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Chapter 1

General Introduction

Biodiversity has both fascinated and puzzled biologists. Early experimental and modeling work led to the principle of competitive exclusion. This states that, among two or more species competing for a shared resource, only the best competitor will survive. The apparent contradiction between competitive exclusion and the species richness found in nature has been a long-standing problem.

In order to resolve this problem, many hypotheses explaining species coexistence against competitive exclusion have been proposed. For instance, niche partition, disturbance, habitat heterogeneity, environmental fluctuation, and so on were considered to be factors promoting species coexistence. Both laboratory and field studies have tested these hypotheses, and shown that these factors actually play a role in promoting species coexistence.

Here, we propose an additional important factor affecting species coexistence, especially for animal communities. The factor is behavioral interactions between individuals. We define behavioral interaction as any behavior of individuals in the interactions, for example, the aggressive behavior, territorial behavior, and so on. In nature, animals always recognize the surrounding individuals and thereby, always change their behavior in order to obtain their high reproductive success.

The behavioral interactions between individuals would affect the frequency of interaction of among species, the strength of the competitions, and consequently, the occurrence of species coexistence. In this thesis, I focus on this effect of behavioral interaction between individuals on species coexistence.

Chapter 2

The effects of individual interactions and habitat preferences on spatial structure in a grassland bird community

Spatial structure and the distribution of individuals within a community might be influenced by several factors such as habitat heterogeneity and local interactions among individuals of the same and different species. We investigated the spatial distributions of eight bird species in a grassland community during the breeding season and examined whether the spatial distributions of individuals were influenced by interactions among neighboring individuals or different habitat preferences of different bird species. In order to identify the effects of the interactions among neighboring individuals and habitat preference, we developed a randomization test in which species identifications were randomly allocated to the observed individual positions within areas with the same vegetation structure. The randomization test indicated that individuals tend to have territories near the territories of individuals of the same species or of a particular species more frequently (or less frequently) than those expected from random distributions of individuals. Among these associations, only one case was explained by individual interactions, and 19 cases were explained by habitat preference. The results suggest that both individual interactions and habitat preference affected the spatial distributions of individuals and possibly influence the species compositions and diversity in grassland bird communities.

Chapter 3

A new hypothesis for species coexistence: male-male repulsion promotes coexistence of competing species.

We propose a new hypothesis, namely, that repulsive behavior between conspecific males creates space for competing species, which promotes their coexistence. This hypothesis can explain the coexistence of two competing species even when their ecological niches overlap completely. The mechanisms underlying such behavior might play a role in making possible the coexistence of two species immediately after speciation, with little or no niche differentiation, as can occur in cichlid fish communities, for example. Although there is thus for little evidence supporting this hypothesis, nevertheless, it can explain the occurrence of species coexistence and biodiversity that previous theories cannot.

Chapter 4

Does interspecific territoriality reflect the intensity of ecological interactions?: A theoretical model for interspecific territoriality

In many studies, interspecific territorial behaviors among coexisting species have been used to infer the presence and the intensity of underlying ecological interactions between species, mainly resource competition. However, the theoretical background of this inference is insufficient. Hence, we constructed a simple theoretical model for interspecific territoriality assuming that interspecific territorial defense is the optimal behavior. Then factors promoting interspecific territoriality and the relationship between interspecific territoriality and ecological interactions are discussed. The model predicts that (1) a territory holder preferentially exclude intruders of species with high "exclusion efficiency", (2) the decision as to whether or not the territory holder excludes a certain species does not depend on the probability of finding intruders of the species nor on the number of intrusions of the species, and (3) interspecific territoriality does not always reflect the intensity of ecological interactions between species. These results indicate that the observation of interspecific territoriality does not necessarily indicate the intensity of ecological interactions. In addition, if territory holders defend their territories as predicted by the present optimal model, the coexistence of competing species is promoted.

Chapter 5

Conspecies-precedence interference competition and species coexistence: Many individuals lead to many species.

