COURTSHIP, HOSTILE BEHAVIOR, NEST-ESTABLISHMENT AND EGG LAYING IN THE EARED GREBE (PODICEPS CASPICUS)

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THE behavior of North American grebes is little known. This is especially true of their nesting behavior. They are relatively secretive and nest in marshes out of reach of most observers. This paper describes courtship, hostile behavior, nest establishment, nest building, copulation, and egg laying of the Eared Grebe, and discusses some of the comparative aspects of these behavior patterns. In addition, some problems of clutch size and laying interval are considered.

Simmons' work (1955) on the Great Crested Grebe of Europe, *Podiceps cristatus*, has been used extensively for comparison with the Eared Grebe.

THE STUDY AREA

The study area was near Williams Lake in the Cariboo district of British Columbia, 52.00° North latitude, 122.00° West longitude, and 1500 to 3000 feet above sea level. The Cariboo Parklands biotic area or biome as described by Munro and Cowan (1947) is flat to rolling grassland broken by stands of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*). Frequently the bottoms of depressions in the grassland hold shallow lakes varying in size from a few acres to twenty square miles. The Eared Grebes chose lakes about a mile by half a mile.

The study lakes, Westwick and Sorensen, were once one but are now artificially divided by an unpaved road. The lakes are carefully described by Munro (1941). The greatest depth is twelve feet, but more than half the lake area is less than five feet deep. These highly productive lakes have at least a foot of thick black mud on the bottom. The clear water is filled with numerous small invertebrates, but no fish. The concentration of invertebrates is such that food does not appear to limit the populations of any of the birds using the lakes. By the middle of July, the bottom flora reaches to within two feet of the surface and extends over ninety percent of the bottom area. In addition dense mats of floating algae cover one fourth of the surface by the end of July. The bottom plants are *Scirpus, Ruppia, Ceratophyllum, Myriophillum*, and *Potamogeton*, and the floating forms are principally *Aphanizomenon* and *Cladophora*.

Westwick Lake had a colony of two hundred and ten pairs of Eared Grebes, and Sorensen Lake a colony of forty pairs. This study was made during the summers of 1955 and 1956, using ordinary observational methods. Sex of the birds could often, but not always, be told. The males had larger crests and sometimes appeared to be larger in total body size. Diagrammatic drawings of some of the patterns described are shown in figures, and the courtship patterns of the Eared Grebe and the Great Crested Grebe are compared in Table 1.

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COURTSHIP DISPLAYS

Courtship display was seen as soon as the Eared Grebes arrived at the breeding lakes. In 1955 the first grebes arrived on May 1; in 1956 a few were on the lakes when I arrived on May 2. In both years most of the grebes had arrived by the end of the first week of May.

Courtship was mutual; all patterns noted were performed by either sex. The courtship displays were all done on open water in the center of the breeding lakes. There was no territory of any kind involved, and each bird made use of the whole lake area. The Great Crested Grebe (Simmons, 1955) courted on territory and used the defense of territory boundaries as part of its courtship.

Courtship display tapered off abruptly as nesting behavior began. The colony, stimulated by courtship, acted as a unit in the total change in behavior. Simmons (1955) described a similar abrupt change of behavior in the territorial Great Crested Grebe, but each pair had its own change-over time. The increased use of advertising behavior seemed to serve to synchronize courtship in the Eared Grebe and create a true colonial situation.

Advertising Behavior

Advertising behavior was seen where an unpaired bird was in search of a mate, or when a paired bird had temporarily lost touch with its mate. The advertising bird swam up and down approaching other grebes with a characteristic attitude (fig. 1) and call. The feathers of the whole body were fluffed out making the posturing bird seem larger than its fellows. Both crest and neck feathers were raised, the neck was erect, and the bill was directed straight forward and closed during the call.

The call was a three-noted *poo-eee-chk*, but the ending *chk* could only be heard at very close range. It may be produced, as Simmons (1955) suggested for the Great Crested Grebe, by the effort of producing the first two notes. The first two notes were plaintive and slurred, about



advertising



cat attitude



threat



penguin dance



alarm

FIGURE 1. Some behavior patterns of the Eared Grebe.

a musical fifth apart. They sounded much as if played on a flute. The third note was on the same pitch as the first but much quieter and very gutteral.

