

INTERSPECIFIC COMPETITION AND NICHE CHANGES IN TITS (*PARUS* spp.): EVALUATION OF NONEXPERIMENTAL DATA

RAUNO V. ALATALO, LARS GUSTAFSSON, AND ARNE LUNDBERG

Department of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden

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Many recent papers have focused on the question of testing causal processes affecting community structure, in particular, interspecific competition (e.g., Connell 1975, 1983; Wiens 1977, 1983; Connor and Simberloff 1978, 1983; Birch 1979; Strong 1980, 1983; Quinn and Dunham 1983; Roughgarden 1983; Salt 1983; Schoener 1983; Simberloff 1983; Strong et al. 1984; James and McCullough 1985). Without doubt, well-done experiments, when feasible, provide the most convincing tests. The role of nonexperimental results is much less clear, and ecologists largely disagree on their value.

Initially, one of the most promising approaches to the study of interspecific competition was the analysis of niche changes in ecologically closely related species in areas of allopatry and sympatry. Sympatric populations often are less similar in their resource niches or morphological characters than are allopatric populations (Nilsson 1963; Willis 1966; Diamond 1970; Huey et al. 1974; Fenchel 1975). The major problem in interpreting these "natural experiments" is that different geographic areas are never exactly alike in resource availability or in other biotic and abiotic factors (Grant 1972, 1975; Strong et al. 1979; Connell 1980; Arthur 1982). Therefore, in any case of niche change, differences in the environment, irrespective of the putative competitor, could be responsible for the observed changes. It is difficult to identify all the possible alternative environmental causes of niche variation, and none but the most recent studies have even attempted this. There are two ways to test for alternative causes. The first is to do a controlled experiment. The second is to try to identify alternative explanations and gather data that make it possible to refute the alternatives or the competition explanation. The experimental way may be easy, difficult, or impossible depending on the case under study. The nonexperimental way is always tedious.

In recent years, many kinds of neutral community models (e.g., Connor and Simberloff 1978, 1979; Strong et al. 1979; Alatalo 1982c; Diamond and Gilpin 1982; Gilpin and Diamond 1982; Colwell and Winkler 1984; Schlüter and Grant 1984) have been used to evaluate interspecific competition. Random assemblages of communities have been constructed excluding, as far as possible, interspecific competition from the many assumptions of the models. Neutral models are noth-

ing more than complicated null hypotheses allowing a statistical test. We do not believe that such models alone allow us to make strong inferences about causal processes. Communities are far too complexly affected by a plethora of factors (competition, predation, parasitism, mutualism, abiotic factors, among others) to make it easy to exclude alternative explanations for any possible deviation from the neutral models. The chances of making better causal inferences are greater if we instead concentrate on detailed studies of closely interacting populations (see, e.g., Schlüter and Grant 1984).

In this paper, we evaluate niche changes in the well-studied bird genus *Parus* (tits; see reviews in Lack 1971; Perrins 1979; Alatalo 1982a). Are niche changes caused by interspecific competition, or are they a consequence of differences in the environment alone? Three general questions should be kept in mind: (1) Is it possible to make strong inferences of causes on the basis of patterns observed in nature, or are the patterns suitable only for detection and formulation of possible explanations? (2) Is there a definite boundary between the strength of inferences based on experimental tests and those from nonexperimental tests? (3) What kind of nonexperimental data allows the strongest inferences?

GEOGRAPHIC NICHE CHANGES

The Data Base

Tits (*Parus* spp.) are small, resident birds that forage mainly in trees on insects, spiders, and seeds. They frequently participate in mixed-species flocks outside the breeding season. Besides tits, we consider two ecologically related species: the goldcrest (*Regulus regulus*), which gleans insects and spiders in the outer parts of trees; and the treecreeper (*Certhia familiaris*), which gleans insects on the trunk and major branches. Sympatric species of the tit guild do exploit in part the same resources, which are likely to be limited, particularly in winter (see Alatalo 1982a).

Seven geographic comparisons with quantitative data either on foraging niches or on morphological characters are known to us (table 2; for species included, see table 1). Case 2 is based on our data from central Sweden and the Åland Islands, which are compared with the study of Alatalo (1980, 1982b) from northern Finland. (For details and some new information confirming the niche and population expansion of coal tits [*Parus ater*] on the island of Gotland [case 1], see the Appendix.) Studies 1–4 illustrate changes in foraging sites within trees (microhabitats); studies 5 and 6 focus on habitat expansions. Study 7 is based on hoarding sites within trees (foraging and hoarding sites are closely related; see Haftorn 1956). Three of the ecological-niche changes in the tits also involve changes in morphology, the direction of which could be attributable to interspecific competition (table 2, Appendix). However, the morphological data are too few to allow any general tests, and in the following, we consider only ecological changes.

