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ECOLOGICAL ISOLATION IN TEMPERATE NORTH AMERICAN GREBES (PODICIPEDIDAE)

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In his two most recent books, Lack (1968, 1971) has surveyed the current knowledge of ecological isolation in birds and its adaptive basis. Lack's lengthy appendices suggest many groups of related species for which breeding strategies and isolating mechanisms are not fully understood, including the grebes (Podicipedidae) of temperate North America.

Despite a wealth of literature on the elaborate courtship dances of many of the five temperate North American species, little work has been done on correlating the adaptiveness of the various mating systems used with the habitats selected by each species. This is especially true in the glaciated prairie region of north-central North America, where all five species are found.

During the summer of 1972 I gathered data on the habitat preferences of each species in north-western North Dakota in an attempt to understand the mechanisms of ecological isolation of the five species in this area. These observations were augmented with information on behavioral and morphological adaptations and have led to a theory of ecological isolation.

STUDY AREA

The study was conducted in the vicinity of Kenmare, North Dakota, in the midst of the glaciated prairie region. Extending from Kenmare towards 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 fifteen miles west of Kenmare is the "Coteau du Missouri", a rolling terminal morain region that extends in a narrow belt across the Dakotas and that also contains large numbers of potholes and scattered large alkaline lakes. The only large freshwater lakes and marshes occured on the Des Lacs National Wildlife Refuge, a series of artificially controlled water areas that wind up the Des Lacs River valley past Kenmare for nearly thirty miles.

Qualitative observations were made throughout the region, while three study areas totaling twenty-five square miles were selected for quantitative observations and measurements. The largest of these (twelve square miles) was situated just north of Kenmare in typical prairie pothole country. Most of the ponds were small and almost all of the area had been cultivated at one time or another. Over 200 ponds were recorded here, excluding small, ephemeral ponds.

A second study area of six square miles was located ten miles east of Kenmare. This agricultural area is exceptionally flat and in wet years contains some very large, shallow ponds. A total of 43 ponds were recorded

here, including one of over 300 acres.

The third study area (seven square miles) was in the north portion of the Lostwood National Wildlife Refuge, one of the greatest waterfowl production areas in the world with up to 150 water basins per square mile. On the study area 244 ponds were surveyed plus four lakes up to 220 acres in size.

The ponds of the first two areas were similar, with most of the pond types described by Stewart and Kantrud (1971) present. More recently cultivated ponds showed emergent vegetation that would naturally appear in less permanent areas and had fewer of the more typical dominants such as Typha. As water levels were very high in 1972, ponds with shorelines that were cultivated in 1971 had few emergents and those ponds totally cultivated in 1971 often had no emergents or submergents until at least mid-summer.

The potholes of the Lostwood area had a very different vegetation. Apparently due to the more stable surroundings and the somewhat more alkaline waters, these ponds were less variable. Shallow ponds were dominated by sedge (Carex) and the larger potholes had lush growths of white-top (Scholochloa feustacea). The largest ponds and the small lakes were very alkaline and generally had restricted growths of bulrush (Scirpus).

METHODS

In the three study areas, all ponds were surveyed and classified according to the system of Stewart and Kantrud (1971). This system of classification is based upon pond permanency as determined by the presence of various indicator species of acquatic plants (Table 1). It also allows a measure of alkalinity through plant indicators. Of great importance to this study was their system of classification of pond cover types (Table 2), which was based on the abundance and distribution of emergent vegetation. Each pond which contained grebes was classified, the number of pair of grebes was recorded, nests were found if possible, and the size of the pond was determined (either through cover-mapping or aerial photographs).

Qualitative observations were made of all species throughout the region to gain an insight into amounts of aggressive behavior, area of territories defended, and other general habits which might be of importance to ecological isolation.

RESULTS

All five temperate North American species of grebe were observed, but only the three small species, the Horned Grebe (Podiceps auritus), Eared Grebe (Podiceps caspicus), and Pied-billed Grebe (Podilymbus podiceps), were found breeding on the study areas. The two large grebes, the Western Grebe (Aechmophorus occidentalis) and Red-necked

Grebe (*Podiceps grisegena*), were seen breeding only on the Des Lacs National Wildlife Refuge.

