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RED-NECKED GREBES BECOME SEMICOLONIAL WHEN PRIME NESTING SUBSTRATE IS AVAILABLE

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Abstract. During 1995–1998 we studied the dynamics of nesting dispersion in a population of 160–200 Red-necked Grebes (*Podiceps grisegena*) on Lake Osakis, a large, windblown lake in central Minnesota. Breeding grebe pairs arriving on the lake were highly attracted to several large floating cattail (*Typha angustifolia*) mats that had broken off and drifted away from the mainland to become ''islands'' snagged within rooted emergent beds. These mats provided prime nesting habitat protected from waves and predators that was chosen by nearly 40% of the breeding population. Most pairs establishing nests on the islands averaged 5–10 simultaneously active neighbors within 50 m, compared to pairs that established territories along the shoreline, most of which had no neighbors within 50 m. The overall success of the two strategies varied widely from year to year, depending on the water levels, nesting habitat availability, timing of windstorms, and predator activity. During most years, however, pairs that established nests on the mats hatched earlier in the season and had larger clutches and broods. The dense mats appeared to provide protection from wind and wave action, the primary cause of early nest loss. Our blood analysis work showed no genetic structure of the population and no tendency for neighbors to be closely related. However, pairs often returned to the same area and type of nesting situation in subsequent years. The behavioral flexibility of Red-necked Grebe pairs to nest in groups within prime habitat areas may enable them to breed successfully within unpredictable emergent wetland habitats.

Key words: coloniality, intraspecific variability, nesting dispersion, Podiceps grisegena, *Red-necked Grebe, spacing, territoriality.*

Los Zambullidores *Podiceps grisegena* Nidifican Semi-Colonialmente Cuando hay Disponibilidad de Buen Sustrato de Nidificación

Resumen. Entre 1995 y 1998, estudiamos la dinámica de dispersión de nidos en una población de 160–200 zambullidores *Podiceps grisegena* en Lake Osakis, un lago grande afectado por el viento ubicado en Minnesota central. Las parejas de zambullidores que arribaron al lago fueron muy atraidas a varios parches flotantes de *Typha angustifolia* que se habían separado de la costa convirtiéndose en islas. Estos parches representaron el mejor hábitat de nidificación (protegido de las olas y los depredadores), y fueron escogidos por cerca del 40% de la población reproductiva. La mayoría de las parejas que establecieron sus nidos en las islas tuvieron en promedio 5–10 vecinos activos simultáneamente a menos de 50 m, en comparación con las parejas que ubicaron sus nidos a lo largo de la costa, la mayoría de las cuales no tuvieron ningún vecino a menos de 50 m. El éxito general de las dos estrategias varió año a año, dependiendo de los niveles de agua, la disponibilidad de hábitat de nidificación, el momento de ocurrencia de tormentas de viento y la actividad de los depredadores. Sin embargo, durante la mayoría de los años, las parejas que ubicaron los nidos en los parches flotantes tuvieron nidadas que eclosionaron más temprano, nidadas más grandes y un mayor número de nidadas. Estos parches densos parecieron conferir protección ante la acción del viento y las olas, las causas principales de la pérdida temprana de nidos. Nuestros análisis de muestras de sangre no mostraron estructura genética en la población, ni una tendencia a que los individuos vecinos estuvieran estrechamente relacionados. Sin embargo, las parejas a menudo regresaron a la misma área y la misma situación de anidación en años subsecuentes. La flexibilidad comportamental de las parejas de *P. grisegena* para anidar en grupos en las áreas con mejor hábitat les podría permitir reproducirse exitosamente en hábitats de humedales emergentes e impredecibles.

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INTRODUCTION

Birds nest in a wide variety of spatial patterns, ranging from highly dispersed to tightly packed. The nesting pattern typical of a species depends on many ecological and social factors, including the availability and dispersion of good feeding areas or safe nesting sites and the social costs and benefits of defending space around a nest. Although only 13% of all bird species nest colonially (Lack 1968), much attention has been paid to the many costs and benefits of colonial versus solitary nesting (Alexander 1974, Wittenberger and Hunt 1985, Danchin and Wagner 1997, Rolland et al. 1998). Most field studies have compared single-species colonies of different sizes (Hoogland and Sherman 1976, Brown and Brown 1996, Hill et al. 1997). Less common are studies of a population that nests both solitarily and colonially on a regular basis (Snapp 1976, Andersson and Wiklund 1978, Shields et al. 1988, Sasvári 1993). Intraspecific variation in spacing behavior, its causes, and its influence on other behavior are of great interest in examining coloniality and its possible evolution (Møller 1987, Siegel-Causey and Kharitonov 1990, Foster 1999).

Nesting behavior ranging from solitary to highly colonial is found among the 21 species of grebes (order Podicipediformes). In North America, Western Grebes (*Aechmophorus occidentalis*), Clark's Grebes (*A. clarkii*), and Eared Grebes (*Podiceps nigricollis*) are highly colonial. These species often nest in colonies of hundreds of pairs spaced only a few meters apart (Storer and Nuechterlein 1992, Boe 1993, Cullen et al. 1999). At the other end of the spectrum, Red-necked Grebes (*Podiceps grisegena*), Horned Grebes (*P. auritus*), Least Grebes (*Tachybaptus dominicus*), and Pied-billed Grebes (*Podilymbus podiceps*) typically nest in widely spaced, all-purpose territories, often with only one pair to a pond (Cramp and Simmons 1977, Muller and Storer 1999, Stout and Nuechterlein 1999). A similar range in sociality is found among the grebe species of other continents (Cramp and Simmons 1977, O'Donnel and Fjeldså 1997).

Red-necked Grebes are renowned for being extremely aggressive toward each other as well as toward other waterbirds. Pairs may defend territories of 1 ha or more, attacking intruders from underwater (''submarine attacks,'' Wobus 1964, Garner 1991, Stout and Nuechterlein 1999). Yet in some populations, Red-necked Grebe pairs regularly form semicolonial groups of nests spaced within 10–20 m of each other (Munro 1941, Cramp and Simmons 1977, Stout and Nuechterlein 1999).