As an example of ecological changes, figures 1 and 2 illustrate changes in the niches of crested (*Parus cristatus*) and willow tits (*Parus montanus*) in three

TABLE 1
LIST OF SPECIES INCLUDED AND THEIR BODY WEIGHT

Species	Common Name	Weight (g)*	N
<i>Parus major</i>	Great tit (GrT)	19.3	26
<i>Parus palustris</i>	Marsh tit (MaT)	12.6	29
<i>Parus caeruleus</i>	Blue tit (BlT)	11.9	15
<i>Parus cinctus</i>	Siberian tit (SiT)	11.7	12
<i>Parus cristatus</i>	Crested tit (CrT)	11.5	20
<i>Parus montanus</i>	Willow tit (WiT)	11.4	39
<i>Parus ater</i>	Coal tit (CoT)	9.5	10
<i>Regulus regulus</i>	Goldcrest (GoC)	5.3	1
<i>Certhia familiaris</i>	Treecreeper (TrC)	9.2	1

* Our live measurements from central Sweden during winter, except weight of the Siberian tit, which is from Haartman et al. 1972.

northern European study sites (case 2). In northern Finland, coal tits are rare, and goldcrests are relatively few in number. In general, these two species exploit the outermost tree parts for foraging. In northern Finland, they constituted only 10%–15% of the guild, whereas in the two southern areas they accounted for 55%–70%. Only 27% of the flocks with willow or crested tits were joined by goldcrests or coal tits in northern Finland, but in central Sweden the corresponding figure was 72%. Goldcrests and coal tits showed no significant changes in foraging sites over the three areas, but crested and willow tits expanded their foraging to needles in northern Finland. Such a shift could be explained by interspecific competition, but without further information, alternative explanations, such as increased relative food availability on the needles in northern Finland, cannot be excluded.

Directions of Niche Changes

Here, we consider only directions of niche changes because in all seven studies they can be unequivocally defined. Niche changes can be divergent or convergent. In *divergent* changes, species *x* reduces its use of foraging sites used by species *y* in its presence (sympatry) compared with an allopatric situation. If species *x* in sympatry increases the use of the foraging sites of species *y*, niche changes are *convergent*. Divergent changes, if they are caused by interspecific competition, are equivalent to the so-called niche shifts.

We quantified niche changes (see Alatalo 1981) by estimating *actual niche overlap* ($\sum \min [p_{xi}, p_{yi}]$, where p_{xi} is the proportional usage of site *i* by species *x* and p_{yi} is the corresponding proportion for species *y*) between species *x* and *y* in sympatry, and compared it with the *potential niche overlap* that would arise if species *x* had foraged as it did in allopatry. The difference (potential minus actual) between overlap values estimates the effect of a foraging-site change by species *x* on the niche overlap between the two species. If species *x* in sympatry avoids the foraging sites of *y*, the sign of the difference is negative (divergent change). In the case of niche convergence, the sign is positive.

For many purposes, the use of overlap indexes can be criticized since different indexes produce different absolute overlap values, and there is no way to argue

TABLE 2

SUMMARY OF THE GEOGRAPHIC NICHE CHANGES IN TRS

Case	Species Absent in Allopatry*	Species with Shift*	Ecological Changes in Sympatry†	Morphological Changes in Sympatry	Associated Species with No Significant Changes*
1. Gotland-Swedish mainland	CrT, WiT	CoT	Divergent(−.289) (less in inner tree parts)	Divergent	GoC(+.039) TrC(+.003)
2. Northern Finland-central Sweden, and Åland	CoT, GoC	WiT CrT	Divergent(−.216) Divergent(−.307) (less in outer tree parts)	?	GrT(−.012) TrC(+.015) CoI(+.029)‡ GoC(+.040)‡ CoT(−.033)
3. Norway: medium altitude-low altitude	CrT	WiT	Divergent(−.084) (less in outer tree parts)	?	
4. Spain: El Chinche-Caravales	CrT	BiT	Divergent(−.149)§ (less on ground and twigs)	Divergent	GrT(−.074)
5. Åland-central Sweden	MaT	WiT	Divergent(−.249) (less in deciduous habitats)	No shift	BiT(−.061) GrT(−.016) CoT(−.002) CrT(−.059) TrC(−.090) GoC(−.053)
6. Canary Islands-northern Africa	CoT	BiT	Divergent (less in coniferous habitats)	Divergent	—
7. Sweden: Norrbotten-Lappland	SiT	WiT	Divergent(−.415) (less in upper tree parts)	?	—

SOURCES.—1. Ålerstam et al. 1974; this study; U. M. Norberg and R. Å. Norberg, pers. comm. 2. This study. 3. Hogstad 1978. 4. Herrera 1978. 5. Alatalo et al. 1985b. 6. Lack and Southern 1949; Grant 1979. 7. Alatalo and A. Carlson, MS.

