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Variation in the diversity of ducks along a gradient of environmental variability

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Abstract. Tramer (1969) proposed that communities regulated by competition in benign, predictable environments were characterized by (i) damped variation in evenness relative to variation in richness over time, and (ii) high evenness relative to communities regulated by variation in the abundance and diversity of resources in rigorous, unpredictable environments. To test whether patterns of variation in diversity could reflect the mechanisms proposed to regulate community structure, temporal and spatial changes in the diversity, richness and evenness of breeding duck communities were examined along a gradient of variability in wetland conditions using thirty-three years of duck census and climate data from the Canadian prairie and boreal forest regions. Temporal variation in evenness was independent of wetland habitat variability. Changes in richness were more parsimoniously explained by the appearance of ducks displaced (by drought) from rigorous, variable wetland habitats into relatively benign ones, than by competition in benign areas. Evenness was not significantly higher for duck guilds in more constant wetland habitats, as predicted. Variation in richness, evenness and diversity, predicted by Tramer, do not provide a basis for distinguishing the factors that regulate duck community structure.

Key words: Climate – Ducks – Diversity – Multivariate analysis – Prairies

The study of patterns in species diversity and the mechanisms by which they are produced, has recently focused on the relative importance of biotic and abiotic factors (e.g., competition and environmental variability, respectively) in community organization (Strong et al. 1984; Grant 1986; Giller and Gee 1987). The degree to which competition plays a role in structuring communities in ecological time is thought to vary with the magnitude of environmental variability (Wiens 1977, 1986). Tramer (1969) proposed that variation in species diversity through changes in its components – richness (number of species) or evenness (distribution of relative abundances of species) – represented alternative mechanisms which organized communities in places that differed with respect to the degree to which the physical environment and resources were stable over time (i.e., how often species populations were in short term equilibria with local resource abundance). He predicted that:
over time,
(i) in resource-saturated, stable environments, competition for limited resources dampens variation in evenness and diversity, therefore, varies primarily with changes in richness;
(ii) in highly variable, resource-unsaturated environments, interspecific differences in ability of populations to track resources (e.g., through differences in reproductive rates, survival or dispersal), produce changes in diversity that are dominated by changes in evenness; and
over space
(iii) greater interspecific competition and resource partitioning in resource saturated, stable environments, results in greater evenness than in unsaturated environments where competition is weak or absent.

Among avian communities, variation in the components of diversity differs between sites and seasons, and with spatial scale (Kricher 1972, 1975; Austin and Tomoff 1978; Rotenberry 1978; Rotenberry et. al. 1979; Smith and MacMahon 1981; Nudds 1983a). At large spatial scales (Austin and Tomoff 1978; Rotenberry 1978; and Nudds 1983a), there is little agreement with Tramer's predictions. Results of studies conducted over small spatial scales, however, tend to accord with them (Kricher 1972; Rotenberry et al. 1979; Smith and MacMahon 1981; but see Kricher 1975). Fewer investigators have studied changes in the components of avian diversity over time (Rotenberry et al. 1979; Nudds 1983a). The success with which Tramer's (1969) model is able to distinguish between mechanisms structuring communities and under what conditions, remains uncertain (Weins 1989; pp. 136–137). As yet, there have been

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no tests of his model simultaneously at large temporal and spatial scales of analysis, due largely to the paucity of appropriate data to do so.

For several reasons, waterfowl provide an appropriate system with which to examine Tramer's (1969) predictions. Ducks breed in a wide variety of wetland complexes that differ extensively in terms of environmental variablility (Bellrose 1980). In general, they are ecologically and morphologically similar, and therefore represent potentially competing species. Ducks are higher-trophic-level consumers; competition rather than predation, should therefore be relatively more important in organizing species assemblages (Nudds 1983b). Finally, Nudds (1983b) concluded that competition for limited resources on the breeding grounds was important in organizing guilds of ducks where wetland habitat variability was low. Because of their economic importance, annual censuses of breeding ducks have been conducted on a continental basis in North America since 1955. By taking advantage of this existing data base consisting of 33 years of duck census data across the Canadian prairies and parts of the Northwest Territories, we tested Tramer's (1969) predictions.

Materials and methods

Duck census data

Annual surveys to estimate the size of duck populations on the major breeding areas in Canada and the United States became fully operational in 1955. Details regarding survey design, procedures and the reliability of survey results have been described in Benning (1976), Anonymous (1977), Bowden (1973) and Martin et al. (1979). The area surveyed (3.03×10^6 km^2) in the prairie provinces and Northwest Territories of Canada, the northcentral United States, and Alaska is divided into 49 strata based on ecogeographic boundaries, and on the abundance and distribution of the mallard, *Anas platyrhynchos* in order to satisfy the requirement for precision in population estimates (see Bowden 1973; Caughley 1977). In each stratum, surveys are conducted on 0.4 km × 29 km transects, flown east-west at an altitude of 30–46 m using fixed-wing aircraft. Transects are systematically flown, beginning from a randomly selected location, and vary in number between strata according to geographical differences in waterfowl density. The starting date of the aerial census is dependent on the yearly migrational chronology and nesting phenology of ducks in each of the survey strata (Bowden 1973). On approximately 10% of transects, ground surveys are made within two days of the aerial survey to obtain a correction factor for differential visibility of species which is applied to all transects with similar vegatation type, in all strata. Ground surveys are not conducted in northern strata. Instead, long-term average visibility rates for each species in southern strata are used to correct aerial counts in the north. For any stratum then, the total breeding abundance of each species is estimated as the product of the area of the stratum, the aerial count density of birds per km^2, and the visibility rate for the species in the stratum.