In this study, we examined the dynamics of nesting dispersion in a population of Red-necked Grebes on Lake Osakis, a large, windblown lake in central Minnesota. This single population bridged the spectrum from intensely territorial to semicolonial, providing an opportunity to investigate ecological, behavioral, and genetic factors contributing to sociality in this species. We examine the hypothesis that Red-necked Grebe nesting aggregations on the lake are associated with exploitation of temporary, ideal nesting habitats formed by large floating mats of narrowleaf cattail (*Typha angustifolia*) that occasionally break loose from the mainland and become snagged offshore. We compare nest spacing, nest initiation dates, clutch size, egg size, hatching success, brood size, and genetic relatedness for grebes nesting in these floating mats to those nesting in nearby rooted cattails.

METHODS

STUDY AREA AND SPECIES

Lake Osakis covers 2537 ha and is located in central Minnesota (45°53′N, 95°09′W), where winds typically reach 40–50 km per hr several times during a typical 4-week incubation period. The lake is frozen over from November to mid-April, when the ice melts and breaks up. Shortly after ''ice-out,'' when open water appears, 80–100 breeding pairs of Red-necked Grebes return to nest in emergent vegetation, primarily narrowleaf cattail, but also bulrush (*Scirpus acutus*) and phragmites (*Phragmites communis*). Nest sites are usually located where these plants emerge from water that is 0.5–2.0 m deep. Both sexes help build and defend the floating nests, constructed of primarily emergent vegetation debris. Both sexes incubate the eggs, defend, feed, and back-brood the young (Stout and Nuechterlein 1999). After settling on their territories, pairs rarely fly except for brief, low patter-flights of 5–20 m during aggressive interactions. Red-necked Grebes on Lake Osakis feed invertebrates to newly hatched chicks but primarily feed minnows to young that are over two weeks old. Fish of an appropriate size, such as yellow

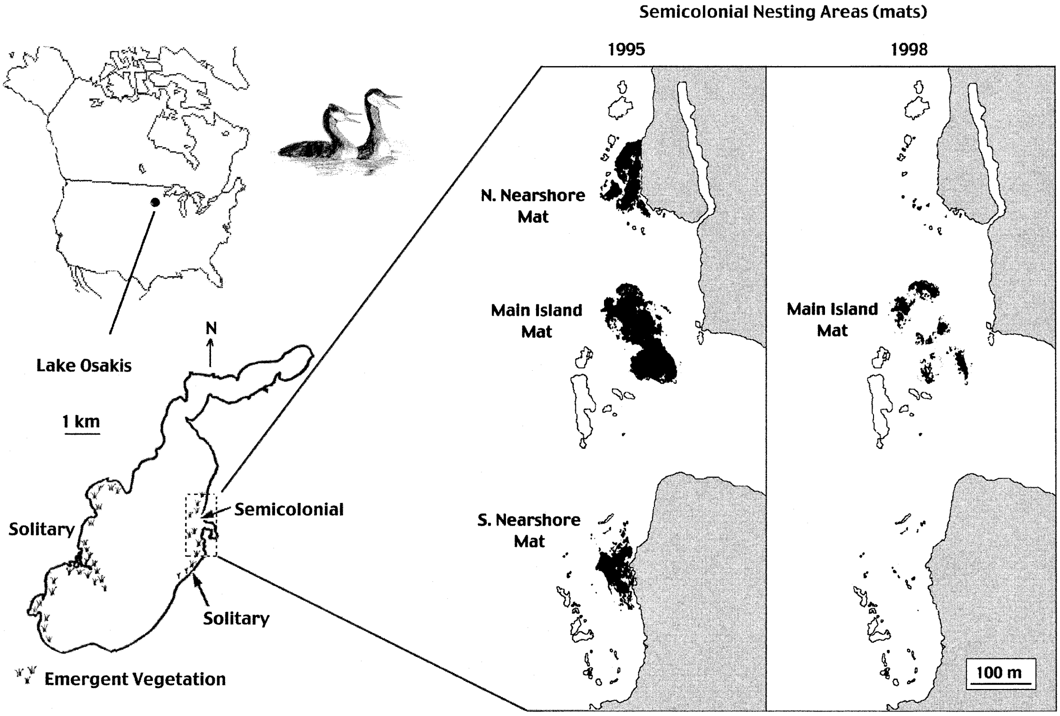

FIGURE 1. The location of solitary and aggregated nesting areas of Red-necked Grebes within Lake Osakis, Minnesota. The detailed maps show the changes in floating cattail mat nesting areas (dark-shaded) between 1995 and 1998. Lighter shading indicates shoreline areas accessible to predators without swimming. Floating mat habitat was highly dynamic compared to rooted cattails and decreased greatly from 1995 to 1998.

perch (*Perca flavescens*) and shiners (*Notropis* spp.), appeared to be abundant and well dispersed on Lake Osakis during the duration of our study (Fraser 1997). Adult grebes spent little time feeding, requiring only 15–30 min to catch several 10–15 cm fish. About 80% of the lake is between 1 and 10 m in depth and easily available to feeding grebes.

FIELD AND LABORATORY TECHNIQUES

From 1995–1998, we searched for and monitored nests along portions of the eastern (2.3 km), and western (3.0 km) shorelines of the lake (Fig. 1). We also monitored nests established within three large floating mats of live cattail that were anchored near the eastern shoreline. The quality and availability of floating mats varied widely among years because the thin, rooted emergent stands in which they were snagged often were sheared off by high winds during spring ice-out, setting them adrift. Further, over several years the well-anchored mats would sink to the bottom and deteriorate. Several lakewide surveys indicated that our nest samples included more than 80% of the breeding population of Red-necked Grebes on the lake.

Between 1995 and 1998 we captured, color banded, and drew blood samples from 87 adults. Using a quick jab with a sterile lancet just above the nail of the rear toe, we collected blood (25–50 μL) with capillary tubes. Another 21 birds had been caught and color banded in 1993–1994. We also obtained DNA samples from blood vessels attached to the shell membranes of 60 hatched eggs and from partly developed embryos of eggs that were abandoned by parents that left the nesting area with early-hatching young. In addition, we drew blood samples from 20 live embryos prior to pipping (Nuechterlein and Buitron 2000). All blood and tissue samples were preserved in microcentrifuge tubes containing 75 mM Tris and 25 mM EDTA in a 1% SDS lysis buffer.

