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Null models of North American prairie duck communities: local habitat conditions and temporal scale influence community patterns

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ABSTRACT

We developed null models that incorporate abundance of individuals at local sites to analyse community patterns of two North American duck guilds, dabbling and diving ducks. We compared patterns of species co-existence and morphological dispersion over two temporal scales, the entire breeding season and at weekly intervals. We found that patterns of co-existence depended on temporal scale and guild and that morphological dispersion depended on guild, temporal scale, character and local habitat features. Co-existence was non-random at all scales for both guilds but departures from the null model depended on scale for some individual species pairs. Generally, the most common species were negatively associated and less common species were positively associated. Dabbling ducks were not different from random communities for lamellar density at any scale or for body length at the seasonal scale, but were under-dispersed at the weekly scale. Diving ducks were over-dispersed in morphology at the breeding season scale but under-dispersed at the weekly scale. Patterns of morphology depended on local habitat characteristics because dabbling duck body length was only over-dispersed on the largest, most permanent, wetlands. Taken together, these results reveal that density compensation, temporal scale and local habitat characteristics influence patterns of co-existence in these wetland bird communities.

Keywords: community structure, null model, randomization test, species co-existence, waterfowl.

INTRODUCTION

The analysis of ecological communities using a null model has had a long and controversial history (reviewed in Gotelli and Graves, 1996). Most controversy has involved inferring an ecological process, such as competition, from the patterns in species presence or absence among a variety of sites or islands. Central to this debate is how to constrain the null

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model so that the model contains the processes that are not of interest (e.g. species–area effects, dispersal due to distance from mainland, habitat affinities of species) and does not contain the processes that are of interest (e.g. competition, which may cause a lack of co-existence between species: Graves and Gotelli, 1983, 1993; Colwell and Winkler, 1984; Wilson, 1989; Gotelli *et al.*, 1997). It is generally agreed that a series of null models of varying levels of constraints should be used to analyse community patterns (Jackson *et al.*, 1992; Kelt *et al.*, 1995; Gotelli, 2000). Most such analyses, however, have used an ordinal scale (presence–absence), even though processes such as competition fundamentally occur between individuals at local sites and produce effects on density that may, under some equilibrium conditions, lead to patterns in presence–absence data (Haila and Järvinen, 1981; James and Boecklen, 1984).

The main controversy in null model analyses has centred around the constraints imposed on presence–absence matrices (Gotelli and Graves, 1996; Manly, 1995; Gotelli, 2000; Gotelli and Entsminger, 2001). The data are usually arranged in a matrix where species are along rows and sites are along columns. The debate then is whether to keep the row totals, column totals or both fixed during randomization. By fixing row totals, each site must receive the same number of species as was observed and this controls for differences in site size and species–area relationships. By fixing column totals, each species must occur on the same number of sites and this controls for differences in dispersal probability of the species. Fixing both column and row totals leads to an appropriately constrained null model but also to computational difficulties (Manly, 1995; Sanderson *et al.*, 1998; Gotelli, 2000; Gotelli and Entsminger, 2001; Manly and Sanderson, 2002). The computational difficulties arise because of the need to randomly sample from the entire space of possible matrices that have the observed row and column sums. This space is very constrained by the row and column sums but still very large. Sanderson *et al.* (1998) pointed out that algorithms used to date are biased in their search of this sample space and introduced an algorithm that more thoroughly sampled from the universe of null matrices. However, Gotelli and Entsminger (2001) pointed out problems with the algorithm of Sanderson *et al.* (1998) and introduced a modification. All of these problems arise by randomizing a matrix of 1's and 0's under the constraints of maintaining the row and column sums.

In this paper, we take a different approach. We use the abundances of different species, not simply their presence or absence. There are still constraints on both row and column totals in the null models, but they are less difficult to implement. First, we know that some sites will hold more individuals than others (due to size or quality of the site), so the null hypothesis must fix the total number on each site to match the observed total. The number of species on each site, however, does not need to be constrained because the number of species observed under the null hypothesis is simply a function relating individuals sampled to species richness. Second, some species are more common than others, so the null hypothesis must fix the total abundance of each species across all sites to match the observed total. Under these two constraints, the null model algorithm is a simple randomization problem of assigning individuals to sites and very easy to implement with simple programming skills.

For example, consider two species (P, Q) and three sites (A, B, C). Observed values for P are 2, 2 and 3 (total number of individuals = 7) and for Q are 0, 1 and 4 (total = 5). Total abundance for each site is 2, 3 and 7. There is only one way to derive the presence–absence species-by-site matrix and so there is no flexibility in the null hypothesis. But there is substantial flexibility in the abundance species-by-site matrix. P occurring 1, 1 and 5 times

and Q occurring 1, 2 and 2 times is one entry in the null hypothesis, for example. There are many other entries that are possible under the null hypothesis and should be included with equal probability.

Waterfowl (*Anatidae*) communities in the prairies of central North America are a particularly suitable group for the development of a null model analysis. Waterfowl, from two foraging guilds, form moderately diverse species assemblages that occupy the same small wetlands. There is an extensive base of organismal- and population-centred work due to the economic importance of this group (Batt *et al.*, 1992), and studies of functional morphology and foraging behaviour provide a good basis for the use of morphology as an index to ecology of each species (Pöysä, 1983a,b; Nudds and Bowlby, 1984; Nudds *et al.*, 1994; Pöysä *et al.*, 1996). Null model studies of waterfowl communities have been limited to regions of low alpha-diversity and density at the northern limit of many species' ranges (e.g. Toft *et al.*, 1982; Pöysä, 1984; Pöysä *et al.*, 1994) or to analysis of species' ranges on a continental scale (e.g. Nudds and Wickett, 1994). However, communities in the centre of these species' ranges, where density and diversity are high and communities vary mostly in relative abundance (Nudds, 1983, 1992), have not been analysed using null models. In this paper, we analyse patterns in waterfowl communities on individual wetlands in the prairie-parkland region of southwestern Manitoba and compare patterns between guilds, morphological characters, temporal scale and local habitats using null models that incorporate abundance of individuals within species.

