The Relationship Between Competition and Morphology. I. Morphological Patterns Among Co-Occurring Dytiscid Beetles

Steven A. Juliano; John H. Lawton

THE RELATIONSHIP BETWEEN COMPETITION AND MORPHOLOGY. I. MORPHOLOGICAL PATTERNS AMONG CO-OCCURRING DYTISCID BEETLES

By STEVEN A. JULIANO*† AND JOHN H. LAWTON†‡

*Department of Biological Sciences, Ecology Group, Felmley 206,
Illinois State University, Normal, IL 61761-6901, U.S.A. and
†Department of Biology, University of York, Heslington, York YO1 5DD, U.K.*

SUMMARY

(1) We tested for widely and regularly distributed body forms in assemblages of small dytiscid beetles using four null models. Body form was determined by measurements of length, width, depth and head width, and was quantified using canonical discriminant function analysis in order to produce independent morphological variables. Our null models were based on different assumptions about where patterns should be evident and the appropriate pool of species' body forms.

(2) We tested for patterns among either all species in an assemblage or only among species above median abundance (by biomass). The pool of species was either the real species present in the area, or synthetic species formed by choosing values of the canonical functions from continuous distributions.

(3) Real assemblages fall into two distinct groups. For seven sites that are primarily small, acidic, and lack fish, we find little evidence for widely or regularly spaced body forms. For two sites that are large, well buffered, and have fish, we find significantly wider and usually more regular dispersions of body forms than expected under the null models. This is especially true of the abundant species, suggesting that morphological similarity influences abundance as well as presence/absence. There were slight differences in the conclusions obtained from using real vs. synthetic species, suggesting that the pool of real species may itself tend toward widely and regularly dispersed body forms (the Narcissus effect, Colwell & Winkler 1984).

(4) Our results support the contention that some water beetle assemblages show morphological patterns consistent with limiting similarity, and lead to different testable predictions about competitive interactions at the two groups of sites. Other biotic influences (e.g. predation) cannot be ruled out without experiments.

INTRODUCTION

A variety of theoretical considerations suggest that there is a limit to how morphologically similar co-occurring species can be (Ricklefs & O'Rourke 1975; Horn & May 1977; Pearson 1980; Ricklefs & Travis 1980; Jeffries & Lawton 1984). Morphologically similar species often use similar resources in similar ways (e.g. Ricklefs, Cochran & Pianka 1981; Warren & Lawton 1987) and may therefore compete more strongly than less similar species. Similar community patterns may also result from the influence of predation

‡ Present address: Center for Population Biology, Department of Pure and Applied Biology, Imperial College, Silwood Park, Ascot SL5 7PY.

(Jeffries & Lawton 1984; Mithen & Lawton 1986). Although community ecologists have long considered morphological patterns among co-occurring species to be important aspects of community structure (Hutchinson 1959; Greene 1987), it is only in the last decade that objective methods to detect morphological patterns have been developed (Strong, Szyska & Simberloff 1979; Ricklefs & Travis 1980; Hendrickson 1981; Dillon 1981; Simberloff & Boecklen 1981; Colwell & Winkler 1984; Findley & Findley 1985; Gotelli, Lewis & Young 1987; Schiebe 1987). Typically, this involves use of null models in order to determine whether observed morphological patterns depart significantly from those expected under some sort of random assembly of species (Schoener 1986a).

The use of null models has led to acrimonious debate (Strong *et al.* 1984). Early enthusiasm for the objectivity of these methods has been tempered with increased understanding of the limitations imposed upon them by initial assumptions, many of which are implicit rather than explicit (Harvey *et al.* 1983; Colwell & Winkler 1984; Greene 1987). But despite problems, null models have yielded several important benefits for community ecology. First, they have encouraged a more critical approach to conclusions drawn from data. Second, the debate on the subject has clarified the distinction between patterns, which may be consistent with several different underlying processes, and the biological processes that cause the patterns. Objectively identified patterns suggest hypotheses to be tested by observations and experiments.

Colwell & Winkler (1984) pointed out several flaws in the way in which null models have been constructed. Most null models have been constructed by reshuffling a pooled group of real species from a range of sites (e.g. islands, Strong, Szyska & Simberloff 1979). Colwell & Winkler (1984) showed that using pooled real species from many sites may bias the test toward failure to reject the null hypothesis of random assembly. This can occur if competition has influenced the body forms of species present in the entire pool of species by eliminating species that are too similar to another species. Colwell & Winkler (1984) called this the Narcissus effect. One way to avoid this problem, at least in model systems, is to use the precompetitive pool of species, i.e. including any species eliminated from the total pool. Unfortunately, identifying species that have been eliminated from a real pool of species is usually impossible. A solution, however, may be to define species not by observed body forms, but rather by a continuous distribution of body forms spanning the range of observed values (e.g. Ricklefs & Travis 1980). By using such 'synthetic species', the species pool would include the full complement of body forms that could exist within the limits defined by existing species.

Most null models of morphological patterns ignore the abundances of species (Ricklefs, Cochran & Pianka 1981; Ranta 1982; James & Boecklen 1984; Nilsson 1986). This is likely to weaken the tests for patterns for two reasons. First, rare species may be transients, either as individuals or as populations, and therefore not strongly influenced by organizing forces such as predation or competition (Ranta 1982; Nilsson 1986). Second, rarity itself may be a result of being too similar to another species (James & Boecklen 1984). When all species in an assemblage are considered, no significant departure from null expectation may result because of similarities between rare and abundant species. However, strong and significant patterns of morphological distinctness may exist among the abundant species. One solution to this problem is to eliminate from consideration species below a threshold abundance.

In this paper, we compare morphological patterns in assemblages of small dytiscid beetles with those produced by null models. We will address several general questions

about how appropriate null models can be constructed, as well as testing for morphological patterns in these assemblages.

NATURAL HISTORY OF DYTISCIDS AND PREDICTIONS TO BE TESTED

Water beetles in the family Dytiscidae are predators both as adults and as larvae. Two subfamilies, Hydroporinae and Laccophilinae, composed of small (< 5·5 mm long) species are considered in this study. Hydroporines are a diverse subfamily (sixty-three species in Britain), whereas laccophilines are much less diverse (three species in Britain) (Friday 1988). Laccophilines and hydroporines frequently co-occur in ponds, ditches, and lakes. Both subfamilies are included in these analyses because of their similar morphology as adults and common co-occurrence.

In Britain, adults of these dytiscids are present throughout the year. Teneral adults appear primarily in late summer and early autumn. Larvae are common in summer. Adults feed on a variety of small aquatic invertebrates (Nilsson 1986; personal observation). Adults of most species have well developed wings and some species have seasonal dispersal, though a few hydroporines are flightless (Jackson 1952).

