Ritualized signals in the red-crowned crane: how and why do they perform various displays?

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Doctoral thesis

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ABSTRACT

Ritualized signals are essential in social communication as it affects to both survival and reproduction. Although several studies described ritualized displays in birds, quantitative analyses have rarely been done. To understand a role of ritualized signals, I investigated both characteristics and function of the following displays in the red-crowned crane (*Grus japonesis*); (1) arch displays after joining to a flock, (2) duet displays in a flock, (3) structure of pair dances and (4) function of pair dances. By behavioural observation on mainly banded cranes during the winter seasons in 2011-2015, I analysed both characteristics and social contexts of these displays.

(1) Arch display after joining to a flock: Behavioural observations indicated that the arch functions as a signal of both threat motivation and individual strength. Singletons had disadvantages in terms of competition over resources and were, therefore, expected to have higher threat motivation than pairs or families. Indeed, singletons performed the arch more frequently than did pairs or families. Performance of the arch was related to dominance: males and adults were more likely to perform the arch than females and sub-adults. The likelihood of performing the arch was positively associated with local group density, indicating that joiners arched in more competitive situations. Contextual analyses indicated that subsequent behaviour by a joiner was more aggressive and that nearby individuals more frequently showed behavioural responses when a joiner arched than when it did not. Together, this study shows that cranes demonstrate functional displays to potential competitors, and represents a rare example of the functional analysis of ritualized signals in non-songbird species with fission-fusion social dynamics.

(2) Duet displays (DDs) in a flock: Families performed DDs more frequently than pairs. Relative to pairs without juveniles, families were supposed to have high motivations for an access to food resources. That was because families needed more foods than pairs in order to care their juveniles. Therefore, this result suggests that the DDs reflected the motivation for resource competition. Particularly, whether DDs were overlapped by vocalization of other pairs (overlapped DDs) or not (non-overlapped DDs) depended on the social situations. The frequency of overlapped DDs but not non-overlapped DDs, increased as the flock size increased. Finally, the performance of non-overlapped DDs, but not overlapped DDs, increased a possibility of staying at the favorable area. These results suggest that non-overlapped DDs function as cooperative resource defense. These findings were consistent with the idea that the degree of overlapping DDs negatively affected by their competitive ability. This study provides rare data on the function of coordinated vocal displays within a group in birds.

(3) Structure of pair dances: I analysed species-specific structure of pair dances. First, concerning its behavioural sequence, I found that behavioural transitions by one individual affected the partner' transitions. Therefore, pair dances were structured. Second, regarding temporal association within a pair, I found that in according to a partner's behavioural elements, individuals decided which behavioural elements to perform. Finally, regarding sexual difference, I found that a male was more active than a female in their dances. These results suggested pair dances played an important role in mutual communication within a pair.

(4) Function of pair dances: I analysed relationship between the inter-pair variation of pair dances and reproductive success. The results partially supported that pair

dances function as strengthening pair bond (pair bond hypothesis). The supporting results were following. First, dance diversity (i.e., entropy) was correlated between mate partners. Second, the total duration of each dance was longer as the breeding season comes. This indicated that the performance of each dance was related with their reproductive sates. Finally, entropy for pairs, but not entropy for each individual, affected reproductive success. These indicated that simultaneous performance was important factors affecting reproductive success. However, the following results disagreed with the pair bond hypothesis. The general synchrony within each pair (i.e., joint entropy) affected their reproductive success negatively. The general dependency within each pair (i.e., mutual information) was negatively associated to long-term reproductive success. Therefore, both synchrony and dependency within each pair partially caused negative effects on reproductive behaviours of pairs. This inconsistency of results might be caused by vague concept of "pair bond". Efforts for establishing pair bonds were different from ones for maintaining pair bonds. That was because establishment of pair bonds needs to know their characteristics such as their personality with each other. On the other hand, maintaining of pair bonds needs to continue their relationship as the same as they have cooperated before. The results firstly imply it needs to be clear what is pair bond.

Overall, ritualized signals in the red-crowned crane were functional and meaning to exchange between signalers and receivers. These studies filled the gaps between ritualized signals and other type of signals (e.g., acoustic performance) and contribute to our broad understanding of animal communication.

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Chapter 1. General introduction

Animal communication is essential in all aspects of animal behaviour such as in mating, reproduction, parental care, and competition (Brandbury &Vehrencamp 2011). Many previous studies of communication focused on visual or acoustic signals. As an example of visual signals, sexually selected traits such as male's ornaments have been intensively studied. Those studies mainly tested and confirmed that those traits are used as an index of a male quality to females (e.g., long-tailed widowbird *Euplectes progne*: Anderson 1982, barn swallow, *Hirundo rustica*: Møller 1994, trinidadian guppy, *Poecilia reticulate*: Houde 1997, blue grosbeak, *Guiraca caerulea*: Keyser & Hill 2000, satin bowerbird, *Ptilonorhynchus violaceus*: Doucet & Montgomerie 2003). Regarding acoustic signals, information encoded in those signals has been mainly studied. Many studies found that different types of calls represent different external information such as types of predators and contents (e.g., vervet monkey, *Chlorocebus pygerythrus*: Seyfarth et. al 1980, great tit, *Parus majour*: Suzuki 2011, Arabian babbler, *Turdoides squamiceps*: Naguib et. al 1999).

Previous studies of signals, particularly in birds, have following problems. First, as discussed, studies have been biased to acoustic and visual signals (e.g., sexual ornaments and calls). Those signals are relatively easy to measure and quantify by their rate or length. In contrast, complex kinematic or multimodal signals (e.g., ritualized displays and dances) remained less studied (Brandbury &Vehrencamp 2011). Although studies have been described various forms of ritualized displays (e.g., Huxley, 1914; Morris, 1958; van Tets, 1965; Masatomi & Kitagawa, 1975), there are no quantitative studies investigating both characteristics and function of these ritualized signals. Second, previous studies mainly investigated one-way communication and few studies investigated mutual communication in which information is exchanged between two individuals sequentially or at the same time (Wachtmeister, 2001). It is also important to compare types of social relationships (e.g., competitors or mating partners) in which mutual communications were observed with those in which one-way communications were performed, in order to understand adaptive significances of these complex signals.

In addition, sexual factors also play an important role affecting the evolution of these signals. Previous studies suggested mutual sexual ornaments are often present in socially monogamous species (reviewed in Pickering & Berrow 2001). That was because the similar selection pressures works on both males and females. Therefore, it is predicted that both males and females showed the similar performance of ritualized displays in socially monogamous animals. Although many studies focused on visual mutual ornaments (e.g., crested auklet, *Aethla cristatella*: Jones & Hunter 1993, black swan, *Cygnus atratus*: Kraaijeveld et al., 2004, blue-footed booby, *Sula nebouxii*: Torres & Velando 2005), there have been only a few studies analysing sexual difference for ritualized displays or pair dances.

Pair dances or courtship displays are composed of many behavioural elements. Some animals use one of these elements in other social situations such as competition for foods, or non-social situations such as preening (Brandbury & Vehrencamp 2011; Maynard Smith & Harper 2003). For examples, some socially monogamous species perform the similar displays in both aggressive situations to competitors and familiar situations to their mate partner (e.g., butterflyfish, *Chaetodon lunulatu*: Yabuta 2002, herring gulls, *Larus argentatus*; Tinbergen 1959, red-crowned crane *Grus japonensis*: Masatomi & Kitagawa 1975). These similarities are classically understood by "ritualization" of each behavioural element (Maynard Smith & Harper 2003). However, there are a few quantitative studies for analysing these similar displays across different contexts.

Based on these problems, a broad aim of my studies is to uncover both characteristics and functions of ritualized displays and mutual communication in the red-crowned crane (*Grus japonensis*). To fulfill the aim, I investigated both characteristics and functions of the following displays in the red-crowned crane:

I) Arch displays after joining a flock (Chapter 2),

II) Duet displays in a flock (Chapter 3),

III) Pair dances (structure: Chapter 4, function: Chapter 5).

Both the arch displays and duet displays are one-way signals. Interestingly, these displays are used as behavioural elements of pair dances, mutual signals. Studies of not only mutual signals but also its element in a different context will expand our understanding of complex signals and communication in animals.

Study species

The red-crowned crane is the suitable species for investigating ritualized signals. The characters of the crane are summarized into three following points (Johnsgard, 1983; Masatomi & Kitagawa, 1974). First, the cranes are socially monogamous and pairs form long-term pair bond. Their lifespan is long (life expectancy: 15.7-17.2 years; Masatomi et al. 2007). Pairs usually associate all the year around. Second, pairs or families occupy own territory in breeding seasons (April-September). During this period, a pair makes a nesting in the reed wetland. A female lays two eggs at once and both males and females incubate their eggs by turns.

The incubation period is about 31-33 days. After hatching, the chicks start flying in three months. Both males and females engage in caring for their young by late winter (usually March) (Masatomi & Kitagawa, 1974). Third, they usually form a flock during winter. They often migrate from their wetland territory to fields of corn in autumn or to artificial feeding stations in winter. In addition, sub-adults and young non-breed birds also form a small flock (usually more than 10 birds) during breeding seasons. Because of these characteristics, cranes have frequent opportunities to communicate with a mate partner or competitors. Probably relating to this, the crane has a large repertoire of ritualized displays compared to solitary species (Ellis et al., 1998). It is easy to observe their behaviours and displays, since they gather in feeding stations at which visibility is good during winter.

The red-crowned crane is one of large birds in the world. In adults, the total body length is about 136 cm (males) or 124 cm (females), the wing length is about 61 cm (males) or 58 cm (females), and the weight is about 8.1 kg (males) or 7.2 kg (females) (Inoue et al. 2013). Males are slightly lager than females. Adults are overall white with black face, neck, and wing secondaries. They have a red patch of bare skin on the crown, which becomes brighter in the excitement such as aggression. Sub-adults have dark-point wing primaries, which are distinguished from adults. Juveniles have grayish neck, tawny head and dull black wing secondaries without a red patch in the crown. The crane was distributed in two separate areas: the island population in Hokkaido, Japan and the continental population in northeast Asia. The island population is now residential and its number was counted about 1,550 (TKG 2015). Although this population was decreased about some tens of birds in 1920s because of human activities such as hunting, the population has increased from 1950s because of artificial foods in the winter and now is considered as stable. On the other hand, the continental population is migrant and its number is estimated at about 1,400-1,550 (BirdLife International 2016). They breeds in the Amur River Basin, Russia and winters in Yellow river delta, the coast of Jiangsu province, China and the Demilitarised Zone, Korean peninsula. It is said that the number of the cranes is probably decreasing in the continental population (BirdLife International 2016).

The cranes have omnivorous diets (Masatomi & Kitagawa 1974). They eat various foods: corn, parsley, some water plants, bushweat, earthworms, loaches, small fishes, frogs, small crayfishes, snakes, water insects and so on. They shift main diets according to season. In the island population, predators for their early chicks were foxes, cats, crows, raptors, and snakes. Except for molting, there are a few predators for healthy adults.

Birds have sophisticated sensory capacity among vertebrates. In general, birds have high visual capacity compared with human (Gill 2007). Especially, they can see the ultra-violet light which human cannot see. The recent visual study shows the whooping crane (*Grus americana*) has a violent sensory capacity, which is similar to other birds (Porter et al. 2010). Except for special birds like owls, birds in general have limited acoustic capacity (about 1~5 kHz) compared with human (Gill 2007). Especially, they cannot hear small volume of the voice which human can hear. Other sensory capacities showed inter-specific variation. These sensory capacities are almost unknown in the crane. In addition, birds in general exhibit a similar cognitive ability compared with mammals (Jarvis et al. 2005). Even though some birds have relatively small brain compared with primates, they also have sophisticated cognitive ability among animals (Dukas 1998). The graylag geese (*Anser anser*), whose brain size is relatively small among birds, showed high cognitive abilities such as transitive inference in cognitive tests (Weiß et al. 2010; Scheiber et al. 2013). Considering these facts, it is suggested that the crane has the actual capability to used ritualized signals for their communication.

General methods

This study was conducted in the region of the Kushiro-Shitsugen National Park, Hokkaido, Japan (about 43°8'N, 144°8'E). The study sites were three artificial feeding stations: one located at the Akan International Crane Center (AKAN), one located at Tsurumidai (TMD), and one located at the Tsurui-Ito Tancho Sanctuary (SANC). All three feeders have been certified by the Japanese government for conservation purposes. At most, 250 wild cranes use each site during the winter season (from December to March). The most unnatural food item provided by local residents at the feeding stations was dent corn (at AKAN once, scattered at about 8:00 AM; at both TMD and SANC twice, scattered in the early morning and late evening). The volume of dent corn (e.g., scattered around an area of about 10 × 20 m in AKAN) appeared to be sufficient for all cranes at the three sites because some corn was left over each night. At AKAN, an additional food item, Japanese dace (about 40 fish per day), was also scattered at 2:00 PM daily.

During the winter season, some cranes gather at artificial feeding stations during the daytime, while other cranes stay on their breeding grounds if food is sufficient. The number of cranes using feeding stations remains consistent throughout the season (Takeda, 2012). Individuals go back and forth between feeding stations and an unfrozen river as a roosting site.

Cranes that have been banded constitute approximately 10% of all individuals within the population (banding was conducted by the Red-crowed Crane Conservancy [RCC]). Because pairs typically move together, I considered the partner of the banded individual to always be the same individual. Their sex and age, which usually could not be determined by appearance alone, were known by RCC. Sex was determined by blood samples from banding research (Miura et al., 2013), and age was determined by their banded year when they were chicks. Reproductive success at each year recorded by RCC continuous research in the winter season. The reproductive success was defined as whether their chicks survived until the first winter seasons after they had hatched.

Study periods are from November to March in 2011 to 2014 (approximate. 7 hours per day, Table 1.1). I recorded behaviours of ringed cranes (identity of individuals) and others (details of observational methods were explained in each chapter). Crane behaviours were observed at a location where the observer could view the entire feeding station. I used a binocular (Zeiss 8x32 T* FL) or a telescope (Kowa 20-60x) for observation especially in identifying banded cranes. Based on observations or video data, I analysed both characteristics and social contexts of their displays.

Data analyses

Unless otherwise noted, data were analysed using generalized linear models (GLMs) or generalized linear mixed models (GLMMs) in this thesis. To avoid pseudo-replication, the identities of individuals or pairs and other fixed effects were set as random terms in the GLMMs. To determine the most parsimonious model, I used backward stepwise selection of independent terms with likelihood ratio tests. Statistical analyses were conducted using R ver. 3.2.1 (R Development Core Team).

Table 1.1 Summary of total observation days/hours for each year. Each chapter used data collected in different year(s).

Year	Days	Hours	Chapter
2011-12	35	254	2, 4, 5
2012-13	61	446	4, 5
2013-14	58	442	3, 5

Chapter 2. Arch displays after joining a flock

2.1 INTRODUCTION

Individuals often perform ritualized displays during encounters that have the potential for conflict because they need to assess the strengths and motivations of other individuals (Maynard Smith & Harper, 2003). These types of displays are expected to be particularly important in species with fission-fusion social dynamics. In fission-fusion societies, the size and membership of a group frequently changes by successive leaving (fission) and joining (fusion) the group spatio-temporally (Aureli et al., 2008). Fission-fusion dynamics display huge variations according to the strength/stability of the associations among subgroups or individuals within a social network, ranging from relatively stable grouping patterns to highly fluid ones (Aureli et al., 2008; Silk et al., 2014). Flexible membership of a flock decreases the predictability of the behaviours of other members, and individuals may need to signal their strength and/or motivation immediately after joining a group (Aureli et al., 2008). This requirement should be especially high when dominance relationships are poorly established or unstable. In these cases, individuals with high motivation for signalling may need to display their intentions to potential competitors during the first interaction after fusion (Aureli et al., 2008). Alternately, individuals with superior physical characteristics or high resource holding potential (RHP) are expected to have a strong incentive to perform such displays (Muller & Mitani, 2005). This requirement contrasts with that of species with cohesive grouping styles, in which information regarding group members is regularly updated via within-group interactions.

Despite the importance of ritualized displays, their functions have been relatively poorly studied in species with highly fluid fission-fusion grouping styles (but see Aureli & Schaffner, 2007). In birds, for example, several studies have described various forms of ritualized displays (e.g. Huxley, 1914; Morris, 1958; van Tets, 1965; Masatomi & Kitagawa, 1975). However, there have been no quantitative analyses on social factors determining the performance of displays; therefore, detailed analyses on the function of displays have never been performed. In addition, there are fewer quantitative studies of ritualized displays in non-passerines (e.g. Kraaijeveld & Mulder, 2001) than in passerines (Hurd & Enquist, 2001). Therefore, analyses of these ritualized displays would deepen our understanding of the role of communication within fission-fusion social systems.

The red-crowned crane is an ideal species in which to investigate ritualized displays in the context of fission-fusion dynamics. All 15 species of cranes have a large repertoire of ritualized displays (Ellis et al., 1998). Of these, the arch display (hereafter, the "arch") is unique to the red-crowned crane (Ellis et al., 1998). This display is occasionally observed when individuals join groups; it does not appear to be directed toward a specific individual and does not involve behavioural elements of direct aggression by itself (Masatomi & Kitagawa, 1975). Masatomi (1988) hypothesised that the arch functions as a threat display based on observations that joiners were more likely to perform the arch when they landed in a flock than when they first flew into a vacant location. More specifically, this hypothesis can be restated as follows: the arch is an honest signal of willingness to engage in aggression. However, the results of Masatomi (1988) did not completely exclude an alternative hypothesis that the arch is a ritualized signal for avoiding the occurrence of aggression in a potentially competitive situation after joining a group. These two hypotheses, namely an honest signal of aggression and avoidance of aggression, will predict different patterns of subsequent behaviour by both the signaller and its possible receiver. The former hypothesis predicts an increased occurrence of aggression, while the later predicts a reduced occurrence of aggression when a joiner performs the arch than when it does not. As such, contextual analysis is indispensable for testing these two hypotheses, but such analyses have not been performed. I uncovered the two broad questions outlined below.

Which individual factors and contexts affect performance of the arch? If the arch functions as a threat display, both the motivation and social status (strength) of the individual are expected to affect its performance. In terms of motivation, I predicted that individuals that do not belong to a unit (singletons) would be more likely to arch than would pairs or family groups. Singletons are more likely to be displaced by their competitors than are pairs or family groups (unpublished data) because singletons cannot perform acts of cooperative aggression, such as unison calls (Masatomi & Kitagawa, 1975). This observation indicates that singletons are less likely to gain access to resources than are groups, which suggests that singletons can gain greater benefits by signalling their motivation to access resources than can individuals within pairs or family groups.

In terms of individual strength, I predicted that dominants would perform the arch more frequently than would subordinates because costs for performing the arch must be lower for dominants than for subdominants. In cranes, adults are dominant over non-adults (Bautista et al., 1995), and males may be dominant over females because they are larger (Inoue et al., 2013). Hence, I predicted that adults or males would perform the arch more frequently than non-adults or females.

Independent of the effects of individual strength and motivations, the intensity of resource competition might affect the need to show a signal to competitors. Therefore, I predicted that joiners would perform the arch more frequently in intensely competitive situations (i.e., when joining a large flock or when landing where local bird density is high) than in less competitive situations (i.e., when joining a small flock or when landing where local bird density is low).

How do joiners and neighbours behave after the arch? If the arch functions as an honest signal of aggression, both joiners and neighbours (i.e., individuals that are close to the joiner; see Methods) would be more aggressive (e.g., approach or emit unison calls; see Methods for definition) when a joiner performs the arch than when the joiner does not perform the arch. Alternatively, if the arch functions as avoidance of aggression, it is predicted that both joiners and neighbours would behave less aggressively (e.g., escape) when a joiner performs the arch than when the joiner does not. Finally, both hypotheses predict that neighbours may avoid joiners performing the arch (e.g., escape) more frequently than joiners not performing the arch.

2.2 METHODS

Data collection

Observations were conducted from 17 February to 2 March 2012, from 8:30 to 16:30, by K.T. (total of 14 days and approximately 110 hours; average of 8 hours per day). Crane behaviours were observed at a location where the observer could view the entire feeding station.

