HABITAT SELECTION AND TERRITORIAL BEHAVIOR OF THE SMALL GREBES OF NORTH DAKOTA

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The Horned (*Podiceps auritus*), Eared (*P. nigricollis*), and Pied-billed (*Podilymbus podiceps*) grebes all have extensive ranges that overlap in the northern interior of North America. Munro (1940) has suggested some slight habitat differences among these species on the lakes of British Columbia, and he also described differing preferences for fish in the diets of these species there. Storer (1960) described subtle differences in feeding techniques employed by the *Podiceps* grebes on their marine wintering grounds.

The small, shallow lakes and ponds of the glaciated prairie region form the major portion of the zone of sympatry of these 3 species. Fish are not usually present there so all 3 species must feed on insects and other invertebrates. The bills of these species are different, but each shape is the result of evolution throughout the species range, not just in the relatively small zone where these grebes coexist. The foods available to grebes in the glaciated prairie region are more limited, suggesting a large overlap between species despite differences in bill shape. During the summer of 1972 I studied habitat selection, territorial behavior, and nest dispersion in order to identify the ecological conditions allowing coexistence of these 3 species.

STUDY AREAS AND METHODS

The study was conducted in the vicinity of Kenmare, Ward County, North Dakota. Extending from Kenmare to the north and east is a glacial drift plain (Stewart and Kantrud 1972), characterized by slightly rolling terrain, poor drainage, and, in wet years, abundant small bodies of water (potholes). About 25 km west of Kenmare is the "Coteau du Missouri," a rolling terminal moraine region that extends in a narrow belt across the Dakotas and also contains large numbers of potholes and scattered large alkaline lakes.

I selected 3 study areas totaling 65 km^2 for quantitative measurements and observations. The largest of these (31 km^2) is just north of Kenmare in typical prairie pothole country. Even in wet years most of the ponds are small and nearly all of the area has been cultivated at one time or another. Over 200 semi-permanent ponds were recorded here, excluding small, ephemeral ponds.

A second study area of 15.5 km^2 is located 16 km east of Kenmare. This agricultural area is exceptionally flat and in wet years contains some very large, yet very shallow ponds. I surveyed 43 ponds here in 1972, including one of over 120 ha that was just 1 m deep at its deepest point.

I selected a third study area (18 km^2) in the north portion of the Lostwood National Wildlife Refuge in the Coteau region. Here I surveyed 244 ponds plus 4 lakes of up to 89 ha in size.

The ponds of the first 2 areas were similar, with a wide variety of pond types present. Ponds which had been cultivated in dry years had emergent vegetation that would naturally appear in less permanent areas. These ponds had fewer of the more typical emergents such as cattail (*Typha* sp.). Water levels were high in 1972 and ponds with shorelines that were cultivated in 1971 had few emergents; ponds totally cultivated in 1971 had no emergents or submergents until at least mid-summer.

The potholes of the Lostwood area had a very different vegetation, apparently due to more stable surroundings and somewhat more alkaline waters. Sedge (*Carex*) dominated small ponds, while white-top (*Scholochloa feustacea*) predominated on larger ponds. The largest ponds and small lakes were very alkaline and generally had only scattered patches of bulrush (*Scirpus*).

In the 3 study areas, I surveyed all ponds and classified them according to pond permanence as determined by the presence of various indicator species of aquatic plants (following Stewart and Kantrud 1971). Ponds were placed into such classes as ephemeral, seasonal, semi-permanent, permanent, alkali, etc. Pond cover types were graded from 1 to 4, with type 1 having 95% or more of the pond area covered with emergent vegetation and type 4 being 95% or more open water. Thus, the typical cattail-lined pothole is usually classed as a type IV, semi-permanent pond, but its cover type may vary from 1 to 4 depending on the distribution of the cattails.

For each pond with nesting grebes, I recorded the number of pairs, found nests when possible, and determined the size of the pond either through cover-mapping or aerial photographs. When possible, I also observed aggressive behavior, area of defended territories, and other general habits of these grebes.