Community studies of Dytiscidae have emphasized correlations of assemblage composition with physical factors (e.g. Cuppen 1983, 1986; Nilsson 1984; Larson 1985; Ranta 1985; Eyre, Ball & Foster 1986). Ranta (1982) and Nilsson (1986) examined body sizes of co-occurring species of dytiscids and found no strong patterns. In contrast, Lawton & Hassell (1984) reported species lists for hydroporines from several sites in North Yorkshire, and suggested that adults differed considerably in body size; they also noted that body length and mean preferred prey length were highly correlated ($r = 0·99$, $P < 0·001$, $N = 5$; N. G. Webb, unpublished data). These data are therefore superficially consistent with the frequent claim that body size differences facilitate coexistence, although as Lawton & Hassell noted, there is no evidence that dytiscids compete for resources. We therefore set out to examine critically morphological patterns in water beetle assemblages from North Yorkshire. In this paper, we test five specific predictions.

(a) Co-occurring species have mean morphological nearest neighbour distances (defined below) that are large relative to random assemblages (wide spacing).

(b) Co-occurring species have standard deviations of morphological nearest neighbour distances (defined below) that are small relative to random assemblages (regular spacing).

(c) The combination of mean nearest neighbour distance and standard deviation of nearest neighbour distance for real assemblages will be extreme relative to random assemblages. It is possible that neither the mean nor the standard deviation are significantly different from random expectation, but that the combination is extremely far from random. This is likely if the mean and standard deviation are positively correlated, making the combination of a moderately high mean and a moderately low standard deviation exceedingly unlikely.

(d) If drawing from a pool of real species produces the Narcissus effect, we predict that drawing from a pool of synthetic species will accentuate any departure from null expectation.

(e) If biotic processes have influenced abundance as well as presence/absence of similar species, we predict that restricting analyses to abundant species will accentuate any departure from null expectation.

We re-emphasize that detection of one or more of these non-random patterns in assemblages of dytiscids tells us nothing about mechanisms that might cause the patterns.

METHODS

Dytiscids were sampled intensively at nine sites in North Yorkshire and Humberside, England, in 1987 and 1988 (Table 1). All sites held water year-round. Five additional sites were sampled less intensively in order to determine if additional species would be added to the local species list. Sampling was designed to identify the pool of local species, the species present at each site, and the relative abundance of each species at each site. Samples were taken with a pond net using three different techniques, each with its own advantages and disadvantages. Sweep samples consisted of three sweeps of the net through 1 m at 0, 1 and, when possible, 2 m from shore, at three or five randomly chosen locations along the shore. At some sites (Skipwith Ditch) the 2-m sample was not taken

TABLE 1. Sites sampled during 1987–88

Site (typical pH)	Characteristics: total area; bottom; dominant vegetation; flow; size of sampled area (types of samples—date)
Sites at Skipwith Common	
Washdike (4·3)	$c.5000$ m^2 natural permanent pond surrounded by many smaller ponds: bottom sand, moss, or peat; *Juncus* at margin; no flow; 100-m section of east shore sampled (SW—9/87, BX—11/87).
Runway Pond (6·7)	$c.1500$ m^2 man-made permanent pond on abandoned runway with limestone base: bottom silt; *Elodea, Potamogeton, Typha, Glyceria, Sphagnum*; no flow; 100-m section of north shore sampled (SW—10/87, BX—11/87, CL—5/88).
Ditch	1-km permanent ditch, 2-m wide, runs around abandoned runway (sites 1 & 2) then away from the runway (site 3) and onto the common away from limestone (sites 4 & 5). Sampled 5 sites $c.200$ m apart.
Ditch 1 (6·2)	Bottom silt and sand; grasses, sedges, and *Sphagnum*; slow flow; 20-m section sampled (SW—9/87, BX—11/87, 4/88).
Ditch 2 (5·6)	Bottom silt; *Sparganium, Sphagnum, Potamogeton*, and grasses; slow flow; 20-m section sampled (SW—9/87, BX—11/87, 4/88).
Ditch 3 (4·5)	Bottom silt and sand; *Sphagnum*, grasses, and *Potamogeton*; slow flow; 20-m section sampled (SW—9/87, BX—11/87, 4/88).
Ditch 4 (4·5)	Bottom silt and sand; *Potamogeton, Sphagnum*, and sedges; slow flow; 20-m section sampled (SW—9/87, BX—11/87, 4/88).
Ditch 5 (4·4)	Bottom silt and sand; *Potamogeton, Sphagnum*, grasses, and sedges; moderate flow; 20-m section sampled (SW—9/87, BX—11/87, 4/88.
Sites not at Skipwith Common	
Pocklington Canal (7·5)	15-km long disused shipping canal, 10–15 m wide; bottom deep silt; *Sparganium, Typha, Nuphar, Carex, Glyceria*, and *Juncus*; moderate flow; $c.350$-m section of west shore sampled (SW—10/87, 3/88, BX—11/87, CL—6/88).
Gravel Pit (7·7)	$c.15000$-m^2 water-filled quarry: bottom gravel; grasses, sedges; no flow; $c.150$-m section of east shore sampled (CL—3/88, 6/88).

SW, sweep samples.
BX, box samples.
CL, collections using pond net (see text for details).

because the water was only about 2 m wide. Box samples were taken using an open-ended, 317-cm² aluminium box and a net which fitted snugly within the box. At ten randomly chosen locations along the shore, samples were taken 0, 1 and 2 m from shore by placing the box firmly into the substrate and netting the substrate and water column within the box. This sampler provided more quantitative data on beetle density at each site, but did not work well in deep water or in very soft substrates. Simple collections, which involved haphazard netting of the area between 0 and 2 m from shore provided collections from sites where steep slopes, deep water, or sparse beetle populations limited the usefulness of the other two methods. All samples were sorted in the field and all adult dytiscids collected for identification, counting, and measurement. Because different combinations of collection methods were used at different sites (Table 1) comparison of abundances between sites is not possible. However, our goals are first to obtain a list of the species within the assemblage at each site and second to rank species abundances within each site. The different methods usually gave similar rank order of species' numerical abundance, e.g. Pocklington Canal (Kendall's Coefficient of Concordance between: sweep and box samples, $\tau = 0.674$, $P = 0.0071$; sweep samples and simple collections, $\tau = 0.692$, $P = 0.0042$; box samples and simple collections, $\tau = 0.471$, $P = 0.0535$). Adults were identified using keys given in the 1986 test version of Friday (1988).

We estimated species relative abundances by multiplying the mean live mass of an individual of each species by the number of individuals of that species in all the samples from a site. Relative abundances therefore represent biomass abundance within each site. We measured abundance by biomass rather than number of individuals because resource demand should be more closely related to population biomass than number of individuals. For some rare species, we did not have mass determinations. For these species we estimated mass based on multiple regressions of log (mean mass) on log (mean length), log (mean width), log (mean depth), and log (mean head width) for those species that were weighed. In our null models, we make use only of the rank order of abundances; we are therefore confident that these approximate biomass abundances are sufficient for our purposes.

