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Complex sexual signals in the mutual courtship display of blue waxbills

(セイキチヨウの双方向的求愛ディスプレイにおける複雑な性的信号)

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動物のコミュニケーション手段は多様性に富み、しばしば著しい複雑性をみせる。その際たる例に、鳥類が性的な文脈でおこなう儀式化された求愛ディスプレイがある。ゴクラクチョウやマイコドリの雄に見られるような求愛ディスプレイは、以下の点において複雑であると言える。（１）歌とダンスなど複数の行動要素から構成されている。（２）信号のやりとりが視覚や聴覚といった複数のモダリティを介しておこなわれる。（３）歌が複数種類の音素レパートリーからなるように、同一モダリティ内における要素の数が多い。例えば亜鳴禽類マイコドリの雄が左右の羽をこすりあわせることで非発声を発する求愛ディスプレイは、複雑な性的信号の典型として挙げられるだろう。このように複雑な求愛ディスプレイは、雌による雄の選り好みを介した性淘汰の産物であると考えられてきた。

しかしながら一部の社会的一夫一妻制鳥類では、精巧で複雑な求愛ディスプレイを雌雄で双方向的におこなうことが知られている。例えばツルや水鳥では、雌雄が同時に複数の行動要素からなる複雑なダンスをおこなう。またスズメ目鳴禽類の一部の種では、複数の音素レパートリーを組み合わせた歌のデュエットを雌雄でおこなう。近年の系統種間比較解析の研究では、鳴禽類において雌雄が歌を持つ状態が祖先形質であることが報告されている。これらを考え合わせると、鳥類の複雑な求愛ディスプレイの機能と進化を明らかにするためには、雄だけでなく雌の行動を考慮した研究が必要である。鳴禽類は歌とダンスを組み合わせた求愛ディスプレイを雌雄でおこなう種が多く存在するが、歌のデュエットに関する研究が進められている一方で、ダンスを含めたマルチモーダルな求愛ディスプレイについてはほとんど調べられていない。

鳴禽類カエデチョウ科に属するセイキチョウ (blue waxbill, *Uraeginthus* spp.) は、雌雄とも身体運動（ダンス）とそれに付随する歌からなる複雑な求愛ディスプレイを行う。セイキチョウは巣材をくわえることで求愛ディスプレイを開始する。巣材を持ったまま上下運動（以下、ボビング）を繰り返し、歌をうたう。このボビング時に、パチパチと明瞭な音を発する。この行動は視覚信号として重要であるだけでなく、聴覚信号の産出に寄与している可能性がある。

本研究では、雌雄双方向的な視聴覚コミュニケーション信号の進化を理解するため、鳴禽類セイキチョウ雌雄の求愛ディスプレイの信号産出メカニズムと社会的機能に着目し実験をおこなった。第2章ではダンス行動の定量解析、第3章では音響解析をおこない、第4章では求愛ディスプレイに影響する社会要因を検討した。

第2章 セイキチョウ雌雄のマルチモーダルな求愛ディスプレイ

ダンス時に発せられる音の産出メカニズムと、ダンス行動の個体差と性差を明らかにするため、ハイスピードカメラ（300 コマ/秒）による求愛ディスプレイの撮影を行い、行動の定量解析をおこなった。ハイスピード撮影の結果、セイキチョウのボビングには足を止まり木に高速で複数回たたきつける、ヒトのタップダンスのような運動が含まれることが明らかになった。この行動は通常速度のカメラ（30 コマ/秒）による撮影やヒトの肉眼では捉えることのできない非常に高速な運動であった。ダンス行動を定量化し、そのパフォーマンスの個体間・個体内変動を調査したところ、ダンスのパフォーマンスに有意な性差はなく、雌雄が同程度に複雑なダンスを行うことが明らかにな

った。また歌っているときとそうでないとき、異性が近くに滞在しているときとそうでないとき、それぞれでダンス行動を比較したところ、いずれにおいてもダンスのパフォーマンスに個体内変動が生じることが分かった。これによりセイキチョウ雌雄のダンス行動が、視聴覚にまたがる複雑な性的信号を発していること、状況依存的に調節されることを明らかにした。

第3章 聴覚信号としての非発声音

セイキチョウのタップダンス様求愛ディスプレイにより発せられる非発声音について、聴覚信号としての有効性を検証するために音響解析をおこなった。その結果、1 ボビングあたりのタップ回数が大きいほどボビングの着地時の音圧が大きくなることが分かった。ボビング時の音圧は歌の音圧幅と重なっていたことに加えて、ダンス以外での足音の音圧よりも明らかに大きかった。これらのことから、タップダンス様求愛ディスプレイによって産出される非発声音が聴覚信号として有効に機能しうることが示された。

第4章 求愛ディスプレイに対する第三者効果

ツルや水鳥に見られるような雌雄双方向的な求愛ダンスは、つがい内のコミュニケーションに重要な機能を果たすと考えられてきた。このため、雌雄で交わされる視聴覚コミュニケーションに対するペア相手以外の個体（第三者）の影響は、これまでほとんど検討されてこなかった。一方、鳴禽類の歌のデュエットでは、それを聴いている第三者が存在する場合、配偶者防衛や配偶者への忠誠の表明として機能することが示唆されている。ここでは、雌雄のダンス行動も、歌のデュエットと類似した機能を持つと予測した。セイキチョウ雌雄の求愛ディスプレイの社会的機能を明らかにするため、第三者効果に着目した実験を行った。ペアを組ませた雌雄に対し、第三者のいる状況といない状況での求愛行動を比較したところ、雌雄共に第三者の存在する状況でダンスが促進された。このときのダンスは多くの場合第三者ではなくパートナーに向けて行われていた。本結果から、セイキチョウの求愛行動がペア相手だけでなく、ペア相手以外の他個体からも影響を受けることが明らかになった。セイキチョウのダンスが性的アピールのみならず、ペア相手への忠誠の表明や第三者に対する配偶者防衛行動として機能する可能性が示された。マルチモーダルな信号の産出に第三者の存在が大きく影響していたことは、社会状況の複雑さが複雑な信号の進化を促すという社会複雑性仮説の観点からも重要な知見と考えられる。

本研究は、社会的な一夫一妻制であり、複雑な歌を持つ鳴禽類の雌雄が、ダンスによって視聴覚にまたがる複雑な性的信号を産出することを初めて報告した。この行動に性差はほとんど見られず、雌から雄への一方向的な性選択によらずとも、複雑な性的信号が進化しうることを明らかにした。

今回は野外の生態学的な知見が少ない状況で、飼育個体を用いてランダムに組んだペアのダンス行動を調査した。そのため、野生化での行動、信号受信者の詳細な反応、つがい形成後の長期的な観察については今後検討すべき課題である。また本実験で得られた知見が鳥類に見られる雌雄の求愛ディスプレイ全般に適用できるのか結論づけることはできず、他種の行動に関しても調査が必要である。カエデチョウ科の種では両性がダンスをおこなうことは珍しくなく、雌雄が発する信号の複雑性とそのコミュニケーション上の重要性は、そもそも見過ごされている可能性がある。セイキチョウのようにつがい間の絆の形成と維持が重要と考えられる種では、系統的制約の大きい歌の代わりとして、ダンスなどの雌雄双方向的な信号伝達手段が進化しやすいのかもしれない。本研究は、これまで焦点が当てられてこなかった求愛ディスプレイの一側面に光を当て、コミュニケーション信号の機能と進化を考える上で重要な示唆を与えた。

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Chapter 1

General introduction

The evolutionary enigma of mutual sexual signals

Why some animals evolved complex communicative signals has remained a mystery. Bird courtship displays are a fascinating example of the wide variety of complex signals involved in animal communication. For example, manakins (Aves: Pipridae) perform a ritualized courtship display in which their wing movements produce non-vocal sounds (Bostwick and Prum 2005). Such a complex courtship display is composed of multiple behavioral components and modalities. A growing number of researchers have investigated complex sexual signals of courtship display, and revealed some findings about the signal production mechanisms and communicative functions (review in Stevens 2013).

Under strong sexual selection pressure, males have exaggerated sexual signals, such as showy ornamental traits or conspicuous courtship displays (Andersson 1994). In lekking or polygynous species, males often perform elaborate courtship displays (e.g., spiders, Girard et al. 2011; frogs, de Luna et al. 2010; fishes, Amorim et al. 2008; and birds, Cooper and Goller 2004, Dalziell et al. 2013). For example, male peacock spiders have a conspicuously colorful abdomen and perform elaborate body movements to produce visual and vibration signals (Girard et al. 2011). Male superb lyrebirds sing several different songs that each match a unique set of dance displays

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(Dalziell et al. 2013). Under sexual selection pressure in males, strong and efficient signals are favored. Multimodal courtship displays play a crucial role in increasing the efficacy of signaling (Uetz et al. 2009, O’Loghlen and Rothstein 2010).

In contrast, both males and females engage in mutual multimodal courtship displays in some socially monogamous avian species. Elaborate mutual dance displays between sexes are performed by socially monogamous non-passerine birds, which are non-vocal learners, such as grebes (Nuechterlein and Storer 1982) and cranes (Masatomi 1983). Song duetting in passerine birds (review in Hall 2004) is also a well-known example of mutual courtship display within pairs. In some species, both sexes exchange courtship displays between pairs in a temporally well-coordinated manner (e.g., song duets in some songbirds, review in Hall 2004), whereas, in other species, both sexes perform solo courtship displays at different times (e.g., solo songs in both sexes of red-cheeked cordon-bleus, Gahr and Güttinger 1986; and blue-capped cordon-bleus, Geberzahn and Gahr 2011). These varied bidirectional courtship displays are assumed to contribute to pair formation, bonding, and maintenance (Malacarne et al. 1991, Wachtmeister and Enquist 2000) in addition to sex appeal.

The evolution of female sexual signaling is a currently debated issue. Females in some species have similar sexual traits to those of males (e.g., songs of male and female blue waxbills; Gahr and Güttinger 1986, Geberzahn and Gahr 2011). However, female sexual traits are often assumed to have different functions from male sexual traits. For example, females are engaged in competition for ecological resources rather than mate acquisition (Tobias et al. 2012), and it was reported that female songs

are used for same-sex competition (Cain and Langmore 2015, 2016). Although birdsong is classically attributed to males, a recent study revealed that song is widespread among female songbirds, and that female song was most likely present in the ancestor of modern songbirds (Odom et al. 2014). These call for a re-evaluation of the pervasive view of courtship display as an epigamic male trait that has evolved through sexual selection (Odom et al. 2014, Riebel et al. 2005) because mutual courtship display has received relatively less attention than male unidirectional courtship displays, and the functions remain unclear.

Dance is another topic that requires consideration to elucidate courtship display evolution. It is puzzling why dance displays can function and evolve as intersexual communication signals in socially monogamous songbirds, but only songs have received the majority of attention (Soma and Garamszegi 2015). Some studies reported that dances are coordinated with songs in male songbirds (Cooper and Goller 2004, Dalziel et al. 2013, Ullrich et al. 2016), presumably to enhance signal efficacy and sexually stimulate females (O’Loghlen and Rothstein 2010). However, a recent phylogenetic study of Estrildid finch courtship display revealed that the common ancestor was likely to have female dance display, and the dance and song displays evolved in response to different selection factors (Soma and Garamszegi 2015).

Courtship display of blue waxbills (Estrildidae: Uraeginthus spp.)

Estrildid finches perform both song and dance in courtship displays, and the display components are shared between the sexes in some species (Goodwin 1983, Soma and

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Garamszegi 2015). Courtship display in the blue waxbill (Estrildidae: *Uraeginthus* spp.) has the potential to provide new insight into the evolution and function of mutual multimodal courtship display. Both sexes of blue waxbills perform complex multimodal courtship displays that are characterized by singing and simultaneous visual displays, such as holding nest material and bobbing (Movie 1, 2; Goodwin 1982).

Fig. 1-1 shows schematic views of courtship behaviors and partner response. According to one study (Goodwin 1983) and my preliminary observations, blue waxbills started courtship by picking up nest materials and moving to a perch (Fig. 1-1). Subsequently, they started to bob repeatedly and sing songs several times (see also Chapter 2). A highly motivated partner in courtship display can be identified by a triangular head, bill wiping, tail flicking, and tail angling during the courtship display (Movie 3, 4; Fig. 1-1). These behaviors are described as characteristics of sexually motivated responses (Goodwin 1982). A “triangular head” is expressed by erecting head feathers, and it gives the head a distinctive triangular shape (Goodwin 1982). Blue waxbills sometimes wipe their bills against the perch (“bill wiping”, Movie 4, Goodwin 1982). “Tail flicking” consists of vertical flicking movements of the tail (Movie 4, Goodwin 1982). A sexually motivated bird usually angles its tail toward the other individual (“tail angling”, Movie 4, Goodwin 1982). After the courtship display, females start to solicit copulation with a crouched posture and quivering tail (“copulation solicitation display”, Movie 4, Goodwin 1982), and the male mounts her to copulate (Movie 4, Goodwin 1982). However, this behavioral sequence was rare in this study (see also Chapter 2), they usually moved on to the post-courtship phase

without copulation (Fig. 1-1). In the post-copulation phase, they sometimes simultaneously perform “bill mandibulation,” which consists of rapid opening and shutting of the mandibles. “Chasing” was performed by a male and female, and seemed to be a ritualized behavior used as a sexual behavior (Goodwin 1982).

Blue waxbills include three species: the red-cheeked cordon-bleu, *Uraeginthus bengalus*; blue-capped cordon-bleu, *U. cyanocephalus*; and blue-breasted waxbill, *U. angolensis*. I studied red-cheeked and blue-capped cordon-bleus in this thesis (Movie 1, 2). The ecology and behavior of blue waxbills are poorly understood, but they are thought to be socially monogamous, biparental songbirds (Goodwin 1982). They are found in arid areas with bushes and/or trees in Africa (Goodwin 1982). They have sexually dimorphic plumage, and males have red-cheeks and a blue-cap in red-cheeked and blue-capped cordon-bleus, respectively (Goodwin 1982). The only sex difference in blue waxbill song is the slightly shorter song produced by females (red-cheeked cordon-bleu, Gahr and Güttinger 1986; blue-capped cordon-bleu, Geberzahn and Gahr 2011).

Blue waxbill dance displays are unique because they produce distinct sounds from their feet during courtship bobbing (Goodwin 1982). Although other songbirds also perform courtship bobbing, they do not produce such distinct sounds while bobbing (e.g., Java sparrows, *Lonchura oryzivora*; Soma and Mori 2015). Blue waxbill dance movements are expected to have some kinematic mechanisms for producing multimodal signals, similar to those signals produced by rapid wing-snapping in manakins (Bostwick and Prum 2003).

Aims

As a first step toward understanding the evolution of mutual multimodal courtship displays, in this thesis I aimed to reveal multimodal signal production mechanisms (Chapter 2, 3) and social functions (Chapter 4) in each blue waxbill sex. By doing so, I aimed to show the similarities of multimodal courtship display mechanisms and functions between males and females, which could contribute to better understanding blue waxbill courtship display evolution.

In Chapter 2, I reported unique dance movements and signal production mechanisms of blue-capped and red-cheeked cordon-bleus. By recording the courtship display with a high-speed video camera, I discovered that, in addition to bobbing, their visual courtship display includes very rapid step-dancing, which is thought to produce vibrations and non-vocal sounds. I also quantified their dance performances and investigated the among- and within-individual differences.

In Chapter 3, I evaluated the signal efficacy of step sounds in blue-capped cordon-bleus. I tested if their high-speed step movements contribute to producing non-vocal sounds. I predicted that tap-dancing movements would affect the amplitude of non-vocal sounds. If this prediction is true, signals in blue-capped cordon-bleu tap dancing would be conveyed acoustically like songs and can be used more broadly than solely using visual signals.

In Chapter 4, I examined the audience effect to understand why and when both male and female blue-capped cordon-bleus perform multimodal courtship

display. Although mutual dance display is usually considered to function as within-pair communication, song duetting facilitates interaction with bystanders (e.g., magpie-lark song duetting, Hall and Magrath 2007). I expected that multimodal complex courtship display in blue-capped cordon-bleus would increase signal efficacy and enhance communication with both partner and bystanders. If blue-capped cordon-bleu courtship display is facilitated by the presence of an audience, the display would have similar functions to song duetting, such as serving as commitment and/or mate-guarding signals.

In Chapter 5, I reviewed multimodal signal production mechanisms and social functions of blue waxbill courtship displays based on the results of Chapters 2 to 4, and discussed future research directions. I also discussed the possible evolutionary processes that shaped mutual sexual signals.

Figure

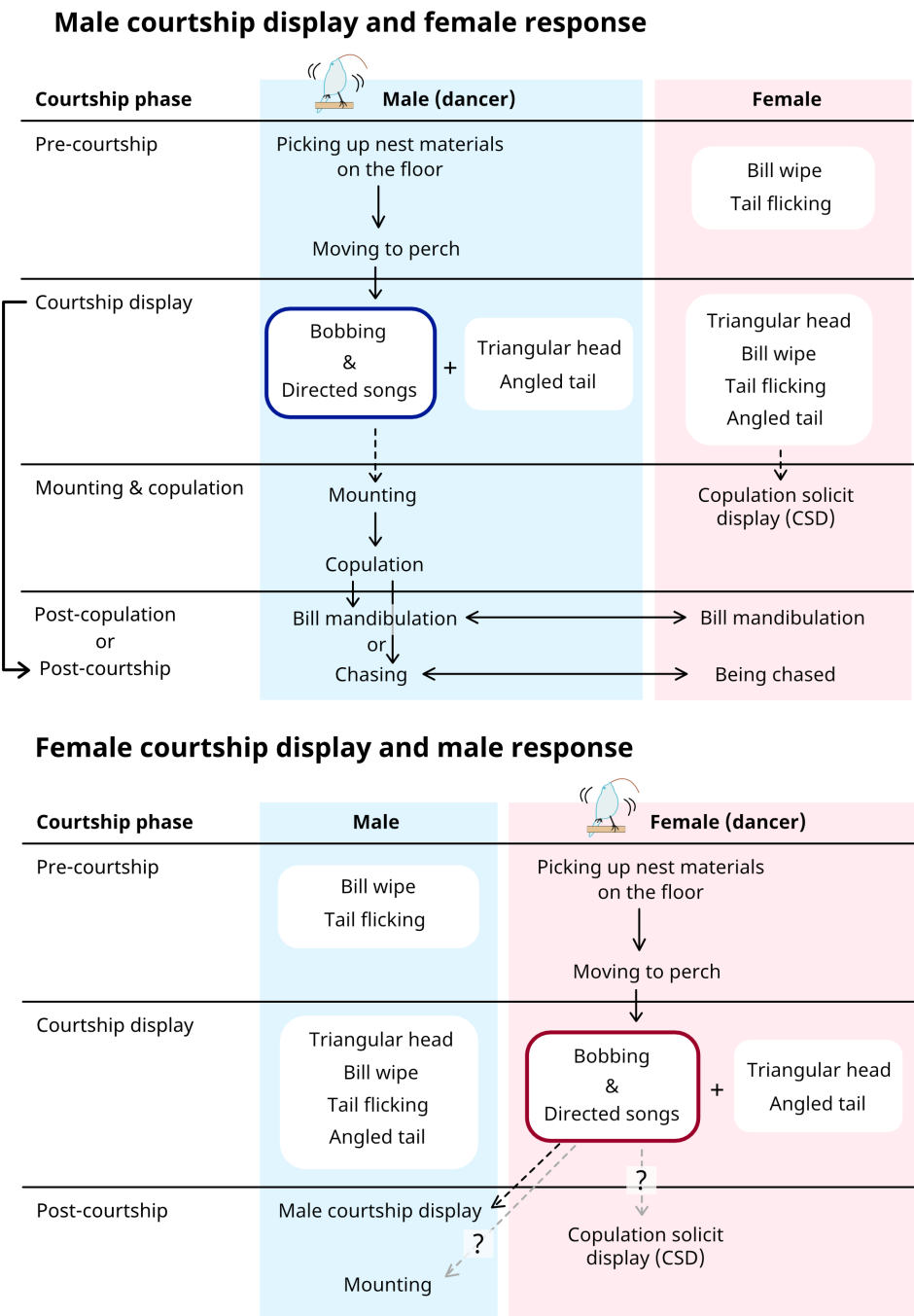


Figure 1-1. Schematic views of courtship behaviors in male and female blue waxbills based on personal observations and Goodwin (1982). Behavioral transitions indicated by dashed arrows were infrequent, at least in this thesis. Gray dashed lines indicate possible transitions that I did not observe.

Captions of supplementary movies

Movie 1.

Courtship display in both sexes of blue-capped cordon-bleus (*U. cyanocephalus*) with normal- (30 frames/s) and high-speed (300 frames/s) video cameras.

Movie 2.