With one exception, any pond with grebes smaller than 45 acres would have only one of the three small species, although in many cases more than one pair of this species was present (Table 3). On ponds larger than 45 acres two or all three species could be found, with many of the pairs using only portions of the marsh (Table 4).

General observations on behavior and habitat preferences are summarized below for each species. Quantified characteristics of pond choice are taken from the study areas, while behavioral observations were made throughout the region.

Red-necked Grebe—Only one pair of this species was observed, nesting in an open area of one of the Des Lacs National Wildlife Refuge marshes. This species has been found by others generally to be a solitary nester that defends an area for feeding and nesting (Palmer, 1962).

Horned Grebe—This species generally preferred small ponds with much open water. Thirty-eight pair were found on 25 water areas, with 27 pair being on twenty small, single-species ponds. Observations showed this species to be very aggressive in defense of its pond or portion of pond, at least during the early stages of nesting. Aggression was stimulated by the sight of an intruding bird and attacks continued until the intruder had been chased out of sight, either into emergent weeds or to another pond.

In those few cases where territories were separated by open water, there appeared to be a territorial border beyond which chasing would not occur. When two or more pairs bred on a pond, nests were either widely dispersed (at least 150 feet if observable over water) or separated visually by some sort of barrier (e.g. a band of emergent vegetation or peninsula of land). An average of only 2.2 acres of water per pair was recorded on the small ponds, and one pair was observed to have raised young successfully on a pond of only three-tenths acre. When this species was found breeding on large ponds, it usually sought out small bays, narrow arms of water, or small openings in extensive areas of emergent vegetation. Rarely was it found nesting on the edge of large areas of open water.

Eared Grebe—In contrast to the previous species, the Eared Grebe was a colonial species of relatively large bodies of water. I recorded 222 nests, only four of which were on ponds smaller than 45 acres in size. On the larger ponds the nests were definitely grouped, with the largest colony of 110 nests situated in an area of only several hundred square feet. Territorial defense seemed to be restricted to the nest itself, and even then nests were often touching.

This species figured in two of the notable variations to the patterns found in the study. The only small pond with two species of grebe was one on which a pair of Eared

Grebe and a pair of Horned Grebe nested. The pond was very small (1.6 acre) but aggressive encounters were observed only around the nests. The Eared Grebe was also the only species present on the only single-species lake found—a large (220 acre) alkaline lake with only a small area of emergent bulrush which the grebes used for nesting.

Pied-billed Grebe—This species used the widest range of pond types. It preferred much emergent vegetation and was present on nearly all ponds and lakes where emergents were common. Only a few territorial encounters were observed, and these usually included much calling in addition to display and fighting.

Western Grebe—This, the largest of the North American grebes, was solely a colonial species found only on large lakes where fish were present. The defended territory includes only a few feet around the nest and birds often ranged over a mile from the nesting colony while feeding.

DISCUSSION

The grebe niche. Before discussing the means by which grebes are ecologically isolated from each other, we should mention why these species are enough alike to make their isolating mechanisms interesting and, also, why they are different enough as a group from other marsh-dwelling birds that competitive interactions between the various groups are not relevant here. In essence, we are looking at the grebe niche and must separate it from the generalized niches of the ducks, loons, and so forth before dividing

it into five component parts.

Grebes are marsh-dwelling diving birds. All of them feed heavily on fish, but the three small species can survive completely well on a diet of small invertebrates, tadpoles, and insect larvae, and thus can breed on the small prairie marshes. On these small ponds, the only diving birds are grebes and certain diving ducks. The latter are primarily vegetarian, thus on small ponds grebes have little competition for the insect larvae and so forth that live on or near the bottom. As long as a pond is deep enough that diving is required to reach these foods the grebe has an advantage over other birds. As pond depth decreases there comes a point where the food resource is available to many other groups of birds, including herons, bitterns, ducks, rails, terns, and large shorebirds. Against these competitors diving is relatively inefficient and grebes are probably excluded.

