

Spatial structure of a diving duck (*Aythya*, *Oxyura*) guild: how does habitat structure and competition influence diving duck habitat use within northern prairie wetlands?

S.M. Torrence and M.G. Butler

Abstract: What circumstances allow the coexistence of similar species is a common but complex question in community ecology. It is often assumed that sympatric species within the same guild must employ some mechanism of niche diversification to coexist. Diving duck (Anatidae: *Aythya* Boie, 1822 and *Oxyura* Bonaparte, 1828) competition is poorly understood and current evidence of coexistence mechanisms is contradictory. In the spring and summer of 2001 and 2002, we tested whether diving ducks foraging within prairie potholes segregate by depth to avoid competition. We sought to explain any segregation by sampling sediment particle size, compactness, and organic content; submergent vegetation; and benthic invertebrate densities in the foraging locations of each species. Our study was conducted at the wetland scale in southwestern Manitoba, Canada. We found that Redheads (*Aythya americana* (Eyton, 1838)), Ruddy Ducks (*Oxyura jamaicensis* (J.F. Gmelin, 1789)), Canvasbacks (*Aythya valisineria* (Wilson, 1814)), and Ring-necked Ducks (*Aythya collaris* (Donovan, 1809)) foraged most often at shallow depths (50–100 cm), while Lesser Scaups (*Aythya affinis* (Eyton, 1838)) foraged at shallow to intermediate depths (50–150 cm). Thus, most divers did not segregate by depth. These results conflict with an earlier study that reported diving ducks segregated by depth to avoid competition. Diving ducks likely forage where prey abundance is greatest relative to the cost of diving to obtain that prey.

Résumé : Les circonstances qui permettent la coexistence d'espèces semblables constituent un sujet de recherche commun mais complexe de l'écologie des communautés. On suppose souvent que des espèces sympatriques d'une même guildoivent utiliser un mécanisme quelconque de diversification de niche afin de pouvoir coexister. La compétition chez les canards plongeurs (Anatidae : *Aythya* Boie, 1822 et *Oxyura* Bonaparte, 1828) est mal comprise et les données actuelles sur les mécanismes de coexistence sont contradictoires. Au printemps et à l'été 2001 et 2002, nous avons vérifié si les canards plongeurs qui se nourrissent dans les dépressions humides (« potholes ») des prairies se séparent en fonction de la profondeur pour éviter la compétition. Nous avons cherché à expliquer la ségrégation possible en échantillonnant, dans les sites de recherche de nourriture de chaque espèce, la taille des particules, la compacité et le contenu organique des sédiments, la végétation submergée et la densité des invertébrés benthiques. L'étude s'est faite à l'échelle d'une terre humide dans le sud-ouest du Manitoba, Canada. Nous trouvons que les fuligules à tête rouge (*Aythya americana* (Eyton, 1838)), les éris-matures rousses (*Oxyura jamaicensis* (J.F. Gmelin, 1789)), les fuligules à dos blanc (*Aythya valisineria* (Wilson, 1814)), et les fuligules à collier (*Aythya collaris* (Donovan, 1809)) recherchent leur nourriture le plus souvent dans les faibles profondeurs (50–100 cm), alors que les petits fuligules (*Aythya affinis* (Eyton, 1838)) se nourrissent à des profondeurs faibles à intermédiaires (50–150 cm). Il n'y a donc pas de ségrégation en fonction de la profondeur chez la majorité des plongeurs. Ces résultats contredisent une étude antérieure qui décrit une ségrégation en fonction de la profondeur pour éviter la compétition. Les canards plongeurs recherchent leur nourriture là où les proies sont les plus abondantes compte tenu du coût de la plongée pour capturer ces proies.

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Introduction

Most theories on the role of competition in structuring natural communities state that competition should vary with the degree of environmental variability (e.g., Wiens 1977; Rotenberry 1978). Wiens (1989a, 1989b) reported that the clearest support for avian competition from studies focused

on narrowly defined guilds at a local scale. However, conclusions about the influence of competition on diving duck (*Aythya* Boie, 1822 and *Oxyura* Bonaparte, 1828) communities relative to habitat variability are based mostly on studies examining large-scale habitat use (e.g., Nudds 1983). If diving ducks make use of resource variability within wetlands, then competition theory would predict that the corre-