The following eight variables were recorded when cranes joined the flock, of which two (v, vi) reflect different density levels that would determine the degree of competition:

i) Joiner’s age (juvenile, sub-adult, or adult). Sub-adults were defined as immature individuals under 3 years old and were distinguished from adults by wing colour (Masatomi & Kitagawa, 1975).

ii) Joiner’s sex, if confirmed. I was only able to identify the sex of an individual when it was banded or emitted unison calls (duet displays). A unison call is a pair’s duet song and exhibits sexual differences in behaviour and song structure (Masatomi & Kitagawa, 1975; Klenova et al., 2008).

iii) Whether a joiner performed the arch within 5 s after landing.

iv) Composition of joiners (singletons, pairs, families with one or two juveniles, or other [more than three adults or sub-adults]). Note that individuals that usually live in a pair or family group occasionally separate and join a flock alone.

v) Number of neighbours present when joiners landed. This variable was defined as the number of cranes within a circular area, whose radius was 4m. If the gap from joiners to the nearest individual was more than 4m, we recorded an instance of no neighbours.

vi) Flock size when a joiner landed on the feeding station. I continuously counted flock size by recording the number of individuals joining and leaving.

vii) Behaviours of a joiner within 1 minute after landing. I chose to observe for 1 minute because this short observation window is suitable for exclusion of the effects of other factors (e.g., behaviours of neighbours and spatial movement of joiners) and for focusing only on the effect of the arch. Indeed, cranes began foraging within around 1 minute after landing in 56% of cases (unpublished data of continuous 5-min observations after landing; n = 75). Social interactions do not usually occur during foraging. This suggests that the most social events occurred frequently soon after the landing events. During these 1-min observations, I continuously recorded aggressive behaviours (pair duet displays and 'struts'; i.e., one aggressive display that cranes exaggerate by slowly taking large steps and stretching their necks vertically; also called the 'adornment-walk') (Ellis et al., 1998; Mastomi & Kitagawa, 1975), foraging (pecking at the corn on the ground), walking (moving within the feeding stations), standing (remain stationary, stretching their neck), preening, and resting (standing and inserting their neck into their wings).

viii) Reactions by neighbours to a joiner within 1 minute. I classified this behaviour into three categories: (a) aggressive behaviours (aggression, see definition above), (b) escape behaviour (escape); i.e., neighbours actively separated from joiners or showed submissive behaviour (i.e., 'cower' [Ellis et al., 1998], also called 'neck-retracted-submission' [Mastomi & Kitagawa, 1975]; cranes shrink their body by curving their neck horizontally), and (c) no behavioural response (inaction), during which neighbours did not change their behaviour/position when joiners were present. When there were two or more neighbours, observations were conducted on the individual that showed a behavioural response. Note that this sampling method could overestimate the occurrence of behavioural reactions. In the present study, observing a randomly chosen neighbour as the focal observation target was not realistic because the occurrence of behavioural reaction was unpredictable and not frequent enough to quantify using this observational method (see below for how this potential problem was addressed).

Data analysis

In total, I observed 821 cases of individuals joining a flock during 370 joining events. Of these, I observed 95 cases of joining by individually-identified cranes; the total number of cranes identified was 48.

I investigated the context and consequences of the arch display when individuals landed in a flock. I used two datasets; the first comprised all observed cases, which was referred to as ‘full data’. The second dataset included cases in which adults were individually-identified using band information (called ‘band data’). By comparing results from two datasets, I checked robustness of the results. To determine the most parsimonious model, I used backward stepwise selection of independent terms with likelihood ratio tests. To avoid pseudo-replication, the same flying events or the identities of each individual were set as random terms in the GLMMs of full data and band data, respectively. Upon analysis of banded individuals, I reported individual means and one SE unit of each probability that individuals performed the arch or other behaviours.

Which factors affected performance of the arch?

To investigate the effects of each independent variable on the occurrence of the arch (a dependent term), I conducted a GLMM featuring a binomial error structure. I conducted two independent analyses. In both analyses, I excluded data for which unit composition was ‘other’ because the heterogeneity of a mixture of different units made it difficult to test and interpret the effects of each independent term.

The first analysis focused on the occurrence of the arch at the unit level because pairs or families usually cooperate to forage in competitive situations (using unison calls) and performance of the arch by one of the unit members may be adequate for other unit members to signal threat intentions to other individuals in a flock. I conducted a GLM with binomial error structure in which whether at least one unit member performed the arch was a dependent term (n = 303). I set a unit composition (singleton, pair or family), a number of neighbors, flock size, and the presence of adults in a unit as independent terms. I did not analyse the effects of sex in this model because pairs or family units included both males and females. I also conducted a GLMM on the band data (n = 51 for 27 individuals).

The second analysis focused on the occurrence of the arch at the individual level; i.e., the data unit was the individual. First, I analysed the effect of age on the performance of the arch using Fisher’s exact probability test because juveniles were never observed performing the arch (n = 821; see Results); therefore, I was unable to include individual age in the GLMMs. Thus, only full data were used in subsequent analyses; I set individual sex, unit composition (family or pair), a number of neighbors, and flock size as independent terms (full data: n = 115; band data: n = 86 for 47 individuals). I also excluded flying data for single individuals because the sample sizes were too small (n = 6 for both full and band data) for comparisons. Hence, my dataset included only families and pairs as the unit type. In addition, I only used data for adults whose sex could be identified. Therefore, this analysis tested the prediction that dominants were more likely to arch than were subordinates (see Introduction).

How did joiners and neighbours behave after the arch?

I analysed the relationship between the occurrence of the arch and subsequent interactions between a joiner and neighbours (full data: n = 544; band data: n = 93 for 48 individuals). I used separate GLMMs with binomial error structure; the subsequent behaviour of a joiner or neighbours was used as the dependent term, and the occurrence of the arch was an independent term. Whether the joiner behaved aggressively was set as a dependent term to test the hypothesis that performance of the arch would increase subsequent aggressive behaviour.

To investigate whether performance of the arch increased behavioural responses by neighbours, I conducted three separate GLMMs with binomial error structure. These GLMMs compared the probability of two categories: aggression or inaction (full data: n = 465; band data: n = 51 for 30 individuals); escape or inaction (full data: n = 386). As mentioned above, my observational method might have overestimated the behavioural response by neighbours. Nevertheless, this overestimation would be unlikely to seriously affect the analyses for the following reasons. First, the behavioural reaction was overestimated in both comparisons (i.e., after the arch vs. no arch); therefore, the effect of overestimation would cancel out. Second, the occurrence of the behavioural response was potentially positively associated with the number of neighbours. To test this possibility, I set the number of neighbours as an additional independent term. I did not observe significant effects of the number of neighbours (P = 0.359, 0.163, 0.187), suggesting that this possibility was unlikely.

Even if I found a significant increase in aggression or escapes by neighbours, it might be that neighbours responded not to the arch *per se* but to the joiner's aggression after the arch. To test this possibility, I conducted further GLMs on data in which joiners did not perform the arch. Joiner aggression (whether the joiner performed aggression) was set as an independent variable. Whether a neighbour performed aggression (n = 360) and whether a neighbour escaped (n =308) were set as dependent variables. I did not conduct the same analyses on band data because of the small sample size.

2.3 RESULTS

Which factors affected performance of the arch? (1) Unit level analysis

Answers: the number of neighbours, singleton or not, and the presence of adults

The analysis at the unit level using the full data revealed significant effects of the number of neighbours, unit composition, and the presence of adults in a unit on the likelihood of a joining bird performing an arch display (Table 2.1a). First, the number of neighbours positively affected performance of the arch (Figure. 2.3). Second, single joiners were more likely to perform the arch than were families or pairs, but the arch performance did not significantly differ between families and pairs (Figure. 2.1). Third, units including at least one adult were more likely to perform the arch than were units including only non-adults (i.e., sub-adults). Flock size did not affect performance of the arch.

On the other hand, the unit level analysis using banded individuals indicated that the above variables were not significantly related to performance of the arch (Table 2.1b). In this analysis, testing the effect of the presence of adults in a unit was not possible due to the small sample size of banded non-adults (n = 2).

Which factors affected performance of the arch? (2) Individual level analyses

Answers: adults or not, sex, and the number of neighbours

Adults performed the arch more frequently than did individuals of other age categories (Figure. 2.2a). The proportions of cases for which the arch was observed significantly differed among adults (28.4%, 179/631), sub-adults (4.5%, 2/44), and juveniles (0.0%, 0/137) (n = 821, Fisher's exact probability test, $P < 0.01$). In addition, significant differences were observed between adults and sub-adults (Fisher's exact probability test, $P < 0.01$) and between adults and juveniles (Fisher's exact probability test, $P < 0.01$), but not between sub-adults and juveniles (Fisher's exact probability test, $P = 0.058$).

Analyses at the individual level indicated that both sex and the number of neighbours affect performance of the arch (Table 2.2a). A GLMM using the full data revealed that multiple factors predicted the occurrence of the arch. First, males performed the arch more frequently than did females (males: 52.3%, 34/65; females: 20.3%, 12/59) (Figure. 2.2b). Second, individuals were more likely to perform the arch when they joined a large number of neighbours, similar to tests at the unit level (Figure. 2.3). In contrast, flock size and the difference between families and pairs did not affect the frequency of the arch. The results of the analysis of data involving banded individuals were very similar to those using the full data (Table 2.2b). A larger number of neighbours led to an increased frequency of the arch, similar to tests with full data (individual mean ± SE; performing the arch: 2.8 ± 0.3, not performing the arch: 1.8 ± 0.1). Males (30.9% ± 8.4%) tended to perform the arch more frequently than did females (18.7% ± 6.9%), although this difference was not significant. Finally, flock size (performing the arch: 68.1 ± 9.6, not performing the arch: 74.8 ± 5.7) and the difference between families and pairs (family: 27.2% ± 7.5%, pair: 19.6 ± 7.3%) did not affect the occurrence of the arch.

How did joiners and neighbours behave after the arch?

Answers: Joiners behaved aggressively and neighbours reacted to the joiners.

As mentioned in the Methods section (Data collection, vii), subsequent behaviour of joiners included aggressive behaviours, foraging, walking, standing, preening, and resting, while other types of behaviour (e.g., interactions within a unit) were not observed. Performance of the arch predicted the occurrence of subsequent aggressive behaviours by joiners (GLMM; b ± SE = 11.771 ± 1.404, $z = 8.381$, $P < 0.01$) (Figure. 2.4). The probability of aggression by a joiner was higher when joiners performed the arch (75%, 113/150) than when they did not (10%, 36/394). The analysis of band data also yielded the same results (performing the arch: 88.3% ± 7.6%, not performing the arch: 12.2% ± 4.1%, GLMM; b ± SE = 3.715 ± 0.697, $z = 5.328$, $P < 0.01$).

The performance of the arch also affected the behaviours of neighbours (inaction or aggression: GLMM; b ± SE = 7.364 ± 1.157, $z = 6.357$, $P < 0.01$; inaction or escape: GLMM: b ± SE = 7.830 ± 2.650, $z = 2.955$, $P = 0.031$) (Figure. 2.5). Behavioural responses (i.e., aggressive behaviours and escape) by neighbours were more likely to occur when joiners performed the arch (aggression: 45%; 61/137, escape: 26%; 36/137) than when they did not (aggression: 16%; 59/369, escape: 1%; 5/369). The band data yielded the same results, in that behavioural responses by neighbours occurred more frequently when cranes performed the arch (80.5% ± 10.0%) than when they did not (16.3% ± 5.4%). These results were confirmed in the inaction or aggression dataset (GLMM; $b \pm \mathrm{SE} = 4.465 \pm 1.201$, $z = 3.719$, $P < 0.01$), but the inaction or escape dataset could not be analysed due to the small sample size ($n = 39$).

It is possible that the behavioural reactions by neighbours listed above were caused by the joiners' aggression, but not by the joiners' arch (see Methods). However, analyses of full data in which the arch was not observed showed neither significant effects of the joiner's aggression on neighbours' aggression (GLMM; $b \pm \mathrm{SE} = 1.141 \pm 2.021$, $z = 0.565$, $P = 0.572$) nor neighbours' escape (GLMM; $b \pm \mathrm{SE} = 2.600 \pm 3.102$, $z = 0.838$, $P = 0.402$). Therefore, the behavioural reactions by neighbours were not a reaction to the aggression by joiners.

2.4 DISCUSSION

Our results support the idea that the arch display in the red-crowned crane serves as a functional signal of threat intentions to neighbouring individuals. As predicted, both motivation and strength were positively associated with performance of the arch (see Introduction). Supporting these predictions, we found that the arch was used for two signalling purposes; one reflected the degree of motivation for possible competition, and the other reflected individual strength; i.e., physical ability of competitive interactions. The analysis at the unit level (Table 2.1a) indicated that singletons were more likely to arch than were families or pairs, and units including adults arched more frequently than did units including only non-adults. The analyses at the individual level (Table 2.2) suggested that within pairs or family units, dominant individuals (adults rather than non-adults, and males rather than females) arched more frequently. In terms of the social context, a higher number of neighbours (used as an indicator of local competition) was associated with an increased likelihood of performing the arch (Tables 2.1, 2.2). In contrast, flock size did not affect performance of the arch. These results suggest that local competition is a more important determinant of arch performance than overall competition (flock size). This also highlights the fact that the arch is directed toward immediate neighbours and not distant individuals within a flock.

Contextual analyses supported the view that the arch is an honest signal of willingness to engage in aggression. Joiners behaved more aggressively when joiners performed the arch than when they did not, indicating that the arch functions as a signal of impeding aggression. At the same time, aggression by neighbours was more frequent after the joiners arched than when they did not. These results clearly refute the alternatively hypothesis that the arch is a ritualized display for avoiding the occurrence of aggression. Neighbours were more likely to escape when joiners performed the arch than when they did not. Note that this result supported both the avoidance of aggression hypothesis and the honest signal hypothesis. Given that behavioural reactions by neighbours would also depend on the individual relationship between the joiner and neighbours (e.g., the difference in motivation or relative strength between two individuals), this result is not powerful enough to distinguish between the two hypotheses.

Based on these results, I conclude that the arch display signals a threat intention to competitors. Note that the arch itself is not aggression, but rather an honest signal of a precursor to aggression. In our dataset, aggression followed the performance of the arch in 75% of cases (see Results), suggesting that the arch does not always lead to aggression. The arch may have functions other than signalling threat intentions to potential competitors. For example, the arch is one behavioural element of the pair dance (Masatomi & Kitagawa, 1975) and might be used in courtship when joining events occur. In addition, pairs occasionally joined a flock as individuals, and in such cases, the arch may be used to communicate an arrival to a partner. However, courtship behaviour and other interactions within a unit were not observed after the arch (see Results), and the main response of neighbours involved aggressive or escape behaviour. These observations conflict the hypothesis that the arch was used for within-pair or within-family communication. Another possibility, which partially overlaps to the avoidance of aggression hypothesis, is that this ritualized display soon after a reunion not only reduces the occurrence of aggression, but also strengthens social bonds. This greeting hypothesis has been confirmed in mammals (e.g., Smith et al., 2011). However, this idea is not consistent with the following facts. The arch was followed by aggression toward other individuals, and neighbours also reacted aggressively. Moreover, affiliative interactions by joiners have never been observed. The frequent occurrence of escape behaviours by neighbours after the arch had been performed was superficially in line with this hypothesis. As discussed above, however, this result is too weak to tease the hypotheses apart; the same pattern is predicted under the hypothesis that the arch represents an honest signal of willingness to engage in aggression. Therefore, this hypothesis is less likely to explain the arch in this species.

Previous studies in birds have documented many examples of ritualized signals during aggressive encounters (see review by Hurd & Enquist, 2001). However, these studies mainly focused on passerines (Hurd & Enquist, 2001); relatively few studies have been conducted in non-passerines (but see Kraaijeveld & Mulder, 2001). There is great potential to advance our knowledge of fission-fusion systems in birds by introducing recently developed methodologies and socio-ecological perspectives (Silk et al., 2014). In particular, the relationships between ritualized displays and fission-fusion systems have been less frequently studied. My study has filled these gaps by demonstrating that cranes, similar to passerines, have ritualized functional displays that convey threat intentions to potential competitors. One unique characteristic is that the necessity of signalling when joining a flock is higher under fluid fission-fusion dynamics than in stable social structure. When fission-fusion occurs rather frequently and social associations are fluid, dominance relationships will not be clearly established and the joining display becomes critical to the flock. Moreover, because individuals need to renew or assess relative dominance relationships among flock members in highly fluid fission-fusion societies, it is believed that individuals must signal their strength and motivation when they join (Aureli et al., 2008). Another unique characteristic is the importance of visual/physical display within a fission-fusion system. Acoustic signals are useful for species with territories in which interactions among neighbours occur over long distances. In contrast, in species like cranes with highly fluid fission-fusion grouping, individuals belonging to the same unit regularly interact with different local competitors. Therefore, cranes may instead rely on visual signals, which can only be transmitted to the receivers over short distances within which they can see signals. Non-passerines such as cranes do not have sophisticated song-like acoustic signals comprising multiple phrases; therefore, behavioural displays may be more important to cranes than to passerines. Birds may use other visual signals such as a ‘badge of status’; i.e., plumage, which is believed to correlate with individual strength (Senar, 2006), although whether red-crowned cranes have such badges of status remains unclear.

The degree of fission-fusion dynamics could affect the form and characteristics of signals. In addition to interspecific differences, variation within the fission-fusion system can produce within-species variation. That is, the degree of fission-fusion can affect dominance relationships among flock members and the degree of resource competition and vice versa (Aureli et al., 2008; Silk et al., 2014). This social flexibility provides new insights about the forms and functions of signals. In terms of dominance, members of highly fluid fission-fusion systems must renew their relative dominance relationships by signalling their resource holding potential (RHP) or motivation when fusion occurs (Aureli et al., 2008). However, few studies have explored this topic in birds with fission-fusion dynamics (Silk et al., 2014). The finding that dominance affects performance of the arch provides a rare example of an often-overlooked relationship between social signals and fission-fusion dynamics. One special feature of red-crowned cranes is that they have a long lifespan among birds (life expectancy is about 15 years) (Masatomi & Masatomi, 2007). Therefore, past interactions with competitors across different seasons or years might affect dominance relationships and consequently performance of the joining display.

In conclusion, the arch, a ritualized joining display in the red-crowned crane, is an honest signal of willingness to engage in aggressive behaviours. Thus, my study provides the most detailed quantitative analysis of a joining display in non-passerines, as well as an example of the value of a contextual analysis that considers sequences of different types of behaviour in birds. My study shows the function of signals within fission-fusion dynamics in birds. As discussed, fission-fusion dynamics represent a continuum, both within and among species, according to the strength and stability of social association (Aureli et al., 2008; Silk et al., 2014). Future studies might investigate how birds in this fission-fusion continuum assess and update information about others upon reuniting. Likewise, the necessity to advertise one’s own strength soon after reunion may also covary along continuum. Whether/how the continuum is associated with the frequency and intensity of signals in birds, remains to be examined. Such studies will contribute to our understanding of the role of animal communication in fission-fusion dynamics.

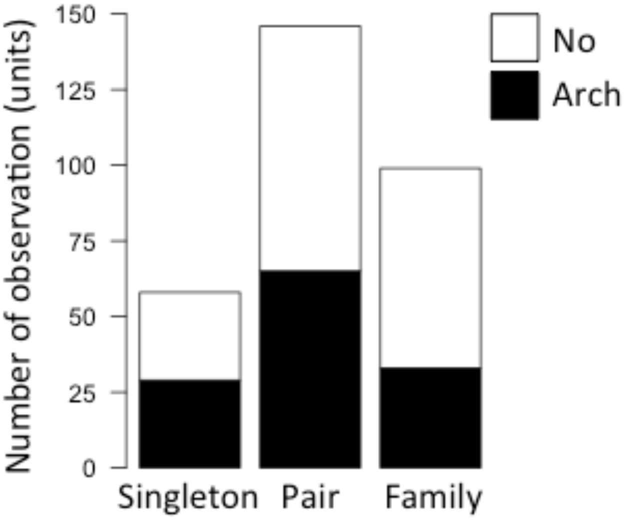

Figure 2.1 Effect of unit composition (classified as singletons, pairs, or families) on performance of the arch, with singletons being more likely to perform the arch compared to pairs or families at the level of units.

