



Fighting for what it's worth: participation and outcome of inter-group encounters in a pair-living primate, the Javan gibbon (*Hylobates moloch*)

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Abstract

When resources are limited and defensible, inter-group encounters in animals are often of aggressive nature. Individuals can participate in inter-group encounters to defend mates, infants, and food resources, but also to attract out-group individuals for additional mating opportunities. Since inter-group conflicts have mainly been studied in group-living species, we examined the mate, infant, and food resource defense and mate attraction hypotheses in pair-living Javan gibbons (*Hylobates moloch*) in Gunung Halimun-Salak National Park, Indonesia. To this end, we investigated factors influencing male and female participation and outcome of encounters (i.e., win vs. lose). We observed 234 complete encounters between three habituated and five unhabituated gibbon groups over 43 months, of which 72% were aggressive. Males were the main participants and they were more likely to participate when cycling females or dependent infants were present, supporting the mate and infant defense hypotheses. Males were also more likely to participate when more fruits were available, contradicting the food resource defense hypothesis. Females participated by singing more often when they were cycling and when there were singing opponents, suggesting an advertisement function of their reproductive status through songs. The probability of winning an inter-group encounter was only higher when cycling females were present, supporting the mate defense hypothesis. The intensity of space use or aggression level had no effect on the outcome of inter-group encounters. Our results highlight that mate and infant defense are crucial for male Javan gibbons, especially in view of their pair-living system, long interbirth intervals, and slow infant development.

Significance statement

While animal groups interact aggressively with each other to defend valuable resources, they can also interact to increase additional mating opportunities. Here, we examined male and female participation and the outcomes of inter-group encounters in a wild pair-living primate, the Javan gibbon. Crucially, we found that the presence of cycling females had a significant impact on male participation, female singing, and the outcome of encounters. Our findings suggest that Javan gibbon females may advertise their reproductive status through singing during inter-group encounters while Javan gibbon males rather participate to defend their mates and infants.

Keywords Inter-group encounter · Mate defense · Infant defense · Outcome of encounter · Pay-off asymmetry · Gibbons

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Introduction

When resources are limited and defensible, inter-group encounters in animals are often of aggressive nature and can affect individual fitness (Kelly 2005; Harris 2010; Koch et al. 2016a). In non-human primates, three main explanations have been accredited to understand the participation of individuals in inter-group encounters. Because female fitness is limited by access to food, females are expected to mostly defend food resources (food resource defense hypothesis; Trivers 1972; Korstjens et al. 2005). Male fitness, however, is limited by access to females; therefore, males are expected to mainly defend females (mate defense hypothesis; Emlen and Oring 1977; Kitchen and Beehner 2007) or food resources for females (food resource defense hypothesis). Males also defend infants from potential infanticides by out-group males (infant defense hypothesis; van Schaik 1996; Steenbeek 1999).

Although these three hypotheses are not mutually exclusive, numerous studies supported the mate defense hypothesis. Males were more aggressive during inter-group encounters in the mating season compared to the non-mating season (bonnet macaques, *Macaca radiata*: Cooper 2004; moustached tamarins, *Saguinus mystax*: Garber et al. 1993; Samango monkeys, *Cercopithecus mitis erythrarchus*: Payne et al. 2003) or when estrous/cycling females were present in comparison to when no estrous/cycling females were present (chacma baboons, *Papio cynocephalus ursinus*: Kitchen et al. 2003; white-faced sakis, *Pithecia pithecia*: Thompson et al. 2012). In contrast, in other studies, the food resource defense hypothesis predicted best participation of individuals in inter-group conflicts (Reichard and Sommer 1997; Cooper et al. 2004; Korstjens et al. 2005; Thompson et al. 2012). For example, female vervet monkeys (*Chlorocebus aethiops pygerythrus*) actively defended access to valuable food resources (Arseneau-Robar et al. 2016) and female Western black-and-white colobus (*Colobus polykomos polykomos*) were more likely to be aggressive in inter-group encounters during months in which they heavily relied on a specific high-quality fruit species (Korstjens et al. 2005). However, other studies revealed that food availability or feeding patch quality had no effect on participation in inter-group encounters (Cowlshaw 1995; Steenbeek 1999; Koch et al. 2016a; Mirville et al. 2018). Finally, infant defense may function differently between sexes (Hrdy 1979). Male may actively defend infants from infanticidal males (Palombit et al. 2000; Wich et al. 2002). In contrast, female Verreaux's sifakas (*Propithecus verreauxi*) participated less often when vulnerable infants were present, potentially to defend infant from injury or infanticide (Koch et al. 2016a).

Inter-group encounters have mainly been studied in primates living in larger groups (Sicotte 1993; Saito et al.

1998; Fashing 2001; Harris 2006; Crofoot et al. 2008; Koch et al. 2016a, 2016b; Lucchesi et al. 2020; Samuni et al. 2020). Yet, only a handful of studies have investigated inter-group encounters in pair-living primates (*Leontopithecus rosalia*: Peres 1989; *S. mystax*: Garber 1993; *Hylobates lar*: Sommer and Reichard 1997; *Callicebus brunneus*: Lawrence 2007; *P. pithecia*: Thompson et al. 2012; *Indri indri*: Bonadonna et al. 2020; *H. moloch*: Yi et al. 2020a). While the food resource defense hypothesis is widely supported in species with diverse social structures (reviewed in Fashing 2001), mate defense might be particularly important for males in pair-living species. The risk that females mate with out-group males during inter-group conflicts may have higher costs for pair-living than group-living males, because pair-living males can sire only a limited number of offspring in comparison to group-living males, which have the potential to mate with several females. Although infanticide occurs more frequently in animals living in larger groups (Lukas and Huchard 2014), infanticides have also been witnessed in pair-living species and may, hence, predict participation in inter-group conflicts (Alfred and Sati 1991; Palombit 1999; Rasoloharijaona et al. 2000; Borries et al. 2011). Because the risk of infanticide has been suggested to be a major selective force for the evolution and maintenance of pair-living in primates (van Schaik and Dunbar 1990; van Schaik and Kappeler 1997; Opie et al. 2013; Kappeler and Pozzi 2019), the mate and infant defense hypotheses are of particular relevance to predict participation in inter-group conflicts.