For this analysis, we used May population estimates for the period 1955–1987 from 23 strata in the Canadian prairies and the Northwest Territories (Fig. 1). Selection of strata was based on 2 criteria: (i) the availability of climatological and hydrological data (each measured in a consistent manner across all areas) with sufficient coverage to adequately classify a given stratum, and (ii) a minimum of two species of dabbling and diving ducks in the stratum over all 33 years. Species selection was based on their overall breeding distribution (Bellrose 1980) relative to the study area (i.e., those species representative of the mixed-prairie, aspen parkland, or boreal forest regions). Fifteen species comprised the duck community for this study including seven dabbling duck and eight diving duck species. The former group consisted of: mallard; gadwall, *A. strepera;* American wigeon, *A. americana;* green-winged teal, *A. crecca;* blue-winged teal, *A. discors;* northern shoveler, *A. clypeata;* and northern pintail, *A. acuta.* The latter group included: redhead, *Aythya americana;* canvasback, *A. valisineria;* lesser scaup, *A. affinis;* ring-necked duck, *A. collaris;* common goldeneye, *Bucephala clangula;* bufflehead, *B. albeola;* scoters, *Melanitta sp.* (which are grouped together in the aerial surveys); and ruddy duck, *Oxyura jamaicensis.*

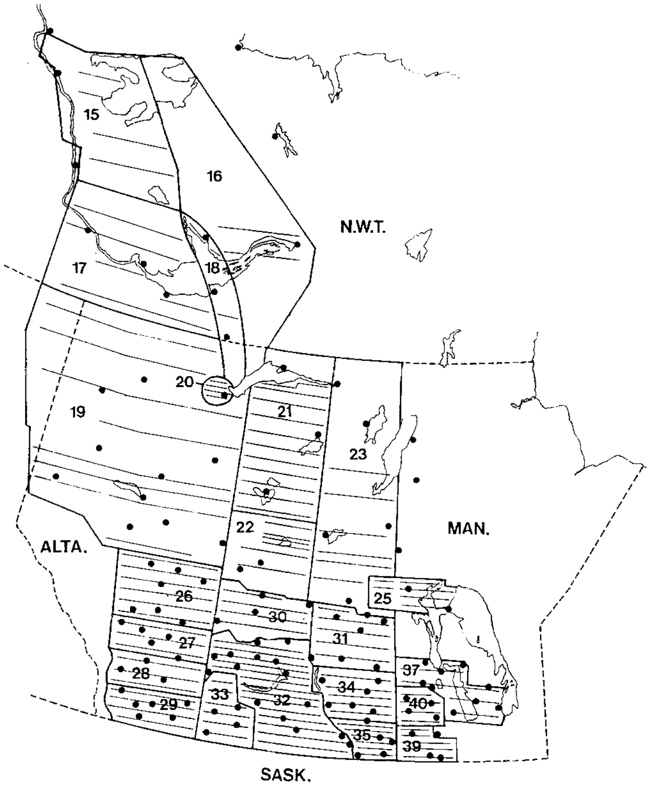

Fig. 1. Location of air-ground survey transects used in the annual waterfowl breeding ground survey by the USFWS and CWS, and the distribution of weather stations (●) in Alberta, Saskatchewan, Manitoba and the Northwest Territories, where climatological variables used to derive multifactorial resource gradients were collected (numbers indicate survey strata)

For each year in each stratum, the following community attributes were calculated: (i) species diversity, (ii) species richness, and (iii) the evenness component of diversity. Diversity (N_2) was the reciprocal of Simpson's index, $1/\Sigma(p_i^2)$, where p_i is the relative abundance of the ith species (Hill 1973). Species richness was the number of species (N_0) and evenness was the ratio N_2/N_1, where $N_1 = \exp(-\Sigma p_i \ln p_i)$ (Hill 1973). A brief discussion regarding the appropriateness of these measures of community attributes is given by Rotenberry (1978).