Courtship display of a male red-cheeked cordon-bleu (*U. bengalus*) with normal- and high-speed video cameras.

Movie 3.

Partners' responses to courtship display in blue-capped cordon-bleus.

Movie 4.

A blue capped cordon-bleu female performing sexually motivated behaviors and copulation.

Movie 5.

An example of male blue-capped cordon-bleu non-vocal courtship sounds and number of steps.

Movie 6.

An example of non-vocal sounds during a courtship dance and other foot movements in a male blue-capped cordon-bleu.

Movie 7.

Dance duetting behavior of blue-capped cordon-bleus in the presence of a female audience.

Movie 8.

Male blue-capped cordon-bleu courtship display directed to its partner in the presence of a female audience.

Chapter 2

Multimodal courtship display in both male and female blue waxbills

Introduction

Elaborate courtship displays are assumed to have evolved under strong sexual selection pressure in males (Andersson 1994, Candolin 2003). Much research has focused on male–female directed courtship displays performed by polygynous male birds, while the occurrence of both male–female and female–male directed courtship displays performed by socially monogamous birds has often been overlooked. Elaborate mutual dance displays between sexes are known to be performed by socially monogamous non-passerine birds, which are non-vocal learners, such as grebes (Nuechterlein and Storer 1982). The evolution and mechanisms of dance duets have received far less attention than have vocal duets. Furthermore, why a few songbird species use both song and dance displays as intersexual communication is a puzzling question (Soma and Garamszegi 2015).

The blue waxbills (*Uraeginthus* spp.) include a few species that have courtship displays in both sexes. During these displays, they hold a piece of nesting material, then bob up and down and sing (Goodwin 1982; Movie 1, 2). Notably, the courtship bobbing produces rhythmical sounds (Movie 1, 2; Fig. 2-1). Here, I analyzed

the audio-visual displays of the red-cheeked cordon-bleu (*U. bengalus*) and the blue-capped cordon-bleu (*U. cyanocephalus*) in detail using high-speed video-camera recordings (Movie 1, 2; Fig. 2-2). As a result, I discovered that their visual courtship display includes quite rapid step-dancing during bobbing (Movie 1, 2; see results). This specific “tap-dance” like behavior has never been reported in songbirds and presumably produces non-vocal sounds and/or vibrations in addition to song.

If the tap dance of blue waxbills serves as a sexual signal, its motor performance varies among individuals, between sexes, and depends on the behavioral context. Specifically, I expected that males would show higher motor performance than females because their dance display is assumed to be more physically demanding and play an important role in both intersexual communication and song. I also expected that, to maximize signal efficacy, blue-capped cordon-bleus adjust their dance performances based on singing activity and their partner’s position. At least in some songbird species, it is known that song production affects dance movements, which likely contributes to avoiding interference and/or coordinating display components (Cooper and Goller 2004, O’Loghlen and Rothstein 2010). Because spatial proximity is a measure that reflects pair bonding in Estrildid finches (Goodwin 1982), partner location is expected to influence dancing performance. Additionally, I investigated partner response to dancing birds, which was expected to vary based on the proximity of the two birds.

Materials and Methods

Subjects and experimental procedure

I used 16 blue-capped cordon-bleus (8 females and 8 males). A male and a female were randomly paired, housed together in a cage (120 × 48 × 48 cm). Conventionally, such housing has been used to record data on courtship behaviors in Estrildid research (e.g., Jarvis et al. 1998). Their behaviors were recorded in a 2-h recording session (2.02 ± 0.40 h) with normal (Q3HD ZOOM, 30 frames/s) and high-speed (GC-PX1 Victor, 300 frames/s) video cameras. If either member of a pair failed to dance, I repeated the recording session using the same pair, or switched their partners. The observation time for each individual was arbitrary (Table 2-1) because I wanted to maximize the sample size by allowing birds to participate as often as they would. I recorded 102 sessions (206.5 hours of footage).

I analyzed the video using Adobe Premiere Pro software (Adobe Systems Inc.) and marked three behavioral measures: (i) the occurrence of dance displays for each individual in each session; (ii) the bobbing tempo (number of bobs/s); and (iii) the number of steps in one bobbing action (Fig. 2-2c). I examined how sex of the performers, partners' positions (same perch or not), and act of singing while bobbing affected performance on these three metrics. For partners' response, I recorded the occurrence of tail flicking, tail angling, and bill wiping, all of which were described as sexually motivated responses for courtship display (Goodwin 1982, Chapter 1, Fig. 1-1). I did not check for a triangular head (Chapter 1, Fig. 1-1) because of the video

resolution and discrimination difficulty. As outcomes of courtships, I recorded the occurrence of mounting of males, copulation solicitation display in females, and copulations (Chapter 1, Fig. 1-1). Using these behavioral scorings, I examined the effect of the location (i.e., the same perch as the dancer or not) on partner response and courtship outcomes, and controlled for the effect of dance bout duration.

All individuals were kept on a 14:10 h light:dark schedule (lights on 07:00–21:00) at about 22 °C and 50% humidity. Birds were provided with finch seed mixture, cuttlebone, water, and cucumber ad libitum. Nests and nesting materials were always available in the cages. Procedures were in accordance with national laws and approved by the Government of Upper Bavaria (approval number 311.5-5682.1/1-2014-021).

Statistical analyses

To examine the effect of sex on the probability that an individual danced during sessions, I used a generalized linear mixed-effect model (GLMM) with a binomial distribution. To examine the effects of sex, partners' position, and singing behavior on dance performance, I used a GLMM with a Poisson distribution to analyse the number of steps, and a linear mixed-effect (LME) model to analyse the bobbing tempo. In these analyses, I considered session number nested within bird ID as a random effect to control for non-independence of the data. To investigate individual differences in dance display, I used a likelihood ratio test to compare this model with a model in which bird ID was removed. To test the effect of partner position and dance bout duration on the occurrence of partner responses (i.e., tail flicking, tail angling, and bill

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wiping) and courtship outcomes (i.e., copulation solicitation display, mounting, and copulation; see also Chapter 1, Fig. 1-1, Movie 4), I used a GLMM with binomial distribution. All statistical analyses were performed using R 3.3.0 (R development Core Team 2016).

Results

Courtship dance

High-speed video recordings revealed that in a single bobbing motion, birds hop with their heads pointed upwards and stamp their feet several times so rapidly that it is invisible to the naked eye (Movie 1, 2; Fig. 2-2b). I confirmed that all blue-capped cordon-bleus that performed courtship displays (7 males and 4 females) included rapid steps while bobbing (Movie 1, Fig. 2). The birds always performed the displays on the perch (Fig. 2-2a). On average, birds performed 3.17 steps (SEM, 0.03; range, 0–6) per bobbing action. One step took 6–12 frames of 300-frames/s video, thus equaling 20–40 ms, at an estimated rate of 25 Hz to 50 Hz. The bobbing tempo was 1.39 bobs/s (SEM, 0.02).

Sex and individual differences

Dance probability, bobbing tempo, and the number of steps during bobs did not differ significantly between males and females (Table 2-2a, Movie 1), although males danced more often (males: 24.8%, females: 10.6%; see Table 2-1a for detailed information) and tended to bob more quickly and take more steps (Fig. 2-3a, b; Table 2-2b, c). Variations in dance probability and the number of steps differed significantly between individuals ($p < 0.05$, Table 2-2a, c), but bobbing tempo did not ($p = 0.425$, Table 2-2b). Although each subject chose to dance display to one or two particular individuals, the birds exhibiting greater motor performance did not tend to receive more dance

displays (Table 2-1b).

Within-individual changes

Both males and females bobbed more quickly and took more steps when their partners were present on the same perch ($p < 0.001$; Table 2-2b, c; Fig. 2-3c, e), which was likely caused by the presence of their nearby partners (Movie 3). Individuals also adjusted the number of steps and the bobbing tempo when singing, bobbing faster ($p < 0.001$, Table 2-2b, Fig. 2-3d) and taking fewer steps ($p < 0.001$, Table 2-2c, Fig. 2-3f). I confirmed that the results were very consistent if I removed the independent data (circles without lines in Fig. 2-3 c–f, Appendix table 1).

Partner responses and courtship outcomes

Both male and female partners responded to subject dances by tail flicking, tail angling, and bill wiping (Chapter 1, Fig. 1-1, Movie 4). When dancers stayed on the same perch, signal receivers were more likely to show sexually motivated responses (Table 2-3a, 2-4), whereas male signal receivers on the same perch showed less tail flicking (Table 2-4). Less motivated birds sat on the perch, sleeping or feeding instead of responding to partners. Dance bout duration also affected the occurrence of partner responses (Table 2-3a). I observed copulations twice, but only when males performed courtship displays (Fig. 1-1, Movie 4, Table 2-4). Although there were no significant effects of partner position on copulation solicitation display (see also Chapter 1, Fig. 1-1, Movie 4), mounting, and copulations, these behaviors were only observed when partners

stayed on the same perch. Dance bout duration did not affect the courtship outcomes (Table 2-3b).

Discussion

Both male and female blue-capped cordon-bleus exhibited quite rapid stepping behavior during courtship displays, which varied among individuals but not across sexes. The evolution of this complex courtship display in both sexes is surprising because male ornaments tend to become exaggerated even in monogamous species because females are generally the choosier sex (Andersson 1994). According to our pairing experiment, both male and female blue-capped cordon-bleus performed courtship display with particular individuals, but high-motor performance individuals were not necessarily popular among the opposite sex (Table 2-1). Assortative mating did not tend to occur with respect to dance performances (Table 2-1). The only sex difference in temporal pattern of the blue-capped cordon-bleus courtship display is the slightly shorter song produced by females (Geberzahn and Gahr 2011). Even if the small sample size prevented us from finding sex-related differences in dance performance, such sex differences would likely be small because the distribution of dance performances overlapped between males and females (Fig. 2-3a, b).

Performing rapid stepping behavior seemed to enable male and female blue-capped cordon-bleus to communicate via multiple modalities. My results suggest that both sexes produce multimodal (acoustic, visual, and tactile) signals for intersexual communication that involves the coordination of several motor systems that control singing, bobbing, stepping, and beak movements. Attention should be paid to where the birds dance in the wild because blue waxbills reportedly dance also

on the ground (Goodwin 1982). However, all dance displays were performed on perches in this captive study. Intensified stepping performance when partners were on the same perch likely enables performers to send vibration signals context-dependently. Considering that the limit of flicker fusion frequency is usually over 100 Hz in many birds (Jones et al. 2007), stepping movements between 25 and 50 Hz could be visible and function as a visual signal for blue waxbills.

The results that the receiver birds usually showed more sexually motivated responses when the dancer was on the same perch support the idea that tap dancing works as an effective multimodal signal (i.e., combination of visual, acoustic, and vibration signals) under these conditions. In contrast to previous results, males showed more tail flicking during female courtship displays when they were not on the same perch. This finding corresponds to Goodwin's (1982) description that female blue waxbills sometimes perform courtship displays when sexual motivation of the male partner appears to be inadequate; in this case, non-vocal sounds produced by dance would be effective for signaling individuals from a distance.

The bobbing movements may exaggerate the sexually dimorphic plumage of their heads and nesting materials that they hold. Intensified bobbing performance when partners stayed on the same perch could make them more visually appealing to highly motivated partners. Fewer steps and more frequent bobbing during singing are likely adaptations that help avoid interference between signals (i.e., stepping sound, song, and body movements). Such coordination could be caused either by physical constraints associated with body movements (e.g., brown-headed cowbirds, Hoepfner

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and Goller 2013), or by deliberately adjusting two independent signals.

Unexpectedly, I observed only a few cases of copulation, copulation solicitation display, and mounting in this study (Movie 4, Table 2-4b). These findings should be cautiously interpreted because this is a pilot study; however, I suspect that their choosiness in mate choice (Table 2-1) is a factor. I expect that repeated courtship display performances would lead to pair formation and copulation over the long-term.

The multimodal (acoustic, visual, tactile) and multicomponent (vocal and non-vocal sounds) courtship display observed was a combination of several motor behaviors (singing, bobbing, stepping). The amazing courtship display of blue waxbills (Movie 1, 2) had features that are analogous to courtship displays in manakins, particularly with regard to multimodality and acrobatic movements (Bostwick and Prum 2005, DuVal 2007, Fusani and Schlinger 2012), but these species differ in vocal learning ability, behavioral mutuality and mating systems. That both sexes of this socially monogamous songbird perform such a complex courtship display is a novel finding and indicates that selective forces other than sexual selection should be considered. Presumably, their multimodal courtship display functions as intersexual communication that contributes to pair formation and bonding (see also Chapter 4).

Figures and Tables

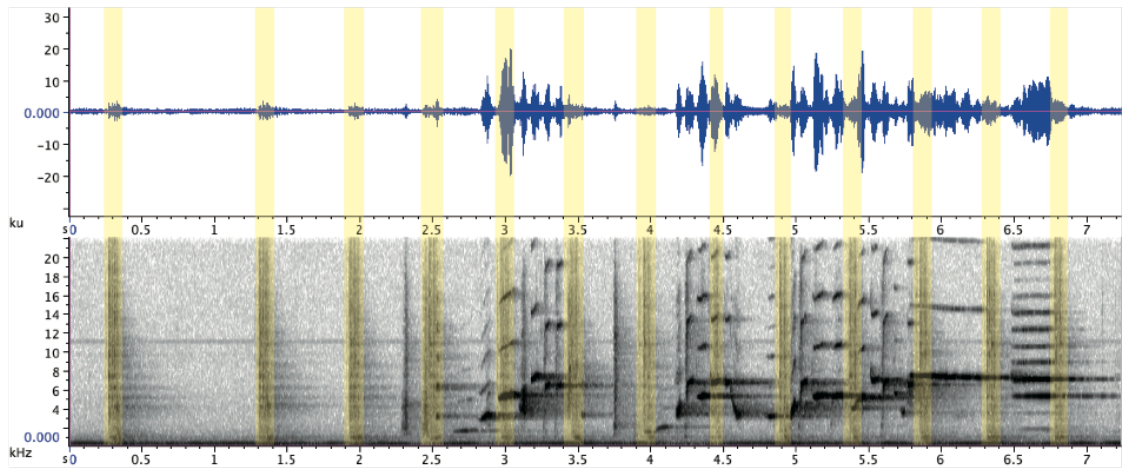


Figure 2-1. The waveform and the spectrogram of sound of courtship display shown by a male blue-capped cordon-bleu in Movie 1, in which stepping sounds are yellow-colored.

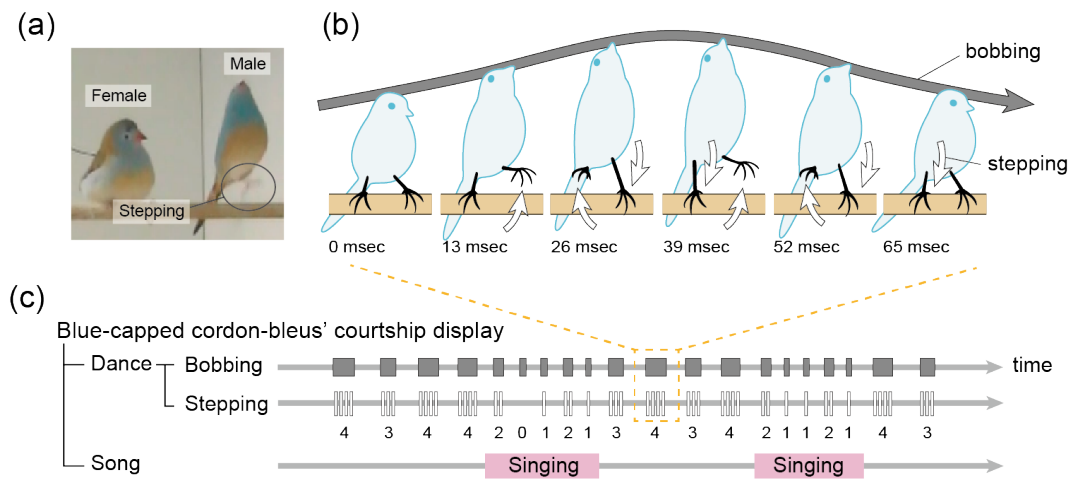


Figure 2-2. Courtship display in blue-capped cordon-bleus. (a) When blue-capped cordon-bleus perform courtship display, (b) they simultaneously bob and step, and (c) sing at certain times. Bobbing (shaded bars) with multiple steps (white bars) is repeated multiple times as indicated in (c), and usually singing occurs several times. White and shaded arrows in (b) correspond with the colour of bars in (c). Note the number of steps in (c) involved in each bobbing action.

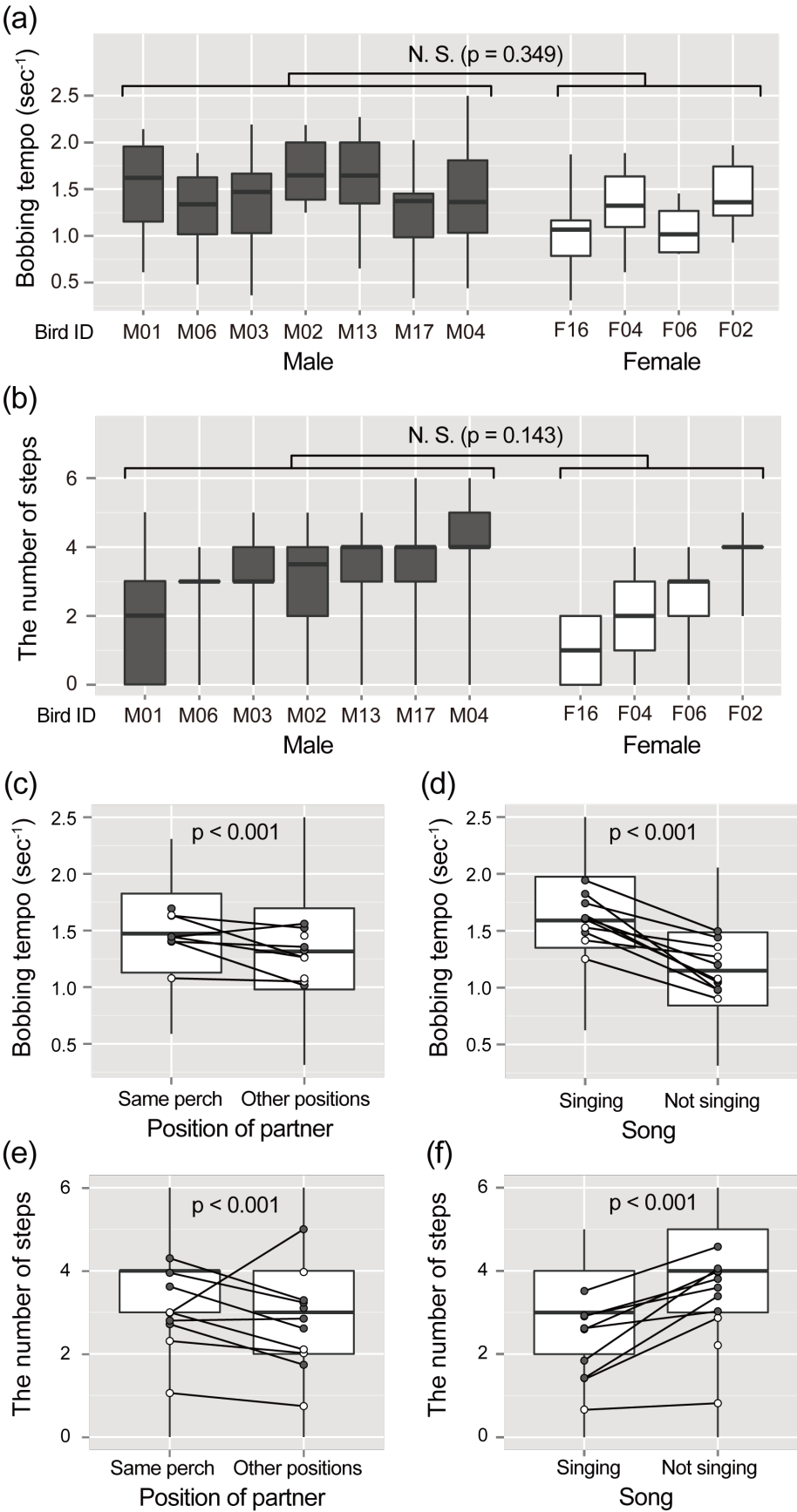


Figure 2-3. Changes of dance performance within and among individuals. Individual differences were calculated in (a) bobbing tempo and (b) the number of steps per bob (shaded bars: males, white bars: females). Bobbing tempo depended on (c) whether the partner was on the same perch, and (d) whether birds were singing. Similarly, the number of steps depended on (e) whether the partner was on the same perch, and (f) whether birds were singing. (a–f) All box plots show median, quartiles, and minimum and maximum values. (c–f) Mean individual values (closed circles: males, open circles: females) and their within-individual changes are indicated. I confirmed that the results of within-individual differences in (c)–(f) did not change if we re-analyzed the data using only paired data (Appendix table 1).

