Biological Station, Wijster

Exclusion, competition or coexistence?
A question of testing the right hypotheses[1,2]

By P. J. Den Boer

Abstract

Since Darwin's "Origin of species", competition was tacitly considered a *necessary* condition for evolutionary processes: important selection should at the same time be competitive selection (Nicholson). Starting from the principle of topicality, data on the possible occurrence of inter-specific competition, both from literature and from field data of the author, is evaluated.

The testing of the "exclusion principle" in biogeography is outlined, and it is concluded that after recent publications of Birch and Den Boer the "exclusion principle" can be replaced by the "coexistence principle". But coexistence does not exclude interspecific competition. However, neither the testing of "character displacement", nor that of "community-wide character displacement" does produce convincing results, not pro and not con dominant effects of interspecific competition. Such effects – if existing – obviously are not very apparent.

From data on carabid beetles the overlap in the breeding seasons of coexisting species under the competition hypothesis is tested against the expectations under the null model (randomly composed local faunas). The occurrence of "niche separation" could not be shown. Only in forest habitats are coexisting carabid species more separated concerning the size of individuals than could be expected under the null hypothesis. There are many reasons however, to suppose that this has nothing to do with interspecific competition.

It is concluded that our present knowledge – though still very fragmentary – is enough to be sure that competition cannot be a *necessary* condition for evolutionary processes. This is evident not only from the above exploration of the possible effects of interspecific competition, but also from the frequency of occurrence of significant intraspecific competition in field populations: in most places most species are rare (Darwin, Williams).

1. Introduction

After having recognized natural selection as the driving force of evolution Darwin (1859, 6th ed. 1878) was left with a primary problem: a variety is positively selected if on the average it has a greater progeny than other varieties, and if this goes on for many genera-tions it is expected – at least by Darwin – that numbers will increase. As carrying capacity is restricted, however, this cannot go on for ever, i. e. there should be some check to in-crease, and this force was apparently thought by Darwin to be competition, either between members of the same population, or between individuals of different species at the same site. As Darwin wrote in this connection: "In each well-stocked country natural selection acts through the competition of the inhabitants, ..." it is not quite clear whether

[1] After a lecture delivered at the 27th Phylogenetic Symposion on 'Competition and Niche Theory' from 30. 11. – 2. 12. 1984 at the University of Bielefeld.
[2] Communication No. 278 of the Biological Station, Wijster.

he considered "capable to compete" to be nearly a synonym of "favoured by selection", or also required that the advantage of an individual at the same time – i.e. by way of a perceptible restriction of resources – should be a significant disadvantage to one or more other individuals. In any case, we will take the latter stand: to speak significantly of "competition" a past or present interaction between some groups of individuals must cause – and not only coincide with – a demonstrable disadvantage for at least one of these groups.

I have the impression that until the present day many biologists understand DARWIN's supposition as: "Competition is a *necessary* condition for evolutionary processes". One hundred years after "The origin of species" NICHOLSON (1960) expressed this view very distinctly, though at the same time extremely: "each significant selection should necessarily be competitive selection". In fact, sticking to this (supposed) stand of DARWIN is somewhat surprising, because already WALLACE (1859) had a different opinion. Moreover, in the course of time, in the field natural selection has appeared usually to be a very complicated and often elusive process, that in many cases seems to be more properly described as "the non-survival of the non-fit" than as "the survival of the fittest". This slogan has to be understood as: sufficient survival and reproduction in many cases can be reached along so many different routes, that the same selective advantage can result from a number of quite different combinations of properties and/or conditions, by which in many – if not most – cases the more persevering changes of the gene-pool on average might appear mainly to result from selecting away of the overall "non-fit", thus leaving intact a great reserve of genetic variability enabling the population to cope with many different situations (spreading of risk: DEN BOER 1968; ANDREWARTHE and BIRCH 1984: Ch. 11). In the midst of such a multitude of individual and environmental events within a generally heterogeneously structured (multipartite) population competition can no more be expected to be a necessary condition for natural selection than for the stability of population numbers (DEN BOER 1968; ANDREWARTHA and BIRCH 1984). Surprisingly, it is again DARWIN (1878), who stresses the relativity of supposing a dominant influence of competition, when he wrote: "Rarity is the attribute of a vast number of species of all classes, in all countries. If we ask ourselves why this or that species is rare, we answer that something is unfavourable in its conditions of life; but what that something is we can hardly ever tell".

Nevertheless, competition could still be important, of course, so that – independent of each presupposed "necessity" – its possible significance should be studied. In this paper we restrict ourselves to the possible part played by interspecific competition. In the course of time the distribution of species in space or the distribution of properties among coexisting species has repeatedly been claimed to be the result of interspecific competition without testing against the proper null hypothesis (cf. POPPER 1968; STRONG 1980).

2. Exclusion

GAUSE (1934) was one of the first who clearly formulated a testable competition hypothesis: "species with the same ecology cannot coexist very long, the superior species will compete out and finally exclude the inferior one". "The same ecology" should obviously be understood as "closely related ecologies", because different species simply cannot have "the same ecology" (cf. COLE 1960; AYALA 1970). During many years this exclusion principle played a dominant part in ecological literature, possibly because GAUSE himself supported it already by elegant laboratory experiments. As taxonomically closely related species can be expected to be also ecologically closely related (DEN BOER 1980) the exclusion principle thus predicts that closely related species, e.g. species in the same genus, will generally not coexist. This could be tested if "will generally not coexist" can be translated into quantitative terms.

ELTON (1946) was the first to try this, when he discovered that on average species are divided among more genera on islands than on the continent, i. e. the species/genera ratio (S/G-ratio) is smaller for islands (1.38 in animals, 1.22 in plants) than for areas on the continent (more than 4.). ELTON explained this as a result of competition between closely related species, which would more readily lead to exclusion on islands than on the continent. WILLIAMS (1947), however, considered this conclusion invalid, because ELTON did not test the distribution of species over genera against the proper null hypothesis: "the number of species of some taxonomic group on an island, together with the distribution of these species over genera, can be considered a random sample of that size and composition (S/G-ratio) taken from the relevant sample space (e. g. on the continent)". WILLIAMS showed, that if the S/G-ratios of islands are thus compared with the expected values under the null hypothesis, the actual ratios are even greater – instead of smaller – than the expected ones. Hence, the exclusion hypothesis should apparently be rejected.

