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Song Functions in Nonduetting Gibbons: Evidence from Playback Experiments on Javan Gibbons (*Hylobates moloch*)

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Abstract Territorial, pair-living primates usually perform long-distance calls as duets in which adult males and females coordinate their calls. Previous studies using playback experiments have shown that gibbon duets convey information about the status of the caller (location, familiarity, sex of the caller, and paired status) and gibbons use this information to respond to achieve several nonmutually exclusive functions, including intragroup contact, territorial defense, and pair-bond advertisement and strengthening. However, not all pair-living gibbons duet, and it is unclear whether the same results should be expected in nonduetting species. We conducted song playback experiments ($N = 47$ trials) to test hypotheses about song functions in nonduetting gibbons on two groups of wild Javan gibbons (*Hylobates moloch*) in the Gunung Halimun-Salak National Park, Indonesia. Javan gibbons initiated movement toward the speaker more quickly in response to songs broadcast in the center of the territory, stranger songs, and songs of unpaired individuals than to songs at the border, neighbor songs, and songs from paired individuals. These results suggest that Javan gibbons can localize songs, and that Javan gibbon songs transmit information about the identity and paired status of the caller. Our results imply that Javan gibbon solo songs are likely to function for territorial defense and pair-bond advertisement like duets in other primates.

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Introduction

Long-distance calls are an important component of intra- and intergroup vocal communication in primates (Byrne 1982; Hohmann and Fruth 1995; Strier 2007; Wich and Nunn 2002). In territorial, group-living primates, long-distance calls can serve several nonmutually exclusive functions (Wich and Nunn 2002), including intragroup cohesion (Cleveland and Snowdon 1982; Riley 2005), companion recruitment (Hohmann and Fruth 1994; Mitani and Nishida 1993), intergroup spacing (da Cunha and Byrne 2006; Waser 1977; Whitehead 1989), mate or infant defense (Harris 2006; Wich *et al.* 2002a, b), and alarm calling (Byrne 1981; Zuberbühler *et al.* 1997).

Territorial, pair-living primates, including gibbons (Hylobatidae), usually perform long-distance calls as duets in which a paired adult male and female coordinate their calls in time. Duets can function for intragroup contact (Geissmann and Mutschler 2006; MacKinnon and MacKinnon 1980), intergroup spacing (Fichtel and Hilgartner 2013; Kinzey and Robinson 1983), and territorial defense (Mason 1966; Nietsch 2003; Pollock 1986), and duets may also serve to advertise and strengthen pair-bonds (Haimoff 1986; Tilson and Tenaza 1976).

Gibbon groups typically consist of an adult pair and their offspring that defend a territory of *ca.* 40 ha (although sizes may vary substantially among populations), with some overlap between the home ranges of neighboring groups (Bartlett 2007). Male–female pairs maintain close spatial proximity and generally display evidence of exclusive pair-bonds (Bartlett 2007). However, resident gibbons may experience the loss of territory or pair-bond exclusivity. Invaders can displace group adults (Fuentes 2000; Koda *et al.* 2012; Reichard 1995), and extrapair copulations (Barelli *et al.* 2013; Huang *et al.* 2013; Kenyon *et al.* 2011; Palombit 1994; Reichard 1995) and more-than-two-adult groups, including stable two-male (Lappan 2007; Malone and Fuentes 2009; Reichard 1995) and two-female (Fan *et al.* 2010; Jiang *et al.* 1999; Srikosamatara and Brockelman 1987; Zhou *et al.* 2008) groups, have been reported in several gibbon species.