Eared Grebes gave the appearance of being paired on arrival in the spring. More than half were swimming in pairs on the day of their arrival at Westwick Lake. When a single bird approached a pair, situations such as the following occurred: "One of the pair swam toward the advertising intruder, and it turned away and left them." "Intruder appeared and swam between the paired birds and around them. The male of the pair ignored the intruder for a while and then rushed at him from a distance of four feet in a threat attitude. Then the pair moved off while the intruder moved into the reeds." Such incidents as these led Munro (1941) to say that the birds were paired on their arrival, and my judgment originally followed his. Closer study of individual pairs, however, showed that none of the Eared Grebes were paired definitively at this stage. Partnerships lasted from three hours to five minutes. An advertising single bird of either sex swam up to the pair and took one of the pair away. The other of the pair then went off and advertised. The number of changes of partners seen dropped off rapidly until pairs were definitive a few days before nesting behavior was first seen.

The advertising position of the Great Crested Grebe described by Simmons (1955) seems the same as that of the Eared except that the crest of the larger species is depressed. The elements of the Great Crested Grebe advertising call seem to be the same as those of the Eared Grebe call. The Great Crested Grebe remained stationary while advertising, which may be related to the territorial nature of its courtship. The Eared Grebe might be either stationary or swimming. It might even swim up to other grebes, but it was not seen to be aggressive.

Habit Preening

Courting grebes floated along in pairs and preened vigorously. This behavior did not differ in aspect from ordinary comfort preening and I saw nothing to indicate that it was a courtship activity. However, between these bouts of comfort preening, a different kind of preening was seen. The two birds drifted within a foot of each other and preened together; either bird might lead, but the other repeated the movements exactly. The timing was so close that it was often difficult to tell which bird was leading. There was no definite sequence of movements, but both birds preened the same feathers at the same time. The movements were a little quicker and not quite so thorough as those of comfort preening. The participants were most frequently side by side but might end up facing each other. I have not seen this pattern except during the courtship period, and I think it must have a courtship function.

Habit preening is by far the most common courtship pattern in the Eared Grebe. It is also reported for the Great Crested Grebe (Simmons, 1955), but in that species head shaking was the more common courtship movement.

Head Shaking

Head shaking was seen both as a separate ceremony and as part of the penguin dance. As a separate ceremony the two birds swam along rapidly, one in front and slightly to the side of the other. Their body feathers were raised, and their position was very high on the water. Their necks were stretched up higher than in the advertising behavior with crest raised and neck feathers depressed. The general effect was taller, higher on the water, and thinner than in the advertising attitude. The head was turned smartly left and right, all in the horizontal plane. The tempo was military, precise but not hurried. Six to twelve turns constituted a ceremony; then both birds usually dove. The timing of both the turns and dive was generally quite precise as the following bird apparently copied the leader. Either sex might lead, and once head shaking was seen done by an unpaired bird. After advertising to a pair, the odd bird did several head shakes, and the female of the pair swam off with him.

The head shaking ceremony was as common as the cat attitude (fig. 1), but not as common as the penguin dance (fig. 1). In about half the instances recorded, head shaking was directed toward other grebes, paired or single birds, as a threat. Once the shaking pair were riding so high on the water that white breast feathers were visible.

In the Great Crested Grebe (Simmons, 1955) head shaking almost replaced habit preening and the penguin dance. In addition to courtship, it is used to cement the pair bond during and after territory-boundary disputes. The use of shaking as threat toward an intruder was the only Eared Grebe counterpart of this. The attitude of the Great Crested Grebe was basically the same as that of the Eared Grebe, but the birds usually faced each other and were always stationary. Often, too, their bills were below horizontal. Faster turns were alternated irregularly with slower ones in the Great Crest, while the tempo was even in the Eared Grebe. The Great Crested Grebe had a special head-shaking call.

Huxley (1914) described Great Crested Grebes head shaking while back to back, but Simmons (1955) had never seen this variation. Wetmore (1920) cited the same for the Eared Grebe, but I have not seen it. Kilham (1954) described a pair of Pied-billed Grebes (*Podilymbus podiceps*) head shaking while they swam near each other.

Penguin Dance

The penguin dance is that peculiar display in which grebes stand up like penguins while treading water. The penguin dance (fig. 1) was more common than the cat attitude or head shaking, but less common than advertising behavior and courtship preening. Both birds would tread water face to face raising their white breast feathers out of the water and seemingly stood on their tails. Their bellies were only a few inches apart, and they paddled their feet alternately and so rapidly that they sometimes splashed. As they stood up they uttered a shrill chittering call and shook their heads violently from side to side. There were from six to twenty head shakes, but the pace was so fast that the birds were usually out of phase. Dropping to the water, they slowed head movements to the pace of the head shaking ceremony, and eight to twenty turns were made from the swimming position facing each other. Only once were Eared Grebes seen shaking face to face without first going through the dance. Sometimes the birds turned during this last head shaking and continued as in a normal shaking ceremony, swimming together down the lake. Sometimes they simply stopped head shaking, drifted apart, and comfort preened. Habit preening was a part of the post-dance ceremony about a third of the time. The beak was dipped eight to sixteen times to the breast feathers or primaries either before or during the head turns. The preening movements were here even more ritualized than was seen in the usual head shaking. The feathers were touched but not stroked, and the rhythm of the ceremony was not broken.