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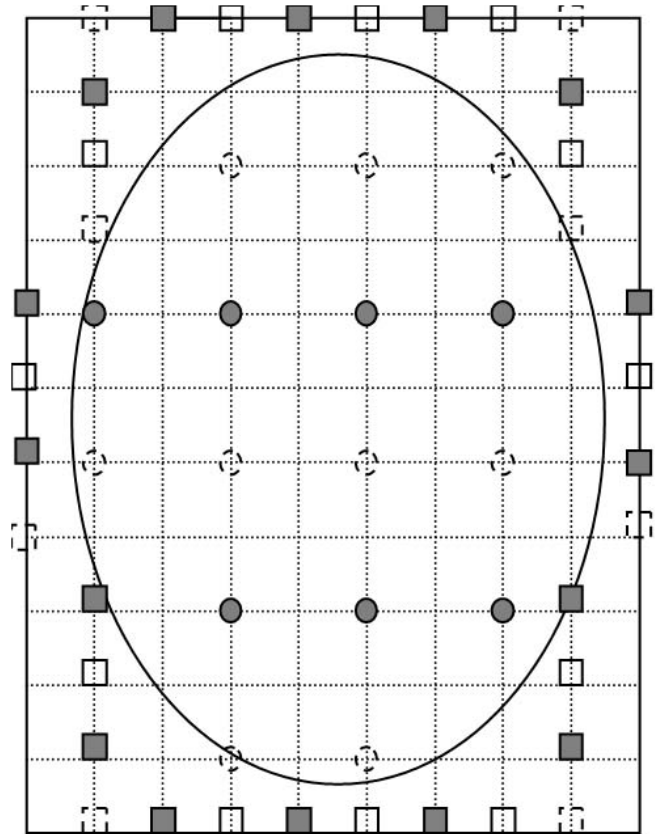
sponding habitat variation would be responsible for patterns in species' distributions.

Diving duck segregation within North American prairie wetlands is poorly understood and current evidence is contradictory (i.e., Siegfried 1976a; Nelson 1983; Simberloff and Conner 1981). Siegfried (1976a) concluded that competition segregated foraging Redheads (*Aythya americana* (Eyton, 1838)) from Canvasbacks (*Aythya valisineria* (Wilson, 1814)) and Lesser Scaup (*Aythya affinis* (Eyton, 1838)) from Ruddy Ducks (*Oxyura jamaicensis* (J.F. Gmelin, 1789)); however, Nelson (1983) found no evidence of such foraging segregation and also observed variability in species-specific foraging locations between years. Diving duck species with differing morphological traits may forage in different habitats within potholes. Depth segregation of North American dabbling ducks while foraging has been explained by differences in lamellar density, which is negatively correlated with the size of the invertebrate prey. Invertebrate size varies with vegetation structure, which in turn is influenced by water depth (Nudds and Bowlby 1984; Armstrong and Nudds 1985). Most diving ducks use their bills to penetrate and sift through benthic sediments for food (Lagerquist and Ankney 1989; Tome 1989; Lovvorn 1994). Given ecomorphological differences among diving ducks (Lagerquist and Ankney 1989), one might hope to explain diving duck foraging patterns within prairie wetlands based on habitat characteristics that influence food availability specific to each species. For example, divers with high lamellar density may forage more efficiently in deeper water where the sediment is less compact and particle size is smaller (e.g., *O. jamaicensis*; Lagerquist and Ankney 1989). In contrast, divers with more stout bills and coarser lamellar spacing may be more effective foragers at shallower depths where the sediment is more compact and particle size is larger (e.g., *A. valisineria*; Lagerquist and Ankney 1989).

The northern prairies, extending from north-central Iowa, USA, to central Alberta, Canada, are important for breeding waterfowl in North America, by some estimates producing >50% of North America's duck population (Baldassarre and Bolen 1994). Ducks meet their nutritional needs during the breeding season by foraging in the wetlands that are so prevalent in this region. There is concern about population declines in some diving duck species such as the Lesser Scaup (Afton and Anderson 2001). The ability to predict where divers forage based on habitat characteristics could aid waterfowl management. Siegfried (1976a) has been cited on multiple occasions (e.g., McKnight 1998; Toft et al. 1982; Pöysä 1983; Nudds 1992; Benoy et al. 2002) in reference to waterfowl habitat use. Our study was aimed at clarifying which habitat characteristics may explain diving duck foraging patterns within northern prairie wetlands.