* For abbreviations, see table 1.

† The direction and effect of niche change on niche overlap with the species absent in allopatry are given in parentheses (niche overlap in sympatry minus expected overlap if species in question had foraged as it did in allopatry; negative values indicate divergence at sympatry, and positive values imply convergence). If several estimates were available, the average of the values is given.

‡ These "missing" species were present in small numbers in the area of allopatry.

§ A statistical test of the ecological shift was not possible, but the corresponding morphological shift was significant.

|| Strictly quantitative data on this habitat shift were not available, but the shift is well established, and corresponding morphological differences are significant.

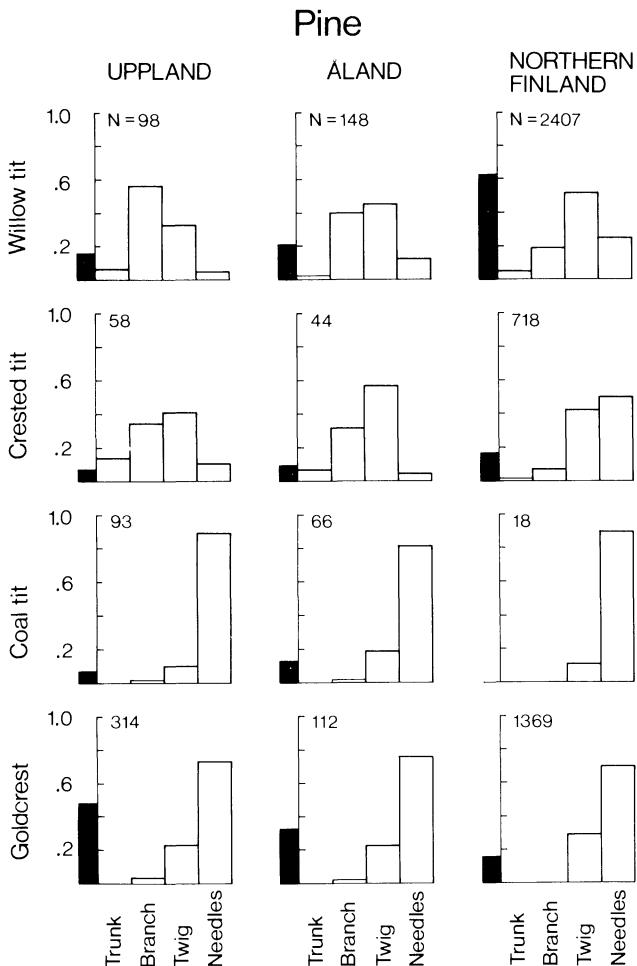


FIG. 1.—The foraging sites of tits and the goldcrest in pine trees during winter in three different areas. Solid columns illustrate the relative proportion of the guild made up by each species in pine.

that the index used here is the only correct one. However, niche-overlap indexes per se cannot produce bias in favor of divergent or convergent changes in a comparison like ours. (Different indexes do yield slightly different results, and one must take care not to select the index that gives the highest significance in tests.)

All seven studies reported at least one ecological niche change in the direction to be expected if interspecific competition restricts foraging niches of sympatric tits (see table 2; divergent change indicated by a negative sign). None of the studies reported significant convergent changes, which should be equally likely if some random factor were responsible for the changes, irrespective of competition.