Gibbon duets may play a role in territorial defense (Carpenter 1940; Ellefson 1968; Leighton 1987; Marshall and Marshall 1976; Raemaekers *et al.* 1984). In playback experiments, Bornean gibbons (*Hylobates muelleri*) and white-bearded gibbons (*H. albibarbis*) showed more intense responses to songs produced in the center of their territory (Mitani 1984, 1985a, b) and songs of unfamiliar individuals (Mitani 1987) than to songs played at the border of the territory and songs of neighboring groups. Gibbon duets may also have functions related to mate defense or pair-bond advertisement (Cowlishaw 1992; Fan *et al.* 2009; Leighton 1987). In playback experiments, Bornean gibbons, white-bearded gibbons, and white-handed gibbons (*H. lar*) showed more intense responses to songs of individuals of the same sex (Mitani 1984, 1987; Raemaekers and Raemaekers 1985), which presumably pose a higher risk of displacement or loss of parentage of future group offspring compared to individuals of the opposite sex. Furthermore, gibbons may derive information about the paired status of the caller based on whether the song is a duet or a solo song (Cowlishaw 1992; Fan *et al.* 2009; Leighton 1987). While Bornean gibbon responses to playbacks of female solo songs and duets did not differ, in white-bearded gibbons, paired males and females reacted more strongly (moving toward playback sites or producing duets) in response to playbacks of solo songs of same-sex individuals than to playbacks of duet songs (Mitani 1984, 1987).

Unlike most gibbon species, Javan gibbons (*Hylobates moloch*) and Kloss's gibbons (*H. klossii*) produce only solo songs (Geissmann 2002; Geissmann and Nijman 2006; Haimoff 1984; Kappeler 1984; Tenaza 1976; Whitten 1982). The reason for the absence of duets in these species is unknown, and songs of nonduetting gibbons may have different functions from those of duetting gibbons. In particular, solo songs may not advertise pair-bonds (Dooley *et al.* 2013; Tenaza 1976). However, the functions of songs in nonduetting gibbon species remain poorly understood, particularly because the responses to solo songs from paired and unpaired individuals have not been compared.

Here, we tested three nonmutually exclusive hypotheses about song functions in paired Javan gibbons: the territorial defense hypothesis, the mate defense hypothesis, and the pair-bond advertisement hypothesis. To test these hypotheses, we conducted a series of playback experiments in which we broadcast songs that varied in four dimensions (location of the playback, familiarity, sex, and paired status of the caller) and quantified the reaction of each adult in two groups of wild, pair-living Javan gibbons. If solo songs function in territorial defense, we predicted that Javan gibbons should start movement toward the speaker more quickly in response to playbacks in the center of their territories than at the border because intruders in the center of a territory may be interpreted as posing a greater threat to the territory (a phenomenon referred to as the "center-edge effect"; Giraldeau and Ydenberg 1987). Furthermore, we predicted quicker initiation of movement toward the speaker in response to songs of strangers than neighbors because reduced aggression between neighbors whose relationships are already settled allows animals to save time and energy (a phenomenon referred to as the "dear enemy effect"; Temeles 1994; Ydenberg *et al.* 1988). If solo songs have a mate defense function, we predicted that Javan gibbons would start movement toward the speaker more frequently or more quickly in response to songs of individuals of the same sex than to songs from individuals of the opposite sex, as same-sex individuals may pose a higher risk of displacement or loss of parentage of future group offspring (Mitani 1984, 1987; Raemaekers and Raemaekers 1985). Lastly, we hypothesized that songs of the nonduetting Javan gibbons, in contrast to those of duetting gibbon species, do not function for pair-bond advertisement, as solo songs in paired gibbons do not carry information about the paired status of the caller. Accordingly, we predicted that we would find no difference in gibbon reactions to simulated intrusions by unpaired as compared to paired individuals.

Methods

Study Site and Subjects

We conducted playback experiments in conjunction with an observational study from September 2009 to March 2010 and from March to November 2011. We followed two habituated gibbon groups 5 days a week at the Citalahab study site in the 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 hill and submontane forest (950–1100 m asl; see Kim *et al.* 2011, 2012 for a description of the study site). The two study groups have been the focus of a long-term research program since 2007. The mean home range size of these groups is 34 ha (Kim *et al.* 2011) and the home ranges are adjacent. Group compositions at the time of the study are shown in Table I.

