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Evidence for interspecific competition among European tits Parus spp.: a review

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Superficial community data allow only weak inferences on the existence of interspecific competition among tit guilds. Only some of the many "niche" studies allow sound tests of null hypotheses that have relevance for interspecific competition.

Foraging site shifts of northern European coniferous forest tits between geographical areas and flocks containing different species are strong evidence of interspecific competition. In particular, the avoidance of foraging sites of putative competitors when these are present in flocks is exceptionally strong non-experimental evidence. In one study these shifts have been confirmed experimentally. The effects of competition on populations are well established, also experimentally, for *Parus caeruleus* and *P. major* in Belgium, England and the Federal Republic of Germany. Three studies give evidence for competition as a factor affecting evolution of morphological characters.

Taken together, the evidence for interspecific competition is already extensive, but it is still difficult to draw firm conclusions about the importance of interspecific competition in structuring tit communities.

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1. Introduction

Niche studies have been very popular during the last decade. The methods of niche separation have been disclosed and it has been assumed that interspecific competition is a major force in the evolution of niche differences. However, the descriptive observations rather seldom allow the testing of null hypotheses, the rejection of which would give solid evidence for interspecific competition. The weakness of much of the data has made many people doubt whether competition is at all important in structuring animal communities (e.g. Wiens 1977, Connor & Simberloff 1979, Connell 1980, Lawton & Strong 1981).

European tits (*Parus*) are perhaps the best studied group of birds as regards population ecology (for reviews see Lack 1966, Perrins 1979). Niche differentiation between tits had been studied extensively already before MacArthur's (1958) seminal paper on North American warblers. Hartley (1953), Gibb (1954) and Betts (1955) worked with tits in English deciduous woodlands, whereas Haftorn (1954, 1956a, 1956b, 1956c) studied feeding and storing behaviour in three tit species of Norwegian coniferous forests. Snow (1954a, 1954b) reviewed the habitat selection of tits of the whole of Eurasia, and he also made some observations of foraging differences in Swedish tits (Snow 1949). As early as 1932 Palmgren wrote a most inspiring paper on the "resource partitioning" of *Parus montanus* and *Regulus regulus* in Finland, with emphasis on "ecomorphological" relations.

Since then, many more papers have been published and I will refer to them only later in the text. In this review I will give emphasis to papers that have given the most rigorous tests of interspecific competition. I will attempt to see whether we have come far enough to make sound conclusions on the role of interspecific competition among tits.

2. Deductions from superficial community data

Superficial data on community structure, e.g. species lists accompanied by abundance estimates or some morphological measures, are of quite restricted value in assessing the importance of competition in structuring communities. It is difficult to rule out the multitude of factors other than competition which affect such parameters, and only few analyses have been made for tits along these lines.

It is hardly to be expected that interspecific competition would produce strictly regular, deterministic size ratios between coexisting species. Instead it may be reasonable to expect that, if interspecific competition is important, morphologically very similar species are less likely to coexist than species that are more different. In fact, in the absence of interspecific competition we should expect the opposite trend since species with similar morphology are likely to be adapted to exploit similar habitats. Herrera (1981) analysed the "assembly rules" of western European tit communities. He found that mean interspecific difference in bill length was significantly higher in those combinations of the six species that did occur than in those that did not occur. Almost all the assemblages included the species with extreme bills (*major* and *caeruleus*), whereas species with average bills (*cristatus, palustris, montanus, ater*) were present only in the largest assemblages. We may question the use of bill length alone in the analysis, as bill shape varies considerably between tit species (Snow 1954a, 1954b, Haftorn 1956c, Lack 1971, Partridge 1976). Differences in other characters, such as foot and leg structure, are also important to the foraging behaviour of tits (Palmgren 1936, Partridge 1976, Norberg 1979). Secondly, Herrera's study is based on a very heterogeneous set of data. From some small areas, he had up to 13 samples representing slightly different habitats, and some areas were represented by several studies, whereas elsewhere whole countries were represented by one census alone.