Environmental gradients analysis

For ducks, the relative abundance and diversity of resources on the breeding grounds depends largely on the nature and dynamics of wetland complexes (Crissey 1969; Smith 1971; Stoudt 1971; Pospahala et al. 1974; Patterson 1976; Bellrose 1980; Nudds 1983b). We sought a number of climatological and hydrological variables that could be used to index variation in wetland diversity and

Table 1. Summary and description of climatic and hydrological variables used in principal components analysis to derive multifactorial wetland habitat gradients

Variable	Attribute[a]	Description	Years
CSMMEAN	A	– weighted precipitation mean (mm) indexed by CSM	1960–1987
CSMRESID	V	– variance in CSM estimates by residuals from mean-variance regression	1960–1987
RUNOFF	A	– annual runoff (mm) from long-term averages on hydrological maps	1957–1966
EVAPOR	A	– mean annual lake evaporation (mm) from hydrological maps	1957–1966
WETLANDP	A	– percent area covered by wetlands from wetland region atlas	1972–1983
MAYTEMPM	A	– mean May temperature (°C)	1958–1987
MAYTEMPV	V	– standard deviation (S.D.) of MAYTEMPM	1958–1987
JUNTEMPM	A	– mean June temperature (°C)	1958–1987
JUNTEMPV	V	– S.D. of JUNTEMPM	1958–1987
JULTEMPM	A	– mean July temperature (°C)	1958–1987
JULTEMPV	V	– S.D. of JULTEMPM	1958–1987
AUGTEMPM	A	– mean August temperature (°C)	1958–1987
AUGTEMPV	V	– variance in AUGTEMPM by residuals from mean-variance regression	1958–1987

[a] A = absolute measure, V = temporal variation

abundance, i.e., the large scale determinants of variability in the quantity and quality of resources such as food, nest sites, and microhabitat structure, at the geographic scale of the analysis.

Values for climatological variables (i.e., precipitation and temperature) were taken from 102 weather stations across the study area (*Monthly Record* – Environment Canada). Measures of total precipitation in each month of the year and mean monthly temperatures for the period from May to August were recorded for each station. For those months when data from a given station were missing (about 1.8% of all records), values were estimated by taking the mean of records from three or four adjacent stations. There were a large number of stations that were not fully operational until the late 1950s and early 1960s, so analysis of climatic data was restricted to the period 1958–1987.

Precipitation in the year(s) preceding a given breeding season on the prairies have been shown to be better predictors of current wetland conditions (Adams 1988) and abundance of breeding ducks than have spring precipitation or aerial pond counts (Pospahala et al. 1974; Boyd 1981). Following Boyd (1981), we used Williams and Robertson's (1965) index of annual conserved soil moisture (CSM) as a measure of wetland conditions. CSM weights monthly precipitation in the 21 months preceding each 1 May because summer rainfall, relative to precipitation in fall and winter, contributes less to persistent soil moisture (Williams and Robertson 1965; Boyd 1981). Williams and Robertson (1965) give the equation for each May as:

$$\begin{aligned}\mathrm{CSM} = {} & 0.36A + [0.37B - 0.2(0.36A)] + 0.13C \\ & + \{0.30D - 0.2[0.36A + (0.37B - 0.2(0.36A)) + 0.13C]\},\end{aligned}$$

where A = total precipitation in August, September and October in year t-2,
B = total precipitation from November in year t-2 to April in year t-1,
C = total precipitation from May to October in year t-1, and
D = total precipitation from November in year t-1 to April in year t.

CSM was calculated for each station for each year for which sufficient data were available.

Weather stations were assigned to each stratum such that as much of the surveyed area as possible was represented. Since these stations were not distributed equally among strata, it was necessary in some cases to make use of stations outside, but nearby, a particular stratum and in other cases to include a station in more than one stratum for calculating stratum level estimates of the climatic variables (see Fig. 1). In each stratum in each year, means of station values for CSM and mean monthly temperature were calculated; these means were used to calculate long-term means and variance estimates for each stratum.

To index environmental variability, coefficients of variation (CVs) have been used commonly (e.g., Kricher 1972; Nudds 1983a; 1983b; Wiens et al. 1987). For statistical analysis, however, ratios such as CVs are inappropriate to standardize variance for differences between the means of different samples (see Atchley et al. 1976). Atchley et al. (1976, p. 147) suggest that because of the unpredictable behavior of such ratio variables, residuals should be used for statistical analysis, and particularly for multivariate procedures. We used regression analysis to test for statistical dependence of variance on the mean (Snedecor and Cochran 1980). Where dependence was evident, residuals were used as variance estimates, otherwise standard deviation was used.

To account for regional differences in hydrology and topology that determine the fate of precipitation, we used hydrological maps giving long-term estimates of annual run-off, mean annual lake evaporation (Anonymous 1978), and the proportion of area covered by wetlands (Anonymous 1986). For each stratum, estimates were made by overlaying a 100 km^2 grid map of the aerial strata onto the hydrological maps (scale of 1:7500000) in order to estimate the area contained between isopleths within each stratum. Stratum means were weighted for the proportion of the total area comprised by the areas between isopleths. Each variable (Table 1) was tested for normality and where departures were evident, appropriate transformations were performed (Snedecor and Cochran 1980; Tabachnick and Fidell 1983). Each variable was then standardized to 0 mean and unit variance, and principal components analysis (Tabachnick and Fidell 1983; SAS Institute 1985) was used to ordinate the aerial strata along synthetic gradients of environmental variability. Varimax rotation was employed after extraction of the first three principal components in order to simplify the factor pattern and facilitate interpretation of the axes (Tabachnick and Fidell 1983).