We tested (i) whether diving ducks segregated spatially by depth within prairie wetlands and (ii) if habitat characteristics and invertebrate densities in dive locations of each species explained differences in dive locations among diving duck species. Our diving duck guild included the Canvasback, Lesser Scaup, Redhead, Ring-necked Duck (*Aythya collaris* (Donovan, 1809)), and Ruddy Duck, which often use the same wetlands simultaneously for foraging and other activities (Osnas 1998). The Bufflehead (*Bucephala albeola*

Fig. 1. Example of pothole mapping technique for locating diving ducks (*Aythya*, *Oxyura*) foraging in prairie wetlands near Minnedosa, Manitoba, Canada. Squares represent perimeter posts and circles represent floats, which were color-coded to distinguish alternate posts and transects. Line intersections are 10 m apart.



(L., 1758)) occurred in this area in low numbers and was therefore excluded from this study.

Materials and methods

Wetland selection criteria

Our study area was in the aspen-parkland area about 10 km south of Minnedosa, Manitoba, Canada, an area described by Kiel et al. (1972). Surveys were conducted on seven wetlands from diving duck arrival in late April through the breeding season ending in mid-July, during 2001 and 2002. Wetlands were semi-permanent with emergent vegetation of cattail (*Typha* L.), sedge (*Carex* L.), common rivergrass (*Scolochloa festucacea* (Willd.) Link), bulrush (*Scirpus* L.), and reeds (*Phragmites* Adans). Sites were accessible from a road and visible from a blind. Study wetlands met size and depth criteria (area < 3 ha, Z_{\max} < 250 cm) for establishment of a survey grid (Fig. 1) and to permit core sampling from an anchored boat. In 2002, we replaced three 2001 sites where diver use was minimal during the first year with wetlands where divers had been observed foraging in 2001 (Table 1). Although this nonrandom selection of sites may bias the study towards finding evidence of competition, observing wetlands with no divers present would provide us with no data relevant to our questions. Informal surveys of study sites replaced in 2001 revealed little diver use of these wetlands in 2002.

Pothole sampling regime and diving duck use

We marked the perimeter of each study wetland at 10 m intervals with 2 m tall, 2 cm × 2 cm color-coded posts to create a grid system for referencing individual duck locations. To minimize the number of foreign objects in the potential diver habitat, (~25 cm × 13 cm) color-coded floats were placed at 20 m intervals in the portion of the grid located in the water (Fig. 1). Observers were able to record diver locations at 10 m resolution because ducks could be recorded as above, below, and left or right of a given float (in relation to the blind). To establish depth contours, we recorded water depth at each 10 m grid intersection. Four values at the corners of a 10 m × 10 m quadrat were then averaged to obtain a mean depth for each quadrat. Each quadrat was assigned to a depth contour. Ideally, vegetation zones would be used, but these zones were not readily apparent early in the season or in wet years; thus, depth contours were used instead. As in Nelson (1983), contour 1 ranged in depth from 0 to 100 cm, contour 2 included depths 101–150 cm, contour 3 included depths 151–200 cm, and contour 4 included depths 201–250 cm. Contour 1 included the zone of emergent vegetation where divers do not forage, and thus spans a greater depth range (as in Nelson 1983). We felt that 50 cm was an adequate contour interval because often middle-depth contours were only a single quadrat wide.

Two observers rotated among study potholes to decrease observer bias. We performed 4 h observations starting at sunrise ~6 mornings/week from ground-level canvas blinds located upslope from wetlands in 2001. Because emergent vegetation concealed shallow areas nearest the blinds in early July 2001, observers used 2.5 m tall blinds in 2002. Location and activity of each individual duck was recorded at 0.5 h intervals. We rarely observed divers “dabbling”, and when we did, this foraging behavior did not occur in the 0.5 h data recording intervals.

Benthic core samples, submergent vegetation data, and penetrometer readings (measuring substrate softness) were collected twice each year, in mid-June and mid-July. To sample vegetation, we collected two 1 m long rake throws (one from each side of the boat) within each quadrat. Each rake sample as a whole (all species) was ranked from one to five based on the abundance of vegetation caught on the rake's teeth and the percent contribution of each plant species was estimated. Because sampling of habitat variables at each diver foraging location was impractical, we subsampled dive locations based on contours. Each pothole was sampled at 10–15 locations. The number of core samples collected from each pothole reflected its size and the number taken from each contour reflected that contour's surface area. When possible, subsamples were randomly chosen for each species using a contour from quadrats in which foraging was observed on more than 1 day. If a species was not observed foraging in a given quadrat on 2 or more days, random subsamples were drawn from quadrats with 2 observed days of foraging by all species combined. If this sampling regimen was not possible, random subsamples were drawn from any foraging locations within the depth contour. Finally, random quadrats were chosen if no diver foraging was observed in a contour. We did not test whether foraging patterns changed through the summer, given the limited number of observed dives.