On large bodies of water several other fish-eating birds can be found co-existing with grebes. These include loons, pelicans, cormorants, mergansers, gulls, and terns. All but loons and mergansers employ quite different feeding adaptations than the grebes, while loons and mergansers, in addition to being rare in the prairie region with which we are concerned, have differently structured bills and use very different nest sites. It is possible, though, that there could be considerable competition between certain grebes and loons in the boreal forest and tundra region,

as the ranges of the Horned and Red-necked Grebes show very restricted areas of overlap with the range of the Red-throated Loon (Gavia stellata)(Palmer, 1962).

Ecological isolation in temperate North American grebes. It is expected that species which share portions of a pool of limiting resources influence each other's abundances reciprocally to the extent of their overlap in the use of this resource (Gause, 1934). Thus, to coexist, closely related species must differ either in habitat, range, or foods (Lack, 1971).

Given the observed habits and habitat preferences for the five North Dakota grebes in their zone of sympatry, a pattern for their ecological isolation emerges. All grebes obtain their food by diving, but the existence of two distinct size classes serves as the most obvious of the isolating mechanisms. The two large species (Western and Red-necked Grebe) are primarily fish-eating, while the three small species eat mainly small invertebrates, at least on the breeding grounds. Even on bodies of water where the two size groups may both exist and feed on similar resources, the weight-ratios between the members of the two classes always exceed two to one, a factor which coincides well with that suggested by MacArthur (1972) as being neccessary for isolation through food sizes in temperate regions. It should be noted that there is no evidence for separation within the size groups by types of food selected. Both Palmer (1962) and my own field observations showed the various

species feed on the same types of food, while a large series of sweep and bottom samples showed as great a variance of available foods within a series of ponds used by one species as between ponds used by two different species. This fact can also be deduced by the data which showed such complete separation of habitats by the grebes. If the species were separating by food types within a size class, one would expect them to pack much more tightly into the same habitats. This was not observed. Thus, given the two size classes and the lack of separation within each class by food types, we now need to see how habitat serves to ecologically isolate the members of each size class in their zone of sympatry.

The most pronounced difference between the habits of the two large species of grebes is that the Red-necked Grebe is almost always a solitary nester that defends a fairly large territory around the nest while the Western Grebe is always colonial and defends only the immediate nest-site. Within the zone of sympatry, the Western Grebe would have the advantage on large, open lakes where nest sites are limited but food is widespread, for the colonial habit allows the birds to concentrate in the limited nesting habitat and scatter over the lake to feed. On smaller bodies of water (but those large enough to support a large grebe species), one would expect the territorial habit of the Red-necked Grebe to be advantageous, as nest-sites are less limiting

here and foraging area is more so. By behaviorally excluding other pairs from an area, the Red-necked Grebe insures an adequate food supply for itself. Thus, through differences in habitat accompanied with the proper social behavior these two species are effectively ecologically isolated.

The observed mating systems are of interest when one looks at the overall distribution of the two species. These species overlap throughout the northern prairie region, from northern North Dakota and southern Manitoba through southern Saskatchewan and much of Alberta. This portion of the glaciated prairie region is probably the most diverse area in North America in the types of water basins available to grebes and, in addition to being the zone of overlap of the two large species, comprises the only area where all five temperate North American grebes are found. Thus, much as increased foliage height diversity in a woodland supports increased bird species diversity (MacArthur and MacArthur, 1961), the area with the greatest diversity of acquatic habitats supports the greatest diversity of grebes. In addition to the prairie region, the range of the Western Grebe extends to the south and west throughout much of the western United States. This region tends to be arid and, in general, permanent surface water tends to be found in the form of large alkaline lakes. The high productivity and scarcity of emergent vegetation that characterize these lakes are ideal for the colonial Western Grebe. On the

other hand, the range of the Red-necked Grebe extends mostly eastward and northward through regions of boreal forest and in some cases tundra. Smaller lakes are common here and productivity tends to be relatively low, thus the territorial characteristics of the Red-necked Grebe are better suited. Palmer (1962) states that this species occasionally nests in loose colonies, and it would be interesting to see if these loose colonies occur in the part of the Red-necked Grebe's range where the Western Grebe is not found. If so, this would parallel the behavior of the Collared Peccary (Tayassu tajacu), which occurs in small groups in the portion of its range which overlaps with the very gregarious White-lipped Peccary (T. pecari), but which is found in large bands in the portion of its range where the White-lipped Peccary does not occur (J. Terborgh, personal comment).

