DETERMINANTS OF COLONY AND NEST-SITE SELECTION IN THE SILVER GREBE (*PODICEPS OCCIPITALES*) AND ROLLAND'S GREBE (*ROLLANDIA ROLLAND*)

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The Silver Grebe and the Rolland's Grebe are common species in Argentina (Olrog 1959) that nest colonially in reed beds. Rolland's Grebe is less colonial (Johnson 1965) and less gregarious (Storer 1967) than the Silver Grebe. Storer (1963, 1967) has described in detail the display behavior of Rolland's Grebe but no studies of either species have dealt with colony and nest-site selection. No detailed study of habitat preference of the grebes has been made although authors have noted that certain species prefer nesting either near open water (Glover 1953; Yocom et al. 1958; Johnson 1965), near channels leading to open water (Munro 1941), or in areas providing high visibility (Chabreck 1963; Weller and Spatcher 1965).

In this study the nesting behavior of the Silver Grebe and Rolland's Grebe was examined from October 1972 through January 1973 in Argentina. Emphasis was placed on environmental factors involved in colony and nest-site selection.

STUDY AREA

Field work was conducted in the marshes on the San Jose Estancia, Murphy, Province of Sante Fe, Argentina. The pampas in this area contain shallow, alkaline lakes with extensive areas of tules (*Scirpus californicus*) and scattered areas of cattails (*Typha* sp.). The marshes studied were extensive and had large areas of open water with a maximum depth of 1.5 m. Water level increases of up to 10 mm were recorded in a 24-hr period. As the summer progressed, water levels dropped due to evaporation.

METHODS

The marshes were thoroughly searched twice a week from 14 October 1972 through 20 January 1973 to locate grebe colonies. Searching was done from horseback, which facilitated nest location, reduced the time necessary to cover the marshes adequately, and lessened the disturbance to nesting birds.

Daily observations were made on the grebe colonies located. Data collected on nests included: species present, sequence of egg laying, size of eggs, width of nest at completion of clutch, distance to closest nest, distance to open water, species of the nearest neighbor, and plant cover characteristics. Random samples were taken by dividing the area in question into equal plots, assigning numbers to those plots, and subsequently selecting plots from a table of random numbers. Methods of analysis of vegetation density will be discussed in a later section.

More extensive observations were made from a stationary blind situated in a Rolland's Grebe colony, and from a movable boat blind in a Silver Grebe colony.

RESULTS

COLONY-SITE SELECTION AND DEVELOPMENT

The grebe's preference for a particular type of habitat was determined by comparing the habitat in grebe colonies to nongrebe colony areas. Nine grebe colonies were initiated between 23 October and 16 November. Four of these were Silver Grebe colonies, two were Rolland's Grebe colonies, and three were mixed colonies. All grebe colonies were adjacent to open water areas. Both species appeared to use the same general habitat.

Visual observation of the available habitat revealed a wide range of tule densities from very dense to very sparse. Low density tule areas contained a small number of dense clumps of tules and/or scattered individual tules. The grebes appeared to select areas of low tule density with small patches of dense tules as colony sites. In order to test this hypothesis, tule density in grebe colony areas was compared to tule density in nongrebe colony areas.

In each of eight grebe colonies, all tule stems were counted in 15 randomly chosen, 80 mm^2 plots. The mean, standard error, and range of tule densities are shown for each colony in figure 1. Fifteen randomly chosen noncolony areas (10 m^2) were sampled in a similar manner. The available habitat ranged from high tule density to low tule density areas. Grebe colonies, however, tended to be in low density areas, with a few clumps of very dense tules. No differences were noted between the species.

Six of the grebe colonies were located sufficiently early to allow an analysis of initiation of egg laying (fig. 2). A higher degree

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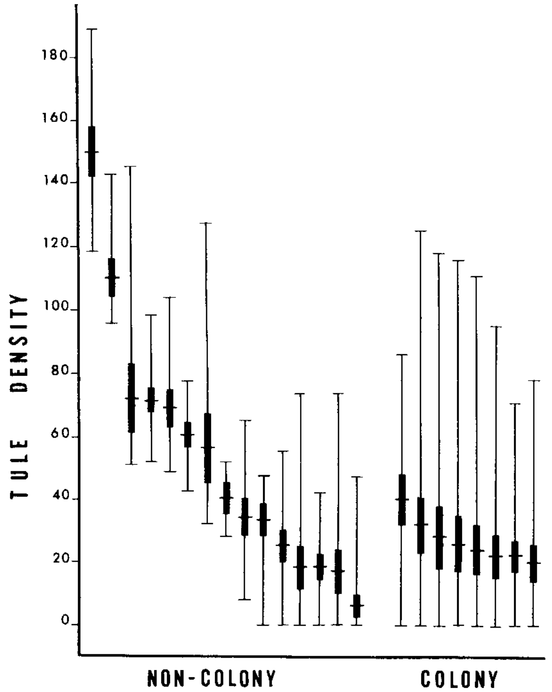