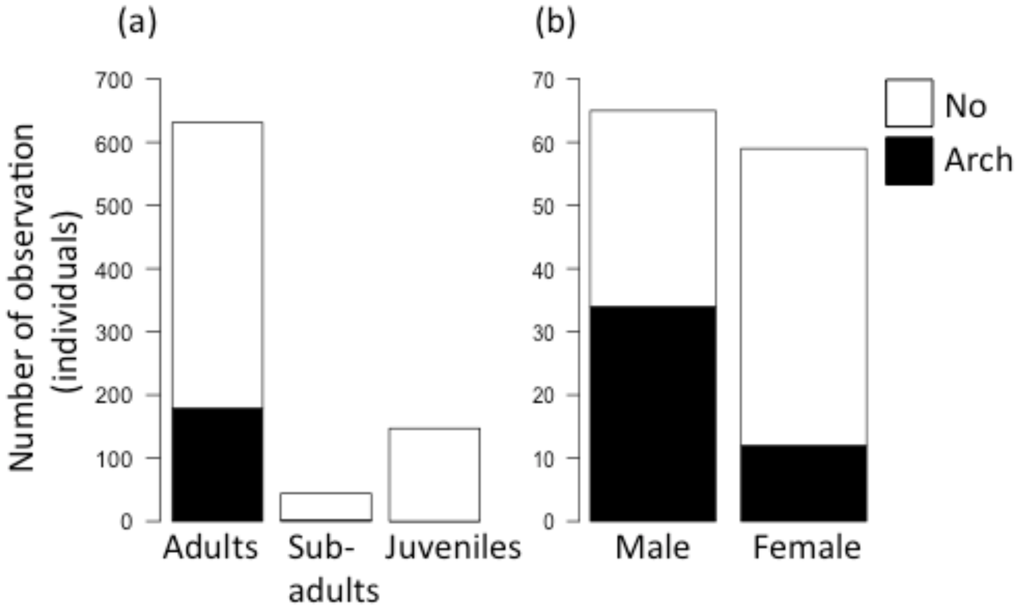

Figure 2.2 Effect of age (a: adults, sub-adults, or juveniles) and sex (b: males vs. females) on performance of the arch.

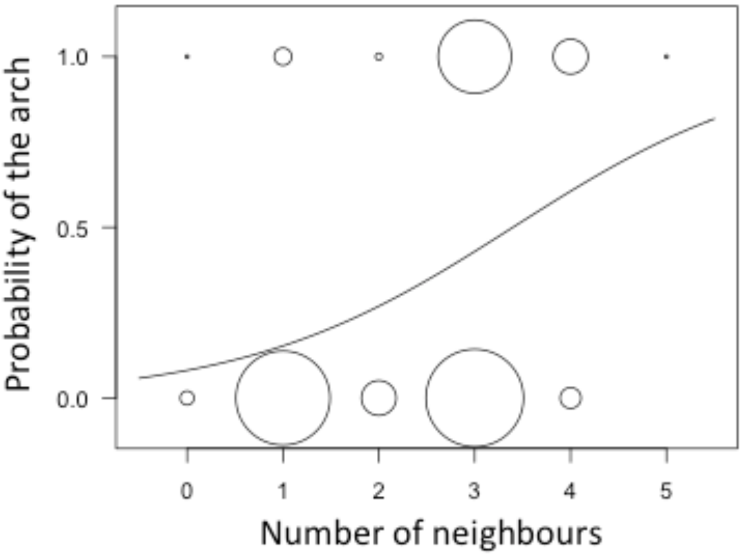

Figure 2.3 Relationship between number of neighbours and occurrence of the arch. Joiners were more likely to perform the arch as the number of neighbours increased. The size of circles corresponds to a number of data (range: 1 to 27) in each case.

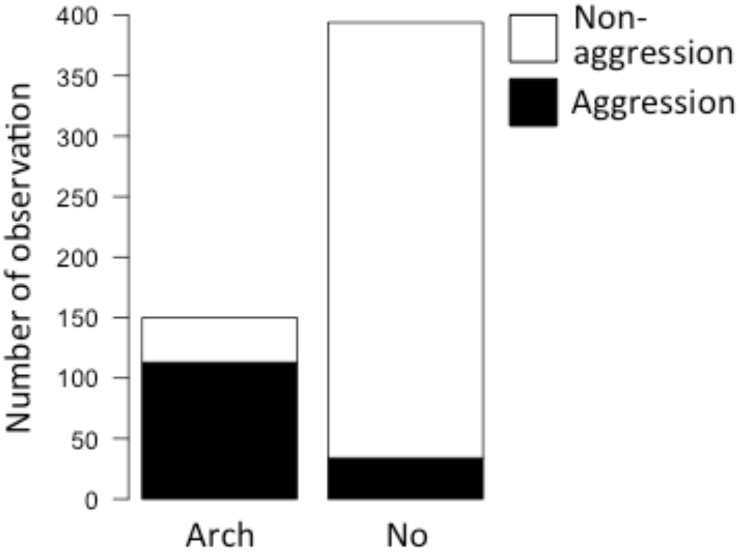

Figure 2.4 Effect of the arch display on subsequent aggression by joiners, with joiners being more likely to behave aggressively when they performed the arch than when they did not.

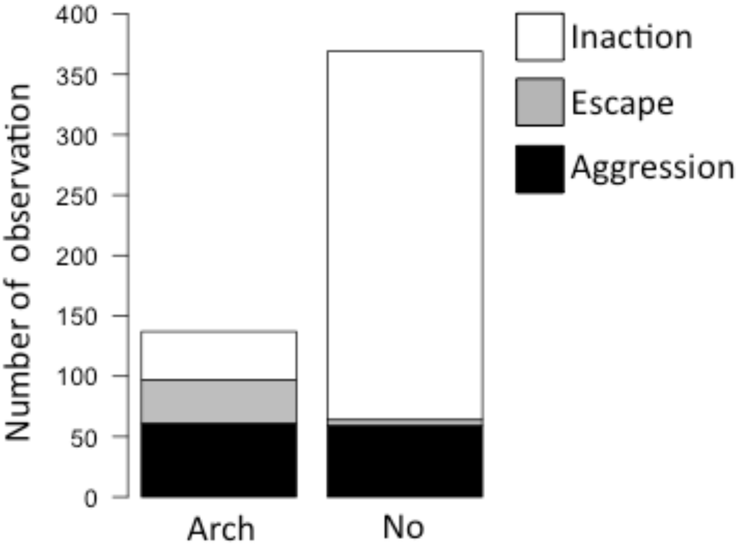

Figure 2.5 Behavioural reaction (classified as aggression, escape, or inaction) by neighbours when joiners arched or did not arch. Neighbours were more likely to display reactions when joiners performed the arch than when they did not.

Table 2.1 Variables affecting the occurrence of the arch at the unit level

a. Full data

Independent terms remained in the final model	*b*±SE	*z*	*P*
(Intercept)	-0.608±0.376	-1.614	0.11
Num. of neighbours	0.541±0.113	4.765	<0.001**
Type		$\chi^2 = 8.886$	0.012*
singleton > pair	0.722±0.359	2.011	0.044*
singleton > family	1.134±0.387	2.929	0.003**
pair = family	-0.412±0.287[a]	-1.436	0.15
The presence of adults in a unit (present > absent)	2.656±1.110	2.392	0.017*
Excluded independent terms	*b*±SE	*z*	*P*
Flock size	0.0002±0.0030	0.080	0.94

[a] estimate of b ± SE when the effect of the right side was set to 0.

GLM, **<0.01, *<0.05.

b. Data for banded adults

Independent term	*b*±SE	*z*	*P*
(Intercept)	-32.989±29.745	-1.109	0.27
Num. of neighbours	15.373±12.716	1.209	0.23
Type		χ^2 =3.726	0.16
singleton = pair	29.970±31.935[a]	0.938	0.35
singleton = family	24.069±33.297[a]	0.723	0.47
pair = family	1.208±21.008[a]	0.058	0.96
Flock size	-0.174±0.250	-0.697	0.49

[a] estimate of *b* ± SE when the effect of the right side was set to 0.

GLMM (the identity of individuals was set as a random term)

Table 2.2 Variables affecting the occurrence of the arch at the individual level

a. Data for sex-identified adults

Independent terms remained the final model	*b*±SE	*z*	*P*
(Intercept)	-16.660±4.235	-3.934	<0.001**
Sex (male > female)	8.013±2.187	3.664	0.002**
Num. of neighbours	3.721±1.304	2.853	0.004**
Excluded independent terms	*b*±SE	*z*	*P*
Type (pair = family)	-1.621±3.337[a]	-0.486	0.63
Flock size	0.056±0.126	0.446	0.66

b. Data for banded adults

Independent terms remained in the final model	*b*±SE	*z*	*P*
(Intercept)	-6.729±1.667	-4.037	<0.001**
Num. of neighbours	1.928±0.556	3.465	0.0005**
Excluded independent terms	*b*±SE	*z*	*P*
Sex (male > female)	1.843±0.969	1.902	0.057
Type (pair = family)	0.564±0.885[a]	0.637	0.52
Flock size	-0.005±0.010	-0.454	0.64

[a] estimate of b ± SE when the effect of right side was set to 0.

GLMM (the identity of individuals was set as a random term), **<0.01, *<0.05.

Chapter 3. Duet displays in a flock

3.1 INTRODUCTION

Coordinated vocal displays play critical roles in animal communication, especially within mated pairs or among social partners (Bradbury & Vehrencamp, 2011). These displays are used in both sexual and social contexts and are seen in various animals (e.g., bush cricket *Ancistrura nigrovittata*: Dobler et al., 1994; magpie-larks *Grallina cyanoleuca*: Hall, 2000; black-fronted titi monkeys *Callicebus nigrifrons*: Caselli et al., 2015). Among these, avian vocal duets have been intensively investigated (reviewed by Hall, 2004, 2009; Dahlin & Benedict, 2014). Duets are defined as “joint acoustic displays where two birds coordinate their songs with a degree of temporal precision” (Hall, 2004). In some species such as black swans (*Cygnus atratus*), duets are usually accompanied by ritualised body movements; therefore, duets in such species are considered to be multimodal coordinated signals including both visual and acoustic components (Kraaijeveld & Mulder, 2002).

Three major hypotheses about the functions of duets have been proposed (reviewed by Hall 2004, 2009): 1) joint resource defence (to serve a pair’s cooperative defence against other competitors), 2) mate guarding (to defend the mated status of a partner against potential competitors of the same sex), and 3) pair bond maintenance (for contact and ensuring reproductive synchrony between males and females). Recent detailed studies have shown that avian duets have multiple situation-dependent functions within the same species (Logue, 2007; Marshall-Ball et al., 2006; Mennill & Vehrencamp, 2008); therefore, these hypotheses are not mutually exclusive. For example, duets can act as signals to both neighbouring competitors (joint resource defence) and one’s mate (mate guarding and pair bond maintenance) simultaneously

(Hall, 2004).

Similar to birdsong, duets sometimes overlap with the vocalisation of other individuals (Masatomi et al., 1999; Maynard et al., 2012). Although many studies have focused on the overlap of male songs for territorial defence or mate choice, it is still controversial whether song overlapping is accidental (Searcy & Beecher, 2009) or has functional meanings (Helfer & Osiejuk, 2015; Naguib & Mennill, 2010). Some studies have suggested that song overlapping is a functional signal that reflects the identities or competitive abilities of the individuals involved. For example, long-tailed manakins (*Chiroxiphia linearis*) change overlapping responses depending on the type of competitor: they avoid overlapping with songs of their neighbouring competitors, but overlap with those of unknown competitors (Maynard et al., 2012). Another study also showed that social rank negatively affected the performance of behavioural responses towards song overlapping by intruders in territorial defence (black-capped chickadee, *Poecile atricapillus*: Mennill & Ratcliffe, 2004).

Duet studies in birds have been biased towards limited species and specific contexts. Regarding species, many studies have been conducted on songbirds or birds that breed in tropical regions (Dahlin & Benedict, 2014). In contrast, there have been few studies on non-songbirds or birds from temperate regions (Kraaijeveld & Mulder, 2002). Regarding context, many studies have focused on duets in territorial species (Hall, 2004), but few quantitative studies have focused on how those species perform duets in a flock (Arrowood, 1988). Some bird species such as cranes perform duet displays (DDs) both when a pair establishes a territory and when a pair stays in a flock. The duet and accompanying displays directed to competitors may play important roles in the latter case, particularly in fission-fusion social dynamics. In a fission-fusion society, both the size and the group membership of competitors frequently vary by the successive joining (fusion) and leaving (fission) of a group (Aureli et al., 2008; Silk et al., 2014). Flexible membership in a flock changes the degree of flock-level or local competition, and it decreases the predictability of the behaviours of potential competitors. Related to this point, previous studies have been restricted to duets for territorial defence (Hall, 2009), and few studies have investigated duets for defending other resources such as food (Kraaijeveld & Mulder, 2002). Food and territory are fundamentally different as the former is sharable among individuals and fluctuates in its availability over time, while the latter is not sharable and is fixed with regard to nest location over time.

As such, the investigation of duets in less-studied species and broad contexts should deepen our understanding of duet signals and expand our knowledge of how animals use them to maintain and/or boost their access to sharable resources. The red-crowned crane (*Grus japonensis*) is suitable for analysing DDs performed in fission-fusion flocks. First, this species performs many ritualised displays in order to signal to competitors (Masatomi & Kitagawa, 1975; Takeda et al., 2015). Those DDs contain "unison calls", a successive chorus lasting a maximum of 45 seconds, which is often seen in situations involving competition for food (Masatomi et al., 1999; Klenova et al., 2008; video.1). At the start and end of a DD, the individuals in a pair perform threat displays such as a "threat walk" (i.e., a display that cranes exaggerate by slowly taking large steps and stretching their necks vertically) (Mastomi & Kitagawa, 1975). Therefore, DDs are composed of both visual and vocal components. Second, cranes form a fluid fission-fusion flock during winter (Johnsgard, 1983). Compared with territorial songbirds in which the same neighbours repeatedly interact, cranes have a high possibility of interacting physically or visually with potential competitors because of their fission-fusion grouping style (Aureli et al., 2008). Thus, it is possible to analyse how the variation in flock size affects the performance of DDs in fission-fusion flocks. Finally, the acoustic structure of each duet differs between pairs (Klenova et al. 2008); therefore, DDs can be an important signal for competitors by signalling pair identities. Masatomi et al. (1999) observed individually unidentified cranes in wintering flocks, and found that the total frequency of DDs was positively related to the number of units joining the flock. From this result, they proposed that DDs function as threatening behaviour. However, no systematic analyses of individually identified cranes have been conducted, and the behavioural consequences of DDs in terms of access to or the defence of resources (food) have been unclear.

To test the hypothesis that pair DDs function as joint resource defence within a flock, I addressed the following two questions.

Which social factors and contexts affect the frequency of DDs?

If a DD functions as joint resource defence, the intensity of competition would be predicted to affect the frequency of DDs positively. I tested this at two levels: flock and individual.

At the flock level, I examined predictors of the total frequency of DDs observed within a flock. In particular, I investigated whether flock size—a proxy of the intensity of within-flock competition—is positively associated with the total frequency of DDs. This is because within-flock competition is expected to increase as the flock size increases. Moreover, I investigated the effect of changes in flock size. In a fission-fusion system, the behaviour of newcomers can be relatively unpredictable for flock members compared with that of flock members who have been staying in the flock (Aureli et al., 2008; Takeda et al., 2015). Therefore, it was predicted that the number of individuals joining a flock would be positively associated with the total frequency of DDs.

Next, I analysed predictors of DD frequency at the individual level. Since DDs include loud vocalisations and can be perceived by all members of a flock, they can be a signal not for potential interactants in the local area, but for those throughout the flock. As mentioned above, the overlapping of signals may have functional meanings. Therefore, I separately analysed the predictors of DDs that were overlapped by the vocalisations of other pairs (overlapped DDs; video.2) and ones that were not (non-overlapped DDs; video.1). I predicted that the intensity of and change in within-flock competition (i.e., flock size and its difference) rather than local competition (i.e., the distance to potential competitors or aggression by these individuals) would be positively associated with the frequency of overlapped DDs by each pair. In addition, I predicted that within-flock competition would not be associated with the frequency of non-overlapped DDs because their frequency would be expected to depend on the membership of other competitors staying in the flock.

If a DD functions as joint resource defence, the individual composition of a unit is also predicted to affect the performance of DDs, independent of the effect of within-flock competition. It is supposed that families are more motivated to access food resources, presumably to care for their young, compared with pairs without any young (Alonso et al., 2004). As such, I predicted that families would be more likely to perform DDs than pairs.

Does the performance of DDs secure access to food resources?

If a DD functions as joint resource defence, it is predicted that the performance of DDs would secure access to food resources. Staying within a food-rich area was considered to reflect success in defending resources in this study. As mentioned above, it is supposed that families are more motivated to secure access to food than pairs without young. In addition, if pairs whose DDs did not overlap with those of others are relatively competitive, it is predicted that these pairs are more likely to succeed at resource defence than pairs whose DDs overlap with those of others. Social interactions with neighbouring individuals, which reflect their relative dominance relationships, can also affect the success of food defence. This leads to predictions that a higher frequency of aggression would increase the level of success in resource defence, but that of submission would decrease it.

3.2 METHODS

Data collection

Observations were conducted from 26 January to 1 March, 2014, from 09:00 to 16:00, by K.F.T. (totalling 25 days and approximately 1950 minutes). One session of observations lasted 30 minutes (n = 65).

At the start of a session, I recorded the following information.

i) The identities of all banded cranes within the food-rich area. These individuals were the targets of our observations and are hereafter called ‘target cranes’ (number of target individuals per session, mean ± standard deviation [SD]: 4.3 ± 1.3, range: 1–7).

ii) The unit composition of each target crane (categorised into three types: singletons, pairs, and families with one or two young; note that individuals that usually live in a pair or family unit occasionally separate) within the food-rich area.

iii) The distance between each target crane and the nearest other crane, except for its partner or family members. I regarded this as the degree of potential competition in the food-rich area. I measured this distance as the 'crane unit' (mean ± SD: 0.9 ± 0.2, range: 0.5–7); here, one 'crane unit' is the width of one crane: approximately 40 cm.

iv) The flock size of all cranes in the feeding station (including both the food-rich area and the non-food-rich area).

During the sessions, I observed the behaviours of all target cranes continuously at the same time. The observation of multiple individuals was possible without bias and oversight because (i) there was a good view with no obstructions, (ii) the recorded behaviours (see below) were conscious, and (iii) the target cranes moved only infrequently in the food-rich area. Even if these target cranes left the food-rich area, it was possible to observe and continue recording their behaviours. During one session, I recorded all bouts of the following behaviours by behavioural sampling methods (Martin & Bateson, 2007). During such observations, other behaviours such as courtship (i.e., dancing and mating) were not observed.

i) DD: a behaviour in which a pair coordinates threat walks and vocal displays with their wings and necks raised dorsally (Ellis et al., 1998; Mastomi & Kitagawa, 1975; Klenova et al., 2008). I also recorded whether each bout of DD overlapped with other individuals' unison calls (overlapped DD: mean ± SD: 0.1 ± 0.5, range: 0–5;

non-overlapped DD: mean ± SD: 0.3 ± 0.6, range: 0–4).

ii) Solo aggression: a behaviour in which an individual rapidly sticks its bill into a nearby opponent's body [i.e., 'bill stab' (Ellis et al., 1998), also called a 'forward peck' (Mastomi & Kitagawa, 1975); mean ± SD: 1.6 ± 1.2, range: 0–7].

iii) Submission: a behaviour in which an individual quickly distances itself from aggressive cranes or shows submissive behaviour towards them [i.e., 'cowering' (Ellis et al., 1998), also called 'neck-retracted submission' (Mastomi & Kitagawa, 1975); cranes shrink their body by curving their neck horizontally; mean ± SD: 0.3 ± 0.5, range: 0–3]. Submission was always performed after other competitors had performed solo aggression.

Since DDs and solo aggression were conspicuous behaviours, I also recorded these behaviours by all members (both banded and non-banded cranes) in the whole flock by all-occurrence methods (Altmann, 1974). Submissive behaviour in the whole flock was not recorded because it was inconspicuous and it was difficult to record all cases in the whole flock.

When the session ended, I recorded data on two variables.

i) Whether the target cranes were in the food-rich area.

ii) The flock size.

Data analysis

In total, I made 265 observations of target cranes in 64 observation sessions lasting 30 minutes each. The total number of banded cranes was 21 [the number of cases per banded individual, mean ± standard error (SE): 13.9 ± 2.6, range: 1–45]. The data were analysed using generalised linear mixed models (GLMMs). To avoid pseudo-replication, the identities of target individuals and the sessions were set as random variables in the GLMMs.

