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Vocalization can mediate male-male sexual interactions in Java sparrows

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Abstract
Same-sex sexual behaviors do not have direct fitness outcomes, but might be adaptive. This issue is often discussed in group-living animals, where social bonding is crucial.In our captive environment, around 33% of the Java-sparrow (*Lonchura oryzivora*) males kept in unisex cages have stable bonded partners. Those bonded males often perch side by side and show allopreening and joint-defensive behaviors towards others. In this study, we aimed to determine how males including such same-sex bonded individuals communicate with each other via vocalizations. We introduced same-sex pairs of Java sparrows, which were bonded or non-bonded, in sound-attenuated boxes and compared their recorded vocalizations with those from male-female pairs. For the male-male pairs, we identified two vocalizations that are usually exchanged between paired partners in intimate contexts: mating trills—which are usually emitted by females during successful copulation—and meowing calls—which are given when both members of the pair are in the nest at the same time. We found that males gave mating trills when their partner males were singing courtship songs, or performed trill duets, which sometimes also included meowing calls. Acoustic analyses revealed that there was no difference between male-male and male-female vocalizations. Meowing calls showed greater within-individual variation in duration and other acoustic parameters, but were similar in same-sex and mixed-sex contexts. Our results indicate that male-male pairs exchanged 31 intimate vocal communications just like male-female couples.

Keywords: Estrildid finch; homosexual; same-sex bonding; vocal communication

Introduction

Same-sex sexual behavior is not necessarily maladaptive (Bailey & Zuk, 2009). It can play a prosocial role and aid animals in avoiding conflict and in forming affiliative relationships with others. For example, female Japanese macaques (*Macaca fuscata*) engage in same-sex mounting after conflict to calm down (Vasey et al., 1998) and Bonin flying foxes (*Pteropus pselaphon*) perform male-male genital licking with rivals presumably for social thermoregulation (Sugita, 2016). Furthermore, same-sex individuals may show pair-bonding just like male-female partners (e.g. Elie et al., 2011, Kindel et al., 2018), which despite tending to be viewed as the result of a mistake, can have adaptive significance. In Laysan albatrosses (*Phoebastria immutabilis*), females maintain long-term pair-bonding and cooperate to raise their extra-pair offspring when the sex ratio is female-biased (Young et al., 2008). Similar female-female cooperation was also reported in feral pigeons (*Colomba livia*), using captive populations of experimentally biased sex ratio by Jankowiak et al. (2018).

Birds are especially rich in species that exhibit same-sex sexual behaviors or bonding. According to interspecies comparative studies, factors associated with reproductive ecology, such as mating systems and parental care, explain why particular sexes tends to show same-sex bonding or same-sex sexual behaviors in birds (MacFarlane et al., 2007, 2010). Specifically, male-male sexual behavior is likely to occur in polygamous species, while female-female behavior is attributed to monogamous species (MacFarlane et al., 2010). Many cases have been reported in sexually dimorphic species, implying that these are not merely cases of mistaken identity.

Even so, a fundamental question yet to be fully answered is whether same-sex pairs correctly discern each other's sex or not. Differentiating between the sexes may be particularly challenging in species that are sexually monomorphic. For example, in long-tailed finches (*Poephila acuticauda*), a sexually monochromatic songbird, males were equally likely to court and copulate with males and females (Langmore & Bennett, 1999). The authors argued that concealing sex is a strategy for reducing the cost of same-sex competition in social life. Alternatively, this result can be interpreted as males being forced to accept an atypical sex role when individuals do not discern between the sexes. Courtship and copulatory behaviors in birds often include sex-specific components, such as male mounting, male singing, or female copulation soliciting displays, but individuals may have some flexibility in which sex role they follow. In graylag geese (*Anser anser*), partnered males tried to mount each other only to fail (Huber & Martys, 1993). In contrast, a female Bengalese finch (Lonchura striata var. domestica) was reported to show pseudo-male behavior, which led to same-sex copulation (Masatomi, 1957).