RESULTS

Habitat selection.—I found one or more pairs of grebes on 75 of the over 500 ponds and lakes surveyed. The ponds used by grebes were easily separable into 2 size classes. Small ponds of 7.3 ha or less had (with 1 exception) 1 species of grebe per pond, although in some cases several pairs were found. These ponds were all seasonal or semi-permanent with many in cultivated areas classed as seasonal-tilled due to past agricultural activity. Ponds of 19.4 ha or more had 2 or 3 species of grebe in nearly all cases. These ranged from large, very shallow seasonal ponds through large alkaline lakes.

I found a single species of grebe (78 grebe pairs) on 67 small ponds (Table 1). Pond type (seasonal, semi-permanent, etc.) appeared to be unimportant to grebes, while pond size and cover-type seemed to be the factors used by grebes in selecting ponds. Of the 67 ponds, 3 were very open and each contained one pair of Eared Grebe. The remaining small ponds were divided between Horned and Pied-billed grebes.

The Pied-billed Grebe avoided the 100% open water, seasonal-tilled ponds but used a wider range of cover types than the Horned Grebe (Table 1).

TABLE 1

CHARACTERISTICS OF SMALL (<7.3 HA) PONDS CONTAINING ONLY ONE GREBE SPECIES PER POND[1]

	Horned	Eared	Pied-billed
Total number of pairs	27	3	48
Number of ponds used	20	3	44
Average number of pairs per pond	1.4	1.0	1.1
Range of number of pairs per pond	1–6	1	1–2
Average area of pond per pair (ha)	0.9	1.5	2.2
Range of pond sizes used (ha)	0.1–5.2	0.4–3.0	0.6–7.0
Frequency of occurrence of pairs by pond classification[2]			
Seasonal Pond	8	1	26
Semi-permanent Pond	9	1	22
Seasonal-tilled Pond	10	1	0
Frequency of occurrence of pairs by pond cover-type[2]			
Type 1	0	0	2
Type 2	3	0	17
Type 3	11	0	23
Type 4	13	3	6
Average cover type used	3.4	4.0	2.7

[1] Only one example of a small pond with 2 species was observed, a 0.6 ha pond with both a Horned and an Eared Grebe pair.
[2] Following the methods of Stewart and Kantrud (1971) as described in the text.

Figure 1 is a finer analysis of the pond-use data and plots pond size against percent open water. The dotted line is added to show the general division of Horned and Pied-billed grebes along these coordinates. The Pied-billed Grebe was also found in a wider range of pond sizes (Fig. 2). Figure 3 shows the distribution of Horned and Pied-billed grebes on ponds less than 2 ha in size. This includes over 80% of the Horned Grebe ponds compared to 45% of the Pied-billed Grebe ponds. Of the 24 Pied-billed Grebe ponds, 13 were rather heavily vegetated (only 20–40% open water), suggesting that where pond size selection overlaps the most, habitat separation is more pronounced. Very small ponds were used almost solely by Horned Grebes, and 60% of all Horned Grebe ponds were less than 1 ha.

The 7 large ponds and lakes used by grebes all had extensive areas of open water which were sometimes bordered by emergent vegetation. The Eared Grebe accounted for 218 of 235 grebe pairs on these ponds (Table 2). All but 6 of the Eared Grebe nests were on large, very open ponds and lakes. The only large lake with just one breeding species was an 89 ha alkaline lake that lacked shore vegetation and had but a few small patches

