Resource variation and the structure of British bird communities

(competition/seasonality/niche overlap)

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ABSTRACT Data on the foraging microhabitats of British birds are reanalyzed with the aim of understanding how fluctuations in resource abundance affect niche relationships and community structure. At Marley Wood, overlap in the foraging sites of resident bird species increased during the late spring and summer and decreased during the fall and winter. Among bird species coexisting in the pine forests at Thetford Chase, spatial overlap and spatial niche widths were positively correlated with food abundance over a 4-year period. These results suggest that in variable environments similarity in spatial niches is an inverse function of the intensity of competition for food. As food supplies drop, consumer species must apparently occupy increasingly different foraging areas in order to coexist. In less variable environments, however, resource stability may allow finer partitioning of the available foraging space and greater spatial overlap within a given foraging area. The results of this paper also suggest a reinterpretation of MacArthur's study of resource partitioning among warbler species in the boreal forests of New England. Rather than providing an instance of niche segregation in order to avoid intense competition, MacArthur's warblers may actually represent another example of increased spatial similarity when food resources are abundant and competition is reduced.

During the 1950s the British ornithologist John Gibb made a series of exceptionally detailed observations on British bird communities at Marley Wood and Thetford Chase (1, 2). In this paper, I reanalyze his data with the aim of understanding how variation in resource abundance affects niche relationships and community structure.

At Marley Wood, Gibb (1) made monthly observations on the amount of time resident bird species spent foraging in various microhabitats such as branches, twigs, buds, leaves, and boles. Using these data, I have calculated spatial overlap values among five species of *Parus* and the Goldcrest (Table 1). The overlap measure employed was the Pianka–May formula (3, 4). Fig. 1 plots spatial overlap between the Great Tit and the Blue Tit and the Great Tit and the Coal Tit from September to August. As Fig. 1 illustrates, spatial overlap was nearly complete during the summer months, then decreased during the fall and winter, and reached a minimum value in the early spring. Of the 15 possible pairs of species, 13 exhibited a similar pattern of high spatial similarity during the summer followed by decreased overlap during the fall and winter.

Unlike the majority of species at Marley Wood, the Coal Tit and the Marsh Tit were very similar in feeding stations throughout the year. However, further data provided by Gibb indicate that overlap between these species actually does decrease during the winter because they begin feeding in different kinds of trees rather than at different foraging stations within trees. Coal Tits feed primarily on oaks during the summer and winter, whereas Marsh Tits feed increasingly less on oaks as the winter progresses and more on elders (1). Coal Tits also feed an

FIG. 1. Spatial overlap between the Great Tit (GT) and the Blue Tit (BT) (Upper) and the Great Tit (GT) and the Coal Tit (CT) (Lower) at Marley Wood from September to August.

average of about 3 m higher than Marsh Tits. The other species pair exhibiting high spatial overlap during all months, Long-tailed Tits and Goldcrests, also begin feeding in different kinds of trees during the winter. The overlap in tree species used for foraging by Longtailed Tits and Goldcrests was 0.846 in September, 0.637 in February, and 0.537 in March. Longtailed Tits also spent considerably more time than Goldcrests feeding in trees (52% vs. 26%) and less time in shrubs and herbage (48% vs. 74%).

In the pine forest at Thetford Chase, Gibb (2) not only recorded the foraging sites of the common bird species but also measured the stock of invertebrate food available from 1953 to 1957. As Table 2 and Fig. 2 show, spatial overlap among Blue Tits, Coal Tits, and Goldcrests increased as food supplies increased. The outlying point in Fig. 2 represents data taken during November and December 1955, when overall food abundance was low yet spatial overlap was high. Closer inspection of Gibb's data reveals that during this period overlap was high because the birds at Thetford Chase were spending unusual amounts of time feeding on pine cones. Subsequent

Table 1. Spatial overlap values from September to August for various pairs of bird species at Marley Wood

Pair	Spatial overlap by month											
	S	O	N	D	J	F	M	A	M	J	J	A
GT-BT	0.797	0.633	0.671	0.616	0.497	0.475	0.236	0.248	0.833	0.997	0.996	0.992
GT-CT	0.950	0.849	0.896	0.817	0.755	0.800	0.595	0.479	0.692	0.907	0.916	—
GT-MT	0.849	0.979	0.902	0.814	0.763	0.649	0.741	0.576	0.870	0.956	0.963	0.712
GT-LT	—	0.187	—	0.199	0.127	0.195	0.147	0.057	0.603	—	0.901	0.633
GT-GC	—	0.289	0.299	0.208	0.086	0.092	—	0.025	—	—	—	—
BT-CT	0.860	0.796	0.771	0.838	0.895	0.644	0.875	0.853	0.849	0.899	0.929	—
BT-MT	0.842	0.696	0.647	0.520	0.648	0.734	0.632	0.850	0.958	0.948	0.956	0.711
BT-LT	—	0.455	—	0.805	0.830	0.659	0.467	0.766	0.850	—	0.907	0.674
BT-GC	—	0.627	0.805	0.798	0.786	0.522	—	0.751	—	—	—	—
CT-MT	0.782	0.898	0.948	0.852	0.855	0.871	0.921	0.926	0.789	0.969	0.981	—
CT-LT	—	0.275	—	0.558	0.695	0.448	0.579	0.758	0.884	—	0.876	—
CT-GC	—	0.522	0.429	0.556	0.651	0.439	—	0.704	—	—	—	—
MT-LT	—	0.271	—	0.231	0.356	0.445	0.601	0.823	0.722	—	0.899	0.787
MT-GC	—	0.490	0.347	0.245	0.268	0.396	—	0.812	—	—	—	—
LT-GC	—	0.914	—	0.998	0.989	0.972	—	0.994	—	—	—	—

GT, Great Tit (*Parus major*); BT, Blue Tit (*P. caeruleus*); CT, Coal Tit (*P. ater*); MT, Marsh Tit (*P. palustris*); LT, Longtailed Tit (*Aegithalos caudatus*); GC, Goldcrest (*Regulus regulus*).

analysis of the insect samples indicated that during November and December of 1955 the pine cone-infesting larvae of the moth *Ernarmonia conicolana* were 5–7 times as dense as in other years (5). Thus, the anomalously high overlap at this time appears to represent the opportunistic exploitation of a super-abundant food source.