During four breeding seasons (1995–1998), we located nests, marked them with inconspicuous, 2 m × 1 cm diameter rusted iron rods, and monitored them for the duration of the breeding season (mid-April to mid-July). From kayaks we checked and labeled any new eggs every 2–5 days, a compromise between obtaining sufficient nesting information and minimizing disturbance. We were especially careful to avoid disturbing nests with hatching eggs, as this could cause abandonment of those eggs that had not yet hatched. Most birds returned to their nests within 10 min of our leaving. Laying order was determined by egg color (Stout and Nuechterlein 1999). We estimated egg development by flotation, as adapted for grebes by Nuechterlein (1975) and Goc (1986). In 1995, we used calipers to measure the length and width of the first three eggs of clutches. Some nest parasitism occurs in grebes, so any new eggs that appeared in a nest after 3 days with no laying were not considered part of the original clutch. Clutches in which more than one new egg appeared within a 24-hr period also were not included in clutch size analyses. Incubation began with the first egg, and hatching occurred over 1–7 days.

Nest failure could usually be attributed to one of three causes: (a) wave destruction (nest sunken or absent usually after severe windstorms, with eggs sometimes located nearby on the lake bottom); (b) predation (nest intact with large pieces of eggshells and attached membranes, or no sign of eggs in an intact nest that had been active 1–2 days earlier); or (c) parental abandonment (nest intact with cold eggs).

At the end of the breeding season, we marked all nest sites with a white plastic bag or milk jug. We then took aerial photos and used these to develop a map. After locating and labeling each nest on the photos, we scanned and aligned them with shoreline features using higher-altitude National Aerial Photography Program photos taken in 1996 (U.S. Geological Survey, EROS data center, Sioux Falls, South Dakota). The Minnesota Department of Natural Resources provided water level data for Lake Osakis.

We devised an artificial nest experiment to obtain information on predator activity at various distances from the shoreline. After cutting pieces of floating cattail mat into artificial islets of three size categories (1 m^2, 4 m^2, and 12 m^2), we placed them in pairs along five stretches of emergent habitat located on the east shore of Lake Osakis. One islet of each pair was attached to the shoreline; the other was anchored at 10, 20, 30, or 40 m from the shore. On each islet, we created an artificial, uncovered nest containing two small chicken eggs and one egg made of soft, nondrying white modeling clay (Sculpey®, Polyform Products Co., Elk Grove Village, Illinois). Between 8 June and 22 June 1998 we randomly set up a total of 15 pairs of islets, with sets placed at least 500 m apart and no more than three islet pairs set simultaneously. We randomly drew which two sizes of islands to use for a pair, which size to place adjacent to the shore, and at which distance to anchor the offshore island. Each islet size was used 10 times, and each distance from shore was used 3–5 times. We checked nests at dawn and dusk for 5 days or until the eggs were depredated. After the experiment was completed, we also set up several dummy nests equipped with a 35-mm camera and automatic trigger to obtain photo documentation of the primary local predators.

We extracted DNA from blood and tissue samples using a proteinase K, phenol-chloroform extraction procedure modified from Mullenbach et al. (1989), or the Chelex (BioRad) procedure. Samples were genotyped at seven polymorphic microsatellite loci described in Sachs and Hughes (1999). DNA amplifications included ^{35}S; resulting products were run out on sequencing gels, dried, and exposed to film. Alleles were assigned sizes according to an M13 sequencing reaction run as a size standard. We calculated genetic relatedness using the method of Queller and Goodnight (1989).

Using the microsatellite genetic data, we tested the hypothesis that kin selection plays a role in allowing colony formation. If aggregated pairs were more tolerant of close relatives than of unrelated individuals, we would expect to find a significant association between genetic distance and spatial distance within the population.

STATISTICAL ANALYSES

To analyze the spatiotemporal patterns of nesting, we developed a time-lapse computer simulation program (using 1 day = 1 sec, 1 km = 1 m) that showed nest initiation and colony formation patterns for each of the four years of the study. In this Supercard™ (Allegiant Technologies, Inc. 1996) program, the following variables were associated with each nest site: distance from shore, *x* and *y* coordinates on a grid, begin date, end date, clutch size, fate, sex, and bird identity (when known).

We used this program to calculate an aggregation index for each nesting attempt, which we defined as the average number of other simultaneously active nests established within a 50-m radius of a nest. By using the average number of close neighbors over the days that the target nest persisted, we avoided a bias associated with using total neighbor numbers for nests of unequal survival duration (2–32 days). Computer simulations revealing this bias demonstrated that short-lived (unsuccessful) nests had correspondingly fewer total close neighbors than longer-lived nests when nests of varied duration were randomly placed on a grid.

We chose 50 m for the aggregation index because it was about twice the mean nearest-neighbor distance of 25.2 m between nests calculated for all pairs. Territorial Red-necked Grebes at other locations also typically establish nests at least 50–70 m apart from each other (Cramp and Simmons 1977, Stout and Nuechterlein 1999). A nest was considered active from three days before egg laying (when nest building and defense of the area began) to three days after hatching or failure (when most pairs usually remained nearby). The aggregation index was used to classify the nest as solitary (0 neighbors within 50 m), intermediate (0.1–1.9 neighbors), or semicolonial (2.0 or more neighbors). These categories subdivided the nesting attempts into three relatively equal-sized samples. For comparisons that focused on nest densities when birds were choosing nest sites, we used aggregation averages for only the first four days (until the first egg was laid).

As in most nesting studies, we considered individual nests as independent samples for the purpose of statistical analyses. For marked pairs, we also calculated breeding success for the season based on number of chicks hatched. Banding data from these marked pairs showed almost no movement of birds from nesting habitats on one side of the lake to the other. The large floating cattail mats were available only to birds nesting on the eastern side of Lake Osakis. We therefore only used nests located on the same side of the lake to compare the characteristics of mat nests to rooted emergent nests.

To examine any clustering of related individuals, we used the Mantel test (Mantel 1967, Sokal 1979), which estimates the association between independent matrices describing the same set of individuals (Sokal and Rohlf 1995). In this case, the matrices compared were pairwise genetic distances of individuals generated from microsatellite genotypes and pairwise spatial distance measured from aerial photographs. Using the program Kinship 1.2 (Queller and Goodnight 1989), we generated the matrix of pairwise relatedness values for all genotyped pairs in the population. The Mantel statistic Z was calculated as a product of the two matrices (Sokal and Rohlf 1995). We used two different sets of matrices for each year of the study. One pair of matrices for each year included all individuals for which we had both genotypic and spatial data, while the other randomly pruned one individual from mated pairs to remove the potential bias of outbreeding. Using microsatellite data, we performed permutation tests with 1000 random iterations.