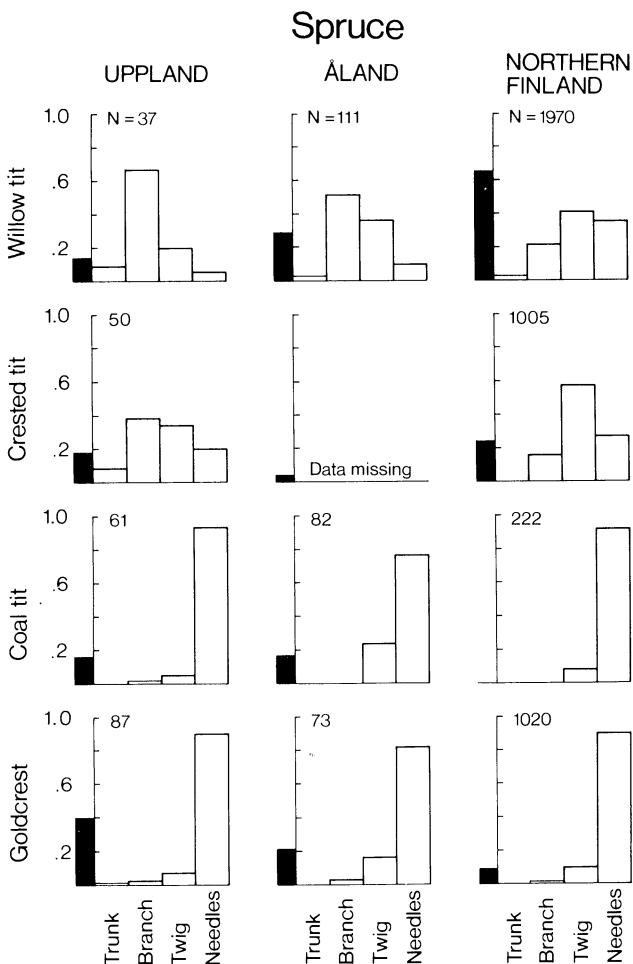


FIG. 2.—The foraging sites of tits and the goldcrest in spruce trees during winter in three different areas. Solid columns illustrate the relative abundance of each species within the guild in spruce.

We can test if the directions of the changes deviate from a null hypothesis of niche changes with no directionality. In eight cases, the foraging niche of a species changed in the direction that would be expected because of interspecific competition. The random probability of all eight changes being divergent rather than convergent is $(\frac{1}{2})^8$, or 0.004 (binomial test). One could argue that we should not exclude the species with no significant changes from this test. In any case, the significant tendency toward divergent rather than convergent niche changes remains if all 21 estimates of niche-change direction from table 2 are considered (Wilcoxon matched-pairs signed-ranks test, $T = 29$, $P < .01$). The result is significant, even though most species made no apparent changes, since in every study one or two species made clear divergent changes.

Species Exhibiting Divergent Niche Changes

If interspecific competition is important, divergent changes should be most likely in species whose fundamental niches are similar (see Pacala and Roughgarden 1982; Schoener 1983). In considering foraging sites within habitats (cases 1–4, 7), one would expect divergent niche shifts in species that most resemble the absent species in body size (for sizes, see table 1). In general, foraging sites of foliage gleaners are related to body size, with the heaviest species foraging in the innermost tree parts and the smallest on the outermost (Alatalo 1982b). An exception is the treecreeper, which possesses special morphological adaptations for foraging on the trunk (Norberg 1979), and it can be assumed to be least likely to shift in the absence of tits. As an example, on the island of Gotland (case 1), the coal tit should be the first species, rather than the goldcrest or the treecreeper, to expand its foraging to the inner tree parts left vacant by absent willow and crested tits.

In case 5 (the Åland Islands), habitat distribution was used for the analysis; hence, differences among species were not related to body size. The bills of coniferous-forest tits are more slender than those of deciduous-forest tits (Snow 1954; Partridge 1976a,b). In the Åland Islands, a deciduous-forest species, the marsh tit (*Parus palustris*), is absent, and a sibling species, the willow tit, is present. Hence, among the coniferous-forest species on Åland, one would expect the willow tit, which closely resembles the marsh tit in morphology, to be the first species to expand to deciduous forests.

In all cases, niche changes were found in the species that most resemble the absent species morphologically. For instance, on Gotland (case 1), in the absence of willow and crested tits, only the coal tit moved into the tree parts generally used by the absent species. Goldcrests and treecreepers did not change their foraging sites. For the studies that involved several species at allopatry (cases 1–5), the probability of such an extreme result was, respectively, $P = \frac{1}{3}$, $P = \frac{2}{5}$ or $\frac{1}{5}$, $P = \frac{1}{2}$, $P = \frac{1}{7}$, and $P = \frac{1}{2}$. The probability that in all the studies it was only the putative competitors that shifted is $P = .0008$, and the pattern is nonrandom.

Figure 3 summarizes estimated niche changes at sympatry (foraging site within trees, cases 1–4, 7) plotted against similarity in size, with the most similar species missing at the area of allopatry. If interspecific competition reduces overlap, we should expect divergent changes in cases where the weight ratio is smallest. As we argued above, the treecreeper should be less likely to be affected than any of the tits. Likewise, we can include two other control cases based on the observations of “missing” species that were present in small numbers at the area of allopatry (case 2, goldcrest, coal tit). There is a significant correlation between morphologically expected and realized niche changes (Spearman rank correlation, $r_s = .83$, $N = 14$, $P < .001$). This implies that divergent foraging changes are to be expected when another tit species of closely similar size (size ratio 1–1.2) is present in the community and no marked changes are found among the less similar species.

