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By: Soojung Ham, **Susan Lappan**, Daniela Hedwig, and Jae Chun Choe


Abstract

Duets in territorial, pair-living primates may function to maintain intragroup cohesion, promote intergroup avoidance, and assist in territorial and resource defense, as well as advertising and reinforcing pair bonds. Despite the absence of duetting in Javan gibbons (*Hylobates moloch*), recent playback experiments suggested that Javan gibbon songs also play a role in pair-bond advertisement as well as territorial and mate defense. However, playback experiments only assess motivations of the listener, which may not reflect the motivations of the caller. We conducted an observational study of naturally occurring female songs in two groups of Javan gibbons from July 2009 to March 2010 and from March to November 2011 in Gunung Halimun–Salak National Park, Indonesia. We investigated female singing rates in relation to singing location, daily path length, occurrence of intergroup encounters, feeding rate, allogrooming rate, and distance between pair mates. The two females produced 47 songs during 164 observation days. Females in the area of their home range that overlapped with neighboring groups sang more frequently than expected based on time spent in the area of overlap vs. the home range interior. Groups also had longer daily path lengths on days when females sang than on nonsinging days, and on days when they visited the area of overlap than on nonvisiting days. Our findings indicate that, like the duets of other pair-living territorial primates, female Javan gibbon songs function for territorial defense, but we found no support for other functions such as intergroup avoidance, resource defense, and pair-bond reinforcement.

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Female Songs of the Nonduetting Javan Gibbons (*Hylobates moloch*) Function for Territorial Defense

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than expected based on time spent in the area of overlap vs. the home range interior. Groups also had longer daily path lengths on days when females sang than on nonsinging days, and on days when they visited the area of overlap than on nonvisiting days. Our findings indicate that, like the duets of other pair-living territorial primates, female Javan gibbon songs function for territorial defense, but we found no support for other functions such as intergroup avoidance, resource defense, and pair-bond reinforcement.

Keywords Nonduetting gibbons · Primate long-distance calls · Ranging behavior · Social monogamy · Song functions

Introduction

Many animal taxa produce long-distance calls, which are conspicuous acoustic signals audible to listeners far from the caller (Ryan and Kime 2003). In primates, these calls appear to play a role in intra- and intergroup communication, and to serve functions including intragroup cohesion (Cleveland and Snowdon 1982; Riley 2005), intergroup avoidance (Chivers 1969; Waser 1977), and territorial or resource defense (Wich *et al.* 2002). In many territorial, pair-living primate species, including members of several major primate radiations, e.g., titi monkeys (Müller and Anzenberger 2002) and tarsiers and gibbons (Haimoff 1986), long-distance calls are performed as duets, in which a paired male and female sing simultaneously in a coordinated manner. Duets appear to serve several of the same functions as solo long-distance calls in other species, including intragroup cohesion (MacKinnon and MacKinnon 1980; Robinson 1979), intergroup avoidance (Kinzey and Robinson 1983), and defense of important food resources (Rasoloharijaona *et al.* 2006) or territories (Gursky 2000; Kinzey and Becker 1983), but duets have also been proposed to function in pair-bond advertisement (Cowlshaw 1992) and reinforcement (Mendez-Cardenas and Zimmermann 2009).

Among duetting primate taxa, gibbons (Hylobatidae) have been the subject of relatively extensive research focusing on the functions of duets. Gibbons include circa 19 species (Chivers *et al.* 2013) of diurnal, arboreal primates that live in the canopies of forests in South and Southeast Asia and southern China. Gibbon groups usually contain a single adult male, a single adult female and up to four immature individuals (Bartlett 2007), although other group structures have been reported (Malone and Fuentes 2009). Pairs are generally stable for long periods of time and usually display evidence of pair bonding such as spatial cohesion, affiliative behavior, and high levels of aggression toward same-sex adults (Bartlett 2007). In most gibbon taxa, each group defends a territory of around 40 ha (range 5 to >100 ha), with some overlap between the home ranges of neighboring groups (Bartlett 2007). When neighbors meet, chases and contact aggression can occur during interactions that can last for ≥ 60 min (Bartlett 2009b; Ellefson 1968; Gittins 1984; Ham *et al.* 2016).

Most gibbons produce long and loud duets, usually in the morning (Geissmann 2000, 2002). Four hypotheses about the functions of gibbon duets have been proposed (Table I). First, duets may play a role in territorial defense by advertising territorial boundaries (Ellefson 1968; Mitani 1985a). Gibbons may interpret songs as indicating ownership of the singing location (Ellefson 1968; Mitani 1985a). For example, Bornean gibbons (*Hylobates muelleri*) usually duet near the area of home range overlap with neighboring

Table I Hypotheses and predictions tested to investigate the functions of female songs in Javan gibbons in Gunung Halimun–Salak National Park