Although most nests were found during the early laying period, we also used the Mayfield correction (Mayfield 1975), as modified by Johnson (1979) and illustrated by Klett et al. (1986) to correct for nesting success biases associated with discovering nests at different stages. A two-factor ANOVA (with mat and year as fixed factors) was used for the comparisons of mat and rooted emergent nests. We used chi-square tests for categorical data and Mann-Whitney U-tests for data that were not normally distributed. SPSS 11.5 (SPSS Inc. 2001) and Minitab Release 13 (Minitab Inc. 2000) statistical software packages were used for statistical analyses. Unless otherwise noted, values are reported as means ± SE, and statistical significance is recognized at $P < 0.05$.

RESULTS

For each of the four field seasons of the study, we documented the fate of between 119 and 148 nesting attempts. Of the 544 attempts that we followed, 132 attempts (24%) hatched at least one young. We attributed the nest losses to wind and wave action (38%), predation (17%), parental abandonment (15%), and other unknown reasons (6%). Of all documented nest attempts, 32% were by pairs with at least one member color banded. When marked pairs failed, they renested from zero to four times. Of 91 marked pairs that failed in their first attempt, 70% began a second clutch, and of the 32 that failed a second time 71% tried again. The number of pairs attempting a fourth clutch was much lower (39% of 23 pairs), and only four pairs tried a fifth time (three of these hatched young). The percentage of marked pairs that eventually hatched at least one young was 39% of 39 in 1995, 66% of 43 in 1996, 49% of 41 in 1997 and 55% of 39 in 1998.

SPATIOTEMPORAL DYNAMICS IN AVAILABILITY OF MATS AND ROOTED BEDS

During both 1995 and 1996, many Red-necked Grebes nesting on the eastern side of the lake used three large, floating cattail mats (Fig. 1). Two of these mats (the North and South Nearshore Mats) drifted away prior to the 1997 season. The third mat (Main Island Mat) persisted over the entire 4-year period, but slowly broke up into smaller pieces as it sank and disintegrated.

Changes in lake water-levels also often meant critical changes in suitability of the rooted emergent beds for nesting grebes. During both 1995 and 1996, water levels on Lake Osakis slowly declined by 0.5–0.6 m over the course of the breeding season. The 1997 season showed an even steeper decline of 1.5 m, while water levels during the 1998 season began and remained at the lowest levels of the 1997 season. These fluctuations had important impacts on nest-site selection by grebes. For example, a peninsula edged with dense cattail on the western side of the lake (Two-mile Bar) was an active and successful nesting area during 1995–1997, with 15–18 nests a year. By late summer in 1997, the water levels were so low that the dense emergent beds were in very shallow water (less than 0.5 m). During the continued low water levels of 1998, only 5 nests were located in this area and none hatched young.

VARIABILITY IN NEST AGGREGATION BY YEAR AND LOCATION

The distance between a nest and its closest, concurrently active neighbor varied from over 450 m to less than 1 m. Over 86% of the nests had an active neighbor within 100 m (Fig. 2). The aggregation index (average number of neighbors within 50 m) varied from 0 to 12 (Fig. 2). As the floating mats deteriorated, nests with five or more near neighbors also became less frequent, from about 19% in 1995 and 1996 to only 6% by 1998 (Fig. 3).

Areas of concentrated nesting were site-specific. Certain areas, such as the Main Island Mat Area (Fig. 1), regularly had high densities of nests, year after year. In these areas, grebes vigorously defended their nests during incubation, but often fed and loafed on the open lake, far away from the defended areas. In other areas, such as the Creek South Shoreline on the eastern side and Two-mile Bar Shoreline on the western side, grebes consistently established solitary nests more typical of Red-necked Grebes (Fig. 1).

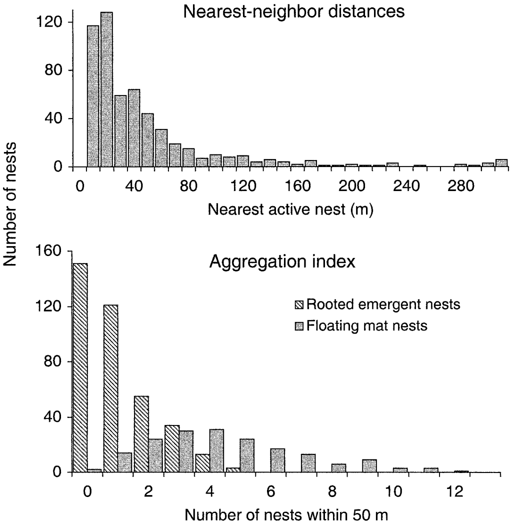

FIGURE 2. Mean distance to the nearest active neighbor for Red-necked Grebe nests on Lake Osakis, Minnesota, calculated at nest initiation (1995–1998, *n* = 554 nests, upper graph). A mean aggregation index was calculated as the daily mean number of actively nesting neighbors within 50 m, over a nest's entire active period (1995–1998, *n* = 554, lower graph). Most aggregated nests were located on floating cattail mats (solid bars).

SEASONAL VARIATION IN AGGREGATION AND NEST FATES

Peak aggregation indices occurred for nests initiated in late May (Fig. 4). In all years but 1997, nesting success peaked during midseason (Fig. 5). In every year of the study, wave action caused by sporadic windstorms was responsible for the most failed nests. Losses to wave action tended to be greatest early in the season before most new emergent growth was above water level and able to act as a breakwater (Fig. 6). In 1998, when there was an unusually early ice-out and initiation of nesting, wave action was a very important cause of early failure.