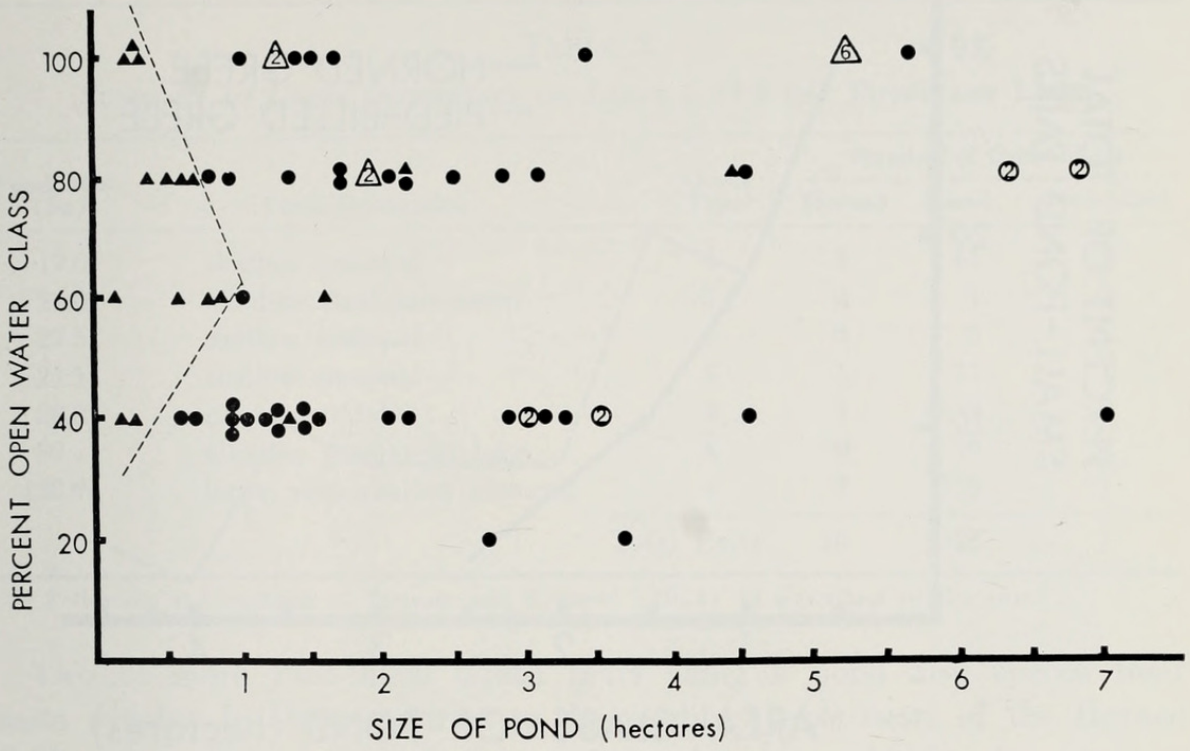

FIG. 1. Size and percentage-cover class of small ponds used by Horned and Pied-billed grebes. Triangles mark Horned Grebe ponds; circles mark Pied-billed Grebe ponds. Figures with numbers represent multiple-pair ponds. Open water classes are designated by the larger value of each class. The dashed line marks the region of pond types used exclusively by Horned Grebes.

of emergent bulrush for Eared Grebe nesting sites. The 10 pairs of Horned Grebes found on large ponds used bays or portions of the lake separated from the main lake by emergent vegetation. Pied-billed Grebes were always associated with dense stands of emergent shoreline vegetation and just 7 pairs were found on these large ponds.

Nest dispersion and territorial behavior.—In most cases the Horned and Pied-billed grebe had but one nesting pair per pond, while the Eared Grebe was usually colonial with all the nests on a lake or pond tightly clumped. Of 222 Eared Grebe nests, only 4 were solitary and one colony included 110 nests.

On ponds with 2 or more Horned Grebe nests, the nests were widely separated either by open water (at least 45 m of water between visible nests) or a barrier of vegetation or land. This species was very aggressive in defense of its pond or portion of pond against other Horned Grebes. Attacks on an intruding bird continued until the intruder was chased out of sight, either into emergent vegetation or out of the pond. An average of only 0.9 ha of water per pair was recorded on the small ponds, and one pair successfully raised young on a pond of only 0.1 ha.