Tests of Tramer's predictions

The PC axis that defined the major gradient of wetland habitat variability was used to examine how diversity, richness and evenness changed over time and space. The position of each stratum along a particular gradient was given by its factor score (Tabachnick and Fidell 1983). The relative contribution of changes in richness and evenness to temporal variation in diversity of ducks was calculated using partial coefficients of determination (Rotenberry et al. 1979; Nudds 1983a). These were then examined with respect to the gradient of wetland habitat variability, to evaluate Tramer's (1969) predictions. To analyze changes in diversity components over space, factor scores were used in correlation and polynomial regression analyses (Meents et al. 1983) to examine the relationships between diversity, richness and evenness, and the wetland habitat variability gradient (Rotenberry 1978).

Results

Three components accounted for approximately 81% of the total variation in the environmental data matrix (Table 2). The first component accounted for 49% of total variance; 8 of the 13 original variables contributed significantly to this axis (Table 2). Factor I consisted of a suite of variables that defined a gradient of wetland habitat variability; at one end, high variability in wetness regimes is compounded by low run-off into few water bodies, that subsequently endure high summer temperatures and high levels of evaporation. At the other, opposite conditions result in wetlands that are relatively more constant or predictable (Fig. 2). Strata with large, positive factor scores on PC I then, are characterized by widely fluctuating food resources (principally aquatic macroinvertebrates), nesting sites and brood rearing areas on a yearly basis. Strata with large negative factor scores, on the other hand, remain largely unchanged from year to year and provide ducks with relatively constant feeding and nesting opportunities. Factors II and III comprised gradients of variability in summer temperatures and absolute amount of precipitation, respectively (Table 2). The geographic distributions of factor scores for each stratum on each of the three components are illustrated in Fig. 3. Our goal was to examine variation in components of diversity relative to major gradients of resource variation, so we concentrated on factor I.

Means and standard deviations of diversity, richness and evenness of ducks in each stratum are given in Appendix 1. Because survey strata differ substantially in area there was a potential bias towards low temporal variation in richness in larger strata, i.e., changes in richness may have been damped because, the larger the stratum, the less chance that some species were absent in a given survey. We tested this by examining the correlation between stratum area and variation in richness (measured as residuals) over time. Variation in richness was independent of area ($r=0.0063$, $p=0.9773$). Changes in richness therefore, reflected real differences between strata in how community structure changed through time, and were not the result of a sampling bias.

Table 2. Rotated factor loadings from principal components analysis on climatic and hydrological data from 23 aerial survey strata. Dominant factor loadings are in boldface

Variable[a]	Factor		
	I	II	III
CSMMEAN	0.173	−0.131	0.917
CSMRESID	0.754	0.266	−0.145
RUN-OFF	−0.891	0.143	0.244
EVAPOR	0.969	−0.166	−0.042
WETLANDP	−0.752	−0.095	0.395
MAYTEMPM	0.903	−0.379	0.134
MAYTEMPV	−0.482	0.759	0.209
JUNTEMPM	0.858	−0.316	0.336
JUNTEMPV	−0.150	0.891	−0.206
JULTEMPM	0.892	−0.179	0.353
JULTEMPV	0.055	0.840	0.147
AUGTEMPM	0.928	−0.212	0.265
AUGTEMPV	−0.055	0.153	0.283
% Variance	48.98	19.73	12.25
Cumulative variance	48.98	68.71	80.97

[a] refer to Table 1 for description of variables

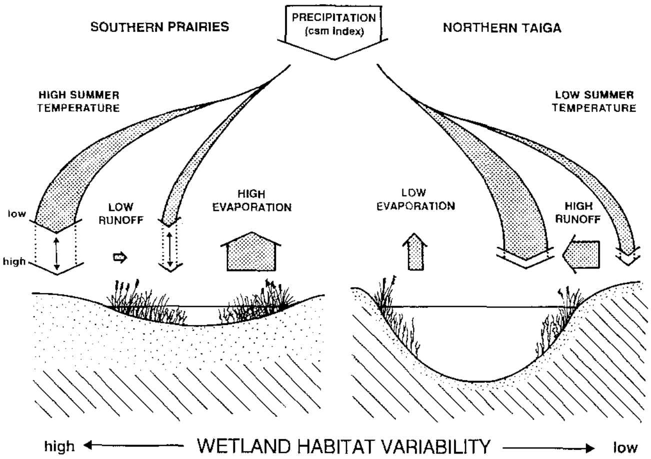

Fig. 2. Schematic illustration of the gradient of wetland habitat variability (PC I) from principal components analysis on climatic and hydrological data from 23 aerial survey strata in Canadian prairies and northern taiga. In the southern prairies, high variability in precipitation (indexed by conserved soil moisture residuals), low run-off into few water bodies, high summer temperatures and high levels of evaporation, result in highly variable wetland conditions from year to year. In the northern taiga, the opposite conditions result in water bodies that have less potential for large fluxes it wetness regimes, and therefore variability in wetland conditions is low. Wetlands in the south and north are characterized by "saucer-shaped" and "bowl-shaped" basin topography, respectively (Sheehan et al. 1987; Adams 1988)