Alatalo (1981a) tested a competitive null hypothesis for tits and other passerines using the bird census data of Soveri (1940) derived from different forest habitats in southern Finland. I expected that passerine species belonging to different genera would be less likely to compete with each other than congeneric species. Therefore, if interspecific competition restricts habitat selection, habitat overlaps between congeneric species should be lower than those between species of different genera. Habitat overlaps between the five tit species (*major, caeruleus, ater, cristatus, montanus*) in all seasons were lower than those between noncongeners, and the difference was significant in two of the four cases. However, this pattern alone provides rather indirect evidence for competition, even though no obvious hypothesis alternative to competition could be identified.

3. Resource utilization studies

Tits are very suitable for niche studies as they are rather easily observable and forage almost continuously. Since the early papers mentioned in the introduction, many more studies have dealt with the foraging sites of tits in Europe:

Finland (Nilsson & Alerstam 1976, Alatalo 1980, 1981b, 1982).

Sweden (Ulfstrand 1962, 1975, 1976, 1977, Alerstam et al. 1974).

Norway (Hogstad 1978).

Denmark (Ulfstrand & Nilsson 1976).

Germany (Ludescher 1973).

England (Gibb 1960, Gibb & Betts 1963, Morse 1978).

Spain (Herrera 1978, 1979, Moreno 1981).

Only a few of these papers provide appropriate tests of null hypotheses which allow us to make inferences about the presence of interspecific competition.

3.1. Resource availability and niche overlap

Competition theory predicts that resource utilization overlaps should decrease with decreasing food availability. Pianka (1974) stated this more precisely in his niche overlap hypothesis, i.e. the maximum tolerable niche overlap should be lower in intensely competitive situations than in environments with lower demand/supply ratio.

In several cases resource utilization overlaps of tits have been studied during different seasons of the year. In Europe, northern Europe in particular, food availability for tits is likely to be lower during winter than during summer. Many studies suggest that foliage-gleaning birds eat only a small part of the available food in summer (Betts 1955, Tinbergen 1960, Gibb & Betts 1963, Lack 1966), whereas in winter they consume a much higher proportion of food resources (Betts 1955, Gibb 1958, 1960, 1966, Solomon et al. 1976, Askenmo et al. 1977, Zajac 1979). Secondly, the provision of extra food during winter has often increased breeding populations of tits:

England — *caeruleus* increased but *major* not affected (Krebs 1971).

Southern Sweden — *major* increased but *caeruleus* not affected (Källander 1981).

Central Sweden — both *cristatus* and *montanus* increased (Jansson et al. 1981).

Finland — *major* increased (von Haartman 1973).

In their careful study, Jansson et al. (1981) showed a doubling of population sizes for tits, and they studied individually marked birds so they could prove that extra feeding increased winter survival. They have also revealed that tits considerably reduce the numbers of spiders on spruce branches during the winter (Askenmo et al. 1977).

Many tit species do hoard considerable quantities of food during autumn for consumption later in the winter (see Haftorn 1954, 1956a, b, c). This behaviour is difficult to interpret if food were not limiting during winter. Furthermore, Gibb (1960) established that winter survival of *ater* was positively correlated with food availability in an English coniferous plantation. In addition, the foraging activity of tits is at its highest during midwinter (Gibb 1954, Ulfstrand 1962). Therefore, food appears to be a limiting factor in winter.

In four out of six studies tits were more separated in terms of their foraging sites or food items during winter than in summer:

England, deciduous forest — feeding sites more segregated in winter (Gibb 1954, see also Lister (1981) who calculated niche overlaps).

England, deciduous forest — diet more segregated in winter (Betts 1955, see Baker & Baker (1973) for overlap values).

England, coniferous plantation — no obvious seasonal trend in foraging site differences (Gibb 1960).

Norway, coniferous forest — more segregation in foraging sites during winter (Haftorn 1956c).

Southern Sweden, coniferous plantation — less segregation in foraging sites during winter (Ulfstrand 1977).

Northern Finland, coniferous forest — more segregation in foraging sites during winter (Alatalo 1980, 1982).

