male home ranges may be less stable, as suggested by the number of males recorded in the study area over time at our study site (see results). As a result, a large number of males may potentially compete over access to each receptive female.

The flanged male's long calls are known to repel male rivals and attract receptive females and can be heard up to 1000 m for human observers on the ground (Galdikas 1983; Mitani 1985a; Delgado, 2003, Mitra Setia and van Schaik, 2007). An additional function of long calls has been described for Sumatran orangutans, namely the female protection function. Non-receptive females try to maintain earshot association with the dominant long-calling flanged male in an area (Mitra Setia and van Schaik 2007), who has a smaller home range than the other flanged males (Singleton and van Schaik, 2001), which serves to avoid sexual harassment by other males and may perhaps also reduce the risk of infanticide (Delgado and van Schaik 2000; Fox 2002; Mitra Setia and van Schaik 2007). However, this protection function has so far not been found in Bornean orangutans (Mitani 1985a, b; Spillmann et al. 2010).

Because of their roving character, flanged males continuously need to decide where to go in order to find food and receptive females and how to behave toward other males. This behavior may depend largely on the number and identity of other males that are present and consequently reflect intra-sexual competition. Since long calls are a sexually selected signal (Delgado 2006), this long-distance communication

system may reveal the nature of intra-sexual competition in male orangutans. Long calls can be assigned to individuals using measurements of the acoustic structure in combination with statistical methods (Delgado 2003; Spillmann et al. 2010) or with a caller recognition approach (Spillmann et al. 2016), and we therefore assume that male orangutans can identify each other by their calls.

Because none of the flanged males in the area are related to the local females (Arora et al. 2012), it is known that males leave their natal range and begin roaming. Given the larger size of the home ranges of flanged males compared to females, we expected the number of males recorded in the study area to increase for longer than the number of females.

Here, we predict as to how Bornean male orangutans adjust their local presence and long-calling activity in response to a variety of ecological and social factors to reveal what intra-sexual competition mechanisms are molding the system (see Table 1). We consider three basic cases: scramble competition, contest competition with stable dominance relations, and contest competition with unstable dominance relations. In the latter case, males must reassess their dyadic dominance status at frequent intervals, perhaps at each encounter (if they have not met for a while). Sumatran males show stable contest competition (Singleton and van Schaik 2002; Delgado 2003; Mitra Setia and van Schaik 2007), but far less is known about Bornean males (see below), who are therefore the focus of this study.

I: number of males

When receptive females are scarce and widely distributed and monopolization is prevented (e.g., because of high costs of association), scramble competition should prevail, and the number of males in an area should

increase with the availability of receptive females. But if stable contest competition prevails, male presence in an area should not change or even decrease because subordinate males should avoid the dominant (see Table 1; cf. Singleton and van Schaik 2002). Under unstable contest, the number of males may increase or stay the same. In Bornean orangutans, the mating skew among flanged males is found to be lower (Mitra Setia et al. 2009) and dominance relations among males more unstable (Galdikas 1983; H. Morrogh-Bernard et al. unpublished manuscript; BS unpublished data) than among Sumatran males. Thus, we predict an increase (which may be small or pronounced) in local male presence with the number of receptive females in the area.

II: call rate

In a roving male promiscuity mating system the expectation is that long call activity should increase as a function of the availability of receptive females. Males need to advertise themselves in order to attract females. This outcome might reflect either scramble competition where males confront each other or unstable contest competition where dominance relations are reassessed at each encounter. On the other hand, under stable contest competition, no relationship should be found or even a decrease in long call activity because only males with higher relative dominance or greater fighting ability are able to increase their call rate and take the risk, whereas males with lower relative dominance or fighting ability will avoid dominant males or reduce their call rate or even stop calling when faced with more dominant rivals (Table 1; cf. Delgado 2003; Mitra Setia and van Schaik 2007). Because of the unclear dominance relations

Table 1 Predictions as a function of the number of sexually attractive females for (I) the number of males present in an area, (II) for average individual long call rate, (III a) for the proportion of responding males, and (III b) the proportion of long call responses