Many songbirds show sexually dimorphic vocalizations (e.g., Yoneda & Okanoya, 1991; Vicario et al., 2001; reviewed in Volodin et al., 2015), which are especially prominent in singing (cf. Catchpole & Slater, 2003; Gahr, 2007). Even so, some are reported to form same-sex pair bonds (e.g. Elie et al., 2011, Boucherie et al.,

2016; Kindel et al., 2018), raising the question of how male-male partners acoustically communicate with each other during bonding. To answer this, we focused on song-induced male-male communications in the Java sparrow (*Lonchura oryzivora*) and other vocalizations, especially mating trill and meowing call, that are usually exchanged between male-female Java-sparrow mating partners.

The Java sparrow is a sexually monochromatic and socially monogamous songbird. Males and females differ slightly in body size, eye-ring thickness, and bill size and color (Restall, 1996; Hasegawa et al., 2011), but because the distributions of these characteristics are highly overlapping between the sexes, sex identification is difficult. Songs are specific to males, and because of the gregarious nature of the species, they are used for courtship but not for territorial defense or male-male competition (Goodwin, 1982; Restall, 1996). Each individual male has one stereotyped song that is composed of 2 to 8 different note types and characterized by note ordering patterns (Hasegawa et al., 2011; Kagawa & Soma, 2013; Ota & Soma, 2014). In response to male singing, females sometimes emit mating trills (Goodwin, 1982). Based on the fact that mating trills are usually heard before or during successful copulation (Goodwin, 1982), we assume that this trill conveys female preference and receptiveness to solicit male mounting. Additionally, males (but probably also females) produce meowing calls when both members of the pair are in or near the nest at the same time (Goodwin, 1982; Restall, 1996). This meowing call is similar to the 'whine' call of a related species (zebra finch, *Taeniopygia guttata*) in that it is soft and long in acoustic structure, and given in the nest (Elie et al., 2010). In the zebra finch, this type of call, sometimes mixed with other calls, is used as a private communication between mating partners during breeding and appears to be associated with the onset of nesting activities (Elie et al., 2010; Gill et al. 2015).

In this study, we recorded the vocal communications of pair-bonded and non-bonded captive Java sparrow males and compared them with those of male-female pairs.

Materials and methods

Java sparrows maintained and bred in our laboratory (Hokkaido Univ.) were used as subjects. In our captive environment, nearly one third of males kept in 5 unisex group cages (46.5×46.5× 113.0cm, 59.1×44.8×63.0cm, or 46.5×46.5×56.5cm) for at least 3 months 103established stable bonds with same-sex partners (13 bonded pairs /78 individuals). The birds were either lab-bred or purchased from several breeders. They were genetically sexed and individually marked with leg rings. They were identified as bonded based on social behaviors that are used as male-female pair-formation criteria in related species: (1) clumping: perching side by side (Fig. 1), (2) allopreening, and (3) joint-threatening display (Baptista & Atwood, 1980; Goodwin, 1982; Clayton, 1990; Restall, 1996). These three behaviors are usually observed only between pair-bonded birds or between parents and young fledglings. As the three behaviors are frequently

Figure 1. Clumping posture of the Java sparrow. Pair-bonded Java sparrows sit in close contact with each other when they rest and sleep on a perch. The male-male bonded pairs do the same.

expressed and can be captured even in short observation period in our captive environment, we defined non-bonded and bonded based on absence/presence of the three behaviors in 30-minute observation. We also confirmed that the three behaviors were always exchanged between fixed pair members.

To observe male-male vocal interactions, we used a total of 19 pair combinations of 28 males (non-bonded: $N = 12$ pairs, $N = 18$ individuals; bonded: $N = 7$ pairs, $N = 14$ individuals; 4 individuals observed for both non-bonded and bonded combinations), and could record vocalizations from 7 pair combinations made up of 13 males (Table 1a). These pairs were always made up of cage mates, which were either bonded or not. As our preliminary observation revealed that males tend to bond with unrelated individuals (i.e., 120non-foster siblings or non-kin), males of each pair were from different families. Each pair of males was isolated in a cage (19.1×37.6×24.5cm) equipped with two perches, food, and water cups, and set in a sound proof chamber and recorded overnight (5:00 p.m. - 14:00 p.m., 21 hours), but some of them were recorded for two nights (42 hours). Audio recordings were made using a digital sound recorder (PMD 661, Marantz, Kanagawa, Japan) through internal microphone at a sampling rate of 44.1 kHz with 16-bit resolution. Sounds under 20dB were not recorded as we used

Table 1. Summary of subject birds, and their sampled vocalizations used for the analyses. Those pairs that we could not sample vocalizations are not included.

