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Seed size diversity, bird species diversity and interspecific competition

P. M. Thompson and J. H. Lawton

We created experimental patches with one, two or three sizes of seeds, and recorded the number of species, and numbers of individuals of each species of birds exploiting the seeds in winter. Bird species diversity increased with seed size diversity. The frequency of visits made by each species of bird to the single-seed plots provided us with a measure of seed-size preference for each species. For example, most Bramblings *Fringilla montifringilla* were recorded on plots with sunflower seeds (the largest seeds); Tree Sparrows *Passer montanus* preferred millet, the smallest seeds, and Blackbirds *Turdus merula* preferred seeds of intermediate size (wheat). Using each species' seed-size preferences we were then able to compute the overlap in seed-size use between species. Dietary overlap was not significantly related to similarity in body-size. Competition between species was assessed by fitting Lotka-Volterra competition equations to species counts on the two- and three-seed plots. Most species-pairs showed no evidence of significant interactions. Of those pairs that did interact significantly, several showed significant mutualistic, not competitive interactions. Both competitive and mutualistic interactions varied with seed diversity. Only two species pairs showed consistent competitive interactions on plots with two seed sizes and on plots with three seed sizes; they were, Blackbird-Greenfinch *Carduelis chloris*, and Blackbird-Tree Sparrow.

We compared our estimates of species' competitive and mutualistic effects on each other with our estimate of dietary overlap. There was no significant relationship between dietary overlap and realised interaction. Our results are briefly discussed in relation to current views on the role of interspecific competition as a force structuring bird communities.

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1. Introduction

Since David Lack's classic study of Darwin's Finches (1947), it has become widely accepted that interspecific competition plays a major role in the structuring of natural communities, and in particular, in limiting the number of species present. Of the many subsequent studies in this area, most have simply looked at differences between close relatives which might permit coexistence (e.g. Lack 1971, MacArthur 1972, Cody 1974). Very few studies have been experimental in na-

ture. Experimental studies on competition in bird communities include Pimm (1978), Williams and Batzli (1979), Högstedt (1980), Slagsvold (1980) and Reed (1982).

In the following study, we experimentally varied food resources using three different sizes of seeds, and then looked at the mixed species flocks of seed eating birds that formed to feed on the seeds, during the winter. Using these data, we first looked for correlations between seed size diversity and bird species diversity. Then, by looking at the diet apparently preferred by

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each species, and estimating niche overlap between species, we went on to see how the species using our experimental seed patches "differed in their ecology". Finally, evidence for contemporary interspecific competition was sought by looking at any changes in the abundance of a species when in the presence of other species.

2. Methods

The study area was on the University of York playing fields (Grid Reference SE 627506). The experimental plots were sown grass which was mown regularly during the growing season, and the whole area was backed by a thin strip of deciduous woodland. Sixteen 2 × 1 m quadrats were marked out in a line along the edge of the playing field; a gap of 3 m separated adjacent quadrats. All the quadrats were equidistant from the wooded area, about 20 m away. Although the species composition of the wood varied along the line of quadrats, all were on grass of uniform length and density.

2.1. The experiments

Three sizes of seed were used: millet (mean length 2.25 mm), husked wheat (mean length 6.5 mm) and sunflower (mean length 13.0 mm).

Each plot had one of eight possible treatments assigned to it as follows:

Millet	(M)
Wheat	(W)
Sunflower	(S)
Millet and Wheat	(M.W)
Millet and Sunflower	(M.S)
Wheat and Sunflower	(W.S)
Millet and Wheat & Sunflower	(M.W.S)
Control – no seeds	(C)

There were two replicates of each treatment, assigned at random; the final applications are given in Tab. 1.

To encourage the birds to feed around the plots, the area in between them was baited with bread and a mixture of seeds every three or four days for three weeks preceding the experiment. For the experiment, a standard volume (200 ml), of seeds was scattered as evenly as possible over each quadrat. Two seeds plots therefore received 100 ml of each seed type, and three seed plots 66.7 ml of each. These experimental applications were made at 9.00 a.m. on 1 December, 11.45 a.m. on 4 December, and 9.55 a.m. on 8 December 1981. (The 2nd and 3rd applications were carried out when it was judged that the birds had eaten most but not all the seeds on the experimental plots.) The study area was watched as intensively as possible during this period, all observations being made from behind a church-yard wall, approximately 35 m from the plots, through 8 × 40 binoculars. Every five minutes throughout the observation periods a scan was made along the plots from left to right and numbers of each species on each plot were recorded using a portable tape-recorder.

Tab. 1. Total numbers of each species seen on each quadrat throughout the experiment.