Four simple morphological measurements were made on a sample of non-teneral beetles of each species. We measured total length, width, and depth, and head width to the nearest 0·1 mm using an ocular micrometer. These measurements served to characterize the body form of each species. For most species we also weighed a set of living non-teneral individuals to the nearest 0·005 mg.

Logs of the four morphological measurements were used in a canonical discriminant analysis (Stevens 1986; SAS Institute Inc. 1987, Procedure CANDISC). This is a multivariate technique related to principal components analysis, but which is appropriate when the groups are characterized by the centroid of a set of multivariate observations. Canonical discriminant analysis produces canonical functions, which are linear combinations of the original variables. The first canonical function maximizes the discriminatory power among groups (i.e. species). The second canonical function is uncorrelated with the first and accounts for the maximum fraction of the between-group variance remaining after the first canonical function is taken into account. With four original variables, four canonical functions can be derived, with the third and fourth having interpretations analogous to the second. Some of the morphological analyses could have been conducted using the original morphometric variables; however, random construction of synthetic species requires random selection of independent values for each morphological variable. Canonical functions provide such independent morphological variables. We used the

canonical functions in the randomization of the pool of real species in order to maintain consistency among our analyses.

All analyses made use of morphological nearest neighbour distances, which were computed for each species in each assemblage using simple Euclidean distances among species means in the space defined by the canonical functions (SAS Institute Inc. 1987, Procedure FASTCLUS). Only nearest neighbour distances were used because distances to nth nearest neighbours are much more sensitive to the Narcissus effect (Colwell & Winkler 1984). Mean morphological nearest neighbour distances (MEANNND), standard deviation of morphological nearest neighbour distances (SDNND), and the difference $D = \text{MEANNND} - \text{SDNND}$ were computed within each community. D is large when species are widely and regularly spaced, and decreases as morphological spacing becomes narrower or more variable. D is used as a simple measure of the unusualness of the combination of MEANNND and SDNND. We chose a difference rather than a ratio (coefficient of variation) because ratios often have undesirable statistical properties (Atchley, Gaskins & Anderson 1976).

Six null models were constructed using the species lists, canonical morphological variables, and rank abundances. Two of these null models involved all species in an assemblage.

(1A) All, real species: MEANNND, SDNND, and D were determined for all species in each real assemblage and compared to those from at least 400 assemblages with the same total number of species randomly formed by drawing without replacement from the list of all available species.

(1B) All, synthetic species: real values of MEANNND, SDNND, and D were compared to those of at least 400 assemblages formed by randomly drawing four canonical functions for each synthetic species. Canonical functions were drawn from normal distributions with the same mean and standard deviation as those observed for all real species for canonical functions 1, 3, and 4. For canonical function 2, the real values were skewed, and departed significantly from a normal distribution. Random values were drawn from a gamma distribution with a shape parameter of 3 and displaced 3 units below 0. This distribution did not differ significantly from the distribution of real values of canonical function 2 (Kolomogorov–Smirnov two-sample test, $P \gg 0.1$).

Two null models tested for patterns among the abundant species in each assemblage. We designated species as 'abundant' if they were at or above median abundance by biomass. Choice of median abundance as the cut-off was arbitrary; however, using this cut-off did eliminate primarily the very rarest of species. In the nine real assemblages, $92.0 \pm 0.9\%$ of the total biomass and $89.7 \pm 1.5\%$ of all individuals (means $\pm$ S.E.) were included in the 'abundant' species, indicating that eliminating species below median abundance left the vast majority (by biomass or individuals) of the assemblage intact. There were two models involving abundant species.

(2A) Abundant, real species: MEANNND, SDNND, and D were determined for those species at or above median abundance in the real assemblage. At least 400 assemblages with the same total number of species were randomly formed by drawing without replacement from the list of all available species. One-half of the species in each random assemblage were randomly designated as being above median abundance. MEANNND, SDNND, and D were determined for each assemblage among these abundant species.

(2B) Abundant, synthetic species: as in model 2A, but with at least 400 assemblages formed by randomly drawing four canonical functions for each synthetic species.

Distributions from which canonical functions were drawn were as described for model 1B.

At some of the study sites, assemblages of small dytiscids were dominated by a single genus, *Hydroporus* (see below). In using null models, ability to detect real patterns declines as analyses are expanded to higher taxonomic groups ('J. P. Morgan Effect', Colwell & Winkler 1984). Therefore, for the sites dominated by *Hydroporus*, we tested null models drawn from a restricted taxonomic species pool consisting of all *Hydroporus* species, plus one species in the genus *Suphrodytes* (closely related to *Hydroporus*, and sometimes considered a subgenus). We tested null models involving:

(3A) All, real *Hydroporus/Suphrodytes*: MEANNND, SDNND, and *D* were compared to those from 500 assemblages with the same total number of species assembled by drawing at random without replacement from the list of all available *Hydroporus/ Suphrodytes*.

(3B) Abundant, real *Hydroporus/Suphrodytes*: MEANNND, SDNND, and *D* were determined for those *Hydroporus/Suphrodytes* species at or above median abundance in the real assemblage. In 500 randomly formed assemblages with the same total number of species, one-half of the species were randomly designated as being above median abundance. MEANNND, SDNND, and *D* for these abundant species in the random assemblages were determined.

We used 'sampled randomization tests' (Sokal & Rohlf 1981) to determine which, if any, of the real assemblages show patterns of widely spaced or uniformly spaced body forms. For each real assemblage, the null hypothesis of random assembly was rejected in favour of wide morphological spacing if the observed value of MEANNND exceeded 95% of those from the random assemblages. The null hypothesis was rejected in favour of regular morphological spacing if SDNND was less than 95% of those from the random assemblages. The combination of MEANNND and SDNND was judged to depart significantly in the direction of wide and regular spacing if *D* for the real assemblage exceeded 95% of those from the random assemblages. We evaluate each assemblage separately, in contrast to many past studies that have used combined tests for all assemblages (e.g. Strong, Szyska & Simberloff 1979; Ricklefs & Travis 1980; Hendrickson 1981; Schoener 1984; Schiebe 1987). We do this because there is no *a priori* reason to expect all assemblages to show patterns.

RESULTS

Twenty-eight species were present in the samples, with assemblages composed of up to sixteen species (Table 2). The list of locally available species did not increase when the five additional sites were included. This suggests that we have sampled a wide enough range of sites so that adding new sites adds no new species. Seven sites located at Skipwith Common were dominated by *Hydroporus* species. Two large bodies of water, Pocklington Canal and Gravel Pit had fewer *Hydroporus* species and more members of other genera (Table 2).