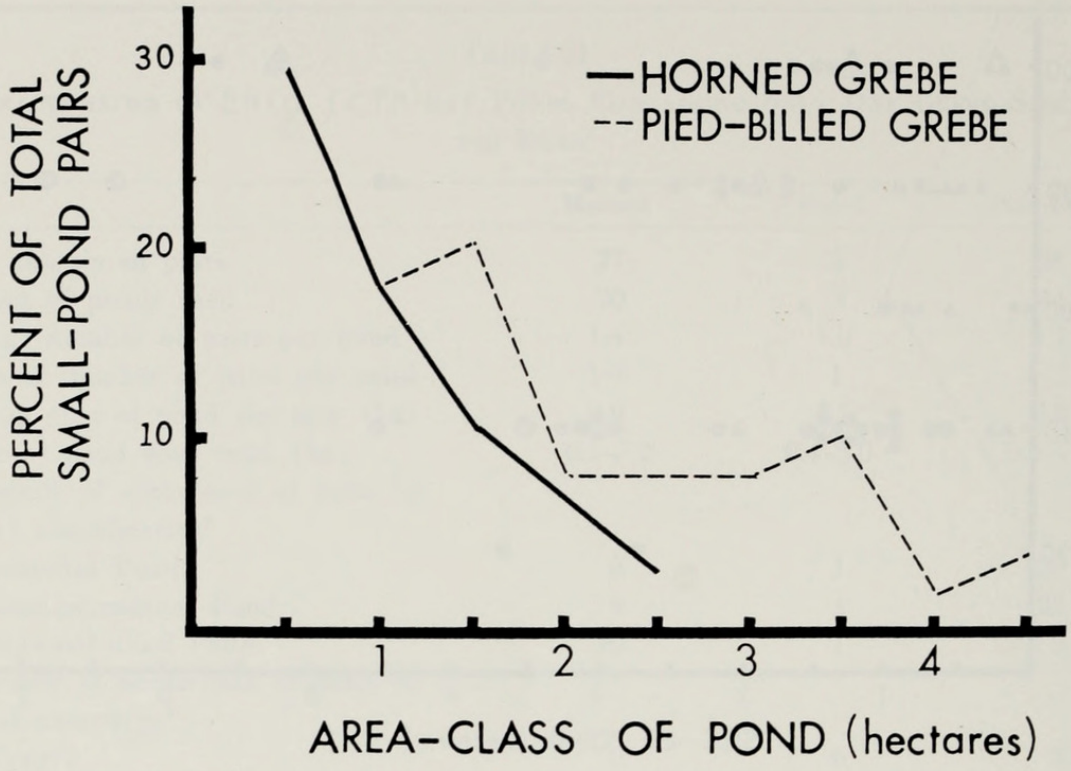

FIG. 2. Frequency distribution by pond size for Horned and Pied-billed grebe ponds computed as the percentage of total small pond pairs for each species.