METHODS

Study area

This study was conducted in the prairie-parkland southeast of Minnedosa, Manitoba, Canada (50°16′N, 99°50′W) in 1997. Fields in cereal grain and oil seed production surround most wetlands. Pasture, grassland and woodlots make up a smaller proportion of surrounding uplands. Variation in size and depth among wetlands creates a permanency gradient, which, in turn, affects plant communities associated with each wetland (Stewart and Kantrud, 1971). Plants dominating smaller, more ephemeral wetlands or outer margins of larger wetlands were *Juncus* spp., *Carex* spp., *Scolochloa festucacea* and various forbs. Larger, more permanent wetlands were lined with emergent vegetation consisting of *Typha* spp., *Scirpus* sp., *Phragmites australis*, *Scolochloa festucacea* or heterogeneous stands of two or more species (Stewart and Kantrud, 1971). Permanent wetlands contain one or more of the submergent plants *Ceratophyllum demersum*, *Chara* spp., *Potamogeton pectinatus*, *Myriophyllum* spp. and *Lemna trisulca*. By midsummer, some wetlands had dense floating mats of filamentous algae or *Lemna minor*; a few wetlands had small patches to large mats of aquatic moss (*Drepanocladus* spp.).

Waterfowl guilds

Ducks in this region are easily classified into one of two guilds, dabbling ducks or diving ducks, based on foraging behaviour, morphology and habitat use. Because members of both guilds feed on aquatic invertebrates and some plant parts (Krapu and Reinecke, 1992), this classification is based mostly on foraging behaviour. Dabbling ducks feed by filtering small food items from the water or by picking larger items from the surface of the water. They also

feed in open water or shallow margins of wetlands by submerging their head and neck or by 'tipping up' to strain food items from benthos or deeper areas of the water column (Pöysä, 1983a,b; DuBowy, 1988). These ducks inhabit all wetland types along the size–depth permanency gradient. Seven species of dabbling ducks breed in southwestern Manitoba: American wigeon (*Anas americana*), blue-winged teal (*A. discors*), gadwall (*A. strepera*), green-winged teal (*A. crecca*), mallard (*A. platyrhynchos*), northern pintail (*A. acuta*) and northern shoveler (*A. clypeata*). Diving ducks feed by swimming down through the water column and filtering or picking food from the water, straining food from surface benthos, or probing into benthos to extract food items (Tome and Wrubleski, 1988). These ducks utilize deeper, more permanent wetlands. Seven species of diving ducks were present in our study area: canvasback (*Aythya valisineria*), lesser scaup (*A. affinis*), redhead (*A. americana*), ring-necked duck (*A. collaris*), ruddy duck (*Oxyura jamaicensis*), bufflehead (*Bucephala albeola*) and common goldeneye (*B. clangula*). Both bufflehead and common goldeneye nest in tree cavities and were uncommon in this region; consequently, only data from the five common species were used in our morphological analysis.

Wetland selection and bird surveys

In mid-April of 1997, 180 wetlands that were entirely visible from a road were selected. Wetlands were chosen to represent the entire permanency gradient and emergent vegetation types in the area. Large wetlands (> 2 ha) were over-sampled to ensure a reasonable sample ($n > 10$) of bird communities using these uncommon wetlands. Weekly point counts of ducks, by species, began on 27 April when most wetlands were ice-free and birds had begun to arrive. Counts continued through the summer brood rearing season until 29 August. In this paper, counts of dabbling and diving ducks from 14 surveys conducted from 27 April to 10 July are used. The data used here extend later into the summer than most studies of breeding waterfowl, but corresponded to the nesting season of 1997. Because large amounts of rain caused smaller wetlands to persist into late summer, most duck species continued to nest well into July.

Early in the season, we used binoculars and a spotting scope to count ducks from a vehicle at one to three locations at each wetland. Later in the season, when vegetation growth partially obscured the view of some wetlands from the roadside, counts were conducted from the vehicle and by walking to high points around the wetland. Ducks were identified to species and recorded as either a breeding pair or an indicated pair. Indicated pairs were a lone female, a lone male, or each male in a group of five or less (Dzubin, 1969). Pairs and indicated pairs were summed to provide an estimate of total breeding pairs on each wetland during each survey. Breeding pairs are the appropriate unit of analysis in ducks because they are socially monogamous during most of the breeding season.

The null model

A null model analysis consists of four parts. First is the metric that is used to describe the community. Second is the randomization algorithm that is used to generate the distribution of the metrics under the null hypothesis or 'null distribution'. It is the randomization algorithm that defines a set of constraints that allow inferences to be made from comparisons between the observed metric and the randomization distribution. The randomization algorithm is the most controversial step of a null model analysis (see Gottelli and Graves,

1996, for a review). Third is the randomization pool, which is the data that the randomization algorithm draws from to create the null distribution of metrics. Constraints can also be put on the randomization pools that affect inferences when comparing the observed metric to the null distribution. Fourth is the comparison of the observed metrics with the null distribution by the calculation of a *P*-value. Each aspect of a null model analysis can be varied to produce a different analysis. In our study, we used two different metrics, co-existence between species-pairs and morphological dispersion, one randomization algorithm and two different randomization pools for each of the two duck guilds. The first randomization pool was all the breeding pairs observed over all the surveys. The second randomization pool was all the breeding pairs observed for each survey separately. We describe each part of the null model analysis in detail below.

Community metrics

The first metric used to describe the duck community was co-existence between species. We defined co-existence between species *i* and *j* as:

$$C_{ij} = \sum_{w=1}^{N} x_{iw} x_{jw}$$

In this equation, x is the number of breeding pairs that were counted on wetland w, and N is the number of wetlands surveyed. This metric incorporates abundance of species i and j instead of the usual metric of the sum of the number sites in the study region where both species i and j are present (e.g. Toft *et al.*, 1982; Jackson *et al.*, 1992; Manly, 1995; Gotelli, 2000). For example, on a wetland that had two blue-winged teal and three mallard pairs, C_{ij} for this wetland would be six because there are six different two-way interspecific comparisons between breeding pairs. This metric is the numerator of Lloyd's (1967) 'mean crowding between species' and reflects the total perceived density of individuals between species i and species j.