Playback Stimuli

We recorded songs of wild and captive Javan gibbons at distances of *ca.* 20 m (wild gibbons) or *ca.* 5 m (captive gibbons) from the caller. We made recordings at a 44.1-kHz sampling rate with 16-bit amplitude resolution using a Sony PCM-D50 digital recorder and a Sennheiser directional microphone (ME66 recording head, K6 power module, and MZW66 pro windscreen). We recorded male songs from two unpaired and two paired captive gibbons at the Javan Gibbon Center (JGC) in the Gunung Gede-Pangrango National Park (GGPNP) and female songs from one paired captive individual at Ragunan Zoo, Jakarta; one unpaired and four paired captive individuals at the JGC; and one unpaired and two paired wild individuals in Cagar Alam Leuweung Sancang (CALS) for use as stranger songs. At Citalahab, we recorded female songs from paired individuals in the two study groups for use as neighbor songs in playbacks for the other group. Other researchers also provided recordings for use in this study as stranger songs (one unpaired and one paired captive male at Howletts Wild Animal Park recorded by Thomas Geissmann, one wild habituated and unpaired female in CALS by Agung Ismail, one paired wild female in the GGPNP by Dirk Meyer) or neighbor songs (one female song of the focal group A by Rahayu Oktaviani). For playback stimuli, we selected high-quality recordings with low background noise and normalized the peak level of the maximum amplitude of digital recordings to –15 using Cool Edit Pro 2.1. We standardized the duration of each stimulus to *ca.* 10 min and broadcast these 27 stimuli with a Visonik David Speaker connected to a Sony D-SJ301 S2 Sports CD Walkman.

Table I Composition of the two study groups of Javan gibbons in the Gunung Halimun-Salak National Park (GHSNP) between September 2009 and November 2011

Group	Individual	Sex	Age class	Remarks
A	Aris	Male	Adult	Paired
	Ayu	Female	Adult	Paired, parous
	Asri	Female	Adult	Unpaired, nulliparous, emigrated 2011
	Amran	Female	Juvenile	
	Amore	Male	Infant	Born 2011
B	Bang Kumis	Male	Adult	Paired
	Bu Keti	Female	Adult	Paired, parous
	Bayi Kumkum	Male	Juvenile	Born 2007
	Bayi Kimkim	Male	Infant	Born 2011

Age-class and paired status are based on Brockelman *et al.* (1998): infant (0–2 yr), juvenile (2–5 yr), adolesecent (5–8 yr), adult (8+ yr). Physiologically adult individuals were further distinguished as either breeding (paired) or nonbreeding (unpaired and, in the case of females, nulliparous).

Playback Procedure

We randomized the order of playback conditions broadcast to gibbons. We conducted 47 experiments: 24 with group A and 23 with group B. The number of trials varied across playback conditions (location: 24 trials in the center and 23 at the border; familiarity: 14 neighbor songs and 33 stranger songs; sex of the caller: 35 female songs and 12 male songs; paired status: 36 songs from paired individuals and 11 from unpaired ones), and the factors were crossed. We also presented a call of the Javan surili (*Presbytis comata*) to the study groups 10 times as a control stimulus to determine whether the playback equipment or procedure influenced gibbon responses. The Javan surili is a primate species inhabiting the same forest area at Citalahab, with home ranges overlapping those of the focal groups, but aggressive behavior toward this species was never observed.

We conducted playbacks in the morning (range: 07:22–12:23 h) during all-day follows, because Javan gibbons usually sing in the morning (Geissmann and Nijman 2006; Kappeler 1984). To ensure that the gibbons were not distracted, we conducted playbacks when the group was stationary, i.e., when resting, feeding, or grooming. To avoid any influence of previous singing or intergroup encounters on the days of the experiments, we conducted experiments ≥30 min after singing from the study group or neighboring groups or intergroup encounters on days when these behaviors occurred naturally. To prevent gibbons from being accustomed to the playbacks, we never conducted playbacks to the same groups on consecutive days (mean trials = 1.71 ± SD 1.33 per month for group A; 1.64 ± SD 0.93 per month for group B). We used each recording only once for each study group. We conducted playbacks, including the test and control stimuli, either at the home range border (defined as the area of overlap between groups) or in the center of a territory (defined as the area exclusively utilized by a single group; Waser 1977). We broadcast neighbor songs in the area of overlap between two study groups.