However, comparisons of this kind may suffer because factors other than food availability do vary between seasons, and it is difficult to rule out their effects on the foraging habits of tits. For instance, we cannot be sure how breeding (see Alatalo 1981a) and the presence of migrants in summer affect the situation (see Ulfstrand 1977).

A much more direct way of testing the relationship between food availability and niche overlap is provided by Gibb's (1960, see also Lister 1981) excellent study of tit populations in an English pine plantation. He measured food availability during four winters and at the same time recorded the foraging behaviour of the birds. I estimated the overlap in the utilization of tree parts in Scots pine during January-February for the three most abundant foliage-gleaning species (*Parus caeruleus, Parus ater, Regulus regulus*) using the simple niche overlap index (e.g. Colwell & Futuyma 1971 Eq. 3, Hurlbert 1978 Eq. 1):

$$O_{ij} = 1 - 1/2\ \Sigma|p_{ih} - p_{jh}|,$$

where p_{ih} is the proportional use of resource category h by species i and p_{jh} is the same proportion for species j. Gibb estimated the availability of food (insects and spiders) in the living foliage of pines, where the three species spend two thirds of their foraging activity during the crucial mid-winter. As a measure of food availability I used the monthly minimum invertebrate stock in Scots pine during January-March. The average overlap in tree part utilization increased significantly with the increasing availability of food (Fig. 1). The increase in niche overlap was particularly prominent between *Parus caeruleus* and *Regulus regulus.* However, even this pattern may not be very strong evidence for interspecific competition, since it is reasonable to expect that species in any case change their foraging sites, in some way, with increasing food availability.

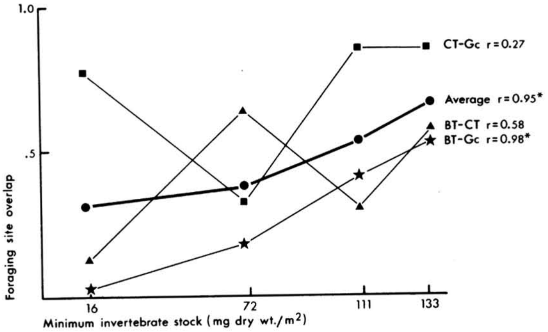

Fig. 1. Foraging site overlap in Scots pine between *Parus caeruleus* (BT), *Parus ater* (CT) and *Regulus regulus* (Gc) against the minimum food supply of the winter in a pine plantation in England (based on Gibb 1960). Asterisks after correlation coefficient indicate significance at $P < 0.05$.

3.2. Geographical niche shifts

Changes in foraging niches in the absence of putatively competitive species give some of the most direct non-experimental tests of interspecific competition. Alerstam et al. (1974) studied foraging sites of tits on both the Swedish mainland and the island of Gotland. In the southern Swedish mainland there are three tit species specialized on coniferous trees (*montanus, cristatus, ater*), but only *ater* is present on Gotland. On the mainland *ater* is strictly specialized to forage on needled twigs of both spruce and pine, whereas *cristatus* and *montanus* forage in the inner parts of trees (Fig. 2). On Gotland, *ater* utilized the inner parts much more frequently than on the mainland. Alatalo (1981) used a similar categorization of foraging sites while studying tits in the coniferous forests of northern Finland where *ater* is