The second metric used to describe the duck community was community-wide morphological dispersion. We first calculated average morphological difference at each wetland and then averaged this over all wetlands. Average morphological difference at wetland w was evaluated as:

$$M_w = \frac{\sum_{i=1}^{S-1} \sum_{j=i+1}^{S} (|\, m_i - m_j \,| \cdot x_i x_j)}{\sum_{i=1}^{S-1} \sum_{j=i+1}^{S} x_i x_j}$$

In this equation, m is the morphological value of species i or j, x is the number of breeding pairs that were counted on wetland w, and S is the number of species in the guild. Note that each interspecific morphological comparison ($m_i - m_j$) is weighted by the number of two-way comparisons between species i and j at each wetland (C_{ijw}). Community-wide morphological dispersion was calculated as the arithmetic mean of M_w over all wetlands where more than two species of dabbling or diving ducks were present.

For dabbling ducks, we used average number of lamellae per centimetre (lamellar density) on the posterior region of the upper bill (from Table 1 in Nudds and Kaminski, 1984) and total body length (tip of bill to base of tail, from Bellrose, 1980) as two ecologically relevant morphological characters. Lamellar density correlates with food particle size (Nudds and Bowlby, 1984; Mott, 1993; Nummi, 1993) and, to a lesser extent, with microhabitat use (Nudds *et al.*, 1994; but see Pöysä *et al.*, 1996). Lamellar density also is important for microhabitat-specific foraging efficiency (Tolkamp, 1993). Total body length was used because it relates to foraging behaviour and feeding depth (Pöysä, 1983a,b, 1986; DuBowy, 1988) and is correlated with other ecologically relevant traits (e.g. neck length) but not correlated with lamellar density. Smaller ducks forage more often by dabbling at the water surface, whereas larger ducks forage more often with their head under the water surface. We used the midpoint between the mean of males and of females for both characters because dabbling ducks are sexually dimorphic in both and were recorded as breeding pairs.

For diving ducks, the average position of each species' head and bill morphology on the major axis of discriminant space was interpolated from Figure 2 of Lagerquist and Ankney (1989). This axis, which we name 'head–bill', was a measure of head and bill length and bill width. Species had bills that varied from long and narrow to short and wide as described by this axis. This axis was important in the discrimination of species in morphological space and correlated with feeding method and diet of these species (Tome and Wrubleski, 1988; Lagerquist and Ankney, 1989).

Randomization algorithm

We wrote a randomization program in SAS (SAS Institute, 1990) to estimate the expected distribution of each community metric under the hypothesis of random community assembly. The program randomly allocated individual breeding pairs to wetlands, without replacement, from either of two randomization pools. Each wetland received the same number of total breeding duck pairs as was observed during the season or the survey, depending on the randomization pool used (i.e. row and column totals of a species $\times$ site matrix of total breeding pair abundance were held constant). Holding total breeding pair abundance constant incorporated any area effect or differences in site suitability that may have affected overall abundance of individuals. Because species richness increases with the total number of individuals observed through a simple sampling effect, holding total breeding pair abundance constant during randomization controlled for these effects. Given the constraint of constant total abundance and those imposed by the randomization pool (see below), species richness at each wetland and frequency of occurrence for each species among wetlands were allowed to vary randomly. After each randomization, the program calculated each metric as above, and then for comparisons using the Survey Pool, metrics were averaged over surveys (see below). Randomization and calculation of the null metric was repeated 4999 times.

Randomization pools

We determined the randomization pool from which breeding pairs were randomly allocated to wetlands in two different ways. In each pool, the data were all individual breeding pairs of each species observed on study wetlands. This is analogous to a species pool in other null model studies, but here the pool is made up of all individual breeding pairs of dabbling or

diving ducks, not species' populations. This created a pool in which the probability of a wetland receiving a given species depended on the proportion of breeding pairs of that species in the pool. Because the randomization pool is fixed for absolute abundance of each species, the pool is an estimate of the regional distribution of abundance among species and is a major constraint on the randomization.

The first randomization pool, the Breeding Season Pool, was the sum of all breeding pairs observed during the 14 surveys. When this pool was used in the randomization algorithm, assemblages created on any particular wetland contained the same number of breeding pairs as was observed over all 14 surveys. Therefore, the Breeding Season Pool can be thought of as one species × site matrix of abundance.

The second randomization pool, the Survey Pool, was all of the breeding pairs that occurred on wetlands during a single survey. Because there were 14 surveys during the breeding season, there are 14 different Survey Pools. Random assemblages created from each Survey Pool contained the same number of pairs as was observed during that survey. In all cases, the survey used to calculate observed metrics was the same as used to create the Survey Pool from which random communities were drawn. For comparisons involving the Survey Pool, the randomization algorithm first averaged (M_w) or summed (C_{ij}) each metric over all wetlands and then averaged or summed over all surveys. This allowed easy comparison to the Breeding Season Pool results. The main data structure of the Survey Pool comparisons can be thought of as 14 species × site matrices in series, where the order of the series is fixed. The fixed order of the data matrices introduces a chronological constraint on the randomization. This constraint is important because species differ substantially in breeding chronology, and these patterns are well documented.

These randomization pools differ in three important ways. First, each observation of each wetland in the Breeding Season Pool is more species-rich than in the Survey Pool because the Breeding Season Pool has 14 times the sampling effort per wetland. Second, temporal patterns in community composition are lost in the Breeding Season Pool due to amalgamation of the 14 surveys – that is, the assemblage of individuals used to calculate the observed values of each community metric for the Breeding Season Pool occurred on the same wetland but not necessarily at the same time. In contrast, assemblages used to calculate the observed metric for the Survey Pools only included individuals that occurred on the same wetland at the same time. Third, the Survey Pool adds the additional constraint of the observed species' breeding chronology. The data used in these randomization pools are shown in Fig. 1.