Which social factors and contexts affect the frequency of DDs?

In the analysis of DDs at the flock level, I conducted a GLMM (n = 60 sessions) featuring a Poisson error structure; the total frequency of DDs during each session was used as a dependent variable. Independent variables included the number of individuals joining a flock and the mean flock size. Throughout this study, the number of individuals joining a flock was calculated using the value of the flock size after a session minus the flock size before it (range: −91 to 56). Throughout this paper, mean flock size is defined as the mean of its values at the start and end of a session. I excluded four sessions in which the data of total DD frequency were incomplete.

In the analysis of DDs at the individual level, I conducted a GLMM (n = 221 for 14 individuals) featuring a Poisson error structure. I analysed the DDs that overlapped or did not overlap with others separately. I included the following as independent variables: unit composition of the target cranes (pair or family), the total frequency of others' aggression, the frequency of submission by the target individuals, the frequency of aggression by the target individuals, the total sum of their past reproductive success (the total number of offspring, mean ± SD: 1.9 ± 2.5, range: 0–8), the distance to potential competitors (crane unit), the number of individuals joining a flock, and the mean flock size. Throughout this study, the total frequency of others' aggression was calculated by the value of the frequency of aggression by all members of a flock minus the frequency of aggression by the target cranes. I excluded singletons (n = 30 observations) from the data because they could not perform DDs. I also excluded 14 observations of banded cranes for whom past reproductive success had not been recorded.

Does the performance of DDs secure access to food resources?

I analysed the relationship between the performance of DDs and the movement of the cranes (n = 265 for 19 individuals). I used a GLMM featuring a binomial error structure; whether target cranes stayed or had moved at the end of one session from the food-rich area was used as a dependent variable. Independent variables included the unit composition of target cranes (singleton, pair, or family), the frequency of DDs (not overlapped or overlapped) by the target cranes, the frequency of submission by the target cranes, the frequency of aggression by the target cranes, the distance from competitors, the number of cranes joining a flock, and the mean flock size. I reported the individual mean and SE of each probability that individuals stayed or did not.

3.3 RESULTS

Which social factors and contexts affect the frequency of DDs?

Answers: the number of cranes joining a flock, the mean flock size, and the unit composition.

At the flock level, the total frequency of DDs observed in each session was positively correlated with both the number of cranes joining a flock and the mean flock size (Table 3.1 and Figure 3.1).

At the individual level, the mean flock size was positively correlated with the frequency of overlapped DDs by the target cranes (Table 3.2a). Independently of these variables, the unit composition of the target cranes affected the performance of both overlapped and non-overlapped DDs (Table 3.2). Families were more likely to perform DDs than pairs without young (Figure 3.2). Other variables did not affect the performance of DDs (Table 3.2).

Does the performance of DDs secure access to food resources?

Answers: Yes, frequencies of non-overlapped DDs were positively related with the retaining of food access.

The frequency of three behaviours and the unit composition of the target cranes affected whether individuals could stay in the food-rich area during one session (Table 3.3 and Figure 3.3). Target cranes were more likely to stay in the food-rich area as the frequencies of non-overlapped DDs and aggression increased (individual mean ± SE; non-overlapped DDs, stay: 0.246 ± 0.060 bouts, leave: 0.122 ± 0.068 bouts; aggression, stay: 0.246 ± 0.121 bouts, leave: 0.095 ± 0.062 bouts). On the other hand, they were less likely to stay in the food-rich area as the frequency of submission increased (stay: 0.299 ± 0.093 bouts, leave: 0.537 ± 0.107 bouts). Families were more likely to stay than pairs or singletons, and there was no significant difference between pairs and singletons (the probability of staying; families: 76.8 ± 10.7%, pairs: 41.1 ± 10.9%, singletons: 14.7 ± 5.5%). The probability of staying was not affected by the frequency of overlapped DDs, the number of cranes joining a flock, the mean flock size, and the distance from competitors (Table 3.3).

3.4 DISCUSSION

The results obtained from this study support the hypothesis that DDs function as joint resource defence within a flock, but also reveal that their consequence depends on whether the DDs overlap with those of others. As predicted, both the number of joining individuals and the mean flock size were positively associated with the total frequency of DDs observed in each session in the analysis at the flock level (Table 3.1). This indicates that the intensity of and change in flock-level competition positively affected the performance of DDs by flock members.

At the individual level, the unit composition of target cranes affected the performance of both overlapped and non-overlapped DDs: families were more likely to perform DDs than pairs without young (Table 3.2). Families were more likely to stay in the food-rich area than pairs (Table 3.3). Given that families should be more motivated to access food resources than pairs, this result suggests that the motivation for accessing resources is one determinant of the performance of DDs.

I also found a difference between social factors affecting the frequencies of overlapped and non-overlapped DDs (Tables 3.2 and 3.3). The mean flock size positively affected the performance of overlapped DDs (Table 3.2), but was independent of the frequency of non-overlapped ones. In contrast to the result at the flock level, the number of cranes joining a flock was associated with neither the frequency of overlapped DDs nor that of non-overlapped ones. These results suggest that the performance of overlapped DDs was related to the mean intensity of competition, but not the change in competition. Individuals joining a flock often landed outside the food-rich area within a flock. Because my observations were focused on pairs staying in the food-rich area (i.e., the target cranes), these individuals might not have responded to individuals joining the flock by performing DDs. In contrast, some pairs outside the food-rich area had the possibility of interacting with these newcomers, whose behaviour was unpredictable, and might have needed to perform DDs in response. The independent variables regarding local characteristics (i.e., the distance from competitors and behaviours when interacting with local competitors) did not affect the performance of DDs (Table 3.2). The fact that DDs are composed of a loud acoustic signal fits the result that the DDs were directed at the flock as a whole, not at local members alone.

In addition, the frequency of non-overlapped DDs, but not that of overlapped DDs, was positively associated with the success of resource defence: target individuals were more likely to stay in the food-rich area as the frequency of DDs increased (Table 3.3). This result was confirmed after controlling for the significant effects of other types of social interaction (aggression and submission; Table 3.3).

These patterns suggest that the relative difference in competitiveness (e.g., social stature) determined the overlap by potential competitors; namely, DDs performed by pairs with low competitiveness overlapped with those of others. Each duet can signal the individuals' identities because the features of the duets have been shown to differ among pairs (Klenova et al., 2008). Therefore, according to the relative competitiveness between themselves and others, cranes might decide whether their DDs should overlap with those of others. These results have similarities with the pattern of song overlap, in which a signal is informative of an individual's level of competitiveness (Helfer & Osiejuk, 2015; Naguib & Mennill, 2010).

In this competitive situation, other hypotheses do not seem to fit the observed patterns. The mate guard hypothesis predicts that behaviours (or calls) by solitary individuals affect the performance of DDs. This is because an individual should react to solo behaviours by potential sexual competitors to prevent them from pairing with its partner or being usurped (Hall, 2004). However, my analyses show that single behaviours (i.e., aggression) were not related to the performance of DDs, which did not support this hypothesis. The observation period in this study did not include the mating season; therefore, defence against extra-pair mating, which forms part of the mate guard hypothesis, was not applicable to the social context associated with my observations. Another major hypothesis, the pair bond hypothesis, predicts that the performance of DDs is related to reproductive success. However, my analyses show that reproductive experience was not related to the performance of DDs (Table 3.2), suggesting that this prediction was not supported. In addition, neither hypothesis could explain the significant relationship between the performance of DDs and whether the individual stayed in the food-rich area. However, these hypotheses might be applied to DDs in other situations or seasons. For instance, it was supposed that pairs sometimes perform DDs at the end of dances for communication within a pair, and they also perform DDs to defend their territory or mate during the breeding season (Mastomi & Kitagawa, 1975).

Overall, this study provides one of the most detailed quantitative analyses of the performance of DDs in a flock of non-songbirds. The results provide a unique opportunity to compare the performance of duets in a flock and in a certain territory. The first identified similarity with earlier findings is that the duets contribute to resource defence both in this species (Table 3.3) and in territorial songbirds (Hall, 2009). Second, previous studies of territoriality using playback experiments showed that territorial pairs performed duets to songs of intruders (Hall, 2000). This is consistent with the finding that the total frequency of DDs by flock members is related to the number of joining cranes (Table 3.1). Therefore, the qualitative difference between territory and food as resources did not affect the performance of duets, especially in behaviours by competitors. It is suggested that this joint resource defence is common to these two kinds of resource. Territory is usually fixed over time and exclusive to neighbours. On the other hand, the amount of available food can change within a day and pairs cannot always monopolise it. However, the context or social factors did not vary in these different situations, and cooperative signalling to competitors occurred in all of these situations. This study also indicates that the cranes gave out functional joint signals to potential competitors, like tropical songbirds shown in previous studies (Logue, 2005).

The stability of membership in a flock may also be one of the most important factors affecting the performance of DDs. There have been few analyses of how unit composition determines the performance of duets. In contrast to the result that families were more likely to perform DDs than pairs without young, the number of chicks was previously shown to be negatively correlated with the performance of duets in black swans (*C. atratus*) (Kraaijeveld & Mulder, 2002). This may reflect the difference in grouping styles between cohesive fixed membership and flexible membership. In black swans, relative dominance relationships are established among pairs during the breeding season since social interactions usually occur among stable individuals. Therefore, swans with a high dominance rank (families with many chicks) may not need to perform duets to advertise their dominance. On the other hand, the membership of cranes in wintering flocks is flexible, and relative dominance relationships with potential competitors are not always established. Thus, cranes may need to perform

DDs to signal their motivation to defend resources. It is interesting that the stability of membership affects the necessity of performing DDs. To clarify this factor, future research should compare the frequency of DDs between two flocks that differ in the stability of dominance relationships in a group.

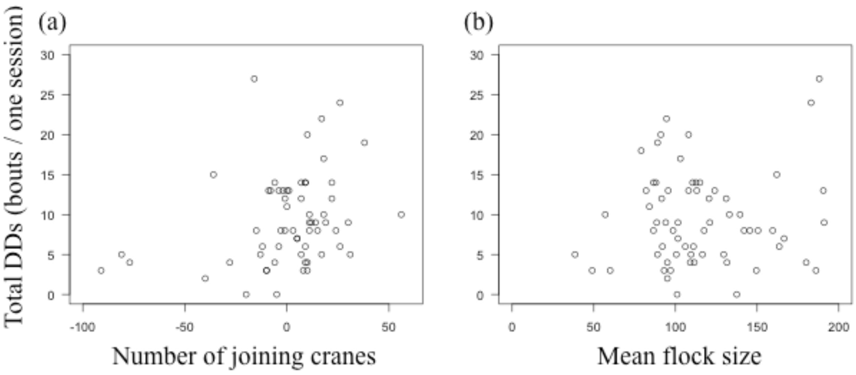

Figure 3.1 Relationships between the total frequency of DDs observed within a flock (bouts/session) and proxies of competition intensity [(a) the number of cranes joining a flock and (b) the mean flock size]. Each point indicates data from each session.

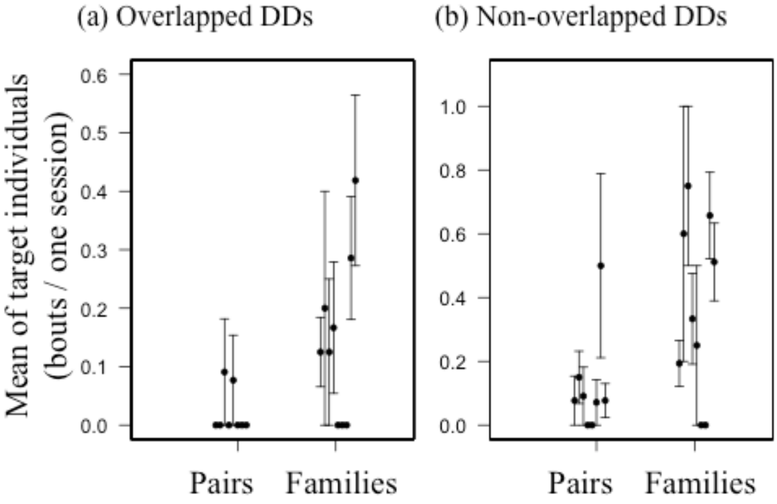

Figure 3.2 Relationships between unit composition (classified into pairs without young and families) and the frequencies of overlapped DDs (a) or non-overlapped DDs (b) of the target individuals. Each point indicates the mean of the behavioural frequency by each target individual during a session. Each bar indicates its SE. The vertical axis indicates the frequency (bouts/session) of each type of DD, while the horizontal axis indicates the unit composition (pairs or families).

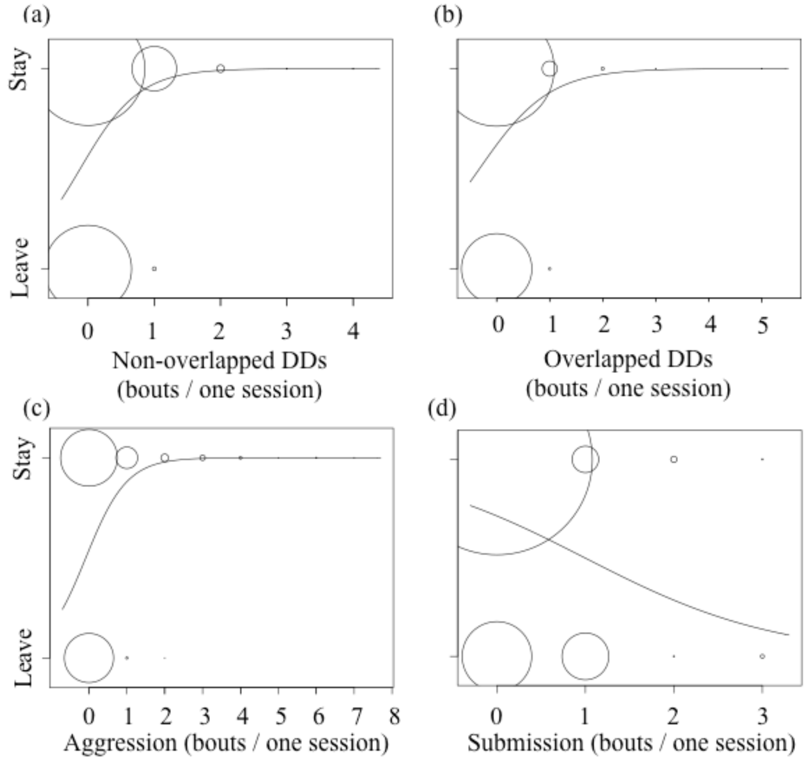

Figure 3.3 Relationships between four types of behaviour [(a) non-overlapped DD, (b) overlapped DD, (c) aggression, and (d) submission] by the target individuals and whether these individuals stayed in the food-rich area when the observation period ended. The size of the circle corresponds to the number of values (range: 1–152) in each case. The horizontal axis indicates the frequency of each behaviour by target individuals (bouts/session), while the vertical axis indicates the probability of staying.

Table.3.1 Variables affecting total frequency of DDs at the flock level.

Independent terms remained in the final model	b±SE	z	P
(Intercept)	1.759±0.15	11.746	<0.001**
The number of cranes joining to a flock	0.009±0.002	4.629	<0.001**
Mean flock size	0.004±0.001	3.195	0.001**

GLM, **<0.01, *<0.05.

Table 3.2 Variables affecting performance of DDs at individual level.

a. Overlapped DDs

Independent terms remaine the final model	*b*±SE	*z*	*P*
(Intercept)	-5.588±1.039	-5.377	<0.001**
Unit type (family > pair)	1.323±0.664	1.992	0.046*
Mean flock size	0.014±0.006	2.119	0.034*
Excluded independent terms			
Reproductive experience	-0.287±0.241	-1.192	0.233
Aggression by target cranes	0.021±0.138	0.150	0.880
Submission by target cranes	0.201±0.315	0.638	0.523
Total aggression by flock members	-0.015±0.042	-0.344	0.731
Distance with competitors	-0.220±0.176	-1.248	0.212
The number of cranes joining to a flock	0.002±0.009	0.258	0.796

GLMM (the identity of individuals and the sessions were set as a random term)

**<0.01, *<0.05.

b. Non-overlapped DDs

Independent terms remained in the final model	b±SE	z	P
(Intercept)	-2.242±0.322	-6.975	<0.001**
Unit type (family > pair)	1.31±0.368	3.561	<0.001**
Excluded independent terms			
Reproductive experience	0.091±0.105	0.867	0.386
Aggression by target cranes	-0.061±0.107	-0.568	0.570
Submission by target cranes	0.122±0.227	0.538	0.590
Total aggression by flock members	-0.024±0.024	-1.001	0.317
Distance with competitors	-0.019±0.115	-0.166	0.868
The number of cranes joining to a flock	0.005±0.005	0.965	0.335
Mean flock size	0.000±0.004	-0.123	0.902

GLMM (the identity of individuals and the sessions were set as a random term)

**<0.01, *<0.05.

Table 3.3 Variables affecting whether target individuals stayed or not within food-rich area during the session.

Independent terms remained in the final model	*b*±SE	*z*	*P*
(Intercept)	0.640±0.441	1.451	0.147
Unit type		$\chi^2 = 13.143$	0.001**
Family > pair	2.218±0.658	3.373	0.001**
Family > singleton	2.757±0.864	3.190	0.001**
Pair = singleton	0.539±0.771[a]	0.699	0.485
Non-overlapped DDs by target cranes	-1.784±0.648	-2.755	0.006**
Aggression by target cranes	-0.927±0.467	-1.986	0.047*
Submission by target cranes	0.652±0.318	2.053	0.040*
Excluded independent terms			
Overlapped DDs by target cranes	-0.689±0.899	-0.766	0.443
Distance with competitors	-0.063±0.206	-0.310	0.756
The number of cranes joining to a flock	-0.005±0.008	-0.664	0.506
Mean flock size	-0.009±0.006	-1.466	0.142

[a] estimate of *b* ± SE when the effect of the right side was set to 0.

GLMM (the identity of individuals and the sessions were set as a random term)

**<0.01, *<0.05.

Chapter 4. Structure of pair dances

4.1 INTRODUCTION

Coordinated displays play critical roles in social or sexual communication especially within mating pairs or social partners (review in Wachtmeister 2001). A form of mutual displays varies widely, ranging from a simple greeting ceremony to a complex dance including multiple behavioural elements. These displays are seen in many animals (e.g., messmate pipefish, *Corythoichthys haematopterus*: Sogabe & Yanagisawa 2008, wandering albatross, *Diomedea exulans*: Pickering & Berrow 2001, red-bellied titi, *callicebus moloch*: Moynihan 1966, blue-capped cordon-bleu, *Uraeginthus cyanocephalus*: Ota et al., 2015). Although many studies described behavioural forms of pair dances, to our knowledge, there have been only a few quantitative studies that analysed pair dances. One of the most detailed analyses was done in albatross (Pickering & Berrow 2001). This study analysed four transition matrices from their behavioural sequences: they are for male to male, female to female, male to female, and female to male transitions. This study showed that 115 of 632 kinds of observed transitions were shown to be statistically significant transitions by a modified chi-squared test, and it further showed that there were sexual differences in these transition patterns (Pickering & Berrow 2001). In this study, however, temporal association between males and females, which is believed to be one of important factors for animal communication (Brandbury & Vehrencamp 2011), have not been analysed.

For comprehensive understanding of the structure of pair dances, it is necessary to consider both transitions and temporal association among behavioural elements in studies of pair dances. Unfortunately there are no methodological frameworks that enable us to analyse these aspects at the same time. Therefore, it is required to combine multiple methods to analyse details of dance structure; such attempts will contribute to promoting our general understanding of mutual communication within a pair.

In this chapter, I analysed species-specific structure of pair dances in the red-crowned cane (see chapter 5 for the inter-pair variation of dances). In order to reveal detailed structure of pair dances, particularly their behavioural transitions and temporal association within a pair, I addressed three questions outlined below.

Do pair dances have a structured behavioural sequence?

I analysed whether a given behavioural element increased the probability that another particular behavioural element occurs subsequently, both within an individual and between partners. In addition, I analysed whether a given behavioural element by one partner increased the probability of synchronous occurrence of the same or another behavioural element by the other. These analyses tested the null hypothesis that the transition occurred at random without considering the temporal association between behavioural elements.