Mayfield analyses showed a large yearly variation in the survival probabilities of aggregated

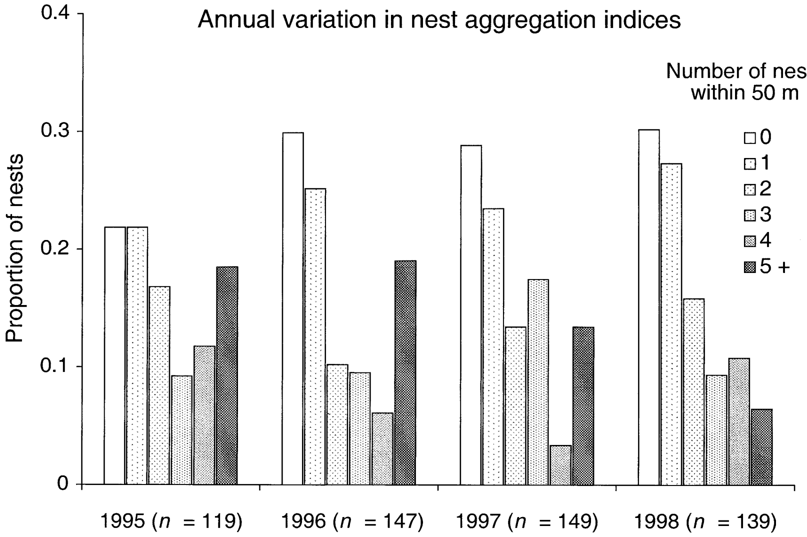

FIGURE 3. Nest aggregation indices for Red-necked Grebes at Lake Osakis, Minnesota, varied widely from year to year. As the availability of floating mats decreased from 1995 to 1998, highly aggregated nests became increasingly rare.

and solitary nests. In 1995, solitary nests (no neighbors within 50 m) were more likely to survive the incubation period of 28 (range 25–30) days than were nests of either the intermediate or most aggregated categories, as indicated by their non-overlapping 95% confidence intervals (Fig. 7). However, the reverse was true in 1998: nests with two or more neighbors were more likely to survive than nests with no neighbors. Seasonal success rates of marked pairs also varied widely between years (Fig. 8).

COMPARISONS BETWEEN NESTS IN MATS AND NESTS IN ROOTED EMERGENTS

Nest initiation. During all four breeding seasons, the most closely spaced nests were on the large floating cattail mats located along the eastern shore. The size, shape, and location of floating

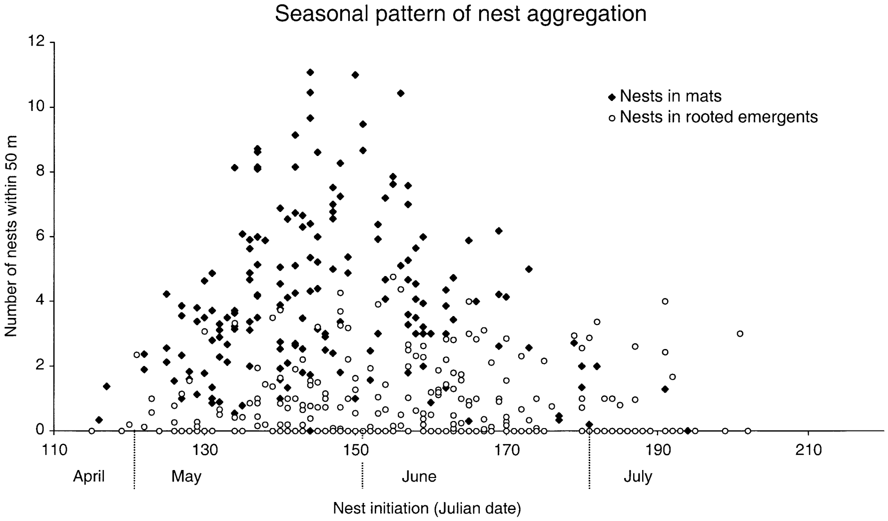

FIGURE 4. Aggregation of Red-necked Grebe nests peaked in late May at Lake Osakis, Minnesota. Each data point represents the mean number of neighbors within 50 m over the active period of a nest.

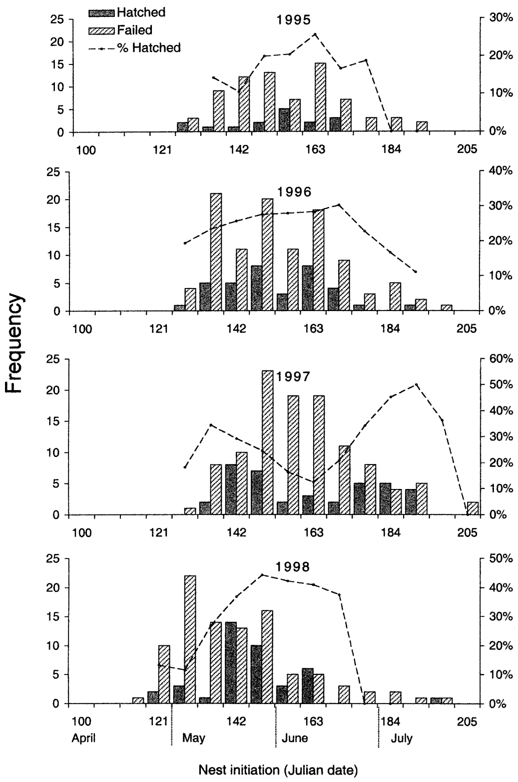

FIGURE 5. Seasonal variation in nesting success of Red-necked Grebes at Lake Osakis, 1995–1998. The dashed line provides a 3-week running average of percent nesting success, as read on the right ordinate axis. Except in 1997, nesting success peaked during midseason.

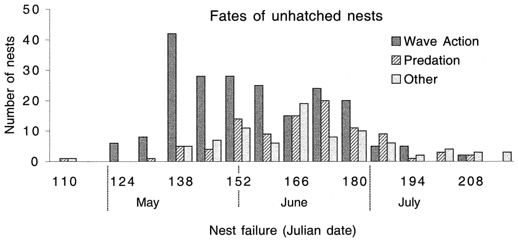

FIGURE 6. There was predictable seasonal variation in the causes of nest failure for Red-necked Grebes at Lake Osakis, 1995–1998. Wave action caused by wind was most important early in the season, before the new emergent vegetation reached the surface to act as a breakwater.

mats were relatively stable within a year, but varied between years as wind action during ice breakup sheared or moved them. Their distance to the mainland also varied widely. Nests on the Main Island Mats averaged 152 ± 40 m (SD; $n = 211$) from shore while those on the North and South Nearshore Mats averaged only 51 ± 7 m ($n = 62$) and 83 ± 53 m ($n = 53$). Nests in rooted cattails along the eastern shore varied greatly in distance to the mainland as well, from an average of 64 ± 52 m for the Creek South Shoreline nests (SD; $n = 75$) to an average of 167 ± 34 m for the First Bay Islets ($n = 34$).

