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Interspecific Competition and the Structure of Bird Guilds in Boreal Europe: the Importance of Doing Fieldwork in the Right Season

Lauri Oksanen

Bird studies have gained a central role in the debate on the importance of interspecific competition in nature. Thus, the negative results reported from a breeding bird community in a North American shrub-steppe area have created ripples throughout community ecology. However, the set of coexisting breeding birds might be an inappropriate operational definition of a bird community, because the intensity of interspecific competition can be expected to peak in autumn–winter. A review of North European data on wintering birds suggests that the case for the competition theory remains strong when bird communities are defined on the basis of winter coexistence.

The idea that stable communities only consist of especially efficient competitors and that the coexisting species must differ in the way they use resources was born in plant ecology at the turn of the century^{1,2}. However, the pursuit of theoretical

perspectives was then overshadowed by vegetation classification, and only recently has the general idea of niche differences become rigorously formulated for plants³. During the intervening period, ornithologists, especially MacArthur^{4,5} and his students⁶, were able to translate the idea of differential use of resources into theoretical models and to use these to interpret data from real communities. Consequently, ornithology took a leading role in community ecology.

The emergence of birds as model organisms for niche and community studies has led to rapid advances of the theory but has also placed it in a rather precarious position. The applicability of the theory to other types of organism has been questioned, especially by ecologists working on folivorous insects⁷ (this criticism is valid but not especially severe: if birds compete intensely then their food items should be subjected to severe predation^{8,9}). Another consequence of the narrow taxonomic basis is that the theory has become very vulnerable to negative results obtained by ornithologists. If it can be shown that the theory does not work with birds, its credibility is sev-

erely damaged with respect to other organisms as well.

The challenge

Exactly such ripples are currently spreading in community ecology, in response to a paper by Wiens and Rotenberry on the bird community of an American shrub–steppe area, where the data seemed to be in conflict with almost all imaginable predictions of competition theory¹⁰. Size ratios between coexisting birds were irregular and the species were poorly segregated with respect to diet and habitat use. Wiens¹¹ suggested that this was due to the assumption of equilibrium in the theory and the non-equilibrium nature of real communities. In his view, populations may be well below the carrying capacity for several generations. During this time, both competition and natural selection are relaxed. Different species can converge in their niches and a wide variety of phenotypes can survive and reproduce. The times of plenty end in ‘crunches’ which severely reduce all populations and also represent periods of intense natural selection. Supposedly, the characteristics and effects of each ‘crunch’ are highly individual, and thus the species will drift in the niche space.

There is a less dramatic explanation for the apparent discrepancies. Birds are extremely mobile, and the sets of coexisting species during breeding and non-breeding seasons can be entirely different. Studies on competition should focus on those sets that experience acute shortage of food. Shortages are possible during the breeding season, since reproduction requires high resource

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levels. However, it is also possible that resource competition becomes relaxed during the summer, especially in extremely seasonal ecosystems. Lack¹² suggested that resource competition intensifies in autumn–winter, when increased populations try to subsist on diminishing resources (see also Fretwell's analysis¹³). Thus, studies on seasonal bird communities, defined on the basis of summer coexistence, might not be the best critical tests of competition theory.

Guild structure among wintering birds in boreal Europe

A rough idea of the applicability of the standard competition theory to wintering terrestrial birds can be obtained by looking at dietary data and size distributions among coexisting bird species of boreal Europe, where the number of species is manageable (i.e. diffuse competition cannot be introduced as a blanket excuse for negative results) and fairly accurate information on ranges, habitats, diets and body weights is available¹⁴. The theory predicts that truly coexisting species either have qualitatively different diets, or (in the case of continuous resource distributions) fairly constant and large body weight ratios (usually about 2), because each species must have a substantial resource base that others are unable to exploit efficiently¹⁵.

