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| 学位(専攻分野) | 博士(理学) |
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論文内容の要旨

Summary of thesis contents

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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# 博士論文の審査結果の要旨
# Summary of the results of the doctoral thesis screening

学位申請者（武田浩平）は、タンチョウ*Grus japonensis*（鳥類ツル目ツル科）における、儀式化された信号とコミュニケーションについて研究した。背曲げ(arch)、デュエットディスプレー(duet display)、つがいによるダンス(pair dance)という三種類の信号に関して、行動頻度の決定要因、およびその機能に関して、４年間にわたる野外調査によって明らかにした。

博士論文は六章からなる。第一章では、動物のコミュニケーション研究の現状、その問題点、研究対象種タンチョウの特徴を手短に解説した。第二章では、個体が群れに参加する時に行う背曲げディスプレーを分析し、この行動に他個体を威嚇する機能があることを報告した。この研究は、*Behaviour*誌に掲載されている（博士論文に含むことは共著者による承諾済み）。第三章では、つがいが同時に発するユニゾンコール(unison call)と特有の動作によって構成されるデュエットディスプレーについて、その機能を分析した。その結果、このディスプレーが群れ内の餌資源をめぐる競争、自己主張の機能を持つことを報告した。

第四章・第五章では、つがいが行うダンスを研究した。タンチョウのダンスは鳥類の儀式化された行動のなかで、構成行動要素が顕著に多く、持続時間も長い。このため、その行動学的分析は、挑戦的な研究テーマとして残されていた。第四章では、ダンスには特定の遷移パターンがあり、相手の行動直後に同じ行動を行う行動パターンがあることを、複数の分析手法によって明らかにした。第五章では、ダンスを特徴付ける指標と、つがいの過去の繁殖履歴・将来の繁殖成功との関連を検証した。これらの研究によって、古典的動物行動学において提唱されたpair bond仮説（ダンスは、つがいの絆を強め高い繁殖成功を導くという仮説）の検証を行った。その結果、ダンスの相互性を示す行動指標が、つがいの繁殖成功が負の関係を示し、pair bond仮説からの予測を支持しなかった。この結果から、pair bondという概念、および仮説の曖昧さを指摘し、より詳細な仮説が必要であることを考察にて提唱している。総合考察である第六章では、本研究の新規性と今後の課題が述べられている。

申請者の研究は、野生タンチョウのコミュニケーションの機能を明らかにする分厚い研究といえる。第二・三章で報告された研究は、鳥類における儀式化された信号の機能を明らかにした数少ない研究である。第四章・第五章で行われたダンスの構造分析、pair bond仮説の定量的検証も世界で初めての研究である。これまでの鳥類におけるコミュニケーション研究は、鳴禽類がおもに縄張りで発する歌形質、または配偶者選択の対象となる性的装飾に集中してきた。申請者の研究は、その他の分類群の大型種を扱い、個体が離合集散する群れにおいて見られる信号を扱っている。これらの点で、本研究は既存のコミュニケーション研究の幅を大きく広げるもので

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あり、高く評価できる。博士論文は英語で書かれており、申請者は十分な英語能力を有すると判断される。これらの点から、申請者が博士（理学）に値すると判定した。