(a) Male-male pair

Male ID	Male ID	Bonding	No. of trill bouts	Analyzed no. of trill notes	No. of meowing call	No. of songs
M-85	M-204	bonded	8	79	30	0†
M-68	M-211	bonded	0	0	35	0
M-165	M-272	bonded	0	0	40	3
M-124	M-146	non-bonded	1	8	0	32†
M-85	M-271	non-bonded	0	0	2	95
M-130	M-195	non-bonded	0	0	3	25
M-254	M-275	non-bonded	0	0	2	4

(b) Male-female pair

Male ID	Female ID	No. of trill bouts	Analyzed no. of trill notes	No. of meowing call
M-118	F-180	1	6	0
M-66	F-141	1	11	0
M-102	F-180	2	59	0
M-207	F-232	3	14	0
M-217	F-182	2	18	0
M-187	F-209	0	0	65

†: Recorded for two nights.

Silent Skip mode of the recorder. All sound files were bandpass-filtered under 200Hz for the below analyses.

To examine the sampled mating trills and meowing calls, we compared them to 9 bouts of mating trills and 65 meowing calls from opposite-sex pairs (N = 6; Table 1b) that we extracted from archived data of video-recorded male-female courtship interactions (cf., Soma & Iwama, 2017). Due to the heterogeneity in the archived videos, sound files extracted from the videos were either at a sampling rate of 44.1 kHz with 16-bit resolution, 44.1 kHz with 32-bit, or 48 kHz with 16-bit, which did not affect the acoustic parameters that we took. For acoustic comparisons of male-male and male-female vocalizations, we measured the duration of mating-trill bouts and calculated the trill rate as the number of trill notes per second. We also measured peak frequency of trill notes by picking out the trills that did not overlap with other sounds. For example, we focused on trill notes that were not overlapped with song notes (see the first trill note in Fig. 2a) in a sequence of repeated trill notes. We measured the duration of meowing calls but did not look at acoustic frequency as they were highly variable even within individuals (see results). For these analyses, we used the sound-analysis software Raven Pro 1.4 (Charif et al., 2010). We could identify which individual was vocalizing in male-female pairs with the help of video images, but not in male-male pairs, except for a case that one male was singing and the other was responding with mating trill.

We compared the four acoustic measures between male-male and male-female vocalizations by conducting liner mixed-effects (LME) model analyses, in which pair attribute (i.e., male-male or male-female) was treated as an explanatory variable and pair or bird identity was entered as a random effect to deal with the non-independence of the data from the same individual or pair. When it was impossible to determine which individual was vocalizing, pair identity was substituted for bird identity. In addition, we also compared these four acoustic measures between bonded and non-bonded pairs by conducting liner model analyses, in which pair attribute (i.e., bonded or non-bonded) was treated as an explanatory variable. For trill parameters, we did not enter a random effect of pair identity because we could record trills from one bonded and one non-bonded pairs. For the analysis of meowing call durations, we entered a random effect of pair identity. All statistical analyses were performed using R ver. 3.0.3 (R Core Team, 2014).

All the animal experiments was conducted with approval from the Institutional Animal Care and Use Committee of the National University Corporation at Hokkaido University in accordance with Hokkaido University Regulations of Animal Experimentation.