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Table 2-1. (a) The list of subject birds and the percentage of the sessions with dance. (b) Behavioral matrix showing the dance rate observed in each male-female combination. Upper triangles correspond to female dance probability rate, while lower triangles show those of males. Blue and pink areas indicate combinations in which males and/or females danced, respectively. Grey parts indicate that the corresponding male and female were not paired. Median no. steps (green) and bobbing tempo (yellow) are indicated. Medians of no. steps per individuals are shown in descending order because it differed significantly among individuals, while bobbing tempo did not.

(a)

Bird ID	Sex	Total number of sessions	Number of sessions with dance	Dance probability
M04	Male	9	5	55.6 %
M17	Male	6	1	16.7 %
M13	Male	8	4	50.0 %
M02	Male	15	1	6.7 %
M03	Male	10	2	20.0 %
M06	Male	17	1	5.9 %
M01	Male	17	6	35.3 %
M07	Male	20	0	0 %
Average				23.8 %

F02	Female	15	3	20.0 %
F06	Female	15	3	20.0 %
F04	Female	9	1	11.1 %
F16	Female	6	2	33.3 %
F01	Female	17	0	0 %
F03	Female	10	0	0 %
F07	Female	19	0	0 %
F13	Female	11	0	0 %
Average				10.6 %

(b)

		Female ID							
		F02	F06	F04	F16	F01	F03	F07	F13
Male ID	No. steps	4	3	2	1	-	-	-	-
	bobbing tempo	1.36	1.02	1.32	1.07	-	-	-	-
M04	4	1.36		1/7			0/2		
M17	4	1.37	0/3	3/7	1/1		2/2	0/1	0/1
M13	4	1.65	0/3					0/1	0/7
M02	3.5	1.65	2/12			0/3			
M03	3	1.47	1/12	0/2		0/3	0/8		
M06	3	1.34		2/2	1/3		0/2	0/1	
M01	2	1.62	1/3	0/11	0/3	0/14		0/2	1/1
M07	-	-	0/1		0/2	5/14		0/15	0/2

Examples:  Not paired  Paired

a: total no. sessions
b: no. sessions with female dance
c: no. sessions with male dance

Table 2-2. Effect of sex on (a) dance probability (GLMM, binomial) and the effects of sex, position of partner and song on (b) the bobbing tempo (LME) and (c) the number of steps in one bob (GLMM, poisson).

Response variable		Coefficient	SE		p
(a) Dance probability	Fixed effect	Sex ^a	0.380	0.259	z = 1.466
	Random effect	Bird ID			$\chi^2 = 9.352$
(b) Bobbing tempo	Fixed effect	Sex ^a	0.089	0.090	t = 0.988
		Partner position ^b	0.440	0.036	t = 12.103
		Song	0.186	0.046	t = 4.003
	Random effect	Bird ID			$\chi^2 = 0.636$
(c) Number of steps in one bob	Fixed effect	Sex ^a	0.380	0.259	z = 1.466
		Partner position ^b	0.201	0.027	z = 7.429
		Song	-0.305	0.023	z = -13.266
	Random effect	Bird ID			$\chi^2 = 58.844$

^a Estimated values for effects that contain a “subject sex” term are for males.

^b Estimated values for effects that contain a “partner position” term are for the same perch (Fig. 2-3).

Table 2-3. Effect of partner position and dance bout duration on the occurrence of partner response (a) and courtship outcomes (b) (GLMM, binomial).

	Response variable	Fixed effect	Coefficient	SE	z-value	p
(a) Partner responses	Tail flicking	Partner position ^a	5.455	0.914	5.676	< 0.001
		Dance bout duration	0.078	0.026	3.053	0.002
	Tail angling	Partner position ^a	6.905	1.319	5.233	< 0.001
		Dance bout duration	0.077	0.028	2.787	0.005
(b) Courtship outcomes	Bill wiping	Partner position ^a	3.008	0.968	3.107	0.002
		Dance bout duration	0.073	0.020	3.705	< 0.001
	Mount	Partner position ^a	40.331	1024.005	0.039	0.969
		Dance bout duration	0.040	0.075	0.535	0.593
	Copulation solicitation display	Partner position ^a	20.000	1192.000	0.002	0.999
		Dance bout duration	0.014	0.040	0.261	0.794
	Copulation	Partner position ^a	20.000	1192.000	0.002	0.999
		Dance bout duration	0.014	0.040	0.261	0.794

^a Estimated values for effects that contain a “partner position” term are for the same perch.

Table 2-4. List and frequency of partners' behaviors, postures, and courtship outcomes in response to dancing birds (see also Chapter 1, Fig. 1-1, Movie 4).

	Response to male dance			Response to female dance		
	The number of observations	Positions *		The number of observations	Positions *	
		Same	Other		Same	Other
Partners' behavior or posture	Tail flicking	70 /150= (46.7 %)	62 + 8 =	11 /36= (30.6 %)	2	9
	Bill wipe	19 (12.7 %)	14 5	2 (5.6 %)	2	0
	Angled tail	54 (36.0 %)	52 2	2 (5.6 %)	2	0
	Copulation solicit display	2 (1.3 %)	2 0			
	Mounting	4 (2.7 %)	4 0	0 (0 %)	0	0
Courtship outcomes	Copulation	2 (1.3 %)	0 0	0 (0 %)	0	0
	Total number of male courtship dances 150			Total number of female courtship dances 36		

* Positions indicate that dancer and the partner stayed on the same perch or other positions.

Chapter 3

Non-vocal sounds as an acoustic signal

Introduction

Although birds generally rely on vocalization for acoustic communication, non-vocal sounds are known to be used in some species, such as manakins (Pipridae; Bostwick and Prum 2003, Fusani et al. 2007, Prum 1998), snipes (*Gallinago coelestis*, Bahr 1907), flappet larks (*Mirafra rufocinnamomea*, Norberg 1991), greater sage grouse (*Centrocercus urophasianus*, Koch et al. 2015), ruffed grouse (*Bonasa umbellus*, Garcia et al. 2012), hummingbirds (Trochilidae, Clark et al. 2011), woodpeckers (Picidae, Stark et al. 1998), oriental white storks (*Ciconia boyciana*, Eda-fujiwara et al. 2004), and palm cockatoos (*Probosciger aterrimus*, Wood 1987). Generally, these species produce non-vocal sounds for courtship using their wings, tails, bills, or tools, and these non-vocal sounds are poorly understood in the context of acoustic communication evolution compared with vocalizations.

Vocalization has been well studied in songbirds, whereas less attention has been paid to non-vocal sounds. However, recent studies revealed that both males and females of some songbird species also produce non-vocal sounds in addition to song (Soma and Mori 2015, see also Chapter 2). For example, in Java sparrows, which are socially monogamous songbirds without female song, both sexes produce bill-click

sounds that are well-coordinated with male song (Soma and Mori 2015). These findings are rather surprising for at least two reasons. First, past studies of acoustic communication in songbirds have typically shed light on their vocalizations, because they are vocal learners and can acquire complex songs (Catchpole and Slater 2008). Therefore, non-vocal sounds in songbirds have been largely overlooked, although some songbirds were suggested to be able to produce non-vocal sounds (Clark and Prum 2015). Second, courtship displays to produce non-vocal sounds are usually considered to have evolved via strong sexual selection pressure on males of polygynous or lekking species (Andersson 1994, Byers et al. 2010, Fusani and Schlinger 2012, Prum 1998). Although a recent study found that vocalization is both widespread and ancestral in female songbirds (Odom et al. 2014), it is still unclear why and how non-vocal sounds evolved in males and females of some songbirds.

As reported in Chapter 2, tap dance-like behavior of the blue-capped cordon-bleu (*U. cyanocephalus*) is accompanied by distinct non-vocal sounds (Fig. 2-1, Movie 5). I have revealed that their visual courtship display includes multiple rapid steps while bobbing and produces non-vocal sounds (Chapter 2; Fig. 2-1, 2; Movie 5). The tap dance-like behavior is invisible to the naked eye and appears as a single pulse on the spectrogram (Fig. 2-1, also see Fig. 3-1a, b). My findings (Chapter 2) suggest that performing rapid step behavior enables male and female blue-capped cordon-bleus to communicate via multiple acoustic signals (i.e., vocal and non-vocal sounds).

Clark (2016) proposed that one criterion to diagnose a non-vocal sound is voluntariness: whether the sound is produced intentionally and production is

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modulated by the animal. My previous study revealed that their tap dance-like behavior is performed only during courtship, and the performance is adjusted in a context-dependent manner (Chapter 2). For example, they take more steps when their partner stayed nearby and fewer steps when they were singing (Chapter 2). These context-dependent performance changes seem to modulate non-vocal sounds but the relationship between the kinematics and sounds remains unclear. Investigating this relationship would improve our understanding of the role of non-vocal sounds. The effective range of acoustic signals is generally broader than that of visual signals, although many environmental factors (e.g., substrates as media for the transmission of signals, light intensity, and noises) affect the signal efficacy. If non-vocal sounds are as loud as songs, blue-capped cordon-bleus dance displays could function as sexual advertisement to potential mates or mate guarding toward potential rivals from a distance (see also Chapter 4).

In this chapter, I investigated whether taking multiple steps contributed to producing non-vocal sounds in two ways. First, I quantified dance performances by evaluating the number of steps in one bob and step speed, and investigated how the dance performances affected sound amplitude. I predicted that if taking multiple steps plays an important role in producing non-vocal sounds, the step sound would be louder as the number of steps increased. I also expected that step speed (i.e., the number of steps / bobbing duration) would have an influence on step sound amplitude, because step speed would be associated with the velocity and/or force when their feet land on the perch. Second, I compared step sound amplitude with that of feet

movement sounds in a non-courtship context and song notes to assess the efficacy of step sounds as acoustic signals. If they produce step sounds as acoustic signals, the sound would be louder than non-communicative sounds, such as feet movement sounds in a non-courtship context (Movie 6), and the amplitude would overlap with that of communicative vocal sounds (i.e., song notes).

Materials and Methods

Subjects and experimental procedure

I analyzed courtship dances of 12 male and five female adult blue-capped cordon-bleus (> 6 months old). One male and one female were arbitrarily paired and housed together in a cage (120 × 48 × 48 cm) in a sound-proof chamber. Their behaviors were recorded in a 2-h observational session with normal (Q3HD ZOOM, Tokyo, Japan; NTSC, 30 frames / s) and high-speed (GC-PX1 Victor, Yokohama, Japan; 300 frames / s) video cameras. Procedures were in accordance with German National Laws and approved by the Government of Upper Bavaria (approval number 311.5-5682.1/1-2014-021).

Sound analysis

I collected sound data with a sampling rate of 44.1 kHz and 16-bit resolution, which was recorded with a unidirectional microphone (angle: 120°, max SPL: 130 dB) under fixed gain settings in a normal-speed camera. I sampled, on average, 41.1 step sounds from each individual (range, 13–50). I sampled step sounds that did not include any noise detected above background levels and were only produced on the same perch position in one session to minimize sound amplitude changes related to the distance of the birds to microphone (Fig. 3-1a, Movie 5). I also sampled 10 feet movement sounds that are not step sounds from each individual as controls (Fig. 3-1a). I sampled the movement sounds when the birds moved on the perch where they also danced (Movie

6). In addition, 20 song notes that did not overlap with step sounds or other noises were arbitrarily sampled. I could not sample song notes from two females because they did not sing (see also Fig. 3-4).

I measured average and peak amplitude of step sounds, feet movement sounds, and song notes using Raven Pro 1.4 (www.birds.cornell.edu/raven). The durations of step sounds were also measured to quantify step speed (see Behavioral analysis). Average amplitude was based on average values of sound pressure level during sound production (Charif et al. 2010). Peak amplitude was considered the sound pressure level at the darkest point in the sound spectrogram (Charif et al. 2010). Because blue-capped cordon-bleus usually sing songs with 10–30 note types (Geberzahn and Gahr 2011) that have quite different amplitudes, their songs cover a wide range of amplitude (Fig. 3-1a). To compare step sound amplitude with that of the lower limit of song notes, I selected the three lowest-amplitude song notes from the 20 song notes mentioned above.

Sound amplitude values measured in this study were expressed in decibels, which reflected relative values within each recording (Charif et al. 2010). The distances from microphones to birds (67–76 cm) and positions on the perch (i.e., edge or center) differed among individuals, although I controlled for these issues at the within-individual level as described above. For these reasons, I could not investigate sound amplitude differences at an among-individual level in this study, but focused on the within-individual changes and statistically controlled for these changes (see also Statistical analysis).

Behavioral analysis

I analyzed two candidate factors that can affect step sound amplitude: the number of steps in one bob and step speed index. From the high-speed movie images, I counted the number of steps in one bob that were analyzed in sound analysis (Figure 3-1a, c; Movie 5). As a variable that is independent of the number of steps, I calculated 'step speed index' (Fig. 3-2); I plotted the step sound duration against the number of steps and calculated the distance of each residual from the regression line (Fig. 3-2). A higher step speed index value indicates less time required for a particular number of steps (Fig. 3-2).

Statistical analysis

To assess whether dance performances influence sound amplitude, I investigated the effects of the number of steps and step speed index on sound amplitude using linear mixed-effect models (LME). To compare sound amplitude between sound categories (i.e., step sounds, feet movement sounds, and song notes), I investigated the effect of each sound category on sound amplitude using LME. I also compared amplitude between the lowest-amplitude song notes and step sounds using LME. In these analyses, I considered bird ID as a random effect to control for non-independence of data from the same individual. All statistical analyses were performed using R 3.3.0 (R development Core Team 2016).

Results

Both average and peak sound amplitude increased as the number of steps increased (Fig. 3-3, Table 3-1), which was also clear at the within-individual level (Fig. 3-4). Increased step speed index values negatively affected peak sound amplitude, but not average sound amplitude (Table 3-1)

Step sounds were significantly louder than feet movement sounds but quieter than song notes (Fig. 3-3; average amplitude: $df = 1149$, $F = 970.943$, $p < 0.001$; peak amplitude: $df = 1149$, $F = 644.887$, $p < 0.001$; see also Movie 6). Although amplitude of arbitrarily chosen song notes was clearly higher than step sound amplitude (Fig. 3-3), the significant difference disappeared when I compared step sound amplitude with that of the lowest-amplitude song notes (Fig. 3-3; average amplitude: $df = 725$, $F = 2.765$, $p = 0.097$; peak amplitude: $df = 725$, $F = 1.702$, $p = 0.193$).

Discussion

My results showed that step sounds satisfy the criterion of non-vocal sounds as an acoustic signal (Clark 2016), at least under my captive conditions. As predicted, non-vocal sounds changed depending on the dance performances at the within-individual level. This suggests that context-dependent changes of dance performance (Chapter 2) modulate the non-vocal sounds. Step sound amplitude correlated with the number of steps in one bobbing and taking multiple steps played an important role in producing louder sounds (Fig. 3-3, Table 3-1). Additionally, step speed index had a negative effect on step sound amplitude (Table 3-1).

There are two possible mechanisms that explain these sound amplitude changes. First, the sound amplitude may be amplified by overlap of multiple step sounds. This may not be the case, however, because the experiments were conducted in a sound-proof chamber where sound reflections were substantially reduced. My behavioral observations revealed that these birds usually tap their feet alternately (Fig. 3-1a, Movie 5) and rarely tap simultaneously (6.4% of all bobbing actions in this study), which indicates that the tap dancing is not performed to make overlapping sounds. In addition, their step speed negatively affected peak sound amplitude (Table 3-1b). This finding indicates that higher step speed can increase the amount of overlap between consecutive sounds, but did not produce louder sounds. However, we should be cautious about the interpretation of these results, because it is not clear how step sounds are affected by reverberations in the eco-acoustic environment of the natural

habitat of blue-capped cordon-bleus.

The second mechanism is strong tapping of their feet against the perch when they take certain steps. Considering that step speed negatively affected peak but not average sound amplitude, birds may more strongly tap during one step among the multiple steps at the cost of step speed. Taking multiple steps may positively increase the landing velocity of their feet on the perch, but I could not directly measure the landing velocity, force, and the interval durations between taps, because neither image nor time resolution of my cameras were sufficient (see Movie 5).

My results of the comparison among sounds that the blue-capped cordon-bleus produce in various contexts also support the idea that step sounds are not just by-product sounds of movements. Step sounds were distinct from other feet movement sounds (see Movie 6; Fig. 3-3) and were as loud as the lowest-amplitude song notes (Fig. 3-3). Presumably, step sounds may serve as communicative signals, especially when the distance between birds is short.

Unfortunately, it is too early to conclude if their non-vocal sounds function as an acoustic signal in the wild, because blue waxbill ecology and behavior in the wild are poorly understood. Blue waxbills live in arid habitats with bushes and trees (Goodwin 1982), and the subjects I used in this thesis always performed dance displays on perches. Therefore, I suspect that in the wild they perform courtship displays on similar substrates to those used under the experimental condition in this study (i.e., slender branches). Observation in the wild, and experiments under captive conditions that control for substrate structure or material and environmental noise would also

Chapter 3: Non-vocal sounds as an acoustic signal

provide useful insight into understanding acoustic function of blue waxbill courtship display.

Figures and Tables

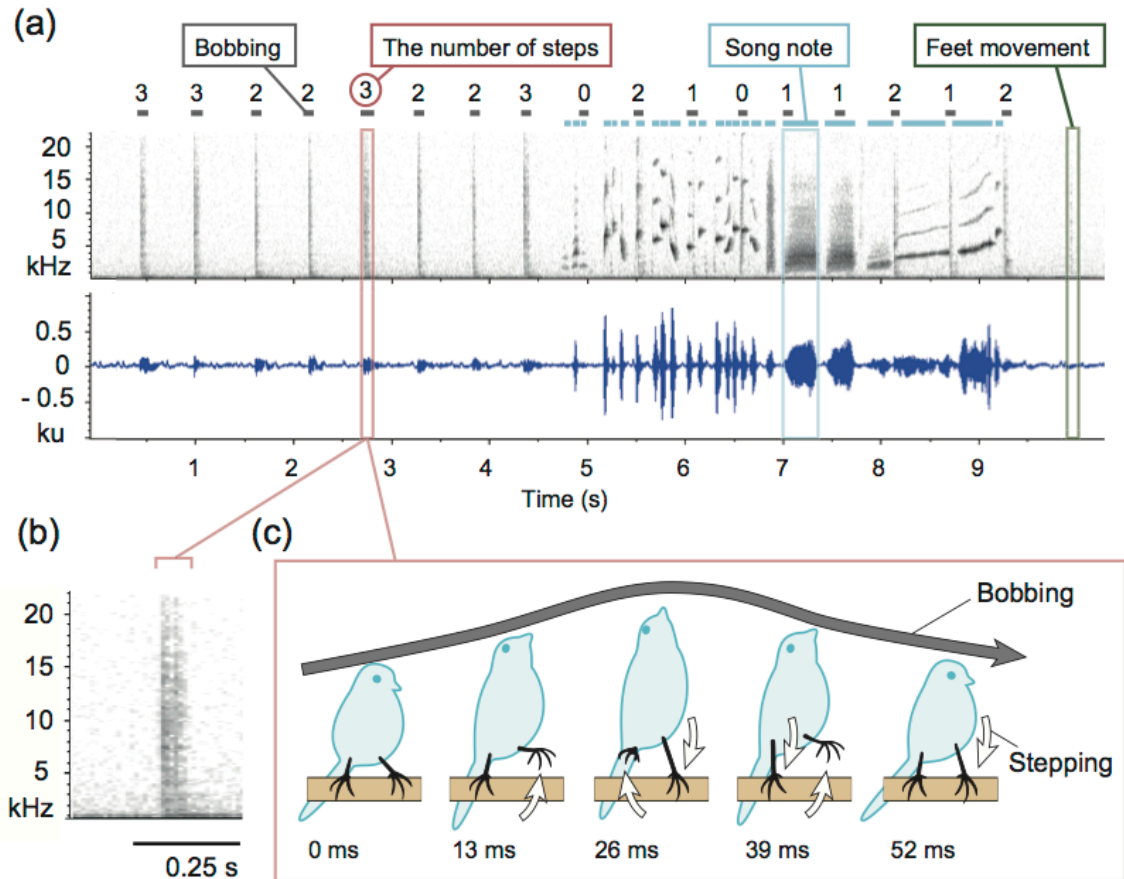


Figure 3-1. Blue-capped cordon-bleu step behavior and sounds. (a) A spectrogram and waveform of blue-capped cordon-bleu step sounds and song. These birds simultaneously bob and step, and sing at certain times. Numbers at the top of the spectrogram indicate how many steps were performed to produce the sounds. Feet movement sounds and song notes were arbitrarily sampled from each individual. (b) Enlarged view of the step sound spectrogram. (c) Diagram of step behavior that produces non-vocal sounds.