The information on ranges, diets and body weights is not without pitfalls. For instance, a pair of species may coexist locally, because both populations get reinforcements from areas where the other one is absent. Thus, birds must be regarded as allopatric if their ranges overlap peripherally. It is also difficult to decide whether a given set of size ratios is sufficiently variable and contains sufficiently small values to pass as evidence against the competition theory. However, weight ratios smaller than 2 between coexisting birds with qualitatively similar diets clearly imply intense competition if the theory is valid. Thus, data on distributions, habitats, diets and body weights can be used to distinguish between static cases where only low or moderate levels of interspecific competition should be observed, and dynamic cases where a closer look should reveal much competitive activity.

Excluding the herbivorous grouses, birds that are undeniably dependent on human settlements and birds that only winter in agricultural areas (coastal Sweden, southwest Finland), the wintering terrestrial avifauna of truly boreal

and non-maritime Europe (roughly, east of the Scandinavian mountains and north of 60°N – see Ref. 16) consists of 31 species that can be divided into five ecological groups.

There are seven species that rely on live vertebrates. Only one of them – the goshawk (*Accipiter gentilis*) – is a diurnal raptor; it is chiefly a predator of gallinaceous birds, a prey group that does not figure substantially in the diet of any of the six owl species. At least two boreal owl guilds can be distinguished: a relatively southern guild, consisting of the pygmy owl (*Glaucidium passerinum*), Tengmalm's owl (*Aegolius funereus*), the hawk owl (*Surnia ulula*), the Ural owl (*Strix uralensis*) and the eagle owl (*Bubo bubo*); and a more northern guild, where the Ural owl is replaced by the great grey owl (*Strix nebulosa*). Successive body weight ratios in the southern guild are 2.0, 2.4, 2.7 and 3.3; in the northern guild they are 2.0, 2.4, 3.6 and 2.4 (calculations based on means of both sexes, ratios listed in order of increasing weights). The ratios are clearly large enough to permit competitive coexistence, and are as regular as could be expected in an area where small microtines are much more abundant than medium-sized prey.

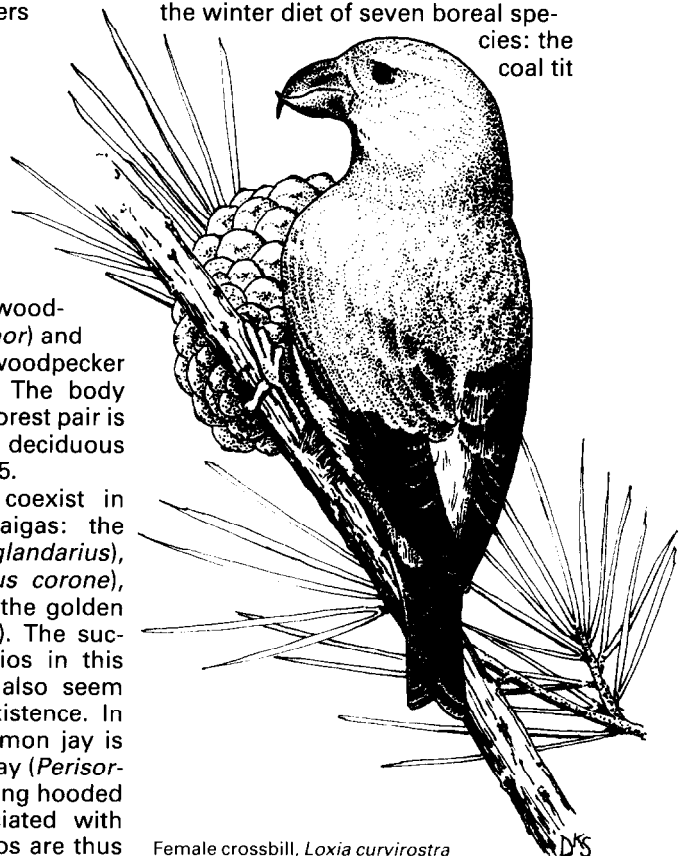
The second non-passerine group consists of six woodpeckers. One – the three-toed woodpecker (*Picoides tridactylus*) – forages on dead spruces, while all the others shun spruce forests. Two species inhabit pine forests: the great spotted woodpecker (*Dendrocopos major*) and the black woodpecker (*Drycopus martius*). The latter is also found in old deciduous forests, which harbour two additional species: the lesser woodpecker (*Dendrocopos minor*) and the white-backed woodpecker (*Dendrocopos leucotos*). The body weight ratio for the pine forest pair is 3.8; the values for the deciduous forest guild are 3.1 and 4.5.