P-values and statistical tests

The *P*-value for each community metric was calculated as the proportion of values in the randomization distribution that were more extreme or equal to the observed value (Manly, 1991). Values equal to the observed value were rare, except for co-existence metrics (C_{ij}). We used the overall Type I error rate of $\alpha = 0.10$ to indicate a significant two-tailed test. We did not evaluate Type II error rate of our null model, as this requires specifying additional parameters (e.g. Kelt *et al.*, 1995).

We tested for statistically significant departure from the null model for co-existence of species pairs for the entire guild by using a chi-squared test. We summed the squared deviation of the observed C_{ij} to the expected C_{ij} and divided by the expected C_{ij} over all species pairs. The expected value of C_{ij} was estimated as the mean of the 4999 random

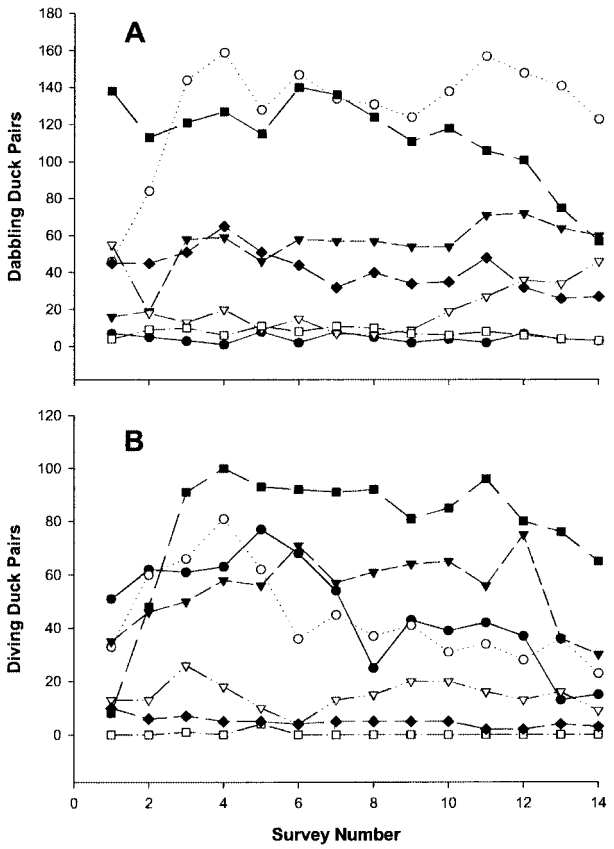

Fig. 1. Counts of dabbling duck pairs (A) and diving duck pairs (B) over the study period. Each survey represents one Survey Pool for the null model. The sum of all ducks by species represents the Breeding Season Pool. For dabbling ducks: ○, blue-winged teal; ■, mallard; ▼, gadwall; ◆, northern shoveler; ▽, green-winged teal; □, northern pintail; ●, American wigeon. For diving ducks: ■, ruddy duck; ○, lesser scaup; ▼, redhead; ●, canvasback; ▽, ring-necked duck; ◆, bufflehead; □, common goldeneye.

values (Manly, 1995). Comparing the observed value to the randomization distribution as described above tested the significance of χ^2. Bonferroni's correction was used to establish significance of each of the 21 species pairs with an overall Type I error rate of 0.10 (Manly, 1995). This resulted in a significant two-tailed test when $P \leq 0.002$.

Morphological dispersion and habitat variation

We correlated the deviation of observed to expected morphological dispersion on individual wetlands to habitat characteristics of those wetlands to test the hypothesis that patterns in morphology are related to local habitat conditions (Weiher *et al.*, 1998; Nudds *et al.*, 2000). Communities for this analysis were only constructed from the Breeding Season Pool and were given the same number of individuals as was observed over the entire season. *Z*-scores

of the deviations from the mean of 100 random values of morphological dispersion on individual wetlands were correlated with the first principal component of wetland physical characteristics. Wetlands were measured for open water area, emergent vegetation area (*Typha* spp. and *Scirpus* spp; water depth ≤ 1 m), edge vegetation area (*Juncus* spp., *Carex* spp., *Scolochloa festucacea* and various forbs; water depth ≤ 0.5 m), total wetland area and length of the emergent vegetation–water interface, measured with a digital planimeter from aerial photographs taken in late June. Photographs of each wetland were taken from a fixed-wing aircraft flying at approximately 700 m. Wetlands were visited on foot in July and each habitat zone was outlined on the photograph to validate photographic representations of vegetation zones. The scale of each photograph was determined in the field by measuring the distance between landmarks with a metre tape. Also, maximum depth of each wetland was measured in early spring (late April to early May).

All habitat variables were not normally distributed, which violated an assumption of principal component analysis. This was due to either the natural distributions of the variable in the wetlands sampled (total area and maximum depth) or to a detection threshold effect (open water area, area of edge vegetation, area of emergent vegetation, vegetation–water interface). A detection threshold effect was known because zeros were recorded from aerial photographs even when positive values of the variable were observed in the field. Therefore, variables were $\log_{10}$-transformed if the minimum of the variable was greater than zero. If the minimum of the variable was zero (i.e. there was a detection threshold effect), the variable was transformed as $\chi = \log_{10}(MR)$, where χ is the new transformed variable, M is the minimum non-zero value of the original variable among all wetlands, and R is a uniform random variable between 0 and 1. After transformation, these variables were approximately normally distributed as determined by inspection of histograms and normal probability plots.

RESULTS

Bird surveys

In both duck guilds, we observed seven species (Fig. 1). All species were observed breeding as indicated by male–female pairs early in the summer (Dzubin, 1969) or broods in the late summer, except for common goldeneye. Common goldeneye were only observed on a few wetlands for a short period of time and were probably migrating individuals. In both guilds, counts of duck pairs for each species were variable early (surveys 1–4) and late (surveys 11–14) in the breeding season. Counts were relatively stable in the middle of the breeding season (Fig. 1).