The three small species of grebe also overlap in the northern prairies, but differ from the larger species in their ability to live on the tiny potholes which are so abundant in this region. Two of these three, the Eared Grebe and Horned Grebe, have habits, ranges, and presumably, mechanisms of isolation remarkably parallel to those of the two large species. The third small grebe, the Pied-billed grebe, is the most unusual in terms of morphology, habits, and range, and it apparently fills a void left by the other four species.

The Eared Grebe is in many ways a small version of the

Western Grebe. It is a highly colonial species and was found on relatively large ponds and lakes. (Of course, because of its much smaller size, the Eared Grebe colonies occured on much smaller ponds than the Western Grebe.) Its range also parallels that of the Western Grebe by including nearly all of the western United States. Unlike the exclusively colonial Western Grebe, the Eared Grebe is somewhat flexible and even in the area of overlap with the Horned Grebe occasional single pairs on small ponds can be found (four pair out of 222 total pair on the North Dakota study areas.) This factor would allow the species to use small ponds when they were available, but in drought periods it would still be able to survive on the larger alkaline ponds that are the characteristic form of relatively permanent water throughout much of the species range.

The Horned Grebe is a smaller counterpart of the Red-necked Grebe in that it defends the area within which it forages and generally nests solitarily. It prefers ponds with open water in the middle, especially small, open ponds. Twenty-seven of the 38 pairs observed on the study areas were on small ponds that averaged only 2.2 acres per pair. Of those eleven pair found on larger ponds, all selected areas such as bays or openings in vegetation where barriers defined smaller portions of the lake which were then defended. The Horned Grebe's range is remarkably similar to that of the Red-necked Grebe and through much of their

northern ranges they are the only grebe species.

The Pied-billed Grebe was the only species which was equally common on both small and large ponds where emergent vegetation was present. In the small ponds of the study areas, it was found on those with extensive emergents or at least widely scattered emergent vegetation. On larger bodies of water it could almost always be found in areas with emergents, and this species was exceedingly common and widespread on the extensive marshes of the Des Lacs National Wildlife Refuge. Like the Horned Grebe, this species defends a territory, which was described by Glover (1953) as an arc of 150 feet around the nest. Unlike the Horned Grebe, which seemed to rely purely on visual cues in territorial defense, this species has a very loud and distinctive call which apparently is used as a spacing mechanism much in the manner of the typical woodland bird. The adaptiveness of such a call is obvious when one considers the density of the emergent vegetation in which this species lives. Another characteristic of this species is the large clutch size. Often eight to ten eggs are laid instead of the four or five typical of the other grebes. Larger clutch sizes are typical of birds that live in less permanent environments (Cody, 1966), and, in the sense that this species uses the small, weed-filled ponds which are so due either to their shallowness or recent flooding, this species could be called a "second-growth" species. On the

other hand, the species is abundant on many large, permanent marshes throughout its range, so further work is needed to ascertain the adaptiveness of such a large clutch size.

Since the generalized behavior of the Pied-billed Grebe with its territorial defense and vocal spacing mechanism parallels the behavior which is so common in terrestrial birds, it is interesting to note that the range of this species extends continuously from Hudson Bay to central Argentina. Apparently less-specialized behavior has allowed it such an extensive range, for it is the only of these grebe species which is adapted to using heavily vegetated ponds. In warmer regions shallow water quickly chokes with acquatic emergents and is the ideal situation for a Pied-billed Grebe. Another factor of its generalized behavior may be its bill size. In general, a larger bill allows a larger variety of foods and food sizes to be taken. In North Dakota, where the Pied-billed Grebe apparently is taking the same foods as the small-billed Horned and Eared Grebes, this large bill may be unneccessary. Through the extensive range of the species it may be very adaptive, and thus would occur throughout the interbreeding population.