How are the same behavioural elements temporally associated between partners?

Temporal coordination of the same behavioural elements between mate partners is one of important parameters reflecting mutual communication within a pair (Brandbury & Vehrencamp 2011; Hall & Magrath 2007). Therefore, I analysed whether the same behavioural elements were temporally associated within a pair by introducing a new method (see Methods).

Is there sexual difference in pair dances?

I analysed sexual differences in the structure and rules of pair dances. This analysis aimed to clarify which sex played a leading role in a pair dance. Sexual difference, especially the cost of producing gametes or the role of parental care (Gowaty 1996), might affect their motivation to perform their dances and change their contents. If divorce or extra-pair mating occurs more than once in their life, it is beneficial for individuals to manipulate their partner to pay more reproductive cost than themselves (Wachtmeister, 2001). Indeed, previous studies showed that extra-pair fertilizations (EPF) occurred in socially monogamous birds that perform pair dances (EPF rate: 14-21 % in waved albatross, *Phoebastria irrorata* [Huyvaert et al., 2006], 4.4-11% in Sandhill Cranes, *Grus Canadensis* [Hayes, et al., 2006]). In addition, the different sexual role per se may affect characteristics of pair dances. For example, in territorial defense males mainly chase and attack intruders, and females support their partners by performing duet displays (Masatomi & Kitagawa, 1974). Previous studies showed that male behaviour triggered sexual behaviour of females (Adkins-Regan 2005). Therefore, males may be more likely to lead females in dances than vice versa.

4.2 **METODS**

Data collection

I used "behaviour sampling" (Martin & Bateson, 2007) by videotaping pair dances of banded cranes in the feeding stations. I checked positions of banded cranes every 30 minutes. When banded cranes showed a sign of starting dances or performed dances, I videotaped them.

During behavioural coding of video data, I classified pair dances into 14 types of behavioural elements based on the previous studies (Ellis et al., 1998; Mastomi & Kitagawa, 1975). The following are the list of these elements.

i) Bill-stab: a behaviour in which an individual rapidly stick its bill into its nearby partner's body without touching (Ellis et al., 1998; Mastomi & Kitagawa, 1975: "upright-peck").

ii) Bow: a behaviour in which an individual bends its bill down with stretching its neck. An individual sometimes opens its wings simultaneously (Mastomi & Kitagawa, 1975; Ellis et al., 1998: "Hoover" or "Neck-crane").

iii) Arch: a behaviour in which an individual curves its neck over its back with raising its wings up (Mastomi & Kitagawa, 1975; Ellis et al., 1998; see also Takeda et al., 2015).

iv) Kick: an aggressive behaviour in which an individual strikes its talon to its nearby partner with leaping up (Mastomi & Kitagawa, 1975; Ellis et al., 1998: "Jump-rake").

v) Leap: a behaviour in which an individual jumps up its body (Mastomi & Kitagawa, 1975; Ellis et al., 1998). Object-toss (i.e., crane throw tiny light things [e. g., snow] with leaping; Mastomi & Kitagawa, 1975; Ellis et al., 1998) is also included in this behaviour.

vi) Peck-ground: a behaviour in which an individual picks down with its bill or picks some objects (e.g., snow) up into the air (Mastomi & Kitagawa, 1975: Picking-up).

vii) Neck-moving: a behaviour in which an individual moves its neck with a vertically short step.

viii) Stoop: a behaviour in which an individual moves its body vertically with elevating its head (Mastomi & Kitagawa, 1975; Ellis et al., 1998: "Tuck-bob").

ix) Shaking: a behaviour in which an individual rapidly rotates its body with opening its beak largely and lifting its head (Ellis et al., 1998: "Gape").

x) Rush: a behaviour in which an individual runs with opening its wings (Mastomi & Kitagawa, 1975). Chasing its partner or others is also included in this behaviour.

xi) Turn: a behaviour in which an individual changes its direction to walk (Mastomi & Kitagawa, 1975)

xii) Duet displays (cf. Chapter 3).

xiii) Stand: remaining stationary, stretching their neck without performing any ritualized displays.

xiv) Walk: moving within the feeding stations without performing any ritualized displays.

Next, I coded the order and duration of all behavioral elements of both males and females from video data (see figure 4.1 for its example). Duration is the continuous time length of each state element. Minimum interval of the duration was 0.1 seconds.

Data analysis

I used 99 bouts (21 pairs) for answering the following questions. Except for analyses of sex differences, all data were pooled for investigating general characteristics of pair dances.

Do pair dances have a structured behavioural sequence?

This analysis considered all elements as an "event" and did not consider its duration or time interval between the successive behavioural elements. This means that information of particular behavioural elements with duration (neck-moving, stoop, shaking rush, turn, duet display, stand and walk) was simplified. I analysed five types of transitions: (i) ones from males to females, (ii) ones from females to males, (iii) synchrony between males and females, (iv) ones from a previous element to the next in males and (v) ones from a previous element to the next in females. I used residual analyses for investigating whether the observed frequency of a particular transition pattern was higher than the expected value calculated under the assumption of random occurrence. If the frequency of transitions were statistically higher than the expected frequency, these transitions were regarded as characteristic transitions or synchrony.

How are the same behavioural elements temporally associated between partners?

Since the first analysis did not take into account the time interval between elements, I conducted the second analysis by focusing on the temporal interval between elements in each pair. Note that this analysis did not consider duration of each element.

The aim of this analysis is to test whether the performance of a given element (X) by one individual (e.g., male) triggers the occurrence of the same element

(Y) by its partner (e.g., female). In order to do so, I defined two time periods: activation window and normal period (Figure. 4.2). The activation window is the time window during which we suppose element X activates the occurrence of element Y. It is defined as within T^* seconds since the last initiation of element X, where the supposed activation duration T^* was set a priori (see below). The total duration of activation window was denoted by T_{act}. I counted the number of element Y that was started within the activation window, which was denoted by N_{act}. As a result, the frequency of Y during the activation window of X, which we denote by P_{act}, can be calculated as

$$P_{\text{act}} = N_{\text{act}} / T_{\text{act}}.$$

Similarly, the normal period is defined as time other than activation window, and I denote its total duration by T_{norm} (Figure. 4.2). I counted the number of element Y that was started within the normal period, which was denoted by N_{norm}. As a result, the frequency of Y during the normal period of X, which I denote by P_{norm}, can be calculated as

$$P_{\text{norm}} = N_{\text{norm}} / T_{\text{norm}}.$$

Next, I calculated K, the degree that X activated the occurrence of Y. K was defined as

$$K = P_{\text{act}} / P_{\text{norm}}.$$

This parameter K is an index of temporal association between particular elements within a pair. In the case that X activated the occurrence of Y, P_{act} should be large compared to P_{norm}. Therefore, $K > 1$ indicates that the temporal association exists between X and Y. When X did not trigger or suppress the occurrence of Y, P_{act} should be equal to or less than P_{norm}, respectively. In such cases, K will be 1 or less.

To judge whether *K* significantly differs from 1 (accidental occurrence of X followed by Y), I conducted a likelihood ratio test for the following model. I assumed that element Y occurs at rate λ_{act} in the activation window but occurs at rate λ_{norm} in the normal period. The likelihood (*L*) of this model can be calculated as

$$L = e^{-\lambda_{\mathrm{act}} T_{\mathrm{act}}} \frac{\left(\lambda_{\mathrm{act}} T_{\mathrm{act}}\right)^{N_{\mathrm{act}}}}{N_{\mathrm{act}}!} \cdot e^{-\lambda_{\mathrm{norm}} T_{\mathrm{norm}}} \frac{\left(\lambda_{\mathrm{norm}} T_{\mathrm{norm}}\right)^{N_{\mathrm{norm}}}}{N_{\mathrm{norm}}!} .$$

The maximum likelihood estimates can be calculated as

$$\begin{aligned} \hat{\lambda}_{\mathrm{act}} &= P_{\mathrm{act}} = \frac{N_{\mathrm{act}}}{T_{\mathrm{act}}} \\ \hat{\lambda}_{\mathrm{norm}} &= P_{\mathrm{norm}} = \frac{N_{\mathrm{norm}}}{T_{\mathrm{norm}}} \end{aligned} ,$$

and the maximum likelihood is

$$\hat{L} = e^{-N_{\mathrm{act}}} \frac{N_{\mathrm{act}}^{N_{\mathrm{act}}}}{N_{\mathrm{act}}!} \cdot e^{-N_{\mathrm{norm}}} \frac{N_{\mathrm{norm}}^{N_{\mathrm{norm}}}}{N_{\mathrm{norm}}!} .$$

In contrast, in our null model I assume that $\lambda_{\mathrm{act}} = \lambda_{\mathrm{norm}} = \lambda$, meaning that there exists no difference in the rate of occurrence of element Y between the activation window and the normal period (i.e. K=1). The likelihood (L_0) of the null model can be calculated as

$$L_0 = e^{-\lambda T_{\mathrm{act}}} \frac{\left(\lambda T_{\mathrm{act}}\right)^{N_{\mathrm{act}}}}{N_{\mathrm{act}}!} \cdot e^{-\lambda T_{\mathrm{norm}}} \frac{\left(\lambda T_{\mathrm{norm}}\right)^{N_{\mathrm{norm}}}}{N_{\mathrm{norm}}!} ,$$

the maximum likelihood estimate is

$$\hat{\lambda} = \frac{N_{\mathrm{act}} + N_{\mathrm{norm}}}{T_{\mathrm{act}} + T_{\mathrm{norm}}} ,$$

and the maximum likelihood is

$$\hat{L}_0 = e^{-N_{\mathrm{act}}} \frac{T_{\mathrm{act}}^{N_{\mathrm{act}}}}{N_{\mathrm{act}}!} \cdot e^{-N_{\mathrm{norm}}} \frac{T_{\mathrm{norm}}^{N_{\mathrm{norm}}}}{N_{\mathrm{norm}}!} \cdot \left(\frac{N_{\mathrm{act}} + N_{\mathrm{norm}}}{T_{\mathrm{act}} + T_{\mathrm{norm}}} \right)^{N_{\mathrm{act}} + N_{\mathrm{norm}}} .$$

Therefore, the log-likelihood ratio statistic (θ) was calculated as

$$\begin{aligned}\theta &= 2\log\frac{\hat{L}}{\hat{L}_0} \\ &= 2\left[N_{\mathrm{act}}\log\left(\frac{N_{\mathrm{act}}}{T_{\mathrm{act}}}\right)+N_{\mathrm{norm}}\log\left(\frac{N_{\mathrm{norm}}}{T_{\mathrm{norm}}}\right)-(N_{\mathrm{act}}+N_{\mathrm{norm}})\log\left(\frac{N_{\mathrm{act}}+N_{\mathrm{norm}}}{T_{\mathrm{act}}+T_{\mathrm{norm}}}\right)\right]\end{aligned}.$$

It is known that θ asymptotically follows the chi-square distribution of 1 degree of freedom. Based on this fact I performed log-likelihood tests. In a similar vein, the confidence interval ($P < 0.05$) of the value of K can be calculated in the following way; the real number k is included in that confidence interval if the null hypothesis "H_0: $\lambda_{\mathrm{act}} = k\lambda_{\mathrm{norm}}$" is not rejected against the alternative hypothesis "H_1: λ_{act} and λ_{norm} can be any values", the condition of which can be written as

$$\begin{aligned}&\theta_k = 2\log\frac{\hat{L}}{\hat{L}_{0,k}} \\ &= 2\left[N_{\mathrm{act}}\log\left(\frac{N_{\mathrm{act}}}{kT_{\mathrm{act}}}\right)+N_{\mathrm{norm}}\log\left(\frac{N_{\mathrm{norm}}}{T_{\mathrm{norm}}}\right)-(N_{\mathrm{act}}+N_{\mathrm{norm}})\log\left(\frac{N_{\mathrm{act}}+N_{\mathrm{norm}}}{kT_{\mathrm{act}}+T_{\mathrm{norm}}}\right)\right] < \chi_1(1-0.05)\end{aligned}.$$

Solving this inequality with respect to k gives us the confidence interval.

I varied the supposed activation duration T^* continuously from 0.1 to 5s, and estimated K for each T^*. Rare elements (turn, kick and call) were excluded from this analysis because small sample sizes resulted in a large confidence interval and led to an inappropriate conclusion. Non-ritualized elements (walk and stand) were also excluded from these analyses because these elements were supposed to be non-functional signals.

Is there sexual difference in pair dances?

I examined sexual difference in behavioural elements in pair dances. I conducted analyses of GLMMs. Sex of individuals (males or females) was used as an independent variable in these analyses. To avoid pseudo-replication, identity of pairs, bouts and years were set as random effects in the GLMMs. I analysed the effects of two dependent variables: total length of dance elements and frequency of each element. The error structure of these analyses depended on the type of dependent variables: the analyses of total length of dance elements and frequency of continuous elements featured Gaussian error structure, and the analyses of frequency of counting elements featured Poisson error structure. Total length of dance elements was calculated by subtracting both the length of "walk" and "stand" from the length of total duration. The non-ritualized elements (walk and stand) were excluded from the analyses of frequency of elements. That was because these elements were supposed to be non-functional.

The peck-ground elements were also excluded from the analyses of frequency of elements because its analysis seemed to be incorrect; all *P* values in the results were extremely small compared with other analyses.

4.3 RESULTS

Do pair dances have a structured behavioural sequence?

Answers: Yes. Three behavioural elements were structured.

Three behavioural elements (i.e., bill-stab, bow, arch) were key patterns in transitions of pair dances (Figure. 4.3). Table 4.1 lists the transition patterns and synchrony whose frequency was higher than the expected values. Three frequencies of transition and synchrony between bill-stabs, bows, and arches were higher than expected. The frequencies of other transition or synchrony were not statistically different from the expected ones.

How are the same behavioural elements temporally associated between partners?

Answers: Part of elements was temporally associated.

Frequencies of seven elements (i.e., stoop, leap, rush, neck-moving, bill-stab, bow, and arch) increased immediately after the partner performed the same ones (i.e., when activation duration T^* was set as 0.1 seconds) (Figure 4.4). The estimated values of K differed between elements. In particular, three structured elements (bill-stab, bow, and arch) had larger values of K (5~50) than non-structured ones (stoop, leap, rush, and neck-moving) (K=1~4). In addition, there was sex difference in the association of elements within a pair; female arch was more likely to activate male's arch than vice versa. On the other hand, neither shaking nor peck-ground element was temporally associated between partners.

Is there sexual difference in pair dances?

Answers: Yes.

Males performed longer in the total length of dance elements than females (GLMM; b ± SE = 9.785 ± 2.496, $t = 3.920$, $P < 0.01$). The sexual difference depended on the type of elements (Table 4.2); the frequencies of bill-stab, kick, rush elements were higher in males than in females. However, the frequency of bow, leap, arch, rush, shaking, stoop, or neck-moving element did not differ between males and females.

4.4 DISCUSSION

My three results supported that pair dance had specific structure. First, a preceding element affected the occurrence of the subsequent element in behavioural transition in males and females, and in transition and synchrony within a pair (Figure 4.3, Table 4.1). It was shown that three behavioural elements (bill-stab, bow and arch) were key elements in their transition between partners. Second, seven behavioural elements showed temporal association within a pair, and other elements did not (Figure 4.4). This result indicated that individuals decided which behavioural elements to perform next according to partner's behavioural elements. Taken together, I conclude that both intervals of elements and behavioural sequences are important signals in their dances. Finally, males performed longer in the total length of dance elements than females did (Table 4.2). Frequencies of three elements were higher in males than in females. Therefore, this result suggested that males were more active than females. It implied males played a leading role in pair dances. This was the first study showing sex difference in pair dance in birds. However, the frequency of other elements did not differed between males and females. This indicated that both males and females equally needed to perform these aspects of pair dances.

The finding of this chapter also implied that pair dance plays an important role in mutual communication within a pair. In fact, my results showed there were temporal association between males and females in some behavioural elements. It indicated that there were behavioural responses within a pair. Therefore, other hypotheses for pair dances did not fit these results. First, the previous study claimed that dances are not functional signals, but classified them as play behaviours according to definitions of "play" (Dinets 2013). This was not supported by these results. Spontaneous or voluntary behaviour, which was one of the criteria for play (Burghardt 2005), did not fit these responses between males and females observed in our data.

Second, the hypotheses that pair dance are for communication with their chicks or neighbouring competitors was rejected. That was because it also did not explain the behavioural response within a pair.

Although the crane is a monogamous species in which both males and females equally care for their chicks, my study suggested that there is sexual difference in pair dance. This result indicated that reproductive efforts might be different between males and females. The frequency of pair dances was highest before the breeding season (Masatomi & Kitagawa, 1975). Therefore, males might stimulate female reproductive preparations such as ovulation by performing pair dances.

The analyses on this chapter are based on pooled data because my aim was to examine species-specific features of pair dances in the red-crowned crane. However, it was that dance structure varied among pairs and even among bouts of the same pair. Such variation had not been analysed in this chapter, but will be conducted in the next chapter (cf. Chapter 5).

The studies also provided more comprehensive understandings of pair dances compared than previous studies. The previous study analysed only behavioural transition in albatross (Pickering & Berrow 2001). My new temporal analyses found that there was significant behavioural association within a pair, which was not identified by the transition analysis only. In addition, the transition analysis clarified only whether transitions were significantly frequent or not, but the temporal analysis additionally revealed intensity of association between two behavioural elements in a quantitative manner via the index *K*. Therefore, it became possible to compare two different transitions by the temporal analyses, even if both of them were shown to be characteristic patterns. For example, arch elements were more likely associated within pairs than bow or bill-stab elements (Figure 4.4). It is interesting to apply my temporal analyses to other species that perform pair dances, such as albatross and grebes. These future studies will unveil universal rules determining the structure of pair dances beyond taxonomic groups. These detailed analyses will give us a deep understanding of mutual communication within a pair.