A 7.62 cm diameter steel core sampler with clear plastic liners was used to collect sediment samples for examination of benthic invertebrates, detritus, sediment particle sizes, and bulk density. Cores typically were collected to a depth of 10 cm, taken back to the laboratory in the liner tubes, and allowed to settle. Core lengths were sometimes less than 10 cm. The depth of the sample in these cases was measured, and invertebrate, particle size, and bulk density data were corrected to represent a 10 cm core. An unconsolidated layer of sediment, rarely thicker than 5 cm, sat above a clay layer that served to plug the core tube, thus facilitating the collection of unconsolidated sediment.

Sediment particles were fractionated wet with screens of 19, 11.2, 4.75, 1.0, 0.71, 0.5, and 0.045 mm mesh, and the volume of each size fraction was determined by water displacement. All core fractions >0.5 mm were stored in 70% ethanol to preserve invertebrates. The remainder of each core sample was frozen for later analysis of other sediment characteristics.

Bulk density (g/cm³) was calculated as an index of the amount of organic material, which is lighter and more porous than other substrate components (Mitsch and Gosselink 1993). Following removal of invertebrates, the entire ethanol-preserved portion of each core sample (the courser fractions) was dried at 105 °C for 72 h. After thawing, a subsample of each frozen core sample fraction was dried because the volumes of these finer fractions were too large to dry in a reasonable length of time. Bulk density was then calculated by summing the dry-mass values for all frozen and preserved fractions of each core sample.

Penetrometer readings were taken to measure substrate softness. A pointed 3.4 kg stick with gradation marks was held next to a wooden measuring stick and we recorded the distance the penetrometer sank into the sediment. We calculated a mean of three penetrometer readings per quadrat.

Invertebrates were sorted from the core samples, identified to the appropriate taxonomic classification based on waterfowl diet studies (Krapu and Reinecke 1992), and measured to the nearest tenth of a millimetre. We calculated biomass using length–dry mass equations in the literature (Smock 1980; McCauley 1984; Stein et al. 1984; Doetkott 1989; Traina and von Ende 1992; T.D. Noraker and K.D. Zimmer, unpublished data).

Habitat measurements (depth, vegetation data, and invertebrate data) from a quadrat were applied to duck foraging observations recorded in that quadrat (after Nudds 1982; Osnas 1998). Total open water area was mapped in mid-summer (9 and 10 July) each year to estimate habitat available to foraging divers in contour 1. The area of contour 1, therefore, excluded the portion of water with emergent vegetation. To map open water, we used the same maps used for mapping dive locations. Quadrats with no emergent vegetation were summed and quadrats with complete emergent vegetation cover were labeled as unavailable to divers. Quadrats partly covered by emergent vegetation, regardless of the amount, were given a value of 0.5 (assuming equal numbers of quadrats with >0.5 and <0.5 coverage) and then summed. This sum was then added to the “open water” area of contour 1 (Table 1).

Statistical analysis

Observed dive frequencies for each species within each

Table 1. Contour areas for study wetlands near Minnedosa, Manitoba, Canada.

Pothole	Year	Contour	Contour area (ha)	Wetland area (ha)	Open water (ha)	Percentage of open water
A	2001	1	0.145			
		2	0.745			
		3	0.4	2.73	1.29	47
	2002	1	0.46			
		2	0.83			
		3	0.14	2.6	1.43	55
B	2001	1	0.16			
		2	0.2			
		3	0.28			
		4	0.09	0.975	0.73	75
	2002	1	0.345			
		2	0.27			
C	2001	1	0.135			
		2	0.15			
		3	0.16			
		4	0.04	0.765	0.485	63
	2002	1	0.41	0.5	0.41	82
		2	0.155			
D	2001	1	0.145	0.81	0.3	37
		2	0.485	0.64	0.485	76
		3	0.17			
E	2001	1	0.17	0.315	0.25	79
		2	0.08	0.4	0.4	100
F	2001	1	0.32	0.4	0.4	100
		2	0.24	0.585	0.41	70
		3	0.17	0.36	0.36	100
G	2002	1	0.36	0.36	0.36	100
		2	0.275	0.52	0.395	76
H	2002	1	0.12	0.52	0.395	76
		2	0.33	0.48	0.34	71
I	2002	1	0.33	0.48	0.34	71
		2	0.01	0.48	0.34	71