A team of four observers conducted playbacks at a distance of *ca*. 100 m from a study group (mean distance = 99.47 ± SD 33.27 m; $N = 47$ trials) while communicating via two-way radios. First, a person held the speaker at a height of 1.5 m and hid under dense vegetation to prevent the gibbons from observing the equipment and habituating to the artificial stimuli. If any group member approached within 10 m of the playback site before the playback had finished, we turned off the sound. A different person mapped the location of the gibbons and of the speaker using *x*/*y* coordinates with a compass and rangefinder to calculate distances between the gibbons and the playback sites at the onset of playbacks.

From the onset of a playback, the two other observers conducted continuous sampling (Altmann 1974) of behaviors of the male and female adults in the focal study group for 60 min. To evaluate the responses of the gibbons to each stimulus, we recorded the following behaviors: which adult moved first (the adult male or adult female) and whether the movement was toward or away from the speaker. These definitions were unambiguous as we observed no lateral movement, i.e., movement neither toward nor away from the speaker. We recorded the start and end time of playbacks and the time that each individual started and ended movement, as well as the time when the gibbons entered the tree under which the speaker was hidden (arrival at the playback site; hh:mm). Using these data, we calculated latency to move and latency to arrive at the playback site in minutes for males and females. If there was no movement during the first 10 min after the playback, we considered this as no response and stopped continuous sampling.

Data Analysis

We used generalized linear mixed models (GLMMs; Baayen 2008) to examine effects of the four factors (location, familiarity, sex of the caller, and paired status) on gibbon behavioral responses. We ran three models, one for each response variable: 1) which adult moved first (sex of the adult to initiate movement [female/male] using a binomial error structure and a logit link, 2) latency to move (in min) using a Poisson error structure and a log link, and 3) latency to arrive at the playback site (in min) using a Gaussian error structure and an identity link. Although we measured both latencies to move and latencies to arrive in whole minutes, we treated the former as a count variable because the range of the latencies to move was relatively small (0–9 min) compared with the range of latencies to arrive (0–60 min). The models were fitted in R 3.0.2 (R Development Core Team 2013) using the functions lmer or glmer of the R package lme4 (Bates *et al.* 2013).

We excluded three trials that resulted in no reaction from the analysis, leaving a sample of 44 trials (23 trials for group A and 21 trials for group B). For model for latency to arrive, we excluded seven additional trials in which the gibbons did not arrive at the playback sites.

We included four test predictors (location, familiarity, sex of the caller, and paired status) in all models as fixed effects. We also included study group and its interactions with the four test predictors as additional fixed effects to control for differences between two study groups. In models for latency to move and latency to arrive, we included sex of the study individual and its interactions with the four test predictors as additional fixed effects to examine whether there were sex differences in gibbon response to playbacks. To control for the effect of date, which may reflect the influence of habituation to playbacks, we included it as a fixed effect. We also included time of the day as a fixed effect to control for potential changes in activity patterns and/or sound propagation during the day. Date and time were approximately symmetrically distributed and *z*-transformed (to a mean of 0 and a standard deviation of 1). Because the playback distance was not precisely standardized across experiments, we also included distance, which was also symmetrically distributed and *z*-transformed, to control for the possible effects of distance on song transmission and gibbon reactions (Fischer *et al.* 2001; Maciej *et al.* 2011). Finally, we included recording condition (wild/captive) as an additional fixed effect to control for the effect of different distances at which recordings were made from wild vs. captive individuals. Each category of playback conditions included both wild and captive individuals except the category "neighbor," which included only wild individuals, and the category "male," which included only captive individuals.

We also included random intercepts for recording ID. We did so because even though we did not repeatedly use the same recording within one study group, our two groups live in adjacent territories and may be able to hear songs broadcast in their neighbor's home range. In addition, we included random intercepts for the identity of the individual that provided the stimulus (to control for the songs from the same individuals) and recording location (to control for the different locations in which recording was conducted). Furthermore, in models for latency to move and latency to arrive we included random intercepts for trial ID to control for nonindependence of the male and female responses, as data were collected from both the male and the female of each group for each trial. No random slopes of fixed effects within each random effect were needed because the fixed effects did not vary within each level of the random effects (Barr *et al.* 2013; Schielzeth and Forstmeier 2009).