In spite of this correction by WILLIAMS (1947), MOREAU (1948) concluded – again without formulating and testing the proper null hypothesis – that 172 bird species belonging to 92 genera were distributed in such fashion over 32 types of habitat in East Africa, that interspecific competition between related species must have a great part in it. WILLIAMS (1951) again formulated the proper null hypothesis, and tested this against the data of MOREAU, and again the exclusion hypothesis had to be rejected. In that case WILLIAMS made use of the diversity index proposed by SIMPSON (1949), in the form of "Generic diversity" (G. d.), i. e. as $N(N-1)/2$ – the total number of species pairs that can be taken from a collection of N species – divided by $\Sigma n_i(n_i-1)/2$ – the summed numbers of pairs that can be taken from the n_i species within each genus – (the congeneric pairs). Hence, G. d. estimates how much the species in the sample are distributed over different genera, and therefore to what extent closely related species apparently "avoid" each other in space. The exclusion hypothesis predicts that for the species in a restricted area G. d. would have a higher value than for the fauna or flora as a whole. For the data of MOREAU WILLIAMS (1951) found instead the inverse relationship.

Unfortunately, the papers of WILLIAMS did not result in a more critical attitude towards the principle of competitive exclusion. In succession GRANT (1966), MAC ARTHUR and WILSON (1967) and COOK (1969) "discovered" the same as ELTON (1946), and again without formulating a null hypothesis. Now it was SIMBERLOFF (1979), who tested these data against the proper null hypothesis, and again the exclusion hypothesis should be rejected. But *all* these rejections do not yet suffice! LACK (1976) was, and DIAMOND (e. g. 1978) is still convinced, that the distribution of bird species among islands is determined to a high degree by interspecific competition between closely related species.

3. Coexistence

A paper by BIRCH (1979) stimulated me (DEN BOER 1980) to have a new try in telling ecologists that the principle of competitive exclusion is past since the paper of WILLIAMS, i. e. some thirty years. To show that this is true not only for birds, I tested the distribution of 149 carabid species over 41 genera (pitfall catches during 9 years at 73 sites: DEN BOER 1977), against the Generic diversity (G. d.) expected under the proper null hypothesis. Again, it appeared very convincingly that at restricted sites G. d.-values are lower on average than expected under the null hypothesis: "species are distributed at random over sites" (Fig. 1). Note, that these low G. d.-values were not only obtained from sites where part of the closely related species "avoid" each other in time, they were equally low at "wet" and at "dry" sites (Fig. 2). Even when we take into account that exclusion is a process that takes time no indications of its occurrence were found (see: Figs. 3 and 4).
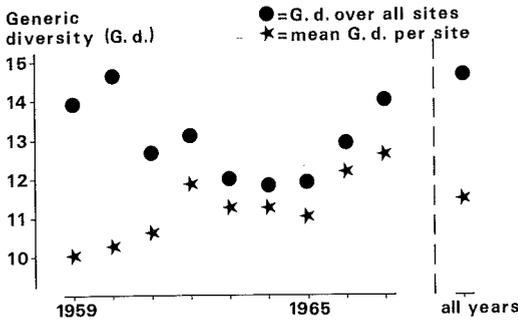
Fig. 1. Mean values of "Generic diversity" (G. d.) over sample sites for a number of years (stars) as compared with expected values (for the carabid fauna as a whole). (From: DEN BOER 1980: Table 4). Further explanation in the text
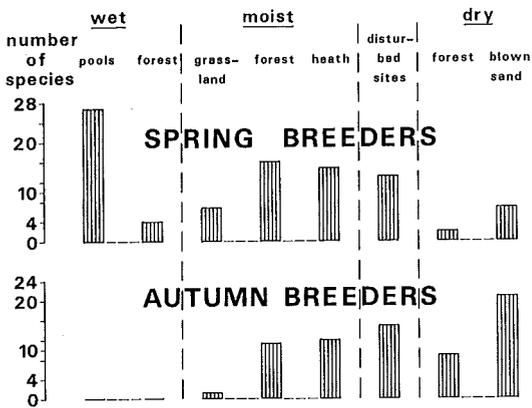

Fig. 2. Numbers of spring resp. autumn breeding carabid species in different kinds of habitat from wet (and unstable) at left to dry at right. (From: DEN BOER 1980: Table 3)
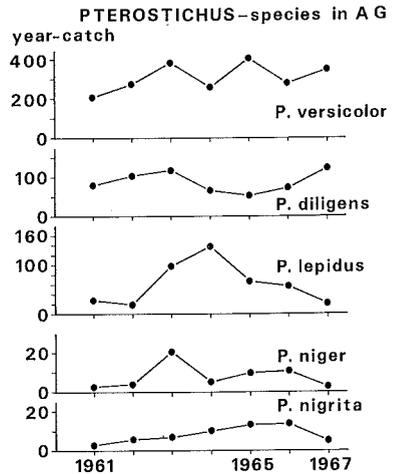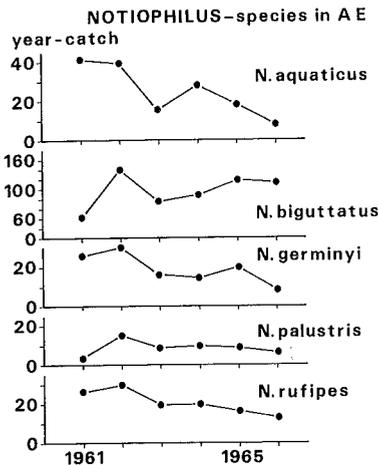

Fig. 3 (left). Year-catches of five Notiophilus-species (Carabidae) in the same set of pitfalls (in a small birch wood) during six succeeding years. (From: DEN BOER 1980: Table 5) – Fig. 4 (right). Year-catches of five Pterostichus-species (Carabidae) in the same set of pitfalls (at a mosaic heath) during seven succeeding years. (From: DEN BOER 1980: Table 5)

Therefore I suggested (DEN BOER 1980) to replace the principle of competitive exclusion by the coexistence principle: "As taxonomically closely related species usually are also ecologically closely related, related species will be found living together more frequently than could be expected with a random distribution of species". The coexistence principle nicely fits the field observations on exclusion which were collected from the literature by BIRCH (1979), and which show that exclusion must be a rare and rather exceptional phenomenon. This study also demonstrates that excluded, and excluding species need not necessarily be closely related: a necessary condition is only that some resource, that is indispensable for one of the species, is destroyed or otherwise made unavailable by the other (e. g.: monkeys that eat the fruits in which some kind of insect is accustomed to lay its eggs).