Four carrion feeders coexist in southern and central taigas: the common jay (*Garrulus glandarius*), the hooded crow (*Corvus corone*), the raven (*C. corax*) and the golden eagle (*Aquila chrysaetos*). The successive body weight ratios in this guild (3.4, 2.8 and 3.3) also seem sufficient to permit coexistence. In northern taigas, the common jay is replaced by the Siberian jay (*Perisoreus infaustus*) and wintering hooded crows are strictly associated with settlements. The size ratios are thus

14.6 and 3.4. The large size ratios between the two northern carrion-feeding passerines and the falling out of the middle species corresponds to the implications of the competition theory in a gradient of diminishing resource inputs.

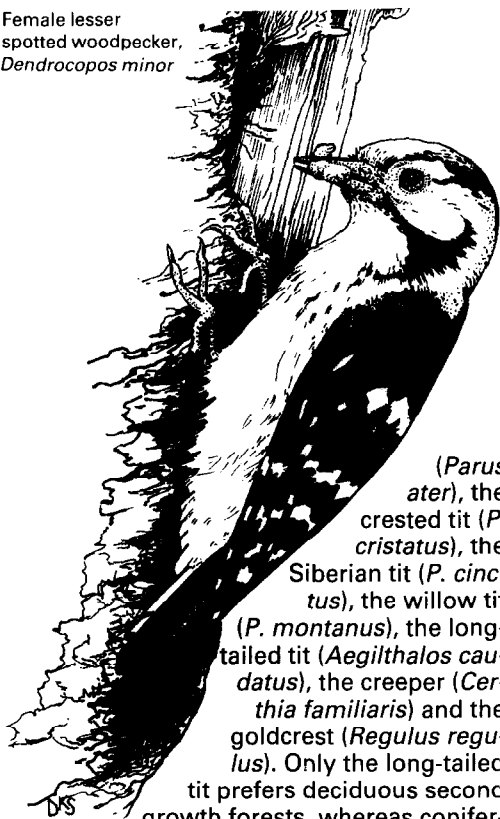
The granivore–frugivore guild consists of eight species. Each of the taiga conifers with different cone morphology – spruce/fir, pine and larch – has its specialist granivore: the common crossbill (*Loxia curvirostra*), the parrot crossbill (*L. pytyopsittacus*) and the two-barred crossbill (*L. leucoptera*), respectively. The only dissonance is the fact that the seeds of Scots pine are also consumed by the great spotted woodpecker, providing a case where competition should act in ecological time. Seeds and buds of angiosperms are used by two similar-sized but largely allopatric granivores: the bullfinch (*Pyrrhula pyrrhula*) in the southern and central taiga and the pine grosbeak (*Pinicola enucleator*) in the northern taiga. The third granivore – the redpoll (*Carduelis flammea*) – has less than half the body weight of the others. The only frugivore regularly wintering in the taiga proper is the waxwing (*Bombycilla garrulus*). Thus, the granivore–frugivore guild seems to be characterized by clear niche differences, and species with similar niches are segregated in space.