Note: Areas were estimated from 9 to 10 July in 2001 and 2002, with contours 1, 2, 3, and 4 describing depth ranges 0–100, 101–150, 151–200, and 201–250 cm, respectively.

contour were adjusted by the proportional contribution of each contour to the total open water surface area of each wetland. This adjustment ensured equal likelihood of dives within each contour, regardless of a contour's absolute area. These adjusted dive frequencies were summed for each pothole by year (after Nelson 1983; for a sample calculation see Appendix Table A1) as a means to compare densities among contours. Differences in habitat availability owing to impenetrable emergent vegetation were accounted for in contour 1 by defining only "open water" as available habitat. We used a goodness-of-fit χ^2 test to test for the nonrandom distribution of diving duck foraging among contours (Neu et al. 1974).

We used ordination techniques in the program CANOCO version 4.0 (ter Braak and Smilauer 1998) to explain the variation in foraging locations of diving ducks for 2001 and 2002 combined. We first performed a principal component analysis (PCA) on a matrix of environmental variables to explore relationships among depth contours and the environmental variables benthic particle size, sediment softness, submerged plant species, and submerged plant cover.

We used direct gradient analysis to look for effects of the environmental variables mentioned above on foraging locations of each diver species. For these comparisons, we first

performed detrended correspondence analysis (DCA) on the species foraging data alone (no environmental data) to determine gradient lengths in standard deviations (SD) to decide whether linear ($SD < 3.0$) or unimodal ($SD > 3.0$) direct gradient analysis (ter Braak 1995) was most appropriate. As the SD value of the DCA for the foraging data was 2.6, we used redundancy analysis (RDA), which is a linear method of direct gradient analysis (ter Braak 1995). In the full-model RDA, environmental variables were tested for significance ($\alpha = 0.10$) using a Monte Carlo permutation procedure (199 iterations) with forward selection, and only significant variables were included in the reduced RDA model. The significance of the axes in the reduced RDA model was tested using a Monte Carlo permutation procedure (1000 iterations).

To determine the influence of food sources on foraging locations, we developed a RDA matrix of diving duck foraging locations, with invertebrate data as the environmental variables. The mean (\pm SE) proportions of chironomids (Chironomidae) (0.74 ± 0.34) and amphipods (Amphipoda) (0.14 ± 0.28) in core samples were higher than other invertebrate taxa; therefore, the remaining invertebrate taxa in each core sample was grouped as "other". Forage variables were abundance, total biomass, and mean biomass per inver-

Table 3. Tests of nonrandom selection of foraging depths by diving ducks in prairie wetlands near Minnedosa, Manitoba, Canada.

	<i>n</i>	Most-used contour(s)	Adjusted observed value	χ^2	df	<i>p</i>
2001						
Canvasback	105	1	61	80.46	3	>0.0001
Ring-necked Duck	50	1	30	37.84	3	>0.0001
Ruddy Duck	385	1	215	245.06	3	>0.0001
Redhead	100	1	64	92.64	3	>0.0001
Lesser Scaup	76	2	37	32.32	3	>0.0001
2002						
Canvasback	88	3	41	6.92	2	0.031
Ring-necked Duck	11	1	8	7.83	2	0.02
Ruddy Duck	171	1	93	73.27	2	>0.0001
Redhead	161	1	74	11.97	2	0.0003
Lesser Scaup	27	1, 2	13, 12	6.57	2	0.038

Note: Adjusted frequency of use of the depth contour most often used by each species (out of four or three contours in 2001 and 2002, respectively) was compared with the expected value with a χ^2 goodness-of-fit test (see text).

RDA environmental variable model included *P. pectinatus* (F ratio = 2.27, p = 0.065), *Ceratophyllum* sp. (F ratio = 1.85, p = 0.085), and benthic particle size class of 11.2–4.4 mm (F ratio = 4.54, p = 0.01). In the reduced model using these variables, axis 1 explained 6.1% of the variation (F ratio = 6.85, p = 0.005), with all three axes together explaining 7.7% of the variation (F ratio = 2.963, p = 0.005).