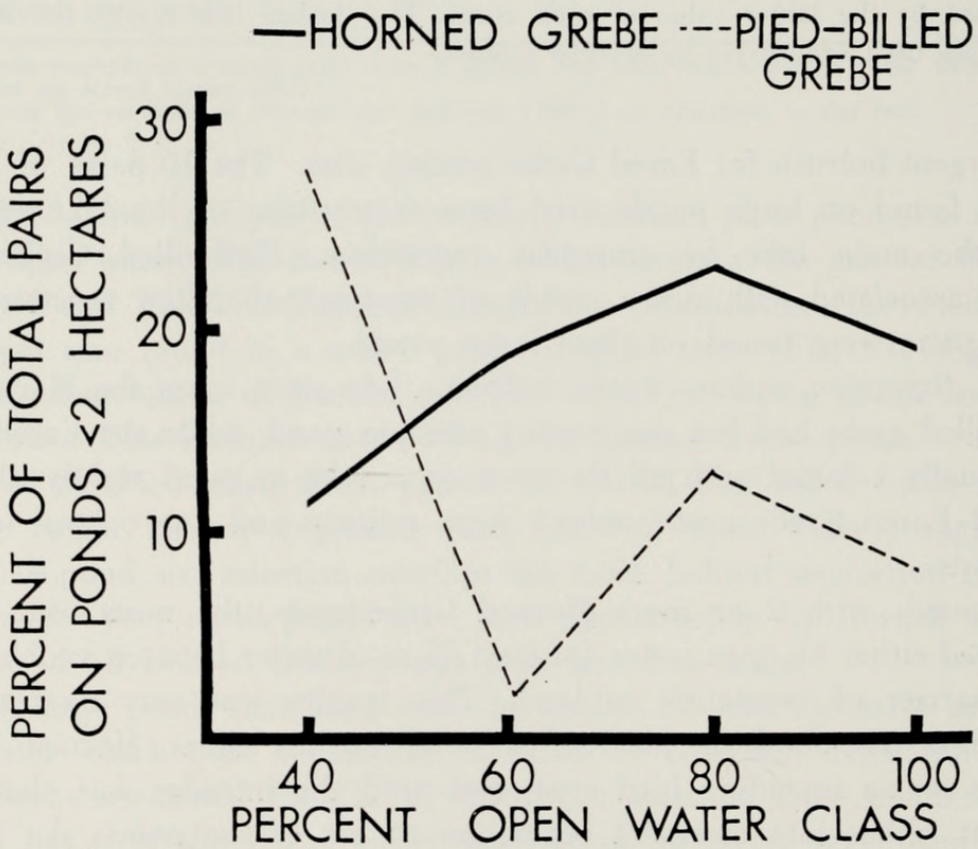

FIG. 3. Frequency of pond use by open water class for those Horned and Pied-billed grebe pairs found on ponds less than 2 ha in size.

TABLE 2

SUMMARY OF GREBE OCCURRENCE ON LARGE (>7.3 HA) PONDS AND LAKES

Pond Size (ha)	Pond Description	Cover Type*	Number of Grebe Pairs		
			Horned	Eared	Pied-billed
19.6	shallow seasonal	4	4	44	1
21.0	alkaline semi-permanent	3	0	4	3
22.5	shallow seasonal	4	0	8	1
24.1	shallow seasonal	4	1	34	1
28.8	permanent lake	3	3	2	0
89.7	alkaline permanent lake	4	0	16	0
128.9	large, very shallow seasonal	4	2	110	1
		Total Pairs	10	218	7

* Following the methods of Stewart and Kantrud (1971) as described in the text.

Two or more Pied-billed Grebe pairs using a pond also spaced their nests widely. In sharp contrast to the readily visible nests of the Horned Grebe, the nests of this species were nearly always hidden in emergent vegetation. Although the species nested in many ponds of about 1 ha, the smallest pond with 2 pairs of Pied-billed Grebe was over 3 ha. Glover (1953) described the Pied-billed Grebe territory as an arc of 150 feet (45 m) around the nest and observed that birds were amicable away from their territories. Of the grebes I studied, only the Pied-billed Grebe had a vocalization that appeared to be associated with territorial behavior.

DISCUSSION

Species which share limited resources likely influence each other's abundances reciprocally to the extent of their overlap in resource use (Gause 1934). Thus, to coexist, closely related species must differ either in habitat, range, or foods (Lack 1971). Range is not a factor here, and studies of the foods used by these species (Munro 1940, Wetmore 1924, Palmer 1962) suggest a high amount of overlap among the species of this area. This suggests that separation by habitat is the most important component allowing the coexistence of these species in the glaciated prairie region.

The separation of the Eared Grebe from the Horned and Pied-billed grebes is obvious, for the former prefers large, open ponds. Here, nesting sites are more limiting than food supply, a condition ideally suited for the colonial nesting habits of the Eared Grebe where only the nest site is defended (Palmer 1962). In contrast, I found the Horned Grebe and Pied-billed Grebe to be solitary nesters and to prefer small ponds or just portions of large ponds. The Horned Grebe was most common on very small, open ponds, a habitat well suited to its observed method of terri-

