SPECIAL FEATURE

Interspecific segregation and attraction in forest birds

INTRODUCTION

How different species coexist in a given habitat or in a given area is one of the central questions in community ecology. During the 1960s and 1970s, MacArthur's niche theory provided a scientific basis for researchers approaching this subject. Niche theory is founded on two basic assumptions: Interspecific competition is an organizing force affecting communities and environments are at equilibrium determined by resource limitation. Because forest birds appeared clearly to fulfil these assumptions, many studies demonstrated their interspecific differences in resource use based on niche theory. Niche differences were often interpreted as the result of interspecific competition for limited resources under equilibrium conditions; yet, hardly any of these studies questioned the intrinsic assumptions of niche theory. Meanwhile, other factors, such as predation, mutualism, disturbance and chance had begun to be focused on as alternative processes affecting community organization. Doubts and criticisms of MacArthur's paradigm resulted in considerable controversy over community organization during the 1980s.

During the 1990s, the approach to biotic communities has become pluralistic. Interspecific competition is now seen as one of several forces organizing communities and resource equilibrium is seen as one of several environmental conditions. When we study how forest birds coexist, we may begin therefore with three questions: firstly, we may ask what kind of segregation is most important and how does it differ among target species. Secondly, we may ask what kind of interspecific interaction is most effective for coexistence. The interaction may be negative, such as competition or predation, or positive, such as mutualism or commensalism. Thirdly, we may ask how interspecific interactions change as environmental conditions vary. In particular, the dynamics of resource abundance and distribution must be examined in order to solve the equilibrium problem.

This special feature is composed of three parts: (1) segregation mechanisms, (2) attraction mechanisms and (3) the effect of food distribution. The first two papers, from Australia, focus on the segregation mechanisms of forest birds. Loyn reviews the pattern of ecological distribution of forest birds in southeastern Australia by examining the incidences of range overlap among congeneric species and mechanisms segregating them. From this broad-scale approach, he confirms that habitat difference is the primary segregation mechanism, and that differences in foraging stratum or substrate are most important for coexistence in the same habitat. As a unique feature of the Australian eucalypt forest environment, Loyn indicates that the indiscriminate interspecific aggression of some communal-breeding species has decreased not only the bird species diversity but also the ecosystem health in forests. Recher and his colleagues compare the foraging ecology of five ground-pouncing birds (Australian robins) in woodlands in western Australia. Ecological segregation among understory-foraging birds has been much less studied than among canopy-foraging birds owing to the simpler structure of foraging substrates. Recher et al. found some fine-scale segregation among species by considering the mosaic of available ground substrates, but recognized that foraging ecology was more similar among different species in the same habitat than among conspecific individuals in different habitats. Loyn's and Recher et al.'s papers indicate that a broader range of species or habitats should be analyzed when studying ecological segregation.

The third and fourth papers focus on attraction mechanisms or positive interactions between species, which have rarely been considered in studies of forest bird communities. Mönkkönen and Forsman review their own original studies on heterospecific attraction, that is, a habitat selection process where colonizing individuals (migrants) use the presence of other species (residents) as cues to profitable breeding sites in relation to food availability or predation risk. From biogeographical, theoretical and experimental studies in Fennoscandia and North America, they conclude that heterospecific attraction is a common and widespread process resulting in high species diversity among forest birds particularly in seasonal environments. Mixed-species flocking is another positive interaction in forest birds. Seki and Sato report that different bird species increase the overlap of

the foraging sites they use and the food they eat by frequent participation in mixed-flocks in the winter following an extremely severe typhoon. Seki and Sato consider interspecific attraction to be a result of increased predation risk following reduction in vegetation cover, but not of decreased food abundance. These two studies indicate the importance of specifying what environmental conditions facilitate a positive interaction over a negative one.

The remaining four papers all pertain to the effects of food-supply on forest birds. The three papers from Japan demonstrate how the abundance and distribution of prey influence the substrate-use difference among canopy-foraging insectivorous birds. Murakami examines how birds respond to the drastic distributional changes of Lepidoptera larvae, which migrate from the canopy to the forest floor. He finds two different responses: some species change their foraging height in parallel with the changing distribution of Lepidoptera larvae, while others switch to different prey without altering their foraging height. Mizutani and Hijii reveal that two closely related and similar-sized species of birds (Parus) differentiated between foraging trees according to their prey-size preference, determined by whether they were single- or multiple-prey loaders. Hino and his colleagues also find interspecifically different use of tree species among Parus, but they relate it to the birds' prey-searching techniques. These three studies indicate that forest-substrate segregation between closely related species can be related to species-specific foraging tactics without considering interspecific competition. Sodhi's paper is the only contribution from tropical forests in this special feature. He reviews the few, but interesting, studies on the effects of food-supply on forest bird ecology in Southeast Asia. Further challenging surveys are expected to be conducted in this region where a range of fascinating phenomena, such as El Nino, mass flowering or fruiting, and year-round mixed-species flocking, occur.

Lastly, we must emphasize that the findings from studies on interspecific interactions and/or food resource distribution affecting species coexistence have significant implications for bird conservation. For example, the numerical changes of some bird species caused by habitat loss or fragmentation decrease overall species diversity through interspecific aggression or attraction. The different responses of birds to varying prey distribution among different tree species demonstrates that tree species composition is an important habitat factor affecting the diversity of canopy-foraging bird species in forests. The mosaic complexity of ground substrates may be an equally significant factor for ground-pouncing birds.

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