FIGURE 1. Mean tule density in sample plots in noncolony areas compared to mean tule density in grebe colony areas. The mean, standard error, and range are given for the 15 plots sampled in each area.

of synchrony in egg laying was noted within colonies than between colonies. Goodall et al. (1951) reported that nests of the Silver Grebe tended to be constructed at the same time. Synchrony of egg laying in the Eared Grebe (*Podiceps caspicus*) was noted by McAllister (1958). The egg-laying period was longer in the Silver Grebe than in Rolland's Grebe. Combining data from all colonies for each species revealed a bimodal distribution of initiation of egg laying (fig. 3); the reasons for this are unknown. However, an extended period of rain and stormy weather occurred from 1 November through 8 November, and may account for the lack of nest building and egg laying during that period.

The egg-laying interval between successive eggs in the Silver Grebe ranged approximately from 1 to 3 days. The mean clutch size for the Silver Grebe was 2.3 (range: 1–4) compared to 2.0 (range: 1–3) for the Rolland's Grebe. However, after a loss of a normal clutch, Silver Grebes often relaid up to three more eggs in the same nest. It is impossible to be positive that relaying was carried out by the same female that laid the first clutch since females were not individually marked. Johnson (1965) reports a range in clutch size for the Silver Grebe of four to six in Chile, I am unable to account for this difference. Silver Grebe eggs

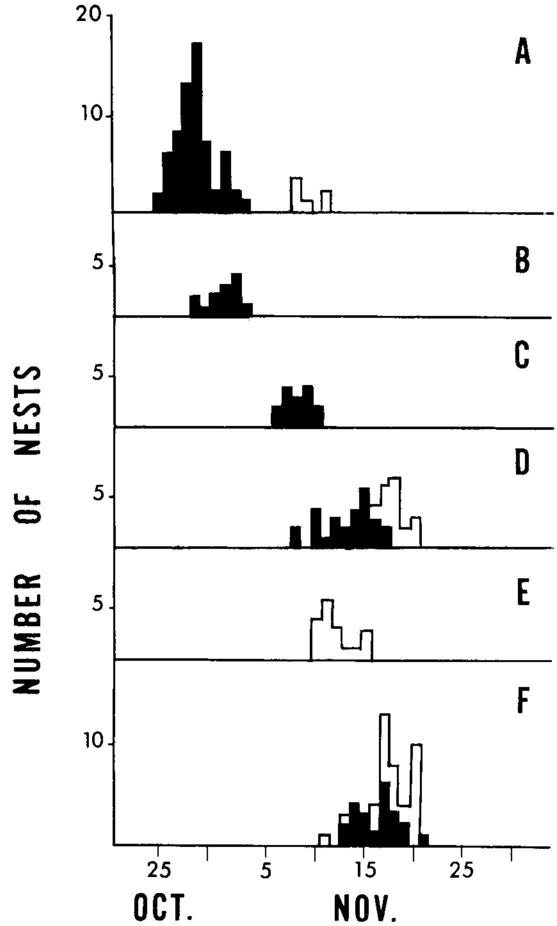

FIGURE 2. Initiation of egg laying in nests of the Silver Grebe (Black) and Rolland's Grebe (White). A through F are separate colonies.

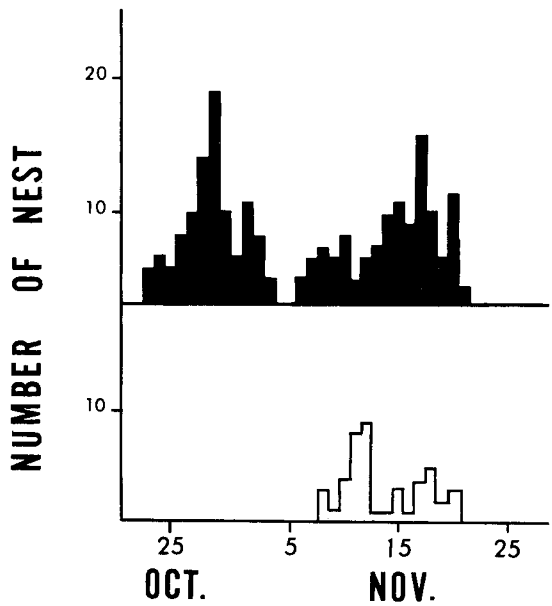

FIGURE 3. Initiation of egg laying in nests of Silver Grebe (Top) and Rolland's Grebe (Bottom). The data are lumped for the San Jose marshes.