	Total numbers of each species seen on each quadrat															
---	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Starling																
Sternus vulgaris	0	0	0	0	0	0	0	0	0	0	0	`0	0	1	0	0
Dunnock																
Prunella modularis	0	11	2	1	0	3	1	7	14	1	0	10	11	4	1	5
Robin																
Erithacus rubecula	0	0	0	0	0	0	1	1	1	0	0	2	5	6	0	2
Blackbird																
Turdus merula	13	22	33	49	3	61	47	17	34	6	0	7	22	10	7	2
Great Tit																
Parus major	3	0	0	0	0	0	0	0	0	0	0	5	1	4	2	0
House Sparrow																
Passer domesticus	8	37	32	8	0	24	7	12	15	14	0	76	14	23	14	24
Tree Sparrow																
Passer montanus	1	31	58	2	0	2	1	66	114	114	0	20	7	35	2	38
Chaffinch																
Fringilla coelebs	47	17	35	30	1	6	24	31	15	24	0	45	14	47	36	21
Brambling																
Fringilla montifringilla	7	2	2	3	0	1	1	0	1	1	0	6	4	22	16	5
Greenfinch																
Carduelis chloris	91	105	49	44	1	69	47	48	19	21	0	77	72	102	101	62
Seed mixture	S	MW	MWS	WS	C	W	WS	MS	MW	M	C	MS	W	MWS	S	M

3. Results and discussion

3.1. General

During the period 1 December to 10 December 1981, the study area was watched for nearly 15 hours with a total of 174 scans. During this time, ten species were recorded feeding on the study plots.

Total numbers of each species seen on individual plots can be found in Tab. 1. The absence of birds on one control plot and the very low numbers on the other, make it safe to assume that the great majority of birds present on other plots were feeding on the experimental seeds.

3.2. Species diversity

Bird species diversity values (B.S.D.) were calculated for each plot using the Shannon-Weiner index (equation 1) (Southwood 1978). This measure of species diversity has been widely used by ornothologists, because it takes into account the relative abundance of each species.

$$B.S.D. = -\Sigma\ p_i\ \log\ p_i, \tag{Eqn 1}$$

where $p_i = N_i/\Sigma N$ and $N_i =$ the abundance of the i:th species. Bird species diversity was linearly related to the number of seed types present (X) as shown in Fig. 1. The equation is: $B.S.D. = 0.195x + 1.132$, ($r^2 = 0.54$; $F_{1,13} = 15.08$; $p = 0.002$).
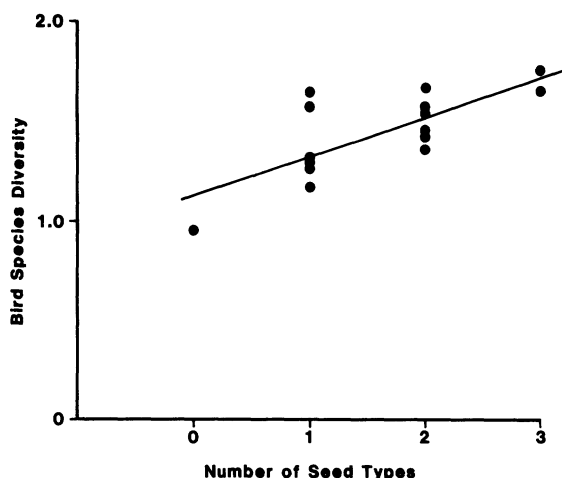

Fig. 1. Bird species diversity calculated using the Shannon-Weiner index plotted against the number of seed types present.

3.3. Resource utilization

By looking at the distribution of birds on the single-seed plots, it was possible to produce 'resource utilization curves' for all species except Starling, which had a sample size of only one. For each species, the number of birds seen on each of these plots was divided by the total number of sightings on all single seed plots. This gave the proportion of time spent feeding on each seed type.
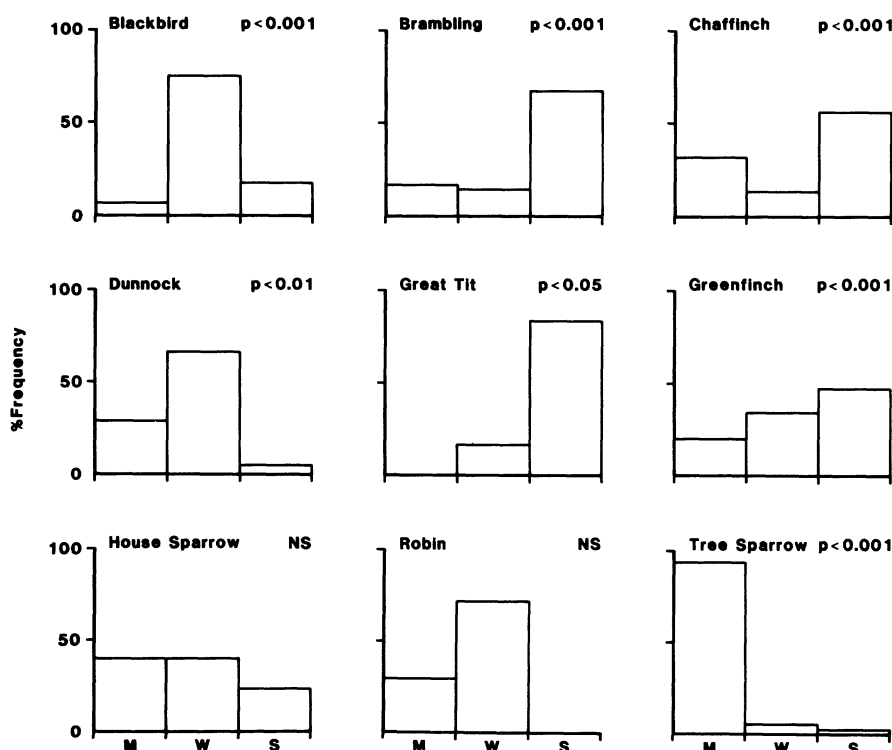