4. Assembly rules

DIAMOND (1978), who is profoundly convinced that the distribution of (bird) species among islands is dominated by interspecific competition, goes further in this than e. g. ELTON (1946) or GRANT (1966). He not only observes that certain closely related species are only exceptionally found together on the same islands, but he even posits "assembly rules" (DIAMOND 1975), which should be answered by the distribution of bird species among islands. The most important one of his "rules" says that the co-occurrences of certain (related) species are so improbable because of interspecific competition that these are even "forbidden", so to say. Examples are the so-called "checkerboard" distributions of *Macropygia*, *Pachycephala* and *Ptilinopus* in the Bismarck Islands (DIAMOND 1975; his Figs. 20, 21, 22) which in my opinion (e. g. his Figs. 20 and 22) rather appear to result from different geographical ranges occupied by the species concerned than from competitive exclusion.

CONNOR and SIMBERLOFF (1979) opposed DIAMOND, saying that one cannot conclude anything from selecting these few examples from a large group of 141 bird species (which potentially form 9870 pairs). They therefore contrasted the observed distributions with those expected if species were randomly placed on islands (in a matrix) subject only to the constraints of the number of species observed on each island (columns) and of the number of occurrences on islands of each species (rows). They could not falsify this null hypothesis. DIAMOND and GILPIN (1982) like WRIGHT and BIEHL (1982) reproach CONNOR and SIMBERLOFF (1979) for diluting the effects of competition by submerging exclusive distributions in an irrelevant mass of distribution data. Hence, they indeed want to restrict the analysis to certain "guilds" of species or even to "potential competitors". But how to assign species to "guilds" or to select "potential competitors" objectively?

GILPIN and DIAMOND (1982) constructed their own null hypothesis based on both the selection of "guilds" and on more degrees of freedom for column and row sums (see above), which is critisized again by CONNOR and SIMBERLOFF (1983). Although this discussion can be expected to go on for some time, because some technical problems of testing have still to be solved, like CONNOR and SIMBERLOFF (1983) I think it promising that "competition-believers" like DIAMOND also now agree that hypotheses should be tested against null hypotheses. Discussions about the features and testing procedures of proper null hypotheses can be very fruitful, indeed. It would be still more fruitful, however, to study very closely the constraints to which "potential competitors" are exposed in the field.

5. Ecological separation in literature

Interspecific competition needs not result in exclusion of one of the species, however. It can also be imagined, that the originally occurring ecological overlap of coexisting species gradually decreases under the influence of interactions. This interesting hypothesis of a

growing "ecological separation" of coexisting species under the influence of competition, which could be in keeping with the coexistence principle of DEN BOER (1980), has been considered – under different names – in so many publications, that I have to restrict myself to a few studies only. Therefore, I shall drop theoretical speculations about "niche separation", such as HUTCHINSON's (1958: fundamental niche), MACARTHUR's (1972), or PIANKA's (1976: niche theory) expositions, which rest on too many assumptions to be testable, and will only discuss some field studies.

The supposition, that closely related species would diverge more ecologically – as a result of interspecific competition – at places where they coexist than when they live separated (allopatrically), was possibly made for the first time by LACK (1947) in his study on "DARWIN's finches" (*Geospiza*) of the Galapagos Isles.

5.1. Character displacement

After the paper of BROWN and WILSON (1956) – in which 15 more examples of "ecological separation" are discussed – this phenomenon is generally called "character displacement", and was widely accepted by the ecological community. At that time only BOWMAN (1961) tried to explain that the morphological-ecological differences between coexisting *Geospiza*-species (LACK 1947) can be understood very well as trivial differences in habitat preference. It was not before 1972 that GRANT tried to formulate null hypotheses for the testing of "character displacement". He tried to quantify the differences between the relevant species, so that the displacement in sympatry can be compared properly with that in allopatry, i. e. he had to eliminate the possible effects of geographical variation. He succeeded in only two cases, and in both he had to reject the hypothesis of character displacement. Interestingly, one of these was the show-example of character displacement – which was treated in all textbooks, e. g. EHRLICH and HOLM (1963: Fig. 10.9) – the bill lengths and facial stripes in two Asiatic nuthatches of the genus *Sitta* (compare GRANT 1972: Table 1, Fig. 4). Even a careful field study of these *Sitta*-species at the sites where they coexist (GRANT 1975) did not reveal indications of significant interspecific competition. On the other hand, GRANT (1972) showed that two of the 16 cases, which were presented by BROWN and WILSON (1956) as examples of character displacement, seem to be sufficiently – though not quantitatively – supported. A more recent survey of the subject (STRONG 1983) does not rehabilitate character displacement, however.

Some of the cases that were already discussed by BROWN and WILSON (1956) concerned morphological tendencies within whole groups of species (guilds); more recently this phenomenon was called "community-wide character displacement". We will call it "character tendencies", because it only concerns ratios between body-measures. It is assumed that related (bird) species can only coexist (on islands) if certain dimensions (length of body, of bill, of wing, etc.) are more different among them than among comparable non-coexisting species, i. e. the sympatric species show higher (size-, bill-, etc.) ratios than the allopatric ones. In other words: The co-occurrences of related species would be such that these ratios will be higher than when the species would have been arranged at random.

With this in mind ABBOTT et al. (1977) again studied the Galapagos-finches and concludes that, though 53 % of the variance of body dimensions between sympatric *Geospiza*-species has to do with differences in the availability of different kinds of food, there are also indications for the occurrence of interspecific competition. STRONG et al. (1979) did not agree at all, because there was no testing against the proper null hypothesis, just as in other cases of "character tendencies" (GRANT and COWAN 1964; POWER 1972). Therefore, they tested the pertinent size-ratios within the sympatric species groups against those in comparable species groups taken at random from those continental bird faunas that might reasonably be considered "source" faunas (null groups). They concluded, that as far as "community-wide character displacement" does exist at all, it will be uncommon.