At Thetford Chase, spatial niche widths also changed as food supplies fluctuated. The Blue Tit, Coal Tit, and Goldcrest all diversified their foraging sites as food supplies increased and contracted their spatial niches as food supplies decreased (Table 2). As Fig. 3 shows, the correlation between spatial niche width and resource abundance was particularly strong for the Blue Tit and the Goldcrest.

What factors generate the changes in spatial niche relationships at Marley Wood and Thetford Chase? Clearly, competition for food must play a major role. However, the exact mechanism of competition is presently uncertain. Elsewhere (unpublished), I have suggested that, as resources decrease, individuals should exclude other members of the community from their foraging areas via interference competition, because allowing spatial overlap with competitors would further reduce rates of energy intake. As food abundance increases, the potential gain in food consumption resulting from spatial exclusion

is reduced and approaches zero when food abundance is so high that individual feeding rates are at their maximum possible values, regardless of the presence or absence of competitors. Thus, as resource levels rise and the benefits of spatial exclusion compared to the costs are reduced, greater spatial overlap should be tolerated.

Foraging theory, on the other hand, suggests that changes in spatial overlap and spatial niche widths within communities may be regulated entirely by changes in exploitative competition (6). As food levels drop, species should theoretically cease foraging in areas where more efficient competitors reduce rates of energy intake to nonprofitable levels. Probably both exploitative and interference competition combine to affect the niche relationships of consumer species in fluctuating environments. At Marley Wood, for example, the number of sup-

Table 2. Average spatial overlap and niche widths for three bird species at Thetford Chase, with concurrent data on invertebrate density

Year	Months	Average spatial overlap	Food supply, g/hectare	Niche width		
				BT	CT	GC
1953–54	N–D	0.830	560	2.26	1.74	1.83
	J–F	0.611	239	1.45	1.75	1.84
	M–A	0.748	120	1.90	2.17	1.52
1954–55	N–D	0.872	31	2.37	1.81	1.71
	J–F	0.371	15	1.34	1.74	1.22
	M–A	0.344	17	1.00	2.93	1.11
1955–56	N–D	0.686	171	2.97	3.83	2.61
	J–F	0.498	78	2.40	5.32	1.39
	M–A	0.409	108	2.39	3.45	1.46
1956–57	N–D	0.675	143	2.54	1.95	1.88
	J–F	0.852	133	2.64	1.62	1.73
	M–A	0.768	217	2.29	3.25	2.08

Niche width is $1/\Sigma P_i^2$, in which P_i is the proportion of total foraging observations in habitat category i . BT, Blue Tit; CT, Coal Tit; GC, Goldcrest. One hectare = 10^4 m².

FIG. 2. Average spatial overlap among Blue Tits, Coal Tits, and Goldcrests in the pine forests of Thetford Chase, plotted against invertebrate food supply for various time periods between 1953 and 1957. The outlying point (O) is for November and December 1955. At this time spatial overlap was higher than expected given the overall supply of resources because bird species at Thetford Chase were feeding primarily on pine cones infested by an outbreak population of *Ernarmonia conicolana*.

FIG. 3. Spatial niche widths of the Blue Tit (BT) and the Goldcrest (GC) at Thetford Chase plotted against invertebrate abundance at various time periods between 1953 and 1957.

planting attacks between species rises during the autumn as resource abundance decreases (1). Dominance hierarchies are also known to exist among the *Parus* species at Marley Wood and Thetford Chase (2, 7). As Morse (8) has shown, increased aggression between dominant and subdominant species often promotes a decrease in niche width and niche overlap.

An inverse correlation between spatial niche segregation and resource abundance has also been documented among other species occurring in seasonal environments, including *Anolis* lizards (unpublished data), Galapagos Finches (9) and temperate and tropical fish (10, 11). To avoid competitive exclusion, then, species in variable environments must apparently occupy increasingly different spatial niches as food abundance drops. In stable environments, however, resources should never drop to such low levels that species are forced to forage in totally different areas in order to coexist. Consequently, species in

stable environments should be able to partition space more finely than species in variable environments, and, within a given foraging area, should tolerate greater spatial overlap.

Finally, Gibb's data suggest a reinterpretation of the classic case of resource partitioning among temperate forest birds: the five warbler species in the genus *Dendroica* that occur together in the boreal forests of New England. The five species are similar in size, breed in the same habitats at about the same time, and forage in the same trees (12). Observations by MacArthur demonstrated differences in foraging microhabitat within trees that presumably allow the species to coexist. However, even within trees considerable similarity exists among species, with 6 of 10 possible pairs having spatial overlap values of 0.5 or greater. Thus, rather than providing a case of niche segregation in order to avoid intense competition, MacArthur's warblers may actually represent another example of increased spatial similarity when food resources are abundant and competition is reduced.

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