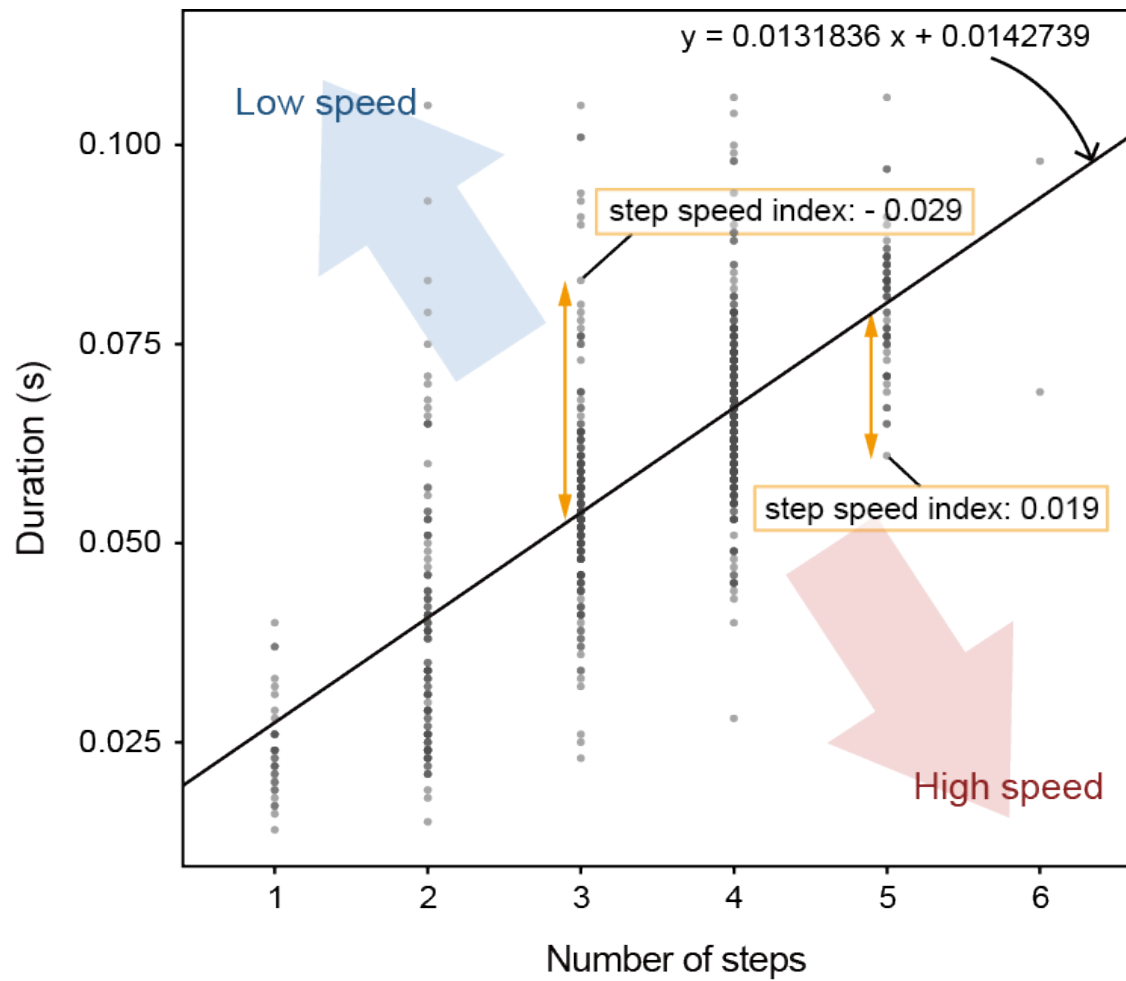


Figure 3-2. Step sound duration gets longer as the number of steps increases. Each semi-transparent point shows the data for one bobbing. Sound durations significantly increased relative to number of steps (regression analysis, $n = 698$, Coefficient = 0.013, $SE < 0.001$, $t = 29.013$, $P < 0.001$). I calculated step speed index based on this scatterplot and regression line.

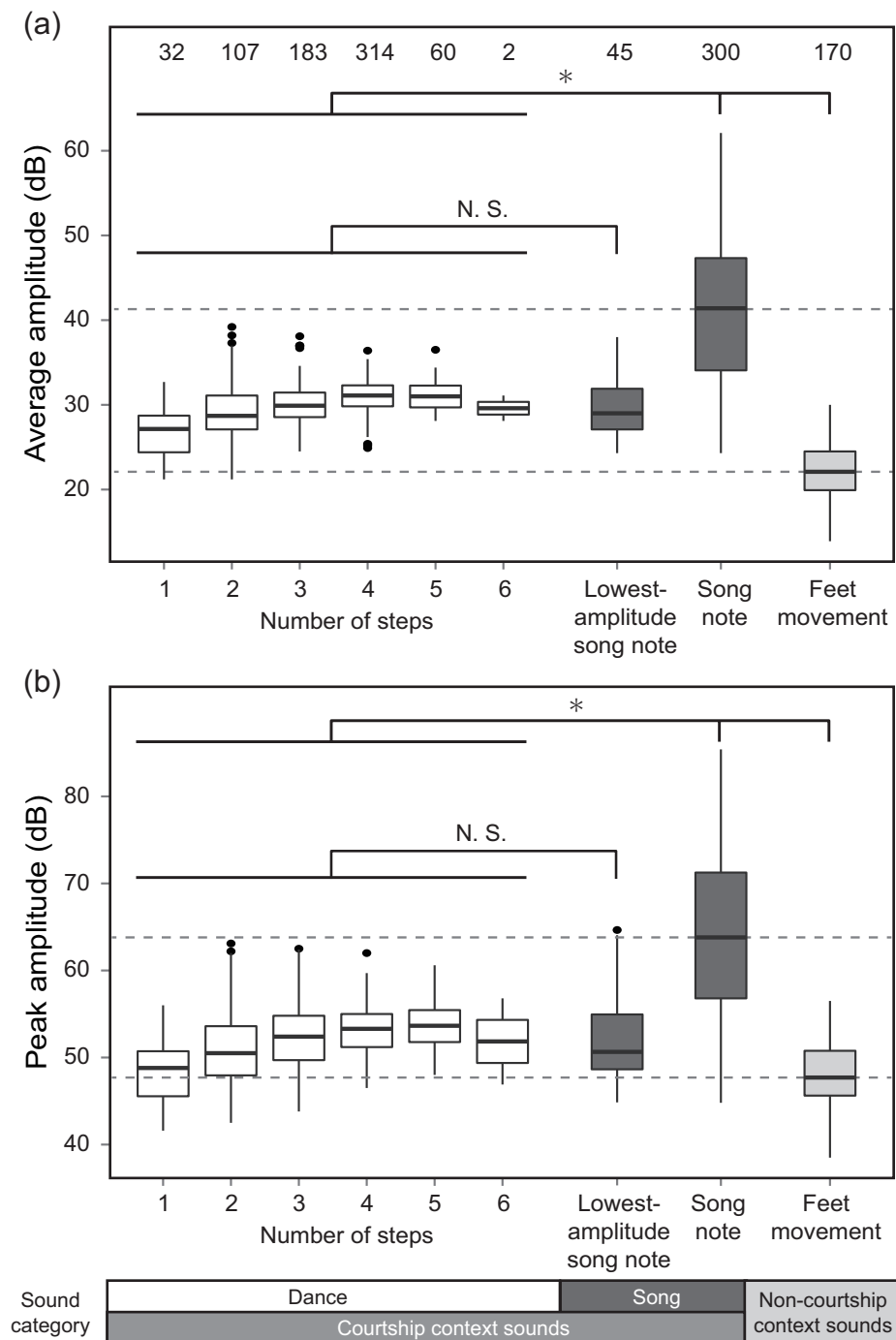


Figure 3-3. Effects of the number of steps on sound amplitude. (a) Average and (b) peak sound amplitude are plotted as a function of the number of steps compared with those of lowest-amplitude song notes, arbitrarily chosen song notes, and feet movement sounds. Numbers at the top of (a) represent sample size for both (a) and (b) (see also Fig. 3-4). All box plots show median and quartiles. Outliers are plotted as points.

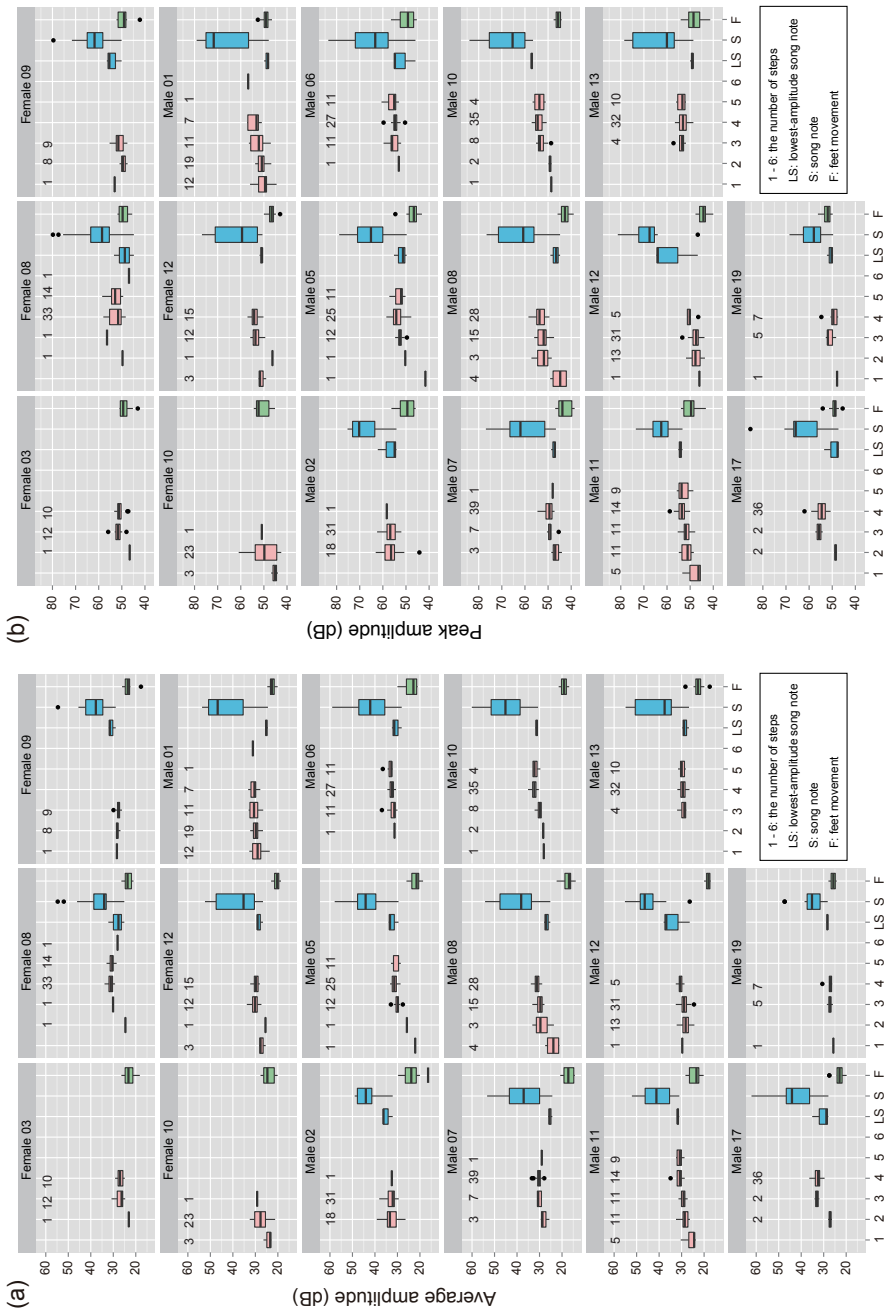


Figure 3-4. (a) Average and (b) peak amplitude plotted as a function of the number of steps for each individual and are shown relative to those of lowest-amplitude song notes (LS), song notes (S), and feet movement sounds (F). Numbers at the top of each graph represent sample size.

Table 3-1. Results of LME analyses of step sound amplitude. The effects of the number of steps and step speed index on (a) average and (b) peak step sound amplitude.

Response variable	Independent variable	Coefficient	SE	t	P
(a) Average amplitude	The number of steps	0.928	0.090	10.307	< 0.001
	Step speed index	4.578	6.458	0.709	0.479
(b) Peak amplitude	The number of steps	1.241	0.129	9.704	< 0.001
	Step speed index	- 42.001	9.191	4.571	< 0.001

Chapter 4

Audience effects on multimodal courtship display

Introduction

Although classic sexual selection theory clearly explains the evolution of sexually dichromatic traits, it is much more difficult to explain why males and females share similarly exaggerated sexual signals. Mutual sexual selection is one possible scenario that explains why both sexes evolved to have equally ornamented morphological or behavioral traits (Andersson 1994, Amundsen 2000). Another possibility is that multi-faceted sexual signals may convey different messages, and be used in multiple contexts to provide information to different receivers (Berglund et al. 1996). Although mutual dance displays exchanged between males and females is usually considered to facilitate within-pair communication (cranes, Masatomi 1983; grebes, Nuechterlein and Storer 1982; blue-footed booby, Torres and Velando 2003), song duet functions in songbirds include appealing to bystanders (Hall 2004). The function of mutual multimodal sexual communication (i.e., song and dance) has not been tested to date because male unimodal signals (i.e., song) is usually analyzed. However, multimodal sexual signals by both sexes are not necessarily only used for within-pair communication. For example, the magpie lark performs song duetting that is

accompanied by body movements to signal coalition quality (Hall and Magrath 2007, Røk and Magrath 2016).

Evaluating sexual communication in the presence of other individuals (e.g., territory neighbors and mating rivals) can provide insight into the evolution of mutual sexual signals. Therefore, I analyzed the effect of an audience on blue-capped cordon-bleu courtship displays. Audience effect refers to changes in the signaling behavior of individuals caused by the mere presence of other individuals (Zuberbühler 2008). Audience effects in the context of mate choice are reported in a wide range of animals (e.g., insects, Fitzsimmons and Bertram 2013; fishes, Nobel and Witte 2013, Auld and Godin 2015; mammals, Townsend and Zuberbuhler 2009, Overduin-De Vries et al. 2012). To gain reproductive benefit, for example, male crickets show aggressive behavior toward rivals in the presence of male or female audiences (Fitzsimmons and Bertram 2013), and non-alpha male macaques copulate with females when the alpha male is out of sight (Overduin-De Vries et al. 2012). Some studies also reported audience effects on bird behavior in a sexual context (Baltz and Clark 1994, Striedter et al. 2003, Ung et al. 2011, Dubois and Belzile 2012), but few studies focused on their courtship display (Kniel et al. 2016, Ung et al. 2011). For example, male canaries suppress courtship behaviors including singing toward a female in the presence of their female mate (Ung et al. 2011). Moreover, whereas a few studies investigated the audience effects on both males and females' behaviors (e.g., distance calls in zebra finches, Vignal et al. 2004; mate choice in zebra finches, Kniel et al. 2016; approach behavior in associated bearded reedlings, Hoi and Griggio 2012), as far as I know, no

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prior studies investigated audience effects on courtship displays exchanged by both sexes using an audience of both sexes.

Mutual courtship display (e.g., duet singing and dancing) can be either dyadic interactions between pairs or signaling other individuals (Hall 2004). Considering the findings of previous studies on duet singing (review in Hall 2004), I hypothesized that paired birds perform mutual courtship displays for (1) mate attraction, (2) mate/territory guarding, and/or (3) signaling commitment to their partner (Fig. 4-1). For example, if courtship display is performed for more than one potential mate, the display would function as mate attraction, and solo courtship display would be facilitated in the presence of potential mates (Fig. 4-1, hypothesis 1). Courtship display toward a partner in the presence of a same-sex audience as the performer would function as mate guarding (Fig. 4-1, hypothesis 2; Hall 2004). If the display is directed to their partner and facilitated by the presence of an opposite-sex audience as the performer, it would signal commitment to ensure a partnership (Fig. 4-1, hypothesis 3; Hall 2004). Duet display can also function as mate guarding and commitment signaling because it reflects coalition quality between pairs (Hall and Magrath 2007). If the courtship display functions as mate guarding and/or commitment signaling, achieving precise temporal coordination of a dance display with a partner would be an effective signal. However, it is still unclear if these explanations fit each component of multimodal sexual signals, because past studies usually only focused on duet singing and not dancing (Hall 2004).

Estrildid finches are a notable example of multimodal courtship display.

Generally, male Estrildid finches produce song that is sometimes accompanied by dance. Moreover, females of some Estrildid finches also have similar courtship displays as males that are composed of song and dance (Goodwin 1982, Soma and Garamszegi 2015). Although Estrildid finches do not perform song duetting, some Estrildid finches perform dance duets between sexes (Goodwin 1982). Like other Estrildid finches, blue waxbills are non-song duetting species, although courtship song and dance are similar between the sexes (song, Geberzahn and Gahr 2011; dance, Chapter 2). In Chapters 2 and 3, I never observed dance duetting of blue waxbills. However, if blue waxbill dance displays have similar functions to song duetting, dance duets may be facilitated by the presence of an audience.

The aim of this study is to investigate the social functions of multimodal courtship display in various social contexts in blue-capped cordon-bleus (*U. cyanocephalus*). I tested whether the presence of an audience influences the number of courtship displays. I investigated audience effects on three types of courtship display: directed and undirected songs, and dance. Directed song is accompanied by courtship dance, whereas undirected song is not (Morris 1954, Zann 1996). Directed song is generally produced under paired conditions (Morris 1954), and undirected song under solitary conditions (Zann 1996, Geberzahn and Gahr 2011). If the display is only performed for within-pair communication, the number of courtship displays would not change with or without an audience. If the display is directed to both partners and audiences, the number of courtship displays would change based on audience presence. Courtship display frequencies that signal mate guarding are expected to

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increase in the presence of a same-sex audience as the performer (Fig. 4-1). Courtship display frequencies can increase in the presence of an audience of the opposite sex as the performer when it functions as a commitment signal to the partner or when the performer increases behavioral investment in the face of multiple potential mates (partner and audience, Fig. 4-1). If the courtship is for mate guarding or signaling commitment, it is also expected that the frequency of duet display would increase in the presence of an audience. By comparing the pattern of audience effects on male and female behaviors, it is also possible to elucidate if the function of courtship display is similar between the sexes. In addition, because the attentiveness of the audience and partner (see also Chapter 2) can influence display activity, I tested if the dance performance (i.e., duration) changes based on the positions of partners and audiences.

Materials and Methods

Subjects and experimental procedure

I arbitrarily matched 20 pairs of males and females using 18 male and 11 female adult blue-capped cordon-bleus (> 6 months old). Because of the limited number of subjects, two males and five females were used as subjects twice, and two females were used as subjects three times in the experiment. Subjects were also used as audiences because of the limited number of subjects.

Paired birds experienced four conditions: pre-experimental control (no-audience 1), male audience, female audience, and post-experimental control (no-audience 2) conditions on consecutive days except otherwise stated (Fig. 4-2). Five pairs experienced male and female audience conditions on the same day, and I tested if the results were consistent with and without these five pairs (see Results). Each pair was introduced into an experimental cage (60 × 48 × 48 cm) one day before pre-experimental control conditions for habituation, and then observed during a pre-experimental control. The next day, I introduced a bird as an audience (male or female) into a cage (60 × 48 × 48 cm) adjacent to the subject pair's cage. Then, I repeated the audience conditions by switching audience sex. The two cages were separated by a fine wire-mesh partition, therefore, they could interact visually and auditorily but not physically (Fig. 4-1). The order of presentation of male and female audiences was randomized for each pair. Fifteen pairs experienced the four conditions on different

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days, and five pairs experienced male and female audience conditions on the same day. On the last day of the experiment, pairs were observed without an audience for a post-experimental control.

I recorded the behavior of subject pairs and audience for 2 h under each condition with a normal-speed camera (Q3HD ZOOM, Tokyo, Japan; NTSC, 30 frames/s). The camera was placed close to the wall of the audience cage (c.f., Movie 7, 8). The two cages for the subject pair and audience were placed in a sound-proof chamber to minimize disturbance. Before and after experiencing all four conditions, subject birds were kept in same-sex home cages. Similarly, audience birds were housed together in a sound-proof chamber except for when they took part in the experiment. Two nests and abundant nesting materials were always available in the subject cages. To minimize the effect of courting activity of the audience, I did not provide nest materials in the audience cage (c.f., Chapter 1, Fig. 1-1). Birds were provided with a finch seed mixture, cuttlebone, water, and cucumber ad libitum. All individuals were kept on a 14:10 h light:dark schedule (lights on 07:00–21:00) at approximately 22 °C and 50% humidity. Procedures were in accordance with national laws and approved by the Government of Upper Bavaria (approval number 311.5-5682.1/1-2014-021).