This conclusion is vigorously combated again by GRANT and ABBOTT (1980). Although their biological objections should be taken seriously, in my opinion they did not completely understand the logic of the testing procedure. Given that the null groups are indeed comparable with the subject-groups, and that the statistics used are adequate, the conclusion of STRONG et al. (1979) can hardly be disputed. But the comparability of the null groups can be doubted, and there may be difficulties with the statistical techniques applied (see e. g. HENDRICKSON1981). I myself have not only serious statistical objections against the use of (size) ratios, but also biological ones: body dimensions often obey certain allometric rules, which can lead to irrelevant distortions of the ratios. Moreover, rather small morphological differences between species need not have – and often will not have (e. g. SCHMITT and COYER 1982) – important ecological consequences; differences in behaviour will often be more to the point (PULLIAM 1983).

Hence, to learn something about the frequency of occurrence of interspecific competition as a direct or indirect cause of ecological separation between coexisting species, morphological character displacement seems not to be a promising field of research. It is more obvious to study directly ecological separation itself, i. e. to go into the field and to compare the ecological similarities and differences of both sympatric and allopatric species, as was started by BOWMAN (1961) and was progressed during the last decade (cf: STRONG 1983).

6. Ecological separation in carabid beetles

Recently some students (MÜLLER 1983, 1985; LOREAU, in press) attributed the separation of coexisting carabid species in respect of certain ecological features to interspecific competition (niche separation), again without formulating and testing null hypotheses. I thought this an excellent opportunity to test against the expectations under proper null hypotheses the degree of separation (or overlap) in breeding season or in mean size of individuals of those carabid species that during a number (3–12) of succeeding years appeared to coexist in relatively high numbers at one or more of the 30 sites we studied in our area (Drenthe): DEN BOER (1977).

6.1. Reproductive separation (resp. overlap) in time

Both MÜLLER (1983, 1985) and LOREAU (in press) claim that the most abundant carabid species in their study areas (some forest sites) show as little overlap in time of reproduction as they do, because only in this way will siginificant interspecific competitions be "avoided" (niche separation). In other words: the distribution of the breeding seasons of these species over the year is supposed to be significantly connected with the possibility to coexist, and will thus be different from distributions that ar not connected with coexistence. The proper null hypothesis thus says: "the reproductive periods of a number of coexisting carabid species will not be separated more in time than those of carabid species in samples (of the same size) that are randomly chosen from the carabid fauna as a whole".

In connection with another project my wife (WIL DAANJE) already delimited the breeding seasons of the 68 most abundant carabid species of our area, by making use of the seasonality parameters of WOLDA (1979), thus fixing the central 95 % of the reproductive activities of the females in time as one or more sequences of weeks during an average year: Fig. 5. The activities of immature and/or spent adults are not included, which was possible, because in nearly all species immature adults can be recognized externally, and in most species samples of active females (pitfall-catches) were dissected to check whether or not ripe eggs were present in the ovaries. As the reproduction period of a certain (carabid) species within the same year only exceptionally differs by more than a single fortnight between sites, whereas within the same site the differences between years are

Fig. 5. Reproductive periods of the 68 most abundant carabid species in Drenthe (Netherlands) averaged over all sites and over more than 20 years. Further explanation in the text. The numbers at right, which refer to the species, are explained in DEN BOER (1977: Table 2). Pter. = *Pterostichus*, Ag. = *Agonum*, Am. = *Amara*, Car. = *Carabus*, Not. = *Notiophilus*, Harp. = *Harpalus*, Cal. = *Calathus*, Cym. = *Cymindis*, Bemb. = *Bembidion*, Trech. = *Trechus*, Leist. = *Leistus*, Trich. = *Trichocellus*, Brad. = *Bradycellus*

usually greater, for each species she could attain the best possible estimate of the breeding season (in weeks) as the average over more than 20 years of the overall (over all sites) reproductive period. In Fig. 5 these estimates are arranged in time-order. More details of these reproductive cycles will be published separately.

The reproductive periods presented in Fig. 5 could immediately be fed into the computer as 68 sequences of 52 characters (0 or 1) each, from which random samples could be taken to compare the mean amount of overlap in time of reproduction with that found in

Table 1

Mean amount of overlap in time of reproduction (O) between the most abundant coexisting species (n) at some site as compared with O under the null hypothesis

100 samples taken at random from 68 species

	site	n	% overlap (O) coexisting	random	P (LE)		site	n	% overlap (O) coexisting	random	P (LE)
I	CC	9	38.8 (36.6)	41.0	0.41	II	N	14	38.2 (32.9)	40.6	0.39
	B	9	45.9 (38.5)	38.8	0.76		Z	17	37.6 (36.4)	40.3	0.37
	C	12	44.8 (47.2)	39.4	0.73		AG	16	40.3 (44.5)	39.7	0.60
	X	10	36.2 (32.7)	38.9	0.45		CF	12	35.8 (43.6)	40.0	0.29
	AM	9	40.4 (52.6)	39.5	0.54		AT	7	56.7 (60.6)	41.6	0.90
	AL	12	41.4 (34.0)	40.2	0.64		BH	9	51.5 (48.5)	39.7	0.89
	G	6	38.7 (19.7)	39.2	0.56		BJ	8	52.0 (54.1)	39.6	0.89
							AU	10	36.5 (26.7)	38.9	0.43
III	P	6	71.4 (67.3)	40.6	0.98		AV	10	35.1 (41.1)	39.7	0.32
	O	6	58.9 (72.0)	39.7	0.93		AZ	8	33.3 (31.1)	40.1	0.24
	CG	8	40.5 (35.3)	39.7	0.61		BB	14	39.2 (55.2)	39.3	0.55
	M	8	53.5 (57.6)	40.6	0.90		AY	14	40.0 (36.3)	40.5	0.52
	BZ	11	37.8 (27.5)	39.8	0.41						
	CA	10	55.0 (49.1)	40.4	0.93		CD	11	45.5 (40.4)	39.8	0.76
	CE	18	50.5 (59.9)	40.0	0.94		AE	12	41.1 (31.6)	40.2	0.59
	BU	9	57.8 (47.5)	39.8	0.97						
	Q	4	36.9 (47.2)	40.4	0.44						

