DOI: 10.61782/fa.2023.1025

forum acusticum 2023

NON-VOCAL MUTUAL COURTSHIP COMMUNICATION IN A SOCIALLY MONOGAMOUS SONGBIRD

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ABSTRACT

Estrildid finches are one of the most studied songbird families for acoustic communication. They often combine their songs with body movements (i.e., dance) during courtship. Past literature has provided detailed descriptions of dance components, but there are still few empirical studies on the behavioral mechanisms and functions of dancing compared to songs. Our study species, blue-capped cordon-bleus (*Uraeginthus cyanocephalus*), perform characteristic dance displays in both sexes. During courtship, they repeatedly bob up and down and sing songs several times. We have previously found that they perform human tap-dance-like high-speed movements, tapping their legs on the perch two to six times in a single bobbing. Their behavior is interesting not only because both sexes perform almost the same display but also because their dance movements can produce sounds and vibrations. Here we present our findings on the dance behavior of cordon-bleus in both captive and wild conditions. Our studies suggest that the sounds and vibrations by dancing can function as communication signals and have multifaced functions depending on the social and environmental contexts. It underscores the importance of studying the non-vocal aspects of songbird courtship displays towards a better understanding of animal communication and its complexities.

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Keywords: Courtship display, Dance, Estrildid finch, Sonation.

1. INTRODUCTION

Vocalization in songbirds has been extensively studied in various fields to elucidate neural mechanisms, communicative functions, and evolutionary trajectories. Many songbirds sing songs in a courtship context, and other behavioral components, such as dance display, often accompany it. The body movements often produce multimodal signals (e.g., non-vocal sounds, vibrations) in addition to visual signals. For instance, our previous studies have reported that some songbirds produce non-vocal sounds by bill clicking [1] and tap dance-like movements [2] (described below) during song production. The multimodal dance displays are likely to play important roles in their sexual communication, as does song. However, less attention has been paid to other courtship components than songs. To deepen our understanding of animal communication systems and their functions, it is essential to know what kind of signals they produce and how each signal works in their communication.

In this paper, we present our findings on the multimodal and multicomponent courtship displays of blue-capped cordon-bleus (*Uraeginthus cyanocephalus*). We describe an overview of their courtship displays and the functions based on behavioral experiments using captive and wild individuals. Then we discuss the possible roles of multimodal signals in their courtship communication.

2. COURTSHIP DISPLAYS OF BLUE-CAPPED CORDON-BLEUS

Blue-capped cordon-bleus (hereafter cordon-bleus) are a socially monogamous estrildid finch species in which both males and females perform multimodal courtship displays comprising song and dance [2, 3]. They are native to East Africa and have sexually dimorphic plumage, with males having a blue-capped head [4].

During the display, cordon-bleus hold a piece of nesting material while bobbing up and down and singing [2, 4]. By recording these displays with a high-speed video camera (300 frames/s), we discovered that in addition to bobbing, their visual courtship display includes quite rapid step-dancing [2] (Fig. 1). This specific "tap-dance"-like behavior is assumed to produce non-vocal sounds [5] (Fig. 1a, b) and vibrations [6]. On average, they performed 3.17±0.03 steps (±SEM; range, 0–6) per bobbing action. One step took around 20–40ms, at an estimated rate of 25 Hz to 50 Hz. There is no sex difference but a significant individual difference in the number of steps in one bobbing [2]. It suggests that the dance movements reflect individual information like physical ability and sexual motivation.

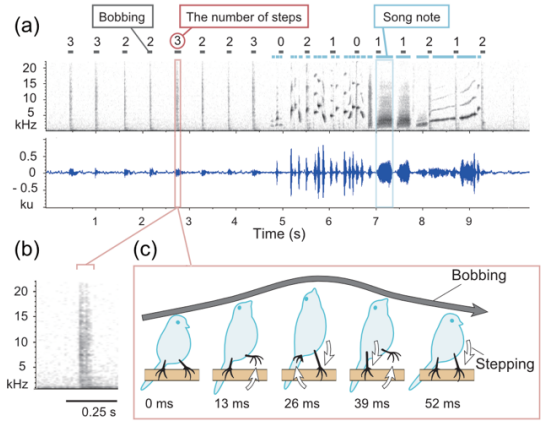

Figure 1. (a) Spectrogram and waveform of cordon-bleu courtship displays. Numbers at the top of the spectrogram indicate how many steps were performed to produce non-vocal sounds. (b) Enlarged section of the step sound spectrogram. Even though cordon-bleus usually perform stepping behavior several times per bobbing, the sound appears as a single pulse on the spectrogram. (c) Diagram of step behavior producing non-vocal sounds (modified from [5] under authors' copyright).