Behavioral measurements

As measures of subject courting activity, I recorded if the birds performed dance and song, and if the dance was a solo or duet under each of the four conditions. Dance duetting was defined as simultaneous expression of dance between a subject male and

female. To quantify the number of courtship displays, I measured the number of (1) dance bouts, (2) directed songs, and (3) undirected songs under each condition (Fig. 4-3). In addition, dance bout duration under audience conditions were measured.

To consider possible effects of audience courting activity on subject behaviors, the number of undirected songs of audiences was also counted. I did not take into account the dance and directed songs of audiences because audience birds were not supplied with nest materials, which are crucial for starting courtship dance (c.f., Chapter 1, Fig. 1-1). This represents one way that I tried to suppress audience dance display (see *subjects and experimental procedure*) to control for the diversity of audience behavior. However, two male audience birds danced during the experiment. I confirmed that the results were consistent if I removed these data (Appendix table 2).

Because it was possible that courtship activity was affected by spatial proximities between the paired birds and between pairs and audiences (see also Chapter 2), I checked the positions of the paired birds and audiences. Positions of paired birds were scored as 1, stayed on the same perch with the dancer; or 0, stayed on another perch. Audience position was scored as 1, stayed on the partition or the perch nearest to the partition without singing and sleeping (c.f., Movie 7, 8); or 0, stayed on another perch.

Statistical analysis

To test if audience presence affected the subjects' courtship displays, I compared the number of courtship displays (i.e., number of dance bouts, directed songs, and

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undirected songs) between no-audience and audience conditions, and between subject males and subject females. Specifically, I compared pre-experimental control and audience conditions. I did not pool pre- and post-experimental conditions to avoid erroneously detecting significant differences between the two conditions; preliminary analyses indicated that the number of dance bouts and directed songs in post-experimental control conditions were quite low, which was presumably because of habituation, which can lower the average of the two controls.

Then, I extracted data under audience conditions to determine how courtship display (i.e., number of dance bouts, directed songs, and undirected songs) is affected by audience. Specifically, I evaluated the following two audience aspects: 1) if the audience is same or opposite sex as the focal subject, and 2) how often the audience sang undirected songs. Additionally, I tested the effects of audience experimental condition order (i.e., first or second audience conditions) and subject sex.

To examine the effect of partner and subject behavior on dance performance, I also tested the effects of the position of partners and audiences (see *behavioral measurements*) on dance bout duration.

For the above three sets of analyses, I used a generalized linear mixed-effect model (GLMM). Numbers of dance bouts, directed songs, and undirected songs were analyzed by Poisson distribution. Dance bout duration was analyzed by Gaussian distribution. In all analyses, I considered pair ID nested within bird ID as random effects to control for non-independence of data. All statistical analyses were performed using R 3.3.0 (R Development Core Team 2016)

Results

Two pairs did not show any courtship dance during any of the four conditions. In the other 18 pairs, both or either of the sexes performed dance at least once during the four experimental conditions (Fig. 4-4). However, bidirectional dance interactions between paired birds were very rare: only one pair performed a duet dance, which was determined based on simultaneous expression of dance display (Movie 7), and in two other pairs, both male and female subjects danced at different times (Fig. 4-4). In the majority of subject pairs ($n = 15$), either a male or female showed dance at least once during the four conditions. Under audience conditions, the number of pairs that danced increased, and duet or bidirectional dances also increased compared with pre- and post-experimental control conditions without audiences (Fig. 4-4). There was no synergetic effect between male and female courting activity, as the number of courtship displays within pairs was not correlated (Fig. 4-5). The number of directed and undirected songs within individuals was also not correlated (Fig. 4-6). Both males and females usually produced either directed or undirected songs (Fig. 4-6).

Comparisons of courtship displays between no-audience and audience conditions

Audience presence facilitated dance display and directed songs. Both males and females performed more dances and directed songs under audience conditions

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compared with no-audience conditions (Table 4-1; Fig. 4-7 a, b). By contrast, they produced fewer undirected songs under audience conditions (Table 4-1). There were significant sex differences in the number of directed songs but not undirected songs (Fig. 4-7 c, Table 4-1a-d). A sex difference in the number of dance bouts was only significant compared with the post-experimental audience control conditions. Males produced more dance and directed songs than females, although the directions of the effects of audience were similar between male and female subjects (Fig. 4-7, Table 4-1).

There were significant or nearly significant differences in the number of courtship displays between pre- and post-experimental control conditions. Subjects performed more dance and directed songs under the pre-experimental control conditions than under the post-experimental control conditions, although the result regarding the number of directed songs was marginally significant (number of dance bouts: Coefficient $\pm$ SE = -0.655 ± 0.137 , $z = -4.786$, $p < 0.001$; number of directed songs: Coefficient $\pm$ SE = -0.212 ± 0.128 , $z = -1.655$, $p = 0.098$). The number of undirected songs significantly increased under post-experimental control conditions (Coefficient $\pm$ SE = 0.275 ± 0.093 , $z = 2.973$, $p = 0.003$).

Effects of audience sex and singing on courtship displays

When the audience was the opposite sex as the subjects, the subjects performed significantly more dances and directed songs, but not undirected songs (Fig. 4-7, Table 4-2). The number of audience songs negatively affected the number of dance bouts, and directed and undirected songs. The order of audience conditions (i.e., first or

second audience conditions) also negatively affected the three variables, and showed that the subjects' courting rates were affected by habituation (Table 4-2). There was a significant subject sex difference in number of directed songs (Table 4-2), and the sex difference for number of dance bouts was marginally significant. I confirmed that the effects of audience sex, number of audience songs, and subject sex were consistent if I eliminated the data of the five pairs of male and female audience conditions that were conducted on the same day (Appendix table 3).

Effects of partner and audience position on dance bout duration

Subjects danced longer when their partner stayed on the same perch, and this was not affected by audience position (Table 4-3). There was no sex difference in dance bout duration (Table 4-3).

Discussion

Although courtship displays are generally assumed to represent private communication between a performer and its potential mate (e.g., cranes, Masatomi 1983; grebes, Nuechterlein and Storer 1982; blue-footed booby, Torres and Velando 2003), this study revealed that courtship display is influenced by the broader social environment. In particular, I found that both sexes as the audience had substantial influence on courtship displays of male and female blue-capped cordon-bleus. Dance displays and directed songs were facilitated by audience presence, especially if the audience was the opposite sex as the subject performer. In contrast, undirected song was suppressed under audience conditions. I observed dance duetting only once, and it was under audience conditions (Movie 8).

Dance function: mate attraction, mate guarding, or commitment?

Dance display was facilitated in the presence of both sexes as the audience. Thus, my results did not reject all of the hypotheses I proposed in the Introduction (Fig. 4-1). Presence of dance display under opposite-sex audience conditions supports the idea that courtship displays can function as both mate attraction and commitment signals (Fig. 4-1). However, function as mate guarding is only partially supported because there were fewer dance displays under same-sex audience conditions than opposite-sex audience conditions, although there were more dance displays compared

with no-audience conditions.

I suggest that dance display mainly functions as mate attraction for a paired partner (but not the audience) and commitment signaling of the partnership. Some behaviors enabled researchers to infer whether the display is directed to the partner. For example, blue waxbills often show “tail angling” during courtship dances that is directed to a target bird (Goodwin 1982, Chapter 1, Fig. 1-1). Based on my observations of tail angling behavior (Movie 8), blue waxbill courtship displays typically seemed to be directed to their partners. Dance bout duration was modulated by the position of partners but not the audience, which further supported this inference.

Although further studies are needed to elucidate the detailed functions of dance display, my study revealed that multimodal signals produced by dance and song are not necessarily only exchanged within a pair.

Sex differences in number of courtship displays and audience effects

The directions of audience effects were similar between male and female subjects. Both sexes of subjects produced more dance and directed songs under audience conditions, and the tendency was greater under opposite-sex audience conditions compared with same-sex audience conditions. This indicates that courtship displays have common functions between the sexes. However, I did find a significant sex difference in number of directed songs; males produced more directed songs than females.

It is not surprising that male investment in courtship display was greater than that of females. Males generally make more efforts to attract potential partners

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because females are generally the choosier sex, even in socially monogamous species (Andersson 1994, Byers et al. 2010). Continuing to perform a courtship display over a long period is likely to be costly in terms of energy expenditure (Franz and Goller 2003) and time lost for other activities (Gil and Gahr 2002). The number of courtship displays may also reflect motivation or body condition, as was reported in other songbirds (David et al. 2012, Casagrande et al. 2016).

Contrast between song and dance

Audience effects on undirected and directed songs showed contrasting results. Although directed songs were performed under audience conditions, undirected songs were suppressed. Generally, undirected songs are produced under solitary conditions and not oriented toward any individual (Zann 1996). Directed songs are produced toward potential mates in social settings (Zann 1996). Song activity can potentially deliver information about the quality or skills of the signaler (Gil and Gahr 2002). It was previously demonstrated that the number of undirected songs is very sensitive to the current nutritional state of a male songbird (Johnson and Rashotte 2002, Ritschard and Brumm 2012, Casagrande et al. 2016, Yamada and Soma 2016). Undirected song may function as sexual advertisement toward potential mates from a distance when the subject does not prefer the surrounding individuals. It is also possible that undirected song is produced in an aggressive context (Searcy et al. 2006). Undirected song suppression under audience conditions may contribute to avoiding conflicts and unnecessary competition.

My results indicate that performing a multimodal dance display provides additional information than song alone and can produce multiple types of messages. Undirected song may function as sexual advertisement and indicate that the singer is single. Directed song is also thought to function as sexual advertisement, and dance display may provide additional information to the individual of interest.

Pair formation

I performed experiments under arbitrarily paired conditions throughout my thesis. Although pair bonding is assumed to be weak in these short-term experimental conditions, these experimental conditions enabled me to observe inter-sexual communication during the pair-formation phase. Therefore, my study can help elucidate how mutual courtship display affects pair formation.

The number of courtship displays under audience conditions was affected by audience sex and order of audience conditions (i.e., first or second audience conditions). The number of courtship displays tended to decrease under second audience conditions, although audience sex still had a significant effect on the displays (Table 4-1). Habituation is a plausible explanation of these changes, but change could have also been caused from progression of pair-bonding formation. Courtship displays I observed in this study were probably used for mate acquisition by mate attraction, mate guarding, and signaling commitment. If pair bonding was formed throughout the experiment, courtship displays in a mate-choice context might have been suppressed as these experiments proceeded.

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Although my results support the idea that dance displays could have similar functions as song duets, I could not narrow the possible functions down from the three hypotheses proposed in the Introduction (mate attraction, signaling commitment, and mate guarding; Fig. 4-1). Long-term observation is an effective way to elucidate detailed functions of courtship display. The intensity of courtship displays and functions can vary between non-breeding and breeding stages. In zebra finches, higher rates of undirected songs performed near the nest were correlated with the presence of paired females in the nest, which indicates within-pair function of undirected song after pair bonding (Zann 1996). The red-cheeked cordon-bleu (*U. bengalus*) also intensifies singing activity during the breeding period (Gahr and Güttinger 1986); however, as far as I know, no study has evaluated dance display performed by both sexes during the breeding period. Investigating when these birds produce multimodal courtship display during the breeding period and how displays contribute to pair bonding and its maintenance would be informative directions for future research.

Figures and Tables

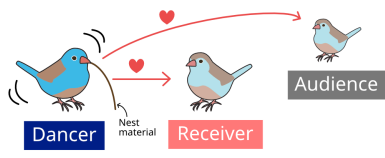
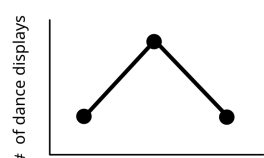
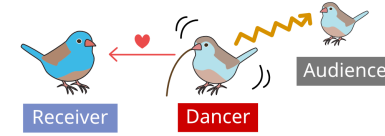
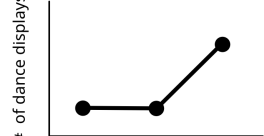
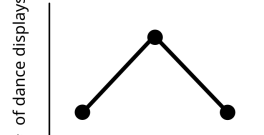
Possible functions of dance	Possible social environment	Predictions	
		The amount of dance displays	Coordinated dance duet
Hypothesis 1 Mate attraction			✗
Hypothesis 2 Mate guarding			✓
Hypothesis 3 Comittment signal			✓

Figure 4-1. Possible functions of dance display and predicted results.

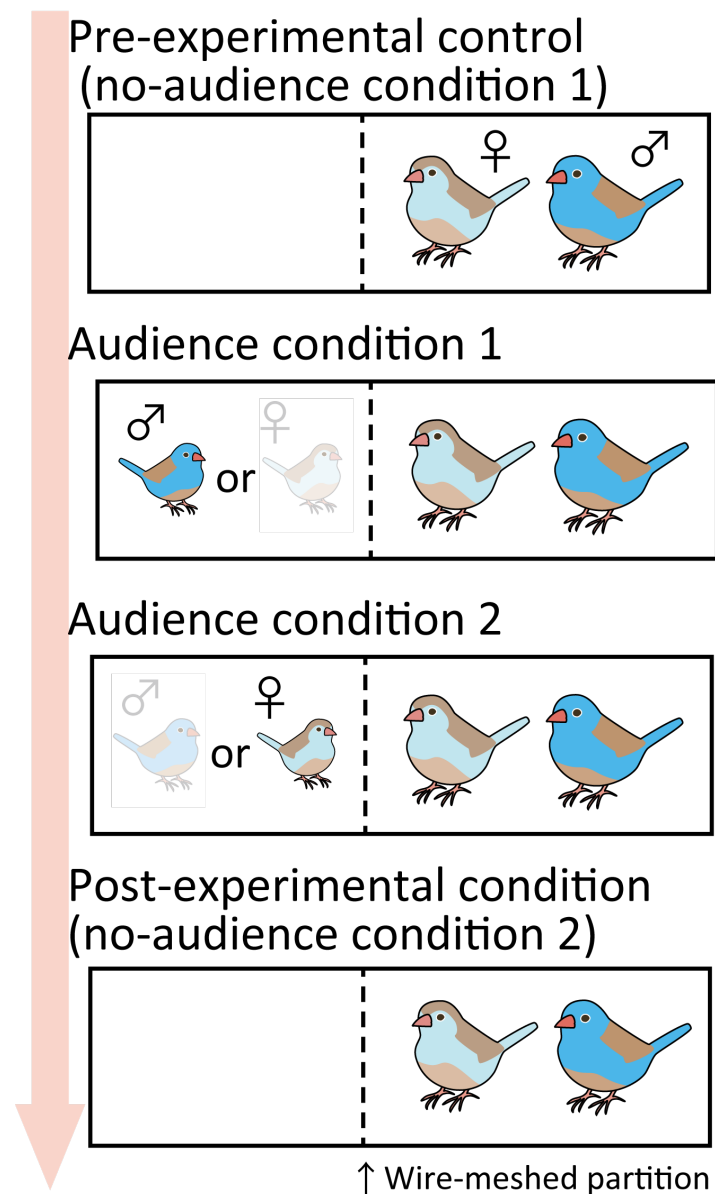


Fig. 4-2. Schematic views of the apparatus used in this experiment and protocol design. Subjects were first recorded without an audience (pre-experimental conditions). Then, we introduced male or female audience as the first audience bird, and the other sex of audience was introduced as the second audience bird. The presentation order of audience sex was randomized for each pair. Subject birds and audiences were separated by a wire-mesh partition. Finally, we recorded subjects without an audience again (post-experimental conditions).

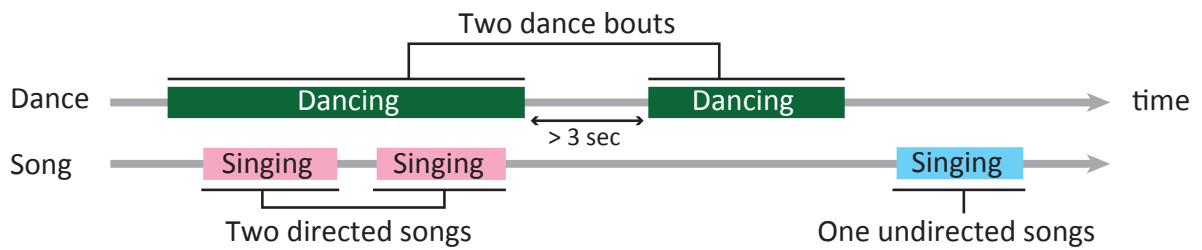


Figure 4-3. Examples and definitions of courtship display measurements. Dance bouts, directed songs while dancing and undirected songs without bobbing were counted. I defined one dance bout as a sequence of bobbings with less than 3-s intervals. In this example, a blue-capped cordon-bleu performed two dances, two directed songs, and one undirected song.

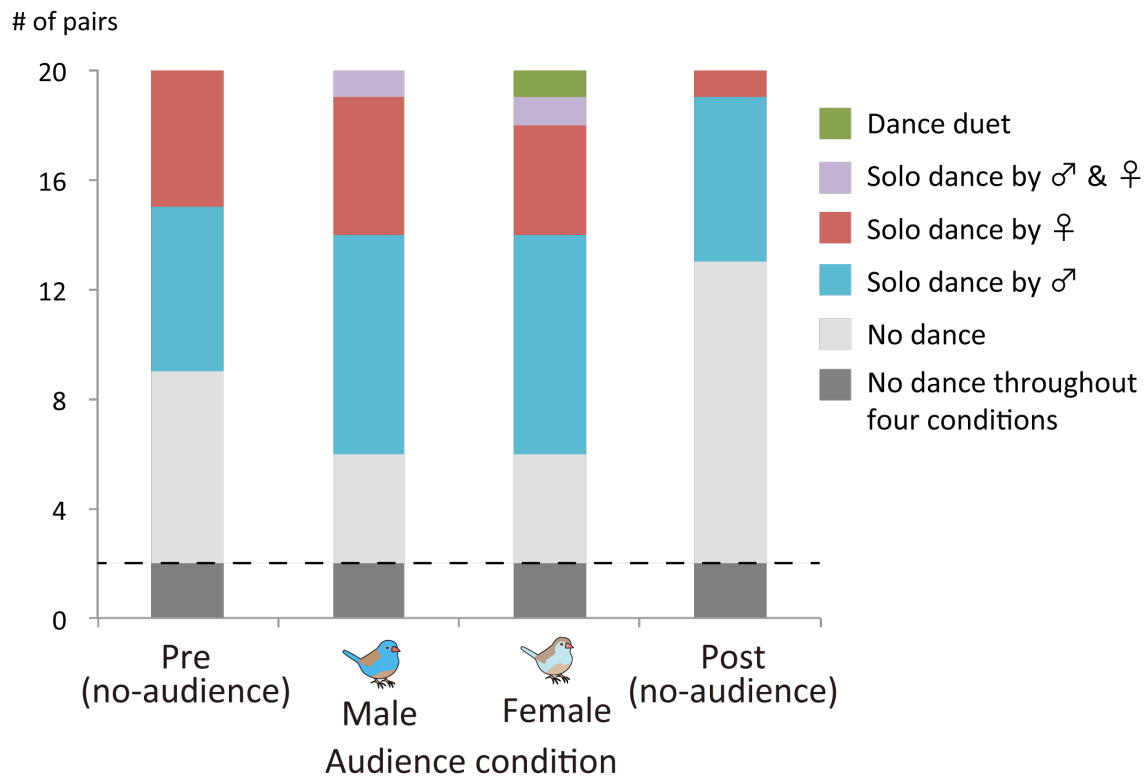


Figure 4-4. Changes in the proportion of courtship display patterns based on audience conditions. The green part indicates that both male and female of the pair danced at the same time. The purple part indicates that both sexes of the pair danced but not simultaneously. Red and blue parts indicate female and male unidirectional dance displays, respectively, that were observed. Pairs in which neither sex danced are represented in gray. Two pairs of both sexes did not dance throughout any of the four conditions and are indicated in dark gray.