The relative contributions of richness and evenness to temporal variation in the diversity of ducks in each stratum are illustrated in Fig. 4. Changes in evenness contributed substantially to temporal changes in diversity across the gradient of wetland habitat variability. Changes in richness contributed more to changes in diversity in constant wetland habitats than in variable wetland habitats (Fig. 4). Seven of 10 strata north of 53° N (strata 15–25) latitude had partial R^2 of diversity and richness≥ 0.50; only 1 of 13 similar coefficients was that large south of 53° N latitude. Spatial changes in diversity and richness along the gradient of wetland habitat variability (PC I) were best described by polynomial functions (Fig. 5). Species diversity and richness increased over the greatest range of wetland habitat variability, but decreased in the most variable wetland habitats (Fig. 5 (a) and (b), respectively). Evenness was not higher in more constant wetland habitats (Fig. 5 (c)).

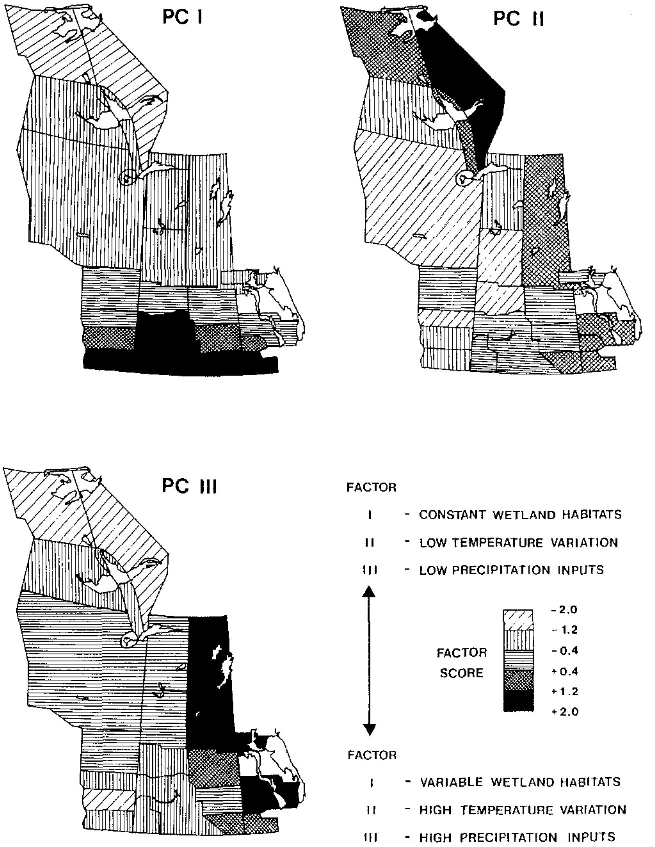

Fig. 3. Geographic distribution of factor scores from principal component (*PC*) analysis of climatic and hydrological variables defining environmental gradients of: wetland habitat variability (*PC I*), variation in summer temperature (*PC II*), and precipitation, over 23 aerial survey strata (*PC III*)

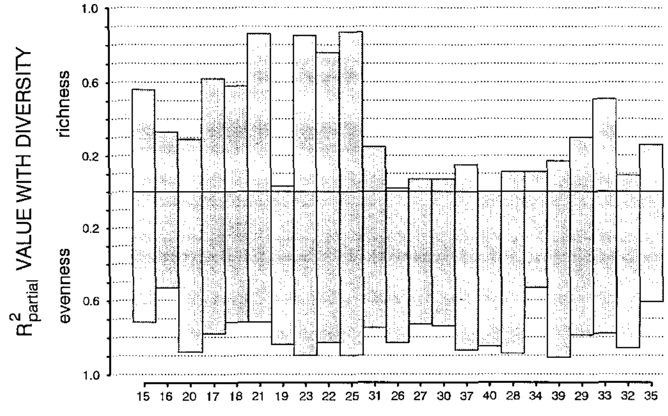

Fig. 4. Relative contribution of changes in richness and evenness to temporal changes in diversity, indexed by partial coefficients of determination (R^2_{partial}) in each survey stratum, ranked along a gradient of wetland habitat variability

Discussion

We tested whether particular patterns of variation in diversity, richness and evenness (e.g., Tramer 1969) could be applied generally to distinguish between mechanisms responsible for organizing duck guilds. Changes in diversity, richness and evenness of breeding ducks over large temporal (33 years) and spatial (regional) scales were generally not in accord with Tramer's (1969) predictions.