Dependent variable	Condition	Predictions as a function of the number of sexually attractive females
I: number of males	Stable contest	Decrease of male presence or no changes
	Unstable contest	Increase of male presence
	Scramble	
II: long call rate	Stable contest	Decrease of long call rate or no changes
	Unstable contest	Increase of long call rate
	Scramble	
III a: response proportion	Scramble	No change in the response proportion
	Stable contest	Response proportion decreases or no changes
	Unstable contest	Increase of response proportion
III b: proportion of responding males	Scramble	No change in the proportion of responding males
	Stable contest	Proportion of responding males decreases or no changes
	Unstable contest	Increase of the proportion of responding males

among Bornean males, we predict no change or an increase in male calling rate when receptive females are present.

III a and b: long call response tendency and the proportion of responding males

Reactions to long calls, both how likely a male is to respond and whether he responds at all (i.e., the proportion of males present that respond to other males' calls) may provide the greatest resolution in disentangling the nature of male-male competition among Bornean orangutans. Assuming scramble competition, the presence of fertile females or other males should not affect the proportion of emitted long call responses, nor, as a consequence, the proportion of contributing males. In the case of stable contest, both the proportion of long call responses and the proportion of contributing males should decrease with both the number of sexually attractive females and the number of males present in the area. However, in unstable contest, we expect the opposite: long call response probability and the proportion of responding males should increase with both the number of sexually attractive females and the number of males present in the area (see Table 1). There is no relevant information on Sumatran males.

Apart from these social factors, ecological factors such as fruit availability and rainfall may also have an effect on calling activity. First, earlier studies reported that fruit availability had no effect on long call activity in Sumatran orangutans (Delgado 2003), suggesting that the energetic costs of long call production are low. However, Bornean habitats show lower overall productivity and higher seasonal variation of fruit availability (Wich et al. 2011; Vogel et al. 2015), which might lead to energetic constraints on long call production, at least during certain time periods. Second, rainfall might have a more direct effect on long call production since sound propagation is highly affected by rainfall (Wiley and Richards 1982). Its effects have so far not been examined, but because males can also call between rain showers, we do not expect this to affect daily rates of long calling.

In traditional observational field studies in a limited study area, it is very difficult to test the predictions derived above (Table 1), because it is impossible to collect accurate information on local male presence. We therefore adopted a novel approach using an automated acoustic localization system (ALS) that allowed us to gather continuous long call data from a recorder grid that encompassed an area of accurate acoustic localization of 450 ha (henceforth called triangulation area) (Spillmann et al. 2015). In this study, we used the data extracted from the triangulation area so as to obtain an accurate estimate of the number of flanged males present in it.

Methods

Study area

Field work was conducted at the Tuanan field station in Central Kalimantan, Indonesia (2.151° South; 114.374° East) from March 2012 until December 2012. The field site is part of the larger Mawas conservation area and covers a 1000 ha trail-system in a peat swamp forest that had undergone selective logging around 20 years earlier. An advantage of swamp forests is the absence of topographic barriers for sound transmission. Researchers and long-term field assistants performed individual focal follows according to a highly standardized field protocol (see: <http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>). In analyses where data of focal follow sampling was used, we included only focal follows lasting >5 h. The ALS data were automatically recorded and analyzed and therefore blind. As to the behavioral data, it was not possible to record data blind because our study involved focal animals; however, none of the observers were aware of the hypothesis we were testing. This research project adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of non-human primates.

Male roving behavior

We compiled data on newly identified individuals, in particular adult females and flanged males, from 2003 to 2014.