We checked for model stability by excluding data points one at a time from the data set and compared the estimates derived with those obtained when including all data points. None of the three models showed instability resulting in considerable changes in the estimates. We derived variance inflation factors (VIFs; Field 2005) for each predictor variable using the function vif of the R package car (Fox and Weisberg 2011) applied to a standard linear model excluding the random effects. This procedure indicated that collinearity was not an issue in the three models, with a maximum VIF of 3.77 (O'Brien 2007). To validate the assumptions of normally distributed and homogeneous residuals in model for latency to arrive, we also visually inspected QQ plots and the residuals plotted against fitted values and detected no indications of violations.

To establish the significance of the test predictors (location, familiarity, sex of the caller, paired status, and sex of the study individual) as a whole (Forstmeier and Schielzeth 2011), we compared the full model with a null model using a likelihood ratio test (R function anova with argument test set to Chisq and R function drop1; Dobson 2002). The null model lacked the test predictors and their interactions, but including the same random effects structure as the full model and also the fixed effects of study group, date, time, distance, and recording condition. We considered $P < 0.05$ as an indicator of statistical significance for the full models, interactions, and main effects. We removed interactions with $P > 0.1$ from the models (Lowry 1992). For nonsignificant results, we interpreted $P < 0.1$ as indicating a trend toward significance for interactions and main effects.

Ethical Note

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

Results

Across the four experimental conditions, 94% of the playbacks (44/47 trials) evoked movement toward the playback sites. The gibbons never moved away from the playback sites. One trial with a paired neighbor female song (played at the border to group B) and two trials with paired stranger female songs (one played at the border to group A, and one played in the center to group B) did not stimulate a response. Males initiated group movement 30 times and females 14 times. None of the 10 trials with the control stimulus of the Javan surili call evoked any reaction.

The full model for which adult moved first fit significantly better than the null model ($\chi^2 = 31.87$, df = 8, $P < 0.001$). However, none of the playback conditions had a significant effect or a significant interaction with group, although sex of the caller showed a trend toward significance ($P < 0.1$; Table II). Females initiated movement mostly in response to female songs (13/32 trials with female songs and 1/12 trials with male songs) whereas males started movement in response to both male (11/12 trials with male songs) and female songs (19/32 trials with female songs). In this model, we found that male initiation of movement was more frequent later in the day (Table II), suggesting that the pattern of animal activities changed throughout the day.

The full model for latency to move had a significantly better fit than the null model ($\chi^2 = 34.65$, df = 18, $P = 0.010$). After we removed nonsignificant interactions between sex of study individual and the playback conditions and between study group and location, we found a clear effect of location and interactions between study group and two test predictors: familiarity and paired status (Table III). Latencies to move were shorter for songs produced in the center of the territory, stranger songs, and songs from unpaired individuals compared to songs played from the home range border, neighbor songs, and songs from paired individuals (Fig. 1). The intensity of the response to familiarity and paired status differed between the two groups, as indicated by the significant interaction terms in the model, but the overall pattern of response was similar in the two study groups. The effect of familiarity was stronger in group A, but the effects of sex of the caller and paired status were stronger in group B (Fig. 1). The interaction between study group and sex of the caller was not significant ($P < 0.1$ but $P > 0.05$; Table III). We also found that latencies to move became longer during the course of the study (Table III), suggesting habituation to the stimuli. Latencies to move were also shorter in response to recordings from wild individuals than from captive individuals (Table III). Sex of the study individual did not affect the individuals' responses in the model, indicating that males and females show similar latencies to move toward

Table II Summary of estimates and standard errors for the GLMM investigating effects on the sex of the adult to initiate group movement in Javan gibbons in the Gunung Halimun-Salak National Park (GHSNP)