Arthropods form a major part of the winter diet of seven boreal species: the coal tit



Female crossbill, *Loxia curvirostra*

Female lesser
spotted woodpecker,
Dendrocopos minor



(*Parus ater*), the crested tit (*P. cristatus*), the Siberian tit (*P. cinctus*), the willow tit (*P. montanus*), the long-tailed tit (*Aegilthos caudatus*), the creeper (*Certhia familiaris*) and the goldcrest (*Regulus regulus*). Only the long-tailed tit prefers deciduous second growth forests, whereas coniferous forests harbour multispecies guilds throughout the region. In the southern taiga, the guild consists of the goldcrest, the coal tit, the crested tit, the willow tit and the creeper. In the Scandinavian part of the central taiga, the composition is otherwise similar but coal tits are absent. The northern taiga (in the east, also the central taiga) is inhabited by willow tits and Siberian tits.

In each area, the set of coexisting species seems to defy the rules of competitive coexistence: only the creeper (which forages on tree trunks) is clearly segregated from the rest, whereas the parids and the goldcrest still form guilds with very tight packing of body sizes and without obvious differences in habitat or foraging technique (weight ratios in the southern taiga: 1.6, 1.3 and 1.03; in the central taiga: 2.0 and 1.03; in the northern taiga: 1.04). The guilds of coexisting insectivores (usually called 'tit guilds' because of the prevalence of parids), can thus be regarded as a litmus test of the competition theory. If interspecific competition is important at all, it must act forcefully and everywhere within these guilds, and, indeed, there must be subtle niche difference permitting competitive coexistence.

The tit guilds: interspecific competition in action

Haftorn¹⁷ had already suggested in the 1950s – before MacArthur had published his famous warbler study⁵ – that similar though more subtle niche differences of the sort that separate the creeper from the tits also occur in the rest of the tit guild, each species having a tendency to

prefer different parts of branches. Willow tits stay closest to the trunk, crested tits use somewhat finer branches, coal tits prefer fine twigs and goldcrests hover among the needles. But did Haftorn observe a mechanism for competitive coexistence, or just minor differences due to individual characteristics of the species?

The next logical step was to discover whether the preferences of different species are sensitive to the presence of postulated competitors. Such studies could be performed by, for instance, comparing normal taiga areas with faunistically impoverished (island) or enriched (suburb) areas and by comparing different subzones with each other. Individually, such comparative studies could only provide weak evidence for (or against) the competition theory, because two areas with different guild structures are likely to show other differences as well. However, enough comparative studies have been performed to allow a statistical evaluation of the results. This was recently done by the Uppsala team of ornithologists¹⁸, and resulted in a clear confirmation of the competition theory. In all cases, sympatry with a species that looked like a close competitor resulted in a divergent niche shift (preference of less similar branches in sympatry than in allopatry). The strongest niche shift was observed in the case of the willow tit and the Siberian tit, which are also very similar in body weight and habit. When the ratio of body weights approached 2, the species ceased to react to the presence of the other.

The ultimate evidence is provided by manipulative experiments. Competition experiments are usually conducted with a design that Tilman¹⁹ calls phenomenological: densities of a supposed competitor are reduced and the response of the other species is observed. With the tit guild, however, the first rigorous experiments, performed by the Gothenburg team, followed Tilman's mechanistic design. This consists of two steps: first, to demonstrate that a resource is in short supply; and secondly, to demonstrate that this shortage is a consequence of consumption. The second point was actually demonstrated first, by enclosing conifer branches with bird-proof nets and comparing

arthropod densities within and outside the nets (which differed by an order of magnitude²⁰). Later, the team showed that supplemental food dramatically increased the winter survival of the tits²¹. This design illuminates the mechanism of competition, but cannot distinguish between intraspecific and interspecific impacts. Fortunately, the Uppsala team has conducted experiments with a phenomenological design, showing that the removal of postulated competitors creates preference shifts towards the niche of the removed species^{22,23}.

An interesting feature of the studies was that strong evidence for resource competition was obtained in spite of the presence of predators. In fact, the Gothenburg team found that virtually all mortality in the tit guild was proximately caused by the pygmy owl²⁴. Their explanation for the apparent contradiction between predation as the main cause of mortality and food as a limiting resource was that predation and food interact: when stressed by food shortages, birds forage in more exposed sites and have less time to watch for predators.