In the full RDA model using invertebrate data to explain diver foraging locations, axis 1 explained 3.5% of the variation (F ratio = 3.58, p = 0.035), while all three axes explained 7.1% of the variation. This model was not significant (F ratio = 0.85, p = 0.63) based on the Monte Carlo permutation test. The reduced RDA model with only the chironomid biomass explained 1.8% of the variation (F ratio = 2.03, p = 0.095). Chironomids, amphipods, and “others” were present in 72.5%, 23.6%, and 30.6% of core samples, respectively, and we found no invertebrates in 19.4% of core samples.

Discussion

Shallow areas of wetlands were important to foraging divers because all species except the Lesser Scaup were found to forage in shallow contours more often than expected by chance. Shallow areas could have higher food densities or biomass. We believe our invertebrate sampling was neither extensive nor intensive enough to relate invertebrate density to water depth, as little variation in diver foraging location was explained by the invertebrate data in the RDA analysis. Such an analysis would require sampling invertebrates on a finer depth interval than the width of our contours, as well as with a larger sample size. However, Nelson (1983) found that invertebrate biomass and abundance in nektonic samples were always highest at shallower depths; results from benthic samples varied, but generally indicated higher biomass and abundance in the shallowest contour. Most studies in prairie wetlands relate invertebrate prey size to predation pressure (e.g., Zimmer et al. 2001), but a void in the literature exists relating benthic invertebrate size in prairie wetlands to water depth.

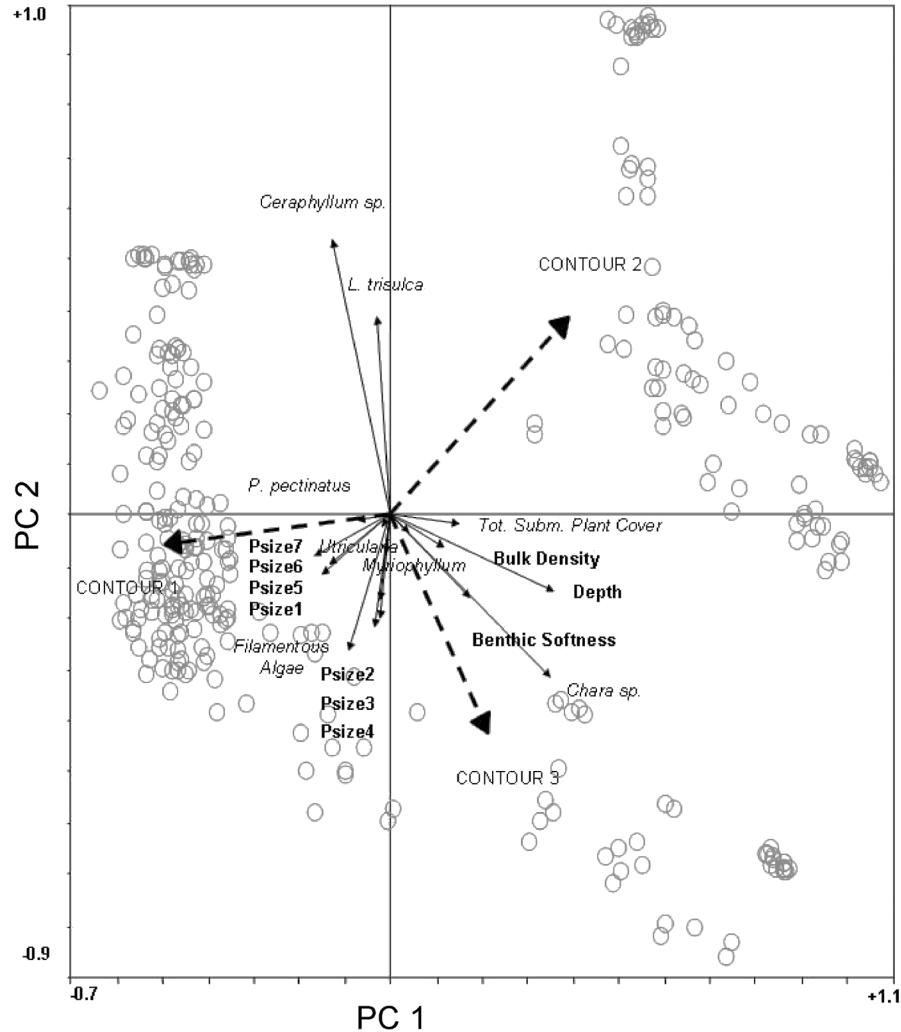
Nelson’s (1983) findings were similar to ours in that she found most divers foraged in shallow to middle depth con-

tours. Nelson (1983) related her observations of dives within contours to food abundance within each contour and found that species generally foraged in the depth contour where their “preferred” food was most abundant. She suggested that divers foraged opportunistically and did not employ a segregation strategy to avoid competition but rather to forage on specific prey (Nelson 1983).