In this study, we investigated inter-group encounters of Javan gibbons (*Hylobates moloch*), a pair-living primate species living in tropical rainforests in Indonesia. For gibbon males, mate defense during inter-group encounters may be critical, as extra-pair copulations occur exclusively during inter-group encounters (*Symphalangus syndactylus*: Palombit 1994; *H. lar*: Bartlett 2003; *Nomascus concolor jingdongensis*: Huang et al. 2013). Moreover, take-over or replacement by extra-group members during inter-group encounters have been reported in several gibbon species, potentially resulting in the permanent loss of opportunities to reproduce (*H. lar*: Brockelman et al. 1998; *N. concolor*: Hu et al. 2018). Gibbon females participate in inter-group encounters mainly by singing and seldom by chasing, whereas males participate exclusively by chasing, even though female gibbons have a similar body and canine size as males, and, hence, a similar fighting ability (Frisch 1963). In contrast, in other species lacking a sexual size dimorphism, as in lemurs, females participate equally often or even more often in inter-group conflicts than males (reviewed in Koch et al. 2016a). Furthermore, Javan gibbon pairs do not duet and mainly females sing solos, while in most other gibbon species, pairs duet to strengthen and advertise pair-bond but also to defend their territory (Ellefson 1968; Raemaekers and Raemaekers 1985b; Geissmann 1993, 2002). Hence, female solo songs

of the non-duetting Javan gibbons may not have pair-bond related functions (Ham et al. 2017), instead solos may serve to attract males from other groups, especially by advertising their reproductive status (i.e., when they are cycling, mate attraction hypothesis; Seiler et al. 2019). Hence, understanding which factors influence female participation in inter-group conflicts in Javan gibbons is of particular interest.

Because the probability of winning an encounter often depends on “the asymmetry in fighting ability” and “pay-off asymmetry” (Smith and Parker 1976), we here also examined factors potentially affecting the outcome of inter-group encounters. In many species, differences in group size can result in asymmetries in fighting abilities during inter-group encounters leading larger groups to win over smaller groups (Sillero-Zubiri and Macdonald 1998; Kitchen et al. 2004; Palmer 2004; Crofoot et al. 2008; Furrer et al. 2011; Majolo et al. 2020). Moreover, if an encounter location has been intensively used by a group, it might be of a higher value than other locations resulting potentially in a higher motivation to defend the area (Kitchen et al. 2004; Crofoot et al. 2008; Wilson et al. 2012; Brown 2013; Koch et al. 2016b). Thus, the encounter location (i.e., location-based pay-off asymmetry) may affect the outcome of inter-group encounters as already indicated in some primate species (Schradin 2004; Crofoot et al. 2008; Markham et al. 2012; Koch et al. 2016b; Roth and Cords 2016). Given gibbons’ high territoriality and small group size, the encounter location rather than asymmetries in fighting ability might affect the outcome of inter-group encounters in Javan gibbons.

In this study, we specifically tested the mate, infant, and food resource hypotheses and the mate attraction hypothesis by investigating which factors predict the male and female participation as well the outcome of inter-group encounters in Javan gibbons (Table 1). For the mate defense hypothesis (1), we predicted that Javan gibbon males participate more often during inter-group encounters when cycling females are present. We also predicted that groups win more often when cycling females are present. For the infant defense

hypothesis (2), we predicted that males participate more often during inter-group encounters when dependent infants are present. We predicted that females participate less often during inter-group encounters to protect dependent infants. We also predicted that groups win more often when dependent infants are present. For the food resource defense hypothesis (3), we predicted that both males and females will participate more often during inter-group encounters when food availability is lower. Furthermore, we assumed that the encounter location predicts the probability of winning an inter-group encounter, with groups being more likely to win an inter-group encounter when the encounter takes place in an area that have been intensively used the months before the inter-group encounter. Finally, for the mate attraction hypothesis (4), we predicted that females sing more often during inter-group encounters when they are cycling.

Methods and materials

Study subjects and site

The local Javan gibbon population in the primary forest of Citalahab area, Gunung Halimun-Salak National Park (6.74° S, 106.53° E), West Java, Indonesia, has been studied regularly since the establishment of the Javan Gibbon Research & Conservation Project in 2007 (Kim et al. 2011, 2012; Ham et al. 2016, 2017; Oktaviani et al. 2018; Yi et al. 2020a, 2020b). This study focused on three habituated adjacent gibbon groups (A, B, and S) and five surrounding unhabituated groups (C, D, E, O, and W). We collected data on inter-group encounters for a total of 43 months over 7 years from 2009 to 2016 (2696.25 h of total observation, see Table S1 in Supplementary Information). During the study period, each group was composed of an adult male–female pair, up to three offspring resulting in a group size between two to five individuals (see Table S2 in Supplementary Information).

Table 1 Hypotheses and predictions tested in the study

	Mate defense hypothesis (when females are cycling)	Infant defense hypothesis (when vulnerable infants are present)	Food resource defense hypothesis (when food is less abundant*/when the encounter location is more frequently used prior to the encounter**)
Model I	↑	↑	↑*
Male participation			
Model II		↓	↑*
Female participation			
Model III	↑ ^a	↑	↑*
Female singing			
Model IV	↑	↑	↑**
Outcome			

^a Mate attraction hypothesis

Data collection during inter-group encounters

We defined an inter-group encounter when two different groups were observed within 50 m of each other, following the definition from previous studies on arboreal primates inhabiting dense tropical forests including gibbons (Sommer and Reichard 1997; Steenbeek 1999; Fashing 2001; Korstjens et al. 2005). We collected data on inter-group encounters between two habituated groups as well as between a habituated and an unhabituated group. We defined participation in an encounter when an individual was chasing an opponent group member for both females and males, and also when females were singing. We included female songs only as male Javan gibbons rarely sing (Kappeler 1984; Geissmann and Nijman 2006) and sang only few times during inter-group encounters during our study period. For each inter-group encounter, we recorded the encounter duration (min), interactive behaviors between all individuals from the focal and opponent groups (i.e., chasing, singing, hitting, grooming, playing, or copulation), initiators and targets of interactions (i.e., chases initiated by and involving whom), and GPS coordinates of encounter locations (see Table S1 in Supplementary Information for detailed data collection). When the opponent group was impossible to identify, we recorded the opponent group as “unknown.”