Fig. 2. Resource utilization curves for the species encountered in the study, measured as the proportion of birds seen on each of the single-seed plots. Probabilities test the null hypothesis of no significant preference. Seeds in order of size are M (millet); W (wheat) and S (sunflower).

The resulting distributions are shown in Fig. 2. χ^2-values were calculated for each resource utilization curve, to see if they differed significantly from a random distribution.

Not unexpectedly, nearly all species show a strong preference for one of the three seed sizes. In all cases except Robin, which had low expected values, and House Sparrow, which showed no marked preference for any one seed type, these preferences were significant at the 5% level (2 d.f.). Great Tit, Chaffinch, Brambling and Greenfinch all preferred sunflower, the largest seed, though they also took smaller seeds in varying proportions. Dunnock and Robin both preferred wheat, and though they took millet in smaller quantities, they hardly ever fed on sunflower seed. Blackbirds too preferred wheat, but they were also feeding on the larger sunflower seeds.

Havlin (1961) noted that Blackbirds could not crush very small seeds, and millet often passed through the gut completely undigested. This could explain why this species was rarely seen feeding on the millet plots. Tree Sparrows were the only species to actually prefer millet, and in fact fed on hardly anything else. Pinowski et al. (1972) also found that in laboratory choice experiments using Tree Sparrows, millet was the most eagerly sought seed.

3.4. Niche overlap

For each possible species pair i and j, a dietary niche overlap value $\alpha_{ij} = \alpha_{ji}$ was calculated for the single seed plots using equation 2, from Pianka (1975) (Tab. 2):

$$\alpha_{ij} = \alpha_{ji} = \frac{\sum\limits_{k}^{n} p_{ki}\, p_{kj}}{\sqrt{\sum\limits_{k}^{n} p_{ki}^2 \sum\limits_{i}^{n} p_{kj}^2}} \quad \text{(Eqn 2)}$$

where p_{ki} and p_{kj} are the proportions of the k:th resource used by the i:th and j:th species respectively.

This formula gives a symmetric measure of overlap, with a maximum value of 1 if the two species' diet are identical, and a minimum value of 0 if they share no food resources at all. The results are given in Tab. 2. These alpha values cannot be equated simply with competition coefficients (see, for example, discussions in Colwell and Futuyma 1971, Pianka 1975, Abrams 1980a, b, Toft et al. 1982 and Pacala and Roughgarden 1982). However, our data allows us to test the relationship between dietary niche overlap as listed in Tab. 2, and the intensity of interspecific competition. We can also test whether overlap and species morphologies are related. Do species pairs with high dietary overlap have similar morphologies? We test this possibility first before moving to a study of the relationship between overlap and competition.

3.5. Morphology, food-type and overlap

To test the idea that morphology is closely correlated with food type, both body size and bill size (length) were plotted against the preferred seed size. Body and bill sizes were taken from Witherby et al. (1940). House Sparrow and Robin were omitted from this analysis because they showed no significant preference for any one seed size. As can be seen in Fig. 3 and Fig. 4 there is no significant correlation between preferred seed size and either body or bill size. We did not test bill depth or more complex bill shape functions in these analyses because we lack the data. Hence, it is possible that a correlation could be found between preferred seed size and some aspect of bill morphology. Body size ratios are plotted against dietary overlap in Fig. 5. Again, no significant relationship was found.

None of these results are very surprising. Although ornithologists have often used bill or body sizes to indicate significant differences in species' feeding ecologies (e.g. Lack 1971, Cody 1974, Ricklefs and Cox 1977 and many others), a growing number of studies suggest that this approach is at best a poor indication of dietary overlap (e.g. Wiens and Rotenberry 1980, Hespenheide 1975). It may be justified where a set of closely related species is involved because differences in morphology

Tab. 2. Dietary niche overlap values for all species pairs, calculated from the data in Fig. 2, and eqn. 2.

|	Dunnock	Robin	Blackbird	Great Tit	House Sparrow	Tree Sparrow	Chaffinch	Brambling	Greenfinch
Dunnock	–	0.998	0.940	0.245	0.883	0.449	0.430	0.348	0.692
Robin		–	0.933	0.183	0.851	0.426	0.366	0.283	0.641
Blackbird			–	0.419	0.783	0.155	0.444	0.443	0.749
Great Tit				–	0.499	0.031	0.884	0.969	0.857
House Sparrow					–	0.699	0.766	0.656	0.869
Tree Sparrow ..						–	0.494	0.276	0.375
Chaffinch							–	0.972	0.924
Brambling								–	0.917
Greenfinch									–