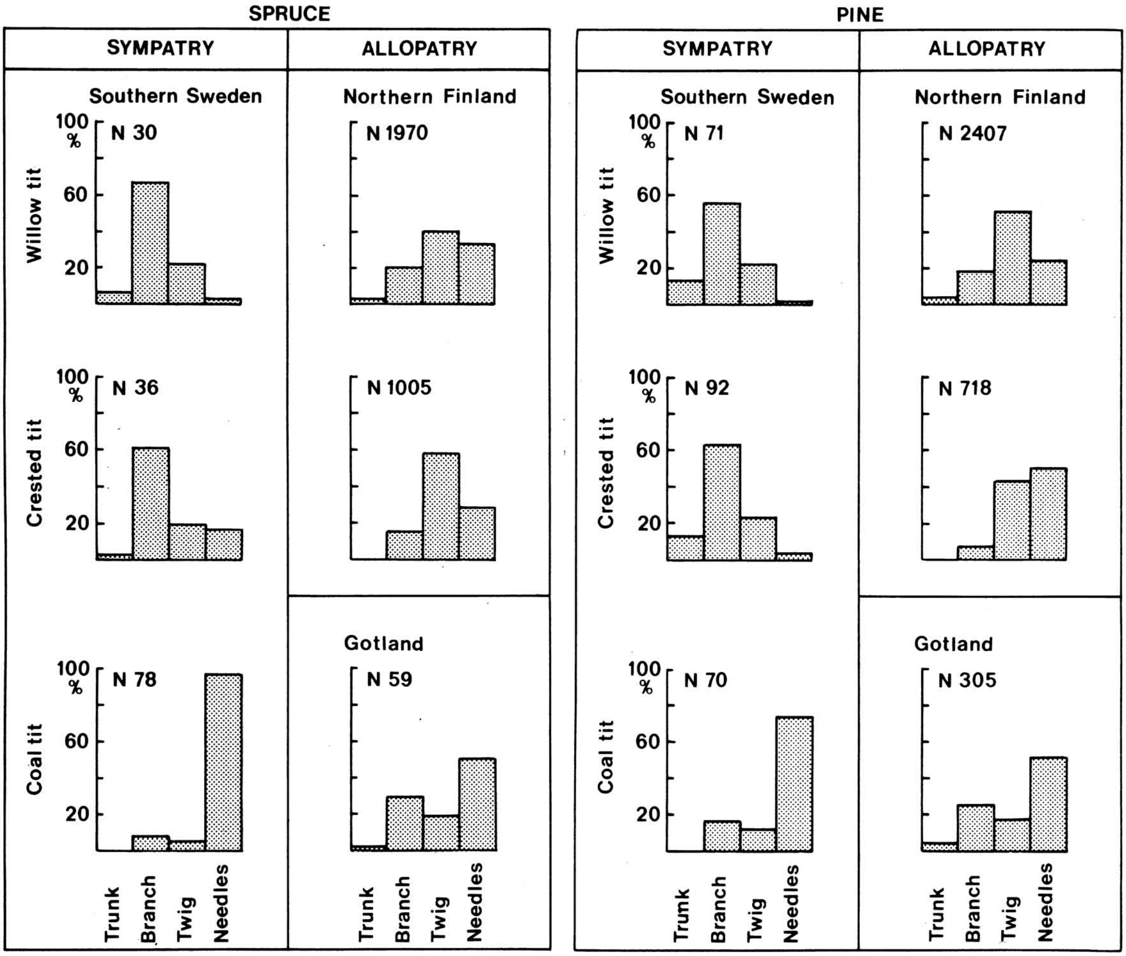

Fig. 2. Foraging sites in spruce and pine for three tit species (*montanus* Willow tit, *cristatus* Crested tit, *ater* Coal tit) during winter in three areas (based on Alerstam et al. 1974 and Alatalo 1982).

not found, but both *cristatus* and *montanus* are present. In both pine and spruce, *cristatus* and *montanus* used needled twigs more frequently than they did in southern Sweden in the presence of *ater* (Fig. 2). For pine the differences are significant at $P<0.001$ (χ^2-test) and for spruce the significance level is $P<0.05$ in *cristatus* and $P<0.10$ (Fisher's exact, 2-tailed) in *montanus*. For testing, to assure independency of observations, I divided the numbers of observations from Oulu by the average number of observations made for each individual at a time (see Alatalo 1982) and from southern Sweden by the applied maximum number of observations per individual (5).

Hogstad (1978) studied the foraging sites of *montanus, cristatus* and *ater* in spruce along an altitudinal gradient in Norway. *Parus cristatus* was present only at the lowest altitudes, and elsewhere *montanus* expanded its foraging activity to those parts of spruce where *cristatus* usually forages. Herrera (1978) studied tits in two similar places (175 km apart) in Spain, only one of which was inhabited by *cristatus*. Among the two other tit species (*major* and *caeruleus*), *caeruleus* in particular changed its foraging sites in the direction of the foraging areas of *cristatus,* when *cristatus* was absent.