Data from the acoustic localization system

We installed an acoustic localization system (ALS) consisting of 20 off-line, time-synchronized (via GPS), SM2+ autonomous recording units in a lattice at 500 m intervals, thus encompassing an area of 300 ha. The ALS was programmed to record continuously from 04:30 to 18:30 local time, to cover the orangutan's entire diurnal activity period. In total, we recorded and localized 3018 long call occurrences on 109 days, spread out over a period of 10 months (March 2012–December 2012). To validate our automated acoustic localization algorithm, we used data from days during the study period on which flanged males were directly observed, either during individual focal follows or when in association with a female focal individual. This revealed a mean localization error of 58 m (SEM = ± 7.2 m) for long calls occurring within the recorder grid, as well as within a peripheral area spanning up to 200 m outside of the grid, covering a total triangulation area of 450 ha. Given that localization accuracy outside of this triangulation area was lower, we restricted our analyses to only consider long calls occurring within the triangulation area ($N = 1615$). For more details

on long call extraction and localization, see Spillmann et al. (2015).

One critical assumption we make for using the ALS method as a proxy of male presence is that each flanged male calls at least once per day while present in the study area. We validated this assumption with focal follow data which showed that males indeed called on 93.8% of observational days (more details see supplemental ESM 1). Therefore, the ALS provides a highly accurate (minimum) estimate of the number of flanged males present within the study area at any day.

Ecological factors

Monthly fruit availability was determined by means of a standardized phenological protocol (<http://www.aim.uzh.ch/Research/orangutanetwork/FieldGuidelines.html>) for ~1500 trees in a 2 ha plot. From these data, a monthly fruit availability index (FAI) is calculated, which is defined as the *number of trees carrying fruit / total number of trees monitored*.

During focal follows, flanged males were rarely observed to give long calls during heavy rain, and we found that hourly long call rates were significantly lower during rain showers (median = 0.0) than during dry periods (median = 0.633; Wilcoxon rank sum test: $W = 98$, $P < 0.013$, $r = -0.552$). The day's total rainfall was therefore measured locally and included in all statistical models.

Number of males in the study area

Because we are not yet able to reliably assign each individual long call to a particular male, we used a validated approach to count the number of males in the area. For this, we used a two-component procedure. First, six of the males could typically be identified by idiosyncratic structures in the spectrograms of their long calls. Second, we applied a time-distance rule that assigned two calls to the same male if they occurred within 4 h and a 300 m radius from each other under the additional restriction that speed of movement did not exceed 550 m/h. This rule was derived empirically from long call data from focal animal sampling over the course of complete follow days ($N_{\text{total LCs}} = 848$ ($N_{\text{focal LCs}} = 242$, $N_{\text{others LCs}} = 606$), 96.8% correct assignments, false pos. = 10, false neg. = 17). This procedure, when complemented with focal follows and additional sightings, allowed us to assign 1615 of the long calls to individual males.

Average long call rate per male

The average long call rate per male was estimated as the total number of long calls given per day divided by the total number of males in the area, as calculated above.

Proportion of long call responses and of responders

We defined responses as any long call that occurs within 5 min at a distance <1300 m of a prior long call given by a different flanged male. We exclusively focused on immediate call responses (<5 min) to capture highly competitive vocal exchanges and omitted responses with longer latencies ($5 < \text{latency} < 18$ min; supplemental ESM 2, Fig. A1). The cut-off distance of 1300 m was chosen, given that distance had no effect on immediate long call responses until this distance. We also calculated a second measure, namely the proportion of responding males among the total number of calling males in the area per day.

Number of sexually attractive females

Unlike chimpanzees and bonobos, orangutan females do not indicate the peri-ovulatory period through sexual swellings (Galdikas 1981). In order to establish the conception time of a female, we calculated 8.5 months back from known or estimated dates of birth of offspring (Graham 1988). A female was taken to be sexually active up to 6 months before, and 2 months after the time of estimated conception, based on patterns in mating activity (L. Dunkel, unpublished data). Using this criterion, two sexually attractive females were identified during the entire observation period, with a slight overlap in their respective periods of sexual attractiveness.