Conclusions

The guild structures among wintering terrestrial birds of boreal Europe conform well to the predictions of the standard competition theory. To some extent, the evidence for the theory comes from guilds where niche differences are so pro-



Ural owl, *Strix uralensis*

found that experiments on inter-specific competition could not be expected to yield large responses, except in some special cases (mainly, contact zones between northern and southern 'ecological sibling' species). Even these cases could be difficult to study experimentally, because of low densities or the mobility of the species, or because of the narrowness of the zone of effective sympatry. This is what makes the studies on the tit guild so significant: the tit guild is exactly the subset of the boreal bird community in which competition should be both intense and easy to study.

The work of Wiens and Rotenberry¹⁰ was important in forcing ornithologists to reconsider their approach to seasonal bird communities. However, the 'crunch' theory of Wiens¹¹ does not look like a promising solution to the problem. The wintering boreal bird community of Europe is characterized by a rather extreme degree of 'boom-crunch' dynamics²⁵. Yet, its guild structure corresponds to the predictions of the competition theory. Also, Grant's²⁶ recent analysis suggests that the occurrence of 'booms' and 'crunches' alone does not generate the kind of drifting discussed by Wiens. The implicit premise of stabil-

ity in the standard competition theory is quite likely to be gravely wrong in many communities, but the theory does not seem to be especially sensitive to the relaxation of this premise.

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Ecological Monitoring

The Handbook of Ecological Monitoring

edited by Robin Clarke, *Oxford University Press (GEMS/UNEP Publication)*, 1986. £30 (xv + 298 pages) ISBN 0 19 854590 8

Remote Sensing and Tropical Land Management

edited by M.J. Eden and J.T. Parry, *John Wiley & Sons*, 1986. £37 (xii + 365 pages) ISBN 0 471 90889 4

Both of these books are about the measuring and monitoring techniques that can be applied to land management of the vast tropical regions of the world. Between them, they cover every method of ecological monitoring of relevance to land management. Their approaches are, however, quite different.

The Handbook of Ecological Monitoring deals solely with the technical aspects of ecological monitoring. The techniques could be used in most of the world's climatological zones, and are not restricted in their application to the tropics. A wide

range of monitoring techniques are covered in the book, ranging from detailed ground survey to the use of satellite imagery. Ground survey and aerial reconnaissance are dealt with in greatest detail, while remote sensing is covered less well.

The balance is redressed in *Remote Sensing and Tropical Land Management*, which uses a series of examples to describe the application of remote sensing to the tropics. Almost all the examples given relate to the mapping of vegetation cover. This highlights one of the limitations of many remote sensors: the images produced by the sensor only represent the surface cover, which in most cases is the vegetation. Radar is the exception to this rule; it can measure some of the features below the surface cover, such as canopy structure and geology. Radar has a further advantage, particularly in the tropics, of being able to penetrate cloud cover. The use of aerial photography and multispectral satellite imagery, on the other hand, are very much restricted by cloud cover.

Eden and Parry's book provides a balanced view of the techniques suit-

able for solving a particular problem. It also makes clear that no one remote sensing technique will provide all the answers. Multispectral scanner images will not replace aerial photography in the foreseeable future, for example. The actual processing of remote sensing imagery is also discussed in detail. The cost of processing remote sensing data can vary tremendously. At the cheapest end, simple photographic prints can be produced from satellite sensor data. These are then interpreted as if they were aerial photographs. At the other extreme, large computer systems can be used to analyse the data: Brazil and India, for example, have invested large sums of money in image processing facilities.

One limitation of both books is that they tend to concentrate on one particular group of techniques (i.e. remote sensing) to solve a particular problem. No one technique gives the best solution; rather, a combination of techniques provides the most effective monitoring strategy. There are three distinct levels of monitoring technique – ground, air and space – and each has a particular