Adaptiveness of grebe species to the marsh cycle. Small marshes of the glaciated prairie region characteristically go through cycles which are controlled by water levels and muskrat populations (Weller and Spatcher, 1965; Weller and

Frederiksen, in press). In general, emergent vegetation can germinate only in very shallow water or mud. Thus, after a dry period, most pond basins are full of emergents. When water again fills these basins, the pond is nearly covered with emergent vegetation. Muskrats soon enter the pond and, in feeding and building dens, start to open patches in the marsh. The muskrat population grows until it eventually eats all the emergents and the marsh is very open with perhaps only a ring of emergent vegetation along the shoreline. It remains open water until drought again allows the germination of marsh emergents.

In looking at the grebe species and the marsh cycle, one finds a pattern of replacement of species that would allow a continual utilization of the grebe niche. In the early, densely emergent stages, one would expect only the Pied-billed Grebe, whose vocalizations adapt it to spacing itself in the dense vegetation. Eventually muskrats would open up holes the the vegetation large enough to attract Horned Grebes or, on larger marshes, Red-necked Grebes. These species are well adapted to defending the open areas while nesting in the surrounding vegetation. Later, when vegetation becomes scarce, these species would be replaced by the colonial forms, the Eared and Western Grebes, which could utilize the available food supply throughout the lake while concentrating their nesting to the now limited supply of emergent vegetation.

Comparison between palearctic and nearctic grebe communities. There are striking parallels between the grebes of temperate North America and those of northern Europe and Asia. Both areas have five species, three of which are the same (Table 5). The major interest is in the similarity of the two differing pairs of species. The largest pair, the North American Western Grebe and the palearctic Great Crested Grebe (Podiceps cristatus), are both large, fish-eating, colonial species that even look remarkably similar in their winter plumages. The other pair, the North American Pied-billed Grebe and the somewhat smaller Little Grebe (Podiceps ruficollis), are similar in their occurence in densely vegetated marshes, in the possession of loud and distinctive calls, in having very large clutch sizes, and in having the thickest bills of the grebes. Although the ranges of the species in the two communities follow the same general pattern, there are some exceptions. For example, the range of the Little Grebe is somewhat more southerly than the Pied-billed Grebe and thus there is a more restricted area where all five palearctic species are sympatric. Whether the interrelationships between range, size, habitat, and mating system which are proposed here hold in the palearctic species would be of considerable interest.

SUMMARY

The three factors used in ecologically isolating species of birds are habitat, range, and foods. Research was done on the five temperate North American species of grebes in their zone of sympatry to see how these factors combined to yield ecological isolation in these closely related diving birds. Observations were also made on social behavior to see how the variations between species in this trait affecting the isolating factors.

The five species can be divided into two size classes which presumably divide food resources in such a manner as to allow a member of each group to coexist within a habitat. The Red-necked Grebe and Western Grebe form the large sized class, while the Horned Grebe, Eared Grebe, and Pied-billed Grebe were the small class. Within each class is one species which is highly aggressive and territorial (Red-necked Grebe and Horned Grebe), each of which prefers relatively small bodies of water with large openings of open water. Also within each size class is one species which is highly colonial and prefers relatively large bodies of water with little emergent vegetation (Eared Grebe and Western Grebe). The Pied-billed Grebe is found on all sizes of ponds as long as there is emergent vegetation. It is territorial, but is the only species which has a distinctive call which is used as a spacing mechanism in its dense habitat.

Further comments are made on how the behavioral systems may affect the overall ranges of each species and how each species may fit into the cycle of marsh vegetation. The many similarities between the North American grebes and those of the palearctic avifauna are also briefly noted.

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Figure 1. A brief summary of a portion of the system of pond classification described by Stewart and Kantrud (1971) and used in this study. Pond classes are separated by the characteristic vegetation of the central (or deepest) part of the basin, provided it occupies 5% or more of the total wetland area.