Results

Meowing calls (N = 105) were frequently produced in the male-male pairs that were already bonded at the start of experiment, while mating trills (N = 8) were infrequent and

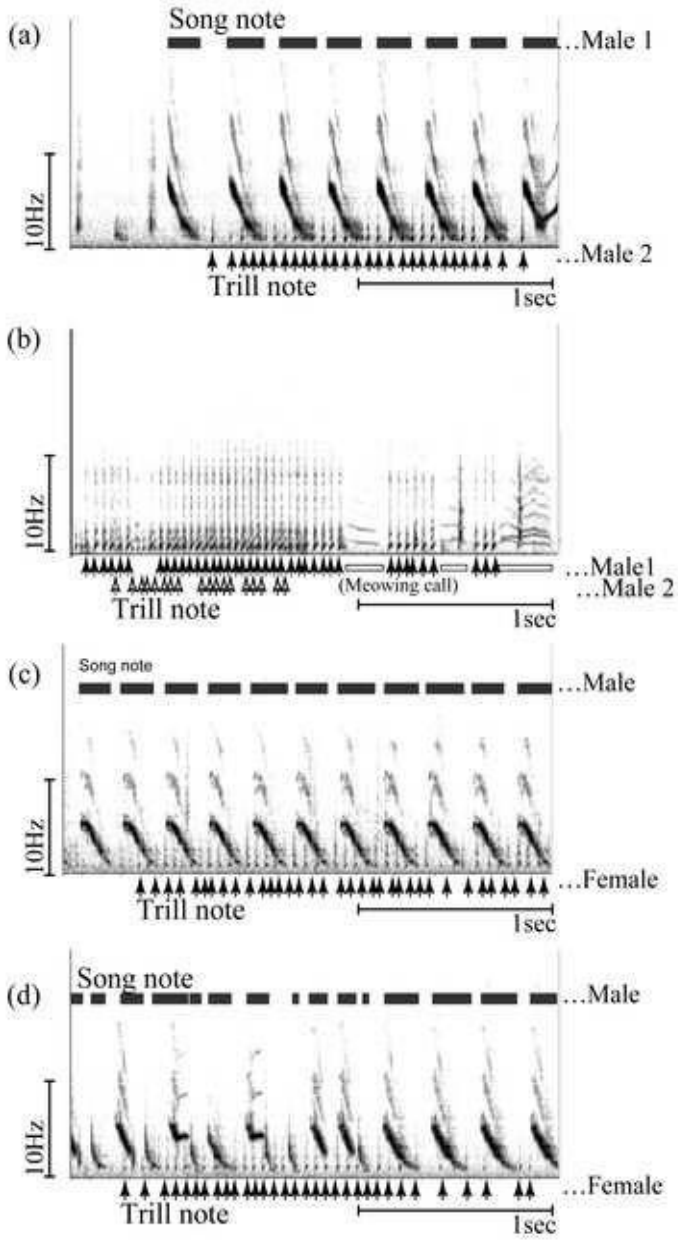

Figure 2. Example spectrograms from Java sparrows' mating trills. In male-male pairs, a non-bonded male emitted mating trills in response to his partner's singing (a), while bonded male-male pairs exchanged trills, which also included several meowing calls (b, see also Fig. 3 for meowing calls). In male-female pairs, females usually produce mating trills during successful copulation (c, d).