We used the number of actively participating opponents to operationalize the fighting ability of an opponent group during an encounter. In addition, we recorded the presence of a singing opponent (yes/no), instead of the exact number of singing opponents, as it was difficult to distinguish singing between adult and sub-adult females from unhabituated groups.

Female reproductive status and infancy

To investigate the mate and infant defense hypotheses, we subdivided female reproductive status into three mutually exclusive phases: (1) cycling females: females who have given birth at least 2 years prior and who were not pregnant, determined a posteriori based on observations on the same population after the study period, (2) dependent infants: females with infants younger than 1 year old, and (3) others: when females were neither cycling or had dependent infants (e.g., a pregnant female or a female who lactates infants older than 1 year). We estimated the pregnancy of females by considering the last birth of infants from our observations and the putative gestation period of 7 months (Ardito 1976; Geissmann 1991). As weaning occurs gradually over a period of 22 months in gibbons (Treesucon 1984; Reichard and Barelli 2008), it would have been inappropriate to consider that the whole lactating period reflects a period of higher infanticide risk. In addition, infant gibbons start consuming solid food by themselves at an age of about 4 months (Berkson 1966) and spent about 70% of time independent from their

mothers at an age of about 1 year (Yi 2020). Therefore, we considered infants younger than 1 year as most vulnerable to infanticide and categorized them as dependent infants.

Fruit availability

Fruit availability was estimated since 2007 during monthly phenology transects of Javan gibbons' feeding trees with a diameter at breast height (dbh) ≥ 10 cm and lianas with dbh ≥ 7 cm, in 25 plots (10 \times 50 m) within the home range of the habituated groups. The plots were randomly selected at the crossroads of grid trails (200 \times 200 m intervals) and also randomly oriented along the trail intersections (Kim 2012). We collected phenology data at the end of each month and considered it to represent fruit availability during the elapsed month. We scored the relative abundance of fruits on a 4-level scale (0: no fruits, 1: present but few, 2: moderately present, 3: abundant; Kim 2012). We added the scores obtained and divided the sum by the total number of trees to represent the fruit availability for each month.

Home range size and encounter location

The home range size was estimated by collecting GPS coordinates of adult females and males at 15-min intervals during animal focal observations, using kernel density estimations (95 %). To investigate the effect of the encounter location on the probability of winning a conflict, we measured the size of the overlapping area between the encounter location and core areas for three timescales: 1, 3, and 6 months preceding to each encounter event (Markham et al. 2012). Thereby, the encounter location was estimated by drawing a circle of 50-m radius around the GPS coordinate that was taken at the beginning of an encounter to represent the “encounter location.” Although groups could move during encounters, we considered the location where the encounter started as biologically more relevant than any other locations during or at the end of the conflict. The “core area” of home ranges of each focal group was calculated using kernel density estimations (50%). The size of the overlapping area between the encounter location and the core area for each of the three timescales was defined as the intensity of space use. All the GPS-data were analyzed using ArcGIS Pro (version 2.0.1; Esri 2018). Finally, we defined the winner of an encounter as the group which stayed longer in the encounter location, and the loser as the group that left the encounter area first (Fashing 2001; Harris 2010). When it was not clear which group left the encounter location first, we recorded it as “draw.” Theoretically, unhabituated groups may have left the encounter location earlier because they were not habituated to the presence of human observers. However, unhabituated groups won or lost in almost all dyads equally often against habituated groups and one unhabituated group even won more often over a

habituated group (see results), making it unlikely that the presence of human observers might have influenced the outcome of conflicts between unhabituated and habituated groups.

Statistical analyses

First, to describe general characteristics of inter-group encounters in Javan gibbons (Table 2), we investigated factors influencing the inter-group encounter frequency. We used a generalized linear mixed model (GLMM; Bolker et al. 2009) with a Poisson distribution to fit the monthly encounter frequency ($N_{\text{month}} = 108$) as a response variable, and female reproductive status and fruit availability as predictor variables. Monthly observation day was set as offset to control the difference in observation days in each month. Focal group identity was set as a random factor to control for possible group differences. For this model, we included encounters we could not observe from the beginning until the end ($N_{\text{encounter}} = 286$). To examine whether there was a sex difference in participation ($N_{\text{encounter}} = 174$), we used a chi-squared test. Finally, we examined whether gibbon groups exhibit dominance relationships among groups by using binomial tests.

Next, we examined factors predicting the probability of participation in inter-group encounters and winning an inter-group encounter. Since our hypotheses were not mutually exclusive, we tested several hypotheses in our models so that all predictors could be simultaneously investigated. In model I (Table 2, male participation model), we ran a binomial GLMM with male chasing (yes/no) for each encounter ($N_{\text{encounter}} = 243$) as a response variable. We included fruit availability, female reproductive status (cycling female, dependent infant, others), and the number of actively participating opponents as predictors. Focal group ID was set as a random factor, and encounter duration as offset to control for the possible effect of group differences and encounter duration.

For model II (Table 2, female participation model) and model III (Table 2, female singing model), we included data collected on female participation during between 2013 and 2016 ($N_{\text{encounter}} = 142$). We fitted separate models for female participation and singing because females participated by chasing and singing, whereas males participated by chasing only. For model II (female participation model), we ran a binomial GLMM with female chasing (yes/no) for each encounter ($N_{\text{encounter}} = 142$) as a response variable and the same predictors, random factor, and offset as in the model I (male participation model). For model III (female singing model), we ran a binomial GLMM with female singing (yes/no, $N_{\text{encounter}} = 142$) as a response variable and fruit availability, female reproductive status, presence of singing opponent as predictors, focal group ID as a random factor, and encounter duration as offset. For all these models, we included random slopes for fruit availability and number of actively participating opponents within gibbon

groups in order to decrease type I error (Schielzeth and Forstmeier 2008; Barr et al. 2013).