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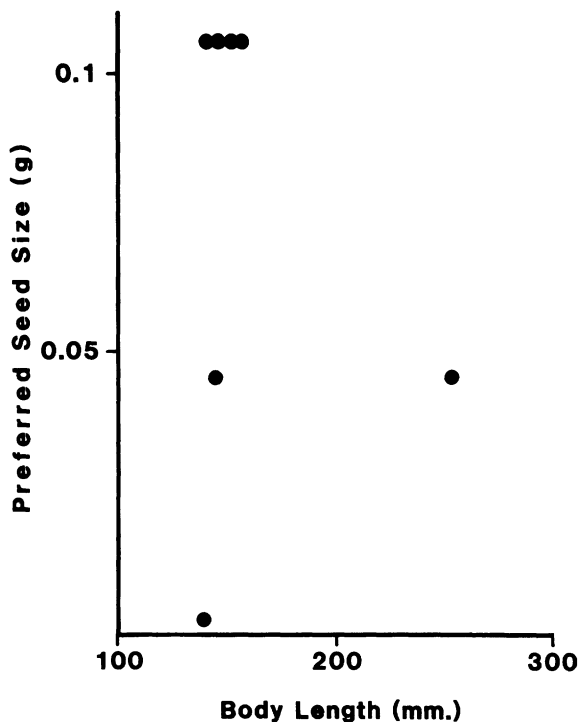
Fig. 3. Body length (mm) vs preferred seed-size (from fig. 2) for all species, except Robin and House Sparrow, where preferred seed-sizes could not be ascertained. There is no significant relationship.
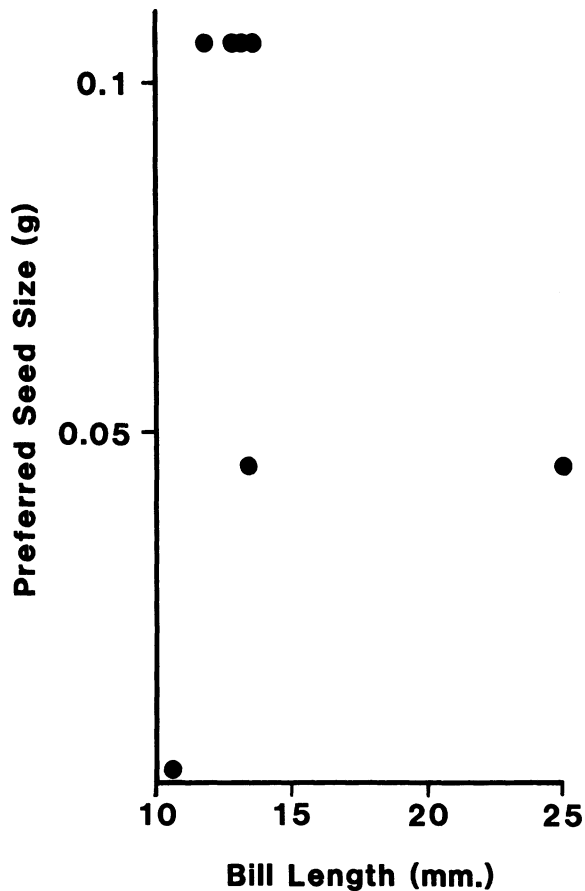
may then reflect differences in feeding ecology. Where distantly related species make up the community under investigation, as here, body and bill sizes may have no significant relationship with food-size.

3.6. Competition and overlap

Tab. 2 shows that many species pairs have a high dietary overlap. Therefore, one might predict that if competition was important, pairs of birds with high dietary overlap should feed together less than expected by chance, whereas those with low food overlap should feed together at least as often as one would expect by chance. In other words, one would expect the proportion of time that each species pair spent together to be inversely correlated with dietary overlap.

This hypothesis was tested by plotting the proportion of time that each species pair spent together on the three-seed plots against the dietary overlap values in Tab. 2. Using data from both the three-seed plots, it was possible to record every occurrence of each member of a species pair, on a presence or absence basis, noting whether the species was alone, or with the other member of the species pair. The number of times that neither species was recorded during a scan was found by subtraction, and all the values were placed in 2 × 2 contingency tables. Using these tables, we estimated the