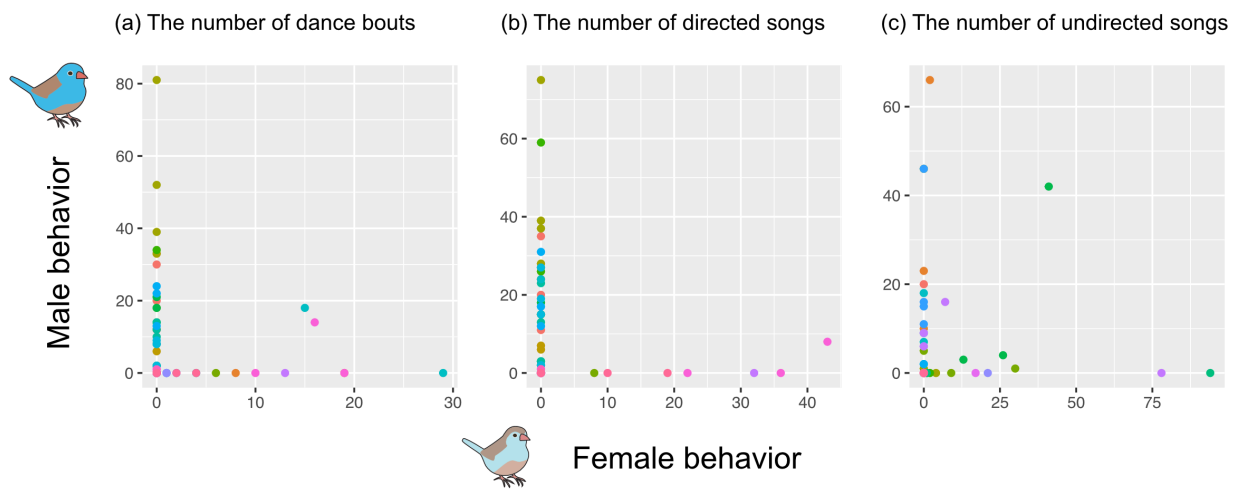


Figure 4-5. Comparison of number of courtship displays between each pair. Number of (a) dance bouts, (b) directed songs, and (c) undirected songs. Each point represents the number of courtship displays of males and females for each recording. Each color represents a different pair.

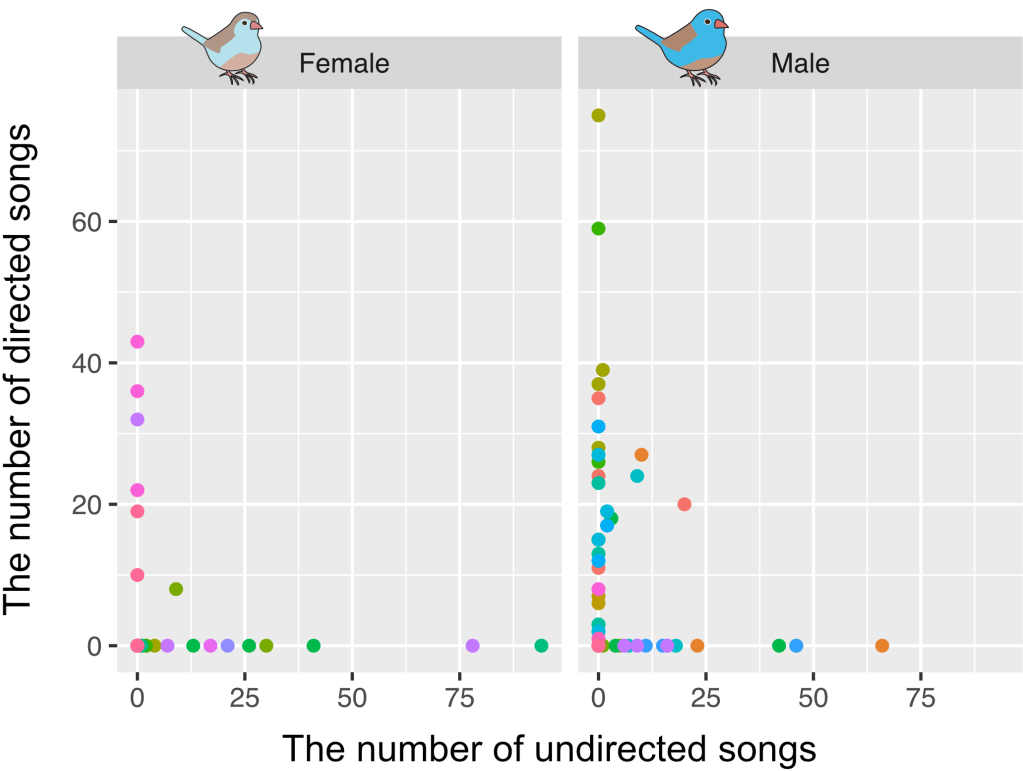


Figure 4-6. Comparison between number of directed and undirected songs among individuals. Each point represents a recording, and each color represents a different individual.

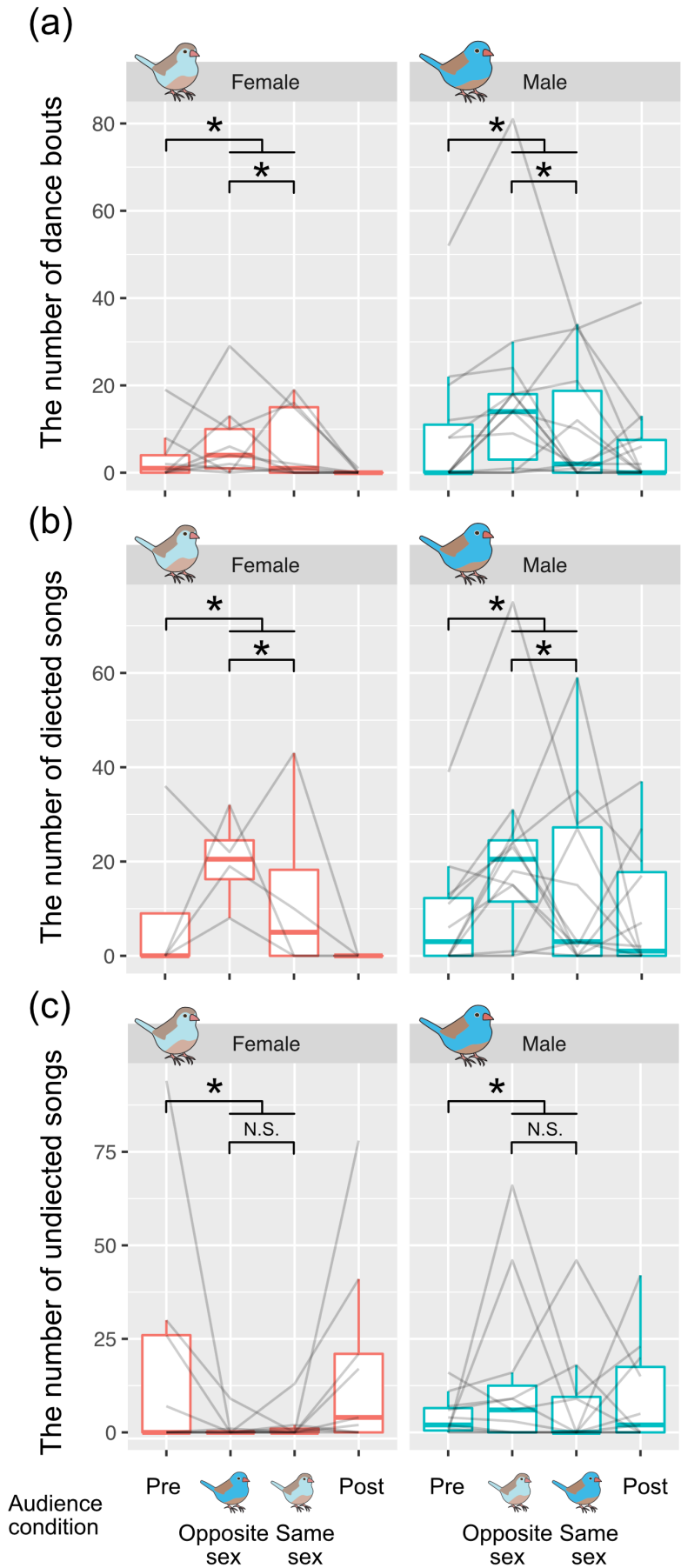


Figure 4-7. Effects of audience and sex on the number of courtship displays. Number of (a) dance bouts, (b) directed songs and (c) undirected songs. I plotted only the data of subjects that performed courtship displays at least once throughout the experiment. All box plots show median and quartiles. Gray lines show within-individual changes.

Table 4-1. Effects of subject sex and audience presence on the number of courtship displays (GLMM, Poisson).

	Response variable	Independent variable	Coefficient	SE	z	p
(a) Comparison between pre-experimental control and audience conditions	The number of dance bouts	Subject sex ^a	1.709	1.011	1.690	0.091
		The presence of audience	0.486	0.092	5.303	< 0.001
	The number of directed songs	Subject sex ^a	4.469	1.494	2.992	0.003
		The presence of audience	0.733	0.096	7.673	< 0.001
	The number of undirected songs	Subject sex ^a	1.628	1.761	0.924	0.355
		The presence of audience	- 0.440	0.093	- 4.729	< 0.001
(b) Comparison between post-experimental control and audience conditions	The number of dance bouts	Subject sex ^a	1.928	0.976	1.976	0.048
		The presence of audience	1.141	0.120	9.535	< 0.001
	The number of directed songs	Subject sex ^a	4.488	1.477	3.038	0.002
		The presence of audience	0.945	0.104	9.069	< 0.001
	The number of undirected songs	Subject sex ^a	0.326	1.447	0.226	0.822
		The presence of audience	- 0.716	0.087	- 8.269	< 0.001

^a Estimated values for effects that contain a "subject sex" term are for males.

Table 4-2. Factors that influence the number of courtship displays under audience conditions (GLMM, Poisson).

Response variable	Independent variable	Coefficient	SE	z	p
(a) The number of dance bouts	Audience sex ^a	- 0.392	0.094	- 4.158	< 0.001
	The number of audience undirected songs	- 0.005	0.002	- 3.049	0.002
	Present order of audience (first or second)	- 0.267	0.099	- 2.707	0.007
	Subject sex ^b	1.710	0.914	1.872	0.061
(b) The number of directed songs	Audience sex ^a	- 0.413	0.088	- 4.704	< 0.001
	The number of audience undirected songs	- 0.004	0.002	- 2.737	0.006
	Present order of audience (first or second)	- 0.160	0.090	- 1.778	0.075
	Subject sex ^b	4.100	1.422	2.884	0.004
(c) The number of undirected songs	Audience sex ^a	- 0.178	0.158	- 1.124	0.261
	The number of audience undirected songs	- 0.009	0.002	- 5.000	< 0.001
	Present order of audience (first or second)	- 0.766	0.165	- 4.628	< 0.001
	Subject sex ^b	1.156	1.780	0.649	0.516

^a Estimated values for effects that contained an “audience sex” term are for same-sex audience conditions.

^b Estimated values for effects that contain a “subject sex” term are for males.

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Table 4-3. Effects of partner and audience position on dance bout duration (GLMM, Gaussian).

Response variable	Independent variable	Coefficient	SE	t	<i>p</i>
Dance bout duration	Subject sex (male)	- 1.370	4.139	- 0.331	0.744
	Partner position	5.558	2.023	2.747	0.006
	Audience position	0.536	1.495	0.358	0.720

Chapter 5

General discussion

The majority of courtship display research has been conducted under the premise that complex courtship displays have evolved in males through female mate choice (Andersson 1994). In contrast, I reported here the first example of a multimodal dance display that is not a uniquely male trait in songbirds. Although Estrildid finches perform both dance and song in their courtship displays (Soma and Garamszegi 2015), blue waxbill displays (blue-capped and red-cheeked cordon-bleus; Movie 1, 2) are exceptional because, as far as I know, they are the only birds to perform dances that produce acoustic and vibratory signals, and are performed by both sexes.

My findings revealed an unexpected form of sexual communication by both sexes of songbirds (Chapter 2, 3). Signal production mechanisms and performances were very similar between the sexes (Chapter 2). In addition, the sexual signals of blue waxbills were not strictly for private communication between the signal producer and potential partners because they were influenced by the broader social environment (Chapter 4). My results indicate that dance display in both sexes cannot be explained by mate attraction alone. Other factors, such as social or natural environments, should be considered to further elucidate courtship display evolution of blue waxbills. In this chapter, I review production mechanisms and social functions of blue waxbill courtship display based on the results of Chapters 2 to 4, and discuss future directions.

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I also discuss the possible scenarios of mutual sexual signal evolution.

Production mechanisms of multimodal sexual signals

In Chapter 2, I revealed that blue waxbills rapidly stamp their feet several times by high-speed video observation. Dance performances did not differ between sexes but varied among individuals. Both male and female blue-capped cordon-bleus intensified their dance performances when their mate was on the same perch. The context-dependent adjustability seems to enable blue-capped cordon-bleus to effectively exchange sexual signals between males and females.

In Chapter 3, I found that tap-dancing behavior affected step sound amplitude. Additionally, the dancing step sounds were substantially louder than foot movement sounds in a non-courtship context, and the amplitude range overlapped with that of song notes. These results support the idea that blue-capped cordon-bleus produce acoustic signals with their feet in addition to song.

One striking aspect of these findings is that these birds simultaneously produce two acoustic signals (non-vocal sounds and songs) (Movie 1, 2; Chapter 2, 3). Future studies should investigate how singing, bobbing, and stepping behaviors are coordinated within individuals and between partners. Past research showed that some species spontaneously synchronize their movements with musical rhythms to which they are exposed (Patel et al. 2009, Hasegawa et al. 2011, Cook et al. 2013, Hattori et al. 2013). Some male songbirds coordinate dance and song (Cooper and Goller 2004, Hoepfner and Goller 2013, Dalziell et al. 2013). However, little is known about how

animals can temporally coordinate naturally produced multicomponent acoustic signals in both sexes (i.e., vocal and non-vocal sounds, Soma and Mori 2015). Fewer steps while singing can be explained by motor constraints because dance displays and singing are both physically demanding (Fusani et al. 2014). In contrast, increased bobbing tempo cannot be explained by trade-offs between singing and dancing signals because sound amplitude and step timing seemed to be coordinated with the songs.

Although I revealed an interesting phenomenon regarding non-vocal sounds in songbirds, detailed communicative functions and the underlying physiological, neuromuscular, and molecular mechanisms of these non-vocal sounds remain unclear. I cannot completely reject the possibility that the non-vocal sounds are just a by-product of vigorous motions that are used as visual signals. Further studies should examine how signal receivers respond to non-vocal sounds (e.g., Freeman and Hare 2015). Perch choice of signal senders should also be tested because perch structures or materials could affect acoustic features of non-vocal sounds. Investigating kinematic characteristics of stepping (e.g., Clifton et al. 2015), associated morphological features (e.g., Bostwick et al. 2012, Clark and Prum 2015), and motor-driven gene expression in song-control brain regions (e.g., Jarvis et al. 1998, Feenders et al. 2008) would further elucidate the mechanisms of non-vocal sounds in blue-capped cordon-bleus; such additional studies could shed new light on multimodal communication in birds.

Social functions of multimodal courtship display

In Chapter 4, I found that audience presence increases multimodal courtship displays.

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Directed and undirected songs frequencies differed based on audience presence. Directed song was present under audience conditions, whereas undirected song was not. In addition, few individuals produced both directed and undirected songs in one recording. These results indicate that multimodal (i.e., dance and directed song) and unimodal courtship display (i.e., undirected song) have distinct functions based on social context. Dance display seemed to contribute to increased signal efficacy of courtship display and gaining information about who is being courted.

Because of the lack of information for the individuals, I could not investigate if blue waxbill dance displays reflect honest signals of individual information, such as developmental stress or current conditions (Zahavi 1975); however, this is highly possible because dance performance varied among individuals (Chapter 2). It would therefore be interesting to determine if the degree of coordination between song and dance serves as an honest signal of individual quality of blue waxbills.

My results in Chapter 4 indicate that multimodal dance display contributes to effectively sending signals to both a potential mate and other individuals. Although I did not examine the vibration signals in courtship displays, vibrations can play an important role as a communicative signal. Vibration signals via a perch would be effective for nearby individuals that stayed on the same perch, whereas acoustic signals would work better to communicate with individuals on different perches. Non-vocal sounds may contribute to relaying the performer's individual information more effectively and precisely to nearby individuals because sound amplitude reflected dance performance (i.e., number of steps and step speed, Chapter 3).

Although most pairs did not simultaneously perform courtship displays between pairs, I observed that only one pair performed duet dance-like behavior (Chapter 4, Movie 7). This may have occurred because I performed experiments on arbitrarily paired birds throughout my thesis. Song duetting improves the coordination between partners that have been together for longer durations (Hall and Magrath 2007). Long-term pair bonding might be critical for performing duet dancing, and long-term observation of paired individuals is needed to test this idea to provide further insight and reveal detailed functions of mutual courtship displays.

Mutual multimodal displays, such as blue waxbill courtship displays, have received little experimental attention and offer rich opportunities for elucidating the roles of signal functions. Although it is too early to conclude based on the available information, I propose that the social functions of blue waxbill courtship displays suggested in my thesis are applicable to other Estrildid finch courtship displays. All Estrildid finches have elaborate dance and song, although the complexity and/or sexual dichromatism vary between species (Soma and Garamszegi 2015). Tap dance-like courtship display in blue waxbills is likely to be unique among Estrildid finches. However, it is also possible that other species might have multimodal signal production mechanisms that were previously overlooked because past studies usually focused on male song in a few species (e.g., zebra and Bengalese finches).

Possible evolutionary scenarios of multimodal courtship display

My findings emphasize the importance of studying multimodal courtship

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display in both males and females based on social factors. Chapter 4's results indicated that social complexity is likely to be a crucial factor that drives communicative complexity in the multimodal courtship display of blue waxbills. Vocal complexity of birds is often subject to testing the "social complexity hypothesis," which posits that groups with complex social systems require complex communicative systems to regulate interactions and relationships among group members (Freeberg et al. 2012, Krams et al. 2012). In chickadees, individuals in larger groups used calls with greater complexity than individuals in smaller groups (Freeberg 2006). Increasing the number of courtship components might have similar functions as increasing vocal repertoire size.

Flexibility of blue waxbill courtship displays for environmental adaptation also seems to be important for understanding their behavior and evolution. The environment plays a substantial role in the way that information is available, gathered, and used, including detection of and response to signals. Some animals adjust their signaling in response to dynamic environmental conditions. A typical example is the Lombard effect, which involves adjusting the volume or frequency of acoustic signals so they can be heard over other noise (Brumm and Todt 2002, Brumm and Zollinger 2011, Schuster et al. 2012). Male wolf spiders prefer to perform courtship displays where the vibration and acoustic signals are maximized (Gordon and Uetz 2011). Male Alpine newts perform multicomponent and multimodal courtship displays, including olfactory and visual signals, and they use more olfactory rather than visual displays in the dark (Denoël and Doellen 2010). Blue waxbill courtship display flexibility is likely

to be effective for sending precise signals in dynamic environmental conditions. Observing courtship behavior of the wild blue waxbills would also help elucidate the eco-acoustic environment and perch properties that affect production of these sounds.

The selective forces on male and female dance displays in Estrildid finches still remain unclear (Soma and Garamszegi 2015). Based on a previous comparative phylogenetic study, ancestral female Estrildid finches are thought to have dance but not song (Soma and Garamszegi 2015). Because Estrildid finches are non-duetting species (Goodwin 1982) and female song is under stronger phylogenetic constraints than dance traits (Soma and Garamszegi 2015), they might require a form of signal production that replaces song to exchange information for within-pair communication. Indeed, it was reported that some display components are shared and exchanged between sexes in courtship or breeding contexts (bill-click sounds in Java sparrows, Soma and Mori 2015; call duetting at the nest in zebra finches, Elie et al. 2010). For example, call duets in zebra finches are involved in mate recognition and mediate pair bonding and its maintenance because the display takes place in the nest and is coordinated within pairs (Elie et al. 2010). It is possible that dance displays have evolved to perform duetting behavior (c.f., Movie 7).

Furthermore, interaction between paired individuals and bystanders might affect complex sexual signal evolution (c.f., Chapter 4) because intraspecific brood parasitism tends to affect dance repertoire size in both sexes of Estrildid finches (Soma and Garamszegi 2015). Well-coordinated mutual signaling behaviors could lead to better reproductive success when both paired individuals need to invest more into

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reproduction when faced with a higher risk of intraspecific brood parasitism. Gregariousness may also affect sexual signal complexity, as discussed above (i.e., the social complexity hypothesis; Freeberg et al. 2012, Krams et al. 2012). Degree of gregariousness is reported to be related to plumage elaborateness in Estrildid finches (Gomes et al. 2016). These perspectives can offer new and informative insights into complex courtship display function and evolution.

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Appendix

Appendix table 1. Results of reanalysis when I removed the independent data of partner position (**a, b**) and song (**c, d**) in Chapter 2 (Fig. 2-3).

Response variables	Fixed effect	Coefficient	SE	<i>p</i>
(a) Bobbing tempo	Partner position	0.161	0.054	0.003
(b) Number of steps in one bob	Partner position	0.173	0.027	< 0.001
(c) Bobbing tempo	Song	0.432	0.037	< 0.001
(d) Number of steps in one bob	Song	- 0.290	0.023	< 0.001

Appendix table 2. Results of reanalysis when I eliminated the data of two pairs, those male audience birds danced during the experiment in Chapter 4 (Table 4-2).