Proposed song functions	Predictions
Territorial defense	1A. Female gibbons sing more frequently when ranging in the area of overlap than expected based on the proportion of time they spend in the area of overlap and the interior of their home range.
	1B. Gibbon groups have longer daily path lengths on days when females sing compared to days when females do not sing.
Intergroup avoidance	2A. Intergroup encounters are less frequent on days when females sing compared to days when females do not sing.
Resource defense	3A. Female singing behavior is temporally associated with high rates of feeding on preferred fruit species near the singing location.
Pair-bond reinforcement	4A. Pair mates groom more frequently on days when females sing compared to days when females do not sing.
	4B. Pair mates maintain closer interindividual distances on days when female sing compared to days when females do not sing.
	4C. Female singing leads to a decrease in distance between the female and her pair mate.

groups (Mitani 1985a; hereafter referred to as the area of overlap). In addition, gibbons may travel throughout their territory to detect and repel intruders (Cheney 1987; Chivers and MacKinnon 1977). Accordingly, singing and traveling may be associated and gibbons may show increased daily path length (DPL) on days when they sing in the morning. However, this possibility has not yet been examined empirically. Second, gibbon songs may promote intergroup avoidance to minimize the costs of aggression between neighbors (Chivers 1976). Playback experiments with gibbons have not found evidence of intergroup avoidance (Ham *et al.* 2016; Mitani 1984, 1985a, b, 1987; Raemaekers and Raemaekers 1985), but observational studies of singing behavior are needed to test this hypothesis further. A third alternative is that gibbon duets may announce ownership of resources (Fan *et al.* 2009; Kinnaird and O'Brien 2005), resulting in higher rates of singing when ranging near important food patches than in other locations. For instance, siamangs (*Symphalangus syndactylus*) and black-crested gibbons (*Nomascus concolor*) sing more frequently near important food patches than in other locations (Fan *et al.* 2009; Kinnaird and O'Brien 2005). Finally, gibbon songs may play an important role in announcing (Cowlshaw 1992; Fan *et al.* 2009; Leighton 1987) or reinforcing pair bonds (Fan *et al.* 2009; Geissmann and Orgeldinger 2000). In siamangs, singing rate correlates positively with other indicators of pair-bond strength, such as the rate of allogrooming and closer proximity between pair mates (Geissmann and Orgeldinger 2000). In addition, paired male and female black-crested gibbons show decreased interindividual distances after singing (Fan *et al.* 2009).

Two gibbon species, Javan gibbons (*Hylobates moloch*) and Kloss's gibbons (*Hylobates klossii*), do not produce duets, but perform solo songs (Geissmann and Nijman 2006; Kappeler 1984; Tenaza 1976; Whitten 1982). Researchers have generally assumed that solo songs are not associated with pair-bond advertisement or reinforcement. For example, researchers have hypothesized that male songs in Kloss's gibbons

may function to attract mates, while female songs may play a role in maintaining territorial boundaries (Dooley *et al.* 2013; Tenaza 1976), but these ideas have not been systematically tested. In addition, songs of female Javan gibbons may function in resource defense, because females appear to sing more frequently close to large fruit patches near the territorial border (Kappeler 1984). However, more quantitative studies are needed to understand fully the functions of songs in nonduetting gibbon species.

The results of a recent study using playback experiments suggest that the solo songs of Javan gibbons convey information not only about individual identity and location, but also the paired status of the caller (Ham *et al.* 2016). These results imply that Javan gibbon songs, like those of duetting gibbon species, may function in pair-bond advertisement as well as for defense of territories or resources. However, playback experiments provide information only about how listeners perceive calls. Additional information about the motivation of the caller is necessary to fully understand the functions of these vocalizations. We used observational data from two groups of wild Javan gibbons to test predictions of the four hypotheses concerning the functions of female solo songs in this species (Table I). Because male Javan gibbons rarely sing (Geissmann and Nijman 2006; Kappeler 1984), we focused on investigating female songs only.

Methods

Study Site and Subjects

We collected behavioral data from two habituated gibbon groups from July 2009 to March 2010 and from March to November 2011 at the Citalahab study area in Gunung Halimun–Salak National Park (GHSNP; 6°42'S, 106°27'E) in West Java, Indonesia. The study site is located in an area of primary submontane forest (950–1100 m asl). Mean monthly rainfall during the study period was $331 \pm \text{SD } 195$ mm/mo (range: 29–712 mm/mo). The two study groups (Table II) have been the subjects of a long-term research program since 2007 (Kim *et al.* 2011, 2012) and were completely

Table II Compositions of the two study groups of Javan gibbons in Gunung Halimun–Salak National Park between July 2009 and November 2011

Group	Adult	Juvenile	Infant
A	Aris (male; paired with Ayu) Ayu (female; paired with Aris; parous) Asri (female; unpaired; nulliparous; emigrated August 2011)	Amran (female)	Amore (male; born January 2011)
B	Bang Kumis (male; paired with Bu Ketu) Bu Ketu (female; paired with Bang Kumis; parous)	Bayi Kumkum (male; born July 2007)	Bayi Kimkim (male; born April 2011)

Age classes are based on Brockelman *et al.* (1998): infant (0–2 years), juvenile (2–5 years), adolescent (5–8 years), adult (8+ years)

habituated to human observers when we initiated this study. Home ranges of the two groups were adjacent to each other.