Fig. 4. As Fig. 3, using bill length (mm). There is no significant relationship.
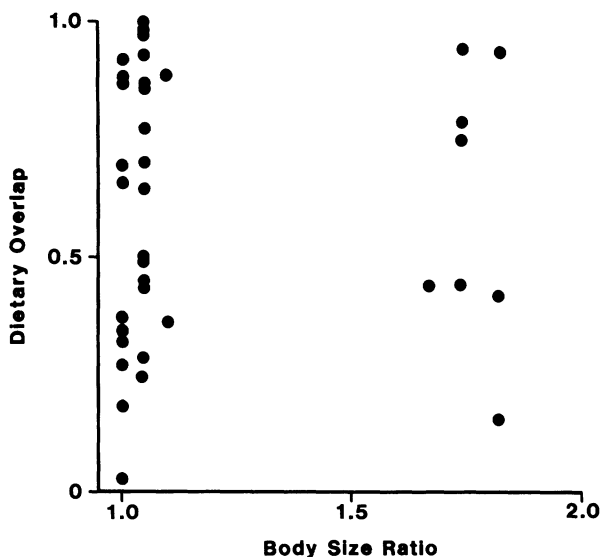

Fig. 5. Body size ratio (largest/smallest member of the pair) against dietary overlap (from Tab. 2) for all species pairs. There is no significant relationship between the two variables.
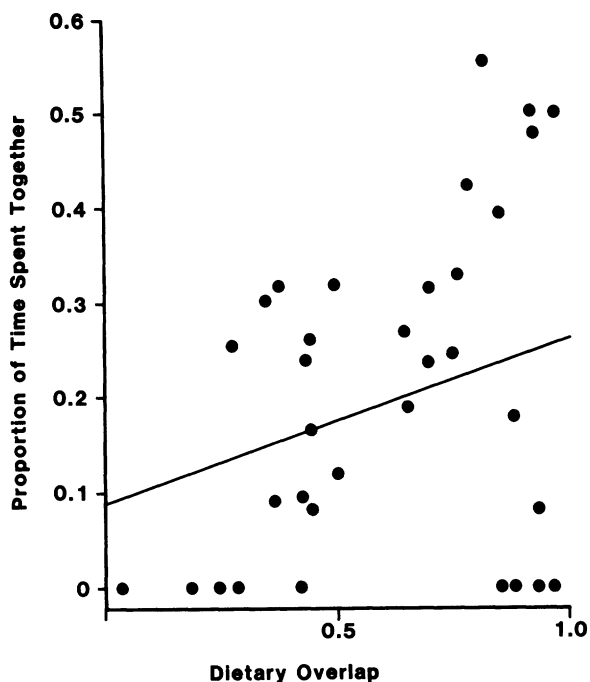
Fig. 6. Proportion of time spent together against dietary overlap for all species pairs. There is a positive relationship between the variables ($F_{1,34} = 3.414$; $p < 0.07$).

expected number of times that the two species should be seen together under the null hypothesis of random association, and compared this with the number of times the pair actually spent feeding together. As some species were relatively rare, expected values were often very low, and χ^2 could not be estimated for most species pairs. Where expected values were >3, χ^2-values were calculated and this gave a measure of whether the pair spent more or less time together than one would expect by chance. The proportion of time spent together was taken as the average of species i's feeding time spent with species j, and species j's feeding time spent with species i.

Fig. 6 shows that although there is only a weak correlation between the proportion of time a pair spends together and their dietary overlap, this result is the *opposite* to that which might be expected in a competitive environment. If competition between species with high overlap was important, they should occur together *less* often than species pairs showing low overlap. Also, no species pairs associated less than one would expect by chance (the competitive hypothesis), but nine were seen feeding together significantly *more* than one would expect by chance (mutualism) ($p < 0.05$; 1 d.f.). What is even more interesting is that these positively associated species all have high dietary overlaps. These results are in direct contradiction to those expected if competition between species was an important process.

3.7. A more detailed test for competition and mutualism

Although the previous analysis provides no evidence for any competitive effects between these species, it would only have done so if one species was totally absent in the presence of another species. A situation where the numbers of one species are simply depressed by the presence of a second species, which could almost certainly be attributed to competition might, therefore, go completely unnoticed. The situation may be even more complicated if individuals from several other species are feeding together on one plot and diffuse competition is important. To overcome these criticisms the Lotka-Voltera competition equations (e.g. May 1981, Toft et al. 1982) can be adapted to produce a model which will show if the numbers of one species are significantly modified by the numbers of individuals of all other species present. If one assumes that the communities on the experimental plots are near equilibrium (i.e. the flocks are not rapidly building up, or declining) then it follows from the basic Lotka-Volterra equation that:

$$N_1 = K_1 - \alpha_{12}^1 N_2 - \alpha_{13}^1 N_3 - \alpha_{1j}^1 N_j \qquad \text{(Eqn 3)}$$

and generally $N_i = K_i - \displaystyle\sum_{j=1}^{n} \alpha_{ij}^1 N_j$

where N_1 = nos. of species 1 on one plot, N_2 = nos. of species 2 on same plot, α_{12}^1 = effect of species 2 on species 1, etc. Here α_{ij}^1 is an interaction coefficient; the prime is used to distinguish it from 'overlap α' (sect. 3.4). K_1 = maximum abundance of species 1 in the absence of potential competitors ($N_j = 0$).