	Estimate	Std. error	χ^2	df	P
Response variable: which adult moved first (female = 0, male = 1)					
Intercept	3.760	1.964	1.92	1	0.056
Location (border = 0, center = 1)	–0.507	0.953	0.29	1	0.593
Familiarity (neighbor = 0, stranger = 1)	–1.984	1.356	2.24	1	0.134
Sex of the caller (female = 0, male = 1)	2.504	1.532	3.24	1	0.072
Paired status (paired = 0, unpaired = 1)	–1.266	1.241	1.07	1	0.300
Study group (A = 0, B = 1)	–0.707	0.882	0.35	1	0.552
Date	–0.781	0.609	0.90	1	0.169
Time of day	1.372	0.659	6.25	1	0.012
Playback distance	0.781	0.607	1.90	1	0.168
Recording condition (captive = 0, wild = 1)	–1.941	1.584	1.70	1	0.192

Table III Summary of estimates and standard errors for the GLMM investigating effects on the gibbon latencies to move in response to playbacks in Javan gibbons in the Gunung Halimun-Salak National Park (GHSNP)

	Estimate	Std. error	χ^2	df	*P*
Response variable: latency to move					
Intercept	2.411	0.572	4.22	1	<0.001
Sex of study individual (female = 0, male = 1)	–0.233	0.185	1.64	1	0.200
Location (border = 0, center = 1)	–0.540	0.270	3.93	1	0.048
Study group (A = 0, B = 1)	0.160	0.406	0.39	1	0.695
Familiarity (neighbor = 0, stranger = 1)	–2.089	0.589	3.55	1	<0.001
Study group: Familiarity	1.334	0.608	4.86	1	0.028
Sex of the caller (female = 0, male = 1)	–0.216	0.551	0.39	1	0.695
Study group: Sex of the caller	–1.102	0.640	3.05	1	0.081
Paired status (paired = 0, unpaired = 1)	0.406	0.573	0.71	1	0.478
Study group: Paired status	–1.822	0.743	6.19	1	0.013
Date	0.462	0.165	7.01	1	0.008
Time of day	0.165	0.171	0.97	1	0.325
Playback distance	–0.075	0.185	0.16	1	0.692
Recording condition (captive = 0, wild = 1)	–1.542	0.482	8.80	1	0.003

":" indicates interactions.

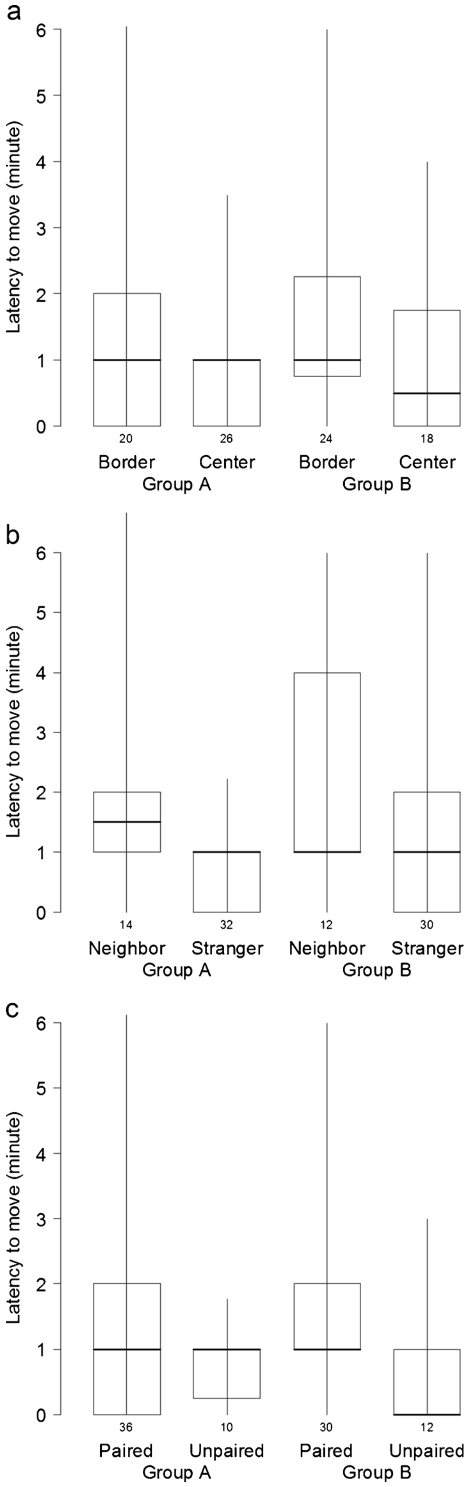
playback sites. We found strong positive correlations between male and female pairmates in their latencies to move (Pearson correlation, $r = 0.84$, $t = 9.92$, df = 42, $P < 0.001$) and their latencies to arrive at the playback site ($r = 0.99$, $t = 54.03$, df = 35, $P < 0.001$).