Response variable	Independent variable	Coefficient	SE	z	p
(a) The number of dance bouts	Audience sex ^a	- 0.546	0.105	- 5.204	< 0.001
	The number of audience undirected songs	- 0.005	0.002	- 3.561	< 0.001
	Present order of audience (first or second)	- 0.092	0.110	- 0.841	0.400
	Subject sex ^b	1.578	0.884	1.785	0.074
(b) The number of directed songs	Audience sex ^a	- 0.711	0.108	- 6.566	< 0.001
	The number of audience undirected songs	- 0.006	0.002	- 3.395	< 0.001
	Present order of audience (first or second)	0.184	0.110	1.674	0.094
	Subject sex ^b	3.874	1.399	2.770	0.006
(c) The number of undirected songs	Audience sex ^a	- 0.177	0.158	- 1.118	0.263
	The number of audience undirected songs	- 0.009	0.002	- 5.000	< 0.001
	Present order of audience (first or second)	- 0.767	0.166	- 4.630	< 0.001
	Subject sex ^b	1.198	1.787	0.670	0.503

^a Estimated values for effects that contained an “audience sex” term are for same-sex audience conditions.

^b Estimated values for effects that contain a “subject sex” term are for males.

Appendix table 3. Results of reanalysis when I eliminated the data of the five pairs those two audience conditions were conducted on the same day in Chapter 4 (Table 4-2).

Response variable	Independent variable	Coefficient	SE	z	p
(a) The number of dance bouts	Audience sex ^a	- 0.665	0.123	- 5.394	< 0.001
	The number of audience undirected songs	- 0.009	0.002	- 4.444	< 0.001
	Present order of audience (first or second)	0.189	0.134	1.416	0.157
	Subject sex ^b	1.067	0.992	1.076	0.282
(b) The number of directed songs	Audience sex ^a	- 0.922	0.134	- 6.864	< 0.001
	The number of audience undirected songs	- 0.010	0.002	- 4.734	< 0.001
	Present order of audience (first or second)	0.519	0.140	3.706	< 0.001
	Subject sex ^b	3.867	1.780	2.172	0.030
(c) The number of undirected songs	Audience sex ^a	0.023	0.197	0.117	0.907
	The number of audience undirected songs	- 0.008	0.002	- 3.444	< 0.001
	Present order of audience (first or second)	- 1.223	0.186	- 6.585	< 0.001
	Subject sex ^b	1.528	2.683	0.570	0.569

^a Estimated values for effects that contained an “audience sex” term are for same-sex audience conditions.

^b Estimated values for effects that contain a “subject sex” term are for males.

Research achievements

List of publications

(1) Ota N, Gahr M & Soma M (2015)

Tap dancing birds: the multimodal mutual courtship display of males and females in a socially monogamous songbird.

Scientific reports, 5, 16614. DOI: 10.1038/srep16614

(2) Ota N, Gahr M & Soma M (2016)

Songbird tap dancing produces non-vocal sounds.

Bioacoustics, online. DOI: 10.1080/09524622.2016.1231080

List of other publications

(1) Ota N & Soma M (2014)

Age-dependent song changes in a closed-ended vocal learner: elevation of song performance after song crystallization.

The journal of avian biology, 45(6), 566–573. DOI: 10.1111/jav.00383

Awards

(1) Best oral presentation by a junior researcher, XXV International Bioacoustics Conference, (Sep. 2015)

(2) Most outstanding presentation award, The Society for Bioacoustics (Dec. 2015)

(3) The top 100 read Scientific Reports article in 2015, Scientific Reports (Apr. 2016)



Presentations

International conferences

- (1) Ota N, Gahr M & Soma M (Oral)

“Tap dancing birds: the multimodal mutual courtship display of males and females in a socially monogamous songbird”

XXV International Bioacoustics conference. Murnau, Germany. (Sep. 2015)

- (2) Ota N, Gahr M & Soma M (Oral)

“Audience promotes courtship dancing exchanged between sexes of a songbird”

International Society of Behavioral Ecology. Exeter, England. (Jul. 2016)

Japanese conferences

- (3) 太田菜央・Manfred Gahr・相馬雅代 (口頭)

「セイキチョウのタップダンス様求愛ディスプレイ」

日本動物行動学会第33回大会 長崎大学 2014年11月

- (4) 太田菜央・Manfred Gahr・相馬雅代 (ポスター)

“Does tap dance contribute to producing louder sounds?: The relationship between dance performance and sound amplitude in the courtship display of a socially monogamous songbird”

The 2nd Annual Meeting of The Society for Bioacoustics 九州大学 2015年12月

- (5) 太田菜央・Manfred Gahr・相馬雅代 (ポスター)

「ルリガシラセイキチョウ雌雄における求愛ディスプレイの第三者効果」

日本鳥学会2016年度大会 北海道大学 2016年9月

- (6) 太田菜央・Manfred Gahr・相馬雅代 (ポスター)

「音を出すためのタップダンス -ルリガシラセイキチョウの求愛ディスプレイ-」

日本動物行動学会第35回大会 新潟大学 2016年11月

Other presentations

International conferences

- (7) Ota N & Soma M (Poster)

“Female preference for syntactically complex trills in the Java sparrow song”

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Tap dancing birds: the multimodal mutual courtship display of males and females in a socially monogamous songbird

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According to classical sexual selection theory, complex multimodal courtship displays have evolved in males through female choice. While it is well-known that socially monogamous songbird males sing to attract females, we report here the first example of a multimodal dance display that is not a uniquely male trait in these birds. In the blue-capped cordon-bleu (*Uraeginthus cyanocephalus*), a socially monogamous songbird, both sexes perform courtship displays that are characterised by singing and simultaneous visual displays. By recording these displays with a high-speed video camera, we discovered that in addition to bobbing, their visual courtship display includes quite rapid step-dancing, which is assumed to produce vibrations and/or presumably non-vocal sounds. Dance performances did not differ between sexes but varied among individuals. Both male and female cordon-bleus intensified their dance performances when their mate was on the same perch. The multimodal (acoustic, visual, tactile) and multicomponent (vocal and non-vocal sounds) courtship display observed was a combination of several motor behaviours (singing, bobbing, stepping). The fact that both sexes of this socially monogamous songbird perform such a complex courtship display is a novel finding and suggests that the evolution of multimodal courtship display as an intersexual communication should be considered.

Elaborate courtship displays are assumed to have evolved under strong sexual selection pressure in males^{1,2}. Males of polygynous species (e.g., spiders³, frogs⁴, fishes⁵, and birds^{6,7}) use multimodal courtship displays to increase the efficacy of signalling^{8,9}. Thus, by coordinating visual and acoustic displays without interference between display components, polygynous male birds can better convey sexual signals^{6,7,10}.

Much research has focussed on male–female directed courtship displays performed by polygynous male birds, while the occurrence of both male–female and female–male directed courtship displays performed by socially monogamous birds has often been overlooked. Elaborate mutual dance displays between sexes are known to be performed by socially monogamous non-passerine birds, which are non-vocal learners, such as grebes¹¹. In socially monogamous non-passerine birds, dance duets may serve similar functions as vocal duets do in songbirds¹²: contributing to pair formation, pair bonding, or mate guarding¹³. The evolution and mechanisms of dance duets have received far less attention than have vocal duets. Furthermore, why a few songbird species use both song and dance displays as intersexual communication is a puzzling question¹⁴.

The blue-capped cordon-bleu (*Uraeginthus cyanocephalus*), a socially monogamous songbird, is one of the few species in which both sexes perform courtship displays. During these displays, they hold a piece

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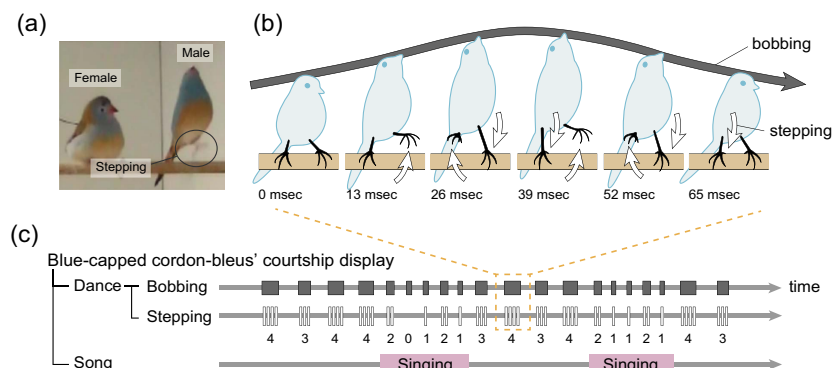


Figure 1. Courtship display in blue-capped cordon-bleus. (a) When blue-capped cordon-bleus perform courtship display, (b) they simultaneously bob and step, and (c) sing at certain times. Bobbing (shaded bars) with multiple steps (white bars) is repeated often, and usually singing occurs several times. White and shaded arrows in (b) correspond with the colour of bars in (c). Note the number of steps in (c) involved in each bobbing action.

of nesting material, then bob up and down and sing¹⁵ (Supplementary Video S1). Notably, the courtship bobbing produces rhythmical sounds (Supplementary Video S1, Supplementary Fig. S1). Here, we analysed the audio-visual displays of the blue-capped cordon-bleu in detail using high-speed video-camera recordings (Fig. 1a). As a result, we discovered that their visual courtship display includes quite rapid step-dancing during bobbing (see results). This specific “tap-dance” like behaviour has never been reported in songbirds and presumably produces non-vocal sounds and/or vibrations in addition to song.

We predicted that such a physically demanding dance display plays an important role in intersexual communication as well as song in cordon-bleus. As a first step toward understanding the function of the stepping-dance display in both male and female blue-capped cordon-bleus, we investigated between- and within- individual variations in dance performance. We expected that male performances would be more exaggerated than those of females, as is observed in plumage¹⁵ and in song^{16,17}. We also expected that to maximize signal efficacy cordon-bleus adjust their dance performances depending on their partner's position and song^{6,8}.

Results

(a) Courtship dance. High-speed video recordings revealed that in a single bobbing motion, birds hop with their heads pointed upwards and stamp their feet several times so rapidly that it is invisible to the naked eye (Supplementary Video S1, Fig. 1b). We confirmed that all cordon-bleus that performed courtship displays (7 males and 4 females) included rapid steps while bobbing (Fig. 1, Supplementary Video S1). The birds always performed the displays on the perch (Fig. 1a). On average, birds performed 3.17 steps (SEM, 0.03; range, 0–6) per bobbing action. One step took 6–12 frames of 300-frames/s video, thus equalling 20–40 ms, at an estimated rate of 25 Hz to 50 Hz. The bobbing tempo was 1.39 bobs/s (SEM, 0.02).

(b) Sex and individual differences. Dance probability, bobbing tempo, and the number of steps during bobs did not differ significantly between males and females (Table 1a, Supplementary Video S1), although males danced more often (males: 24.8%, females: 10.6%; see Supplementary Table S1a for detailed information) and tended to bob more quickly and take more steps (Fig. 2a,b; Table 1b,c). Variations in dance probability and the number of steps differed significantly between individuals ($p < 0.05$, Table 1a,c), but bobbing tempo did not ($p = 0.425$, Table 1b). Although each subject chose to dance to one or two particular individuals, the birds exhibiting greater motor performance did not tend to receive more dance displays (Supplementary Table S1b).

(c) Within-individual changes. Both males and females bobbed more quickly and took more steps when their partners were present on the same perch ($p < 0.001$; Table 1b,c; Fig. 2c,e), which was likely caused by the presence of their nearby partners (see Supplementary Video S2). Individuals also adjusted the number of steps and the bobbing tempo when singing, bobbing faster ($p < 0.001$, Table 1b, Fig. 2d) and taking fewer steps ($p < 0.001$, Table 1c, Fig. 2f).

Discussion

Both male and female blue-capped cordon-bleus exhibited quite rapid stepping behaviour during courtship displays, which varied among individuals but not across sexes. The evolution of this complex courtship display in both sexes is surprising because male ornaments tend to become exaggerated even in monogamous species because females are generally the choosier sex¹. According to our pairing experiment,

Response variable			Coefficient	SE		<i>p</i>
(a) Dance probability	Fixed effect	Sex	0.380	0.259	$z = 1.466$	0.143
	Random effect	Bird ID			$\chi^2 = 9.352$	0.002
(b) Bobbing tempo	Fixed effect	Sex	0.089	0.090	$t = 0.988$	0.349
		Partner position	0.440	0.036	$t = 12.103$	<0.001
		Song	0.186	0.046	$t = 4.003$	<0.001
	Random effect	Bird ID			$\chi^2 = 0.636$	0.425
(c) Number of steps in one bob	Fixed effect	Sex	0.380	0.259	$z = 1.466$	0.143
		Partner position	0.201	0.027	$z = 7.429$	<0.001
		Song	−0.305	0.023	$z = -13.266$	<0.001
	Random effect	Bird ID			$\chi^2 = 58.844$	<0.001

Table 1. The effect of sex on (a) dance probability (GLMM, binomial) and the effects of sex, position of partner and song on (b) the bobbing tempo (LME) and (c) the number of steps in one bob (GLMM, poisson).

both male and female cordon-bleus chose to court with particular individuals, but high-motor performance individuals were not necessarily popular among the opposite sex (Supplementary Table S1b). Assortative mating did not tend to occur with respect to dance performances. The only sex difference in temporal pattern of the blue-capped cordon-bleus courtship display is the slightly shorter song produced by females¹⁷. Even if the small sample size prevented us from finding sex-related differences in dance performance, such sex differences would likely be small because the distribution of dance performances overlapped between males and females (Fig. 2a,b). Although other estrildid finches are known to show both dance and song courtship display¹⁴, the cordon-bleus displays (blue-capped and red-cheeked cordon-bleus; Supplementary Video S1, S3) are exceptional because as far as we know, theirs are the only dances that produce acoustic and vibratory signals, and that are performed by both sexes.

Performing rapid stepping behaviour seemed to enable male and female cordon-bleus to communicate via multiple modalities. Our results suggest that both sexes produce multimodal (acoustic, visual, and tactile) signals for intersexual communication that involves the coordination of several motor systems that control singing, bobbing, stepping, and beak movements. Attention should be paid to where the birds dance in the wild because cordon-bleus reportedly dance also on the ground¹⁵. However, all dance displays were performed on perches in this captive study. Intensified stepping performance when partners were on the same perch likely enables performers to send vibration signals context-dependently. Considering that the limit of flicker fusion frequency is usually over 100 Hz in many birds¹⁸, stepping movements between 25 and 50 Hz could be visible and function as a visual signal for cordon-bleus. The bobbing movements seem to exaggerate the sexually dimorphic plumage of their heads and nesting materials that they hold. Intensified bobbing performance when partners stayed on the same perch could make them more visually appealing to highly motivated partners. Fewer steps and more frequent bobbing during singing are likely adaptations that help avoid interference between signals (i.e., stepping sound, song, and body movements). Such coordination could be caused either by physical constraints associated with body movements (e.g., brown-headed cowbirds¹⁰), or by deliberately adjusting two independent signals. The amazing courtship display of cordon-bleus had features that are analogous to courtship displays in manakins, particularly with regard to multimodality and acrobatic movements^{19–21}, but these species differ in vocal learning ability, behavioural mutuality and mating systems.

The most striking aspect of our findings is that they appear to produce two acoustic signals (non-vocal sounds and songs) simultaneously (Supplementary Video S1, S3, Supplementary Figure S1). Past research showed that some species spontaneously synchronize their movements with musical rhythms to which they are exposed^{22–25}. However, little is known about how animals can temporally coordinate naturally produced multicomponent acoustic signals (i.e., vocal and non-vocal sounds²⁶). Fewer steps during singing can be explained from the perspective of motor constraints because dance displays and singing are both physically demanding²⁷. In contrast, increased bobbing tempo cannot be explained by trade-offs between singing and dancing signals. Sound pressure and the timing of steps seemed to be coordinated with the songs. A next step in the study of blue-capped cordon-bleus courtship display should be to investigate how singing, bobbing, and stepping behaviours are coordinated within individuals and between partners. This would yield insights into how multimodal and multicomponent courtship display evolved.

Material & Methods

Procedure. We used 16 blue-capped cordon-bleus (8 females and 8 males). A male and a female were randomly paired, housed together in a cage (120 × 48 × 48 cm), and their behaviour recorded in a

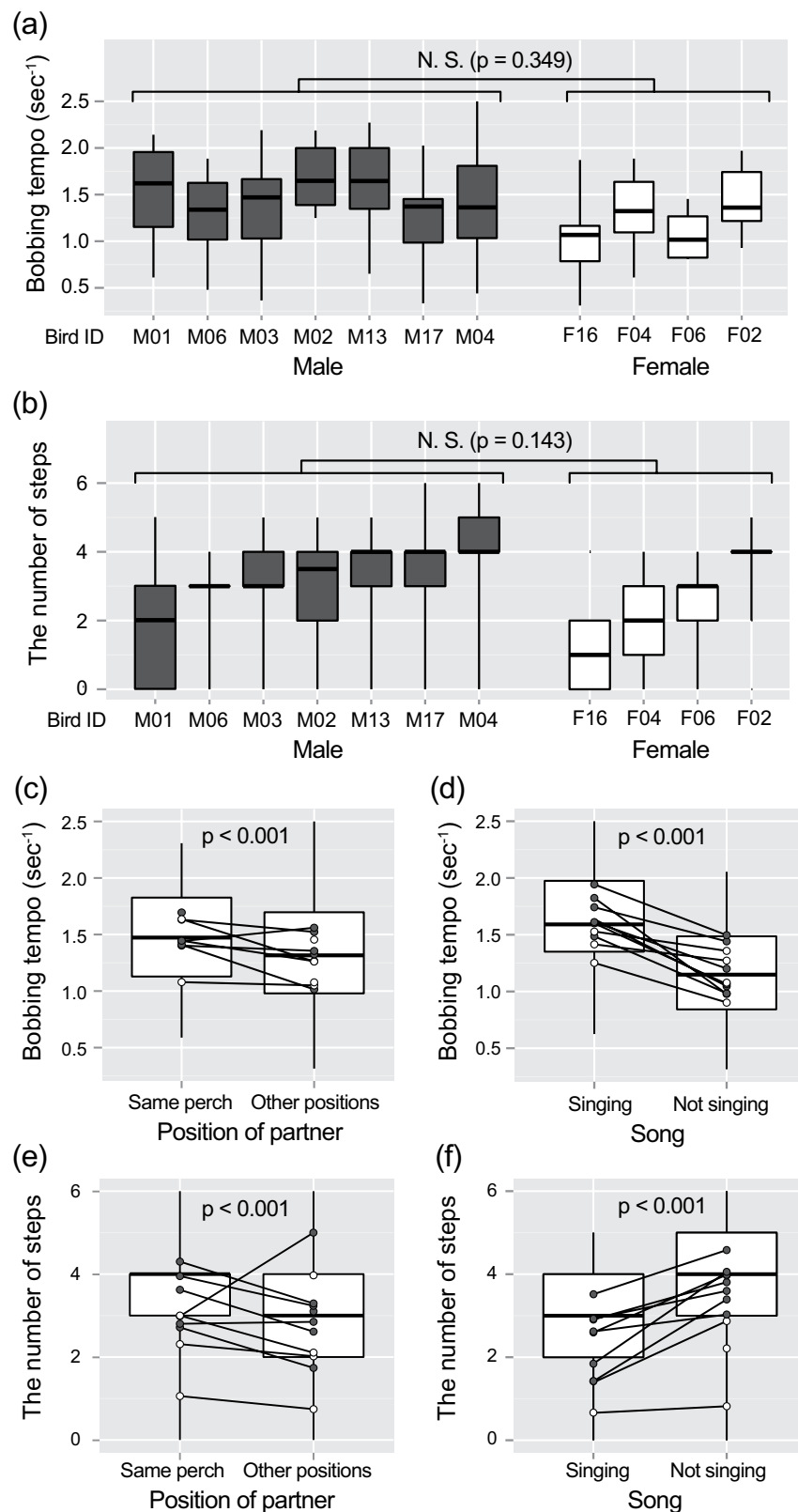


Figure 2. Changes of dance performance within and among individuals. Individual differences were calculated in (a) bobbing tempo and (b) the number of steps per bob (shaded bars: males, white bars: females). Bobbing tempo depended on (c) whether the partner was on the same perch, and (d) whether birds were singing. Similarly, the number of steps depended on (e) whether the partner was on the same perch, and (f) whether birds were singing. (a–f) All box plots show median, quartiles, and minimum and maximum values. (c–f) Mean individual values (closed circles: males, open circles: females) and their within-individual changes are indicated.