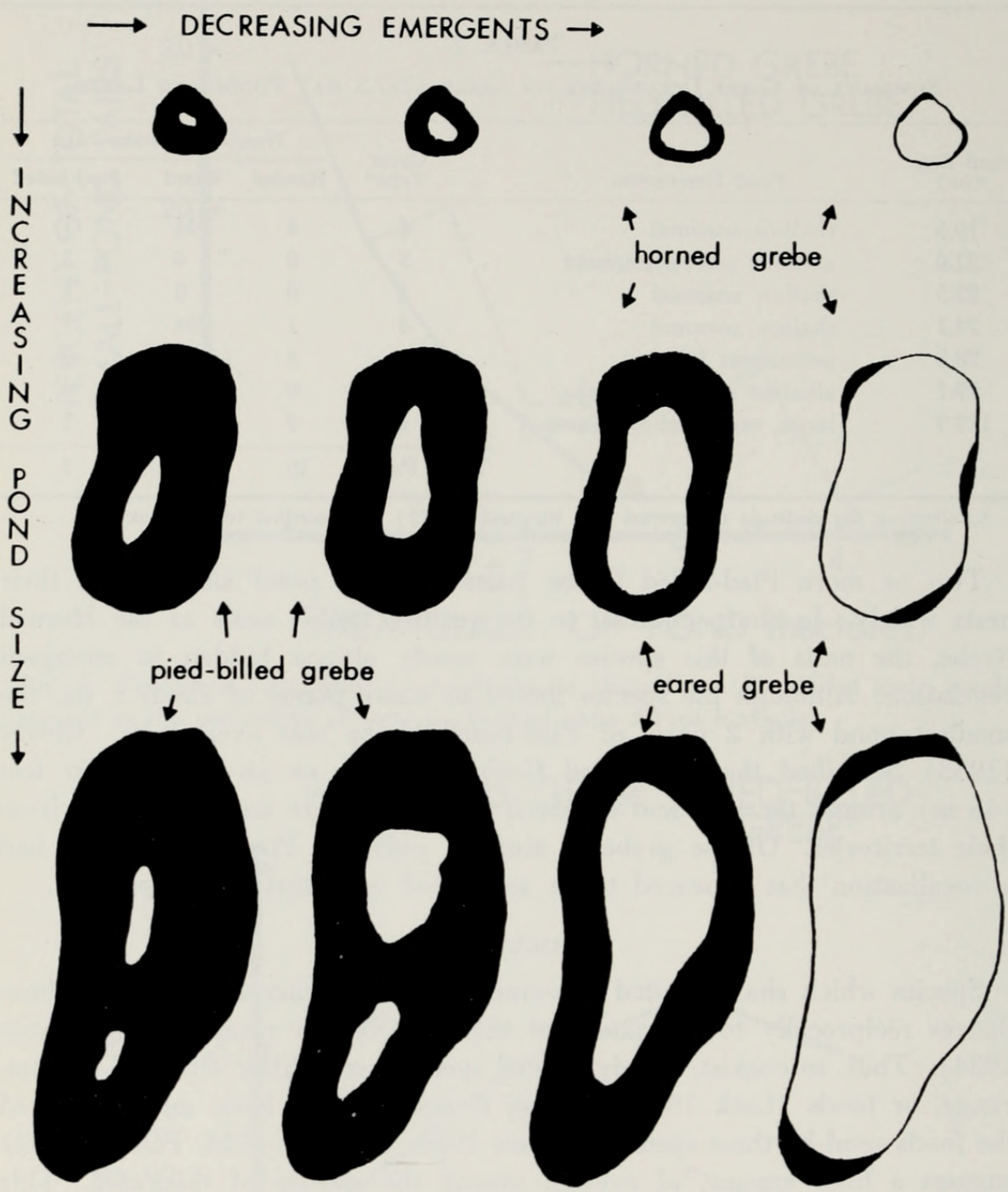

FIG. 4. Schematic diagram showing how the 3 grebe species generally separate their habitat preferences among ponds varying in size and emergent vegetation. Dark areas signify emergent vegetation; species names signify the general area in which they predominate.

torial defense by visual cues. On the other hand, the Pied-billed Grebe used more heavily vegetated and generally larger ponds and used a distinctive vocalization to aid in the defense of its territory in such a visually restricted habitat. Figure 4 illustrates the method used by these species to divide ponds of varying size and cover-type.