Data Collection

S. Ham and three field assistants collected behavioral data on the two study groups during all-day follows (from sleeping tree to sleeping tree) for 3 consecutive days whenever possible, resulting in a total of 202 all-day follows (group A: 119 days; group B: 83 days). We used scan sampling (Altmann 1974) to record the behavior and location of adult individuals in the groups at 15-min intervals. We categorized gibbon behaviors as resting (stationary and not engaging in other activities), feeding (collecting and eating food), traveling (brachiating, jumping, or walking), allogrooming, singing, or other (drinking, defecating, urinating, or playing; we grouped play with these other variables because our focus was on adult behaviors, and we never observed social play involving two adult individuals). To record the location of the gibbons, we mapped the tree occupied by each individual within a system of x/y coordinates established within a 200×200 m grid of trails overlaying the study area (Kim *et al.* 2011, 2012) using a compass and rangefinder. For each occurrence of singing or allogrooming between paired male and female gibbons, we recorded the start and end times of these behaviors. We also recorded the location of the tree that the individuals occupied at the onset of singing. We defined a song as a singing event separated by an interval of >5 min from other songs by the same individual (Geissmann and Nijman 2006). We heard only 10 male songs during the study period, of which only two were produced by the males in the two study groups. We excluded from the analysis 37 days for which <6 h of observational data were available, and 1 day in which the female in group B sang twice. During the remaining 164 days (group A: 96 days; group B: 68 days; observation duration, and start and end times of data collection are shown in [Supplementary Materials](#)) the focal females produced 47 songs (group A: 27 songs; group B: 20 songs). Although previous researchers have suggested several song types for Javan gibbon songs (Geissmann and Nijman 2006; Kappeler 1984), we grouped the two most common types of female song bouts[^] and bscream bouts[^] together, because we did not find a significant difference in start time, duration, context, or location between these song types at our study site (S. Ham, *unpubl. Data*). Whenever we visually detected neighboring groups <50 m from the focal group, we recorded the occurrence of an intergroup encounter.

We recorded total daily precipitation at circa 05:00 h daily using a standard rain gauge set outside of our research station <50 m from the two groups' home ranges. Because of the potential effects of food availability on gibbon behavior (Bartlett 2009a; Fan and Jiang 2008; Kim *et al.* 2012), we monitored plant food production using 15 phenology plots established before our study (Kim *et al.* 2012) at random trail junctions within the grid of trails overlaying the study area. The 10×50 m phenology plots, all of which were located within the home ranges of the two study groups, contained 119 individual trees (diameter at breast height [DBH] >10 cm) of 27 tree species eaten by Javan gibbons at this and other sites (Kappeler 1984; Kim *et al.* 2012). Five food trees died during the study, leaving 114 in November 2011. We calculated monthly food availability as the proportion of food trees producing each type of food item (fruits, flowers, or new leaves) at the end of each month and used this variable as a control predictor in some analyses.

Estimation of Home Range and Overlap Area

We estimated home ranges of the two study groups and areas of overlap with five other neighboring groups (groups C, D, E, O, and S; Fig. 1) using 100% minimum convex polygons (MCPs) that we generated with the function `mcp` in the R package `adehabitatHR` (Calenge 2006) in R 3.0.2 (R Development Core Team 2013) and Geospatial Modeling Environment v0.7.2.0 (Beyer 2012) with ArcMap 10 (ESRI 2011) based on 5533 location points (group A: 3166 points; group B: 2367 points) recorded during scan sampling and 97 locations of intergroup encounters. To achieve a larger sample for home range estimation, we used the location coordinates from adult males because when the paired female moved separately from the male, we followed the male, which led to more missing data for females. This should not be problematic because gibbon group members, including tightly bonded pairs, are usually spatially cohesive (Bartlett 2007; Raemaekers and Raemaekers 1985). The home range of group A was 36 ha in size and the group B home range was 54 ha, with a mean of 4.6 ha (10%) overlap with neighboring groups.

Data Analysis

Territorial Defense Hypothesis To test if female gibbons sang more frequently than expected when ranging in the area of overlap, we used a chi-square test (Table III; prediction 1A). We compared the observed frequencies of singing in the area of overlap and in the interior of the home range to frequencies expected based on the number of scans in which the gibbons were ranging in the area of overlap and the interior. To control for spatial autocorrelation among locations recorded in subsequent scans and for the potential effect of time of day on singing behavior (Geissmann and Nijman 2006; Kappeler 1984), we used a

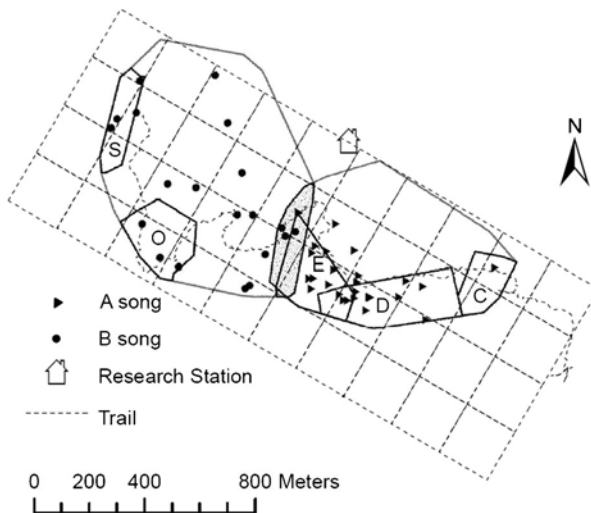


Fig. 1 Home ranges of study groups A and B in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011. The area of overlap between group A and group B is stippled. The letters C, D, E, O, and S indicate the approximate areas of overlap with other neighboring groups.