Our results differed from Siegfried’s (1976a) in that most species in our study foraged at shallow depths. Siegfried (1976a), by comparing the known diets of diver species, suggested that species with similar diets segregated spatially to avoid competition. Siegfried (1976a) supported this conclusion by referring to Weller’s (1964) hypothesis that Canvasbacks and Redheads may have evolved allopatrically, and to his own hypothesis (Siegfried 1976b) that the Ruddy Duck is a new addition to the North American prairies and thus evolved allopatrically with the Lesser Scaup. Siegfried suggested that species pairs evolving in allopatry, such as Canvasbacks and Redheads, or Lesser Scaup and Ruddy Ducks, are more likely to engage in interference competition (Siegfried 1976a). However, these hypotheses by Weller (1964) and Siegfried (1976b) regarding the evolutionary history of diving ducks have not been verified. Because Siegfried (1976a) did not take depth measurements in his wetlands, it is unclear how deep the divers he observed were foraging. Only four and two wetlands in our study had a contour 3 in 2001 and 2002, respectively, but several diver species were observed foraging within shallower wetlands. Evidence that more than one diver species foraged (*i*) in shallow wetlands and (*ii*) most often in the shallowest depth contour of deeper wetlands supports our conclusion that divers do not segregate by depth.

Our finding that most species foraged at shallow depths does not support Siegfried’s (1976a) hypothesis that diving ducks can partition space more efficiently than food. Diet overlap among diving ducks can be high (see review in Krapu and Reinecke 1992) and this overlap may explain the similarity in foraging locations in our study. Because chironomids constitute, on average, 72% of all invertebrates present in core samples and were present in 72.5% of all core samples, they may have been the main food source of

Fig. 2. Principal component analysis (PCA) of environmental variables measured for two habitat sampling periods (mid-June and mid-July) in 2001 and 2002 of prairie wetlands in Minnedosa, Manitoba, Canada, where diving ducks were observed foraging. Circles represent sampling locations. Arrows represent the strength of each variable's influence on axis scores. Psize1, 2, 3, 4, 5, 6, and 7 represent percentage of core samples collected on sieves of sized 19, 11.2, 4.75, 1, 0.71, 0.5, and 0.045 mm, respectively, for each sampling location. Benthic softness represents penetrometer readings and bulk density represents organic content. Tot. Subm. Plant Cover represents an average rank ranging 1–5 for the amount of coverage of a rake sample. Each plant species was scored for its contribution to the total amount of plant material present. Eigenvalues are 32.7 for PC axis 1 and 15.9 for PC axis 2.



all divers observed in our study. The suggestion by Siegfried (1976a), therefore, that diet overlap causes spatial segregation is not supported. Siegfried's (1976a) conclusions may have been influenced by his failure to take depth measurements in his study sites. Thus, a diver in the center of a shallow pothole may have been recorded similarly to a diver in the center of a deep wetland.

There may be a discrepancy between the abundance, versus the availability, of invertebrates as prey for diving ducks. Osnas (1998) found that diving duck communities were less evenly distributed than expected among wetlands in the Minnedosa area and suggested a possible correlation between bill morphology and wetland characteristics. For example, species with a lower lamellar density (i.e., Canvasbacks) may fare better when using coarser wetland substrates with larger particle sizes than species with a greater

lamellar density (i.e., Ruddy Ducks or Lesser Scaup; Lagerquist and Ankney 1989); coarse sediments may impede separation of substrate and prey for species with finer lamellar spacing. Because we found that most divers foraged at shallow depths where particle size was generally larger than in deeper water, we conclude that, at the scale of our measurements, diving duck species do not differentially use habitats based on morphological features such as lamellar density. Furthermore, diving in shallow water may have lower energetic costs than diving in deeper water (Lovvorn 1994).