The full model for latency to arrive at the playback site did not fit significantly better than the null model (GLMM: $\chi^2 = 14.64$, df = 18, $P = 0.687$).

Discussion

We observed differences in latency to respond to playbacks for three of four experimental conditions. Javan gibbons responded more quickly to songs broadcast in the center of the territory (Fig. 1a), stranger songs (Fig. 1b), and songs produced by unpaired individuals (Fig. 1c) compared to songs broadcast at the border, neighbor songs, and songs from paired individuals. Although the size of the effects of two variables (familiarity and paired status) on latency to move differed between two study groups, the results indicate that solo songs in nonduetting Javan gibbons encode information about the identity and paired status of the caller, and that listeners are capable of using this information to distinguish between neighbors and strangers, and paired and unpaired individuals. In addition, the results show that Javan gibbons can localize songs. Supporting our predictions, these findings suggest that Javan gibbon solo songs may function for territory defense, but also for pair-bond advertisement like duets in other primates (Bernstein 2007).

Fig. 1 Effects of the three playback conditions on latency to move in the two study groups. (**a**) Location (border vs. center). (**b**) Familiarity (neighbor vs. stranger). (**c**) Paired status (paired vs. unpaired). Shown are medians (bold lines), quartiles and percentiles (2.5 and 97.5%). The number of trials for each combination is indicated below the boxes.



In our study, gibbons started to move toward the playback sites faster in response to playbacks in the center of a territory than at the border, which is consistent with the territorial defense hypothesis. This result is in line with previous studies, in which Bornean gibbons and white-handed gibbons approached more frequently, produced more vocalizations, and stayed near the playback sites longer in response to playbacks from the center than the border of the territory (Mitani 1985b; Raemaekers and Raemaekers 1985), as is predicted by the "center-edge effect" (Giraldeau and Ydenberg 1987). Moreover, we found that gibbons started to move faster in response to stranger than neighbor songs, which is compatible with the "dear enemy effect" (Temeles 1994; Ydenberg *et al.* 1988). Javan gibbons at Citalahab may acquire the ability to differentiate between familiar and unfamiliar callers during intergroup encounters and by regularly listening to neighbors' songs, as direct encounters are frequent (153 intergroup encounters witnessed during the study period; mean encounter rate = 0.60 ± SD 0.24/day) and adult females sing regularly (0.25 song bouts per day during the study period). A similar mechanism has been proposed for black crested gibbons (*Nomascus concolor*: Sun *et al.* 2011). However, despite the evidence for the "dear enemy effect" in this and other studies, gibbons often display aggression toward neighboring groups in the area of overlap (Brockelman and Srikosamatara 1984; Ellefson 1968; Gittins 1980) and gibbon songs may provoke direct interactions between groups, i.e., approach or aggression (Chivers and MacKinnon 1977; Mitani 1984, 1985a, b, 1987; Raemaekers and Raemaekers 1985). It remains unclear what factors affect the frequency and intensity of territorial aggression. Further investigation of the relationship between the rate at which individuals of territorial species hear songs of other individuals and the intensity of aggression toward that individual may provide valuable information about how the "dear enemy effect" is produced and the factors mediating territorial aggression in primates.