We tested this model for significant α_{ij}^1 values using the data from the three-seed plots. The N_i's and N_j's were numbers of individuals of each species present on one plot during one scan. Nine multiple regression analyses were then run on the computer package I.D.A., in each case having a different species as N_i, the dependant variable.

An indication of how well the model fits the data is given by the multiple r values in Tab. 3. Although these are all significant ($p < 0.01$, 125 d.f.), the r^2 values show that in most cases the model explains very little of the variation in the numbers of different species. Only in two cases, where numbers of Brambling and Greenfinch are the dependent variables, is more than 33% of the observed variation explained by this model.

This analysis provides an estimate of the interaction coefficients between these species. In each multiple regression, the slope of the lines between the dependent (N_i) and each independent variable (N_j) that is the partial regression coefficients, give a measure of the α_{ij}^1's in equation 3. This is a measure of the effect of population size of the independent variable species, on that of the dependent variable species, assuming all other species'

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Tab. 3. Multiple r and r² values from the multiple regression analysis used to test the Lotka-Volterra model on the 3-seed and 2-seed plots.

Dependent variable species N_i	3-Seed Plots		2-Seed Plots	
	r	r^2	r	r^2
Dunnock	0.24	0.06	0.31	0.10
Robin	0.24	0.06	0.29	0.09
Blackbird	0.44	0.20	0.52	0.27
Great Tit	0.32	0.10	0.18	0.03
House Sparrow	0.53	0.28	0.31	0.10
Tree Sparrow	0.29	0.08	0.27	0.08
Chaffinch	0.41	0.17	0.46	0.21
Brambling	0.60	0.37	0.28	0.08
Greenfinch	0.65	0.43	0.30	0.09

populations remain constant. The significance of these values can be tested using a 2-tailed 't' test.

Those values which were significant at the $p < 0.05$ level (120 d.f.), were placed in the matrix in Tab. 4A. Twelve out of the thirty-six species pairs had significant α^1_{ij} values, and of those twelve, seven were positively, and five negatively associated. (It must be remembered that in a sample of this size, one would expect three or four of these associations to be significant purely by chance, at $p = 0.05$.)

Negative α^1_{ij}'s indicate competitive interactions. For example Great Tits and Blackbirds apparently interact competitively, each species adversely affecting the numbers of the other on the three seed plots (Tab. 4A). There are also several examples of apparent mutualism (see, for example, Williamson 1972) where both members of a species pair are more abundant in the presence of the other species than they are in its absence (α^1_{ij} and α^1_{ji} both positive). Brambling and Greenfinch are an example in Tab. 4A.

We also carried out identical calculations for the two-seed plots, using data from every third scan to facilitate comparison with the three-seed plots (recall that there were three times as many two-seed plots as three-seed plots and unequal sample sizes made direct comparison difficult). Significant partial regression coefficients were placed in the matrix in Tab. 4B; multiple r values can be found with those from the three-seed plots in Tab. 3.

Multiple r values for this set of data are again quite low, and the r² values show that on the two-seed plots, the model explains even less of the variation in numbers of each species. Only eight species pairs have significant partial regression coefficients, but seven of these are negatively associated, a much higher proportion than on the three-seed plots.

The performance of the model in the two different situations was then compared by plotting the values for

Tab. 4. Estimates of interaction coefficients α^1_{ij} (effect of species j on species i), using the Lotka-Volterra model, firstly on the 3-seed and secondly on the 2-seed plots. 0 signifies a non-significant relationship. Reading horizontally, the rows in the table show the effects of Robin on Dunnock, Blackbord on Dunnock, Great Tit on Dunnock etc. For example, the interaction coefficient α^1_{ij} describing the effect of Brambling (j) on Dunnock (i) is +0.106, a beneficial effect. Likewise, the effect of House Sparrow (j) on Brambling (i) is −0.101, a negative effect.

A. 3-Seed Plots

	D	R	B	G.T.	H.S.	T.S.	C	BR	G
Dunnock	−	0	0	0	0	0	0	0.106	0
Robin	0	−	0	0	0	0	0	0	0
Blackbird	0	0	−	−0.512	0.158	−0.065	0	0	−0.106
Great Tit	0	0	−0.070	−	0.041	0	0	0	0
House Sparrow	0	0	0.532	1.020	−	0.108	0	−0.469	0.304
Tree Sparrow	0	0	−0.603	0	0.297	−	0	0	−0.235
Chaffinch	0	0	0	0	0	0	−	0.629	0
Brambling	0.312	0	0	0	−0.101	0	0.157	−	0.161
Greenfinch	0	0	−0.792	0	1.650	−0.190	0	1.650	−