2.1 Signal efficacy of non-vocal sounds

Our laboratory experiment and field observation support the idea that the non-vocal sounds by cordon-bleu tap-dancing can serve as communicative signals [5, 7]. As a result of the acoustic analysis of tap-dancing behavior in the laboratory experiment, we found that the non-vocal sounds get louder with the number of steps in one bobbing, and the amplitude range overlaps with that of song notes [5]. They decrease the number of steps when singing [2], which may avoid interference between vocal and non-vocal sounds.

We also confirmed that wild cordon-bleus habit in Tanzania perform tap-dancing behavior as well as captive individuals. Although the non-vocal sounds seemed to be greatly varied depending on the substrate and the position of the birds, we succeeded in recording the non-vocal sounds by tap dancing several times during the field observation [7]. These findings suggest that the non-vocal sounds are sufficiently audible and can convey information on the number of steps that may reflect individual conditions and sexual motivations.

3. WHY DO CORDON-BLEUS PRODUCE MULTIMODAL SIGNALS?

It is intriguing that songbirds, which are supposed to communicate using complex learned songs, also produce multimodal signals by dancing. We assume that the multimodal and multicomponent courtship displays enhance the detectability and/or accuracy of signals, leading to strong pair bonding and its maintenance. Here we offer some perspectives on how and why the multimodal signals of cordon-bleus can be effective in their sexual communication based on our studies.

3.1 Environmental factors

The non-vocal sounds and vibrations of tap dancing might function as backup signals for visual signals under fluctuating environments. Cordon-bleus are non-territorial and opportunistic breeders [3, 4] and have no specific courtship territories [7], unlike lekking birds. During the fieldwork study, we observed that cordon-bleus performed courtship displays in a variety of places: on the perch in an open area (Fig. 2a), shaded area (Fig. 2b, c), and on the perch with leaves that hide their feet (Fig. 2d). Under these highly uncertain environmental conditions, non-vocal sounds and vibrations are useful in ensuring that courtship signals are conveyed.

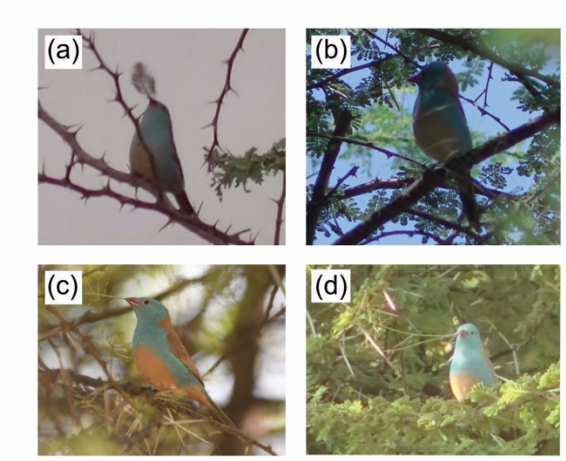

Figure 2. Wild blue-capped cordon-bleus performing courtship displays on the perch in (a) an open area, (b, c) shaded area, and (d) on the perch with leaves that hide their feet.

3.2 Social factors

Social conditions play a crucial role in whether cordon-bleus perform dance displays or not. While cordon-bleus sing songs in various social contexts, including an isolated condition, dance displays are produced only when the birds are close to potential mating partners [8]. We have found that the partners are more responsive to songs with dance displays than songs without [8]. More interestingly, the multimodal courtship displays (song with dance) are promoted by the presence of an audience in addition to the partner [9]. These findings suggest that cordon-bleu courtship displays have different messages according to the attribution of signal receivers. It can send courtship signals to the opposite sex nearby and at the same time advertises mating status to other surrounding individuals, which may lead to mate guarding and pair bonding maintenance.

3.3 Ecological factors

In socially monogamous birds, well-coordinated biparental care is critical for their reproductive success. To achieve this, they need to find a compatible partner and keep the pair bond lasting throughout the breeding. Socially monogamous birds often perform mutual courtship displays even after pair bonding (e.g., red-cheeked cordon-bleus [10]) Blue-capped cordon-bleus also perform courtship displays at the breeding stage (Ota personal observation). In those cases, the courtship displays are likely to serve as a commitment signal toward the paired partner rather than a sexual signal. Mutual courtship displays might be vital in forming pair bonding and maximizing biparental care [11].
Intriguingly, our comparative phylogenetic analysis suggested that intraspecific brood parasitism was associated with dance repertoire size [12]. Mutual courtship display producing complex multimodal signals may have evolved in response to increased reproductive cost, such as a risk of intraspecific brood parasitism.