TABLE 1. Egg dimensions of Rolland's and Silver Grebe.

Species	Length (mm)		Breadth (mm)	
	Mean	Range	Mean	Range
Silver	43.8 ± 1.6	40.3 – 48.8	29.1 ± 1.2	26.1 – 38.7
Rolland's	40.1 ± 2.1	36.7 – 49.1	28.0 ± 1.6	25.0 – 37.9

were larger than Rolland's Grebe eggs (table 1).

NEST-SITE SELECTION

As stated above, grebes choose colony areas having a low mean tule density with a large range. Therefore, within the colony area there are available areas of very low tule density, small clumps of very high density, and larger clumps of high density. Grebes could choose nest sites in any of these or on the interface of these areas. Both species of grebe appeared to select small, dense clumps of tules surrounded by open water as nest sites.

A device was built to test the hypothesis that grebes selected the center of small, dense clumps of tules for nest placement. The device consisted of narrow wooden arms constructed in such a way that an inner area (56 mm^2) could be compared to an outside section of equal area. The device, placed so that the grebe nest was in the center, allowed discrimination between small high density areas,

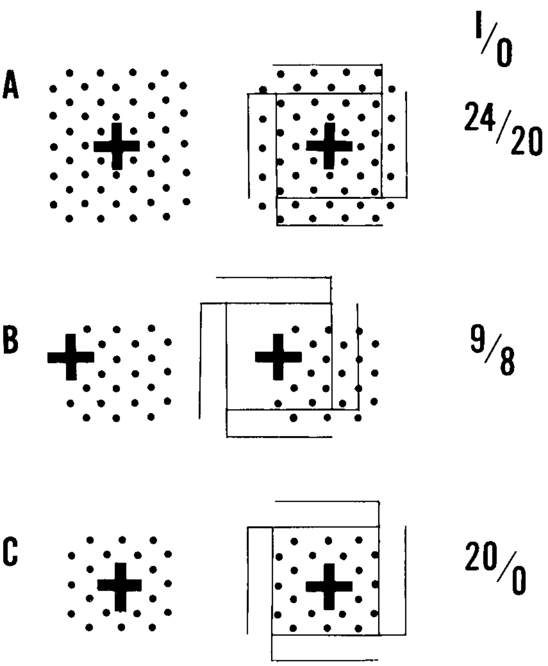

FIGURE 4. Hypothetical nest placement in a large clump of tules (A) and a small clump of tules (B & C) with associated inside/outside measurements. + = the center of the grebe nest, I = inside, and 0 = outside.

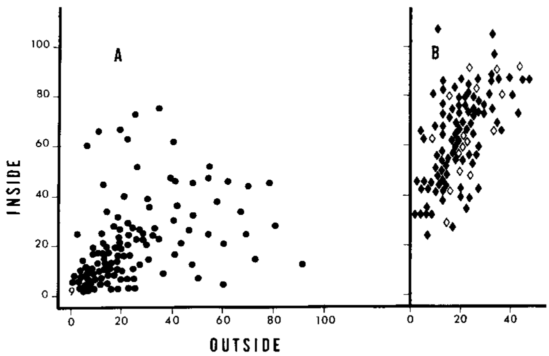

FIGURE 5. Comparison of available nest sites within colony areas (A) and sites selected (B). Note that the grebes selected small clumps surrounded by open water. Closed diamonds are Silver Grebe nests and open diamonds are Rolland's Grebe nests.

large high density areas, and low density areas. For example, a nest located in a large clump would result in a high number of tules in the inside area, and a high number of tules in the outside area (fig. 4A). A nest located in the center of a small clump of tules would yield a high inside-low outside number of tules (fig. 4C). If, however, the nest were placed on the edge of a small clump of tules, a low inside-low outside number of tules would result (fig. 4B).

The number of stems in the inside and outside sections was counted for each of 115 grebe nests, and for 115 randomly chosen locations within the grebe colonies. Figure 5 shows the results of this procedure. The grebes selected the center of small, dense clumps of tules immediately surrounded by open water for nest sites.