Table III Overview of statistical tests and models used to test hypotheses concerning the functions of female Javan gibbon songs in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011

Hypothesis	Prediction	Sample size	Test	Error structure, link function	Response variable	Test predictor	Control predictor
Territorial defense	1A	600 scan samples	Chi-square	—	Female song (yes/no)	Ranging location	—
	1B	115 days	GLM	Gaussian, identity	DPL (m)	Female song (yes/no)	Group ID (in interaction with test predictor) Daily total precipitation (mm) ^a Monthly fruit availability Monthly flower availability Clinging infant present (yes/no) Daily observation duration (offset term) ^a
Intergroup avoidance	2A	146 days	GLM	Binomial, logit	Encounter (yes/no)	Female song (yes/no)	Group ID (in interaction with test predictor) Daily total precipitation (mm) ^a Daily mean distance from animal to closest border point (m) Observation duration after female song (offset term) ^a
Resource defense	3A	47 singing locations	GLMM	Binomial, logit	Female song (yes/no)	Number of feeding scans from preferred fig fruit species/cell Number of feeding from preferred nonfig species/cell	Group ID (in interaction with test predictor) Daily mean precipitation (mm) Number of scans/cell (offset term) ^a Random intercepts for cell ID Random slopes of fixed effects within cell ID

Table III (continued)

Hypothesis	Prediction	Sample size	Test	Error structure, link function	Response variable	Test predictor	Control predictor
Pair-bond reinforcement	4A	163 days	GLM	Binomial, logit	Groom (yes/no)	Female song (yes/no)	Group ID (in interaction with test predictor) Daily total precipitation (mm) ^a Clinging infant present (yes/no) Percentage of valid scans
	4B	163 days	GLM	Gaussian, identity	Daily mean distance between mates ^a	Female song (yes/no)	Group ID (in an interaction with the test predictor) Daily total precipitation (mm) ^a Clinging infant present (yes/no) Percentage of valid scans
	4C	22 songs	Wilcoxon	—	Distance between mates	Before vs. after start of singing	—

The sample size was 164 days, but in some models we excluded days in which the observers terminated all-day follows early because of heavy rainfall or lost contact with one of the focal individuals

^a We log transformed these variables because the distribution was right skewed

randomly selected subsample of the data. For each hour of the day, we randomly selected 50 scans (sampling time range: 06:10–18:05 h) from the available scan data (sample sizes range from 73 to 598 scans for different hours of the day). From this subsample, we calculated the number of scans occurring in the area of overlap and the interior of the home range and the number of singing locations recorded in the area of overlap and the interior using the function `SpatialPoints` in the R package `sp` (Bivand *et al.* 2013; Pebesma and Bivand 2005).

To test if gibbons had longer DPL on days when females sang compared to days when females did not sing, we used a generalized linear model (GLM; McCullagh and Nelder 1989; Table III; prediction 1B). We calculated DPL by summing the straight-line distances traveled during each 15-min interval in a day. Because DPL correlated positively with daily observation duration (Pearson correlation, $r = 0.44$, $t = 5.24$, $df = 113$, $P < 0.001$) even after we excluded days when follows were incomplete, we controlled for the possible effect of daily observation duration on DPL by including observation duration as an offset term in the model. We also included fruit and flower availability as control predictors to control for the effect of food availability on DPL (Bartlett 2009a; Fan and Jiang 2008; Kim *et al.* 2012). In addition, we included the presence of a clinging infant as a control predictor in the model to control for the possible effect of infants on female travel distance because a clinging infant may inhibit movement (Bartlett *et al.* 2016). To examine in addition the possible relationship between the two predictions of the territorial defense hypothesis (prediction 1A and 1B), we used a Mann–Whitney U test to test if gibbons traveled longer on days when gibbons visited the area of overlap compared to days when they did not visit the area of overlap.

Intergroup Avoidance Hypothesis To test if intergroup encounters were less frequent on days when females sang than on days when females did not sing, we used a GLM (Table III; prediction 2A). Because this test aimed to investigate the effect of female singing on the rate of intergroup encounters, rather than the effect of intergroup encounters on female vocal behavior, we excluded 18 days in which gibbons sang after encounters. To control for the effects of proximity to the border on the probability of encounters, we included the daily mean distance from the scans to the closest border point for the home ranges as a control predictor. We calculated distance using the function `mcp` in the R package `adehabitatHR` (Calenge 2006). To control for the possible effect of observation duration on the probability of observing an intergroup encounter, we also included observation duration after female songs as an offset term.