Statistical analysis

Model I: to predict the number of males within the study area at a given day, we fitted a generalized linear model (GLM) with a Poisson error distribution, incorporating the number of sexually attractive females present, fruit availability, and total rainfall as main predictor variables. Next, we fitted a series of models to assess which social (number of males and number of sexually attractive females present) or ecological (monthly fruit availability and total rainfall) variables (fixed effects) best predicted the following aspects of long call activity within our study area: model II for the call rate per male per day (linear model, LM), model IIIa for the proportion of long calls produced as a response to a preceding long call (binomial GLM), and model IIIb for the proportion of males that responded to the calls of other males (binomial GLM). In all models, the interaction between the number of males and the number of sexually attractive females was considered, but this never reached statistical significance and was therefore omitted from the models reported here. The likelihood ratio tests were done by comparing all variables of each model with the null model. Where required, data were transformed prior to analyses, and all models were conducted in R3.1.3 (R Core Team 2015) using packages “car” and “MuMIn” (Fox and Weissberg 2011; Barton 2016).

Results

Male roving behavior

New flanged males did indeed continue to enter the study area (Fig. 1), whereas the number of females remained roughly constant, apart from a sudden increase in 2007–2008, caused by the increase of the study area from 700 to 1000 ha during this time period, and local female recruitment due to maturation. Moreover, because some of the new males were clearly quite old, male ranges may also be far less stable than those of females. This pattern confirms that we are indeed dealing with a roving male mating system.

I: social and ecological correlates of male presence

In our first model, we tested which factors account for the number of males present in the area. A significant Poisson GLM ($\chi^2_{\text{LRT}} = 30.084$, $R^2_{\text{GLM(c)}} = 0.036$, $P < 0.001$, $N = 109$) led us to reject our prediction that the number of sexually attractive females would affect male presence (see Table 2). Only fruit availability had a significant and positive effect on male presence in the area ($B = 0.087$, $\text{SE} = 0.019$, t value = 4.557, $P < 0.001$).

II: average long call rate per male

Using a linear model ($\chi^2_{\text{LRT}} = 4.05$, $R^2_{\text{LM(c)}} = 0.285$, $P < 0.001$, $N = 109$), we found that the average long call rate of a male present in the study area was a function of the number of sexually attractive females ($B = 0.204$, $\text{SE} = 0.06$, t value = 3.423, $P < 0.001$), as well as the number of other

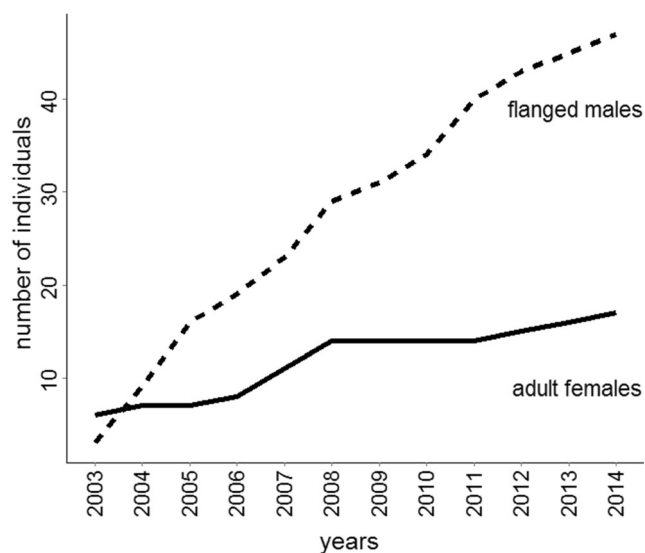


Fig. 1 Cumulative counts of identified individuals over the years at Tuanan field site

Table 2 The effect of food availability, rain, and the number of sexually attractive females on the number of calling males in the area of 109 days spread over a 10-month period. Parameter estimates, associated standard errors, and statistical significance as obtained from a poisson GLM

Fixed effects	Estimate	Std. error	z value	Pr(> z)
(Intercept)	1.084	0.097	11.188	
Ecological factors				
Food availability	0.087	0.019	4.557	<0.001
Rain	-0.004	0.004	-1.106	0.269
Social factors				
nr of attractive females	-0.003	0.093	-0.034	0.973

$$\chi^2_{\text{LRT}} = 30.084, p < 0.001$$

males in the area ($B = 0.054$, $\text{SE} = 0.024$, t value = 2.298, $P = 0.024$) (see Fig. 2 and Table 3).