Floating mats left intact by ice-out created attractive early nesting habitat since their new growth appeared before that of the rooted emergent beds, presumably because their root mass was closer to the warmer water surface. Initiation of mat nests averaged 8 days earlier than that of rooted emergent nests, a significant difference (Table 1). Mats were especially important to early nesters if most rooted emergent beds were sheared off during ice-out, as in 1997.

Nest aggregation. Nests in mats also were more aggregated than rooted emergent nests located in the same general area (Fig. 9). This relationship was significant for all three mat areas (Main Island Area: $F_{1,210} = 105.5$, $P < 0.001$; South Nearshore Area: $F_{1,71} = 133.2$, $P < 0.001$; North Nearshore Area: $F_{1,44} = 38.7$, $P < 0.001$). The highest nest densities occurred at the Main Island Mat Area during 1997. Early pairs vigorously defended the mat areas, and overt fights with bill-to-bill contact sometimes lasted several minutes (see illustrations in Stout and Nuechterlein 1999). However, as the continual pressure from other pairs increased, defended areas in mats rapidly shrank in size and nests were established closer together (Fig. 4). For example, during the first week of nest initiation the mean nest aggregation index in the Main Island Mat

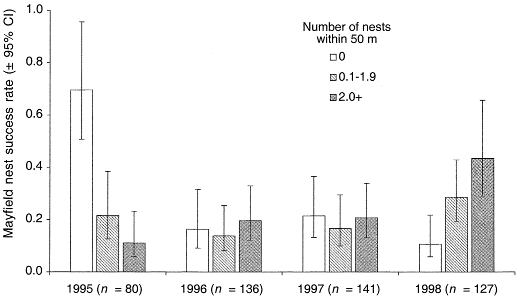

FIGURE 7. Neither solitary nor aggregated nests were consistently more likely to survive the average incubation period of 28 days, as calculated using the Mayfield correction (mean ± 95% CI).

TABLE 1. Mean ± SE characteristics of Red-necked Grebe nests initiated in floating emergent cattail mats versus rooted emergent vegetation at Lake Osakis, Minnesota. Nests in mats were initiated earlier and had larger clutches than nests in rooted emergents. Young also hatched earlier in mats, and brood sizes were larger. Analyses excluded renests within a season.

	n	Floating cattail mats	Rooted emergent vegetation	*F*	*P*
Initiation date (Julian)	248	140 ± 1.4	148 ± 1.4	17.8	<0.001
Clutch size	73	4.7 ± 0.2	3.9 ± 0.2	6.9	0.01
Hatch date (Julian)	93	172 ± 1.9	194 ± 1.6	70.6	<0.001
Brood size	50	3.0 ± 0.2	2.1 ± 0.2	6.8	0.01

Area increased from zero to more than five neighbors within 50 m. Meanwhile, nest densities remained low (0–1 neighbors) for pairs defending more typical territories in the Creek South Shoreline area over the same period.

Clutch and egg size. Clutch sizes tended to decrease over the summer. Before 1 June, 63% of 132 nests had clutch sizes of 4 or greater, while only 19% of the 53 nests initiated in June and July had clutches of 4 or more. Mean clutch sizes of nests initiated in mats were significantly greater than those of rooted emergent nests (Table 1). Egg widths and lengths, however, showed no significant differences between mat and rooted emergent nests (median egg lengths for rooted and mat nests = 530.5 and 542.0 mm, U = 378, n_1 and n_2 = 36 and 15, P = 0.82; median egg widths for rooted emergent and mat nests = 356.8 and 360.7 mm, U = 438, n_1 and n_2 = 36 and 15, P = 0.33).

Hatch date, brood size, and hatching success. On average, young of mat-nesting pairs hatched 22 days earlier than young of pairs nesting in rooted emergents, a difference that was significant (Table 1). In all years, pairs nesting in mats were the first to hatch chicks. In 1995, 1996, and 1997 the first 4–6 pairs to hatch young came from mat nests. Mat-nesting pairs also produced broods that were significantly larger (Table 1).

The percentage of first nests hatching, however, was not significantly greater in mats than in rooted vegetation during any of the four seasons (1995: mat = 19.4, n = 31, rooted = 15.4, n = 13; 1996: mat = 26.1, n = 46, rooted = 22.6, n = 31; 1997: mat = 23.1, n = 26, rooted = 16.3, n = 43; 1998: mat = 18.8, n = 16, rooted = 20.0, n = 35, all $\chi^2_1 \leq 0.5$, all $P \geq 0.48$).

Intraspecific brood parasitism. Although brood parasitism rates were not a focus of this study, our observations and DNA work suggest that they were low for nests in both mats and rooted vegetation. Only one of 20 eggs from eight clutches that were salvaged from females of known genotypes could not be attributed to the appropriate female. We detected no increase in parasitism by birds nesting close together, but our sample sizes were small and not subjected to statistical analysis. We also have a sample of 11 eggs collected from nine clutches of genotyped females that we suspected were being parasitized, either because the clutch was unusually large or because more than one egg was laid in a 24-hr period. For these clutches, only 1 of 6 first or second-laid eggs was parasitic compared to 5 of 5 fourth-laid (or later) eggs. Although sample sizes again are small, these results suggest that the later eggs of a clutch are more likely to be parasitic.

SITE FIDELITY AND RELATEDNESS OF NEIGHBORS

Marked birds regularly nested close to the site of their previous year's attempts: 42–46% of

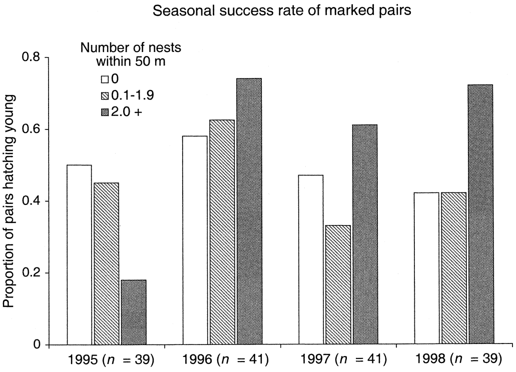

FIGURE 8. Proportion of marked solitary and aggregated pairs hatching young on Lake Osakis from 1995–1998, including all renesting attempts for the season.