All four canonical functions were significant (*F* approximation, $P \leqslant 0.0001$), indicating that all four were correlated with group membership. The correlation structure between the four canonical functions and the four morphological variables (Table 3) indicates that the first canonical function (CANF1) accounted for 85.1% of the between-group variance and had high positive correlations with all of the original variables. CANF1 is therefore interpreted as a measure of overall size. The second canonical function (CANF2)

TABLE 2. Rank abundance of small dytiscids at nine sites near York. Site abbreviations: WD = Washdike; D5, D4, D3, D2, D1 = Ditch sites 5, 4, 3, 2, 1; RW = Runway Pond; GP = Gravel Pit; PC = Pocklington Canal

Species	WD	D5	D4	D3	D2	D1	RW	GP	PC
HYDROPORINAE									
Coelambus									
impresso-punctatus (Schall.)	—	—	—	—	—	—	7	—	—
Graptodytes									
granularis (L.)	—	—	—	—	—	—	16	—	—
pictus (Fab.)	—	—	—	—	—	—	9	4	7
Hydroporus									
angustatus Sturm	—	—	—	—	6	9	15	—	—
erythrocephalus (L.)	1	2	1	2	1	2	1	—	—
gyllenhalii Sch.	6	1	3	1	4	1	11	—	—
incognitus Sharp	7	—	—	—	—	—	—	—	—
melanarius Sturm	—	8	6	—	—	—	—	—	—
memnonius Nic.	—	6	—	—	—	6	8	—	—
neglectus Sch.	—	—	10	9	11	—	13	—	—
obscurus Sturm	2	4	2	11	—	—	14	—	—
palustris (L.)	8	7	4	3	8	7	5	7	5
planus (Fab.)	5	5	—	—	—	—	6	—	3
pubescens (Gyll.)	—	3	8	8	10	—	—	—	—
striola (Gyll.)	—	—	7	4	2	5	10	—	—
tristis (Pay.)	4	9	5	10	9	3	12	—	—
umbrosus (Gyll.)	3	—	9	5	3	4	2	—	—
Hygrotus									
decoratus (Gyll.)	—	—	—	—	7	—	—	—	—
inaequalis (Fab.)	—	—	—	—	—	—	4	1	8
versicolor (Schall.)	—	—	—	—	—	—	—	6	2
Hyphydrus									
ovatus (L.)	—	—	—	—	—	—	—	2	1
Porhydrus									
lineatus (Fab.)	—	—	—	—	—	—	3	—	10
Potamonectes									
assimilis (Pay.)	—	—	—	—	—	—	—	3	6
elegans (Pan.)	—	—	—	—	—	—	—	8	—
Stictotarsus									
duodecimpustulatus (Fab.)	—	—	—	—	—	—	—	—	9
Suphrodytes									
dorsalis (Fab.)	—	—	—	6	5	8	—	—	—
LACCOPHILINAE									
Laccophilus									
hyalinus (Deg.)	—	—	—	—	—	—	—	—	4
minutus (L.)	—	—	—	—	—	—	—	5	—
Species	8	9	10	11	11	9	16	8	10

accounted for 9·8% of between-group variance and was positively correlated with log (depth) and log (width) and negatively correlated with log (length) and log (head). Because the coefficient for log (head) is small, CANF2 can be interpreted as a measure of width and depth relative to length (see Stevens 1986). Species that are deep-bodied and wide relative to their length have large values of CANF2. CANF3 accounted for 4·1% of between-group variance, and was positively correlated only with log (head). Because coefficients for log (depth) and log (width) are small, CANF3 is interpreted as a measure

Table 3. Canonical discriminant analysis of morphology of small dytiscids. Cumulative variance gives the proportion of the variance in the original variables accounted for by canonical functions up to and including the function listed. F-tests test the null hypothesis that proportion of variance accounted for by the canonical function and all subsequent functions is zero (***$P \leqslant 0.0001$). Correlations are between canonical functions and original variates. Unstandardized coefficients are from the linear function for each canonical variate: CANF = constant + coef (loglength) + coef (logwidth) + coef (logdepth) + coef (loghead)

	CANF1	CANF2	CANF3	CANF4
Eigen value	43·03	4·97	2·06	0·50
Cum. % variance	85·10	94·94	99·02	100·00
Appx. F	49·10***	20·90***	12·32***	5·62***
(d.f.)	(108, 1066)	(78, 805)	(50, 540)	(24, 271)
Canonical correlation with				
log (length)	0·830	−0·314	−0·458	−0·049
log (width)	0·819	0·316	−0·088	−0·471
log (depth)	0·548	0·461	−0·413	0·563
log (head)	0·826	−0·124	0·497	0·236
Canonical coefficients				
log (length)	18·21	−61·10	−45·17	−0·85
log (width)	16·64	43·14	5·60	−47·24
log (depth)	3·79	25·75	−12·12	24·77
log (head)	25·53	−13·76	52·94	25·22

of head width relative to length. Species with wide heads relative to length have large values of CANF3. CANF4 accounted for 1·0% of between-group variance, and was positively correlated with log (depth) and log (head) and negatively correlated with the other two variables. CANF4 is interpreted as a measure of depth and head width relative to width. Species with deep bodies and large heads relative to width had large values of CANF4.

For the entire species pool, the plane defined by CANF1 and CANF2 shows clear distinctions among genera (Fig. 1a). One group of species, primarily the genus *Hydroporus*, spans a large range of sizes (CANF1) and is relatively narrow and flat (CANF2). Another group of species in the genera *Graptodytes*, *Hygrotus*, and *Hyphydrus* spans nearly the same range of sizes (CANF1) but is relatively wide and deep-bodied (CANF2). The plane defined by CANF3 and CANF1 further separates generic groups, indicating that *Laccophilus* and *Graptodytes* are relatively large-headed (Fig. 1b).