2-hour recording session (2.02 ± 0.40 hours) with normal (Q3HD ZOOM, 30 frames/s) and high-speed (GC-PX1 Victor, 300 frames/s) video cameras. If either member of a pair failed to dance, we repeated the recording session using the same pair, or switched their partners. The observation time for each individual was arbitrary (see Supplementary Table S1) because we wanted to maximize the sample size by allowing birds to participate as often as they would. We recorded 102 sessions (206.5 hours of footage).

We analysed the video using Adobe Premiere Pro software (Adobe Systems Inc.) and marked three behavioural measures: (i) the occurrence of dance displays for each individual in each session; (ii) the bobbing tempo (number of bobs/s); and (iii) the number of steps in one bobbing action (Fig. 1c). We examined how the sex of the performers, their partners' positions (same perch or not), and the act of singing while bobbing affected performance on these three metrics.

All individuals were kept on a 14:10 h light:dark schedule (lights on 07:00–21:00) at about 22 °C and 50% humidity. Birds were provided with finch seed mixture, cuttlebone, water, and cucumber ad libitum. Nests and nesting materials were always available in the cages. Procedures were in accordance with national laws and approved by the Government of Upper Bavaria.

Statistical analyses. To examine the effect of sex on the probability that an individual danced during sessions, we used a generalized linear mixed-effect model (GLMM) with a binomial distribution. To examine the effects of sex, partners' position, and singing behaviour on dance performance, we used a GLMM with a Poisson distribution to analyse the number of steps, and a linear mixed-effect (LME) model to analyse the bobbing tempo. In these analyses, we considered session number nested within bird ID as random effects to control for non-independence of the data. To investigate individual differences in dance display, we used a likelihood ratio test to compare this model with a model in which bird ID was removed. All statistical analyses were performed using R 3.1.2 (R development Core Team 2014).

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Author Contributions

N.O. and M.S. conducted the experiments and analysed the data. All authors designed the experiments and wrote the paper.

Additional Information

Supplementary information accompanies this paper at <http://www.nature.com/srep>

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Songbird tap dancing produces non-vocal sounds*

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ABSTRACT

Vocalizations have been elucidated in previous songbird studies, whereas less attention has been paid to non-vocal sounds. In the blue-capped cordon-bleu (*Uraeginthus cyanocephalus*), both sexes perform courtship displays that are accompanied by singing and distinct body movements (i.e. dance). Our previous study revealed that their courtship bobbing includes multiple rapid steps. This behaviour is quite similar to human tap dancing, because it can function as both visual and acoustic signals. To examine the acoustic signal value of such steps, we tested if their high-speed step movements produce non-vocal sounds that have amplitudes similar to vocal sounds. We found that step behaviour affected step sound amplitude. Additionally, the dancing step sounds were substantially louder than feet movement sounds in a non-courtship context, and the amplitude range overlapped with that of song notes. These results support the idea that in addition to song cordon-bleus produce acoustic signals with their feet.

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Introduction

Although birds generally rely on vocalization for acoustic communication, non-vocal sounds are known to be used in some species, such as manakins (Pipridae; Prum 1998; Bostwick and Prum 2003; Fusani et al. 2007), snipes (*Gallinago coelestis*; Bahr 1907), flappet larks (*Mirafra rufocinnamomea*; Norberg 1991), greater sage grouse (*Centrocercus urophasianus*; Koch et al. 2015), ruffed grouse (*Bonasa umbellus*; Garcia et al. 2012), hummingbirds (Trochilidae; Clark et al. 2011), woodpeckers (Picidae; Stark et al. 1998), oriental white storks (*Ciconia boyciana*; Eda-Fujiwara et al. 2004), and palm cockatoos (*Probosciger aterrimus*; Wood 1987). Generally, these species produce non-vocal sounds for courtship using their wings, tails, bills, or tools, and these non-vocal sounds are poorly understood in the context of acoustic communication evolution compared with vocalizations.

We recently found that both males and females of some songbird species also produce non-vocal sounds in addition to song (Ota et al. 2015; Soma and Mori 2015). For example,

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in Java sparrows (*Lonchura oryzivora*), which are socially monogamous songbirds without female song, both sexes produce bill-click sounds that are well-coordinated with male song (Soma and Mori 2015). These findings are rather surprising for at least two reasons. First, past studies of acoustic communication in songbirds have typically shed light on their vocalizations, because they are vocal learners and can acquire complex songs (Catchpole and Slater 2008). Therefore, non-vocal sounds in songbirds have been largely overlooked, although some songbirds were suggested to be able to produce non-vocal sounds (Clark and Prum 2015). Second, courtship displays to produce non-vocal sounds are usually considered to have evolved via strong sexual selection pressure on males of polygynous or lekking species (Andersson 1994; Prum 1998; Byers et al. 2010; Fusani and Schlinger 2012). Although a recent study found that vocalization is both widespread and ancestral in female songbirds (Odom et al. 2014), it is still unclear why and how non-vocal sounds evolved in males and females of some songbirds.

Our study species, the blue-capped cordon-bleu (*Uraeginthus cyanocephalus*), performs tap dance-like behaviour that is accompanied by distinct non-vocal sounds (Figure 1(a); Supplementary Video 1; Ota et al. 2015). Blue-capped cordon-bleus are socially monogamous songbirds, and both sexes perform elaborate multimodal courtship displays that are characterized by singing and simultaneous visual displays, such as holding nest material and bobbing (Goodwin 1982). We previously discovered that their visual courtship display includes multiple rapid steps while bobbing and produces non-vocal sounds (Ota et al. 2015; Figure 1(c); Supplementary Video 1). High-speed video observation revealed that they stamp their feet several times rapidly. The behaviour is invisible to the naked eye and appears as a single pulse on the spectrogram (Ota et al. 2015; Figure 1(a) and (b)). Our previous findings suggest that performing rapid step behaviour enables male and female cordon-bleus to communicate via multiple acoustic signals (i.e. vocal and non-vocal sounds).

Clark (2016) proposed that one criterion to diagnose a non-vocal sound is voluntariness: whether the sound is produced intentionally and production is modulated by the animal. Our previous study revealed that their tap dance-like behaviour is performed only during courtship, and the performance is adjusted in a context-dependent manner (Ota et al. 2015). For example, they took more steps when their partner stayed nearby and fewer steps when they were singing (Ota et al. 2015). These context-dependent performance changes seem to modulate non-vocal sounds but the relationship between the kinematics and sounds remains unclear. Investigating this relationship would improve our understanding of the role of non-vocal sounds.

In this study, we investigated whether taking multiple steps contributed to producing non-vocal sounds in two ways. First, we quantified dance performances by evaluating the number of steps in one bob and by evaluating step speed, and investigated how the dance performances affected sound amplitude. We predicted that if taking multiple steps plays an important role in producing non-vocal sounds, the step sound would be louder as the number of steps increased. We also expected that step speed (i.e. the number of steps/bobbing duration) would have an influence on step sound amplitude, because step speed would be associated with the velocity and/or force when their feet land on the perch. Second, we compared step sound amplitude with that of feet movement sounds in a non-courtship context and song notes to assess the efficacy of step sounds as acoustic signals. If they produce step sounds as acoustic signals, the sound would be louder than non-communicative sounds,

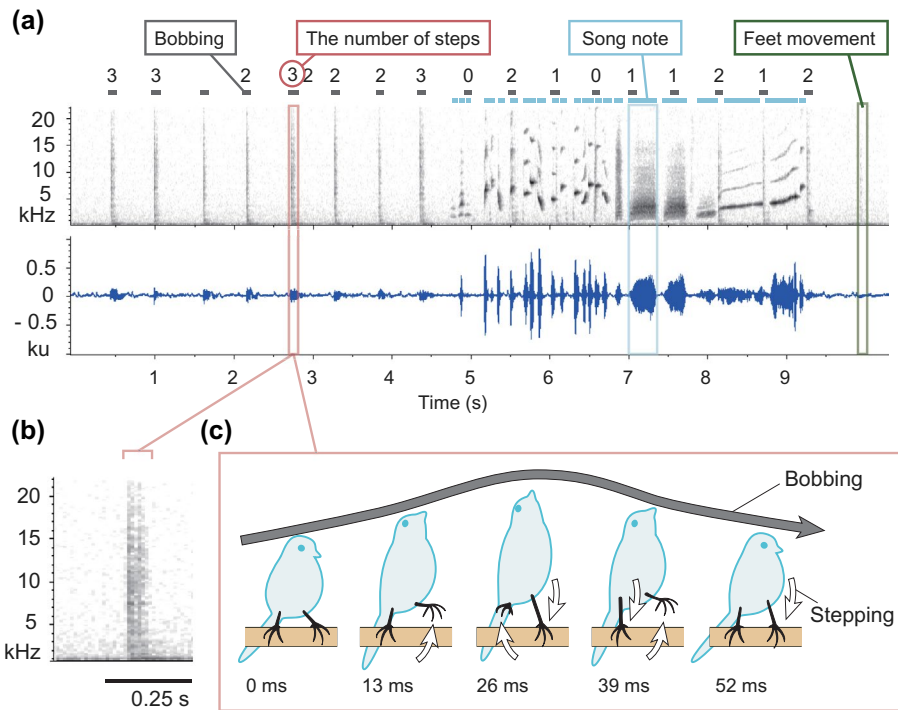


Figure 1. Blue-capped cordon-bleu step behaviour and sounds.

Notes: (a) A spectrogram and waveform of blue-capped cordon-bleu step sounds and song. These birds simultaneously bob and step, and sing at certain times. Numbers at the top of the spectrogram indicate how many steps were performed to produce the sounds. Feet movement sounds and song notes were arbitrarily sampled from each individual. (b) Enlarged view of the step sound spectrogram. (c) Diagram of step behaviour that produces non-vocal sounds.

such as feet movement sounds in a non-courtship context (Supplementary Video 2), and the amplitude would overlap with that of communicative vocal sounds (i.e. song notes).

Materials and methods

Subjects and experimental procedure

We analysed courtship dances of 12 male and five female adult blue-capped cordon-bleus (>6 months old). One male and one female were arbitrarily paired and housed together in a cage (120 × 48 × 48 cm) in a sound-proof chamber. Their behaviours were recorded in a 2-h observational session with normal (Q3HD ZOOM, Tokyo, Japan; NTSC, 30 frames/s) and high-speed (GC-PX1 Victor, Yokohama, Japan; 300 frames/s) video cameras. Procedures were in accordance with German National Laws and approved by the Government of Upper Bavaria.

Sound analysis

We collected sound data with a sampling rate of 44.1 kHz and 16-bit resolution, which was recorded with a unidirectional microphone (angle: 120°, max SPL: 130 dB) under fixed gain settings in a normal-speed camera. We sampled on average, 41.1 step sounds from each

individual (range, 13–50). We sampled step sounds that did not include any noise detected above background levels and were only produced on the same perch position in one session to minimize sound amplitude changes related to the distance of the birds to microphone (Figure 1(a); Supplementary Video 1). We also sampled 10-foot movement sounds that are not step sounds from each individual as controls (Figure 1(a)). We sampled the movement sounds when the birds moved on the perch where they also danced (Supplementary Video 2). In addition, 20 song notes that did not overlap with step sounds or other noises were arbitrarily sampled. We could not sample song notes from two females because they did not sing (see also Supplementary Figure S2).

We measured average and peak amplitude of step sounds, feet movement sounds, and song notes using Raven Pro 1.4 (www.birds.cornell.edu/raven). The durations of step sounds were also measured to quantify step speed (see ‘Behavioural analysis’). Average amplitude was based on average values of sound pressure level during sound production (Charif et al. 2010). Peak amplitude was considered the sound pressure level at the darkest point in the sound spectrogram (Charif et al. 2010). Because cordon-bleus usually sing songs with 10–30 note types (Geberzahn and Gahr 2011) that have quite different amplitudes, their songs cover a wide range of amplitude (Figure 1(a)). To compare step sound amplitude with that of the lower limit of song notes, we selected the three lowest-amplitude song notes from the 20 song notes mentioned above.

Sound amplitude values measured in this study were expressed in decibels, which reflected relative values within each recording (Charif et al. 2010). The distances from microphones to birds (67–76 cm) and positions on the perch (i.e. edge or centre) differed among individuals, although we controlled for these issues at the within-individual level as described above. For these reasons, we could not investigate sound amplitude differences at an among-individual level in this study, but focused on the within-individual changes and statistically controlled for these changes (see also ‘Statistical analysis’).

Behavioural analysis

We analysed two candidate factors that can affect step sound amplitude: the number of steps in one bob and step speed index. From the high-speed movie images, we counted the number of steps in one bob that were analysed in sound analysis (Figure 1(a) and (c); Supplementary Video 1). As a variable that is independent of the number of steps, we calculated ‘step speed index’ (Supplementary Figure S1); we plotted the step sound duration against the number of steps and calculated the distance of each residual from the regression line (Supplementary Figure S1). A higher step speed index value indicates less time required for a particular number of steps (Supplementary Figure S1).

Statistical analysis

To assess whether dance performances influence sound amplitude, we investigated the effects of the number of steps and step speed index on sound amplitude using linear mixed-effect models (LME). To compare sound amplitude between sound categories (i.e. step sounds, feet movement sounds, and song notes), we investigated the effect of each sound category on sound amplitude using LME. We also compared amplitude between the lowest-amplitude song notes and step sounds using LME. In these analyses, we considered bird ID as

a random effect to control for non-independence of data from the same individual. All statistical analyses were performed using R 3.1.2 (R Development Core Team 2014).

Results

Both average and peak sound amplitude increased as the number of steps increased (Figure 2, Table 1), which was also clear at the within-individual level (Supplementary Figure S2). Increased step speed index values negatively affected peak sound amplitude, but not average sound amplitude (Table 1).

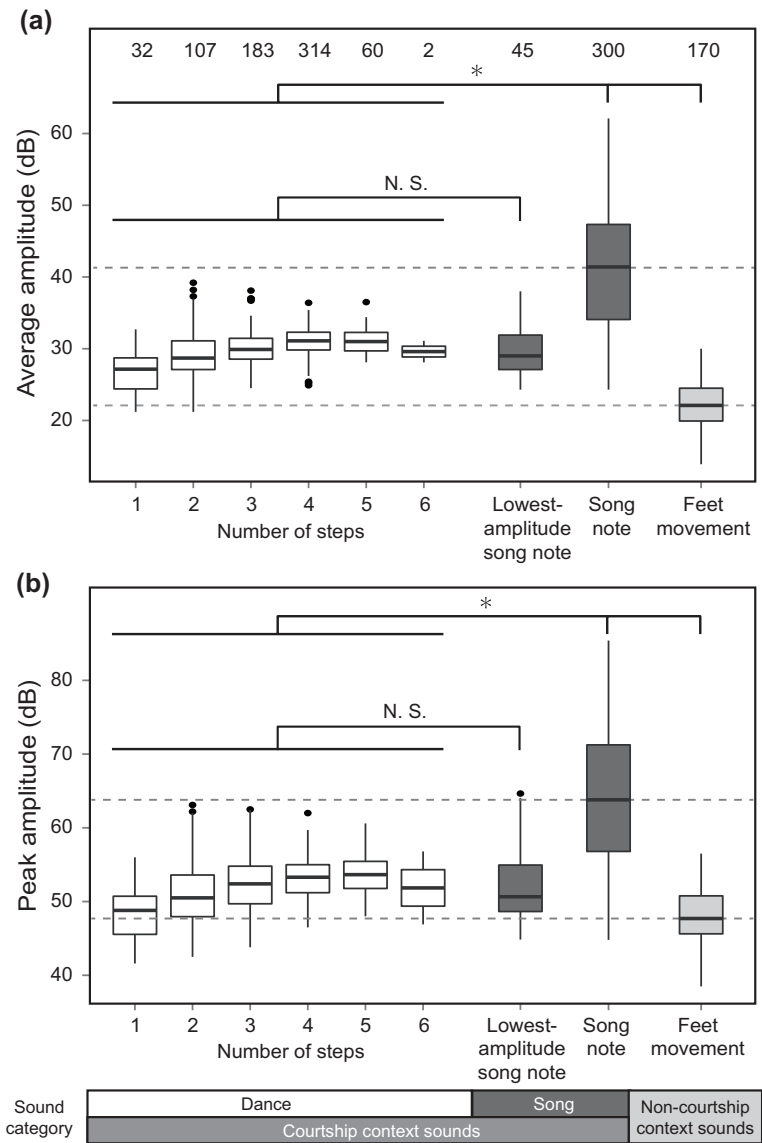


Figure 2. Effects of the number of steps on sound amplitude. Notes: (a) Average and (b) peak sound amplitude are plotted as a function of the number of steps compared with those of lowest-amplitude song notes, arbitrarily chosen song notes, and feet movement sounds. Numbers at the top of (a) represent sample size for both (a) and (b) (see also Supplementary Figure S2). All box plots show median and quartiles. Outliers are plotted as points.

Table 1. Results of LME analyses of step sound amplitude. The effects of the number of steps and step speed index on (a) average and (b) peak step sound amplitude.

Response variable	Independent variable	Coefficient	SE	<i>t</i>	<i>p</i>
(a) Average amplitude	The number of steps	0.928	0.090	10.307	<0.001
	Step speed index	4.578	6.458	0.709	0.479
(b) Peak amplitude	The number of steps	1.241	0.129	9.704	<0.001
	Step speed index	−42.001	9.191	4.571	<0.001

Note: Significant *p* values (<0.05) are given in bold.

Step sounds were significantly louder than feet movement sounds but quieter than song notes (Supplementary Video 2; Figure 2; average amplitude: $df = 1149$, $F = 970.943$, $p < 0.001$; peak amplitude: $df = 1149$, $F = 644.887$, $p < 0.001$). Although amplitude of arbitrarily chosen song notes was clearly higher than step sound amplitude (Figure 2), the significant difference disappeared when we compared step sound amplitude with that of the lowest-amplitude song notes (Figure 2; average amplitude: $df = 725$, $F = 2.765$, $p = 0.097$; peak amplitude: $df = 725$, $F = 1.702$, $p = 0.193$).

Discussion

Our results showed that step sounds satisfy the criterion of non-vocal sounds as an acoustic signal (Clark 2016), at least under our captive conditions. As predicted, non-vocal sounds changed depending on the dance performances at the within-individual level. This suggests that context-dependent changes of dance performance (Ota et al. 2015) modulate the non-vocal sounds. Step sound amplitude correlated with the number of steps in one bobbing and taking multiple steps played an important role in producing louder sounds (Figure 2, Table 1). Additionally, step speed index had a negative effect on step sound amplitude (Table 1).

There are two possible mechanisms that explain these sound amplitude changes. First, the sound amplitude may be amplified by overlap of multiple step sounds. This may not be the case, however, because the experiments were conducted in a sound-proof chamber where sound reflections were substantially reduced. Our behavioural observations revealed that these birds usually tap their feet alternately (Figure 1(a), Supplementary Video 1) and rarely tap simultaneously (6.4% of all bobbing actions in this study), which indicates that the tap dancing is not performed to make overlapping sounds. In addition, their step speed negatively affected peak sound amplitude (Table 1(b)). This finding indicates that higher step speed can increase the amount of overlap between consecutive sounds, but did not produce louder sounds. However, we should be cautious about the interpretation of these results, because it is not clear how step sounds are affected by reverberations in the eco-acoustic environment of the natural habitat of blue-capped cordon-bleus.

The second mechanism is strong tapping of their feet against the perch when they take certain steps. Considering that step speed negatively affected peak but not average sound amplitude, birds may more strongly tap during one step among the multiple steps at the cost of step speed. Taking multiple steps may positively increase the landing velocity of their feet on the perch, but we could not directly measure the landing velocity, force and the interval durations between taps, because neither image nor time resolution of our cameras were sufficient (Supplementary Video 1).

Our results of the comparison among sounds that the cordon-bleus produce in various contexts also support the idea that step sounds are not just by-product sounds of movements. Step sounds were distinct from other feet movement sounds (Supplementary Video 2; Figure 2) and were as loud as the lowest-amplitude song notes (Figure 2). Presumably, step sounds may serve as communicative signals, especially when the distance between birds is short.

Although we have revealed an interesting phenomenon about non-vocal sounds in songbirds, detailed communicative functions and the underlying physiological and neuromuscular mechanisms of these non-vocal sounds remain unclear. We cannot completely deny the possibility that the non-vocal sounds are just a by-product of a vigorous motion that is used as a visual signal. We should examine how signal receivers respond to non-vocal sounds (e.g. Freeman and Hare 2015). Perch choice of signal senders should also be tested, because perch structures or materials would affect acoustic features of non-vocal sounds. Investigating kinematic characteristics of the stepping (e.g. Clifton et al. 2015) and associated morphological features (e.g. Bostwick et al. 2012; Clark and Prum 2015) would further elucidate the mechanisms of non-vocal sounds in blue-capped cordon-bleus. Observing cordon-bleu courtship behaviour in the wild would help elucidate the eco-acoustic environment and perch properties that affect the production of these sounds. Such additional studies would shed new light on acoustic communication in birds.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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