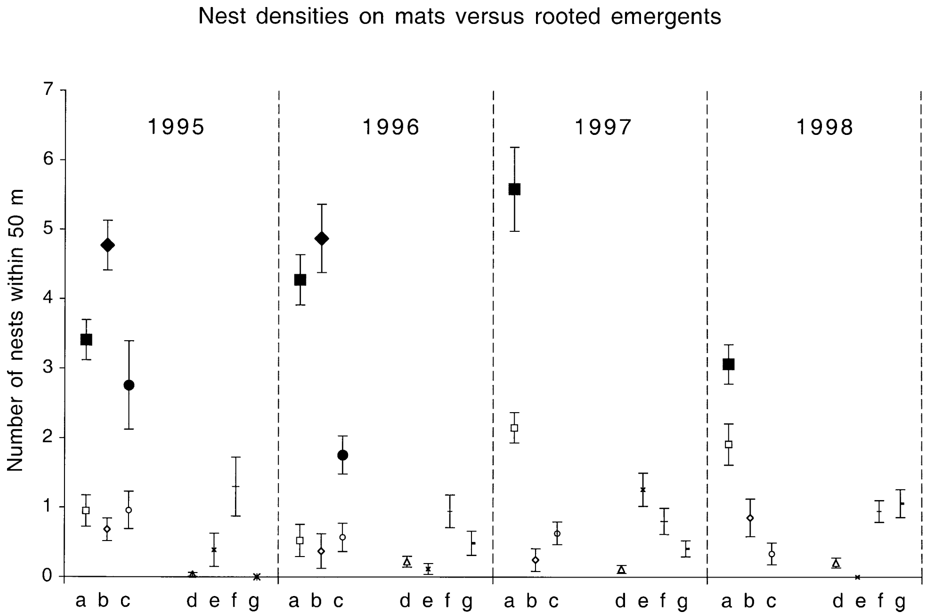

FIGURE 9. Mean aggregation indices (± SE) for nests established in mats (filled symbols) versus in rooted emergent vegetation (unfilled symbols) (for 1995–1998, n = 119, 147, 149, and 139 nests, respectively). Letters on the x-axis represent the following different areas of Lake Osakis: (a) Main Island Area, (b) South Nearshore Area, (c) North Nearshore Area, (d) Creek South Shoreline, (e) Two-mile Bar Shoreline, (f) Rooted Emergent Island, and (g) Public Access Shoreline.

first nests were within 50 m of the previous year's first nest; 83–87% were within 150 m (n = 68). Close neighbors during one year therefore often were close neighbors the next year. Analyzing the microsatellite data using Kinship 1.2, we found no significant association between spatial distance and genetic distance in any of the eight matrix sets ($r < 0.1$, $P > 0.05$).

NEST LOCATION AND RISK OF PREDATION

Our experimental artificial nests confirmed that predators regularly checked the shoreline emergent vegetation. During their five days of exposure, 13 of the 15 nests on islets directly adjacent to the shore were depredated, while none of the 15 nests on islands 10–40 m offshore were disturbed ($\chi^2_1 = 19.5$, $P < 0.001$). Twelve of the 13 depredated nests were found within 48 hr and the thirteenth within 70 hr. Predation was mostly nocturnal (7 of 9 nests for which the timing was known). In most cases the clay eggs had been bitten or chewed into small pieces. Mammalian tooth impressions resembling those of raccoons (*Procyon lotor*) were visible on several clay eggs, and we subsequently obtained several photographs of raccoons preying upon the artificial nests.

DISCUSSION

Several important environmental factors influenced nesting habitat on Lake Osakis. These included (1) predator activity, (2) changes in lake water-levels, (3) the amount of shearing of offshore rooted emergent vegetation during spring ice-out, and (4) the drifting and disintegration of dense floating cattail mats. These four factors had major impacts on the spatial distribution of nests both within and among years. Pairs had anywhere from 0 to 12 simultaneously active neighbors within a 50-m radius, depending on their choice of nest timing and location. The degree of nest aggregation varied greatly from one part of the lake to another, over the breeding season, and from one year to the next. Certain areas of the lake, however, were predictably more likely to have aggregations of nesting grebes than others, and individuals that nested in these aggregations one year were very likely to do so again the next year.

To anchor their floating nests and hatch young, Red-necked Grebes preferred sheltered emergent vegetation in water at least 0.5 m deep. Nests that were located farther from the mainland or over deeper water presumably were safer from terrestrial predators such as raccoons. The experimental nest platforms showed that even 10 m of open water can greatly reduce access to nests by mammalian predators, as was found also for shorebird nests by Frederick and Collopy (1989). Nests farther from shore may still be vulnerable to more aquatic mammals, such as mink (*Mustela vison*), and to aerial predators, such as herons, owls, gulls and corvids. All five adults that died while incubating during our study were decapitated, indicating that mink or Great Horned Owls (*Bubo virginianus*) were their likely predators. Corvids and gulls were almost never seen in the area. Great Blue Herons (*Ardea herodias*), however, commonly fed along the shoreline and around the islands, and in at least two cases were seen destroying and removing the eggs of a clutch. Grebes reacted to the herons with a loud, hissing threat whenever they came close to their nest. This tactic generally was effective against herons, which did not appear to seek out grebe nests.

Nests far from shore may be safer from raccoons, but stem densities of emergents generally decrease with water depth (Goc 1986), and so these nests are more vulnerable to destruction by wind and wave action (Nuechterlein 1975). Wave action causes major nest losses within most grebe species (Cramp and Simmons 1977), especially those nesting on larger lakes (Vlug 1983, Van der Poel 2000). In our study, over 40% of all Red-necked Grebe nest losses were wind related. The impact of wave action varied among nesting areas and years, presumably in relation to the amount and density of the previous year's vegetation that remained to serve as a breakwater. Initiating nests early, and repeatedly replacing destroyed nests, appear to be common tactics among many species of grebes.

Risks from waves (which do not threaten the lives of incubating adults) and predators (which do) therefore appear to play against one another when grebes are choosing nest sites, and actual nest locations may represent a compromise between these factors. When large floating cattail mats snag offshore in deep water, they may provide prime nesting habitat that is otherwise not available on the lake until much later in the spring, when new sprouts from the rooted cattail reach the water surface. A natural experiment within the South Nearshore Mat area impressed upon us the importance of these floating mats to aggregated nesting. In 1995, there were 12 nests in this area, a number that increased to 23 nests in 1996. However just prior to the nesting season in 1997, strong southeasterly winds caused the South Nearshore Mat to drift away. The remaining rooted vegetation was sparse, and was used by only four pairs in 1997 and two pairs in 1998.