What kind of factors other than interspecific competition might produce these geographical niche shifts? The problem with geographical comparisons is that environmental factors other than the presence of putative competitors surely also vary between areas. For instance, food may be distributed in a drastically different way in trees on Gotland and on the mainland. Even though this is highly unlikely in areas so close together, we cannot wholly reject this hypothesis. However, it is less plausible that some other factor(s) had produced all the shifts mentioned above, thus systematically imitating the same direction of effect as can be expected for interspecific competition.

Alerstam et al. (1974) showed that *ater* is much more abundant on Gotland than on the mainland. This fact fits well with the interspecific competition hypothesis, but it also permits alternative explanations (see Wiens 1977). Let us assume that the *ater* population has increased on Gotland for some reason other than relaxed interspecific competition with *montanus* and *cristatus.* The increased intraspecific competition might then cause the expansion of foraging to inner parts of the tree. Nobody has been able to identify any such reasons for the high population density of *ater* on Gotland. Alternative explanations can best be excluded by experiment, where all factors other than the presence of different species are held constant. Such an experiment was performed during winter 1981-82 in central Sweden (Alatalo, Gustafsson & Lundberg, unpubl.). Most of the *montanus* and *cristatus* individuals were removed at the beginning of the winter in a pine-dominated forest area. The remaining individuals of *ater* then used the inner parts of the pines more frequently than those in the control area, and this provides strong evidence for interspecific competition.

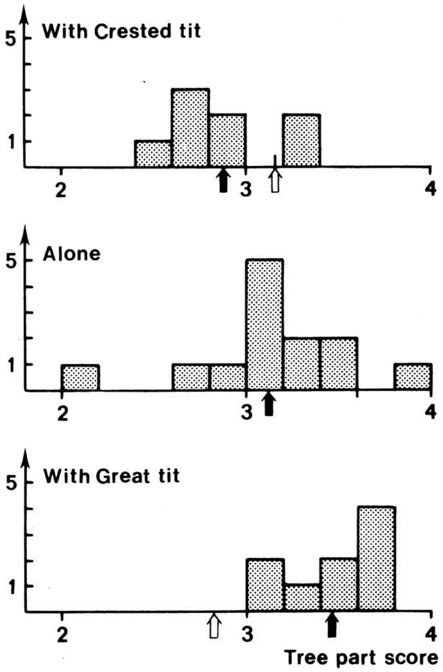

Fig. 3. The average tree part score in spruce for each *montanus* folck: in the presence of *cristatus* (Crested tit), in the absence of *cristatus* and *major* (Great tit), and in the presence of *major*. Observations are from northern Finland during winter (see Alatalo 1981b). Tree parts are scored from larger to smaller diameter (1 = trunk, 2 = branch diameter over 8 mm, 3 = twig, 4 = needled twig). Black arrows indicate the average (over flocks) tree part score for *montanus* in each type of flock, and open arrows give the average tree part score of the putative competitor.

3.3. Foraging shifts and flock composition

Even within the same areas the structure of multispecific tit flocks varies in time and space, making it possible to study foraging behaviour changes related to the presence of other species. Hogstad (1978) observed the foraging sites of *montanus* in the absence and presence of *cristatus* in a coniferous forest area in central Norway. During each of the five study months (November-March) *montanus* moved to the outer parts of spruce, where *cristatus* usually forages, in its absence.

In northern Finland Alatalo (1981b) studied similar foraging shifts in winter tit flocks consisting of *cristatus, montanus, major* (near houses), *ater* (only occasionally in some years) and *Regulus regulus.* Using all possible comparisons, the species avoided one another's foraging sites when moving in the same flock. To illustrate this, Fig. 3 gives the average foraging sites (tree part scores) of *montanus* in spruce in each flock with *major,* with *cristatus* and without these two species. In the presence of *major, montanus* moved to the upper and outer parts of spruce thus avoiding *major*, which forages primarily in the lowest and innermost parts of the tree. On the other hand, in the presence of *cristatus*, which forages in the upper parts of spruce, *montanus* shifted downwards in the tree. The average tree part scores estimated for *montanus* vary significantly between different types of flocks (Kruskal-Wallis test, $H = 10.71$, $P < 0.01$).