Observed values for MEANNND, SDNND, and D, and probabilities of more extreme values under the null hypothesis of random assembly of species are given in Table 4 (models 1A, 1B) and Table 5 (models 2A, 2B). For randomizations involving all, real species (model 1A), one assemblage had MEANNND significantly larger than expected by chance (Pocklington Canal, Table 4). Assemblages from Skipwith Common had MEANNNDs that were very low, so low that for 5 assemblages, MEANNND was less than those of 95% of random assemblages (Table 4). The null hypothesis would have been rejected in favour of an alternative of morphological convergence in these five assemblages. Four assemblages had SDNNDs that were significantly smaller than expected; however, all four were associated with low MEANNNDs (Table 4). For none of the nine assemblages was D significantly larger than expected (Table 4). We conclude that
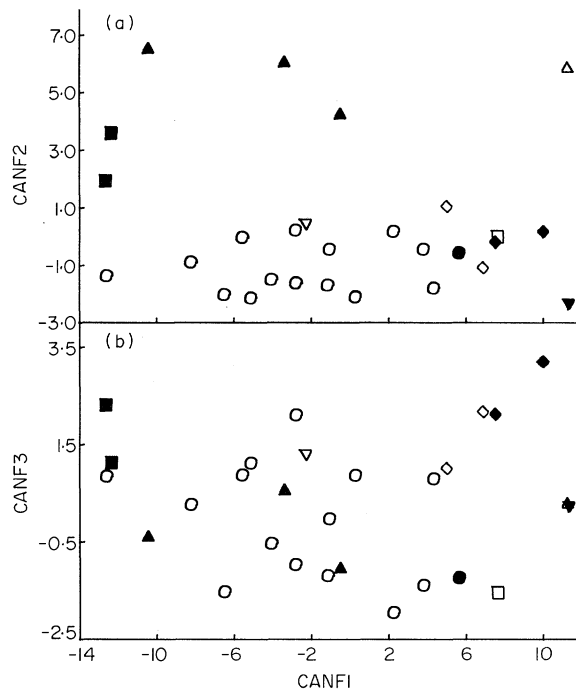
FIG. 1. Plots of CANF1, CANF2, and CANF3 for twenty-eight small dytiscid species present in this study. Plotted points are mean values for each species: *Hydroporus* (O); *Suphrodytes* (●); *Hyphydrus* (△); *Hygrotus* (▲); *Coelambus* (□); *Graptodytes* (■); *Porhydrus* (▽); *Stictotarsus* (▼) *Potamonectes* (◇) *Laccophilus* (◆). (a) CANF2 vs. CANF1. (b) CANF3 vs. CANF1.

when all species are compared to random assemblages drawn from the pool of real species, only one assemblage shows a pattern of widely, but not regularly dispersed body forms.

For randomizations involving all synthetic species (Model 1B) only Pocklington Canal had MEANNND significantly larger than expected due to chance (Table 4). The same four assemblages at Skipwith had SDNNDs that were significantly smaller than those expected due to chance, but once again these low values of SDNND were associated with low values of MEANNND. D for Pocklington Canal was significantly greater than that expected due to chance. This indicates that all species at this site had body forms more widely and regularly dispersed than expected if assemblages were created from any possible species within the morphological space occupied by these beetles. This conclusion was not obtained from randomization of real species. This suggests that the Narcissus effect may be occurring in our randomization of real species, weakening our ability to detect pattern in the Pocklington Canal assemblage. However, the actual difference between $P1A$ and $P1B$ is small. For all sites, observed D were more extreme relative to random assemblages of synthetic species than relative to real species (Table 4), further suggesting that the Narcissus effect influences the tests involving real species.

When only species above median abundance are considered, the results change somewhat (Table 5). For model 2A, none of the nine assemblages have MEANNNDs significantly greater than expected due to chance. Only two assemblages have SDNNDs that are significantly less than expected due to chance, and again all of these are associated

TABLE 4. MEANNND, SDNND, and D from nine real assemblages, and proportion of random assemblages yielding more extreme values under null hypotheses 1A (all, real species; P1A) and 1B (all, synthetic species; P1B). Tests are based on 500 random assemblages, except for Runway Pond, for which only 400 random assemblages were formed due to limited computer memory. All sites except Gravel Pit and Pocklington Canal are at Skipwith Common

Site	MEANNND		SDNND		D	
	(P1A)	(P1B)	(P1A)	(P1B)	(P1A)	(P1B)
Washdike	2·509		0·223		2·285	
(8 spp.)	(0·996)	(0·946)	(0·002)*	(0·006)*	(0·572)	(0·290)
Ditch 5	2·664		0·411		2·252	
(9 spp.)	(0·998)	(0·872)	(0·008)*	(0·014)*	(0·522)	(0·206)
Ditch 4	2·882		0·738		2·145	
(10 spp.)	(0·960)	(0·764)	(0·072)	(0·058)	(0·540)	(0·200)
Ditch 3	2·638		0·626		2·011	
(11 spp.)	(0·998)	(0·882)	(0·020)*	(0·038)*	(0·698)	(0·218)
Ditch 2	3·395		1·618		1·776	
(11 spp.)	(0·750)	(0·338)	(0·598)	(0·584)	(0·864)	(0·354)
Ditch 1	2·756		0·335		2·422	
(9 spp.)	(0·990)	(0·832)	(0·002)*	(0·012)*	(0·412)	(0·154)
Runway Pond	2·955		0·976		1·979	
(16 spp.)	(0·895)	(0·315)	(0·183)	(0·223)	(0·548)	(0·068)
Gravel Pit	4·686		2·723		1·963	
(8 spp.)	(0·188)	(0·096)	(0·936)	(0·834)	(0·788)	(0·438)
Pocklington Canal	4·598		1·953		2·645	
(10 spp.)	(0·040)*	(0·034)*	(0·802)	(0·650)	(0·134)	(0·042)*

* $P < 0.05$.

with very low values of MEANNND. Two assemblages (Pocklington Canal, Gravel Pit) have Ds significantly larger than expected due to chance, i.e. they have a combination of unusually large MEANNND and small SDNND. Figure 2a illustrates the pattern of association between MEANNND and SDNND for abundant species in random assemblages and also shows the positions of two real assemblages with the same number of species. MEANNND and SDNND are significantly and positively correlated ($P \leqslant 0.0001$), and combinations of high MEANNND and low SDNND are therefore very rare. Thus, even though the two assemblages in question have values of MEANNND and SDNND that are slightly but not significantly more extreme than expected when each statistic is considered alone, the combinations of MEANNND and SDNND do depart significantly from that expected due to chance. We conclude that in the Skipwith assemblages there is no evidence of widely and regularly dispersed body forms, but in the other two assemblages, the abundant species are more widely and regularly dispersed than expected due to chance alone.