Resource Defense Hypothesis To test if females were more likely to sing in specific locations during time periods when they fed on preferred fruit species at high rates than during times when they fed on preferred fruit species at low rates, we used a generalized linear mixed model (GLMM; Baayen 2008; Table III; prediction 3A). We compared the number of scans in which gibbons fed on preferred fruits at singing locations during the time periods in which female gibbons produced songs to the number of scans in which the gibbons fed on preferred fruits at the same location during time periods in which we observed no singing. For this analysis, we

created circular cells with a radius of 50 m around each singing location to ensure that we included all candidate food trees within a biologically relevant distance from the calling site within the cells. Gibbon groups often react to the presence of other groups ranging ≤ 50 m away by orienting to the other group, singing, displaying, or initiating chases, indicating the salience of this distance in the context of resource ownership (Ellefson 1968).

For each cell, we then calculated the number of scans during which the female was feeding on food patches of preferred fruit species for a period of 15 days, including 7 days before and 7 days after a singing day. We compared this number to the number of scans during which the female was feeding on preferred fruits at the same location during a randomly selected 15-day period in which we observed no singing. We randomly selected periods with a minimum interval of 30 days from the period in which we observed singing ($437 \pm \text{SD } 266$ days) to avoid sampling adjacent time periods. We defined preferred fruit species as species with a preference index >2.5 in a previous study of Javan gibbons at this site (Kim *et al.* 2012). We investigated the effect of feeding on fig species *Ficus* sp. and nonfig fruit species separately because figs are highly preferred and their large fruit crops and asynchronous fruiting make them particularly important gibbon foods (Kim *et al.* 2012). Because we lacked detailed information about the phenology of each fruit species, we chose a period spanning 15 days for this analysis based on the estimated duration of feeding for a typical patch of highly preferred fruit at this site during a single fruiting event (S. Kim, *pers. comm.*). We chose to base our analysis on a sampling design aimed at measuring feeding rates around singing locations to maximize our sample size, but, based on the assumption that food availability can affect singing but not vice versa, we included the number of feeding scans in the model as test predictors and the occurrence of female song (yes/no) as a response variable (Table III).

To account for potential spatial autocorrelation, we combined cells for songs produced <50 m apart (equivalent to 39% cell area overlap) under the same cell ID in the analysis, as overlapping cells are not independent. To account for the influence of observation duration in the different cells on the number of feeding scans, we included the number of scans per cell as an offset term in the model because the number of scans per cell will approximate the actual observation duration. In addition, we included random slopes of the three fixed effects within cell ID and random intercepts for each level of the variable cell ID (Barr *et al.* 2013; Schielzeth and Forstmeier 2009).

Pair-Bond Reinforcement Hypothesis To test if male–female pairs groomed more frequently and if male–female distances were lower on days when females sang compared to days when females did not sing, we used two GLMs (Table III; predictions 4A and 4B). In these models we excluded one day in which there was an outlier in our measurement of the mean distance between mates because the recorded value of 125.9 m was very large compared to the mean distance between mates of 18.5 m, and almost certainly reflected a recording error. We included the presence of a clinging infant as a control predictor in the two models to control for the possible effect of clinging infants on allogrooming and distance between pair mates because females carrying infants are still lactating, which may influence male–female interactions

(Barelli *et al.* 2011). We could not determine the location of one adult for some scans, and such events likely occur more frequently when pair mates are farther apart. Therefore, to control for the bias produced by the tendency to undersample larger interindividual distances, we also included the percentage of scans when we knew the locations of both pair mates, i.e., valid scans.

To test if male–female pairs maintained closer proximity after the female sang, we used an exact Wilcoxon test (Table III; prediction 4C) using the function `wilcox.exact` in the R Package `exactRankTests` (Hothorn and Hornik 2013) to compare male–female interindividual distances at different times. To compare the distance between mates before and after singing we selected two scans for each song. To estimate the distance between mates after singing began, we used a scan recorded during singing (11 scans, mean interval from song start time to the time of the scan: 9 min, range: 4–18 min) or just after singing (11 scans, mean interval from song end time to the time of the scan: 5 min, range: 1–13 min). For the sample of behavior before singing, we used the scan taken 30 min before the `after` scan (22 scans). For this test, we included all days in which we knew the locations of both pair mates before and during/after singing ($N = 22$ songs).

In all models, we controlled for possible group differences by including interactions between the test predictors and group ID as control predictors (Table III). We also controlled for the possible influence of precipitation in most models because rainfall has been demonstrated to affect gibbon behavior such as traveling and singing (Kappeler 1984; Whitten 1982). The models were fitted in R 3.0.2 using the function `lm` for the GLM (R Development Core Team 2013) and the function `lmer` in the R package `lme4` for the GLMM (Bates *et al.* 2013).