These studies provide exceptionally strong non-experimental evidence for interspecific competition. As is always the case with non-experimental data, we must carefully consider factors other than competitive pressure that may vary between flocks of different structure. The flock structure is surely dependent on the type of habitat (Ulfstrand 1975). It is highly likely that the foraging sites of e.g. *cristatus* are more profitable for flocks with *cristatus* than the same sites in those areas where *cristatus* was not observed in flocks. Therefore, in the presence of *cristatus,* and if competition has no effect, *montanus* should

	Resource availability	Species A	Species B
Habitat 1	o o o o o + o +	o o o o o o +	absent
Habitat 2	o + o + o + o +	o o o + o +	+ + o + o +
Habitat 3	+ + + + o + o +	absent	+ + + + + o +

Fig. 4. A schematic illustration of the null expectation, with regard to interspecific competition, for resource utilization shifts of tit species A in the presence and absence of another tit species B in flocks. Species A prefers 'o' as a resource and B prefers '+'. Therefore in habitat 1, where only 'o' is abundant, species A is alone, and in habitat 3, with '+' abundant, only sp. B is in the flocks. In habitat 2, where both resource types are abundant, the two species are together in the flocks. Both species increase the relative use of their preferred resource type with increase in its availability. In consequence, the resource utilization overlaps of the two species are higher when the species are together in flocks, simply because of the shared similar environment. The figure gives only directions of the shifts, absolute values being of no importance to my argument. The argument is solid if 1) neither species prefers habitats where resource types preferred by it are scarce, and 2) neither species reduces the relative use of their preferred resource type if its availability is increased.

increase rather than reduce its use of the foraging sites preferred by *cristatus* (see also Fig. 4). Thus, in the absence of interspecific competition, we expect that tit species will converge in their foraging sites when in the same flock, which makes the above tests for interspecific competition conservative.

Further evidence for current interspecific competition affecting the foraging sites of Scandinavian coniferous forest tits during winter is provided by the experimental study of Alatalo, Gustafsson & Lundberg (unpubl., see Section 3.2), where both *Parus ater* and *Regulus regulus* expanded their foraging areas in pines when *montanus* and *cristatus* were removed from the flocks. Alatalo (1981b) showed that social subordinates were more likely to change their foraging sites than social dominants. Therefore interference competition seems to be involved, but pure exploitative competition may also be important. Interference between individuals of different species in tit flocks (Hinde 1952, Gibb 1954, Ulfstrand 1962, Morse 1978, Hogstad 1978) also points to the presence of interspecific competition.

4. Population effects

In only a few works has interspecific competition been studied in terms of its effects on population size. This is mainly because of practical problems. However, *major* and *caeruleus* are eminently suitable for population studies as they prefer nest boxes as breeding and winter roosting sites.

Competition between species for nesting and roosting holes has apparently been almost too obvious to be studied in detail. Slagsvold (1975) reviewed the competition for nest boxes between *Parus major* and *Ficedula hypoleuca*. Löhrl (1977, see also Dhondt & Eyckerman 1980a) gave experimental evidence for nest and roosting hole competition between *major* and *caeruleus*. In an area in Germany, where *major* was three times as abundant as *caeruleus*, he reduced the size of the openings of nest boxes so that *major* (the larger species) could no longer use them. As a result *caeruleus* became over three times more abundant than earlier. Dhondt & Eyckerman (1980a) carried out an experiment with a control in Belgium during winter, when tits use boxes as roosting sites. The breeding densities of *caeruleus* were almost doubled in the experimental area. They were able to exclude the alternative hypothesis that *caeruleus* simply prefers nest holes with small openings by selection experiments in an aviary. Thus the two species compete for roosting sites during winter, and it is *major* that excludes *caeruleus* from holes.