Interestingly, our results suggest that solo songs in paired Javan gibbons convey information about the paired status of the caller. Contrary to our predictions, gibbons showed shorter latencies to move toward the speaker in response to songs from unpaired than paired individuals. This may indicate that unpaired gibbons use songs to advertise their unpaired status for purposes such as attracting mates or searching for unoccupied territories (Cowlishaw 1992; Kappeler 1984; Whitten 1982). For paired gibbons, however, recognizing unpaired individuals can play a crucial role in territory and mate defense. It is unclear how paired status is encoded in Javan gibbon songs. Previous studies investigating individuality in the songs of Javan gibbons have shown that high variability in the initiation part of the great calls allows listeners to identify individuals (Dallmann and Geissmann 2001a, b), but whether this part also encodes information about the paired status is not yet clear. Adult male and female gibbons in newly formed pairs develop vocal coordination over time while producing duets together, suggesting that paired individuals adapt their own songs to those of their mates (Geissmann 1986, 1999; Haraway and Maples 1998; Maples *et al.* 1989). Similar comparisons of acoustic structure before and after pair formation should be made for nonduetting gibbons to investigate how solo songs are transformed to transmit information about the paired status of the caller after forming a pair.

Previous studies have found stronger responses to same-sex intruders in Bornean gibbons, white-bearded gibbons, and white-handed gibbons (Mitani 1984, 1987; Raemaekers and Raemaekers 1985). Such sex-specific responses indicate mate defense, because same-sex callers are likely to pose a greater threat to an individual's mated status and parentage of future group offspring than opposite-sex individuals (Mitani 1984, 1987; Raemaekers and Raemaekers 1985). Extrapair copulations, three-adult groups, or both have been reported in most gibbon taxa, including Javan gibbons (Malone and Fuentes 2009). Thus, it seems likely that mate defense is also important in Javan gibbons. Interestingly, contrary to our prediction, we did not detect a significant effect of sex of the caller. However, the results were suggestive ($P < 0.1$; Tables II and III). Our study involved only two Javan gibbon groups, but we found that groups differ significantly in the intensity of their responses to song playbacks. Thus, one cannot rule out the possibility that any effect of caller sex was obscured by other potentially confounding variables in our study. Further quantitative studies should again test the mate defense function in Javan gibbons by including a larger sample of groups and taking into account additional variables such as pair-bond strength, group composition, and home range quality that may affect the intensity of responses to real or simulated intruders.

We found strong positive correlations between males and females in their latencies to move and their latencies to arrive at the playback site, which indicate that the male and female in each group coordinated their movements. These results suggest that one partner is likely to follow the actions of the other, resulting in highly coordinated travel (Raemaekers and Raemaekers 1985). Future researchers designing playback experiments may be able to capture subtle social signaling between pair-mates using video recordings to permit more detailed behavioral analyses resulting in a better understanding of the roles of males and females in territory and mate defense.

Mediating intergroup spacing has been proposed as an alternative hypothesis for the functions of gibbon songs. If songs mediate intergroup spacing by promoting avoidance, gibbons should move away after hearing songs to avoid the cost of aggression during direct encounters (Baldwin and Baldwin 1972; Chivers 1969; Waser 1977). However, in our study and previous studies of other gibbon species (Chivers and MacKinnon 1977; Mitani 1984, 1985a, b, 1987; Raemaekers and Raemaekers 1985), movement away from the speaker was never observed. Furthermore, maintaining intergroup spacing may involve phenomena other than immediate avoidance. To better explore intergroup spacing in gibbons, researchers should conduct detailed observational investigations in which both the caller and the listener are observed simultaneously.

Researchers tend to assume that the evolution of duets is connected to pair-living because all duetting primate species are thought to be socially monogamous (Geissmann 2000; Haimoff 1986). Gibbons provide an interesting opportunity to investigate the relationship between duetting and pair-living. In gibbons, duetting is assumed to be a primitive trait, which was secondarily lost in the two nonduetting species (Geissmann 2002; Groves 1984). However, an adequate explanation for the loss of duetting in Javan gibbons and Kloss's gibbons has not yet been identified. Our results show that song functions are probably similar in duetting and nonduetting species. To understand fully the functions of songs in duetting and nonduetting gibbons, future studies should investigate the context of spontaneous singing behavior in wild gibbons. This approach may be helpful in exploring the functions of song in pair-living primates, and also may shed light on patterns of song evolution in socially monogamous primates.

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