Colony areas did include areas of high and low density. It should be noted that although 56% of the random samples had inside/outside measurements of 22/22 or less, no grebe nests were located in these areas. Although grebes built nests in clumps having as many as 107 stems in the inside quadrant, no nests were built in areas where the outside quadrant had more than 45 stems. This shows that the grebes were selecting small, dense clumps. The ratio of inside to outside in the random samples ranged from + 0.10 to + 10.0, whereas grebes selected only areas where this ratio varied from + 1.6 to + 11.8. No species differences were noted.

In another species of marsh-nesting bird, Franklin's Gull (*Larus pipixcan*), nest placement was shown to be related to visibility (Burger 1972). Visibility was defined as the area visible from the gull's nest and was measured from photographs taken with a camera equipped with a fish-eye lens. A visibility index was then computed from the photographs and correlated with internest distance. This same procedure was followed with the grebes, and no correlation was found. Grebes appear to be selecting nest sites on the basis of environmental factors, and not on the basis of their ability to see other grebes. In fact, in one case, two Silver Grebe nests were touching each other.

NEST STRUCTURE AND INTERNEST DISTANCES

Differences in nest structure between the two species were easily discernible. Nests of the Silver Grebe were larger ($\bar{X}$ at widest point $= 45.2 \pm 8.8$ mm, range = 28–72 mm) than Rolland's Grebe nests ($\bar{X} = 29.2 \pm 5.2$ mm, range = 15–38 mm) ($P < 0.01$). Older nests of both species were smaller due to a gradual sinking of the nest. Nests of Rolland's Grebe were compact and usually wet, whereas those of the Silver Grebe were less compact and dry. Rolland's Grebes tended to cover eggs upon leaving the nest, and Silver Grebes did so infrequently (18%).

The distance between neighboring nests was inversely correlated with the number of nests in the colony ($r = 6.9$). In the largest colony (colony A), the mean internest distance was 1.8 ± 0.9 m. In this colony the internest distances of Silver-Silver Grebes and Rolland's-Rolland's Grebes were not significantly different although Rolland's-Silver Grebes internest distances tended to be larger ($\bar{X} = 3.8 \pm 2.1$ m). In the smallest Silver Grebe colony, the mean internest distance was 4.3 ± 1.4 m, and in the smallest Rolland's Grebe colony, the internest distance averaged 5.0 ± 1.7 m.

EFFECTS OF HEAVY RAINS

On two occasions heavy rains produced rapid increases in water level which resulted in the loss of nests and eggs. On 1 November after 18 mm of rain, there was a loss of 21 Silver Grebe nests (37% nest loss). Another heavy rainstorm (38 mm) on 6–7 November resulted in a loss of 18 nests (34% nest loss) in the same Silver Grebe colony. No major storms were recorded during the incubation period of Rolland's Grebe.

ANTI-PREDATOR BEHAVIOR

The main mammalian predator in these marshes appeared to be a species of weasel. In one case this mammal was observed to kill an incubating Silver Grebe by crushing its head. Because it was dark, I could not follow the path of the animal when it left this nest. However, the following day two additional crushed bodies were located nearby, presumably killed in the same manner. The entire colony of 15 nests was ultimately destroyed. This colony was closer to dry land than other grebe colonies.

Two avian species were predators on eggs and adults: the Chimango Caracara (*Milvago chimango*) and the Crested Caracara (*Polyborus plancus*). The Crested Caracaras nested nearby and were present in the marshes all summer. They were observed eating eggs as well as eating the head and breasts of adults they killed on the nest. Chimangos were very common, and nested in the same marshes. Nonbreeding birds from the surrounding pampas roosted in the marshes at night and it was common to count a flight of 15–25 Chimangos flying into the marsh at one location. Chimangos were observed to eat grebe eggs in 11 nests, but they did not eat adults.

Anti-predator behavior in both species of grebe was minimal and limited to retreat from their nests. The grebes slipped into the water and swam underwater for 15 m or more before surfacing. The grebes then gathered in a tight group on open water. These groups swam slowly back and forth, diving infrequently. In this connection it was interesting to observe a similar behavior pattern in Rolland's Grebe even though predators were not observed to elicit this behavior. During the latter part of the parental care period, groups of up to 150 birds gathered in the middle of open water areas at about 09:00 each morning. The group was composed primarily of adults with a few young, as well as up to 30 Brown-hooded Gulls (*Larus maculipennis*). The birds swam slowly, and the group used the same areas of open water each day, although the direction of movement was often changed. Ten to 50% of the group was often diving. Chimango Caracaras often circled these groups, but invariably left without making a kill. At approximately 16:00 in the afternoon, groups began to break up as individuals swam into the tules and commenced solitary feeding. Weller (1967) reported similar groups of grebes during the nonbreeding season.