For the model involving synthetic species (model 2B) all seven assemblages from Skipwith Common show no significant departures from random expectation for MEANNND, SDNND, or D (Table 5). However, MEANNND for Gravel Pit is significantly larger than expected, and both Gravel Pit and Pocklington Canal have Ds that are significantly larger than expected, indicating that the abundant species at these

TABLE 5. MEANNND, SDNND, and D for abundant species from nine real assemblages, and proportion of random assemblages yielding more extreme values under null hypotheses 2A (abundant, real species (P2A) and 2B (abundant, synthetic species; P2B). Tests are based on 500 random assemblages, except for Runway Pond, for which only 400 random assemblages were formed due to limited computer memory. All sites except Gravel Pit and Pocklington Canal are at Skipwith Common

Site	MEANNND		SDNND		D	
	(P2A)	(P2B)	(P2A)	(P2B)	(P2A)	(P2B)
Washdike	3·991		2·881		1·109	
(8 spp.)	(0·856)	(0·686)	(0·652)	(0·642)	(0·926)	(0·806)
Ditch 5	3·145		0·866		2·280	
(9 spp.)	(0·958)	(0·866)	(0·126)	(0·168)	(0·698)	(0·508)
Ditch 4	2·792		0·664		2·128	
(10 spp.)	(0·982)	(0·938)	(0·086)	(0·108)	(0·722)	(0·574)
Ditch 3	3·292		0·671		2·621	
(11 spp.)	(0·924)	(0·810)	(0·042)*	(0·064)	(0·468)	(0·280)
Ditch 2	3·273		0·613		2·659	
(11 spp.)	(0·928)	(0·812)	(0·038)*	(0·058)	(0·452)	(0·268)
Ditch 1	3·911		0·842		2·549	
(9 spp.)	(0·926)	(0·670)	(0·124)	(0·154)	(0·596)	(0·388)
Runway Pond	3·859		1·475		2·385	
(16 spp.)	(0·620)	(0·355)	(0·355)	(0·452)	(0·458)	(0·213)
Gravel Pit	8·686		0·836		7·851	
(8 spp.)	(0·054)	(0·030)*	(0·190)	(0·176)	(0·014)*	(0·000)*
Pocklington Canal	6·003		0·614		5·389	
(10 spp.)	(0·190)	(0·184)	(0·084)	(0·098)	(0·020)*	(0·020)*

* $P < 0.05$.

two large bodies of water have body forms that are widely and regularly spaced. Figure 2b illustrates the significant ($P < 0.0001$) positive correlation between MEANNND and SDNND among random assemblages, and the positions of two real assemblages with the same number of species. The difference due to randomizing synthetic species vs. real species in our ability to detect patterns among abundant species is minimal (Table 5). With synthetic species, we do find one additional test significant (MEANNND at Gravel Pit); however, the change of randomization also eliminates two significant tests on SDNND.

Comparison of Tables 4 and 5 suggest that for Gravel Pit and Pocklington Canal, patterns are stronger among abundant species than among all species, especially when D is tested. This lends some support to the hypothesis that whatever the source of the pattern in morphology, it also affects abundance of species. However, considering only abundant species did not uniformly enhance patterns in MEANNND and SDNND, so the support for the hypothesis is only partial. Among the Skipwith sites, considering only the abundant species reduces the number of tests showing low SDNND. For the two larger bodies of water, considering only the abundant species increases the number of tests showing large D.

A sceptic might note that each of Tables 4 and 5 involves 54 tests each, and that some of these tests should appear significant simply due to chance. We note that one would expect
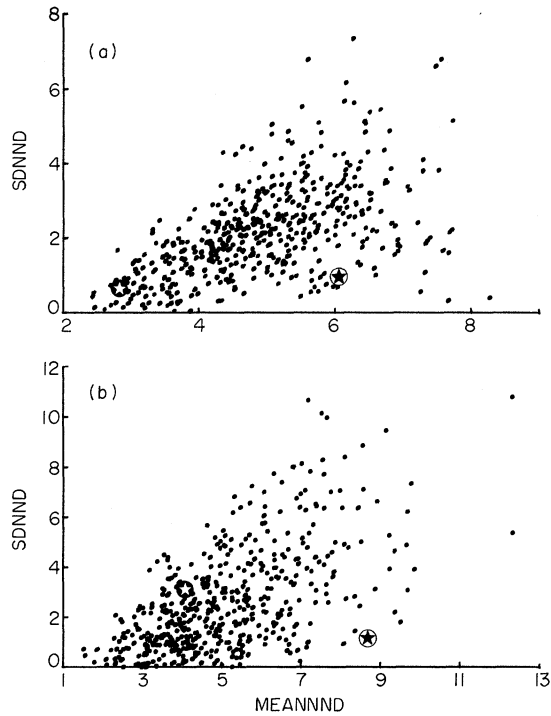
FIG 2. SDNND vs. MEANNND for abundant species in 500 random assemblages. Positions of two real assemblages are indicated on each graph. D (MEANNND − SDNND) increases toward the lower right corner and decreases toward the upper left corner. (a) Assemblages composed of ten species, randomly formed from the list of real species (model 2A): Pocklington Canal (★); Ditch 4 (☆). (b) Assemblages composed of eight species, randomly formed by drawing canonical functions from continuous distributions (model 2B): Gravel Pit (★); Washdike (☆).

2–3 tests out of 54 to yield P values < 0.05. We found 11 and 7 significant tests in Tables 4 and 5, respectively. We further note that all variations on our testing approach lead to the same overall picture: body forms of species from the two larger bodies of water tend to be widely and/or regularly spaced, whereas body forms of species from Skipwith are not. The pattern for the large bodies of water is strongest when abundant species are considered. Although our four separate approaches are not independent tests, they do represent null models incorporating different assumptions about how patterns may be produced. The consistency of the conclusions for Gravel Pit and Pocklington Canal indicates that these patterns are robust with respect to some of the assumptions of the null model used.

Comparisons of assemblages of *Hydroporus/Suphrodytes* to those produced by null models (3A) gave little evidence of significant morphological patterns (Table 6). For tests involving all *Hydroporus/Suphrodytes* species, neither MEANNND nor D was significantly greater than expected for any of the sites (Table 6). One site (Washdike) had SDNND significantly smaller than expected, but this was associated with a very low value of MEANNND (Table 6). Thus, when all *Hydroporus/Suphrodytes* are considered, there is no evidence of widely and regularly dispersed body forms.

For tests involving only abundant *Hydroporus/Suphrodytes* (3B), neither MEANNND nor SDNND were significantly different from expected (Table 6). However, at Ditch site 2,

TABLE 6. MEANNND, SDNND, and *D* based on ALL species or on ABUNDANT species (greater than median abundance) for assemblages of *Hydroporus/Suphrodytes* species, and proportion of random assemblages yielding more extreme values. Tests are based on 500 random assemblages. All sites are at Skipwith Common

Site	MEANNND		SDNND		*D*	
	ALL (*P*)	ABUNDANT (*P*)	ALL (*P*)	ABUNDANT (*P*)	ALL (*P*)	ABUNDANT (*P*)
Washdike (8 spp.)	2·509 (0·976)	3·991 (0·462)	0·223 (0·026)*	2·881 (0·876)	2·285 (0·414)	1·109 (0·932)
Ditch 5 (9 spp.)	2·664 (0·854)	3·145 (0·770)	0·411 (0·214)	0·866 (0·372)	2·253 (0·432)	2·280 (0·548)
Ditch 4 (10 spp.)	2·882 (0·496)	2·791 (0·916)	0·738 (0·667)	0·664 (0·298)	2·145 (0·576)	2·128 (0·664)
Ditch 3 (11 spp.)	2·638 (0·806)	3·292 (0·496)	0·627 (0·472)	0·671 (0·358)	2·011 (0·780)	2·621 (0·196)
Ditch 2 (10 spp.)	2·949 (0·394)	4·002 (0·274)	0·699 (0·608)	0·373 (0·110)	2·251 (0·388)	3·628 (0·012)*
Ditch 1 (9 spp.)	2·756 (0·742)	3·911 (0·594)	0·335 (0·138)	0·842 (0·366)	2·422 (0·140)	2·549 (0·348)
Runway Pond (11 spp.)	2·758 (0·624)	3·047 (0·708)	0·639 (0·500)	0·774 (0·454)	2·120 (0·650)	2·273 (0·554)

* $P < 0.05$.