NICHE CHANGES IN FLOCKS

Alatalo (1981; see also Alatalo 1982a) studied mixed-species flocks of tits and goldcrests during winter in northern Finland. These flocks vary in structure in

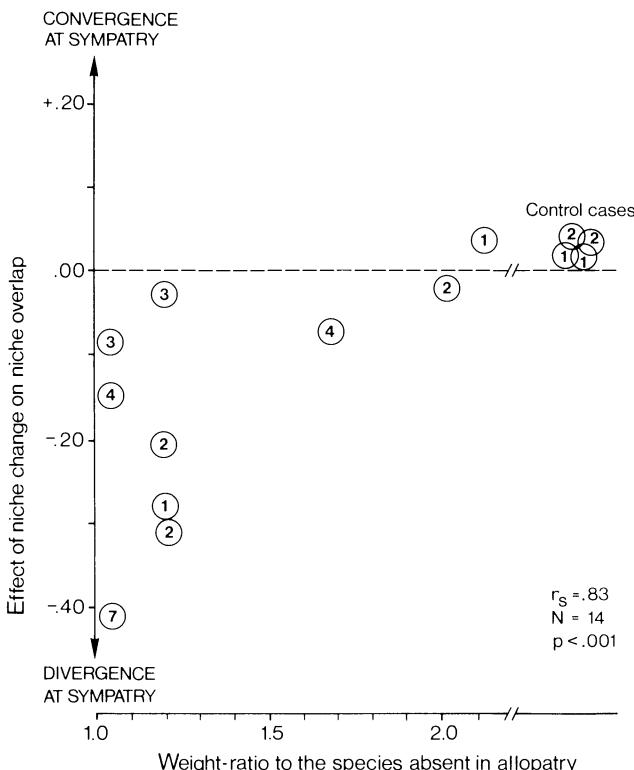


FIG. 3.—The effect of foraging-site change on niche overlap with the species absent in allopatry in relation to the weight ratio with that species. Numbers refer to cases in table 2. Control cases are those in which interspecific competition should not affect foraging sites because of great morphological differences between species (treecreeper compared with tits) or because they are based on observations of a few individuals of the "missing" species at allopatry.

both time and space. Using all the available comparisons, Alatalo found that the species significantly avoided each other's foraging sites in spruce and in pine when foraging together in the same flock. For example, willow tits moved upward and outward in trees in the presence of great tits, which use chiefly the lower and inner tree parts. Among all 40 cases (including even slight and nonsignificant estimates), in 29 cases the foraging change was divergent, in one case there was no change, and in 10 cases the estimated change was convergent.

This implies a significant (binomial test, $P < .01$) tendency toward niche changes lowering the overlap in foraging sites of species when they feed together. On the average, the changes were rather weak, but there are many reasons why these local changes should not be as clear as the geographic changes considered above. The analysis included all possible comparisons so that a general test would be possible, for example, of species as different as goldcrests and great tits (*Parus major*). Often, it was not possible to eliminate all other species when any given

species pair was compared. In many cases, the absence of a species from a flock was only temporary. It is difficult to reach conclusions about the magnitudes of niche changes associated with the presence of each species, but we can conclude that there is a general tendency toward divergence in foraging sites in multispecific flocks.

INTERSPECIFIC COMPETITION OR SOME ALTERNATIVE EXPLANATION?

There is a general pattern of divergent niche changes in sympatric tits. The same pattern holds for tits and goldcrests in mixed-species flocks in northern Finland. The patterns are concordant with the causal hypothesis that interspecific competition restricts foraging-site utilization by these birds. However, differences in the biotic or abiotic environment, irrespective of the presence or absence of putative competitors, may produce changes in foraging sites. The question is whether environmental causes can create *general* tendencies toward divergent rather than convergent changes.

The strongest evidence for interspecific competition is the pattern of divergent changes only in the presence of morphologically similar species (fig. 3). We are not aware of any logically sound alternative explanation for this result, and in the following we consider only the two major ways in which environmental differences could produce generally divergent niche changes.

Variation in Relative Profitability of Foraging Sites

The distribution of food over foraging sites is likely to be variable, and Alatalo (1980) found pronounced monthly variation in foraging-site utilization by tits and goldcrests. The costs and benefits associated with foraging in different parts of trees or habitats can never be the same in two areas, even if interspecific competition does not exist. Yet, if such variation is random with respect to the tit guild structure, it cannot explain the general patterns of divergent changes.

Nonrandom variation could arise if environmental differences are the cause of the absence of putative competitors in allopatry. It is quite conceivable that the resources whose utilization is being observed affect the presence or absence of species. Thus, for instance, in northern Finland, the number of goldcrests and coal tits could be small because of comparatively low food availability at their preferred foraging sites (needles). If so, and if there is no interspecific competition, we would expect the willow and crested tits to forage on needles even less frequently in northern Finland than they do in central Sweden and in the Åland Islands (convergent changes at sympathy).