Co-existence

Co-existence of all species pairs in the dabbling duck guild was different from expected for both the Breeding Season Pool and Survey Pool models (Fig. 2). When observed patterns of species pair co-existence were compared with the Breeding Season Pool model, deviation from the model over all species pairs was large ($\chi^2 = 1493.4$, $P \leq 0.0002$; Fig. 2). Abundance of seven species pairs differed from random expectation after Bonferroni's correction ($P \leq 0.002$; Fig. 2). Blue-winged teal and mallard, blue-winged teal and gadwall, and blue-winged teal and northern shoveler were negatively associated and were among the most

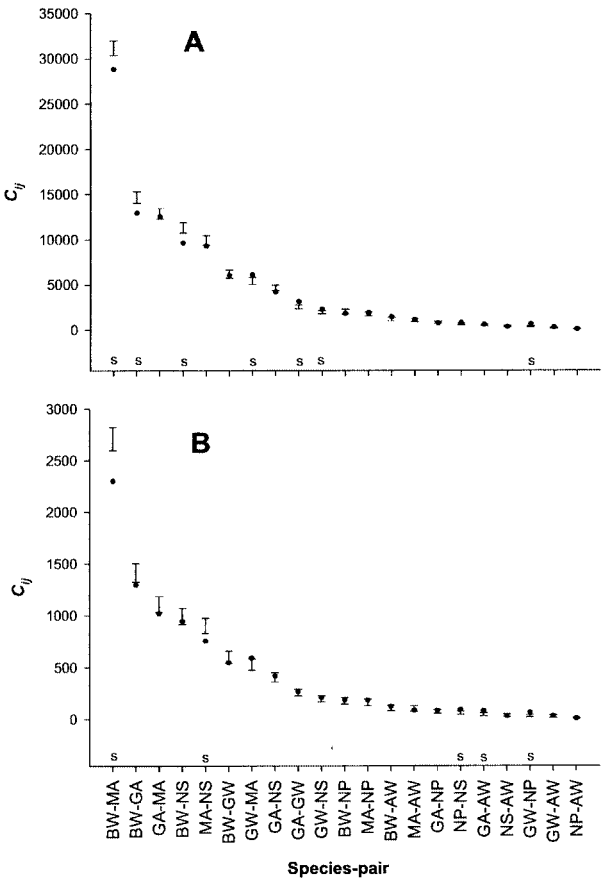

Fig. 2. Co-existence between pairs of dabbling duck species for the Breeding Season Pool model (A) and the Survey Pool model (B). The error bars are 95% prediction intervals for the randomization distribution. The observed values of co-existence are the filled circles. Overall guild co-existence was significantly different from both the Breeding Season Pool model ($\chi^2 = 1493.4$, $P \leq 0.0002$) and the Survey Pool model ($\chi^2 = 231.0$, $P \leq 0.0002$). Statistically significant deviations from the randomization distribution for each species pair are noted by the 's' above the x-axis ($P < 0.002$ after Bonferroni correction for 21 species pairs, overall error rate is $\alpha = 0.10$). BW, blue-winged teal; MA, mallard; GA, gadwall; NS, northern shoveler; GW, green-winged teal; NP, northern pintail; AW, American wigeon.

abundant species pairs. Green-winged teal and mallard, gadwall and green-winged teal, green-winged teal and northern shoveler, and green-winged teal and northern pintail were positively associated and were less abundant than those species pairs negatively associated (Mann-Whitney U-test: $U = 12$, $P = 0.10$; Fig. 2). When observed patterns of species pair co-existence were compared with the Survey Pool model, deviation from the model over all species pairs was large ($\chi^2 = 231.0$, $P \leq 0.0002$; Fig. 2). The abundance of five species pairs was different from random expectation after Bonferroni's correction ($P \leq 0.002$; Fig. 2). Blue-winged teal and mallard and mallard and northern shoveler were negatively associated

and were among the most abundant species pairs. Northern pintail and northern shoveler, gadwall and American wigeon, and green-winged teal and northern pintail were positively associated and were less abundant than those species pairs that were negatively associated, but this relationship was not statistically significant ($U = 6$, $P = 0.20$; Fig. 2).

Co-existence of all species pairs in the diving duck guild was different from expected for the Breeding Season Pool and Survey Pool models (Fig. 3). When observed patterns of species pair co-existence were compared with the Breeding Season Pool model, deviation from the model over all species pairs was large ($\chi^2 = 3065.6$, $P \leq 0.0002$; Fig. 3). The