III: long call interactions

III a: proportion of long call responses

A binomial GLM ($\chi^2_{\text{LRT}} = 33.687$, $R^2_{\text{GLM(c)}} = 0.087$, $P < 0.001$, $N = 109$) found that the tendency to immediately respond to the long call of another male was largely explained by the number of attractive females currently present ($B = 0.676$, $\text{SE} = 0.182$, t value = 3.713, $P < 0.001$), as well as the number of flanged males in the area ($B = 0.255$, $\text{SE} = 0.086$, t value = 2.976, $P = 0.003$), while neither fruit availability nor rainfall had an effect (see Fig. 3 and Table 4).

III b: proportion of responding males

A binomial GLM ($\chi^2_{\text{LRT}} = 48.546$, $R^2_{\text{GLM(c)}} = 0.188$, $P < 0.001$, $N = 109$) showed that the proportion of responding males increased with the number of sexually attractive females

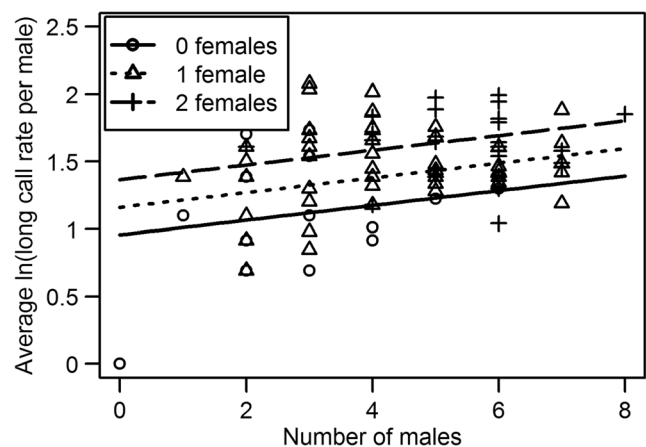


Fig. 2 Probability of average individual ln(long call rate per day) as a function of the number of sexually attractive females and the number of males present in the area. Prediction lines were obtained from a linear model. Data points represent the raw data

Table 3 The effect of food availability, rainfall, the number of sexually attractive females, and the number of males in the area on the average individual call rate per day of 109 days spread over a 10-month period

Fixed effects	Estimate	Std. error	<i>t</i> value	Pr(> <i>t</i>)
(Intercept)	0.985	0.087	11.328	
Ecological factors				
Food availability	−0.006	0.017	−0.360	0.719
Rain	−0.001	0.002	−0.312	0.756
Social factors				
<i>nr. of attractive females</i>	0.204	0.060	3.423	<0.001
<i>nr. of flanged males</i>	0.054	0.024	2.298	0.024

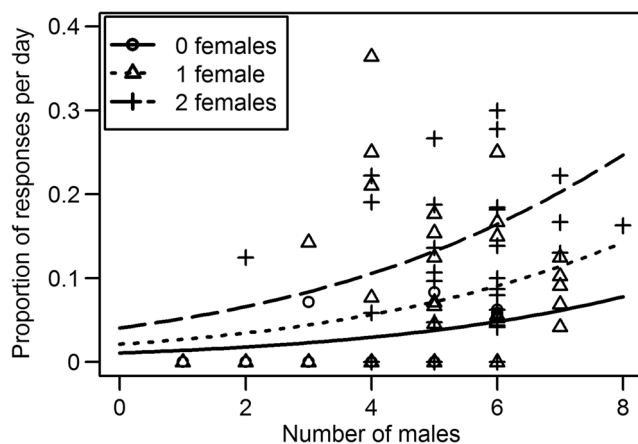
Parameter estimates, associated standard errors, and statistical significance as obtained from a linear model with ln (long call rate per day)

$$\chi^2_{\text{LRT}} = 4.05, p < 0.001$$

($B = 0.657$, $SE = 0.230$, t value = 2.856, $P = 0.004$) and the number of males present ($B = 0.336$, $SE = 0.114$, t value = 2.946, $P = 0.003$) (see Fig. 4 and Table 5). This indicates the presence of a crowding effect, but also that a greater proportion of the males present commit to calling when sexually attractive females are present. Again, neither fruit availability nor rainfall were significant predictors in the model.