If factors other than resource availability determine the absence of species in allopatry (e.g., isolation, which is possible for island cases 1, 5, and 6), there is no reason to expect any bias toward convergence or divergence because of the probable differences in resource distribution.

The expectation of convergent niche changes in the absence of interspecific competition is even clearer in comparisons of flocks of different structure (see Alatalo 1981, 1982a), since the study sites were not isolated from each other. When two birds are foraging together, they are exploiting exactly the same

environment; when they are foraging separately, environments differ. Hence, for environmental reasons, their foraging sites should converge, not diverge, in mixed-species flocks.

Variation in Population Size

Above, we considered the possibility that relative profitabilities of foraging sites vary between areas. It is also possible that the absolute food availability varies, causing changes in population sizes of tits. Likewise, other factors, such as reduced predation pressure, could cause an increase in population size. An increase in population size may lead to increased intraspecific competition, with niche expansion as a consequence. Thus, if allopatric populations are denser for reasons other than reduced interspecific competition, a pattern of divergent niche changes unrelated to interspecific competition may result.

Predators are often fewer on islands. It has also been argued that islands are more productive in general. Both factors could lead to increased population sizes on islands, and three of our comparisons (cases 1, 5, and 6) are between an island area of allopatry and a mainland area of sympatry. On the island of Gotland (case 1), many predators present on the Swedish mainland, such as the stoat (*Mustela erminea*), weasel (*Mustela nivalis*), and pygmy owl (*Glaucidium passerinum*), are absent. Coal tits on Gotland have undergone a clear population expansion (Appendix; Alerstam et al. 1974). The density of coal tits is as high as the summed density of the three coniferous-forest tits (coal, crested, and willow tits) on the mainland of southern Sweden, and it is possible that reduced predation pressure has contributed to this enormous population increase on Gotland. However, Gustafsson (MS) has demonstrated that the dominant, older coal tit individuals forage on twigs on Gotland and the subordinate, younger birds forage in the "mainland niche" (needles). If increased intraspecific competition were the sole explanation for the niche expansion of coal tits on Gotland, we would expect subordinate individuals and not dominant individuals to be forced to the foraging sites not utilized on the mainland. Hence, increased intraspecific competition alone does not appear to be a valid explanation of the niche expansion of coal tits on Gotland.

The Åland Islands (case 5) are connected to the Finnish mainland by "stepping-stone" islands (see Järvinen and Haila 1984). Predators of tits that are found on adjacent mainlands are also present on the Åland Islands. Two other facts argue against the hypothesis that increased intraspecific competition in willow tits, due to some island effect, would have resulted in their expansion to a deciduous habitat. First, in none of the other six species were there any significant habitat changes between central Sweden and the Åland Islands. Second, the density of willow tits in their preferred coniferous habitat was not higher in the Åland Islands, which would be the case if increased intraspecific competition were the cause of the habitat expansion.

We are not well acquainted with the third island case (6, blue tits [*Parus caeruleus*] on the Canary Islands). However, there was a significant tendency toward divergent shifts even excluding this case (test based on 20 quantified ecological changes). Therefore, there is no reason to expect that increased

intraspecific competition at allopatry would have biased the direction of the niche changes in our comparison. Neither is it likely that some unknown island effect would explain the results, since there is a significant tendency for divergent changes if only mainland studies of allopatry are included (cases 2, 3, 4, and 7; Wilcoxon matched-pairs signed-ranks test, $T = 10$, $N = 11$, $P < .05$).

Increased intraspecific competition could explain divergence in foraging sites from monospecific to mixed-species flocks if the numbers of individuals for a given tit species were higher in monospecific flocks. However, there was a slight tendency toward an increase in individual numbers in mixed-species flocks. In 30 of the 40 comparisons, there were more individuals of the species in question in mixed-species flocks (binomial test, $P < .01$; average increase, +6.9%).

In sum, we cannot identify any logically sound noncompetitive explanation for the general pattern of divergent niche changes in tits. We emphasize that this does not mean that foraging-site niches are affected only by interspecific competition. However, when allopatry-sympatry comparisons are restricted to reasonably similar environments (sites in the same tree species or habitats of the same type), the presence or absence of morphologically similar guild members appears to be the primary factor causing geographic niche variation.