For all models we tested for collinearity between the predictor variables by calculating Variance Inflation Factors (VIF; Field 2005) for each predictor variable using the function `vif` in the R package `car` (Fox and Weisberg 2011) applied to a standard linear model. This procedure indicated that collinearity was not an issue, with the largest VIF of 1.46 occurring in the models for allogrooming and distance between mates. To validate the assumptions of normally distributed and homogeneous residuals for the Gaussian models, we visually inspected QQ plots and the residuals plotted against fitted values and detected no signs of violations. We also checked for model stability by excluding data points one at a time from the data set and compared the estimates of the models with those obtained when including all data points. None of the models showed instability resulting in considerable changes in the estimates. As an overall test of the influence of our test predictors on the response variable of each model, we compared the full models with all predictor variables to their respective null model lacking all test predictors, but including the same control predictors as the full model, using a likelihood ratio test and the function `anova` with argument `test` set to `Chisq` (Forstmeier and Schielzeth 2011). We used $P < 0.05$ as an indicator of statistical significance for all tests and models. For significant models, we report both the estimates for slopes and partial R^2 to indicate effect sizes. We calculated the partial R^2 of each predictor variable by first calculating the difference between the residual sum of squares of the full models and that of a reduced model lacking that predictor variable, and then dividing that value by the residual sum of squares of the reduced model (Cohen *et al.* 2003). Slope estimates specify how much

the outcome variable changed in response to changes in the predictor variable, and the partial R^2 how much of the total variation in the outcome variable was explained by variation in the predictor variable. The data analyzed here will be made available by the corresponding author upon reasonable request.

Ethical Note

Our research protocol was approved by the Animal Behavior Research Committee of Ewha Womans University, the Indonesian Ministry of Research and Technology (RISTEK), the Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature (PHKA), and GHSNP. We conducted this research in full compliance with Indonesian law.

Results

Territorial Defense

Females sang in the area of overlap significantly more frequently than expected based on the proportion of scans recorded in the area of overlap (prediction 1A; Table IV; Fig. 2). We also found a significant effect of female song on DPL (prediction 1B; Table IV). After we removed the nonsignificant interaction between female song and group ID ($P = 0.291$), the estimated slope for the song variable indicated that the two study groups traveled an average of 204 m longer on days when females performed songs (Table V; Fig. 3). The groups also had longer DPL when females had clinging infants (Table V). Gibbons also had longer DPL on days when they visited the area of overlap than on days when they did not (Mann–Whitney U test, $U = 135$, $N_{\text{visit}} = 158$, $N_{\text{no visit}} = 6$, $P = 0.002$; Fig. 4).

Table IV Results of the statistical tests and full-null model comparisons conducted to test hypotheses regarding the functions of female songs in Javan gibbons in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011

Hypothesis	Prediction	Test	χ^2	df ^a	P
Territorial defense	1A	Chi-square test	21.57	1	<0.001
	1B	GLM	3.15	2	0.047
Intergroup avoidance	2A	GLM	1.69	2	0.429
Resource defense	3A	GLMM	1.99	4	0.738
Pair-bond reinforcement	4A	GLM	0.36	2	0.834
	4B	GLM	3.72	2	0.026
	4C	Wilcoxon test	101 ^b	22	0.425

^a Indicates the differences in df between null and full models in the likelihood ratio tests

^b Indicates T^+ value of the Wilcoxon test

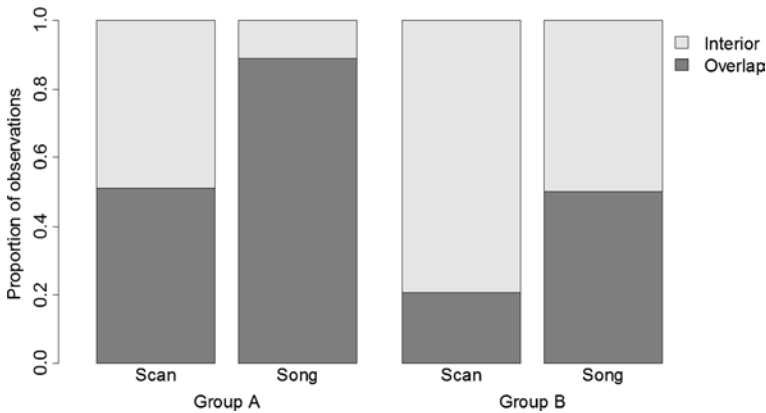


Fig. 2 Proportions of scans occurring in the area of overlap and the interior of the home ranges and the proportion of songs performed in the area of overlap and interior in two groups of Javan gibbons in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011 ($N = 339$ scans, 27 songs for group A; $N = 261$ scans, 20 songs for group B).

Intergroup Avoidance

The full model investigating the effect of female singing on the probability of intergroup encounters did not have significantly better explanatory power than the null model (prediction 2A; Table IV).

Resource Defense

The full model investigating the effect of the rate of feeding on preferred fruit species at specific locations on female singing did not have significantly better explanatory power than the null model (prediction 3A; Table IV).