D was significantly larger than expected, indicating that abundant *Hydroporus/Suphrodytes* at this site were apparently more widely and regularly spread in morphological space than expected due to chance. However, due to chance alone, one would expect 2–3 significant tests among the 48 tests in Table 6. As we have found two significant tests, we conclude that analysis of *Hydroporus/Suphrodytes* provides no evidence for morphological patterns at these small sites. Therefore, for the Skipwith sites, the conclusion obtained from analysing the taxonomically restricted pool of species is the same as that obtained from analysing the total pool of small dytiscids.

DISCUSSION

Lawton & Hassell's (1984) suggestion that morphological patterns were present in assemblages of small dytiscids was based primarily on the assemblage at Pocklington Canal. Our data support this suggestion for that site and for another site with a similar set of species. Lawton & Hassell did not consider sites at Skipwith Common.

Although assemblages of similar species from different sites may be influenced by very different biological processes (e.g. Pearson & Mury 1979; Pearson 1980; Schluter & Grant 1984; Schoener 1986b; Roughgarden, Gaines & Pacala 1987), many tests for patterns proceed under the assumption that morphological patterns should be ubiquitous, and so test whether all examined assemblages show the pattern in question (e.g. Strong, Szyska & Simberloff 1979). However, one of the main virtues of null models is that they provide a preliminary way of sorting assemblages, i.e. those that show morphological (or other) patterns and those that do not. The water beetle assemblages examined in this study fall into two groups, which can be identified based on location, size, taxonomic composition

of the beetle assemblages, and site characteristics, as well as on the basis of the tests of null models. The two largest bodies of water, Pocklington Canal and Gravel Pit, have assemblages composed of many genera, are located on well-buffered soils and hence have neutral to basic pH, are well populated with insectivorous fish, and have beetle assemblages with abundant species widely and regularly distributed in morphological space. The Skipwith sites, in contrast, have assemblages dominated by one genus, *Hydroporus*, are smaller, are located on poorly buffered soil (though some sites are artificially buffered by limestone in the foundation of an abandoned runway), lack insectivorous fish, and all have assemblages that give no evidence of wide, regular dispersion in morphological space.

Overall, our results suggest that different biotic processes have influenced the assemblages in these two groups. If the observed morphological patterns are in fact a result of interspecific competition, we predict that experiments testing for biotic interactions between water beetles, and for differential effects of competitors based on morphological distinctness, should give different results at the two types of sites. At the large sites, interspecific competition should be evident among adults and the intensity of competition should decrease as morphological similarity between species decreases; at the Skipwith sites, interspecific competition should be absent or uninfluenced by morphology. Results of these experiments will be reported in a later publication.

An alternative explanation, that predation influences morphological similarity should also be tested. The observed differences in morphological pattern at the two groups of sites are consistent with the hypothesis that wide dispersion in morphological space is a result of species' requirements for enemy-free space (Jeffries & Lawton 1984), and that insectivorous fish are the principal predators involved. Perch and roach are found at the two larger sites and Pocklington Canal also holds a variety of other fish species including pike and eel. None of these fish are present at the Skipwith sites. In addition, *Notonecta glauca* L. is abundant at Pocklington Canal and present at Gravel Pit. Although *N. glauca* is sporadically present at some of the Skipwith sites, it is common at Skipwith only at Runway Pond. Both fish (Leech & Chandler 1956) and *N. glauca* (Giller 1986; personal observation) prey on adult dytiscids. Other potential predators on adult dytiscids include large odonates and larger dytiscids, both of which were present, but not common, at all sites. These observations suggest that predation on adult dytiscids, particularly by fish, is strongest at sites where assemblages are most widely and regularly dispersed in morphological space, and is thus consistent with the enemy-free space hypothesis.

Morphological pattern, particularly at the two large sites, was slightly more extreme when compared to synthetic species than when compared to real species. This contrasts with a prior study of bird assemblages (Ricklefs & Travis 1980) which showed no consistent difference in the results from null models involving real vs. synthetic species. Our results suggest that the Narcissus effect is influencing the tests. The synthetic species approach may be a generally useful way of avoiding the problem posed by the Narcissus effect. It would be interesting to apply such models to simulations such as those done by Colwell & Winkler (1984) which originally demonstrated the Narcissus effect, to see precisely how much of an improvement the synthetic species models could make.

Patterns of wide and regular morphological spacing, as measured by D, are stronger and more consistent among the abundant species at the large sites than among all the species at these sites. This supports the hypothesis that rare species are less influenced by the processes producing the pattern, or that their rarity is in part due to their similarity to other species. The decision to use species above median abundance as the 'abundant'

group was a reasonable first step in accounting for species abundance in null models, but was arbitrary. It is likely that better criteria could be developed. It is important for future null models to consider species abundance as well as morphology.

The positive correlation between MEANNND and SDNND indicates that the combination of widely and regularly spaced body forms is rare in random communities. This means that it is important to test whether the combination is unusual, not just whether each value is extreme. The composite statistic used in this study gives equal weight to both MEANNND and SDNND. Other weightings (i.e. other linear combinations of MEANNND and SDNND) may give different results. In some cases, the hypothesis of interest may only be that species are widely spaced, and in such cases MEANNND should suffice.

ACKNOWLEDGMENTS

REFERENCES

Atchley, W. R., Gaskins, C. T. & Anderson, D. (1976). Statistical properties of ratios. I. Empirical results. *Systematic Zoology*, **25**, 137–148.

Colwell, R. K. & Winkler, D. W. (1984). A null model for null models in biogeography. *Ecological Communities, Conceptual Issues and the Evidence* (Ed. by D. R. Strong, Jr, D. Simberloff, L. G. Abele & A. B. Thistle), pp. 344–359. Princeton University Press, Princeton.

Cuppen, J. G. M. (1983). On the habitats of three species of the genus *Hygrotus* Stephens (Coleoptera: Dytiscidae). *Freshwater Biology*, **13**, 579–588.