EXPERIMENTS VERSUS COMPARATIVE APPROACH

Far from arguing against the use of experiments (see Alatalo et al. 1985a for an experiment showing divergent niche changes), we believe that well-controlled and repeated field experiments are the most efficient way of testing for interspecific competition. In experiments, complicating environmental factors can be controlled for, and the presence or absence of the putative competitors should be the only factor varying between experimental and control plots. However, it may not be enough to have only one experimental and only one control plot. Two areas can never be exactly similar, and environmental factors may still have an effect. One has to repeat the experiment in many plots so that a statistical test using each plot as an independent observation is feasible. Many competition experiments do not fulfill this criterion (see review in Hurlbert 1984). Furthermore, one has to be careful to preserve the natural situation, for example, the population density of the remaining species, in the study plots.

Recently, Schoener (1983) and Connell (1983) scrutinized the present experimental tests of interspecific competition. There are discrepancies among authors in the kinds of experiments that are judged to give evidence for interspecific competition. The lesson is that even with experiments, we need to make inferences about the strength of the evidence.

The patterns found in nature are crucial for the formulation of hypotheses that provide possible causal explanations of natural phenomena. But they may also be of use for the evaluation of different hypotheses. Manipulative experiments are not always feasible, in particular if we are interested in the evolutionary time scale. Whenever experiments can be done, they are likely to be more efficient than nonexperimental studies with tedious consideration of the alternative hypotheses. In particular, readers of a paper find it easier to evaluate inferences

based on experiments rather than on natural patterns. However, it is not legitimate to omit nonexperimental evidence if reasonable alternative explanations cannot be pointed out. The possibility of an unconsidered alternative explanation is always present. Hidden alternatives are more probable for nonexperimental than for experimental evidence, but their probability should decrease with increased experience regarding the question at hand.

To make the best use of comparative data, it is important that we include all relevant data in the tests rather than selecting the data that fit our expectations (community-wide tests in the sense of Strong et al. 1979). Moreover, we can make stronger inferences with general patterns than with single observations. For instance, a single sympatry-allopatry comparison is unlikely to allow us to reject the possibility that niche changes are caused by some environmental difference. In tits, divergent changes in foraging sites at sympatry and in mixed-species flocks give strong evidence for interspecific competition since there are no reasonable alternative explanations for such general patterns. At least three other studies reported general patterns of divergent changes (character displacement in fishes, Dunham et al. 1979; character displacement in Galápagos finches, Grant and Abbott 1980 and Schlüter and Grant 1984). In some other studies, general tests may be feasible (e.g., Schoener 1975; Lister 1976a,b).

SUMMARY

The role of nonexperimental observations for testing causal processes, such as interspecific competition, has been questioned during the present "competition controversy." Initially, niche changes between areas of allopatry and sympatry were considered to be strong evidence for interspecific competition. However, any single change may be due to alternative causes, in particular, to differences in the environment irrespective of the presence or absence of the putative competitor. We evaluated niche changes in European tits (*Parus* spp.). In all seven cases studied, one or two species showed a clear, divergent ecological shift in the area of sympatry. Likewise, Alatalo (1981) found a general pattern of divergence in foraging sites in mixed-species tit flocks compared with monospecific flocks. These significant tendencies toward divergent rather than convergent shifts in the presence of putative competitors cannot be explained by differences in the environment alone. The strongest evidence that interspecific competition causes niche changes comes from the observation that, within the guild, changes were found only in the species that morphologically most closely resembled the species that were absent in allopatry (weight ratio ≤ 1.2).

In general, we believe that well-done experiments, if feasible, are the best way to evaluate alternative hypotheses. However, it is also possible to make inferences about causal processes without experiments if alternative explanations of the observed patterns can be refuted. The nonexperimental approach is tedious and requires good knowledge of the animals and the question under consideration. Inclusion of several independent comparisons allowing general tests is of great value.

ACKNOWLEDGMENTS

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APPENDIX

UNPUBLISHED DATA ON THE GEOGRAPHIC NICHE CHANGES INCLUDED IN TABLE 2

COAL TIT ON GOTLAND AND SWEDISH MAINLAND

Three tit species (willow, crested, coal) coexist in the coniferous forests on the Swedish mainland. Most tits are strongly resident, and therefore only the coal tit is present on the island of Gotland 100 km off Sweden's east coast. Alerstam et al. (1974) established that in the absence of willow and crested tits, coal tits had expanded their foraging niche toward the foraging sites of the absent species. Likewise, the population size of coal tits was much higher on Gotland than on the southern Swedish mainland.