B. 2-Seed Plots

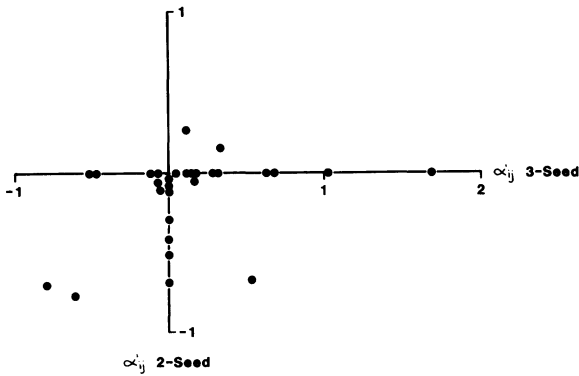|	D	R	B	G.T.	H.S.	T.S.	C	BR	G
Dunnock	−	0	0	0	0	0	−0.119	0.259	0
Robin	0	−	−0.085	0	0	0	−0.056	0	0
Blackbird	0	−0.682	−	0	−0.055	−0.074	−0.299	0	−0.060
Great Tit	0	0	0	−	0	0	0	0	0
House Sparrow	0	0	−0.671	0	−	0	0	0	0
Tree Sparrow	0	0	−0.767	0	0	−	0	0	0
Chaffinch	−0.411	−0.758	−0.506	0	0	0	−	0	0
Brambling	0.155	0	0	0	0	0	0	−	0
Greenfinch	0	0	−0.711	0	0	0	0	0	−

Fig. 7. Values of α^1_{ij} calculated from the two-seed plots (Y-axis) against those calculated for the same species-pair from the three-seed plots (X-axis). The relationship is not statistically significant.

α^1_{ij} calculated from the three-seed plots, against those from the two-seed plots. Fig. 7 shows that the relationship between these two sets of values is not significant. In other words, apparent competition (or mutualism) in the three-seed plots was not significantly related to apparent species interactions on the two-seed plots.

There could be several reasons for this lack of correlation. Firstly, the model may be inadequate for describing these data. For example, flocks may have been a long way from equilibrium over the period of measurement. We think that this is an unlikely reason for the disagreement. The total number of birds on the plots did not vary wildly during periods of measurement, and similar studies based on equation 3 suggest that it should provide reasonably robust estimates of the interaction coefficient (Hallet and Pimm 1979).

Alternatively, interactions between species may be highly non-linear, involving higher-order terms not incorporated into equation 3 (e.g. Case and Bender 1981, Pomerantz 1981). We did not test this possibility because we do not know what form such higher order interaction might take. Finally the model may be basically sound, the lack of correlation in Fig. 7 merely reflecting how sensitive the interaction coefficients are to changes in the resource base. This possibility makes biological sense because it implies that a species may be a better (or worse) competitor, when preferred seeds are present (or absent). Similar comments apply to mutualism.

Despite the overall lack of correlation between the two sets of estimates of α^1_{ij} in Fig. 7, two species pairs, Blackbird-Greenfinch and Blackbird-Tree Sparrow, stand out as having quite similar interaction coefficients in both cases. These results suggest that consistent interspecific competition may occur between a small minority of species pairs. It is interesting that Greenfinches and Blackbirds were the species we most often saw fighting on the grid, suggesting that for this pair, at least, interspecific competition may in part be due to

aggression. Detailed behavioural observations on these and other species-pairs would undoubtedly be valuable in elucidating the interaction coefficients in Tab. 4.

The positive α^1_{ij}'s in Tab. 4 (mutualistic interactions) are interesting because they suggest attraction between species. An anonymous reviewer suggested to us that the apparent mutualisms may be an artifact because some species were commoner on the plots immediately after food was renewed. Alternatively, positive α^1_{ij}'s may represent genuine attractions between species-pairs. Mutual attraction (+ α^1_{ij}) is presumably the mechanism maintaining cohesion in mixed species flocks. It may be relevant that mutualism was commoner when there were three kinds of seeds than when there were only two. We did not predict that this would happen *a priori*; *a posteriori* it does not seem unreasonable that species should be more tolerant to members of other species when there is greater variety of food resources.

Some of the associations are curious. For example, the only consistent association in Tab. 4A and 4B is that between Brambling and Dunnock. We have no idea why. It is much less surprising that Greenfinches and House Sparrows should associate together on three-seed plots and that Chaffinches and Bramblings should do likewise. Whatever the explanation for the cases of apparent mutualism, what is significant is that these species apparently flock together. There is no evidence of significant competition between them.

3.8. Overlap and interaction

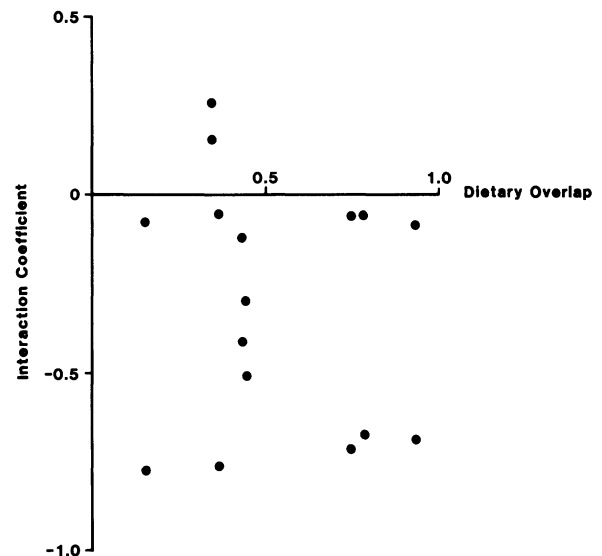Ecologists have often assumed that overlap in resource use should be roughly equivalent to the intensity of in-

Fig. 8. Interaction coefficients (α^1_{ij}) from the two-seed plots plotted against dietary niche overlap, for those species-pairs with significant α^1_{ij} values. There is no significant correlation. Interaction coefficients are taken from Tab. 4B; overlap values from Tab. 2.