For model IV (Table 2, outcome model), we collected data on the outcome of encounters between 2014 and 2016 and included only encounters which had a clear winner or loser to examine factors influencing encounter outcomes ($N_{\text{encounter}} = 86$). For model IV, we ran a binomial GLMM by including winning (yes/no) as a response variable and female reproductive status and intensity of space use in 1 month, number of actively participating opponents, proportion of chasing frequency (i.e., “focal chasing frequency” divided by “focal and non-focal chasing frequency”) as predictors, focal group ID as a random factor, all predictors as random slopes within focal group ID, and encounter duration as offset. We also fitted two additional binomial GLMMs using the two other time-scales for the core area: intensity of space use in 3 months and 6 months.

For all models, quantitative predictors were z-transformed to a mean of 0 and standard deviation of 1 before fitting the models. Only main effects were included when there were no significant effects of interactions between predictors. We also controlled for collinearity among predictors using the package ‘car’ (Fox et al. 2012). Since all variance inflation factors were below or around 1, collinearity was not an issue. We compared full and null models including only random factors and offsets using likelihood ratio tests. We discussed the results of the models with respect to test predictors only when a full-null comparison revealed significance. All *p* values were two-tailed. We discussed the results of a model only when a full-null model comparison revealed a significance or a trend (Forstmeier and Schielzeth 2011; Mundry 2014). All data were analyzed using R (version 3.4.3; R Development Core Team 2018). As we did focal animal observations in the field, blind methods were not applicable.

Results

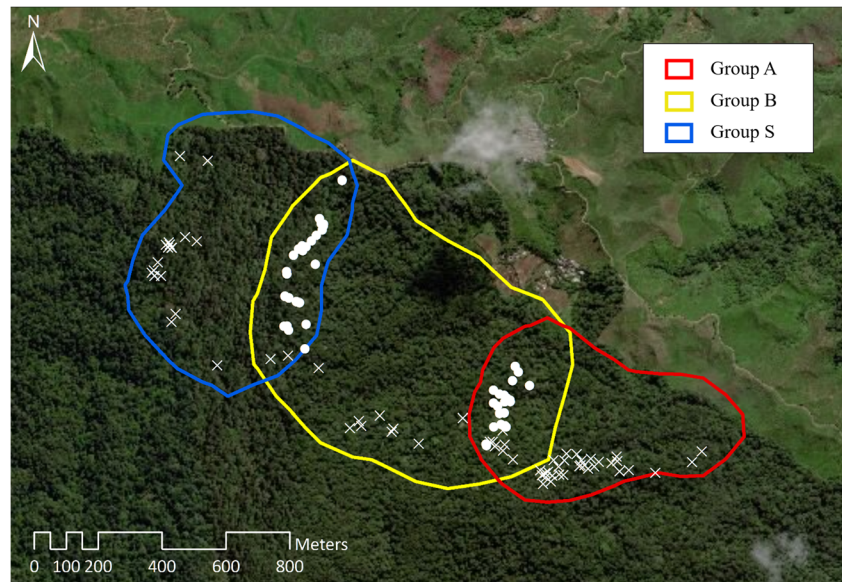
General characteristics of inter-group encounters in Javan gibbons

We observed 234 completely observed and 52 incompletely observed encounters during the 581 days of observations. Gibbons encountered other groups exclusively in the overlapping areas of their home ranges (Fig. 1) with a mean encounter frequency of 0.49 per day (SD = 0.63, range 0–2). The inter-group encounter frequency was not predicted by female reproductive status or fruit availability (full-null model comparison: $\chi^2 = 0.47$, *df* = 3, *p* = 0.925). Mean duration of complete encounters was 80 min (SD = 52, range 3–293). In the 234

Table 2 Statistical tests and models used to test hypotheses regarding inter-group encounters in Javan gibbons (*Hylobates moloch*) from Gunung Halimun-Salak National Park

Model name	Test	Error structure, link function	Response variable	Test predictor	Control predictor	Sample size
General characteristics of inter-group encounters						
Encounter frequency	GLMM	Poisson, log	Monthly frequency of encounters	Female reproductive status (cycling female/ dependent infant/ the rest), monthly fruit availability	Group ID (random), Monthly observation day (offset)	108 months
Sex difference in participation	Chi-squared test			Presence of female and male participation per encounter		174 encounters
Dominance between groups						
Model I	GLMM	Binomial, logit	Winning probability			86 encounters
Male participation				Female reproductive status (cycling female/ dependent infant/ the rest), monthly fruit availability, number of actively chasing opponents	Group ID (random), encounter duration (offset)	243 encounters
Model II	GLMM	Binomial, logit	Female chasing (yes/no)	Female reproductive status (dependent infant/ the rest), monthly fruit availability, number of actively chasing opponents,	Group ID (random), encounter duration (offset)	142 encounters
Female participation				Female reproductive status (cycling female/ dependent infant/ the rest), monthly fruit availability, singing opponents (yes/no)	Group ID (random), encounter duration (offset)	142 encounters
Model III	GLMM	Binomial, logit	Female singing (yes/no)	Female reproductive status (cycling female/ dependent infant/ the rest), monthly fruit availability, singing opponents (yes/no)	Group ID (random), encounter duration (offset)	142 encounters
Female singing				Female reproductive status, intensity of space use (1 month), number of actively chasing opponents, proportion of chasing frequency	Group ID (random), encounter duration (offset)	86 encounters
Model IVa	GLMM	Binomial, logit	Outcome of inter-group encounters (win/lose)	Female reproductive status, intensity of space use (3 month), number of actively chasing opponents, proportion of chasing frequency	Group ID (random), encounter duration (offset)	86 encounters
Outcome (1 month)				Female reproductive status, intensity of space use (6 month), number of actively chasing opponents, proportion of chasing frequency	Group ID (random), encounter duration (offset)	86 encounters
Model IVb	GLMM	Binomial, logit	Outcome of inter-group encounters (win/lose)	Female reproductive status, intensity of space use (6 month), number of actively chasing opponents, proportion of chasing frequency	Group ID (random), encounter duration (offset)	86 encounters
Outcome (3 month)						
Model IVc	GLMM	Binomial, logit	Outcome of inter-group encounters (win/lose)	Female reproductive status, intensity of space use (6 month), number of actively chasing opponents, proportion of chasing frequency	Group ID (random), encounter duration (offset)	86 encounters
Outcome (6 month)						

