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学位論文題目 Ritualized signals in the red-crowned crane: how and why do  
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Abridged version (outline)

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

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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 japonensis*); (1) the arch display after joining to a flock, (2) the 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) The 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 ritualised signals in non-songbird species with fission-fusion social dynamics.

(2) The 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's 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 the kind of behavioural elements performed. 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 dance functions as maintaining pair bond (pair bond hypothesis). The supporting results were following. First, dance diversity (i.e., entropy) was correlated between a pair. Second, the total duration of each dance was longer as the breeding season comes. This indicated that the performance of each dances were related with their reproductive situation. Finally, entropy for pairs not but 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 (joint entropy) affected their reproductive success negatively. The general dependency within each pair (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 understanding broad of animal communication.

(798 words)