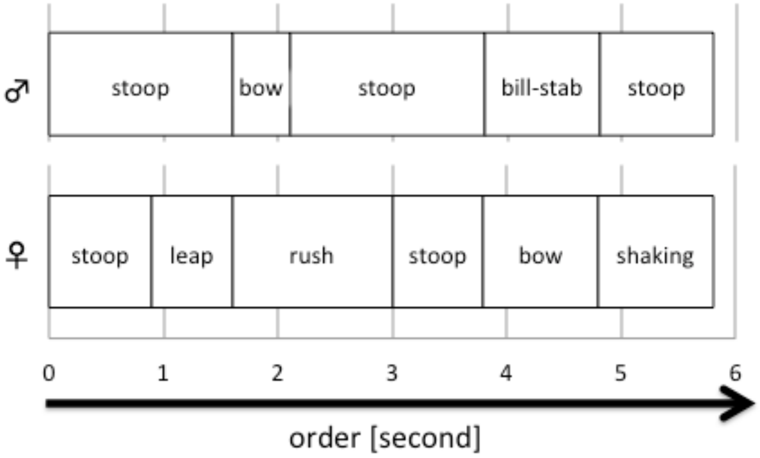

Figure 4.1 the example of sequential data

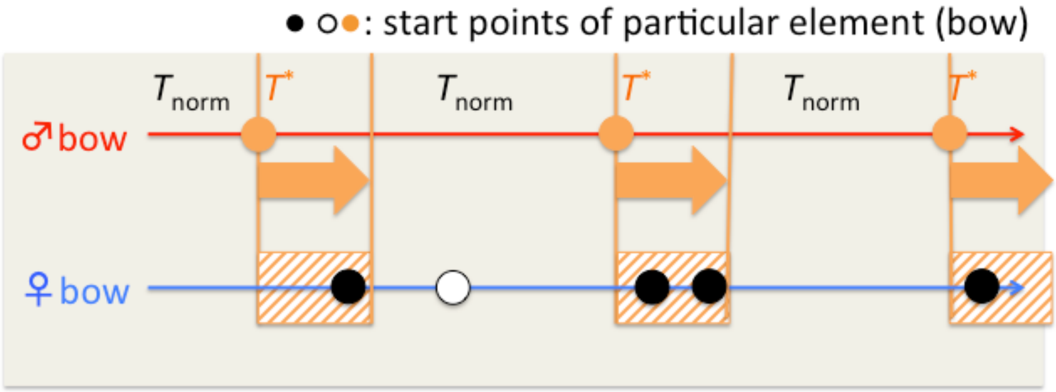

Figure 4.2 the example of analyses for interval within each pair

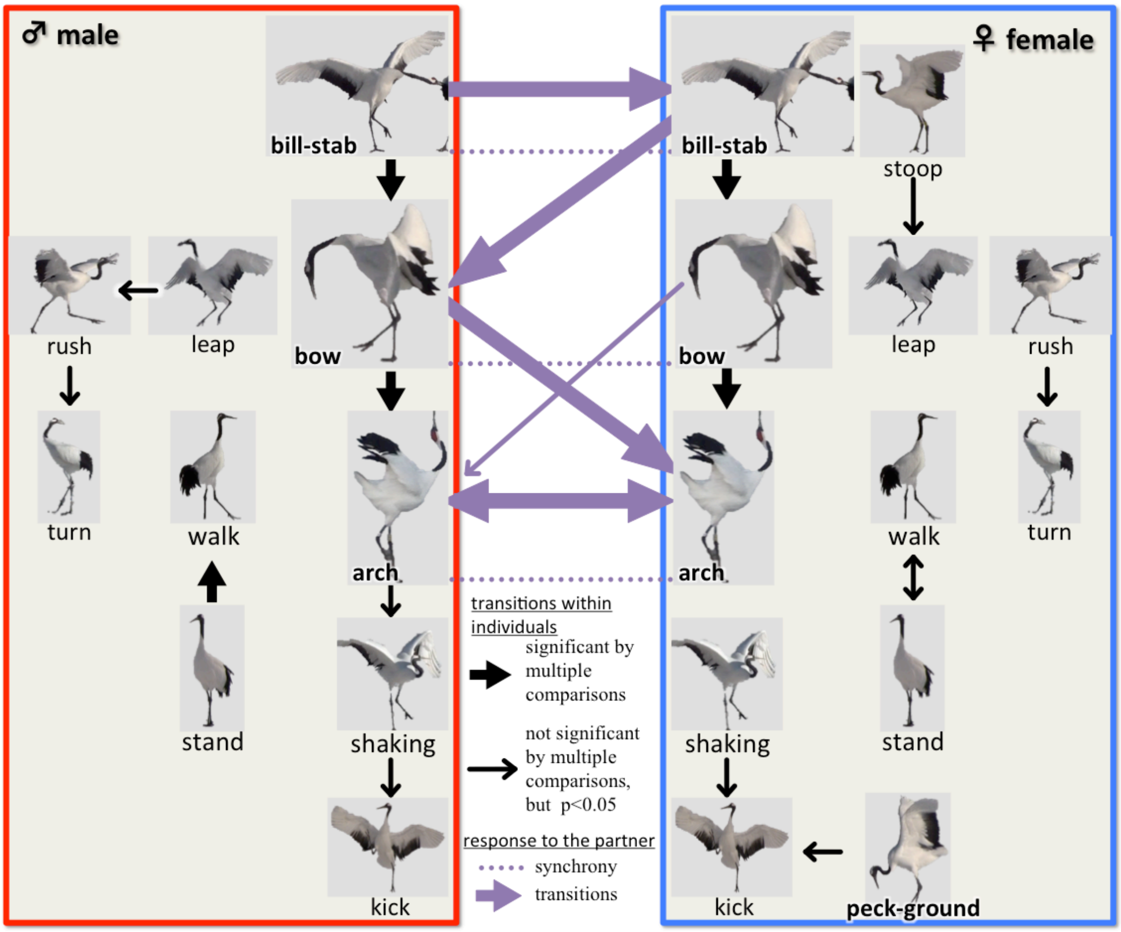

Figure. 4.3 Characteristic transition between males and females

Bold arrows indicated that significant transitions with considering multiple comparison. Narrow arrows indicated that transitions without considering multiple comparison, but their significances were smaller than 0.05. The dash lines indicated that synchrony between males and females.

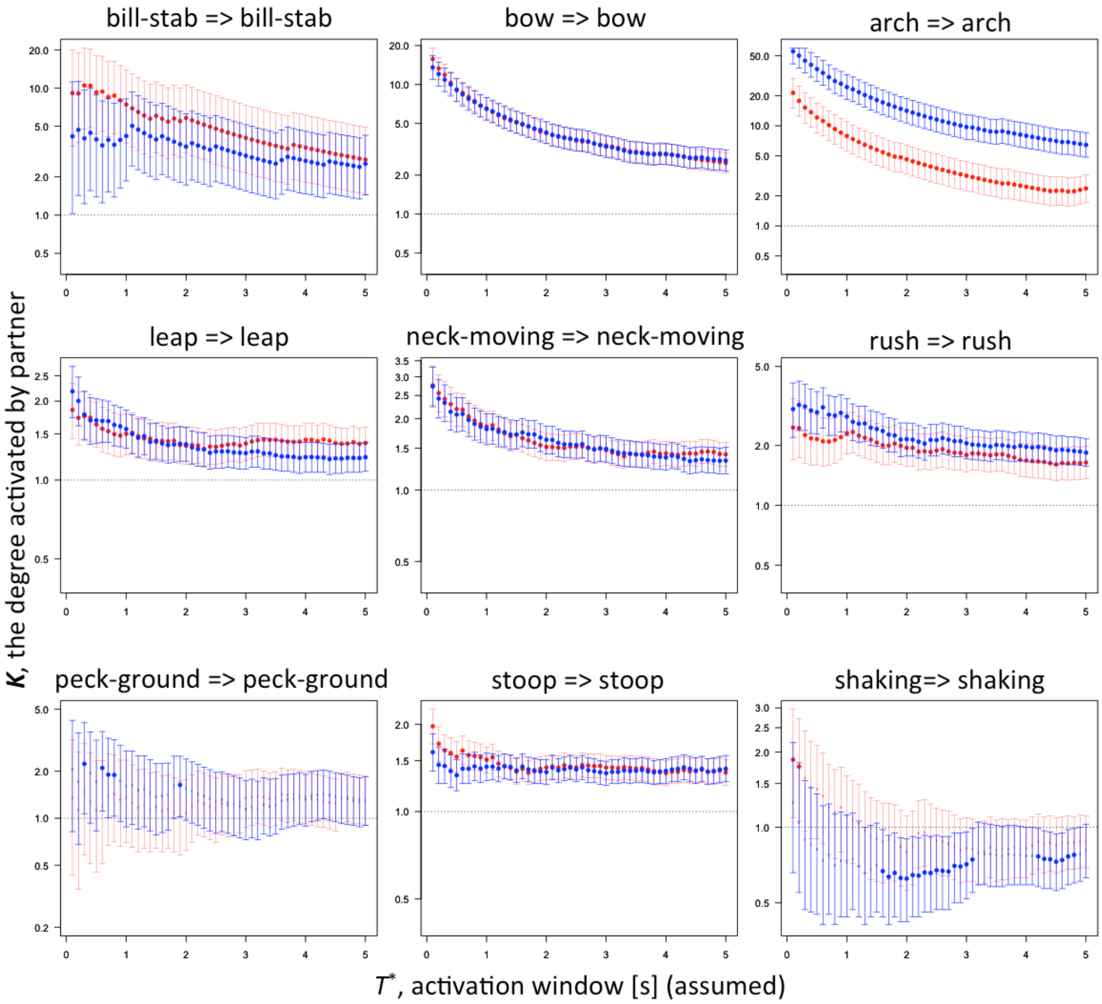

Figure 4.4 the temporal association between males and females.

A horizontal axis showed T^*. A vertical axis showed K, the degree of activated by partner. Red line indicated effects from males to females. Blue line indicated effects from females to males. The circles indicated the significant effects and the points indicated the non-significant effects. Error bar indicate SE.

Table 4.1 the transition patterns and synchrony whose frequency was higher than the expected values.

a. List of significant transition patterns.

Transition pattern	The first element	The second element	Observed frequency	Expected frequency	P value
Male to female	Bill-stab	Bill-stab	0.00155	0.00022	< 0.00001**
Male to female	Bow	Arch	0.01438	0.00202	< 0.00001**
Male to female	Arch	Arch	0.00564	0.00082	< 0.00001**
Female to male	Bill-stab	Bow	0.00318	0.00051	< 0.00001**
Female to female	Arch	Arch	0.00988	0.00082	< 0.00001**
Male to male	Bill-stab	Bow	0.01139	0.00207	< 0.00001**
Male to male	Bow	Arch	0.03002	0.00220	< 0.00001**
Female to female	Bill-stab	Bow	0.00343	0.00072	0.00003*
Female to female	Bow	Arch	0.03405	0.00289	< 0.00001**

With considering multiple comparison, $P < 0.00025$*, $P < 0.00001$**

b. List of significant synchrony between males and females.

Males	Females	Observed frequency	Expected frequency	P value
Bill-stab	Bill-stab	0.00121	0.00022	< 0.00001**
Bow	Bow	0.01970	0.00465	0.00019*
Arch	Arch	0.00916	0.00082	< 0.00001**

With considering multiple comparison, $P < 0.00025$*, $P < 0.000025$**

Table 4.2 Sex difference of each element

a. Bill-stab

Independent terms	*b*±SE	*z*	*P*
(Intercept)	0.303±0.174	1.735	0.083
Sex (males > females)	1.259±0.229	5.493	<0.001**

b. Kick

Independent terms	*b*±SE	*z*	*P*
(Intercept)	0.74±0.264	2.800	0.005**
Sex (males > females)	0.854±0.292	2.921	0.003**

c. Bow

Independent terms	*b*±SE	*z*	*P*
(Intercept)	1.279±0.133	9.610	<0.001**
Sex (males > females)	0.003±0.172	0.015	0.988

d. Leap

Independent terms	*b*±SE	*z*	*P*
(Intercept)	1.67±0.232	7.197	<0.001**
Sex (males > females)	0.057±0.181	0.315	0.753

e. Arch

Independent terms	*b*±SE	*z*	*P*
(Intercept)	0.48±0.128	3.744	<0.001**
Sex (males > females)	0.027±0.147	0.183	0.855

f. Stoop

Independent terms	*b*±SE	*t*	*P*
(Intercept)	23.914±3.115	7.677	<0.001**
Sex (males > females)	0.959±2.529	0.379	0.688

g. Neck-moving

Independent terms	*b*±SE	*t*	*P*
(Intercept)	15.661±4.157	3.767	<0.001**
Sex (males > females)	0.657±1.638	0.401	0.690

h. Rush

Independent terms	*b*±SE	*t*	*P*
(Intercept)	13.405±4.175	3.211	<0.001**
Sex (males > females)	5.769±1.59	3.627	0.001**

i. Shaking

Independent terms	*b*±SE	*t*	*P*
(Intercept)	6.937±1.491	4.652	<0.001**
Sex (males > females)	-0.211±1.091	-0.194	0.857

Chapter 5. Function of pair dances

5.1 INTRODUCTION

Courtship displays have received much attention by researchers since Darwin (reviewed in Montgomerie & Doucet 2007). The development and sophistication of sexual selection theory led both field and experimental researchers to investigate patterns and functions of sexual dimorphic characters in animals (Anderson 1994). On the other hand, studies on characters expressed both in males and females were relative scare (Kraaijeveld et al., 2007). Furthermore, there were a few quantitative studies about mutual displays (exception: Kraaijeveld & Mulder 2002, Soma & Garamszegi 2015). Although pair dances can play an important role in communication within a pair (cf. Chapter 4), quantitative studies about functions of the pair dances had not been conducted. The classical theory of sexual selection predicts that pair dances function for pair formations or mate choice, but could not explain why birds continue to perform pair dances after pair formation (Huxley 1914). That was because after pair formation, there should be no selective pressure of sexual selection for performing the mutual displays. Therefore, "*we still don't know*" functions of pair dances (Birkhead et al., 2014, page 349).

The descriptive studies speculated that a pair dance functions as strengthening pair bond with considering these following facts ("pair bond hypothesis"; Armstrong 1942). This hypothesis is based on common characteristics found in bird species that perform a pair dance (e.g., red-crowned crane, *Grus japonensis*: Masatomi & Kitagawa, 1975, blue-footed booby, *Sula nebouxii*: Torres & Velando, 2003, wandering albatross, *Diomedea exulans*: Pickering & Berrow 2001). First, both males and females care for chicks. Second, the same individuals form a long-term relationship. Third, a pair also performs the dance after pair formation. However, support for this hypothesis remained at a descriptive level, and rigid quantitative analyses for the hypothesis had not been conducted. The lack of the test of pair bond hypothesis is partially because no studies quantifying dance performance.

This chapter quantified performance of each pair dance in the red-crowned cranes by using entropy based on information theory (Vanderbilt et al., 2015). This method was applied to behavioural studies targeting to complex displays or vocal performance (Briefer et al., 2010; Dalziell et al., 2013; Kojima & Doupe, 2011). Entropy is useful to measure a diversity of elements or synchrony between two characters (cf. Chapter 5.2). Therefore, entropy is a good index for analysing individual difference of each pair dance activity.

In this chapter, I address two questions outlined below.

Is a diversity of elements correlated to a partner's one in each dance? If pair dances function as strengthening pair ponds, a diversity of elements is predicted to correlate to a partner's one within each bout of dance. The diversities of elements are supposed to be used as communication tools within each pair. Therefore, individuals may correspond to their partner's performance and the correlation between the diversity of each pair occurs. In addition, I analysed sexual difference in the diversity. If dances function as strengthening pair bonds, a male is predicted to have a similar diversity with a female in each pair. That is because both males and females are supposed to show similar performance of pair dances. I used entropy as a parameter of the diversity of elements. Dance diversity reflects the diversity of behavioural elements in each dance without considering its sequence.

How do characteristics of each dance relate with reproductive state? If pair dances function as strengthening pair bonds, characteristics of each dance is predicted to relate with their reproductive success and vary with seasons. More specifically, high activity of dance is supposed to contribute their cooperation especially in their reproductive behaviours. To quantify the characteristics of each dance bout, I first calculated the total duration of each dance. I predict that their dance duration increases as the breeding season approaches. Second, I calculated four indexes based on information theory: entropy (diversity) for each individual (male and female), joint entropy (asynchrony) and mutual information (dependency). Based on this hypothesis, I predict that 1) a pair index (i.e., joint entropy and mutual information) relates to reproductive success but solo index (i.e., entropy for each individual) did not; 2) synchrony within each pair (low joint entropy) is positively associated to the reproductive success; 3) a dependency within each pair (mutual information) is positively associated to the reproductive success.

5.2 METHODS

Both data collection and data coding are the same to the methods of Chapter 4 (4.2 Methods). In total, we analysed 347 bouts of pair dances for 3 years. Total number of banded pairs was 33 (the number of cases per pairs, mean ± SE: 9.4 ± 10 range: 1-40). Their ages varied two to 23 yr old (mean ± SD: 11.6 ± 4.6 yrs).

I conducted GLMM featuring Gaussian error structure (duration: 347 data for 33 pairs, entropy: 99 data for 21 pairs) in all analyses. To avoid pseudo-replication, the identities of pairs and the year were set as random terms in the GLMMs.

Shannon information entropy provides indexes for investigating the general performance of mutual displays (Vanderbilt et al., 2015). I calculated three types of indexes for each dance (*X* or *Y*);

(1) entropy: *H(X)*,

(2) joint entropy: *H(X, Y)*,

(3) mutual information: *I(X, Y)*.

Theses indexes are calculated as following equations (Shannon, 1948).

$$H(X) = -\sum_{x \in X} P(x) \log P(x)$$

$$H(X,Y) = -\sum_{x \in X} \sum_{y \in Y} P(x,y) \log P(x,y)$$

$$I(X;Y) = H(X) + H(Y) - H(X,Y) = \sum_{x \in X} \sum_{y \in Y} P(x,y) \log \frac{P(x,y)}{P(x)P(y)}$$

Where *P(x)* is a proportion of time with element *x*, i.e., the total duration for which an individual perform a behavioural element (*x*) in each dance, divided by the total duration of each dance.

Similarly, *P(X, Y)* is a proportion of time with two particular elements by two individuals, i.e., the total duration for which one perform a behavioural element (*x*) with another performing a behavioural element (*y*) simultaneously, divided by the total duration of each dance.

Entropy (*H(X)*) reflects the behavioural diversity of contents in each dance. Higher entropy indicates that each dance shows higher diversity of behavioural elements. Joint entropy (*H(X,Y)*) reflects the behavioural asynchrony of contents with summing pairs. Lower joint entropy indicates that each dance shows higher behavioural synchrony within each pair. Mutual information (*I(X,Y)*) reflects the independency of contents within each pair. Higher mutual information indicates that each dance shows higher dependency within each pair.

Is a diversity of elements correlated to a partner's one in each dance?

I investigated whether the diversity of behavioural elements was symmetrical within a pair. After controlling for the number of elements used in each dance and duration of each dance, I analysed two cases by GLMMs: the analysis whose dependent term was entropy for males and independent term was entropy for females, and vice versa. I did those two analyses because it was hard to decide which individual, a male or a female, should be set as an independent term in the case of mutual communication. Because of this problem, I also calculated a correlation coefficient (r) between entropy of males and females. Note that this correlational analysis was based on pooled data and did not consider pseudo-replication caused by the identity of pairs.

How do characteristics of each dance relate with reproductive states?

In the analyses, I included following variables as independent terms; dates of observation, whether their juveniles were present or absent when pairs performed the dance, whether pairs succeeded for caring chicks or not in the next year (cf. Chapter 1), the number of years with their reproductive success, and their ages. In the analysis of entropy, I controlled for the effect of a number of elements used in each dance and duration of each dance.

5.3 RESULTS

Is a diversity of elements correlated to a partner's one in each dance?

Answers: Yes.

The entropy of males was related to those of females in each dance and vice versa (Table 5.1, Figure 5.1). The correlation value between males and females was 0.37. In addition, there were not significantly sexual differences in their entropy (Table 5.2).

How do characteristics of each dance relate with reproductive states?

Answers: Pair synchrony/dependency was negatively associated with reproductive success.

The duration of each dance increased as the breeding season approached (Table 5.3). Other parameters of reproductive states did not affect the duration of each dance.

The entropy for males associated to neither reproductive success nor the seasonal change (Figure. 5.2, Table 5.4). The entropy for females also associated to neither reproductive success nor the seasonal change (Figure. 5.2, Table 5.5).

On the other hand, the pair indexes were associated with reproductive success. Joint entropy of pairs (i.e., asynchrony within each pair) positively affected the reproductive success of a next year (Table 5.6). Mutual information (i.e., dependency within each pair) was negatively associated to the number of years with their reproductive success (Table 5.7). Other parameters of reproductive states did not affect these indexes.

5.4 DISCUSSION

The results partially supported the pair bond hypothesis. The supporting results were summarized as follow. First, dance diversity (i.e., entropy) was correlated within a pair (Table 5.1, Figure 5.1). This suggested that individuals responded to the performance of their partner. Second, there were not sexual differences in the diversity of elements (Table 5.2). Third, the total duration of each dance was longer as the breeding season approached (Table 5.3). This indicated that the performances of each dance were related to their reproductive conditions, i.e., these might be correlated with the change of sexual hormone depending on dates (Adkins-Regan 2005). Fourth, the pair indexes but not the solo indexes, affected reproductive success (Figure. 5.2, 5.3, 5.4, Table 5.4, 5.5, 5.6, 5.7). These indicated that the synchronous pair dance was an important factor affecting the reproductive success.

However, the following results disagreed with the pair bond hypothesis. The joint entropy was positively associated with short-term reproductive success (Figure. 5.3, Table 5.6). This indicated that overall synchrony within each pair affected their reproductive success negatively. The overall dependency within each pair (mutual information) was also negatively associated to long-term reproductive success (Figure 5.4, Table 5.7). Therefore, both synchrony and dependency within each pair partially caused negative effects on reproductive behaviours of pairs.

Why did some results disagree with the pair bond hypothesis? For discussing this, it is necessary to point out that the concept of “pair bond” is vague. In general, “pair bond” should include an individual’s contribution for reproductive success and negotiation for cooperative parental care (Armstrong 1942; Black 1996). However, these arguments need to be discussed with cautions. Below, I discussed three possibilities.