Note: 22 of these 30 sites are described in DEN BOER (1977: Appendix A, Part II).
Between brackets: O, if only pairs with about equally abundant year-catches (DEN BOER 1977) are considered. P (LE) = chance to find the same or an even smaller overlap in random samples. I = forest sites, II = sites in heath, peatmoor or blown sand (dry heath), III = unstable sites (agricultural fields or wet, periodically inundated sites in health); CD and AE are transitional sites between forest and open country.

the sample from some site in the field. The mean amount of overlap is estimated as the weighted average of the overlaps between all pairs of species that can be taken from the sample, i.e. $O = [\Sigma\ 2o_{i,j}/\Sigma\ (a_i+b_j)] * 100\ \%$, in which a_i and b_j are the reproductive periods in weeks of species A_i and B_j respectively, and of which $o_{i,j}$ is the overlap in weeks (i and j indicate the species of Fig. 5, $i \neq j$). The 100 (or 200) random samples taken for comparison with some sample from the field give the relevant probability distribution of O, from which can be estimated the probability that the degree of reproductive separation (100-O) computed from the field sample will be attained or even exceeded under the null hypothesis. The results of this test are shown in Table 1.

Table 1 convincingly demonstrates that nowhere in our study area (Drenthe) there can be found even the slightest indication that coexisting carabid species would have a tendency to "avoid" each other in (reproduction) time, neither when all possible pairs of coexisting abundant species are taken into account, nor when only pairs of about equally abundantly caught species are considered. Forest sites are no better in this respect than sites in heath, peat-moor or blown sand areas; some unstable sites show very high overlap values, because such habitats are often highly dominated by spring breeders (see also Fig. 2). If we divide our 68 most abundant species up into the three most natural groups: D-species that highly prefer stable forest, species that prefer stable open sites, i.e. old heath, old peat-moor or blown sand fixed by vegetation (E- and F-species), and the remaining species, viz. H-species that inhabit both stable and unstable sites together with G-species that only occupy unstable places (see further: DEN BOER 1977), as shown in Fig. 6, and in forest sites (I) only take into account D-species, in heath, peat-moor and blown sand sites (II) only consider E- and F-species, and in unstable sites (III) only H- +
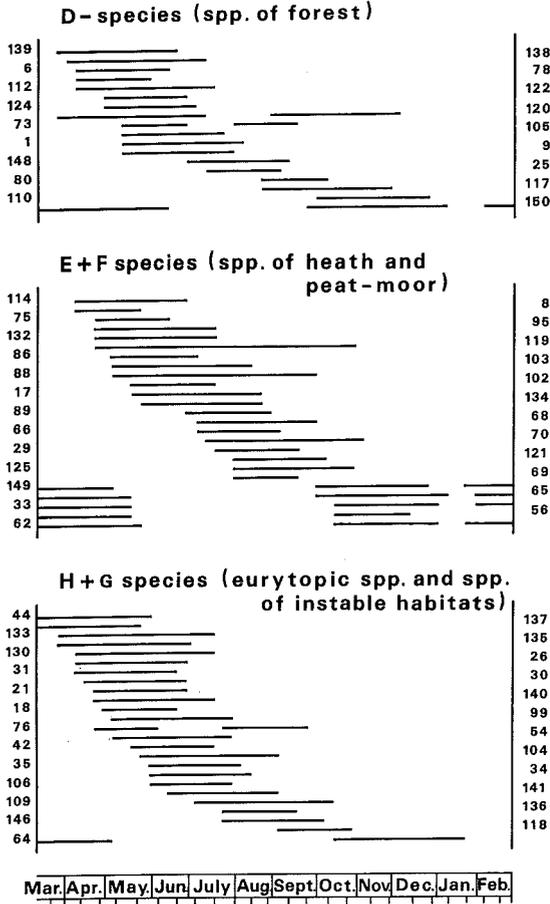
Fig. 6. The same as Fig. 5, but the species are divided up into three groups according to the preferred habitats: species of forest (D), species of heath, peat-moor and blown sand (dry heath) (E + F), eurytopic species (both in stable and unstable habitats) and other species of unstable habitats (H + G). The numbers, which refer to the species, are explained in DEN BOER (1977: Table 2)

G-species, our test gives the same kind of results (in 19 cases even worse) as those given in Table 1: there is not even the slightest indication of niche (reproductive) separation in coexisting carabid species.

Hence, we must reject the hypothesis of MÜLLER (1983, 1985) and of LOREAU (in press).

6.2. Separation according to the size of individuals

MÜLLER (1983, 1985) was also struck by the differences in mean size of individuals between carabid species coexisting at the same (forest) sites. He hypothesized that these size differences will not only be correlated with differently sized prey, but that also these coexisting species will thus significantly "avoid" interspecific competition for food. In other words: on average the differences in mean individual-size between carabid species are expected to be greater for coexisting species than for non-coexisting ones, whereas the proper null hypothesis will say that comparable coexisting and non-coexisting carabid species on average will not be different in this respect.

Some years ago already, I divided the carabid species occurring in our area into four rather natural size-classes (the groups I, II, III and IV of Table 1 in DEN BOER 1980). To get at somewhat more similar frequencies of species in these groups I again subdivided the classes II and III into two further (also rather natural) groups each. The frequencies of the

68 most abundant species (cf. 6.1) in these 6 classes are given at the foot of Table 2. To compare the actual distribution among these 6 size-classes of the most abundant carabid species at some site with the distribution expected under the null hypothesis I again used the diversity index proposed by SIMPSON (1949); compare: DEN BOER (1980). In this case it took the form of »Size-diversity« (S. d.), i. e. $N(N-1)/2$ – the total number of species pairs – divided by Σ $n_i(n_i-1)/2$ – the summed numbers of pairs that can be taken form the n_i species in each of the 6 size-classes (cf. section 2). Just as in DEN BOER (1980: 4.3, Table 4) we now compare mean S. d. over all sites, as the average distribution of coexisting abundant species among the 6 size-classes, with S. d. of the 68 most abundant species as a total, which at the same time is the expectation value for random samples: Table 2.