Fig. 1 Home ranges of three habituated gibbon groups (A, B, and S) and inter-group encounter locations between the habituated groups (circle) and between habituated and unhabituated Javan gibbon (*Hylobates moloch*) groups (cross) in Gunung Halimun-Salak National Park, Indonesia, between 2009 and 2016



completely observed encounters, chasing occurred in 72% of cases, and was mostly observed between adult males (87%). In general, males participated more often than females in inter-group encounters (chi-squared test; $\chi^2 = 43.16$, $p < 0.001$). During each encounter, we observed on average 3.9 chases by both sexes (SD = 4.7, range 0–25). We did not observe males preventing females from approaching another group by forcing them to stay away from opponent groups (i.e., herding). However, when females were chased by an opponent male, males almost always chased immediately the opponent male back within a minute (14 out of 20 times). Between 2013 and 2016, females participated by chasing in 18 out of 142 encounters, and only after the male partner initiated chasing. Females from either focal or non-focal groups sang in 32% of inter-group encounters ($N_{\text{encounters}} = 46$). Female songs lasted on average for 12 min (SD = 7, range

1–32). In seven encounters, we observed 16 cases of gibbons hitting each other with their fist. In all cases, an adult male hit an opponent male except in a single case in which an adult male hit a sub-adult female. Nonetheless, no serious injuries or lethal attacks during encounters were observed in this study, while it occurs, albeit very rarely, in other gibbon species (*H. lar*: Palombit 1993; *H. albibarbis*: Cheyne et al. 2010). We did not observe any affiliative interactions between adult individuals from different groups, neither grooming nor copulation. We observed playing twice between juveniles from two different groups (group B and S), which lasted only for a few seconds as they were immediately chased by the parents from the opponent group. The average home range size of three habituated groups was 38.3 ± 14 ha. The size of area overlapping was both 6 ha between group A and B, and between group B and S.

Table 3 Total number of encounters between the eight Javan gibbon groups (*Hylobates moloch*), and the frequency of won encounters for each group in Gunung Halimun-Salak National Park between 2014 and 2016

Group 1	Group 2	Number of encounters	Frequency of winning group 1	Frequency of winning group 2	Binomial test p
A	B	40	21	19	0.875
A	C	25	6	19	0.01**
A	D	15	4	11	0.119
A	E	3	2	1	1
B	S	28	17	11	0.345
B	D	3	1	2	1
B	O	5	3	2	NA
S	O	1	0	1	NA
S	W	14	5	9	0.424

* < 0.05; ** < 0.01; *** < 0.001—significance levels

Finally, gibbon groups did not exhibit clear dominance relationships, except one group dyad (group A and C; see Table 3, Fig. S1 in Supplementary Information).

Model I: male participation

Male participation was predicted by fruit availability, female reproductive status (cycling female/dependent infant), and the number of actively chasing opponents (full and null model comparison: $\chi^2 = 19.12$, $df = 5$, $p = 0.002$; Table 4). Males were significantly more likely to participate in inter-group encounters when the female was cycling and when a dependent infant was present (Fig. 2(a)), when fruit availability was higher (Fig. 2(b)) and when more individuals of the opponent group participated in the inter-group encounters (Fig. 2(c)).

Model II: female participation and model III: female singing

Neither female reproductive status, fruit availability, nor number of chasing opponents predicted female participation in inter-group encounters (full and null model comparison: $\chi^2 = 4.74$, $df = 3$, $p = 0.192$). The probability of females singing during inter-group encounters was predicted by the female reproductive status and presence of singing opponents (full and null model comparison: $\chi^2 = 9.75$, $df = 4$, $p = 0.045$; Table 5; Fig. 3(a), (b)), with females being more likely to sing when they were cycling and when individuals in the opponent group also sang.

Model IV: outcome

In all three models examining the influence of space use for each time category (1, 3, and 6 months) on the probability of winning an encounter, only female reproductive status predicted the probability of winning an encounter. Focal groups were more likely to win an encounter when females were cycling compared to when females were not cycling (full

and null model comparison: 1-month overlap: $\chi^2 = 12.64$, $df = 5$, $p = 0.027$; 3-month overlap: $\chi^2 = 13.26$, $df = 5$, $p = 0.021$; 6-month overlap: $\chi^2 = 13.28$, $df = 5$, $p = 0.021$). The intensity of space use (1, 3, and 6 months), number of actively participating opponents, or proportion of chasing frequency did not predict the probability of winning an encounter (Table 6).

Discussion

Inter-group encounters in Javan gibbons occurred every other day and were mostly aggressive, without any affiliative interactions between groups such as grooming or extra-pair copulation, which have been frequently reported in other gibbon species (*S. syndactylus*: Palombit 1994; *N. gabriellae*: Kenyon et al. 2011; *H. lar*: Bartlett 2003; Barelli et al. 2013; *N. concolor jingdongensis*: Huang et al. 2013). The frequency of inter-group encounters did not co-vary with any socio-ecological factors investigated and we did not find any dominance relationships among groups. Male Javan gibbons participated more often in inter-group encounters than females, especially when females were cycling or dependent infants were present, supporting both the mate and infant defense hypotheses. In addition, males also participated more often when more opponents were actively participating in the inter-group encounters. They also participated more when food availability was high, contradicting the food resource hypothesis. In contrast to males, female participation by chasing in inter-group encounters was not predicted by any socio-ecological factors investigated in this study, probably because female chasing was too rare to draw a significant conclusion. Females participated more often in singing when they were cycling and when females in the opponent group also sang, supporting the mate attraction hypothesis. The probability of winning an encounter was best predicted by the presence of cycling females but not by the intensity of space use, providing additional support for the mate defense hypothesis. Hence, in pair-living Javan gibbons the mate and infant

Table 4 Effects of fruit availability, female reproductive status, and the number of actively participating opponents on male chasing (yes/no) in inter-group interactions in Javan gibbons (*Hylobates moloch*) in Gunung Halimun-Salak National Park between 2013 and 2016

	CI (lower, upper)	Estimate	Std. error	z	p
Fruit availability ¹	−0.036, −1.384	0.693	0.260	2.663	0.008**
Female reproductive status					
Cycling female	−0.361, −1.956	1.145	0.406	2.822	0.005**
Dependent infant	−0.581, −2.667	1.573	0.527	2.985	0.003**
Number of actively participating opponents ²	−0.105, 0.948	0.541	0.188	2.874	0.004**