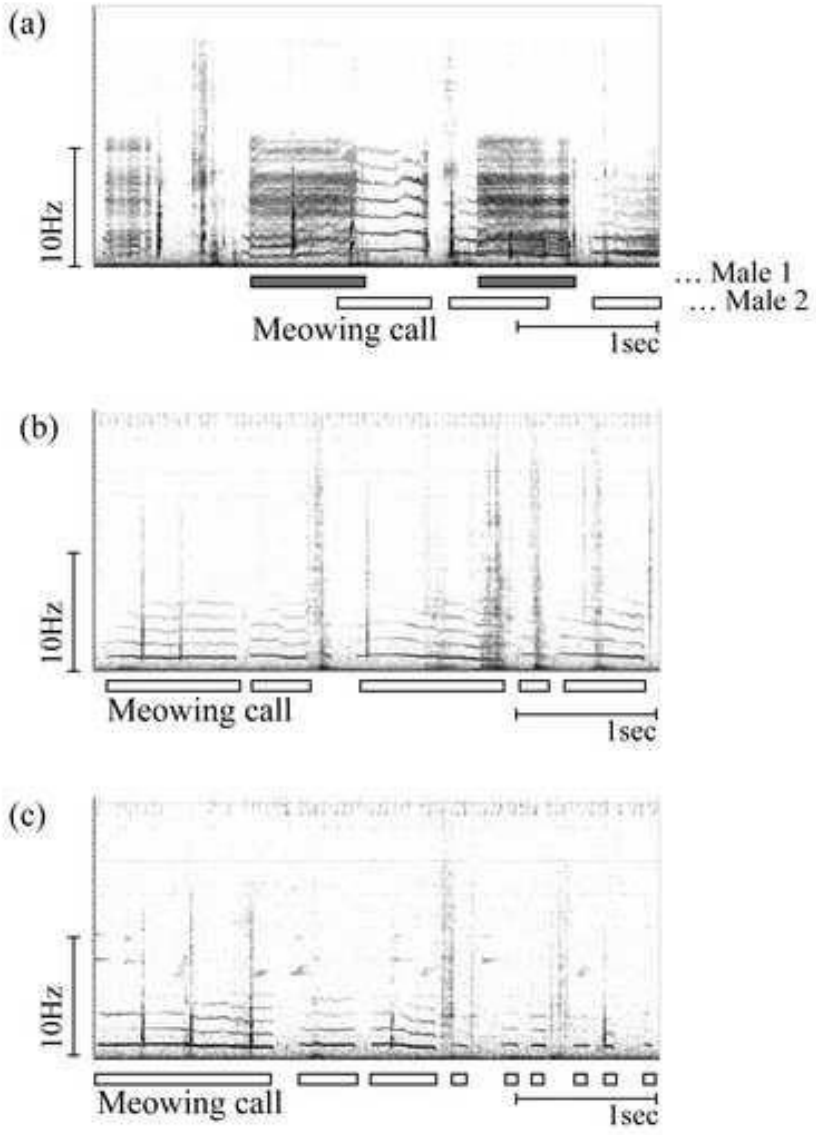

Figure 3. Example spectrograms from Java sparrows' meowing calls. Bonded males produced meowing calls in a duet-like manner (a), while in a non-bonded pair, a male also gave the same calls (b). This call is usually used male-female communication when breeding (c).

observed only in one male-male bonded pair (Table 1a; Fig. 2, 3). Additionally, meowing calls ($N = 7$) were heard in several non-bonded male-male pairs, and a trill bout ($N = 1$) in another. Therefore, in total seven out of nineteen pairs exchanged vocalizations that are usually attributed to courting/breeding interactions in male-female pairs. While in a non-bonded pair, a male produced mating trills in response to his partner's singing (Fig. 2a)

just as females usually do (Fig. 2c, d), the bonded males produced mating trills simultaneously, like duets, which sometimes included meowing calls (Fig. 2b, 3a).
As shown in the spectrograms (Fig. 2, 3), both mating trills and meowing calls were similar in male-male and male-female contexts. Mating trills were composed of fast repetition low frequency notes, and meowing calls had harmonic structures with variable duration (Fig. 2, 3, Table 2). Comparison of acoustic parameters revealed no statistically significant differences between male-male and male-female communications for either type of vocalization (Table 2). In addition, comparison of non-bonded and bonded male pairs revealed no statistical significant differences in the three parameters of mating trills (Bout duration of mating trills: $N_{\text{bonded}} = 8$, $N_{\text{non-bonded}} = 1$, $t = 1.58$, $P = 0.16$; Trill rate: $N_{\text{bonded}} = 8$, $N_{\text{non-bonded}} = 1$, $t = 1.27$, $P = 0.244$; Peak frequency: $N_{\text{bonded}} = 79$, $N_{\text{non-bonded}} = 8$, $t = 1.94$, $P = 0.056$), and in the duration of mowing calls ($N_{\text{bonded}} = 105$, $N_{\text{non-bonded}} = 7$, $t = 1.50$, $P = 0.21$), which might be partially attributable to the very small sample sizes of some data.