Table 2 shows that, averaged over all sites, species with more similarly sized individuals have a weak tendency to coexist: mean S. d. (5.76) is smaller than S. d. of the total (6.16). This could already be expected since congeneric species often have about equally-sized individuals (DEN BOER 1980: Table 2) and tend to coexist (cf. section 3). In fact, this already suffices to reject the hypothesis of MÜLLER (1983, 1985). But forest sites in particular (MÜLLER worked with forest carabids) do show higher S. d.-values than expected: Table 2. However, this does not mean that at forest sites the distribution of carabid species should necessarily have the significance of "niche separation", because of the following reasons:

1. Forest sites are not the only sites with S. d.-values higher than 6.16: 16 out of the 30 sites show this (Table 2) which could just be expected under the null hypothesis. Moreover, these high S. d.-values were in all kinds of habitats, including about half of the unstable sites. – 2. An excess of both species with small and species with big individuals,

Table 2

Frequency of the most abundant coexisting species (n:Table 1) at some site(s) in 6 classes of mean size of individuals, evaluated as "Size-diversity"

S.d. compare G. d., section 2

S.d. at individual sites		group (mean) S.d.	difference (χ^2) (d.f. = 5)
forest sites:	CC (7.2), B (9.0), C (6.6), X (7.5), AM (7.2), AL (6.6), G (5.0)	6.98	20.99 (P ≈ 0.001)
moist-health sites:	N (5.1), Z (5.0), AG (5.7), CF (4.7)	5.16	
grass-heath sites:	AT (7.0), BH (7.2), BJ (5.6)	6.54	6.22 (P ≈ 0.30)
unstable wet heath and peat-moor:	P (7.5), O (5.0), CG (5.6), M. (14.0), Q (6.0)	7.08	
blown sand (dry heath) sites:	AU (9.0), AV (6.4), AZ (7.0), BB (5.7), AY (3.8)	5.35	16.61 (P ≈ 0.01)
agricultural fields:	BZ (3.9), CA (3.8), CE (6.7), BU (7.2)	5.35	16.09 (P ≈ 0.01)
transitional sites:	CD (9.2), AE (5.2)	6.37	
all sites taken together (mean S.d.)		5.76	9.72 (P ≈ 0.10)
all 68 species together (S.d. of total)		6.16	

size classes	1	2	3	4	5	6	Σ
mm	(< 5)	(5–6.8)	(7–8.5)	(9–10)	(10.5–12.5)	(> 13)	
number of spp.	13	16	11	10	9	9	68
spp. summed over all sites	58	72	55	32	55	37	309
	(12.8)	(15.8)	(12.1)	(7.0)	(12.1)	(8.2)	(68)

Between brackets: S.d.-values for individual sites; "difference (χ^2)" = difference between the frequency distribution summed over some sites and that summed over all sites (at the bottom of the Table).

which is the cause of high S. d.-values, is not typical only of forest sites; it is also found in unstable sites (wet heath, agricultural fields): Fig. 7. – 3. If we arrange the coexisting carabid species in order of their year-catches this ranking does not correspond at all with an increasing order of size-differences between about equally abundantly caught species, as should be expected under the competition hypothesis (the greatest differences in size of individu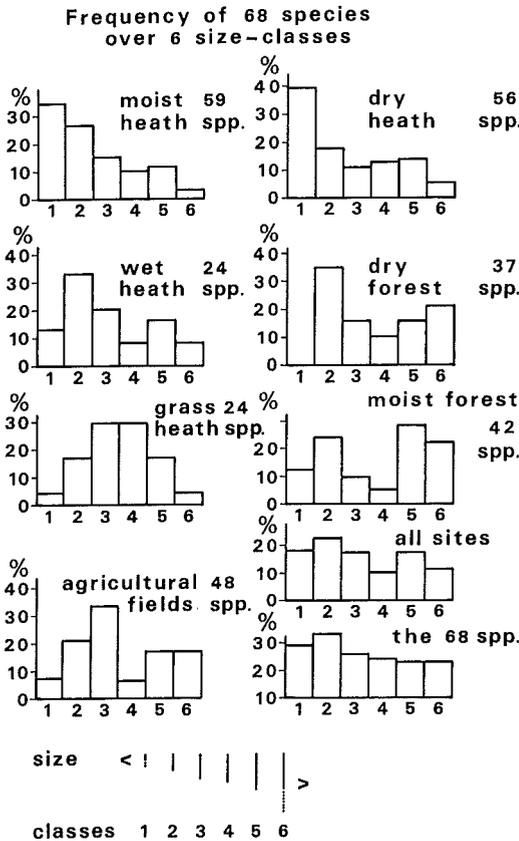als between the most abundant species). – 4. Although we have the impression that in litter and soil of our forests the availability of prey is much better than in old (moist) heath areas, our forests are poor in carabids – both in number of species and in numbers of individuals – as compared with moist heath areas (which all show low S. d.-values: Table 2). – 5. Szyszko (1984) showed that with the aging of the (pine) forest the carabid fauna gradually shifts from species with small towards species with big individuals which seems to be passively connected with a shift from a dominance of small prey (e. g. mites, collembolans) towards larger prey (e. g. worms, snails, caterpillars). I suggest that our forests are somewhere half-way in this process (note, that the dry forests sampled are indeed evidently younger than the moist ones; compare Fig. 7). I propose that even in general the distribution of carabid species among size-classes of individuals passively results from the size-distribution of prey, and does not reflect something like "niche separation".

Fig. 7. Frequency distribution over 6 size-classes of individuals of the 68 most abundant carabid species of Drenthe (Netherlands) occurring at 30 sites. The distributions for a number of sites of the same type are summed. The class-limits are given in Table 2. (See further the text)

7 Discussion

This survey has shown, I hope, that it is not very probable that the distribution of species in space or the distribution of properties among coexisting species will often be significantly dominated by interspecific competition, either directly nor indirectly. Holding the principle of topicality I thus expect that interspecific competition will only exceptionally have influenced the course of evolution significantly. This does not mean, of course, that interspecific competition, or even competitive exclusion, does not exist at all; on the contrary, highly convincing cases are found among plants and among sessile animals (see e. g. Connell 1971); see further Zwölfer (1979); Birch (1979) for other examples. But in ecology one cannot make science by selecting cases that agree with our preconceived

ideas. We will have to place these examples back into the sample space from which they were selected, i. e. we can only rightly judge their *general* significance against the original background. This is just what is done by testing against proper null hypotheses.