* < 0.05; ** < 0.01; *** < 0.001—significance levels

^{1, 2} z-transformed; mean ± SD of the original value: ¹ 0.33 ± 0.09, ² 0.69 ± 0.58

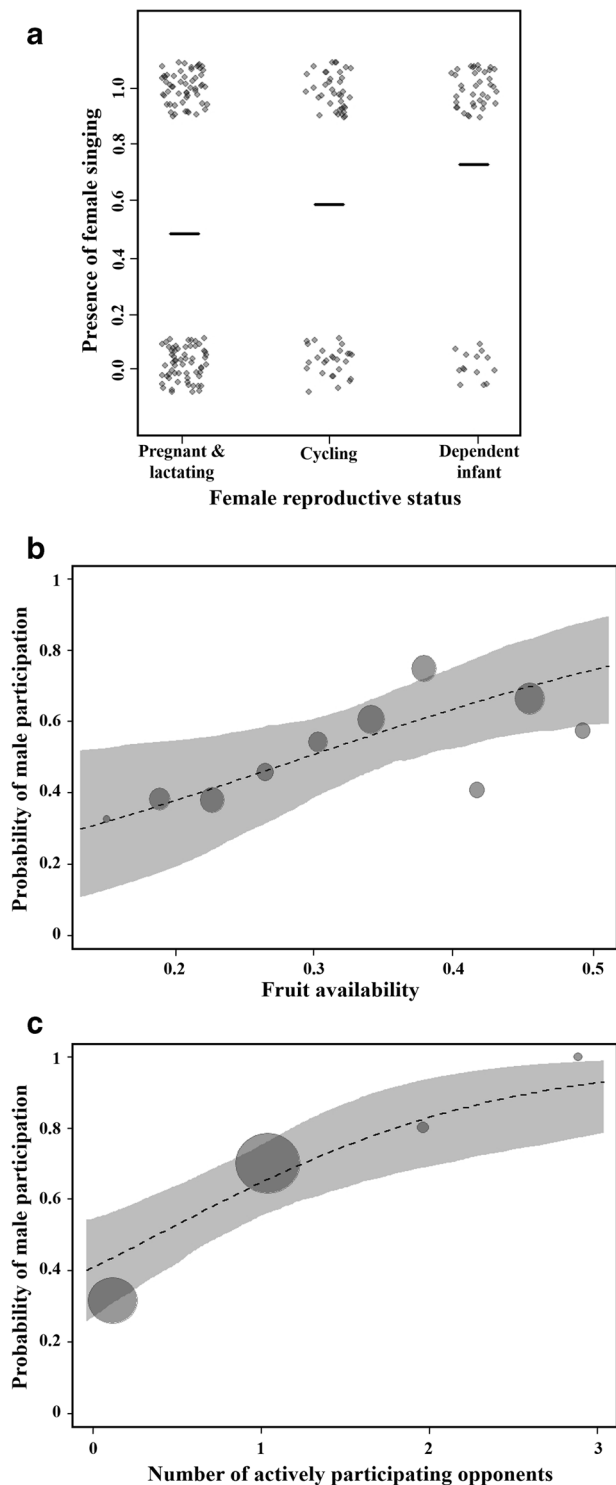


Fig. 2 Effects of (a) female reproductive status (other period, cycling, or dependent infant), (b) fruit availability, and (c) the number of actively participating opponents on probability of male participation in Javan gibbons (*Hylobates moloch*) in Gunung Halimun-Salak National Park, Indonesia, between 2009 and 2016. The bars indicate mean values of the probability of male participation for each female reproductive status when male participation absence and presence were coded into 0 and 1 respectively. The bubble size indicates the sample size for each data point (b) $N = 3$ to 22, (c) $N = 3$ to 142) and the shaded areas represent the 95% confidence intervals

defense hypotheses best predicted male participation in inter-group encounters.

Mate defense hypothesis

Javan gibbon males participated more often when cycling females were present, supporting the mate defense hypothesis. Moreover, Javan gibbon males immediately chased opponent males back when their pair-mates were chased, also supporting the mate defense hypothesis. This appears to be a highly effective strategy to defend females and/or to prevent potential extra-pair copulations, considering that extra-pair copulations occur exclusively during inter-group encounters in other gibbon species (*S. syndactylus*: Palombit 1994; *H. lar*: Bartlett 2003; *N. c. jingdongensis*: Huang et al. 2013). Males also participated more often when in the opponent group more individuals were actively participating in the inter-group encounters, suggesting that they actively adjust their fighting power to that of the opponent group, a phenomenon that has also been observed in Verreaux's sifakas (Koch et al. 2016b).

The probability of winning an encounter was only predicted by the presence of cycling females in a group, which again supports the mate defense hypothesis. Interestingly, winning in Javan gibbons was not achieved by higher levels of aggression (i.e., chasing frequency). Inter-group encounters in Javan gibbons lasted on average for 80 min and often ended long after the last aggressive interaction took place. In contrast, in blue monkeys (*Cercopithecus mitis*), a losing group usually retreated almost immediately after the last aggressive interaction (Roth and Cords 2016). Hence, Javan gibbons may use a different tactic to win a conflict, and probably to defend their mate, by withstanding and not giving up on the area by moving away. The mate defense hypothesis might be of particular importance for male gibbons, because gibbons have a relatively slow development with long interbirth intervals (ca. 41 months: *H. lar*: Reichard and Barelli 2008; about 43 months: Javan gibbons in the study population), and males may face high reproductive costs when females copulate with extra-pair males.