Discussion

The aim of this study was to characterize the nature of male-male competition in the roving male promiscuity mating system of Bornean orangutans through an examination of their long-distance communication system. Given that with conventional field methods (such as focal animal sampling), it is not feasible to obtain a comprehensive record of all long-distance vocalizations within a sufficiently large area, we

**Fig. 3** Probability of the proportion of long calls that elicited responses on a given day in the area as a function of the number of males in the area and the number of sexually attractive females. The prediction lines refer to the binomial GLM predictions**Table 4** The effect of food availability, rainfall, the number of sexually attractive females, and the number of males in the area on the proportion of long call responses of 109 days spread over a 10-month period

Fixed effects	Estimate	Std. error	<i>z</i> value	Pr(> <i>z</i>)
(Intercept)	−4.157	0.426	−9.749	<2e-16
Ecological factors				
Food availability	−0.064	0.044	−1.455	0.146
Rain	−0.015	0.010	−1.608	0.108
Social factors				
<i>nr. of attractive females</i>	0.676	0.182	3.713	<0.001
<i>nr. of flanged males</i>	0.255	0.086	2.976	0.003

Parameter estimates, associated standard errors, and statistical significance as obtained from a binomial GLM

$$\chi^2_{\text{LRT}} = 38.687, p < 0.001$$

instead relied on an automated grid of recorders in the study area. We used data from this acoustic localization system (ALS) to investigate which social or ecological factors underlie male ranging and long-calling decisions. We were able to show that: (i) male presence in the area is a function of local fruit availability, (ii) call rates reflect the number of sexually attractive females and the number of males present in an area, and (iii) the proportion of long call responses and the proportion of responding males show a positive relationship with the number of sexually attractive females as well as with the number of males present in the area.

As expected for a species with a roving male mating system, the number of males present within our study area varied considerably (range: 0–8 males, with a mean of 4.211 males) over the 10 months period. We found that fruit availability was the only significant predictor (Table 2). Interestingly, local fruit availability did not affect the long-calling behavior of males once present (Tables 3, 4, and 5), suggesting that flanged males are looking for areas with high fruit availability,

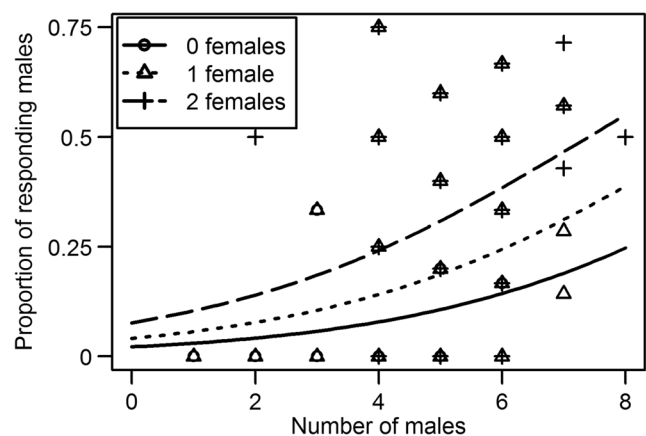
**Fig. 4** Probability of the proportion of males that responded to long calls in the area as a function of the number of males present and the number of sexually attractive females. The prediction line refers to the binomial GLM predictions

Table 5 The effect of food availability, rainfall, the number of sexually attractive females, and the number of males in the area on the proportion of responding males of 109 days spread over a 10-month period

Fixed effects	Estimate	Std. error	z value	Pr(> z)
(Intercept)	−3.745	0.561	−6.673	0.000
Ecological factors				
Food availability	0.010	0.057	0.178	0.859
Rain	−0.015	0.010	−1.467	0.142
Social factors				
<i>nr. of attractive females</i>	<i>0.657</i>	<i>0.230</i>	<i>2.856</i>	<i>0.004</i>
<i>nr. of flanged males</i>	<i>0.336</i>	<i>0.114</i>	<i>2.946</i>	<i>0.003</i>

Parameter estimates, associated standard errors, and statistical significance as obtained from a binomial GLM

$\chi^2_{\text{LRT}} = 48.546$, $p < 0.001$

and subsequently vocally react to the presence of fertile females and other males.