4. CONCLUSIONS AND DISCUSSION

Cordon-bleu courtship displays are unique and interesting in at least two ways. First, cordon-bleus perform this complex multimodal courtship displays in males and females [2]. Our findings that both sexes of cordon-bleus perform multimodal courtship displays are puzzling from the pervasive view of complex courtship signals as a male trait evolved via female mate choice. The courtship display of cordon-bleus exhibits features analogous to dance displays of male manakins in that it includes acrobatic movements [13, 14]. Manakins are a lekking and non-song-learning species, so they differ from cordon-bleus in vocal learning ability and behavioral mutuality.
Second, this specific tap dance-like display presumably produces non-vocal sounds and substrate-borne vibrations in addition to visual signals [5, 6]. It is a novel finding that songbirds produce multimodal signals by dancing since they were previously assumed to use songs as a primary sexual communication tool, as the name suggests.
Our studies on cordon-bleus emphasize the importance of investigating the multimodality and mutuality of courtship signals in songbirds. We still have only indirect evidence regarding the signal efficacy of non-vocal sounds (Section 2.2). Therefore, empirical studies would be required to test the communicative functions (e.g., playback experiments of non-vocal sounds). It would also be worthwhile to explore the sex differences in multimodal signal production and the response. Despite the fact that female song and dance are found in many species of Estrildid finches [12], the behavioral mechanisms and functions regarding female signal production have rarely been investigated. These approaches would provide new perspectives on discussing animal communication systems and their complexity.

5. REFERENCES

[1] M. Soma and C. Mori: "The songbird as a percussionist: syntactic rules for non-vocal sound and song production in Java sparrows." *PLoS One* 10, no. 5: e0124876, 2015.

[2] N. Ota, M. Gahr and M. Soma: “Tap dancing birds: the multimodal mutual courtship display of males and females in a socially monogamous songbird.” *Scientific reports*, 5(1), pp.1-6, 2015.

[3] N. Geberzahn and M. Gahr: "Undirected (solitary) birdsong in female and male blue-capped cordon-bleus (*Uraeginthus cyanocephalus)* and its endocrine correlates." *PLoS One* 6, no. 10: e26485, 2011.

[4] D. Goodwin: *Estrildid finches of the world.* Ithaca: Cornell University Press, 1982.

[5] N. Ota, M. Gahr and M. Soma: "Songbird tap dancing produces non-vocal sounds." *Bioacoustics* 26, no. 2: 161-168, 2017.

[6] N. Ota and M. Soma: “Vibrational signals in multimodal courtship displays of birds.” In *Biotremology: Physiology, Ecology, and Evolution* (pp. 237-259). Cham: Springer International Publishing, 2022.

[7] N. Ota: "Tap dancers in the wild: field observations of multimodal courtship displays in socially monogamous songbirds." *The Science of Nature* 107, no. 4: 30, 2020.

[8] N. Ota and M. Gahr: "Context-sensitive dance–vocal displays affect song patterns and partner responses in a socially monogamous songbird." *Ethology* 128, no. 1: 61-69, 2022.

[9] N. Ota, M. Gahr and M. Soma: "Couples showing off: Audience promotes both male and female multimodal courtship display in a songbird." *Science Advances* 4, no. 10: eaat4779, 2018.

[10] M. Gahr and H. R. Güttinger. "Functional aspects of singing in male and female *Uraeginthus bengalus* (Estrildidae)." *Ethology* 72, no. 2: 123-131, 1986.

[11] C. A. Wachtmeister: "Display in monogamous pairs: a review of empirical data and evolutionary explanations." *Animal behaviour* 61, no. 5: 861-868, 2001.

[12] M. Soma and L. Z. Garamszegi: "Evolution of courtship display in Estrildid finches: dance in relation to female song and plumage ornamentation." *Frontiers in Ecology and Evolution* 3: 4, 2015.

[13] K. S. Bostwick and R. O. Prum: "Courting bird sings with stridulating wing feathers." *Science* 309, no. 5735: 736-736, 2005.

[14] L. Fusani and B. A. Schlinger: “Proximate and ultimate causes of male courtship behavior in Golden-collared Manakins.” *Journal of Ornithology*, 153, pp.119-124, 2012.