Infant defense hypothesis

Because male Javan gibbons also participated more often in inter-group encounters when their own infants were dependent, participation may also serve to defend dependent infants from a potential risk of infanticide. Losing an infant might be especially costly for Javan gibbons due to the slow development and long interbirth intervals. However, the presence of infants did not influence the probability of participating in an inter-group encounter in females. Since female Javan gibbons mainly participate by singing and not by chasing, infants

Table 5 Effects of fruit availability, female reproductive status, and the presence of a singing opponent female on the presence of female song during inter-group encounters in Javan gibbons (*Hylobates moloch*) in Gunung Halimun-Salak National Park, Indonesia, between 2013 and 2016

	CI (lower, upper)	Estimate	Std. error	z	p
Fruit availability ¹	−0.613, 0.906	0.183	0.277	0.659	0.510
Female reproductive status					
Cycling female	−0.278, 2.885	1.319	0.594	2.223	0.026*
Dependent infant	−0.984, 1.997	0.562	0.747	0.753	0.451
Presence of a singing opponent female	0.813, 3.698	2.224	0.537	4.139	<0.001***

* < 0.05; ** < 0.01; *** < 0.001—significance levels

¹ z-transformed; mean ± SD of the original value: ¹ 0.39 ± 0.05

might not be exposed to potential injuries or infanticide during inter-group encounters in contrast to other primates such as vervet monkeys or Verreaux's sifakas (Arseneau-Robar et al. 2016; Koch et al. 2016a).

Food resource defense hypothesis

Javan gibbon males participated more often in inter-group encounters, when fruit availability was higher, contradicting prediction of the food resource defense hypothesis (Reichard and Sommer 1997; Cooper et al. 2004; Korstjens et al. 2005; Thompson et al. 2012). Since participation might be energetically costly, males may participate more often when more food is available. Similarly, Tai chimpanzees were engaged more often in territorial activities during periods of high food availability because individuals might have been in a better physical condition, a direct correlate of fighting abilities (*Pan troglodytes verus*: Herbinger et al. 2001).

Moreover, figs, the preferred food item for Javan gibbons (Kim et al. 2012), are difficult to defend because they are fruiting asynchronously (Janzen 1979; Kinnaird et al. 1999). In contrast, other gibbon species usually defend their main fruiting trees of non-fig species, whereas figs serve only as fallback food (Leighton 1983; Reichard and Sommer 1997; Harrison and Marshall 2011). Therefore, the food defense may have a different mechanism for Javan gibbons in comparison to other gibbon species (*H. lar*: Reichard and Sommer 1997). For instance, male Javan gibbons may participate in inter-group encounters more often when food availability is high because they might be in better condition. When less food is available, they may focus more on foraging and saving energy, rather than competing with other groups over limited food sources which anyway may not be defensible.

While fruit availability can be a temporal index to test the food resource defense hypothesis, the intensity of space use prior to an encounter can represent a spatial index to test the (food) resource defense hypothesis. Considering that the universally used definition of

outcome of inter-group encounters (i.e., a winning group stays longer in the encounter location) is location-based, the intensity of space use prior to an encounter can well reflect the spatial perspective of food resources for animals. However, the intensity of space use at the encounter location in any time period (i.e., 1, 3, and 6 months preceding encounter events) did not predict the outcome of inter-group encounters in Javan gibbons in this study. On the contrary, in other territorial primates such as Verreaux's sifakas (Koch et al. 2016b), yellow baboons (*Papio cynocephalus*: Markham et al. 2012), and blue monkeys (*Cercopithecus mitis*: Roth and Cords 2016), the relative intensity of space use predicted the outcome of inter-group conflicts, with groups using the area more intensively being more likely to win the encounter because these areas might have been more valuable for them (i.e., probably more feeding occurred in the area). In addition, in Verreaux's sifakas and yellow baboons winning groups used the encountered area after an encounter more often than losing groups, indicating that losing an encounter can result in longer-term disadvantages (Markham et al. 2012; Koch et al. 2016b). It is possible that the intensity of space use may not represent a good proxy to assess the potential value of the used area in Javan gibbons. However, the fact that Javan gibbons did not win conflicts more often in intensively used areas may suggest that the outcome of encounters might not be associated with critical dis/advantages in Javan gibbons. For instance, regardless of the outcome of inter-group encounters, Javan gibbons rather avoid potential inter-group encounters by sleeping further away from aggressive encounter locations (Yi et al. 2020a). Given the frequent inter-group encounters in overlapping areas, winning Javan gibbon groups might not be expected to monopolize the area for long-term because they share a large portion of their home ranges with other groups' and are able to cross their home range multiple times a day (mean home range 38.8 ha (range 25.6–53.5 ha); this study, mean daily path lengths 1488 m (range 638–3300 m); Ham et al. 2017). Hence, the (food) resource