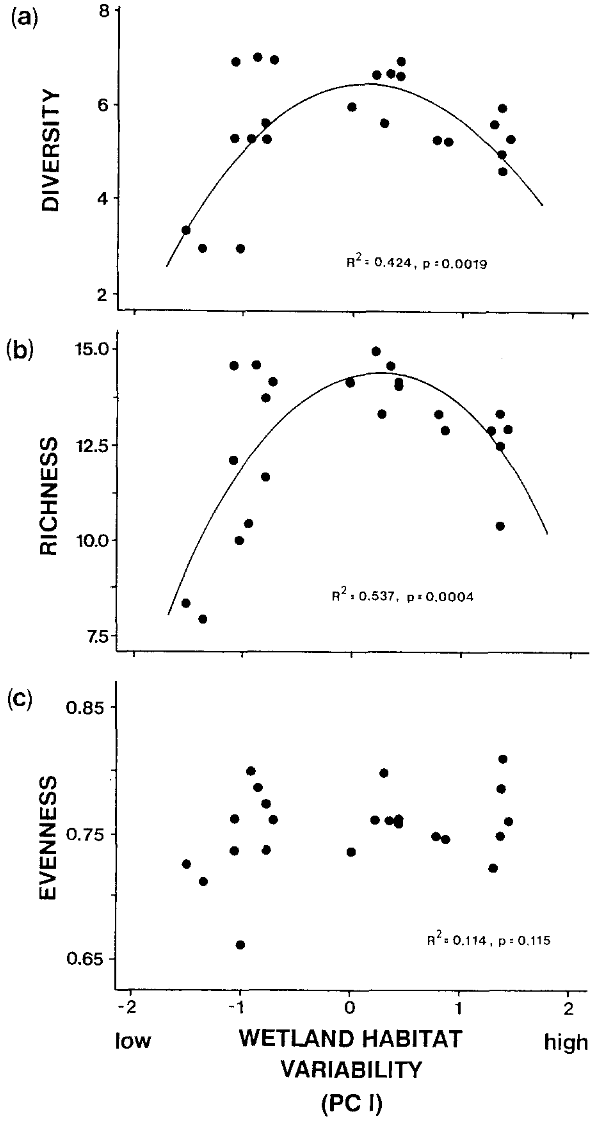

Fig. 5a–c. Relationships between wetland habitat variability (*PC I*) and (**a**) diversity, (**b**) richness, and (**c**) evenness, for breeding ducks. Equations for the curves are: (**a**) $Y = 0.359X - 1.002X^2 + 6.449$, and (**b**) $Y = 0.81X - 1.763X^2 + 14.349$

Temporal variation in diversity, richness and evenness

The contribution of changes in richness to temporal changes in diversity in a general way appeared to be in agreement with Tramer's (1969) predictions, i.e., variation in richness contributed more importantly to variation in diversity in relatively constant, northern wetland habitats than it did in the variable southern prairies. Nudds (1983a), however, found that changes in diversity correlated with changes in richness in variable wetland habitats, in contrast to Tramer's predictions. There may be 2 related reasons for this. First, Nudds' (1983a) data came from small sites within larger strata and it seems that scale influences results of these types of studies (see Introduction). Second, those sites were in strata 26 and 35, which are areas of moderate to high wetland habitat variability (see Fig. 4). In this range of variability, we found that virtually all variation in duck diversity was due to variation in evenness. The sites Nudds compared, therefore, may not have been sufficiently different in terms of environmental variability to test adequately Tramer's predictions, and Nudds may have prematurely rejected Tramer's hypothesis.

However, Tramer (1969) also argued that competition for limited resources in constant environments would, over time, damp fluctuations in evenness. Consequently, temporal changes in diversity would come about through changes in richness as species dropped in and out of the assemblage with relatively small changes in resource saturation. In the northern taiga and boreal forest, relatively constant wetland conditions provide ducks with nesting and feeding sites that remain relatively unchanged from year to year. We think that populations in the north might, therefore, experience more frequent periods of resource-based interspecific competition than those in the south (see also Rotenberry et al. 1979). Similarly, at a site within a region of moderate wetland habitat variability (stratum 26), Nudds (1983b) found evidence of competitively induced adjustments to niche parameters among diving ducks. Where wetland habitat variability was higher (stratum 35), he found that changes in duck community structure were more related to habitat heterogeneity than to competition. So, it appears that temporal changes in richness and diversity we document here, might, in fact, correlate with the degree to which competition or resource heterogeneity are important in organizing duck communities, but not for the reasons postulated by Tramer (1969). The contribution of variation in evenness to temporal variation in diversity was high in most strata and independent of wetland habitat variability. Furthermore, the relative contributions of richness to changes in diversity were never greater than the contributions of evenness. These findings are inconsistent with Tramer's (1969) hypothesis, i.e., variation in evenness was not damped relative to variation in richness where wetland habitat variability was low. Nudds (1983a) may have been correct, then, to reject Tramer's hypothesis, though for the wrong reason.