Class*	Title	Dominant Vegetative Zone	Characteristic Plants
I	Ephemeral pond	wetland-low prairie	*Poa pratensis*, *Solidago altissima*
II	Temporary Pond	wet meadow	*Poa palustris*, *Hordeum jubatum*
III	Seasonal Pond or Lake	shallow marsh	*Carex atherodes*, *Scholochloa feustacea*
IV	Semipermanent Pond or Lake	deep marsh	*Scirpus* sp., *Typha* sp.
V	Permanent Pond or Lake	permanent open-water zone	*Typha* sp., *Scirpus* sp.
VI	Alkali Pond or Lake	intermittent alkali zone	*Ruppia maritima*

*A suffix t can be added to those ponds whose vegetation is judged to have been altered through tillage in the past.

Figure 2. A summary of the pond cover-type classification system designed by Stewart and Kantrud (1971) and used in this study.

Cover Type	Description
1	Open water less than five per cent of wetland area
2	Open water five to ninety-five per cent of wetland area, emergents in scattered patches or spread thinly throughout
3	A central expanse of open water that is greater than five per cent of the area of the wetland, plus a broad band of emergent vegetation around this.
4	Open water greater than ninety-five per cent of the wetland area; on small ponds emergents in a band less than six feet in width along shoreline.

Figure 3. Characteristics of small (<18 acres) ponds selected by the three small grebe species and containing only one species per pond.[1]

	Horned Grebe	Eared Grebe	Pied-billed Grebe
Total number of pairs	27	3	48
Total number of ponds utilized	20	3	44
Average number of pairs per pond	1.35	1.0	1.09
Range of number of pairs per pond	1-6	1	1-2
Range of pond sizes used (acres)	.3-12.9	1.0-7.3	1.5-17.2
Average area of pond per pair (acres)	2.2	3.6	5.4
Frequency of occurrence[2] by pond classification			
Seasonal (Type III) Pond	8	1	26
Semipermanent (Type IV) Pond	9	1	22
Seasonal tilled pond (Type III-T)	10	1	0
Frequency of occurrence[2] by pond cover type			
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 two species was observed, a 1.6 acre pond with both a Horned and Eared grebe pair nesting.

[2]Following the method of Stewart and Kantrud, 1971.

Figure 4. Summary of grebe occurrence on large (>18 acre) ponds and lakes surveyed on the North Dakota study areas.

Pond Size (acres)	Pond description and classification*	Cover Type*	Occurence of Grebes (number of pair) Horned Grebe	Eared Grebe	Pied-billed Grebe
48.5	shallow seasonal pond (III)	4	4	44	1
51.8	alkaline semiper-manent marsh (IV)	3	0	4	3
55.5	shallow seasonal pond (III)	4	0	8	1
59.6	shallow seasonal pond (III)	4	1	34	1
71.3	permanent lake (V)	3	3	2	0
221.7	alkaline permanent lake (VI)	4	0	16	0
318.6	large, very shallow seasonal pond (III)	4	2	110	1

*Following the method of Stewart and Kantrud, 1971.

Figure 5. Brief summaries of the habits, habitats, and ranges of the grebes of the palearctic region taken from Dement'ev (1968) and Bruun (1970).

Species	Length (in.)	Range	Natural Vegetation	Habitat	Mating System	Clutch Size
Podiceps cristatus	18	All but very N. Europe, much of Asia south of 60° N.	Plains and mixed forest north to boreal forest	Lakes with vegetation	Colonial on large lakes, also single pairs	usually 3-4
Podiceps grisegena	17	NE Europe and much of E. Russia	Plains, forests, including boreal forest	Marshy lakes and ponds with vegetation.	Territorial, single nests	usually 4-5
Podiceps auritus	14	Narrow band east from Baltic Sea	Plains and mountains, mixed and boreal forest	small stagnant water bodies	Individual pairs or small colonies	usually 4-5
Podiceps caspicus	12	Much of Asia and Europe S. of 55°N.	Mixed, decid. forest and plains	Various ponds often with much open water	Colonial	usually 4
Podiceps ruficollis	10	All of Europe SW of line from Baltic Sea to Caspian Sea	Varied forests and plains	Small ponds with much vegetation	Nests in pairs and small colonies	4-5 but often 8-10