Pair-Bond Reinforcement

The full model investigating the effect of female singing on allogrooming rates between mates did not have significantly better explanatory power than the null model

Table V Summary of estimates and standard errors for the generalized linear model investigating the effect of female song on daily path length in Javan gibbons in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011

	Estimate	SD	χ^2	df	<i>P</i>	R^2
Intercept	1291.015	279.267	4.62	1	<0.001	—
Female song (no = 0, yes = 1)	203.743	89.634	2.27	1	0.025	0.046
Group ID (group A = 0, group B = 1)	563.976	82.322	6.85	1	<0.001	0.303
Daily total precipitation	-26.735	34.500	0.78	1	0.440	0.006
Monthly fruit availability	24.609	1238.600	0.02	1	0.984	<0.001
Monthly flower availability	-1039.165	602.042	1.73	1	0.087	0.027
Clinging infant present (no = 0, yes = 1)	173.964	86.394	2.01	1	0.047	0.036

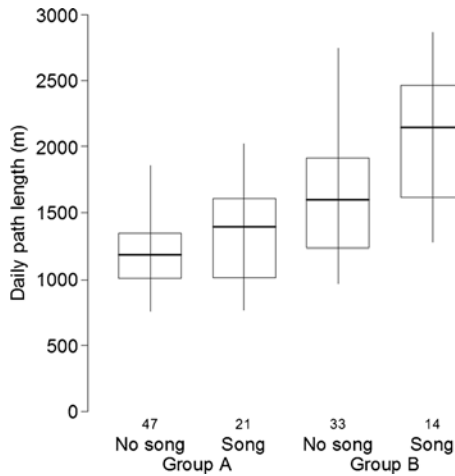


Fig. 3 Effect of female song on daily path length in two groups of Javan gibbons in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011. Shown are medians (bold lines), quartiles, and percentiles (2.5% and 97.5%). The number of samples for each combination is indicated below the boxes.

(prediction 4A; Table IV). The full model investigating the influence of female singing on daily mean distance between mates showed significantly better explanatory power than the null model (prediction 4B; Table IV). After we removed the nonsignificant interaction between group ID and female song in this model ($P = 0.064$), we found that the effect of female song was not significant (Table VI). Distances between mates were larger in group A than group B, and when the female had a clinging infant (Table VI). The mean distance between mates did not differ between measurements 30 min before singing and after female singing (prediction 4C; Table IV).

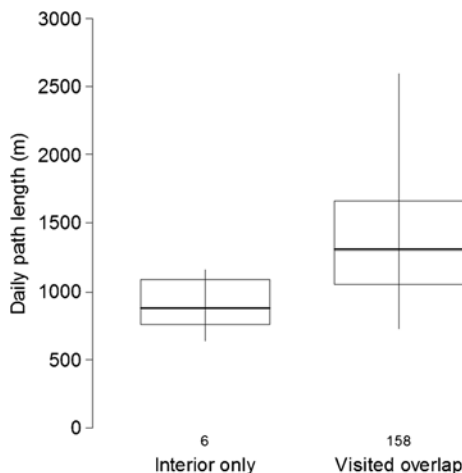


Fig. 4 Daily path length on days on which Javan gibbons visited the area of overlap and days on which they did not visit the area of overlap in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011. Shown are medians (bold lines), quartiles, and percentiles (2.5% and 97.5%). The number of samples for each combination is indicated below the boxes.

Table VI Summary of estimates and standard errors for generalized linear model investigating the effect of female song on the daily mean distance between mates in Javan gibbons in Gunung Halimun–Salak National Park from July 2009 to March 2010 and from March to November 2011

	Estimate	SD	χ^2	df	<i>P</i>	<i>R</i> ²
Intercept	2.797	0.264	10.61	1	<0.001	—
Female song (no = 0, yes = 1)	0.180	0.091	1.97	1	0.050	0.024
Group ID (A = 0, B = 1)	-0.201	0.089	2.25	1	0.026	0.031
Daily total precipitation	0.004	0.030	0.13	1	0.900	<0.001
Clinging infant present (no = 0, yes = 1)	0.201	0.093	2.15	1	0.033	0.029
Percentage of valid scans	-0.074	0.332	0.22	1	0.824	<0.001

Discussion

Our results indicate that female Javan gibbon songs function for territorial defense, but we found no support for other song functions. Females sang more frequently than expected in the area of their home ranges that overlapped with other groups, which suggests that songs may function to advertise territorial boundaries or to contest disputed areas. This is in line with studies on Bornean gibbons (Mitani 1985a) and titi monkeys (*Callicebus moloch*: Robinson 1979) showing that they call more frequently near the boundaries of their home ranges than in other areas. In addition, our study groups traveled farther on days when they visited the area of overlap compared to days when they ranged only in the interior of their home ranges. They also traveled farther on singing than on nonsinging days. The ratio of DPL to home range size is an important predictor of territoriality in primates, suggesting that territorial species need to visit opposite borders of the home range daily to monitor and prevent intrusions (Mitani and Rodman 1979). Therefore, an increase in DPL can indicate increased investment in territorial defense. For instance, chimpanzees change their movement patterns and travel longer distances on days when they patrol their territories' border (Amsler 2010).