Dhondt (1977, see also Minot 1978, Dhondt 1978, Dhondt & Eyckerman 1980b) gives correlative evidence for interspecific competition between *caeruleus* and *major* during the breeding season in Belgium. He studied the variation in breeding success in relation to population density of the two species. In particular, *caeruleus* appeared to have a negative effect on the reproductive outcome of *major*. Minot (1981) carried out experiments on food competition between *major* and *caeruleus* during the breeding season in England. The breeding success of *major*, in terms of nestling weight, increased in an area where all *caeruleus* nestlings were removed on hatching.

5. Evolution and interspecific competition

The evidence for competitive co-evolution among animals is very scanty (e.g. Connell 1980) and chiefly consists of cases of character displacement, i.e. sympatric populations of two putative competitors being morphologically more distinct than allopatric populations (Grant 1972, Connell 1980).

Herrera (1978) also measured bill lengths in the study mentioned in Section 3.2, and in the absence of *cristatus, caeruleus* had longer bills (resembling *cristatus*) and foraged more like *cristatus*. However, one must be careful in interpreting such morphological shifts, which may have arisen for reasons other than competition. If morphological shifts have evolved for other reasons, there is a 50 % chance that they are in the direction expected from the competitive hypothesis. For instance, in the case studied by Herrera, the importance of the relation between foraging behaviour and bill length is not considered. The classical example of competitive character displacement among tits is that of *caeruleus* of the Canary Islands (Lack & Southern 1949), where *ater* is not found: *caeruleus* resembles *ater* in both ecology and morphology. Snow (1954a, 1954b) suggested an alternative climatic explanation for this morphological shift. Grant (1979), having considered the two hypotheses thoroughly, found it plausible that both factors have been working in the same direction.

The foraging shift of *ater* on the island of Gotland is accompanied by a morphological shift (Alatalo, Gustafsson & Lundberg, unpubl.). On Gotland *ater* individuals are bigger, thus resembling *montatus* and *cristatus* also in this respect. In general, smaller foliage-gleaners use twigs of smaller diameter (Alatalo 1982), and small size may well be economical for birds foraging on the outermost foliage. Thus the larger size of *ater* on Gotland fits well with its shift to thicker branches. Since the ecological shift of *ater* in the absence of *cristatus* and *montanus* has been verified experimentally (Section 3.2), this study gives strong evidence for competition as an evolutionary force.

6. Concluding remarks

Many studies suggest that European tit species do compete with each other. As always, it may be a matter of taste to define how strong or weak this evidence is. All interpretations of causal relations between natural phenomena give rise to some doubts. We are dealing with hypotheses that are only more or less likely to be true. I argue that the present evidence for interspecific competition between tits is quite strong.

The most rigorous tests of competition between tit species consist of experiments or of careful studies of interacting populations. Superficial community data only seldom allow useful tests.

Experiments, when available, give the most efficient tests, but non-experimental data, with careful consideration of other factors involved, may be equally useful. In many cases, in particular with evolutionary phenomena, experiments are impossible, and then careful scrutiny of natural observations is all we have to work with. We cannot ignore the evolutionary time scale because of the difficulty in studying it, but of course we have to accept the weakness of our explanations in this area.

Even after having established the existence of interspecific competition among coexisting tit species it is difficult to form an opinion of the effects of interspecific competition in the tit guild. It may well partly restrict population densities and resource utilization of all the species in every community, though this may not be true during all seasons and in all years. In this way it is likely to be an important evolutionary force as well. Evidence for interspecific competition in restricting geographical distribution or habitat selection (in other words the species number of each local guild) is much less persuasive, but no rigorous tests have been carried out in this respect. Cases of non-overlapping geographical distribution among European *Parus* spp., probably caused by interspecific competition are few: *cyanus-caeruleus* (Lack 1971, Perrins 1979), *lugubris-palustris* (Lack 1971, Perrins 1979) and *cristatus-cinctus* (Lack 1971, Järvinen & Väisänen 1979).

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