Another factor possibly contributing to the distribution of these species was the aggressiveness of the Pied-billed Grebe towards the *Podiceps* species. Wetmore (1920) observed the Pied-billed Grebe harassing Eared Grebes and he states (1924) that the Pied-billed is a savage fighter that even attacks coots (*Fulica americana*). No direct confrontations between Horned and Pied-billed grebes were observed, but in 2 cases Pied-billed replaced Horned grebes which had appeared first on a pond. This suggests that the Pied-billed may have been dominant on the wide variety of pond sites it occupied. The Horned Grebe used ponds either too small or too open for the Pied-billed, while the Eared Grebe could effectively populate large, open ponds where vegetation might have been limiting for the Pied-billed Grebe. The amount of overlap in habitat preferences might have been related to the presence of many more available ponds than breeding grebe pairs in 1972. Even so, each species had one type of pond that it occupied exclusively.

Since both *Podiceps* species commonly build their nests in shallow water away from emergent vegetation, the idea that nest sites may be relatively more limited on a large, open pond should be clarified. Glover (1953) found that 50% of the destruction of Pied-billed Grebe nests in Iowa could be attributed to wind damage. A similar pattern prevailed in North Dakota in 1972 with many nests destroyed by the rough water resulting from strong prairie winds. These winds varied greatly in direction during the spring and thus limited the number of sheltered nesting sites. On large, open ponds containing several pairs of Horned Grebes, the first pair arriving in the spring usually picked the most sheltered site and nested successfully. Late arriving pairs were forced to put their territories and nests in portions of the pond more vulnerable to wind and water damage and were correspondingly less successful. Contrastingly, when Eared Grebes nested on large ponds or lakes they effectively put the whole colony of nests in the most sheltered location and thus greatly reduced nest loss.

The fairly complete division of these species by habitat implies indirectly the highly overlapping or identical foods that I discussed earlier. If foods were different, 2 or 3 species might be able to coexist on smaller ponds. Even though 2.2 ha per pair was needed on small ponds, a pond of nearly 20 ha was needed to support 2 species. The existence of 2 or 3 species on a pond may be the result of the larger area being able to supply separately the habitat requirements of each species. This suggests certain parallels between grebe distribution and bird species packing on islands (MacArthur and Wilson 1967). Large ponds may act like large islands which contain more species than small islands because they contain more habitats and thus can support more habitat specialists. Large

islands also contain more species because they allow closely-related species with overlapping habitat or dietary requirements to coexist. On a small island, this may not be possible and perhaps only one of these species could survive. In this way small ponds may act like small islands which can support just one of a set of similar species. Certain of these ponds may match the habitat specifications of only one species of grebe, while others could be suitable for 2 species. In the latter case, the species present may be a matter of who arrived first, dominance behavior between species, subtle differences in available foods, or, perhaps, habitat differences finer than those analyzed here. Further work would be needed to determine this, but it is apparent that even if we allow a certain amount of variation among the diets of these species, small ponds would still be able to support just one species while the overlapping diets could be tolerated on larger ponds and lakes.

SUMMARY

Patterns of habitat selection and territorial behavior of the Horned, Eared, and Pied-billed grebes were examined in North Dakota. Each species seemed to prefer a distinct pond type which could be explained in part by the species-specific methods of nest dispersion and territorial defense. The Eared Grebe preferred large, open ponds with abundant feeding grounds but where a compact colony of nests could be situated in a sheltered site. Horned Grebes seemed to prefer small ponds with open water where they could defend a territory visually. The Pied-billed Grebe occupied the widest variety of pond types but was always associated with heavy emergent vegetation. As this species has a distinct vocalization, it was suggested that it was the best adapted of the species for defending its territory in low-visibility habitats.

Possible dominance interactions were discussed to explain the presence of certain species on ponds suitable for 2 or more species. The advantages of being colonial on open ponds were also discussed. Parallels between pond selection by grebes and island biogeography were noted.

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Dr. Walter D. Maddox of Kankakee, Illinois, is a life member of the Wilson Ornithological Society whose professional interests and research are in oral surgery. Dr. Maddox's ornithological interests include avian biogeography and evolution. He is also a member of the AOU, the COS, Sigma Xi, and several professional dental organizations. He is married and has 2 sons and 2 daughters. In addition to his professional and ornithological interests, Dr. Maddox is a student of Civil War history and the Illinois Community College Movement, and he enjoys golf and photography.