Why, then, do changes in richness in the north and south appear to accord with Tramer's predictions? Changes in richness in relatively benign areas may be largely the result of a phenomenon known as "flyover" (Bellrose 1980; Johnson and Grier 1988), rather than an outcome of competition for limited resources. During drought years on the prairies, the number of ponds (generally the ephemeral, highly productive potholes) are reduced, causing many dabbling ducks to fly over the prairies to the northern parklands and boreal forest regions (e.g., Hansen and McKnight 1964; Crissey 1969). Species otherwise absent or infrequent in northern regions (e.g., gadwall, blue-winged teal and northern shoveler) thus appear and disappear from assemblages in benign habitats as a result of conditions elsewhere, rather than conditions there. Thus, although it is possible that this influx of birds into these habitats may result in, or heighten, competition for limited resources (i.e., where resident populations may already be in equilibria with local resource levels), the immigration and emigration of species in benign, northern environments do not appear to be caused by competition as Tramer (1969) argued.

Spatial variation in diversity, richness and evenness

Across the gradient of wetland habitat variability, changes in diversity were paralleled by changes in richness; evenness, however, was not greater in more benign areas as Tramer predicted. In contrast, Rotenberry (1978) found that species diversity decreased from constant to variable environments due mainly to decreases in evenness. Similarly, Nudds' (1983a) found that changes in diversity from relatively benign aspen parkland to variable mixed prairie habitats were related more to changes in evenness than richness for dabbling and diving ducks. The direction of changes in evenness, however, were opposite for each guild. Only for dabbling ducks was evenness lower in more variable environments, consistent with Tramer's (1969) hypothesis.

Synthesis

The observation that changes in diversity were paralleled by changes in richness is consistent with several other studies relating changes in diversity and richness to environmental variability at both small (e.g., Kricher 1972, 1975; Kushlan 1976; Uetz 1975; Rotenberry et al. 1979; Smith and MacMahon 1981) and large (Pianka 1967; Austin and Tomoff 1978) spatial scales. Unlike these studies, however, duck diversity and richness tended to increase, rather than decrease, with increasing environmental variability. Several authors have reviewed and/or formulated a number of hypotheses attempting to explain geographical gradients in species diversity (Pianka 1966; Connell 1978; Shmida and Wilson 1985). In general, these hypotheses attempt to explain continental patterns of species diversity in terms of some underlying gradient of resource abundance, resource saturation, or temporal or spatial heterogeneity. In the prairie ecosystem, moderate to high levels of climatic variability generally enhance wetland habitats for waterfowl in a manner consistent with Connell's (1978) intermediate disturbance hypothesis. According to this hypothesis, high diversity is produced and maintained by intermediate levels of disturbance that reduce the numbers of competitively dominant species and thereby allow competitively inferior species to persist in the community. Periodic drought in the southern prairies has been shown to maintain high levels of primary and secondary productivity (Sheehan et al. 1987; Adams 1988) and habitat heterogeneity (Kaminski and Prince 1981; Murkin et al. 1982; Sheehan et al. 1987; Adams 1988).

Figure 6 illustrates several gradients of resource variability, structure and abundance that underlie variation

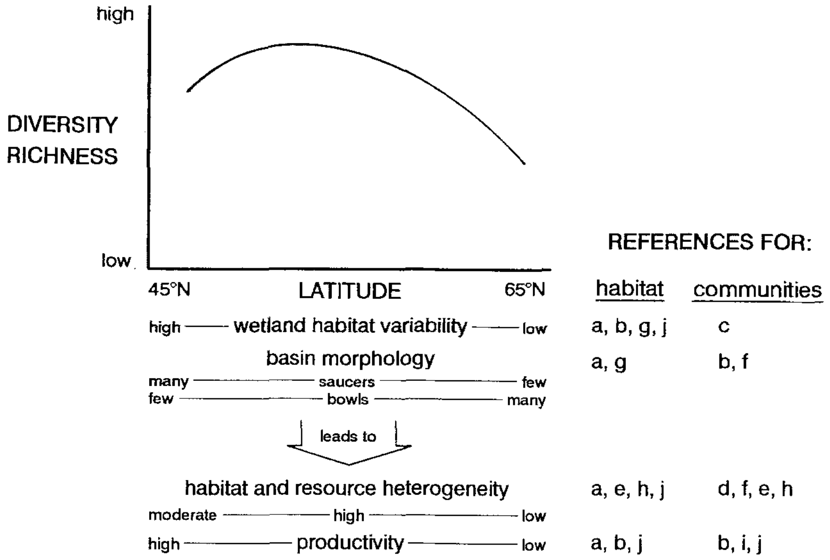

Fig. 6. Schematic illustration of changes in duck diversity and species richness along geographic gradients of resource variability, heterogeneity and abundance. A latitudinal decline in wetland habitat variability combined with changes in basin morphology appears to be a driving force behind regional differences in habitat (and resource) heterogeneity and productivity, that in turn determine duck diversity. See text for full explanation. References: (*a*) Adams 1988; (*b*) Bellrose 1980; (*c*) this study; (*d*) Dannell and Sjöberg 1982; (*e*) Kaminski and Prince 1981; (*f*) Kantrund and Stewart 1977; (*g*) Millar 1982, 1983, 1984; (*h*) Murkin et al. 1982; (*i*) Pöysä 1984; (*j*) Sheehan et al. 1987