In section 4 was shown that it is not always easy to formulate the proper null hypothesis, which may partly depend – as in that case – on the formulation of the alternative hypothesis to be tested. Therefore, I should like to invite ecologists to take into account the formulation and testability of the proper null hypotheses when proposing any "mechanism"; for hypothesis + null hypothesis have completely to fill up the sample space of possibilities. As, in most cases treated in this paper, the projectors of null hypotheses answered this condition we can already safely state that interspecific competition cannot be a necessary condition for evolutionary processes. But what about intraspecific competition, which in general can be expected to be more apparent, because coexisting individuals of the same species will be more similar ecologically than co-occurring individuals of different species?

One cannot deny that a variety that is favoured by selection on average will have a greater progeny than other varieties. That is true indeed, since it is a tautology synonymous with "survival of the fittest". But it does not necessarily lead to selection being competitive selection (NICHOLSON 1960). Under natural conditions a variety that is "fit" at present, may no longer be so under slightly different conditions, i. e. possibly already tomorrow. In the same way, individuals of some variety that are "fit" in this place, may be not in another possibly adjacent one. Under the heterogeneous and variable field conditions this will often be true for many "fitness"-properties, whereas only the eventual size of the progeny counts. This will result in a variable degree of selection of a number of more or less connected "fitness"-properties at the same time. Natural selection "plays" simultaneously, so to say – and with variable "success" – against a number of different "opponents", and if in some "plays" some "profits" are made these results are naturally (and indissolubly) included into the pool of "scores and positions" as a whole. The positive selection of some property will thus be accompanied by many and often quite independent genetic changes, which represent as many genetic compromises together enabling the population to survive many different and more or less frequently occurring conditions (spreading of risk: DEN BOER 1968; see also: ANDREWARTHA and BIRCH 1984: Ch. 11).

Hence, though it is evident that a variety that is favoured by selection will on average have a greater progeny than other varieties (by definition) the base of comparison – the other varieties in the population – has changed at the same time (and often profoundly) because this is inherent in naturally occurring selective processes. As not all these changed gene-combinations – probably only a minority – will have overall favourable effects, it is impossible to predict anything about trends in population numbers as a consequence of natural selection. Apart from some short-term and/or local effects, population density will most probably appear to be quite independent of significant selection processes. Therefore, in my opinion, there cannot exist a necessary connection between "favoured by selection" and "capable to compete" (NICHOLSON 1960), because many – if not most – selective processes will have little or nothing to do with competition. See also: ANDREWARTHA and BIRCH (1984: Ch. 11).

Apart from this rather fundamental criticism of a highly deterministic view on selection processes the experience of the field ecologist raise other objections to the assumption that in most populations during most of the time mean density would be close to carrying capacity. For instance:

1. DARWIN (1878) already observed that rarity is much more common than numerousness (cf. section 1). WILLIAMS (1964; see his Fig. 24), found that in large fauna-samples the 50 % rarest species account for only 0.2 to 3.8 % of the individuals, whereas the very most numerous species formed 16 to 88 % of the individuals. My experiences with the continuous sampling of carabid beetles in many sites are similar (e. g. in 1962: 1.4 % and

22 % respectively). See also: DEN BOER (1971). – 2. Under natural conditions vital resources are only incidentally exhausted (MILNE 1962), and in most of these exceptional cases usually by the same few species. Not so much because in most places during most of the time alle individuals easily get enough, but more often – especially in arthropods – because they can only get at a small part of the resources (WHITE 1978), either because of only modestly developed searching capabilities (e. g. in carabid beetles) and/or because they are too frequently manipulated by environmental conditions (ANDREWARTHA and BIRCH 1954), among which is the varying availability of the critical resource itself (DEMPSTER and POLLARD 1981). – 3. Usually local populations do not survive very long (ANDREWARTHA and BIRCH 1954; DEN BOER 1985), so that in many cases there simply will not be enough time to reach carrying capacity. Therefore, in my opinion the greatest problem for a population is not: "How to keep down density?", but: "How to prevent extinction?" – 4. Most organisms are heavily attacked by predators, parasites and pathogens which together usually will keep down population numbers, and will thus prevent exclusion (cf. CORNELL 1971). As the enemies are also open to selection – and thus able to "adapt" – this "natural control" (MILNE 1962) will not easily be broken, though it need not have anything to do with "regulation" (DEN BOER 1968, 1971).

Holding the principle of topicality my conclusion thus is, that neither interspecific nor intraspecific competition are *necessary* conditions for evolutionary processes. It is time to release natural selection from its galling bonds with competition.

Acknowledgement

Zusammenfassung

Ausschluß, Konkurrenz oder Koexistenz –
ein Problem der Prüfung der richtigen Hypothesen