Partially sunken mats provide preferred nesting sites until they break up. In 1995, when this study began, the Main Island Area consisted of a solid 200 × 80 m dense mat of floating cattail that was nearly impenetrable and sank beneath us when we checked nests. Grebe nest densities in this area were highest in 1997 (5.8 neighbors within 50 m), at which time the mat had broken into four smaller, partly sunken islands. Little of the original Main Island Mat remained by early 2001, when aggregated nesting within the area largely ceased.

Color banded birds often re-paired and showed high rates of returning to nesting areas used in previous years, with some individuals nesting within a 100-m radius for all four years of the study. However, the dynamics of cattail beds in marshes and lakes are such that grebes are faced with an ever-changing array of potential nest sites. Wave-sheltered locations continually change between and within years, and occur at different depths and distances from the mainland. Therefore, a location that was ideal one year may not be suitable the next. In addition to vegetation changes, the behavior, density, and type of predators of an area may change, altering the vulnerability of a site to predators.

The dramatic increase in aggregation indices for Red-necked Grebes nesting on cattail mats on Lake Osakis appears to be largely the result of social pressure. Attack distances by birds that claimed this prime, early nesting habitat diminished rapidly as more and more neighbors established nests. Successful rearing of young under such crowded conditions probably requires abundant fish resources outside of the territory as a prerequisite. Red-necked Grebes carry and brood newly hatched young on their backs, and pairs with young in the aggregated nesting areas immediately left their small nesting territories to exploit the rich food resources along shorelines throughout the lake. Although Red-necked Grebes on most lakes defend exclusive territories in which both feeding and chick rearing occur, instances of loose colonies have been described as far back as 1902 (Bent 1919).

Aggregated nesting also has been reported in other grebe species that are typically aggressive and widely spaced, including Horned Grebes (Clase et al. 1960, Fjeldså 1973, Fournier and Hines 1999), Great Crested Grebes (*Podiceps cristatus*; Venables and Lack 1934, 1936, Simmons 1970, Cramp and Simmons 1977, Vlug 1983, Goc 1986, Moskal and Marszalek 1986, Bukacinska et al. 1993, Van der Poel 2000), Little Grebes (*Tachybaptus ruficollis*; Cramp and Simmons 1977) and White-tufted Grebes (*Rollandia rolland*; Burger 1974). As in the case of Lake Osakis, these aggregations often are located on large lakes where food for young may be plentiful. The ability of grebes to carry their young on their back allows aggregated-nesting pairs to abandon their small territories and exploit food-rich areas that lack suitable nest sites.

Limited availability of safe nesting sites has long been suggested as one of the factors that promote aggregations of breeding waterbirds (Lack 1968). A shortage of safe nest sites has been used to explain the occasional loose colonies in several otherwise territorial grebes (Simmons 1974, Cramp and Simmons 1977, O'Donnel and Fjeldså 1997). However, colonies of up to 500 pairs of Great Crested Grebes, some with nests only 1 m apart, also have been described on large lakes in continental Europe, even when habitat did not appear to be limiting (Vlug 1983, Bukacinska et al. 1993, Van der Poel 2000). As in our study, Bukacinska et al. (1993) found that colonial pairs nested earlier and had larger clutches than solitary pairs. In contrast, Van der Poel (2000) found that the colonial pairs began breeding later (apparently waiting for growth of suitable emergents) and had lower breeding success.

Changes from territorial to colonial breeding have been documented in other bird groups, and have been correlated with limited availability of safe nesting sites, sudden changes in type or number of predators, or changes in food abundance (Lott 1991). Mallards (*Anas platyrhynchos*) and Gadwalls (*A. strepera*) that normally nest in well hidden and spaced nests sometimes nest on predator-safe islands at very high densities, with average nearest-neighbor distances of 2 m (Lokemoen et al. 1984). In Mute Swans (*Cygnus olor*) a particular allele has been found to be associated with coloniality (Bacon and Andersen-Harild 1989).

Timing of breeding is a second, very flexible aspect of grebe reproduction on Lake Osakis. Initiation of new nests or renests spanned the entire period from ice-out to early August. Pairs nesting in mats initiated their nests earlier, which was associated with a larger clutch and brood size, as in many other species. Early grebe nests often are initiated before there is sufficient vegetation to protect the nests from high waves during storms. These nests appear to be a low-cost gamble that unusually calm weather might allow the clutches to hatch early despite a lack of nesting cover, and early pairs were able to quickly and repeatedly replace clutches (up to four times). We suggest that the ease of obtaining fish on Lake Osakis increases the advantages of nesting early in the floating mats, even when other pairs are already settled there. For pairs that first claim mat areas, large feeding territories may not be economically defensible (Brown 1964) because intruder pressure from neighboring pairs increases rapidly. This ability of Red-necked Grebes to adjust the distance at which they tolerate a neighbor is of great interest, and behavioral differences in territorial and aggregated pairs have been reported separately (Klatt 2002).

Kinship theory predicts that as the relatedness between group members and potential ''joiners'' increases, the resistance to allowing these individuals into the group should decrease. This will be true as long as any loss of individual fitness is compensated for by a gain in inclusive fitness (Rodman 1981, Higashi and Yamamura 1993, Rannala and Brown 1994). However, our comparisons of subpopulations nesting in different parts of the lake failed to show any genetic substructure in the population. It therefore appears as though subgroups on Lake Osakis are a freely interbreeding population. Although in almost no case were we able to obtain blood samples for all four members of two neighboring pairs, the pairwise relatedness data did not reveal any tendency for birds to nest near relatives. Taken together, these genetic data provide no support for the hypothesis that grebes breeding in loose colonies were closer relatives than were those defending large territories. Possibly, the transient nature of the emergent mats keeps the colonies in such flux that genetic differentiation is unlikely. Familiarity may also facilitate aggregated nesting (McNicholl 1975), and we documented at least 26 cases where marked birds remained close neighbors for two or more years.

We conclude that grebe pairs may nest semicolonially, not because there is a shortage of suitable habitat, but because they are attracted to the same prime nesting habitat. On Lake Osakis, this prime habitat consisted of floating cattail mats that became temporarily anchored over deep water, where adults and their nests were safe from mammalian predators and waves. Behavioral flexibility in nesting strategies may allow a variety of species to nest successfully within habitats that are becoming increasingly fragmented and altered by human activity.

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