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terspecific competition (e.g. Cody 1974). However, just as there is no relationship between differences in body size and overlap in resource use (Fig. 5), nor is there any relationship between overlap (Tab. 2) and the α^1_{ij} values in Tab. 4A or 4B. Fig. 8 shows the α^1_{ij} data for the two-seed plots (i.e. those most likely to agree with the overlaps in Tab. 2, because most of the significant interactions in Tab. 4B were competitive). There is no correlation.

This result is in general agreement with recent theoretical studies (e.g. Abrams 1980a, b, and Lawlor 1980). Despite some evidence to show that overlap and competition may sometimes vary together (e.g. Pacala and Roughgarden 1982), in general there are no sound theoretical or practical reasons why they must.

4. Concluding remarks

The relationship between bird species diversity and seed size diversity (Fig. 1) is similar to that found by other workers studying resource diversity and species diversity (e.g. MacArthur and MacArthur 1961, Cody 1975, Karr 1975, 1976, Gatz 1980). Cody (1975) went on to suggest that such patterns must have been produced by competitive interactions between species. Other workers believe that there is no reason to *assume* that competition is producing these observed patterns (e.g. Connor and Simberloff 1979, Connell 1980).

If interspecific competition is important, then evidence for it ought to be found in one of two ways. Firstly, if some aspect or morphology such as body size is significantly correlated with preferred seed size, then one could argue that competition acting in the past has moulded species niches to minimize contemporary competitive interactions (e.g. Hutchinson 1959, Hespenheide 1966, 1975, Lack 1971, but see Connell 1980). Secondly, competition may be contemporary and apparent from studies of species' population dynamics (e.g. Alatalo 1981, Minot 1981, Toft et al. 1982, Grant and Grant 1982).

This study produced no evidence for a relationship between morphology and diet which might have suggested that competition has shaped these species' feeding preferences. Other studies where direct relationships have been found, for example between culmen size and mean seed size taken (Pulliam 1975), or body weight and size of fruit eaten (Diamond 1975), have tended to look at a group of closely related species rather than more disparate sets of finches, tits, thrushes etc. as here. However, our data agree with a growing body of similar evidence which fails to support any simple relationship between morphology and feeding ecology, either in constant body-size ratios between coexisting species (e.g. Wiens and Rotenberry 1981, Simberloff and Boecklen 1981, Roth 1981), or clear relationships between morphology and diet (e.g. Wiens and Rotenberry 1980).

It is, of course, possible that this and other studies have used the wrong parameters when looking at bird morphology, or that the food preferences found at the time of the investigation do not reflect the natural food preferences under situations of occasional severe resource limitation. Bearing these caveats in mind, our results suggest that it is dangerous to presume that 'morphology can be used as an index to ecological relationships among species coexisting in the same habitat' (Ricklefs and Cox 1977). Resource use must be measured, not guessed.

The Lotka-Volterra model does provide some evidence that competition is occurring between certain species pairs, the presence of one species reducing the numbers of a second, as in the case of Blackbird and Greenfinch. However, in many cases there are no statistically significant interactions between members of a species pair, and there are, amongst those which are significant, several positive, not negative associations. In other words, mixed species flocks are forming, often where the species involved have high dietary overlaps.

Of course, we have only measured species abundances, not feeding rates or other components of fitness. Hence, it is possible that subtle competitive effects have gone unrecorded in this study. Another obvious criticism of this work, is that seed supplies were artificial. This is probably inevitable if resources are to be manipulated experimentally. However, the range of seed sizes used is similar to that available naturally and seeds are naturally patchy resources. Wintering flocks of birds are expert at locating good feeding sites. Hence the "artificiality" of our experiment is probably more apparent than real. Obviously, it remains possible that smaller quantities of seeds, distributed on different spatial scales may have revealed stronger evidence for interspecific competition than our simple experiment. In particular we have not tested for the effects of exploitation competition over longer periods of time (weeks or days rather than minutes). These important caveats aside, our data do not support the notion that competition was an important process structuring a wintering flock of seed-feeding birds. Dietary overlap bore little or no relationship to morphological overlap, and species did not differ in any systematic way in either body sizes or bill sizes. Most species pairs showed no evidence of significant interactions, and when pairs did interact, they often did so mutualistically, not competitively.

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