For animals, intraspecific competition is often more important than interspecific competition because the former is more related to their reproductive successes than the later. So, we assume that, in interference competition, individuals of animals compete preferentially with conspecific competitors (we name this assumption as conspecies-precedence interference competition) and then, examine how this assumption affect species coexistence by developing a theoretical model. As the result, species coexistence is promoted by the present assumption. The coexistence is more promoted in the guild in which the intensity of interference competition is stronger or the density of species is higher. These results indicate that the present assumption can play a role in maintaining species coexistence in the guilds in which densities of these species are high and there are interference competitions among individuals (e.g. African cichlids, coral reef fishes). Furthermore, this model provides an additional explanation for the positive relationships between productivity and animal species biodiversity.

Chapter 6
General Discussion

In this thesis, I showed, by theoretical models, that behavioral interactions between individuals of animals lead to species coexistence. In Chapters 2 and 3, I showed the repulsive behavior between conspecific males in establishing territory (male-male repulsion) creates space for heterospecific individuals and then, promotes their coexistence. In Chapter 4, I developed a mathematical model on interspecific territoriality and showed that optimal territorial behavior leads to species coexistence. In chapter 5, I assumed that, in interference competition, individuals of animals compete preferentially with conspecific competitors (conspecies-precedence interference competition) and showed that it promotes species coexistence.

From the four studies in the present thesis, adaptive animal behaviors are very important factors to promote species coexistence. Generally, animals behave to obtain resources and mating opportunities, ultimately to maximize their fitness. In many cases, these behaviors reduce other individuals' fitness, especially conspecific individuals' fitness, because the niche overlap between conspecies is larger than that between heterospecies and the competition for mating opportunities occurs only between conspecies. Consequently, these behaviors result in increasing intraspecific competition and thereby, it prevents competitive exclusion. Of course, the present models cannot be applied to all the animals. For example, for animals whose reproductive success increases by aggregations, male-mal repulsion and conspecific-precedence interference competition are not adaptive, and thus, different models should be considered. However, because behaviors that reduce conspecific individuals' fitness are commonly observed in nature, the mechanisms of species coexistence which were provided by the present models can be explanations of species coexistences in animal communities.

Investigations of such behavioral interactions of individuals constitute an important future direction for community ecology. The influences of behavior on the structure of an ecological community may be play important roles in ecology and ethology.

論文審査の結果の要旨

三上修氏の博士論文について，3名の論文審査担当者により，本提出論文の意義，方法の妥当性，得られた結果に関する記述，考察の妥当性について検討が行われた。

本論文は，群集における共存メカニズムを個体間の行動的な相互作用の観点から捉えた研究である。群集生態学において，「どうして似たような資源を要求する種が共存できているのか」，「どうして地域や環境により共存している種数が大きく異なるのか」は，古くからの疑問であり，未だ多くの論争が行われている研究でもある。このような問題に対して，従来の群集生態学では，ニッチ分割，捕食や寄生，環境の時間的・空間的変動をはじめ，様々な仮説が提唱されている。本研究では，このような問題に対して，個体間の行動的な相互作用（個体による生息場所の選択・競争相手の選択など）を考慮するという新しい切り口で，解決に当たっている。ここで考えられた個体間の行動的な相互作用は，行動生態学において既存の，また行動生態学的知見から考えると矛盾のない行動である。このような行動を，実際に野外でデータを取る，仮定として組み込んで数理モデルを構築する，またはコンピューターシミュレーションを行うという方法を用い，共存への影響の解析を行っている。その結果，個体が適応的な行動をとると共存が容易に起こること，資源幅の増大を伴わない単に資源量の増加だけでも共存種数が増えること，そして，高密度でいること自体が多種の共存を促進すること，などの結果が得られている。これらの結果は，群集生態学における既存の知見とは異なる新しい知見であり，現実において多種が共存していることを，うまく説明できる可能性がある。また，このように個体間の行動的な相互作用を考慮することは，群集生態学に行動生態学的知見を導入することであり，これまで別々に考慮されてきた領域を結びつける重要な研究でもある。

以上のような，新たな視点を持ち込む独創性，それを適切な方法で解析する能力，そしてそこから新規性のある結果が得られることは，三上修氏が，自立して研究活動を行うために必要な高度の研究能力と学識を有することを示している。したがって，三上修氏提出の博士論文は，博士（理学）の学位論文として合格と認める。