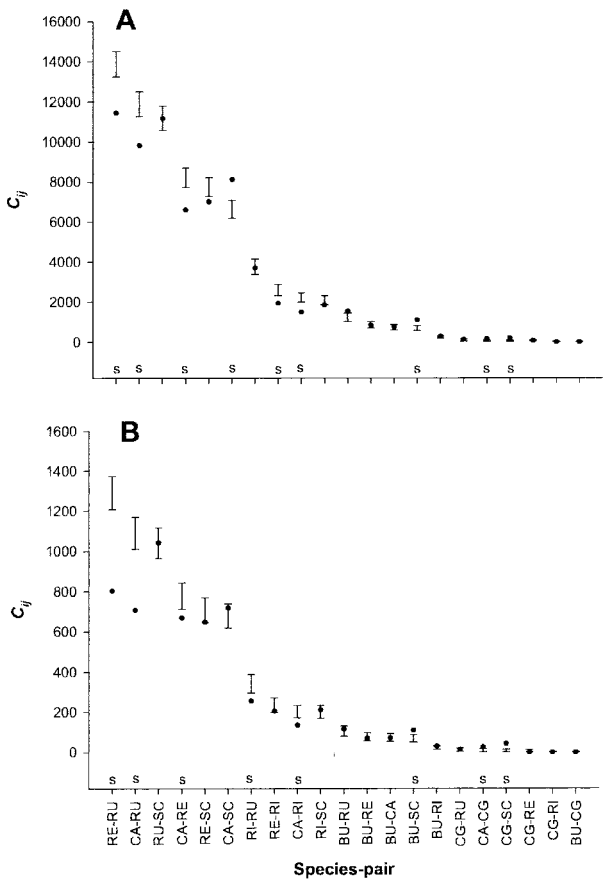

Fig. 3. Co-existence between pairs of diving duck species for the Breeding Season Pool model (A) and the Survey Pool model (B). The error bars are 95% prediction intervals for the randomization distribution. The observed values of co-existence are the filled circles. Overall guild co-existence was significantly different from both the Breeding Season Pool model ($\chi^2 = 3065.6$, $P \leq 0.0002$) and the Survey Pool model ($\chi^2 = 646.8$, $P \leq 0.0002$). Statistically significant deviations from the randomization distribution for each species pair are noted by the 's' above the x-axis ($P < 0.002$ after Bonferroni correction for 21 species pairs, overall error rate is $\alpha = 0.10$). RE, redhead; RU, ruddy duck; CA, canvasback; SC, lesser scaup; RI, ring-necked duck; BU, bufflehead; CG, common goldeneye.

abundance of nine individual species pairs was different from random expectation after Bonferroni's correction ($P \leq 0.002$; Fig. 3). Redhead and ruddy duck, canvasback and ruddy duck, canvasback and redhead, and redhead and ring-necked duck were negatively associated and were among the most abundant species pairs. Canvasback and lesser scaup, bufflehead and lesser scaup, canvasback and goldeneye, and goldeneye and lesser scaup were positively associated and were less abundant than those species pairs that were negatively associated (Mann-Whitney U-test: $U = 18$, $P = 0.10$; Fig. 3). When observed patterns of species pair co-existence were compared with the Survey Pool model, deviation from the model over all species pairs was large ($\chi^2 = 646.8$, $P \leq 0.0002$; Fig. 3). The abundance of eight individual species pairs was different from random expectation after Bonferroni's correction ($P \leq 0.002$; Fig. 3). These species pairs were the same as for the Breeding Season Pool model except that the canvasback and scaup were no longer significantly different from the null model. All positively associated species pairs were less abundant than those species pairs that were negatively associated, but this relationship was not statistically significant ($U = 12$, $P > 0.20$; Fig. 3).

Morphological dispersion

In dabbling duck communities, neither lamellar density nor body length differed from random expectation when compared with the Breeding Season Pool model ($P = 0.116$ and $P = 0.340$, respectively; Fig. 4). Lamellar density was not different from random expectation for the Survey Pool model ($P = 0.403$), but body length was under-dispersed compared with the Survey Pool model ($P \leq 0.0002$; Fig. 4).

In diving duck communities, head–bill was over-dispersed ($P = 0.003$) when compared with the Breeding Season Pool model and under-dispersed when compared with the Survey Pool model ($P = 0.0498$; Fig. 5).

Morphological dispersion and habitat variation

The first principal component (PC) of the habitat variables had a positive loading on all original variables (Table 1). This principal component was interpreted as wetland permanency in which wetlands varied from small and shallow (low PC scores) to large and deep (high PC scores). No other principal components were interpreted because they explained much less variation and did not lead to straightforward predictions of how they should covary with morphological dispersion (Nudds *et al.*, 2000).

In dabbling duck communities, deviations from the null model were dependent on habitat variation for body length but not lamellar density. Z-scores for lamellar density were not correlated to wetland permanency (Pearson's $\rho = -0.066$, $P = 0.391$; Fig. 6A), but Z-scores for body length were positively correlated to wetland permanency ($\rho = 0.220$, $P = 0.004$; Fig. 6B). When the extreme point was removed from the data set, the correlation between body length and wetland permanency was still significant ($\rho = 0.183$, $P = 0.017$; Fig. 6B). Note that Z-scores for body length were consistently positive only on the wetlands with the largest PC scores.

Deviations from the null model in morphological dispersion of diving duck communities were not related to habitat variation ($\rho = -0.101$, $P = 0.257$).

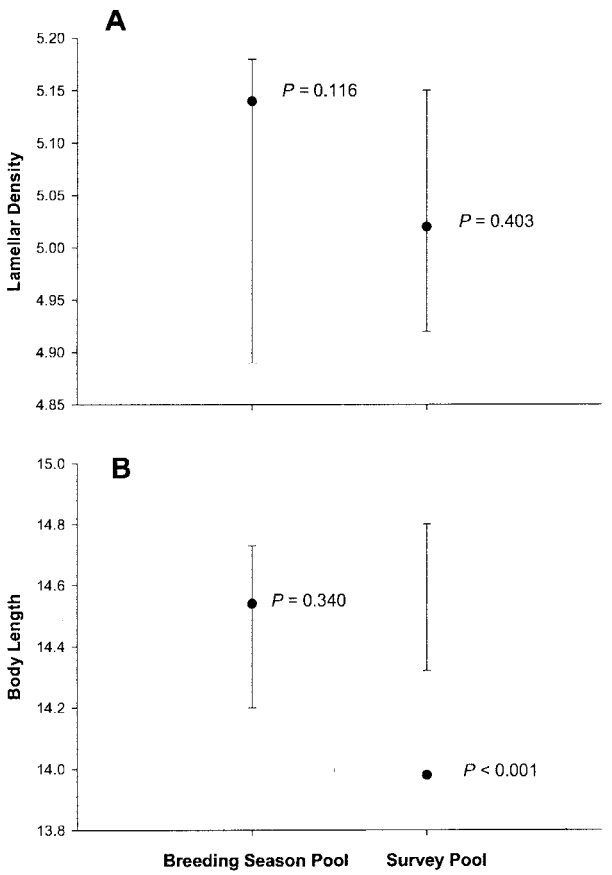

Fig. 4. Average morphological dispersion for lamellar density (A) and body length (B) of dabbling duck communities. The error bars are 95% prediction intervals for the randomization distribution based on the Breeding Season Pool model or the Survey Pool model (see text for description of these two models). The observed values of morphological dispersion are the solid circles.