First, there was a possibility that efforts for establishing pair bonds might be qualitatively different from ones for maintaining pair bonds. Pairs need to assess the characteristics of the partner such as their compatibility within each pair during the establishment of pair bonds. On the other hand, for maintaining of pair bonds, pairs need to continue their relationship as they have cooperated before. Therefore, it was predicted that the length of pair bonds positively associated with the dance characteristics such as synchrony within a pair. If pair bonds continue for lifetime (i.e., divorce never occurred), their ages could be used as a proxy of the time length of pair bonds. Still, their ages did not affect any dance characteristics (Table 5.3, 5.4, 5.5, 5.6, 5.7), which suggested that the results might not support this prediction. In addition, it might be inaccurate to use their age as the time of pair bonds. Previous studies reported that divorce occurred in the sandhill crane (*Grus canadensis*) (its divorce rate: 3.9 %: Black 1996, appendix 19.1). The genetic evidence of extra-pair fertilizations was also reported in this species (Hayes et al. 2006). In order to collect accurate time of pair bonds, it is necessary to study captive cranes in which the time of pair bonds has been recorded in detail.

Second, it was possible that dance characteristics of each pair was the *consequence* of their past reproductive performance. This idea is opposite to my prediction that dance characteristics were the *cause* of their reproductive success. For instance, a pair with low reproductive success might need to communicate intensively for reproductive cooperation within a pair. On the other hand, pairs with high reproductive success might not need to do so if pair bond has already been well-established. Following this idea, it is predicted that the past reproductive success negatively relates with dance characteristics. This prediction was partly supported by the negative relationship between the pair index and long-term reproductive success (Table 5.7). However, the current past reproductive success (i.e., whether their juveniles were present or absent when pairs performed the dance) did not affect any indexes (Table 5.3, 5.4, 5.5, 5.6, 5.7), which disagreed with the possibility that dances may be the consequence of the preceding reproductive performance. It is necessary to clarify this possibility by detail future analyses dealt with other parameters of pair dances.

Third, there was a possibility that low synchrony/dependency of pair dances may facilitate cooperation within a pair, and consequently may result in future reproductive success. Previous studies suggested that temporal synchrony of songs or displays within a group were positively associated with coalition quality or mate quality (e.g., Australian magpie-lark, *Grallina cyanoleuca*: Hall & Magrath, 2007, katydids, *Neoconocephalus spiza*: Greenfield & Roizen, 1993, long-tailed manakin, *Chiroxiphia linearis*: Trainer & McDonald, 1995). In this study, however, synchrony/dependency of pair dances was negatively associated with their reproductive success (Table 5.6, 5.7). Although pair dances with low synchrony/dependency may appear to be less structured, it also indicates that behavioural combination is not concentrated on specific patterns – i.e., large number of behavioural combination is included in the pair dance. Therefore, a number of behavioural combination rather than synchrony/dependency may be a critical factor of reproductive success.

Together, these three possibilities clarifies that the concept of the pair bond proposed by Armstrong (1942) was too vague. It will be important to update the concept of the pair bond and test predictions by the accumulation of data.

This study showed that pair indexes, but not solo index, affected to the reproductive success (Figure. 5.2, 5.3, 5.4, Table 5.4, 5.5, 5.6, 5.7), meaning that a reductive approach could miss an importance of signals. This suggests an importance of quantifying mutual signals itself rather than divining it to signals by each individual. Still, it should be noted that this study did not use full information contained in pair dances. It is difficult to quantify characteristic variations of pair dances compared with solo displays. In solo displays, it is enough to analyse one-way interaction from a sender to receiver. On the other hand, the analyses for mutual communication such as pair dances quantify complicated interactions between two performers simultaneously. For such difficulty, the following aspects were not analysed in my studies. First, the analyses did not consider variations of behavioural sequences or temporal associations in pair dances. It should be noted that the sample size required for data analyses will be large in the case that the number of behavioural elements is large (14 in this study) and further that researchers test inter-pair variation. Second, the analyses ignored variation of behavioural contents in pair dances. The kinds of behavioural elements may be one of important factors for mutual communication within each pair, since individuals of pairs should decide which behavioural elements to perform according to the partner's behavioural elements (cf. chapter 4).

In summary, these results provided the first evidence that supported the pair bond hypothesis. These studies showed there were significant complex relationships between synchrony of dances and reproductive success. My studies also gave us an opportunity to reconsider what pair bond means exactly. Therefore, these findings provided newly understanding of mutual communication in animals.

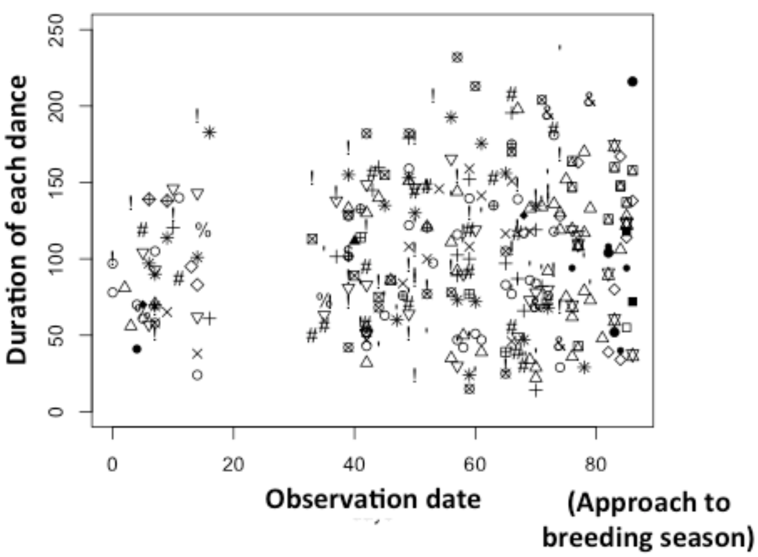

Figure 5.1 A relationship between dance duration and a date when each dance was observed.

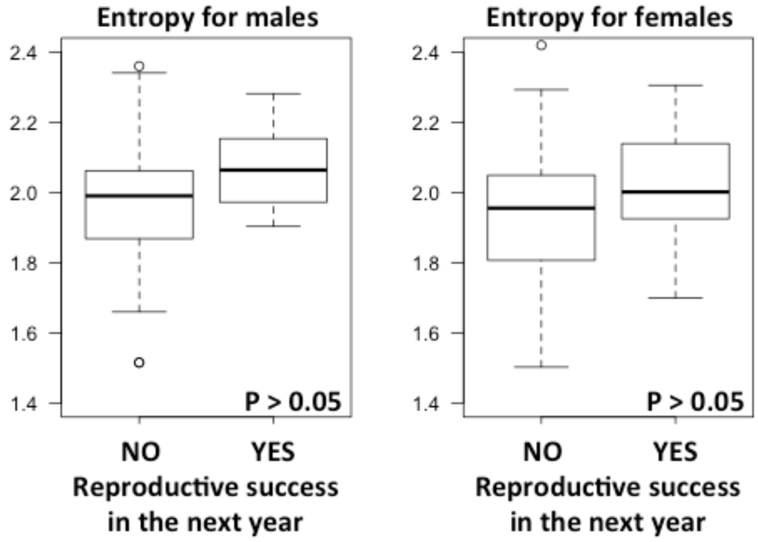

Figure 5.2 Relationships between entropy for males and females and reproductive success in a next year.

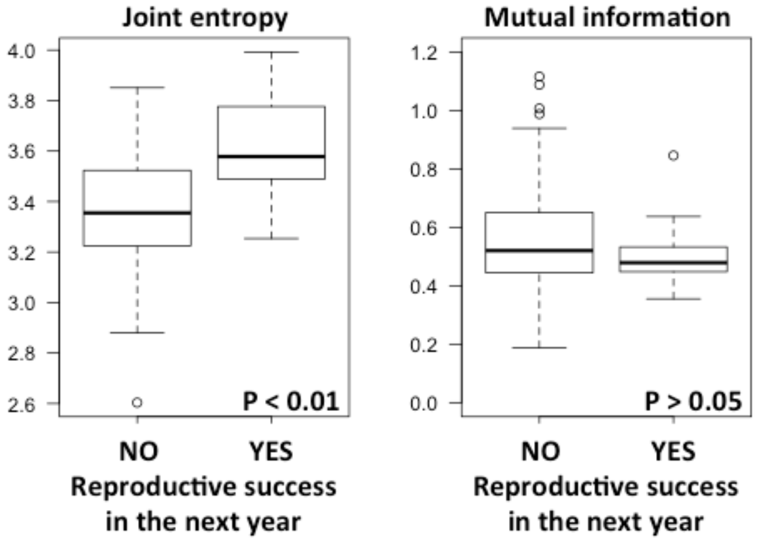

Figure 5.3 Relationships between entropy for pairs and reproductive success in a next year.

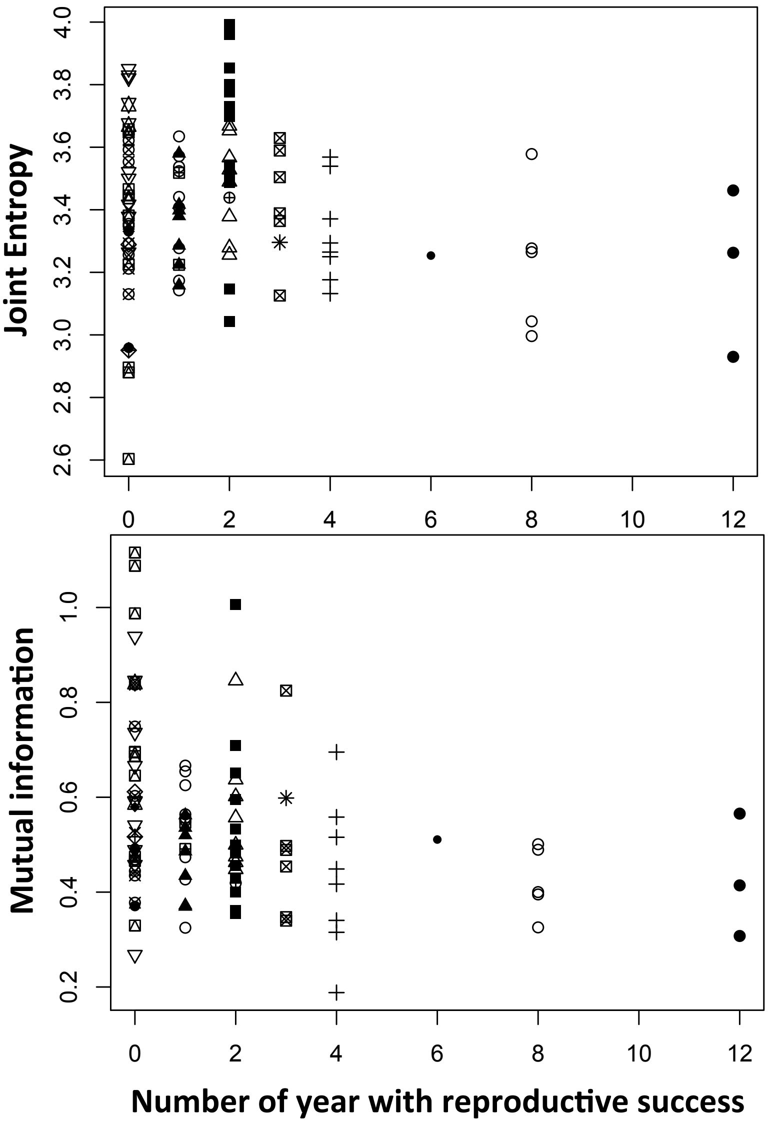

Figure 5.4 Relationships between entropy for pairs and the number of year with reproductive success. The types of each sign correspond to each pair.

Table 5.1

a. Male entropy (independent term)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	0.939±0.13	7.227	<0.0001**
Female entropy	0.176±0.066	2.688	0.008**
Duration	-0.001±0.000	-3.242	0.001**
The number of elements	0.074±0.009	8.182	<0.0001**

b. Female entropy (independent term)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	0.520±0.157	3.319	0.001**
Male entropy	0.230±0.075	3.060	0.003**
The number of elements	0.090±0.009	10.199	<0.0001**
Excluded independent terms			
Duration	0.000±0.000	-0.409	0.673

(n = 99)

**<0.01, *<0.05.

Table 5.2 Sex difference of entropy (n = 198)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	1.042±0.069	15.083	<0.001**
The number of elements	0.09±0.007	13.277	<0.001**
Duration	-0.001±0	-1.991	0.037*
Excluded independent terms			
Sex (male > female)	-0.003±0.022	-0.116	0.909

**<0.01, *<0.05.

Table 5.3 Duration of each dance (n = 363)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	84.385±10.108	8.348	0.001**
Date	0.308±0.11	2.802	0.006**
Excluded independent terms			
Age	-0.930±0.581	-1.601	0.118
Reproductive experience (year)	-0.059±0.873	-0.068	0.946
Future RS (0,1)	5.897±5.795	1.018	0.313
Juveniles in the year (0, 1)	5.970±5.239	1.140	0.262

**<0.01, *<0.05.

Table 5.4 Male entropy (n=37)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	1.241±0.123	10.099	<0.0001**
The number of elements	0.069±0.01	6.949	<0.0001**
Excluded independent terms			
Reproductive experience (year)	-0.022±0.044	-0.492	0.656
Future RS (0,1)	-0.022±0.049	-0.450	0.657
Juveniles in the year (0, 1)	-0.024±0.039	-0.624	0.547
Duration	-0.001±0.000	-1.681	0.103
Age	-0.01±0.016	-0.585	0.603
Date	-0.001±0.001	-1.755	0.088

**<0.01, *<0.05.

Table 5.5 Female entropy (n = 64)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	0.884±0.103	8.623	<0.0001**
The number of elements	0.099±0.01	10.244	<0.0001**
Excluded independent terms			
Reproductive experience (year)	-0.007±0.005	-1.430	0.157
Future RS (0,1)	0.057±0.041	1.377	0.173
Juveniles in the year (0, 1)	-0.01±0.049	-0.196	0.845
Duration	-0.001±0.000	-1.267	0.209
Age	0.000±0.003	-0.150	0.881
Date	-0.001±0.001	-1.203	0.233

**<0.01, *<0.05.

Table 5.6 Joint entropy (n=99)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	2.141±0.22	9.721	<0.0001**
Future RS (0,1)	0.171±0.056	3.063	0.003**
Duration	0.003±0.001	5.039	<0.0001**
The number of elements	0.077±0.019	4.135	<0.0001**
Excluded independent terms			
Reproductive experience (year)	-0.015±0.010	-1.420	0.129
Juveniles in the year (0, 1)	-0.056±0.053	-1.072	0.248
Age	-0.01±0.005	-1.784	0.062
Date	-0.001±0.001	-1.912	0.051

**<0.01, *<0.05.

Table 5.7 Mutual information (n=99)

Independent terms remained in the final model	*b*±SE	*t*	*P*
(Intercept)	-0.127±0.169	-0.753	0.453
Reproductive experience (year)	-0.017±0.006	-2.967	0.005**
Duration	-0.002±0.000	-5.801	<0.0001**
The number of elements	0.075±0.014	5.317	<0.0001**
Excluded independent terms			
Future RS (0,1)	-0.004±0.046	-0.088	0.931
Juveniles in the year (0, 1)	0.005±0.041	0.129	0.898
Age	-0.004±0.005	-0.752	0.463
Date	0.000±0.001	-0.505	0.614

**<0.01, *<0.05.

Chapter 6. General conclusion

I summarize three originalities of my studies as follow. First, I uncovered quantitative characteristics of ritualized displays (Chapter 2, 3). These studies provide one of a few examples investigating the determinants and consequences of those displays especially in birds. Second, this is first detail quantitative study of pair dances, mutual signals (Chapter 4, 5). Third, this is the first quantitative test of the pair bond hypothesis, which proposes a necessity of conceptual update of the hypothesis (Chapter 5). Together, these studies contribute to the understanding of animal signals by clarifying functions of ritualized displays.

Interestingly, my studies found that the kind of social relationships may affect the type of signals such that the degree of complexity and directionality of signals (one-way communication vs. mutual communication). Arch and duet displays are one-way social signals to potential competitors (Chapter 2, 3). A social relationship between senders and receivers is relatively short-term, at maximum about one hour in a fission-fusion flocking system. On the other hand, a pair dance is a mutual sexual signal within each pair (Chapter 4, 5). A relationship between a sender and a receiver is long-term, spanning for over years.

My studies also imply that important information to a mate or competitors is coded in the ritualized displays. Previous studies focused on information of both sexual ornaments and calls (Brandbury & Vehrencamp 2011). However, there are a few studies on what information is coded in ritualized displays and pair dances. The studies in this thesis are not designed to answer this question directly, but provide some implications on this topic. One cue is that both arch and duet displays are included in pair dances (Chapter 4). These single displays function as aggressive signals to their competitors (Chapter 2, 3). On the other hand, pair dances including these displays function as strengthening pair bonds to their mate partner (Chapter 5). Therefore, the results showed that functions of these displays depended on social contexts. Two following results suggested that some meanings are coded in pair dances. First, a pair dance was structured within a pair (Chapter 4). Second, dance performance, especially the mutuality measured by the synchrony and dependency, was related with reproductive success (Chapter 5). The candidates of information coded in pair dances might be cooperative intentions for reproduction, compatibility within a pair, a physiological state and so on. Regarding physiological synchrony, previous studies showed that within-pair testosterone co-variation was positively related with long-term reproductive success in greylag geese (*Anser anser*) (reviewed in Hirschenhauser 2012). Sexual hormone, such as testosterone, regulates internal reproduction and controls sexual behaviours (Adkins-Regan 2005). If sexual hormone co-variation within pair is an important factor for boosting reproductive success in the crane, pairs may use dance performances as signals to send their physiological states and encourage reproductive preparation each other. Therefore, it is interesting to investigate the relationship between characteristics of each dance and co-variation of their sexual hormone within each pair. These studies will contribute to clarify what candidate information is coded in the pair dances.

It is unclear why so many behavioural elements compose of a pair dance. Although the function of each display depends on social contexts, the meaning of each display may be similar across contexts (Bradbury & Vehrencamp 2011). For example, some affiliative displays toward a mate partner are structurally similar to aggressive displays toward competitors in some monogamous species (e.g., butterflyfish, *Chaetodon lunulatu*: Yabuta 2002, herring gulls, *Larus argentatus*; Tinbergen 1959, red-crowned crane *Grus japonensis*: Masatomi & Kitagawa 1975). Based on this, it may be that each element codes different meanings according to meanings of other contexts (behavioural meaning hypothesis). For example, some behavioural elements may cause a negative effect on their reproductive performance, but other elements may cause a positive effect on their reproductive performance. Therefore, it is interesting to examine whether different behavioural elements play different roles in pair communication. Future studies need to clarify this possibility by investigating more detailed analyses on pair dances.

Although reproductive costs for males were supposed to be equal to that for females in monogamous birds (cf. Chapter 1), my studies found the sexual difference in both arch displays (Chapter 2) and pair dances (Chapter 4). In particular, some parameters of male activity were higher than ones of female activity. This indicated that males might lead females in their pair dances. These sexual differences of dances might be related to differentiated investment to gametes or different parental role. For example, males mainly chase or attack to their intruders in territorial defense, and females support their partners by performing duet displays (Masatomi & Kitagawa, 1974). In addition, the sexual difference of pair dances might be caused by be sexual conflict for investing the amount of reproductive efforts in each year (Wachtmeister 2001). When there is a conflict between a sender and a receiver, an intensity of signals occasionally evolve to be stronger than its necessary level for a receiver (Seary & Nowicki, 2005). For instance, intensity of begging calls was stronger than the minimum level that parents responded (Wright & Leonard, 2002). Similarly, pair dances might function as a signal to “manipulate” the mate partner for necessary amounts of reproductive efforts. If one of a pair succeeds to manipulate his/her partners to invest greater reproductive efforts than its own by performing pair dances, that individual can use other resource for future reproductive success. Therefore, evolutionary arms race with a pair might occur, and as a result, dance performances may become complex and sexually differentiated. This explanation might only fit when their divorce or extra-pair copulation occurred. Extra-pair fertilizations (EPF) were reported in socially monogamous species that perform pair dances (EPF rate: 14-21 % in waved albatross, *Phoebastria irrorata* [Huyvaert et al., 2006], 4.4-11% in Sandhill Cranes, *Grus Canadensis* [Hayes, et al. 2006]). Therefore, EPF might occur in the observed individuals. However, the occurrence of EPF was unknown in the red-crowned crane because of limited researches for banded individuals.

Pair dances of the red-crowned crane seem to be one of the most complex structures among animals. Why do they perform complex pair dances? My studies suggested that a pair send some reproductive information each other by performing pair dances. Cooperative reproduction or reproductive negotiation may be essential for pairs compared with other birds. I speculate that two factors explain the uniqueness of pair bond in the red-crowned crane.