in duck diversity over a latitudinal gradient in central North America. Coupled with latitudinal gradients in basin morphology, wetland habitat variability appears to be a driving force behind regional differences in habitat (and resource) heterogeneity and productivity (see Fig. 6, for references). Wetland complexes in the north are dominated by deeper, "bowl" shaped water bodies, with narrow vegetated margins. Turnover of nutrients, with attendant increases in primary and secondary production, is relatively low in these basins resulting from relatively constant wetness regimes. Consequently, these structurally simple habitats, with lower resource productivity and diversity, support fewer species (Fig. 6). In the southern prairies, a high degree of variability in wetness regimes rejuvenates wetlands and thus maintains high levels of productivity, but: (i) intense, frequent droughts do not permit the development of late successional plant species that increase habitat heterogeneity (Sheehan et al. 1987; Adams 1988), and (ii) wetlands are dominated by shallow, ephemeral "saucer-shaped" water bodies, with few of the semipermanent and permanent bodies that are used by many diving ducks. These habitats therefore are capable of providing breeding habitat for many species of dabbling ducks, but for only a few species of diving ducks (Fig. 6).

In the south-central prairies, however, climatological and topographical attributes converge to produce structurally diverse and highly productive habitats (Adams 1988), and we offer this hypothesis as an extension to Connell's (1978), to explain the "hump" in the diversity – wetland habitat variability relationship (Fig. 5). Wetland complexes in this region consist of an array of basin types that experience moderate levels of climatic variability. Periodic droughts in this region maintain high levels of vegetative interspersion in shallower wetlands, and relatively high productivity in all wetland types (Sheehan et al. 1987; Adams 1988). Consequently, wetland habitats in areas of intermediate climatic variability do support highly diverse species assemblages (Fig. 6; Bellrose 1980), but at this scale of analysis other factors appear also to contribute to geographical gradients in diversity, e.g., spatial heterogeneity, and productivity (see also Nudds 1992).

Based on our analysis of long-term census data for ducks collected at a regional scale and broad-scale indices of wetland habitat variability, we found little evidence consistent with Tramer's (1969) hypothesis. Temporal variation in diversity and richness appeared to accord with Tramer's hypothesis, but better reflected the effects of dispersal in response to climatic conditions than to reflect mechanisms (like competition) that might organize local species assemblages (see also Wiens 1984, 1989: pp. 136–137). Changes in the diversity of ducks over space appeared to be related more to geographical gradients of habitat and resource heterogeneity, and productivity than to levels of competition in differentially variable environments (see also Wiens et al. 1987). We conclude, contrary to Rotenberry et al. (1979, p. 504) that, regardless of whether patterns are "statistically valid and logically consistent", they need not necessarily indicate the mechanisms, like competition or variability in the diversity and abundance of resources, that are important in regulating community structure.

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Appendix 1. Means and standard deviations of diversity, richness, and evenness by aerial survey stratum for the period 1955–1987

Stratum	Diversity		Richness		Evenness	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
15	3.23	0.74	8.52	1.82	0.719	0.070
16	2.85	0.71	7.91	1.21	0.714	0.056
17	5.23	1.06	12.18	2.05	0.738	0.073
18	2.98	0.78	9.85	1.52	0.658	0.048
19	6.94	0.98	14.76	0.50	0.785	0.042
20	6.95	1.64	14.55	0.79	0.759	0.076
21	5.17	1.51	10.30	2.94	0.797	0.073
22	5.53	1.50	13.61	1.85	0.732	0.059
23	5.20	1.38	11.55	2.05	0.778	0.067
25	6.98	1.64	14.36	1.65	0.761	0.063
26	6.67	0.89	14.94	0.24	0.758	0.040
27	5.67	0.62	13.30	1.19	0.799	0.037
28	5.24	1.19	13.24	1.12	0.756	0.061
29	4.77	0.94	12.70	1.36	0.746	0.050
30	6.51	1.12	14.79	0.48	0.758	0.059
31	5.88	0.97	14.24	0.75	0.735	0.053
32	5.94	1.01	13.15	0.97	0.807	0.053
33	4.86	0.92	10.58	1.32	0.788	0.050
34	5.36	1.10	12.82	1.04	0.749	0.045
35	5.25	1.11	12.79	1.36	0.764	0.056
37	6.85	1.47	14.03	0.68	0.763	0.062
39	5.52	1.60	13.03	0.92	0.725	0.079
40	6.71	1.33	14.03	0.73	0.766	0.056

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