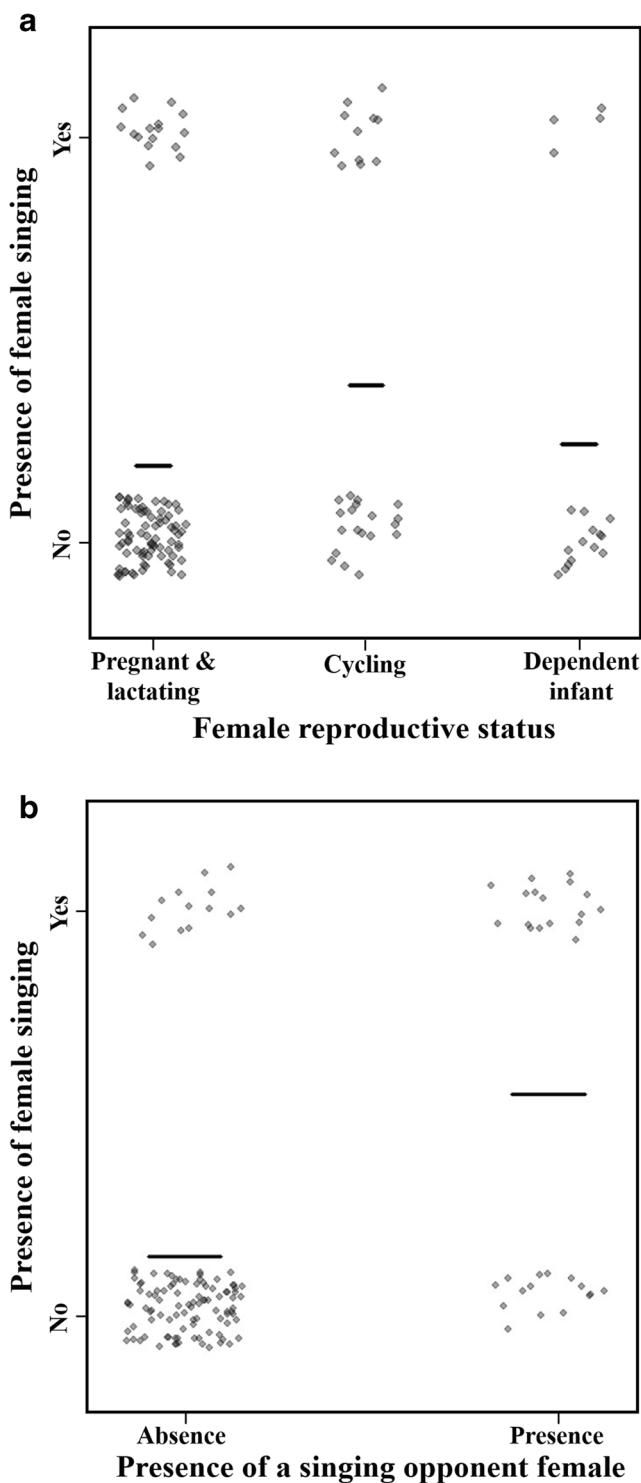


Fig. 3 Effect of (a) female reproductive status (other period, cycling, or dependent infant) and (b) presence of a singing opponent female (absence or presence) on the presence of female song during inter-group encounters in Javan gibbons (*Hylobates moloch*) in Gunung Halimun-Salak National Park, Indonesia, between 2013 and 2016. The bars indicate mean values of the probability of female singing. Presence and absence of singing opponent female were coded into 0 and 1 respectively

defense hypothesis may not explain participation in inter-group encounters in Javan gibbons.

Mate attraction hypothesis

Javan gibbon females participated more often in inter-group encounters by singing, when they were cycling and when the female of the opponent group also sang. Hence, female songs of this non-duetting species might function to attract extra-group males when they are cycling, which in turn may trigger opponent females to follow singing to advertise their presence. Since singing, especially the long-distance calls that female gibbons produce, is costly, it might have evolved to signal female's physical condition and, hence, fighting ability (Vehrencamp 2000; Terleph et al. 2016). In other gibbon species, female-female replacements have been observed several times (*H. lar*: Reichard et al. 2012; Terleph et al. 2016), suggesting that females may face strong intra-sexual competition over territories (Sommer and Reichard 1997). In addition, the song of females during inter-group encounters has been suggested for some gibbon species to function in intra-sexual competition (Raemaekers et al. 1984; Mitani 1985; Raemaekers and Raemaekers 1985a; Cowlshaw 1992). Hence, the song of female Javan gibbons during inter-group encounters may have a dual function: to attract extra-group males when females are cycling but also in intra-sexual competition.

Conclusion

In conclusion, our results indicate that in Javan gibbons, socio-ecological factors affected individual participation in inter-group conflicts, differently in males and females. Males participate mainly by chasing opponents to defend mates and infants but not food resources. Females, in contrast, participate mainly by singing, most likely to advertise their reproductive status. The probability to win an encounter was predicted by female's reproductive status but not by the relative intensity of space use providing additional support for the mate defense hypothesis for males but no support for the food resource defense hypothesis. Since Javan gibbons frequently encounter neighboring groups and easily cross their home ranges several times a day, they may rely on a strategy of frequently checking overlapping areas and exhibit moderate levels of aggression such as non-lethal chasing of their "dear enemy" (Fisher 1954) during inter-group encounters. The mate and infant defense appear to predict best participation during inter-group encounters in pair-living species because costs of extra-group copulations and infanticide risk might be relatively higher in pair-living than in group-living species.

Table 6 Effects of the female reproductive status, intensity of space use over 1 month, 3 months, and 6 months, the number of actively participating opponents, and proportion of chasing frequency (“focal chasing frequency” divided by “focal and non-focal chasing frequency”)on the outcome of the inter-group encounter (win vs. lose) in Javan gibbons (*Hylobates moloch*) in Gunung Halimun-Salak National Park, Indonesia, between 2014 and 2016

	CI (lower, upper)	Estimate	Std. error	z	p
1-month overlap					
Female reproductive status					
Cycling female	0.373, 2.860	1.568	0.628	2.496	0.012*
Dependent infant	-2.255, 0.941	-0.577	0.804	-0.718	0.473
Intensity of space use (1 month)	-0.383, 0.651	0.132	0.259	0.507	0.612
Number of actively participating opponents ¹	-0.847, 0.393	-0.202	0.307	-0.658	0.510
Proportion of chasing frequency	-0.372, 0.927	0.270	0.327	0.825	0.409
3-month overlap					
Female reproductive status					
Cycling female	0.432, 2.944	1.635	0.635	2.577	0.010**
Dependent infant	-2.162, 1.041	-0.483	0.805	-0.600	0.549
Intensity of space use (3 months)	-0.277, 0.796	0.251	0.270	0.929	0.353
Number of actively participating opponents ¹	-0.906, 0.357	-0.241	0.313	-0.770	0.441
Proportion of chasing frequency	-0.451, 0.872	0.207	0.333	0.622	0.534
6-month overlap					
Female reproductive status					
Cycling female	0.406, 2.949	1.620	0.641	2.527	0.012*
Dependent infant	-2.309, 0.888	-0.632	0.803	-0.787	0.431
Intensity of space use (6 months)	-0.290, 0.855	0.270	0.288	0.936	0.349
Number of actively participating opponents ¹	-0.879, 0.371	-0.223	0.309	-0.722	0.470
Proportion of chasing frequency	-0.437, 0.880	0.217	0.332	0.654	0.513

* < 0.05; ** < 0.01; *** < 0.001—significance levels

¹ z-transformed; mean ± SD of the original value: ¹ 1.11 ± 0.41

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Data availability The data used for this study are available from the corresponding author on request.

Compliance with ethical standards

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

Ethical approval This study involved observation of animals in their natural habitat and was not disruptive to the subjects and the ecosystem. Our research protocol was approved by the Indonesian Ministry of Research and Technology (RISTEK; SIP: 375/SIP/FRP/SM/X/2014, 91/P/TNGHS/2015, 652/FRP/SM/VI/2015), the Indonesian Ministry of Forestry’s Department for the Protection and Conservation of Nature (PHKA), and the Gunung Halimun-Salak National Park.

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