Cuppen, J. G. M. (1986). The influence of acidity and chlorinity on the distribution of Hydroporus species (Coleoptera: Dytiscidae) in the Netherlands. *Entomologica Basiliensia*, **11**, 327–336.

Dillon, R. T., Jr (1981). Patterns in the morphology and distribution of gastropods in Oneida Lake, New York, detected using computer-generated null hypotheses. *American Naturalist*, **118**, 83–101.

Eyre, M. D., Ball, S. G. & Foster, G. N. (1986). An initial classification of the habitats of aquatic Coleoptera in north-east England. *Journal of Applied Ecology*, **23**, 841–852.

Findley, J. S. & Findley, M. T. (1985). A search for pattern in butterfly fish communities. *American Naturalist*, **126**, 800–816.

Friday, L. E. (1988). *A Key to the Adults of British Water Beetles*. AIDGAP. Field Studies Council, Dorset Press, Dorchester.

Giller, P. S. (1986). The natural diet of Notonectidae: field trials using electrophoresis. *Ecological Entomology*, **11**, 163–172.

Gotelli, N. J., Lewis, F. G. III & Young, C. M. (1987). Body-size differences in a colonizing amphipod–mollusc assemblage. *Oecologia*, **72**, 104–108.

Greene, E. (1987). Sizing up size ratios. *Trends in Ecology and Evolution*, **2**, 79–81.

Harvey, P. H., Colwell, R. K., Silvertown, J. W. & May, R. M. (1983). Null models in ecology. *Annual Review of Ecology and Systematics*, **14**, 189–211.

Horn, H. S. & May, R. M. (11977). Limits to similarity among coexisting competitors. *Nature*, **270**, 660–661.

Hendrickson, J. A. Jr (1981). Community-wide character displacement reexamined. *Evolution*, **35**, 794–809.

Hutchinson, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.

Jackson, D. J. (1952). Observations on the capacity for flight of water beetles. *Proceedings of the Royal Entomological Society of London (A)*, **27**, 57–70.

James, F. C. & Boecklen, W. J. (1984). Interspecific morphological relationships and the densities of birds. *Ecological Communities, Conceptual Issues and the Evidence* (Ed. by D. R. Strong, Jr, D. Simberloff, L. G. Abele & A. B. Thistle), pp. 458–477. Princeton University Press, Princeton.

Jeffries, M. J. & Lawton, J. H. (1984). Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.

Larson, D. J. (1985). Structure in temperate predaceous diving beetle communities (Coleoptera: Dytiscidae). *Holarctic Ecology*, **8**, 18–32.

Lawton, J. H. & Hassell, M. P. (1984). Interspecific competition in insects. *Ecological Entomology* (Ed. by C. B. Huffaker & R. L. Rabb), pp. 451–493. John Wiley & Sons, New York.

Leech, H. B. & Chandler, H. P. (1956). Aquatic Coleoptera. *Aquatic Insects of California* (Ed. by R. L. Usinger), pp. 293–371. University of California Press, Berkeley.

Mithen, S. J. & Lawton, J. H. (1986). Food-web models that generate constant predator–prey ratios. *Oecologia*, **69**, 542–550.

Nilsson, A. N. (1984). Species richness and succession of aquatic beetles in some kettle-hole ponds in northern Sweden. *Holarctic Ecology*, **7**, 149–156.

Nilsson, A. N. (1986). Community structure in the Dytiscidae (Coleoptera) of a northern Swedish seasonal pond. *Annales Zoologici Fennici*, **23**, 39–47.

Pearson, D. L. (1980). Patterns of limiting similarity in tropical forest tiger beetles (Coleoptera: Cicindelidae). *Biotropica*, **12**, 195–204.

Pearson, D. L. & Mury, E. J. (1979). Character divergence and convergence among tiger beetles (Coleoptera: Cicindelidae). *Ecology*, **60**, 557–566.

Ranta, E. (1982). Animal communities in rock pools. *Annales Zoologici Fennici*, **19**, 337–347.

Ranta, E. (1985). Communities of water beetles in different kinds of waters in Finland. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **137**, 33–45.

Ricklefs, R. E., Cochran, D. & Pianka, E. R. (1981). A morphological analysis of the structure of communities of lizards in desert habitats. *Ecology*, **62**, 1474–1483.

Ricklefs, R. E. & O'Rourke, K. (1975). Aspect diversity in moths: a temperate-tropical comparison. *Evolution*, **29**, 313–324.

Ricklefs, R. E. & Travis, J. (1980). A morphological approach to the study of avian community organization. *Auk*, **97**, 321–338.

Roughgarden, J., Gaines S. D. & Pacala, S. W. (1987). Supply side ecology: the role of physical transport processes. *Organization of Communities, Past and Present* (Ed. by J. H. R. Gee & P. S. Giller), pp. 491–518. Blackwell Scientific Publications, Oxford.

SAS Institute Inc. (1987). *SAS/STAT^{TM} Guide for Personal Computers, Version 6 Edition*. SAS Institute Inc., Cary, NC.

Schiebe, J. S. (1987). Climate, competition, and the structure of temperate zone lizard communities. *Ecology*, **68**, 1424–1437.

Schluter, D. & Grant, P. R. (1984). Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist*, **123**, 175–196.

Schoener, T. W. (1984). Size differences among sympatric, bird-eating hawks: A worldwide survey. *Ecological Communities, Conceptual Issues and the Evidence* (Ed. by D. R. Strong, Jr, D. Simberloff, L. G. Abele & A. B. Thistle), pp. 254–281. Princeton University Press, Princeton.

Schoener, T. W. (1986a). Resource partitioning. *Community Ecology: Pattern and Process* (Ed. by D. J. Anderson & J. Kikkawa), pp. 91–126. Blackwell Scientific Publications, Melbourne.

Schoener, T. W. (1986b). Overview: kinds of ecological communities—ecology becomes pluralistic. *Community Ecology* (Ed. by J. Diamond & T. J. Case), pp. 467–479. Harper & Row, New York.

Simberloff, D. & Boecklen, W. (1981). Santa Rosalia reconsidered: size ratios and competition. *Evolution*, **35**, 1206–1228.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*, 2nd edn. W. H. Freeman & Co., New York.

Stevens, J. (1986). *Applied Multivariate Statistics for the Social Sciences*. Lawrence Erlbaum Associates, Inc. Hilsdale, N.J.

Strong, D. R. Jr., Simberloff, D., Abele, L. G. & Thistle, A. B. (Eds) (1984). *Ecological Communities. Conceptual Issues and the Evidence*. Princeton University Press, Princeton.

Strong, D. R., Szyska, L. A. & Simberloff, D. S. (1979). Tests of community-wide character displacement against null hypotheses. *Evolution*, **33**, 897–913.

Warren, P. H. & Lawton, J. H. (1987). Invertebrate predator–prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, **74**, 231–235.