We believe it noteworthy that in our study Canvasbacks, Ruddy Ducks, Redheads, and Ring-necked Ducks foraged in contour 1 in both a wet year and a dry year. In our study, 2001 was a very wet year and 2002 was a fairly dry year. Sequential wet-dry cycles greatly influence prairie habitats (van der Valk 1989; Euliss et al. 2004), and Murkin et al.

(1997) stated that wet–dry cycling is important to production in prairie wetlands. One result of wet–dry cycling is the promotion of vegetative decomposition (Ryder and Horwitz 1995), which can influence invertebrate composition within wetlands. Sediment organic content can have a positive relationship with invertebrates, such as chironomids, that are important in the diet of divers (Topping 1971; Moss and Timms 1989). Briggs and Maher (1985) recommended that wetlands managed for waterfowl be allowed to dry out periodically, because this promoted growth of submerged plants such as *Potamogeton tricarinatus* F. Muell. and A. Benn. ex. A. Benn., which in turn promoted increased benthic organic matter that increased benthic invertebrate densities, especially large species like *Chironomus* spp. Such wet–dry cycling may affect wetland edges the most, where we observed the majority of divers foraging. Our finding that bulk density was greater in deeper contours (and thus more organic matter was present in shallower contours), albeit a weak association, alludes to this. To make stronger conclusions regarding food availability to divers based on invertebrate distributions and substrate type in prairie wetlands, we recommend a more rigorous benthic invertebrate sampling program that is paired with a dive tank study in which substrate type is varied while holding prey density constant. A study relating benthic invertebrate distributions to habitat characteristics such as water depth, organic content, and benthic particle size would also be useful. Our results regarding shallow foraging of divers should not be extrapolated to waterfowl habitats with a greater range in depths. Habitat conditions in shallow and deeper habitats in lakes and coastal lagoons may vary more than what we encountered in the present study. Diving ducks may distribute themselves in different patterns when a wider array of habitats is available to them.

Our results indicate that habitat variables may play a strong role in determining diving duck use of wetland habitat. Additionally, variation influenced by abiotic factors subject to temporal changes, such as wet–dry fluctuations, may have important influences on diver foraging. If resources are limited, then diving ducks may experience competition, especially if these wet–dry fluctuations are present on the continent as a whole. However, competition appears not to cause segregation of diving duck species by depth within prairie wetlands. We focused on studies supporting competition as a consequence of resource limitation on the breeding grounds, but there is support for resource limitation in the wintering grounds as well (Heitmeyer and Fredrickson 1981; Kaminski and Gluesing 1987; DuBowy 1988; for a contrasting study see Smith et al. 1986). Thus, a study examining the relationship of water level and foraging depth of diving ducks on the wintering grounds would be interesting, especially if management units could “cycle” through wet and dry years. Moist soil management areas with the ability to control water levels would be an ideal place for such an experimental study.

Diving duck foraging is not random, because divers forage preferentially in shallow water of prairie wetlands, yet segregation by depth is not a mechanism for avoiding competition. Most likely, divers forage in shallow water because shallow foraging is more energy efficient than foraging in deeper water, and (or) because the benthic food resources

are denser in shallower areas. Given the similarity we found in use of foraging habitat among species in this guild, management for diving ducks in prairie wetlands should focus on managing the guild in general, as opposed to managing individual species.

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Appendix A

Method for adjusting number of dives per contour

To test for differences in the number of dives per zone, diving duck observations were first adjusted to allow for equal probability that a duck would dive in each zone regardless of zone area.

These adjustments were made by first summing the original dive counts (F) for each pothole (F_O). The number of observed dives in each zone was divided by the proportional area of that zone, scaled to zone 1, to create an intermediate dive count (I) that was rounded to the nearest whole number. All I values for one pothole were summed to create F_A , which was rounded to the nearest whole number.

To calculate the final adjusted number of dives as a proportion of the original dive counts (to avoid changing sample sizes for the χ^2 test), we multiplied each I value by the ratio F_O/F_A (Table A1).

Table A1. Sample calculation.

Pothole	Zone	Original dive counts (F)	Ratio between zone area and zone 1	Intermediate dive counts (I)	Adjusted dive counts ($I \times F_O/F_A$)
A	1	31	1	31	72
	2	72	5.14	14	32
	3	7	2.76	3	6
Total		$F_O = 110$		$F_A = 48$	110