(a) Mating trill					**LME**	
	Male-female		Male-male		*t*	*P*
Bout duration (s)	2.20 ± 0.33	(*N* = 9)	0.82 ± 0.19	(*N* = 9)	1.49	0.42
Trill rate (/s)	20.49 ± 0.92	(*N* = 9)	22.27 ± 1.4	(*N* = 9)	0.99	0.37
Peak frequency (Hz)	1100.7 ± 35.2	(*N* = 108)	980.1 ± 9.0	(*N* = 87)	0.85	0.44
(b) Meowing call						
Duration (s)	0.25 ± 0.03	(*N* = 65)	0.42 ± 0.03	(*N* = 112)	0.87	0.42

Table 2. Comparison of acoustic parameters for mating trills (a) and meowing calls (b) between male-female and male-male pairs. Means ± SE are shown for each acoustic parameter.

Discussion

The present study revealed same-sex vocal interactions that might possibly play a role in male-male sexual bonding. We observed that males produced mating trills in response to singing, mating trills, and meowing calls of their partner males (Fig. 2), and also that they exchanged meowing calls with each other (Fig. 3). These vocalizations exchanged between males can be seen as affiliative because they were also observed in male-male bonded pairs, 188and were quite similar to vocalizations that are common in male-female pairs (Table 2).

The most striking aspect of our finding was that some males were capable of producing female-specific vocalization, i.e., mating trills. This type of vocalization is supposed to solicit male mounting (Goodwin, 1982), and was not described in other

behavioral contexts, to our knowledge. We observed that one non-bonded male produced the trill in response to singing, which means that he acted like a female in response to male-specific vocalizations. Although we cannot deny the possibility of sex misidentification, it is more likely that sex-specificity in singing can give sufficient clues of sex identification. As Langmore and Bennett (1999) argued, concealing their sex to reduce the cost of same-sex competition can sometimes be adaptive, especially in gregarious and monochromatic species like the Java sparrow.

The behavior we observed in the male-male bonded pairs suggests more than simple concealment of sex. The pairs showed duet-like vocal interactions, using both mating trills and meowing calls. Duet-like vocal communication is often observed between mating pairs of birds and plays roles in mutual territorial defense, mate guarding, and courting (reviewed by Hall, 2004). In the zebra finch (a species related to the Java sparrow), pairs often give call duets when nesting, suggesting that such private vocal communication 205contributes to reproductive cooperation (Elie et al., 2010; Gill et al. 2015). Call duets are similar between the zebra finch and the Java sparrow in several aspects. Meowing calls (Java sparrow) and whine calls (zebra finch) are acoustically similar, and both species mix different call types when they duet (Elie et al., 2010; Fig. 3). Although we are not sure whether male-female pairs of Java sparrows exhibit similar duets, we predict that Java-sparrow pairs generally rely on duet-like vocal communications for pair-bond maintenance.

The present finding is preliminary and cannot be used to judge the adaptiveness of male-male sexual behavior and bonding. However, it shows that the Java sparrow has the potential to form male-male bonds, aided by vocal communication. The Java sparrow is a highly gregarious species even in the breeding season (Goodwin 1982; Restall, 1996), and shows strong preference for staying with conspecifics (Watanabe, 2002). This social nature might underlie the phenomenon that we observed. However, group-living is not always peaceful. Indeed, the Java sparrow is characterized by a range of agonistic displays (Baptista & Atwood, 1980) and can become aggressive toward conspecifics, which explains why they need to reduce social costs by having a bonded partner. This idea is supported by our preliminary observation that bonded individuals (including both male-female and same-sex pairs) become socially dominant and secure the highest perch position in the aviary.

Same-sex sexual behavior and bonding tend to occur when sex ratios are biased (Bailey & Zuk, 2009) and male-female mating opportunities are limited. This was indeed the case in the present study conducted in captivity, and was also confirmed in another study of feral pigeons (Jankowiak et al., 2018). However, interestingly, in the Crimson finch (*Neochima phaeton*), a species related to the Java sparrow, male-male pair-bonding was reported to be maintained for months in the wild, resulting eggs of unknown origin in the nest (Kindel et al., 2018). We expect that what we observe in captivity can help to explain what happens in the field. To conclude, Java sparrow males vocally interact with

each other and show bonding like male-female pairs, which might be an adaptive strategy to cope with social life with dominance relationships (MacFarlane et al., 2010). In the future, we should look into whether or not females show similar same-sex bonding (cf., Tomaszycki et al. 2014), and associate it with the social structure of the species.

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