Although Brown-hooded Gulls are not predators in the usual sense, they were observed to take over and use active Silver Grebe nests ($N = 19$). The gulls added material to grebe nests, then laid an egg on the same day. In two of these nests, a complete clutch of grebe eggs was replaced by one gull egg; subsequently the gull egg was pecked, removed, and a grebe egg was laid in the same nest. In two other nests, individual gull eggs were laid with the grebe eggs. These nests were incubated by grebes until the grebe eggs hatched; the gull egg was then abandoned by the grebe. In three cases, grebe nests in which the eggs had hatched were used by gulls. Brown-hooded Gulls did not use nests of the Rolland's Grebe. The nests of this species are quite small, and thus do not resemble as closely the nest construction of Brown-hooded Gulls.

DISCUSSION

Darling (1938), working in a colony of gulls, suggested that in colonial species increased "social stimulation" produces greater breeding synchrony resulting in an earlier and shorter egg-laying period. Several authors have presented evidence for increased synchrony with increased colony size (reviewed by Coulson and White 1956), but other authors have failed to find such a correlation (Orians 1961; Vermeer 1963). In this study, the greatest degree of egg-laying synchrony was found in the smallest colonies.

Colony-site selection in these two species of grebe seems to involve two factors: proximity to deep open water, and tule density. Proximity to deep open water would be advantageous because it allows greater visibility and rapid escape from predators. Areas of low tule density would facilitate underwater entrance and exit from nests. Presumably, a greater tule density would result in more obstruction to underwater swimming. Both species were observed to enter and exit only underwater.

Both species of grebe studied selected small clumps of dense tules as nest sites. Clumps of tules provided adequate support for nest attachment. Such nest attachment prevented winds from dislodging nests. Loss of nests and eggs as a result of wind and rain was reported for the Pied-billed Grebe (*Podilymbus podiceps*) (Chabreck 1963) and Horned Grebe (*Podiceps auritus*) (Munro 1941). Small clumps of dense tules may also provide protection from avian predators.

The formation of Rolland's Grebes into tight groups during the day might be selected for because it decreases predation, increases feeding efficiency, or both. Members of the groups I observed did dive and often had material in their beaks. Grebes are known to form commensal feeding associations with species of the Anatidae (see review in Siegfried 1971), Rallidae (Ashmole et al. 1958), and Laridae (Dusi 1968; Weller 1967).

Large groups of grebes similar to those I observed of Rolland's Grebe were reported for the Eared Grebe (Palmer 1962), Western Grebe (*Aechmophorus occidentalis*) (Palmer 1962), Silver Grebe (Wetmore 1926), Hoary-headed Grebe (*Podiceps poliocephalus*) (Hobbs 1958), and Little Grebe (*P. novaehollandiae*) (Hobbs 1958). Hobbs (1958) further noted that a Whistling Eagle (*Haliaster sphenurus*) hovered over a mixed flock of Little and Hoary-headed Grebes, appeared "confused by the constant diving," and eventually killed a bird that lagged behind the group. I frequently observed Chimango Caracaras circling over groups of Rolland's Grebes, but eventually the hawks left without success. These Caracaras probably are unable to kill adults, but the young in the group are small enough to be taken as prey.

In conclusion, colony-site selection in Rolland's and Silver Grebes was determined by low mean tule density, while nest-site selection was determined by the presence of small, dense clumps of tules.

SUMMARY

The nesting behavior of Silver and Rolland's Grebe was studied for 4 months in a marsh in the pampas of Argentina. Five Silver Grebe colonies, two Rolland's Grebe colonies, and two mixed colonies were located. All colonies were in reed beds adjacent to open water. Although a wide range of tule densities was available, the grebes selected areas of low density that contained a few dense clumps of tules for colony sites. Nests were located in the center of small, dense clumps of tules immediately surrounded by open water. Low mean tule density areas provided a minimum of obstruction for underwater swimming; dense clumps provided adequate support for nest attachment and some protection from avian predators.

The egg-laying period was from 23 October through 25 November for the Silver Grebe, and from 10 November through 25 November for the Rolland's Grebe. A higher degree of synchrony was noted within colonies than in the marshes as a whole. Heavy rains were observed to cause loss of nests and eggs.

A weasel and two hawks were predators on the grebes and their eggs. Anti-predator be-

havior consisted of an underwater retreat to open water and the subsequent formation of tight groups. A similar grouping not elicited by predators was observed daily during the latter part of the breeding season in Rolland's Grebe only. A number of Brown-hooded Gulls took over and used active Silver Grebe nests.

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