Because male distribution is widely believed to be primarily driven by mating opportunities (Emlen and Oring 1977; Kappeler and van Schaik 2002), the obvious expectation is that males rove in search of females and decide based on cues of the presence of receptive females (Dunbar 2000). The empirical data on Bornean orangutan males perhaps revealed that the availability of receptive females had no direct effect on male presence. Since female orangutans do not advertise their reproductive status, this may be the best males can do. Moreover, since female orangutans are generally ready to conceive when they exceed a certain condition threshold after a long and energetically draining period of lactation (van Schaik and van Noordwijk 1985; Knott 2001, 2005), which is likely to happen when local food abundance is propitious (MAvN, unpublished data). Thus, local fruit availability is perhaps the most reliable environmental proxy available to males to gather information on the distribution of mating opportunities. Fruit abundance may actually vary considerably over short distances, even in a swamp forest (Harrison et al. 2016), and it therefore pays for males to base their ranging decisions on this ecological variable. Doing so, moreover, helps males to maintain a good physical condition, which seems crucial in the energetically demanding acts of mate guarding and engaging in aggressive male-male conflict (see below).

Although fruit abundance affected a male's local presence, it did not affect his calling behavior, which was exclusively driven by social variables. Average long-calling rates were best predicted by the number of sexually attractive females and the number of other males in the area (Fig. 2, Table 3). This relationship may simply reflect attempts to attract females, and therefore scramble competition. However, closer examination of the nature of long call interactions between males suggests otherwise. Both the proportion of long call responses and the proportion of males that responded to the

long calls of other males increased with both the number of sexually attractive females and the number of males in the area (Figs. 3 and 4, Tables 4 and 5). Competition thus becomes more intense when more receptive females are around but also with more rival males present, a pattern in line with predictions from unstable contest competition (Table 1). Comparable results were also found in humans and gorillas but they do not engage in confrontational assessment (Flinn 1988; Sicotte 1994).

It remains somewhat puzzling exactly how males locate sexually attractive females. We can envisage three different mechanisms. First, as mentioned above, males' ranging decisions seem to depend on fruit availability. The likelihood to meet receptive females in areas with better food supply might be higher and therefore males in such areas are willing to confront others. However, since receptive females are rare as a result of 7-year birth intervals and virtually no infant mortality (Wich et al. 2004, for Tuanan: MAVN, unpublished data), this does not appear to be plausible. Second, females should maximize the probability to mate with the best male, especially when there is no male investment in rearing offspring, or to mate with different males in order to confuse paternity and reduce the risk of infanticide, especially when dominance ranks among males are unstable (Andersson and Iwasa 1996; van Schaik 2000; Andersson and Simmons 2006). Either way, females gain from provoking interactions between a mate-guarding (consorting) male and another calling male by simply approaching the calling male (Cox and Le Boeuf 1977; Fox 2002). The guarding male either drops off or meets the challenge, allowing the female to either select the strongest male as mate or confuse paternity by mating with multiple males. In this case, then, the females are responsible for the escalation among the calling males—a suggestion supported by observations on both Sumatran and Bornean orangutans (Utami and Setia 1995; Fox 2002; Tuanan: BS, unpublished data). Third, because males increase their call rate when informed about the presence of receptive females and increase their competitive call interactions toward rivals, information about the presence of fertile females will automatically spread. Thus, non-intended listeners will be informed immediately. It has been shown that context is encoded in orangutan long calls. This makes it possible for eavesdroppers to extract information by listening to long calls and long call interactions (Spillmann et al. 2010). It is therefore likely that males use a combination of overall calling rate, response rates, and the acoustic properties of long calls to assess the presence of receptive females in the area, even before they have directly observed their presence.