First, the difficulty of mating may play an important role in this uniqueness. The mating in the red-crowned crane has two features. One is that mating may be physically difficult for their heavy bodies. The other feature is that the height of conjugation is very high among birds since their legs are very long. In the red-crowned crane, pairs attempt to mate multiple times during a mating season. They often fail in mating especially in the early season (early March). Both perfect timing and high motivation may be important factors for the success of mating, speculated from the fact that males always perform rhythmical calls before mating (Masatomi & Kitagawa 1975). The red-crowned crane has one of the heaviest body weights among the crane family. Other birds with relatively long legs, such as the stilt (*Himantopus himantopus)*, have more light bodies than the crane. Other heavy monogamous birds, such as albatrosses, can perform low height of conjugation in their mating compared with the crane. Therefore it may be physically easier for these birds to mate than the red-crowned crane. Future studies need to investigate the relationship between physical difficulty of mating (e.g., heights of conjugation and body weights) and the complexity of dances by using phylogenetic comparisons within the crane family.

The second uniqueness of this species is the role of molting. Molting occurs once in two years, which is critical to their survival. They cannot fly completely during molting, which they may be more likely to be attacked by their predators such as foxes than the normal states. Molting occurs during the period of parental care. Therefore, pairs need highly cooperation in this season compared with other periods. Considering these facts, the necessity for highly pair cooperation and negotiation may be one of the critical factors for the evolution of complex pair dances.

As future studies, it will be interesting to apply the methods used in this thesis (i.e., transition analysis, analysis for temporal association, and entropy) to solo dances performed by sub-adults or singles. Many previous works have been conducted in song development of passerines (Marler & Slabbekoorn 2004). On the other hand, there have not been quantitative analyses about development of signals using other modules, resulting in poor understanding of the development of ritualized displays and dances. Dance characteristics may be determined by both hard-wired genetic background and individually acquired component by learning. Regarding genetic background, the kinds of behavioural elements were common among pairs in the red-crowned crane (Masatmi & Kitagawa, 1975; Chapter 4). Regarding learning, inter-pair variation was present and associated with reproductive performance (Chapter 5). Future studies about comparison between solo dances and pair dances will contribute to the understanding of pair bond. That is because whether pair bond exists is one of critical differences between pair dances and solo dances.

Finally, my studies can be indirectly applied to effective management and conservation of the crane. The red-crowned crane is an endangered species (BirdLife International, 2013). Application of these behavioural results can provide an efficient way of investigating their social and sexual relationships quantitatively for conservation. Regarding arch displays or duet displays, it is possible to assess the gathering patterns of the cranes. In Japanese populations, high densities at feeding stations are a serious problem because of the increased risk of infectious diseases (Masatomi & Masatomi, 2009). In practice, the degree of competition at feeding stations could potentially be assessed by simply measuring the frequency of the arch displays or duet displays (Chapter 2, 3). It will provide our understanding of dominance and the potential problems associated with high densities. Regarding pair dances, it is possible to assess the quality of relationship between each pair in captivities. The captive breeding of the crane is also important for conservation breeding projects. It is one of difficult problems to form pair bonds and have chicks in captivities. In practice, a possibility that pair succeeds in reproduction could potentially be assessed by measuring indexes of dance performance (Chapter 5). Therefore, these indexes may offer one of the cues about pair formation. These behavioural monitoring at feeding stations or captivities could provide basic knowledge of the species, and lead to more effective conservation.

In summary, ritualized signals in the red-crowned crane were functional and have some biological meanings exchanged between signalers and receivers. These studies filled the gaps between ritualized signals and other types of signals (e.g., acoustic performance), and contribute to our broad understanding of animal communication.

REFERENCES

Adkins-Regan, E. (2005). Hormones and Animal Social Behavior. Princeton University Press.

Alonso, J. C., Bautista, L. M., & Alonso, J. A. (2004). Family - based territoriality vs flocking in wintering common cranes *Grus grus*. Journal of Avian Biology, 35(5), 434-444.

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour, 49(3), 227-266.

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. Nature, 299(5886), 818-820.

Andersson, M. B. (1994). Sexual Selection. Princeton University Press.

Armstrong, E. A. (1942). Bird Display. Cambridge University Press.

Arrowood, P. C. (1988). Duetting, pair bonding and agonistic display in parakeet pairs. Behaviour, 106(1), 129-157.

Aureli, F. & Schaffner, C. (2007). Aggression and conflict management at fusion in spider monkeys. – Biology Letters 3: 147–149.

Aureli, F., Shaffner, C., Boesch, C., Bearder, S., Call, J., Chapman, C., Connor, R.Di., Fiore, A., Dunbar, R.I.M., Henzi, S.P. et al. (2008). Fission-fusion dynamics: new research frameworks. – Curr. Anthropol. 49(4): 627–654.

Bautista, L.M., Alonso, J.C. & Alonso, J.A. (1995). A field test of ideal free distribution in flock-feeding common cranes. – Journal of Animal Ecology 64(6): 747-757.

BirdLife International (2013). *Grus japonensis*. The IUCN red list of threatened species. version 2014.2. <www.iucnredlist.org>. Downloaded on 7th October

2014.

BirdLife International (2016) Species factsheet: *Grus japonensis*. Downloaded from http://www.birdlife.org on 8th February 2016.

Birkhead, T., Wimpenny, J., & Montgomerie, B. (2014). Ten Thousand Birds: Ornithology since Darwin. Princeton University Press.

Black, J. M. (Ed.). (1996). Partnerships in Birds: The Study of Monogamy: The Study of Monogamy. Oxford University Press, UK.

Bradbury, J.W. & Vehrencamp, S.L. (2011). Principles of Animal Communication, 2nd ed. – Sinauer, Sunderland.

Briefer, E., Osiejuk, T. S., Rybak, F., & Aubin, T. (2010). Are bird song complexity and song sharing shaped by habitat structure? An information theory and statistical approach. Journal of Theoretical Biology, 262(1), 151-164.

Burghardt, G.M. 2005. The Genesis of Animal Play. Cambridge: The MIT Press.

Caselli, C. B., Mennill, D. J., Gestich, C. C., Setz, E. Z., & Bicca‐Marques, J. C. (2015). Playback responses of socially monogamous black-fronted titi monkeys to simulated solitary and paired intruders. American journal of primatology.

Dahlin, C. R., & Benedict, L. (2014). Angry birds need not apply: a perspective on the flexible form and multifunctionality of avian vocal duets. Ethology, 120(1), 1-10.

Dalziell, A. H., Peters, R. A., Cockburn, A., Dorland, A. D., Maisey, A. C., & Magrath, R. D. (2013). Dance choreography is coordinated with song repertoire in a complex avian display. Current Biology, 23(12), 1132-1135.

Dinets, V. (2013). Crane dances as play behaviour. Ibis, 155(2), 424-425.

Dobler, S., Heller, K. G., & Von Helversen, O. (1994). Song pattern recognition and an auditory time window in the female bushcricket *Ancistrura nigrovittata*

(Orthoptera: Phaneropteridae). Journal of Comparative Physiology A, 175(1), 67-74.

Doucet, S. M., & Montgomerie, R. (2003). Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. Behavioral Ecology, 14(4), 503-509.

Dukas, R. (1998). Cognitive ecology: the evolutionary ecology of information processing and decision making (Vol. 1). University of Chicago Press.

Ellis, D.E., Swengel, S.R., Archibald, G.W. & Kepler, C. B. (1998). A sociogram for the cranes of the world. – Behavioural Processes 43: 125–151.

Gill, F. B. (2007). Ornithology. 3rd edition, Macmillan.

Gowaty, P. A. (1996). 2 Battles of the sexes and origins of monogamy. Partnerships in Birds: The Study of Monogamy: The Study of Monogamy (edited by Black, J. M.), pp21-52.

Greenfield, M. D, & Roizen, I. (1993). Katydid synchronous chorusing is an evolutionarily stable outcome of female choice. Nature 364, 618–620.

Hall, M. L. (2000). The function of duetting in magpie-larks: conflict, cooperation, or commitment?. Animal Behaviour, 60(5), 667-677.

Hall, M. L. (2004). A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology, 55(5), 415-430.

Hall, M. L. (2009). A review of vocal duetting in birds. Advances in the Study of Behavior, 40, 67-121.

Hall, M. L., & Magrath, R. D. (2007). Temporal coordination signals coalition quality. Current Biology, 17(11), R406-R407.

Hayes, M. A., Britten, H. B., & Barzen, J. A. (2006). Extra-pair fertilizations in

Sandhill Cranes revealed using microsatellite DNA markers. The Condor, 108(4), 970-976.

Helfer, B., & Osiejuk, T. S. (2015). It takes all kinds in acoustic communication: a new perspective on the song overlapping phenomenon. Ethology, 121(4), 315-326.

Hirschenhauser, K. (2012). Testosterone and partner compatibility: evidence and emerging questions. Ethology, 118(9), 799-811.

Houde, A. E. (1997). Sex, Color, and Mate Choice in Guppies. Princeton University Press.

Hurd, P.L. & Enquist, M. (2001). Threat display in birds. – Can. J. Zool. 79: 931–942.

Huxley, J. S. (1914). The courtship-habits of the great crested grebe (Podiceps cristatus); with an addition to the theory of sexual selection. Proceedings of the Zoological Society of London, 35, 491–562.

Huyvaert, K. P., Anderson, D. J., & Parker, P. G. (2006). Mate opportunity hypothesis and extrapair paternity in waved albatrosses (*Phoebastria irrorata*). The Auk, 123(2), 524-536.

Inoue, M., Shimura, R., Uebayashi, A., Ikoma, S., Iima, H., Sumiyoshi, T., Teraoka, H., Makita, K., Hiraga, T., Momose, K. & Masatomi, H. (2012). Physical body parameters of red-crowned cranes *Grus japonensis* by sex and life stage in eastern Hokkaido, Japan. – The Journal of veterinary medical science/the Japanese Society of Veterinary Science 75(8): 1055-1060.

Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., ... & Striedter, G. (2005). Avian brains and a new understanding of vertebrate brain evolution. Nature Reviews Neuroscience, 6(2), 151-159.

Johnsgard, P. A. (1983). Cranes of the World. –University of Nebraska, Lincoln.

Jones, I. L., & Hunter, F. M. (1993). Mutual sexual selection in a monogamous seabird. Nature 362, 238 – 239.

Keyser, A. J., & Hill, G. E. (2000). Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. Behavioral Ecology, 11(2), 202-209.

Klenova, A. V., Volodin, I. A., & Volodina, E. V. (2008). Duet structure provides information about pair identity in the red-crowned crane (*Grus japonensis*). Journal of Ethology, 26(3), 317-325.

Kojima, S., & Doupe, A. J. (2011). Social performance reveals unexpected vocal competency in young songbirds. Proceedings of the National Academy of Sciences, 108(4), 1687-1692.

Kraaijeveld, K., & Mulder, R. A. (2002). The function of triumph ceremonies in the black swan. Behaviour, 139(1), 45-54.

Kraaijeveld, K., Gregurke, J., Hall, C., Komdeur, J., & Mulder, R. A. (2004). Mutual ornamentation, sexual selection, and social dominance in the black swan. Behavioral Ecology, 15(3), 380-389.

Kraaijeveld, K., Kraaijeveld-Smit, F. J., & Komdeur, J. (2007). The evolution of mutual ornamentation. Animal Behaviour, 74(4), 657-677.

Logue, D. M. (2005). Cooperative defence in duet singing birds. Cognition, Brain, Behavior, 9, 497-510.

Logue, D. M. (2007). Duetting in space: a radio-telemetry study of the black-bellied wren. Proceedings of the Royal Society of London B: Biological Sciences, 274(1628), 3005-3010.

Marler, P. R., & Slabbekoorn, H. (2004). Nature's Music: the Science of Birdsong. Academic Press.

Marshall-Ball, L., Mann, N., & Slater, P. J. B. (2006). Multiple functions to duet singing: hidden conflicts and apparent cooperation. Animal Behaviour, 71(4), 823-831.

Martin, P. R., & Bateson, P. P. G. (2007). Measuring Behaviour: an Introductory Guide, 3rd edition. Cambridge University Press.

Masatomi, H. & Kitagawa, T. (1974). Bionomics and sociology of Tancho or the Japanese Crane, *Grus japonensis*, I.:Distribution, habitat and outline of annual cycle. – J. Faculty of Science. Hokkaido University, Series VI. Zoology 19(3): 777-802.

Masatomi, H. & Kitagawa, T. (1975). Bionomics and sociology of Tancho or the Japanese crane, *Grus japonensis,* II. ethogram. – J. Faculty of Science. Hokkaido University, Series VI. Zoology 19 (4): 834–878.

Masatomi, H. (1988). Arching behaviour of the Tancho *Grus japonensis* landed on the feeding stations in 1998. – J. Senshu Univ. Hokkaido (Nat. Sci.) 21: 145-153 (In Japanese with an English abstract).

Masatomi, H., Koga, K., Matsumoto, F., & Tmiyama, N. (1999) Frequency of unison-calls among Flocks of the Tancho at the wintering feeding stations, J. of Environ. Sci. Lab., Senshu Univ., 6:399-410 (In Japanese with an English abstract).

Masatomi, Y., Higashi, S., & Masatomi, H. (2007). A simple population viability analysis of Tancho (*Grus japonensis*) in southeastern Hokkaido, Japan. - Population Ecology 49(4): 297-304.

Masatomi H. & Masatomi Y. (2009). Promoting the coexistence of humans and Tancho in Japan. – Japanese Journal of Conservation Ecology 14: 223-242 (In

Japanese with an English abstract).

Maynard, D. F., Ward, K. A. A., Doucet, S. M., & Mennill, D. J. (2012). Calling in an acoustically competitive environment: duetting male long-tailed manakins avoid overlapping neighbours but not playback-simulated rivals. Animal Behaviour, 84(3), 563-573.

Maynard Smith J. & Harper D. (2003). Animal Signals. – Oxford University Press, New York.

Mennill, D. J., & Ratcliffe, L. M. (2004). Overlapping and matching in the song contests of black-capped chickadees. Animal Behaviour, 67(3), 441-450.

Mennill, D. J., & Vehrencamp, S. L. (2008). Context-dependent functions of avian duets revealed by microphone-array recordings and multispeaker playback. Current Biology, 18(17), 1314-1319

Miura, Y., Shiomi, A., Shiraishi, J., Makita, K., Asakawa, M., Kitazawa, T., Hiraga, T., Momose, Y., Momose, K., Masatomi, H., & Teraoka, H. (2013). Large-scale survey of mitochondrial D-loop of the red-crowned crane *Grus japonensis* in Hokkaido, Japan by convenient genotyping method. – The Journal of Veterinary Medical Science / the Japanese Society of Veterinary Science 75(1): 43-47.

Montgomerie, R., & Doucet, S. M. (2007). Courtship and copulation. Reproductive biology and phylogeny of birds. Sexual selection, behavior, conservation, embryology, genetics, 6 (edited by Jamieson B. G.M.), pp161-238.

Morris, D. (1958). The comparative ethology of grassfinches (Erythrurae) and mannikins (Amadinae). – Proceedings of the Zoological Society of London 131: 389–439.

Moynihan, M. (1966). Communication in the titi monkey, Callicebus. Journal of

Zoology, 150(1), 77-127.

Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. Advances in the Study of Behavior, 35, 275-331.

Møller, A. P., & Gregersen, J. (1994). Sexual Selection and the Barn Swallow (Vol. 8). Oxford: Oxford University Press.

Naguib, M., & Mennill, D. J. (2010). The signal value of birdsong: empirical evidence suggests song overlapping is a signal. Animal Behaviour, 80(3), e11-e15.

Naguib, M., Mundry, R., Ostreiher, R., Hultsch, H., Schrader, L., & Todt, D. (1999). Cooperatively breeding Arabian babblers call differently when mobbing in different predator-induced situations. Behavioral Ecology, 10(6), 636-640.

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.

Pickering, S. P. C., & Berrow, S. D. (2001). Courtship behaviour of the wandering albatross *Diomedea exulans* at Bird Island, South Georgia. Marine ornithology, 29(1), 29-37.

Porter, M. L., Kingston, A. C., McCready, R., Cameron, E. G., Hofmann, C. M., Suarez, L., ... & Robinson, P. R. (2014). Visual pigments, oil droplets, lens, and cornea characterization in the whooping crane (*Grus americana*). Journal of Experimental Biology, jeb-108456.

Rosenthal, G.G. & Ryan, M.J. (2000). Visual and acoustic communication in non-human animals: a comparison. – Journal of Biosciences 25(3): 285-290.

Scheiber, I. B., Weiß, B. M., Hemetsberger, J., & Kotrschal, K. (2013). The social life of Greylag Geese. Cambridge University Press.

Searcy, W. A., & Beecher, M. D. (2009). Song as an aggressive signal in songbirds. Animal Behaviour, 78(6), 1281-1292.

Searcy, W. A., & Nowicki, S. (2005). The Evolution of Animal Communication: Reliability and Deception in Signaling Systems. Princeton University Press.

Senar, J. C. (2006). Color displays as intrasexual signals of aggression and dominance. ‒ In Bird Coloration volume.Ⅱ (Hill, G.E. & McGraw, K.J., eds.). MA: Harvard University Press, Cambridge, p.87‒136.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science, 210(4471), 801-803.

Shannon, C. E. (1948). A note on the concept of entropy. Bell System Tech. J, 27, 379-423.

Silk, M.J., Croft, D.P., Tregenza, T. & Bearhop, S. (2014). The importance of fission–fusion social group dynamics in birds. – Ibis 156: 701–715.

Smith, J.E., Powning, K.S., Dawes, S.E., Estrada, J.R., Hopper, A.L., Piotrowski, S.L. & Holekamp, K.E. (2011). Greetings promote cooperation and reinforce social bonds among spotted hyaenas. –Animal Behaviour. 81(2): 401-415.

Sogabe, A., & Yanagisawa, Y. (2008). Maintenance of pair bond during the non-reproductive season in a monogamous pipefish *Corythoichthys haematopterus*. Journal of Ethology, 26(1), 195-199.

Soma, M., & Garamszegi, L. Z. (2015). Evolution of courtship display in Estrildid finches: dance in relation to female song and plumage ornamentation. Frontiers in Ecology and Evolution, 3, 4.

Suzuki, T. N. (2011). Parental alarm calls warn nestlings about different predatory threats. Current Biology, 21(1), R15-R16.

Takeda, K. (2012). Individual dependence on a feeding station in the red-crowned crane, - China Crane News 16(1): 18-20.

Takeda, K. F., Hiraiwa-Hasegawa, M., & Kutsukake, N. (2015). Arch displays signal threat intentions in a fission–fusion flock of the red-crowned crane. Behaviour, 152(12-13), 1779-1799.

Tinbergen, N. (1959). Comparative Studies of the Behaviour of Gulls (Laridae): a Progress Report1). Behaviour, 15(1), 1-69.

TKG (Tancho kihon-chosa Group) (2015). TKG news letter No58, Red-crowned crane conservancy (in Japanese).

Torres, R., & Velando, A. (2003). A dynamic trait affects continuous pair assessment in the blue-footed booby, *Sula nebouxii*. Behavioral Ecology and Sociobiology. 55, 65–72.

Torres, R., & Velando, A. (2005). Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxii.* Animal Behaviour, 69(1), 59-65.

Trainer, J.M., and McDonald, D.B. (1995). Singing performance, frequency matching and courtship success of long- tailed manakins (*Chiroxiphia linearis*). Behavioral Ecology and Sociobiology. 37, 249–254.

van Tets, G.F. (1965). A comparative study of some social communication patterns in the Pelecaniformes. – Ornithol. Monogr. 2: 1–88.

Wachtmeister, C. A. (2001). Display in monogamous pairs: a review of empirical data and evolutionary explanations. Animal Behaviour, 61(5), 861-868.

Weiß, B. M., Kehmeier, S., & Schloegl, C. (2010). Transitive inference in free-living greylag geese, *Anser anser*. Animal behaviour, 79(6), 1277-1283.

Wright, J., & Leonard, M. L. (2002). The Evolution of Begging: Competition, Cooperation and Communication. Springer Science & Business Media.

Yabuta, S. (2002). Uncertainty in partner recognition and the tail-up display in a monogamous butterflyfish. Animal behaviour, 63(1), 165-173.