DISCUSSION

We have shown that both dabbling and diving duck communities are structured in both species co-existence and ecologically relevant morphology. This was true under a variety of constraints. Generally, common species were negatively associated and rare species were positively associated. Morphological structure of duck communities depended on temporal scale and, for dabbling ducks, on local habitat characteristics.

This study represents an advance for the analysis of duck communities because it was conducted in the central part of the species' breeding range where density and diversity are high. Only Nudds (1983) and DuBowy (1988) have studied duck communities in this important area for waterfowl breeding but neither of these authors used a null model perspective. Only Toft *et al.* (1982) have used null models to analyse duck communities on individual wetlands, but their study was done at the northern limit of most species' ranges

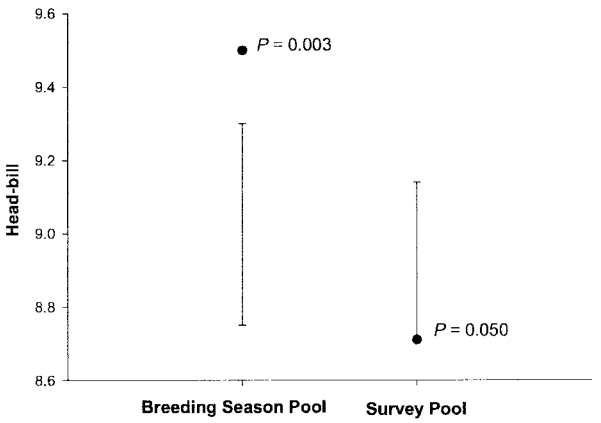

Fig. 5. Average morphological dispersion for diving duck communities. Head–bill is a multivariate measure of head and bill size and shape. The error bars are 95% prediction intervals for the randomization distribution based on the Breeding Season Pool model or the Survey Pool model (see text for description of these two models). The observed values of morphological dispersion are the solid circles.

Table 1. First principal component of the $\log_{10}$-transformed wetland variables

Variable	Coefficient
Total area	0.973
Water area	0.900
Emergent vegetation area	0.654
Edge vegetation area	0.694
Vegetation–water interface	0.917
Maximum depth	0.669
Eigenvalue	3.955
Percent variance	65.92

where diversity was low on each wetland. This allowed them to use a simple chi-squared technique to test for patterns of co-existence between species. In contrast with their results, we did not find a strong negative association between ring-necked duck and scaup, two relatively similar species, for either randomization pool (Fig. 3). Presumably, the interactions that mediate these patterns differ between areas or have changed since earlier studies were completed.

We have also found novel patterns in this duck community, such as morphological under-dispersion of dabbling and diving duck communities (Figs 4 and 5). Under-dispersion of the dabbling and diving duck communities (i.e. morphologically similar individuals found together) could be caused by two processes. First, there may have been fewer than expected

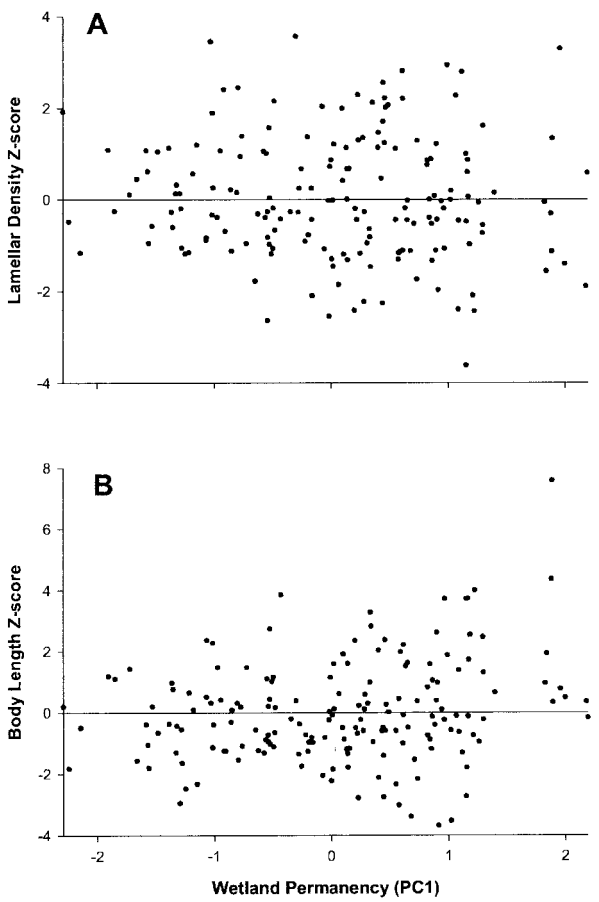

Fig. 6. Scatter plot between the *Z*-score of lamellar density (A) and body length (B) dispersion on individual wetlands and wetland permanency for dabbling ducks. The line marks *Z*-scores of zero and is not a regression line. *Z*-scores for each wetland were calculated from 100 random communities generated from the Breeding Season Pool model. Wetland permanency is the first principal component of wetland physical characteristics. Negative values represent small and shallow wetlands and positive values represent large and deep wetlands (see Table 1 and text).