Our new data confirm the foraging shift of coal tits on Gotland to inner tree parts. During two winters (January–February 1981 and 1982), the proportions of foraging observations in different parts of pine on Gotland were trunk, 0.07; branch, 0.40; twig, 0.29; and needled twig, 0.24 ($N = 3189$). At the same time, coal tits in central Sweden and the Åland Islands foraged primarily on needled twigs (fig. 1). For testing, we divided observation numbers by the maximum number of observations allowed for each individual on each occasion (20 on Gotland and 5 at the other sites). This approach ensured that observation numbers did not exceed the numbers of independent observations. We rounded decimals so as to reduce the difference between the study sites and used Fisher's exact probability test. The foraging sites of the coal tit both on Åland and in central Sweden were significantly different ($P < .001$) from those on Gotland.

Our data confirmed the elevated population density of the coal tit on Gotland. In a color-banded population, the wintertime density (January–February) of coal tits on Gotland was estimated at 90–110 individuals in a 1-km² pine-dominated forest. At the same time, in a similar forest of 35 ha in central Sweden, we found only seven coal tits, or a density of 20 individuals per km². These estimates are based on at least 20 visits to each area.

The niche change of the coal tit on Gotland is accompanied by an increase in body size (U. M. Norberg and R. Å. Norberg, pers. comm.; Gustafsson, MS). As a result, the coal tit approaches willow and crested tits in morphology, as it does in foraging behavior. In general, small foliage-gleaning species forage on outermost twigs, and larger species use thicker branches (Alatalo 1982b). This trend also holds when individual coal tits of different size in a Gotland population are compared (Gustafsson, MS). Hence, it is reasonable to assume an interrelationship between the morphological and ecological changes of the coal tit on Gotland compared with coal tits on the mainland.

CRESTED TIT AND WILLOW TIT IN CENTRAL SWEDEN, THE ÅLAND ISLANDS,
AND NORTHERN FINLAND

In northern Finland, only a few coal tit stragglers are present. Thus, the situation offers an opportunity to examine whether the crested and willow tits change their foraging sites in the absence of the coal tit. Alatalo (1980, 1982b) recorded the foraging sites of tits during three winters near the city of Oulu in northern Finland. During the winters of 1981 and 1982 (January–March), we used a similar method to study the foraging sites of tits in coniferous forests around the city of Uppsala in central Sweden and on the Åland Islands. We moved

along transects in the forests and made up to five observations of the foraging sites of each individual bird encountered, with an interval of at least 15 s between each record.

In both pine and spruce, the willow and crested tits used outer tree parts much more frequently in northern Finland than at the other sites (figs. 1, 2). To achieve independence of the observations in the tests, we divided the number of observations by the maximum allowed number of five records per individual in central Sweden and the Åland Islands, and by the average number of observations per individual in northern Finland (willow tit, 7.5; crested tit, 13.4). These figures refer to the total number of observations scored for each individual, including observations from different trees. Hence, the approach is conservative. In both pine and spruce, willow and crested tits in northern Finland differed significantly in foraging sites (χ^2 test, $P < .05$) from the two other areas. From Åland, we had only six observations of the crested tit in spruce, and no comparison was possible. In the winter of 1981, spruce had a plentiful seed crop in central Sweden. Only data from 1982 were used for spruce in this area, since it would not make sense to include the data for 1981, when all the species except the goldcrest specialized on the temporarily superabundant spruce seeds.

The goldcrest and the coal tit did not change foraging sites over the three areas ($P > .05$). Neither was there any significant difference between Åland and central Sweden for the willow and crested tit. The scarcity of coal tits might contribute to the niche changes of the willow and crested tits in northern Finland. The other needle specialist, the goldcrest, is also a much less abundant component of the tit guild in northern Finland than in the two southern areas. In central Sweden and Åland, the combined density of needle specialists was higher than that of the willow and crested tit together (abundance relation in pine, 2.4 and 1.6; and in spruce, 1.8 and 1.2, respectively). In northern Finland (January–March), the abundance relation between the two types of birds was reversed. The total density of willow and crested tits in pine was 5.1 times the combined density of coal tits and goldcrests; in spruce, willow and crested tits were 10.5 times as plentiful.

Alatalo (1980) established considerable short-time variation in foraging sites of tits in northern Finland. However, such variation is unlikely to confound our geographic comparison. During all six winter study periods, both the crested and willow tits foraged more in the outer parts of pine and spruce in northern Finland than they generally did during winter in central Sweden and the Åland Islands. In northern Finland during the last two winters of the study, eggs of lachnids (Lachnidae) were abundant on pine needles. This may have contributed to the increased use of pine needles as foraging sites by willow and crested tits. However, such eggs are also common on pine needles in central Sweden, where they are exploited by goldcrests and coal tits alone.

The great tit and the treecreeper, which seldom forage on needles (Alatalo 1982b) and which are morphologically dissimilar to the coal tit, did not show any significant foraging-site changes in spruce or pine over the three areas.

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