If long call production per se were energetically costly, we should have found a relationship between fruit availability and a male's long call activity. Since this was not the case, we can assume that long call production, at the observed rate of 3.31 (SD = ± 1.41) per day, is not costly

in the energetic sense but rather costly in the social sense because calling males and especially responding males accept the risk of physical fights. Rain as a more direct ecological factor did not influence call activity in the area. Wiley and Richards (1982) argued that long-distance communication is strongly affected by noise (i.e., rainfall) that influences detection and discrimination by the receiver. The absence of a relationship between rainfall and long call activity and long call responses in our ALS models, suggests that rain affects the actual timing of long calls, but not the calling rates over the whole day.

Overall, then, males zoom in on particular areas based on local food abundance and adjust their long-calling behavior to the presence of both other males and sexually attractive females. The responses to other males in the absence of sexually attractive females allow the males to update their information on each other's relative fighting ability, which presumably undergoes appreciable fluctuations (see below). Our observations are not consistent with scramble competition, but rather with the unstable form of contest competition (terminology following van Schaik and van Noordwijk 1988) we call *confrontational assessment*: increased advertising and assessment of rivals' fighting ability when there are sexually attractive females present. This is consistent with the known differences between the social systems of the two orangutan species. In Sumatran orangutans, long call activity is affected by neither social nor ecological factors, indicating that call activity is relatively stable in an area. This is because the dominant male creates an acoustic safety zone that subordinate flanged males avoid and females tend to stay in earshot association with the dominant male in the area (Singleton and van Schaik 2002; Delgado 2003; Mitra Setia and van Schaik 2007). In contrast, in Bornean orangutans the dominance hierarchy among flanged males is much less stable and females with dependent offspring do not seek to remain in earshot association with them (Mitani 1985a; Spillmann et al. 2010), probably because doing so would not guarantee reduced harassment (Bornean flanged males are known to force matings: MacKinnon 1974; Galdikas 1981; Schurmann 1982; Mitani 1985a; Knott 2009) given the rapid fluctuations in conditions and thus dyadic dominance status.

Indications for a less stable dominance system in Bornean flanged males are higher rates of chases between rivals and more observed physical fights among Bornean flanged males compared to Sumatran flanged males. This is also reflected in a significantly higher incidence of scars and mutilated or missing fingers and toes in Bornean males (L. Dunkel, unpublished data). In addition, the proportion of flanged males to unflanged males is much higher in Borneo than in Sumatra, consistent with the lack of developmental arrest of unflanged males in Bornean compared with Sumatran orangutans (Utami et al. 2002; Pradhan et al. 2012; Dunkel et al. 2013; Marty et al. 2015). Moreover, a larger number of

flanged males converging around a single female will act to reduce the monopolization ability of the top-dominant male, and thus create mating opportunities for non-dominant males (Watts 1998).

These results, based on the long-distance communication system alone, suggest that a certain fairly small proportion of flanged males do commit to contest. Another proportion emit long calls but only when circumstances permit it, so as to avoid escalated male aggression that might lead to energetic costly chasings or even more costly physical fights. Field data (BS unpublished data) show quite a bit of turnover between the competitive and non-competitive strategy. Flanged males might extensively compete until they fall below a minimal condition threshold, upon which they cease call interactions to recover from their poor physical condition. This temporally exaggerated competitive behavior resembles the system observed among male elephants: bulls in musth compete intensely over access to females and their condition declines over the course of their musth period (Poole 1987; Poole et al. 2011). Other males avoid contests with musth males, even if these are smaller.

In conclusion, this study shows a combination of scramble and contest components in male-male competition in a roving male mating system among Bornean flanged males. This mix seems to be based on confrontational assessment, where flanged males increase their call rate to attract females and continuously update their dominance relations through commitment in long call interactions, which may result in close encounters and even fights. We suggest that the use of ALS can also enhance our knowledge of male strategies in other species with roving males that call.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Informed consent This study was conducted on non-human animals and is therefore not relevant.

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