Long-distance calls appear to help neighboring groups reduce the frequency of costly intergroup encounters in several primate species: for example, mantled howler monkeys (*Alouatta palliata*: Baldwin and Baldwin 1973; Chivers 1969) and gray-cheeked mangabeys (*Lophocebus albigena*: Waser 1977). However, our results, combined with those of previous studies, suggest that intergroup avoidance is not an important function of gibbon songs for duetting or nonduetting species. Female songs of nonduetting Javan gibbons in this study did not decrease the probability of intergroup encounters. Playback experiments also found no evidence for the intergroup avoidance hypothesis in duetting gibbon species, as movement away from the speaker was never shown (Mitani 1984, 1985a, b, 1987; Raemaekers and Raemaekers 1985). To explore further the intergroup avoidance hypothesis in gibbons, researchers need to collect detailed data on the movement of several neighboring groups simultaneously to model the effects of song on the movement trajectories of singing and listening groups.

Previous studies of the resource defense hypothesis in duetting species have provided mixed results. There are no indications of a spatial association between singing

locations and important food trees for Bornean gibbons (Mitani 1985b), but siamangs, black-crested gibbons, and Milne-Edwards's sportive lemurs (*Lepilemure edwardsi*) sing more frequently at feeding sites (Fan *et al.* 2009; Kinnaird and O'Brien 2005; Rasoloharijaona *et al.* 2006). We found no relationship between rates of feeding on important food species near singing locations and song production. However, sampling constraints forced us to test this relationship only in areas within the home range where songs were actually produced. Studies using a more refined measure of the importance of food resources and using a random set of locations to examine the relationship between availability of important foods and song production will be required for a more thorough test of this hypothesis for Javan gibbons.

Previous studies have found positive correlations between singing rates and other indicators of pair-bond strength. In siamangs, singing leads to increases in proximity between mates and allogrooming rate (Geissmann and Orgeldinger 2000). In addition, interindividual distances in black-crested gibbons decrease after singing (Fan *et al.* 2009). However, we did not detect a decrease in interindividual distances after songs nor did pair mates show significantly higher rates of allogrooming on days when the female sang in the morning. In fact, pair mates tended to have a larger mean interindividual distance on singing days than nonsinging days, which is opposite to the prediction of the pair-bond reinforcement hypothesis, although the result was not significant ($P = 0.05$). Female Javan gibbon songs may not play a role in pair-bond reinforcement, but rather may function for pair-bond advertisement. Although pair-bond reinforcement and advertisement are often grouped together, pair-bond advertisement is communication directed at individuals outside the social group, whereas pair-bond reinforcement involves communication between the pair mates. Playback experiments on Javan gibbons have demonstrated that female solo songs convey information about their mated status, suggesting that they function to advertise pair bonds in intergroup communication (Ham *et al.* 2016). We did not consider pair-bonding behaviors other than grooming and interindividual distances. However, singing can also increase behavioral synchronization between pair mates, as has been demonstrated in Milne-Edwards's sportive lemurs (Mendez-Cardenas and Zimmermann 2009) and siamangs (Geissmann and Orgeldinger 2000). Future studies should examine the relationship between solo song production and behavioral synchronization within Javan gibbon groups to investigate further whether female song may function for pair-bond reinforcement in this species.

While we found support only for the territorial defense hypothesis, our study included only two gibbon groups, which limits our ability to draw conclusions about the behavior of the population. Moreover, although there was an effect of female song on DPL, supporting the territorial defense hypothesis, the partial R^2 was low, indicating that little of the variation in DPL is explained by song production. DPL is responsive to a large number of factors, such as food availability, group composition, weather, and duration of the active period (Bartlett 2009a), none of which could be controlled in a refined manner in this study. In addition, gibbon vocalizations exhibit context-specific variation in their acoustic structure (Clarke *et al.* 2006), suggesting that songs produced in different contexts may deliver different information and have different functions (Mennill and Vehrencamp 2008). Although we could acoustically distinguish the two most common song types in Javan gibbons, female song bouts and scream bouts (Geissmann and Nijman 2006), here we grouped these songs for our analyses.

However, the functions of the two song types have not been adequately explored. Future studies investigating the social and ecological contexts in which different song types are produced by Javan gibbons will contribute to a better understanding of territoriality and the functions of solo songs and duets in gibbons.

Like female white-handed gibbons (*Hylobates lar*; Barelli *et al.* 2008), female Javan gibbons in this study appeared to lead group movements. Our results suggest that female Javan gibbons may defend their territories by announcing territorial boundaries in the area of overlap through singing and by leading daily ranging movement that includes visits to contested areas. In contrast, male Javan gibbons rarely vocalize but appear to have primary responsibility for chasing neighboring males during intergroup encounters (Kappeler 1984). Further investigation of sex differences in the costs and benefits of different types of territorial behavior may help to explain the function of songs and the loss of duetting in Javan gibbons.

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