interspecific pairs with an above average difference in morphology. Interspecific species pairs with similar morphology that chose similar wetlands could cause this pattern. For both diving ducks and dabbling ducks, this mechanism could contribute to the observed patterns of under-dispersion because the two most abundant species pairs were also some of the most different in morphology and were less abundant than expected (Figs 2 and 3). Second, intraspecific clumping, where wetlands contain more breeding pairs of the same species than expected, could also produce morphological under-dispersion. The null model presented here did not test for intraspecific clumping and cannot distinguish between these patterns. Moreover, these two mechanisms are not mutually exclusive and we believe that both are occurring in these communities. Regardless, under-dispersion is consistent with a community structured by 'environmental adversity' (Weiher and Keddy, 1995). Environ-

mental adversity could be manifest in many ways. For example, limited nutrient-rich food could be important because of high nutrient demands during reproduction and growth (Alisauskas and Ankney, 1992; Sedinger, 1992). Recent experimental studies in Northern Europe have shown that manipulations of dabbling duck density on individual wetlands do not affect heterospecific density and increases conspecific density (Elmberg *et al.*, 1997). Additionally, ducklings foraging on fertile wetlands in Northern Europe gained more weight than did ducklings foraging on less fertile wetlands (Sjöberg *et al.*, 2000). These studies suggest that nutrient limitation is important for waterfowl community organization in Northern Europe. It would be interesting to know whether similar patterns exist in our study area. Our finding of under-dispersion in dabbling duck communities, together with published studies on the high nutrient demands of breeding ducks and the lack of competitive effects in other regions, suggests that the duck community as a whole was not structured by competition in our study area. Instead, the community patterns are more consistent with a community that tracks temporally and spatially variable resources.

Common species were negatively associated and rare species were positively associated (Figs 2 and 3). This pattern suggests that interspecific competition may be important for some of the common species and common habitat preferences may be important for some rare species. Limitation by the number of suitable wetland types may be important for the rare species (e.g. green-winged teal, northern pintail and wigeon) because they are known to be habitat specialists (Paquette and Ankney, 1996; Osnas, 1998). Green-winged teal and northern pintail were often found together on the same wetlands and these wetlands tended to be shallower, more vegetated and had higher water conductivity than average wetlands (Osnas, 1998). The most common species in each guild (the blue-winged teal–mallard pair for dabblers and the redhead–ruddy and canvasback–ruddy pairs for divers), however, were negatively associated. This could be due to competition being important only for these most common species. These species pairs were also some of the most different in morphology for both guilds; therefore, density compensation could be acting to control patterns of abundance of these common species even though the morphological analysis did not suggest that competition was important for the community as a whole.

The results of all of our analyses depended on the temporal scale of analysis. Scale dependency has been found before in dabbling ducks of northern Europe (Pöysä *et al.*, 1996) and seems to be a general result of community studies (Wiens, 1989; Weiher and Keddy, 1995). In the present study, we used two scales of analysis: the Breeding Season Pool and the Survey Pool. The scale dependency is most evident for the morphological analyses in dabbling and diving ducks. For dabbling duck body length, morphological dispersion was not different than expected for the Breeding Season Pool but under-dispersed for the Survey Pool (Fig. 4B). Diving duck morphology was over-dispersed for the Breeding Season Pool and under-dispersed for the Survey Pool (Fig. 5). Because these two pools differed only in how observed and random communities were constructed, any differences in results are due to the different methods used. For the Breeding Season Pool, observed communities were constructed by amalgamating breeding pairs over all surveys for each wetland and randomizations were drawn from all breeding pairs observed during all surveys. For the Survey Pool, observed communities were those breeding pairs observed on a wetland during a survey, and random communities were drawn from all breeding pairs observed during that same survey. Metrics for the Survey Pool were then averaged over surveys. This

methodology for the Survey Pool incorporated the observed temporal chronology of breeding pair abundance (Fig. 1) into both observed and random metrics. Conversely, the Breeding Season Pool does not contain temporal patterns in either the observed or random communities. Therefore, these two methods create two different 'snapshots' of the breeding duck community. Because differences in breeding chronology between species are well documented and could be due to historical reasons or processes that operate outside our study region (weather on migration routes or wintering areas, etc.), we believe that the Survey Pool is most appropriate for detecting patterns that are relevant to processes occurring in our study area, such as differences in habitat preferences or interactions between species. The scale-dependent nature of the results, however, could be problematic for other researchers trying to detect patterns in communities for which less natural history is known. For other systems, a comparison between many models and scales of analysis will be essential.

Local habitat conditions also influenced community patterns for dabbling ducks. Over most of the range of wetland PC1 scores there was no relationship between habitat and morphological dispersion, but body length was over-dispersed on those wetlands with the largest PC1 scores. These wetland types were very rare in the study area and had relatively little habitat diversity. As these wetlands were the largest and deepest, they had relatively little edge vegetated area and more open water areas compared with the other wetland types. Therefore, resource partitioning by foraging depth might only be important on those wetlands with few opportunities for habitat partitioning within the wetland. Alternatively, these wetland types may be resource-poor in terms of the number and types of food resources as compared with the other wetland types. Therefore, competition for food might be important on these wetlands but not on others, and this competition causes communities to become over-dispersed. Our results on morphological dispersion partly agree with the hypothesis of Nudds *et al.* (2000) that dabbling ducks should be over-dispersed in body length on wetlands with low microhabitat diversity, and that communities should be over-dispersed in lamellar density on wetlands with high microhabitat diversity. The results of our study support the hypothesis that segregation along a depth gradient (body length) occurs on wetlands with little microhabitat diversity. However, we found no evidence that dabbling duck communities on smaller wetlands were structured in terms of morphology as hypothesized by Nudds *et al.* (2000).

In conclusion, we found evidence that both diving and dabbling duck communities on individual wetlands are not random samples of individual duck pairs from our study region. We found that both guilds have non-random patterns of co-existence between species and are structured in terms of ecologically relevant morphological characters. Importantly, the community patterns found here depended on the temporal scale of analysis. Our null model study is one of the few that incorporates abundance of individuals among species in a region at local sites. Because we incorporated abundance into the null model and used community metrics sensitive to changes in abundance, we were able to analyse patterns in breeding duck communities that have not been previously subject to null model analysis of community structure. We urge future null modellers to collect data on abundance, to incorporate abundance into models so as to better reflect the actual frequency of the interaction they wish to model, and to compare results among models and scales. Doing so may lead to insights into community patterns that have been overlooked before, or to analyses of data sets that were not thought to be amenable to a null model analysis.

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