Seit DARWINS ‚Origin of species' wurde Konkurrenz als eine notwendige Voraussetzung für Evolutionsprozesse, jede bedeutsame Selektion als „competitive selection" (NICHOLSON) betrachtet. Zur Überprüfung dieses Ansatzes wird die Frage, ob sich die Wirkung von interspezifischer Konkurrenz nachweisen läßt, an Hand der Literatur und eigener Felduntersuchungen des Autors überprüft. Es werden die vorliegenden Untersuchungen zum „exclusion principle" in der Biogeographie kurz dargestellt, mit dem Ergebnis, daß nach einigen neueren Publikationen von BIRCH und DEN BOER, das sogenannte „exclusion principle" durch das „coexistence principle" ersetzt werden kann. Freilich wird durch die Möglichkeit von Koexistenz interspezifische Konkurrenz nicht ausgeschlossen. Es bringt jedoch weder der Test der Beispiele für „character displacement", noch der für „community-wide-character displacement" überzeugende Ergebnisse, die für oder gegen eine bedeutende Beteiligung von interspezifischer Konkurrenz sprechen. Falls eine solche existiert, ist sie offensichtlich nicht sehr auffällig. Ein an Carabiden gewonnenes Datenmaterial wird im Hinblick auf die zeitliche Überlappung der Fortpflanzungsperioden koexistierender Arten untersucht, wobei der „Konkurrenz Hypothese" ein „Null-Modell" (das von einer zufälligen Zusammensetzung einer Lokalfauna ausgeht) gegenübergestellt wird. Dabei ließ sich keine „Nischen-Separation" nachweisen. Lediglich in Waldbiotopen sind die koexistierenden Carabiden-Arten im Hinblick auf die Körpergröße stärker verschieden, als es nach der Null-Hypothese zu erwarten wäre. Es gibt jedoch viele Gründe für die Annahme, daß diese Sonderung hinsichtlich der Körpergröße nichts mit interspezifischer Konkurrenz zu tun hat. Es wird der Schluß gezogen, daß unsere vorliegenden Erkenntnisse, auch wenn diese noch sehr fragmentarisch sind, ausreichen, um sicher zu sein, daß Konkurrenz keine *notwendige* Bedingung für Evolutionsprozesse darstellt. Die relative Bedeutungslosigkeit der interspezifischen Konkurrenz zeigt sich nicht nur in den hier diskutierten Fällen, sondern gilt auch bezüglich ihres Wirkens in Freilandpopulationen. Die meisten Arten sind an den meisten Plätzen ihres Vorkommen selten (DARWIN, WILLIAMS).

Literature

ABBOTT, I.; ABBOTT, L. K.; GRANT, P. R., 1977: Comparative ecology of Galàpagos ground finches (*Geospiza* Gould): Evaluation of the importance of floristic diversity and interspecific competition. Ecol. Mongr. **47**, 151–184.

ANDREWARTHA, H. G.; BIRCH, L. C., 1954: The distribution and abundance of animals. Chicago: Chicago Univ. Press.

– – 1984: The ecological web. More on the distribution and abundance of animals. Chicago: Chicago Univ. Press.

AYALA, F. J., 1970: Competition, coexistence and evolution. In: Essays in evolution and genetics in honor of THEODOSIUS DOBZHANSKY. Ed. by HECHT, STEERE. Amsterdam: North-Holl. Publ. Co. 121–158.

BIRCH, L. C., 1979: The effects of species of animals which share common recources on one another's distribution and abundance. Fortschr. Zool. **25**, 2/3, 197–221.

BOWMAN, R. I., 1961: Morphological differentiation and adaptation in the Galàpagos finches. Univ. Calif. Berkeley Publ. Zool. **58**, 1–302.

BROWN, W. L., WILSON, E. O., 1956: Character displacement. Syst. Zool. **5**, 49–64.

COLE, L. C., 1960: Competitive exclusion. Science **132**, 348–349.

CONNELL, J. H., 1971: On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Dynamics of populations. Ed. by DEN BOER, GRADWELL. Wageningen: Pudoc. 298–312.

CONNOR, E. F.; SIMBERLOFF, D. S., 1979: The assembly of species communities: change or competition? Ecology **60**, 1132–1140.

CONNOR, E. F.; SIMBERLOFF, D. S., 1983: Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. Oikos **41**, 455–465.

COOK, R. E., 1969: Variation in species density of North American birds. Syst. Zool. **18**, 63–84.

DARWIN, CH., 1859: The origin of species by means of natural selection. (6th ed. 1878). London: John Murray.

DEMPSTER, J. P.; POLLARD, E., 1981: Fluctuations in resource availability and insect populations. Oecologia **50**, 412–416.

DEN BOER, P. J., 1968: Spreading of risk and stabilization of animal numbers. Acta Biotheor., Leiden, **18**, 165–194.

– 1971: Stabilization of animal numbers and the heterogeneity of the environment: the problem of the persistence of sparse populations. In: Dynamics of populations. Ed. by DEN BOER, GRADWELL. Wageningen: Pudoc. 77–97.

– 1977: Dispersal power and survival. Carabids in a cultivated countryside. Miscell. Papers L. H. Wageningen **14**, 1–190.

– 1980: Exclusion or coexistence and the taxonomic or ecological relationship between species. Neth. J. Zool. **30**, 278–306.

– 1985: Fluctuations of density and survival of carabid populations. Oecologia **67**, 322–330.

DIAMOND, J. L., 1975: Assembly of species communities. In: Ecology and evolution of communities. Ed. by CODY, DIAMOND. Harvard: Harvard Univ. Press. 342–444.

– 1978: Niche shifts and the rediscovery of interspecific competition. Amer. Scientist **66**, 322–331.

DIAMOND, J. M.; GILPIN, M. E., 1982: Examination of the "null" model of CONNOR and SIMBERLOFF for species co-occurrences on islands. Oecologia **52**, 64–74.

EHRLICH, P. R.; HOLM, R. W., 1963: The process of evolution. McGraw-Hill Book Comp, New York. 231.

ELTON, C. S., 1946: Competition and structure of ecological communities. J. anim. Ecol. **15**, 54–68.

GAUSE, G. F., 1934: The struggle for existence. Baltimore: Williams & Wilkins Co. (1934). New York: Hafner Publ. Co., Inc. (Repr. 1964).

GILPIN, M. E.; DIAMOND, J. M., 1982: Factors contributing to non-randomness in species co-occurrences on island. Oecologia **52**, 75–84.

GRANT, P. R., 1966: Ecological compatibility of bird species on islands. Amer. Natur. **100**, 451–462.

– 1972: Convergent and divergent character displacement. Biol. Journ. Linn. Soc. **4**, 39–68.

– 1975: The classical case of character displacement. In: Evolutionary biology. Ed. by DOBSZANSKY, HECHT and STEERE. New York: Plenum Press. **8**, 237–337.

GRANT, P. R.; ABBOTT, I., 1980: Interspecific competition, island biogeography and null hypotheses. Evolution **34**, 322–341.

GRANT, P. R.; COWAN, I. McT., 1964: A review of the avifauna of the Tres Marias Islands, Nayarit, Mexico. Condor, **66**, 221–228.