Very occasionally the Eared Grebes turned while still standing and ran a short distance on the water before settling down to head shake. Usually the birds stood up actually facing each other, but occasionally they stood up facing the same direction, but turned while standing to face each other. This turning seemed to be the same as that seen in the Great Crested Grebe discovery ceremony (Simmons, 1955). In diving the Great Crested Grebe most often overshot its mate, came up facing away from it, and turned to face it. The mate was in a cat attitude, and the diving bird slowly dropped to the water, head shaking with it. I have not considered the discovery ceremony under a separate heading, because I think that it is an incomplete form of the penguin dance. This incomplete form is the more common form for the Great Crested Grebe, and the complete form was rarely seen. When it did occur, Great Crested Grebes dove and each of the pair brought to the surface a bit of pond weed, swam toward its mate and rose in the penguin dance. The Eared Grebe may begin its dance from a dive or from the surface; but the use of weed was not seen.

The Great Crested Grebes leaned against each other during the penguin dance (Simmons, 1955), but the Eared Grebes stood without leaning.

The chittering call of the Eared Grebe penguin dance consisted of the two notes of the advertising call uttered more quickly and in wild excitement. In construction it is the same as the threat call, but the quality seemed more musical. Simmons (1955) did not describe any call for the penguin dance of the Great Crested Grebe. Perhaps, since head shaking was so closely related to the dance, the head shaking call was used. The Eared Grebe was not heard to call during head shaking.

Occasionally in the Eared Grebe an unmated bird flapped in high intensity threat at a pair doing the penguin dance. Often it came from

quite a distance at the sound of the dance. This was more likely to happen later in the season when the odd bird had been advertising for a long time.

In the Eared Grebe I did not observe the penguin dance after a pair had begun nest building. Lawrence (1950) said that the upright rush of the Western Grebe (*Aechmophorus occidentalis*) was seen in reduced intensity all summer; but the upright rush may not be homologous to the penguin dance of other grebes.

Cat Attitude

In the cat attitude the head was drawn down on the breast with the crest and neck feathers raised (fig. 1). The raised body feathers made the birds look much larger than usual, and the wings were away from the body but bent. The carpal joint was tipped forward and down to almost touch the water. The posturing bird exactly faced the bird eliciting the display, thus making more striking the orange circle of plumes in the center of the larger black circle of the wings and body. The attitude of the Great Crested Grebe seems to be the same.

The cat attitude was quite rare compared to the other courtship patterns. Apparently the Great Crested Grebe (Simmons, 1955) uses it more than the Eared Grebe. Its function is not clear. Both grebes used the cat attitude when an unmated bird had been advertising. Another grebe swam toward the advertising bird and dove. The advertising grebe assumed the cat attitude, and the approaching bird rose in the penguin attitude. Paired Eared Grebes used the same ceremony without previous advertising. In the Eared Grebe the penguin dance seemed always to follow; in the Great Crested Grebe head shaking followed. Once a female Eared Grebe assumed the cat attitude facing an advertising male as he passed. Her mate immediately drove the odd bird away. Rarely in either species one bird flapped over the water a little way and did a cat attitude turning to face its mate. Or it might just patter away and swim back without using the cat attitude. The penguin dance or head shaking followed respectively as seen before. In addition the Great Crested Grebe unmated female used the attitude when threatened by a mated male. I have included this section under courtship and made no mention of it under threat as Simmons (1955) did. because I think that it is not related to threat behavior.

HOSTILE BEHAVIOR

Threat Attitudes

Threat behavior was seen under two sets of circumstances. During the courtship period, advertising birds (fig. 1) swam up to courting

TABLE 1

Advertising Behavior:	Eared Grebe	Great Crested Grebe
neck erect, bill forward	x	x
crest and neck feathers raised	x	
crest down		x
body feathers fluffed	x	x
body high on water	x	x
call: poo-eee-chk	x	
grr-owp row-ah		x
done while: moving	x	
stationary		x
done by lone bird mated or not	x	x
Habit Preening:		
precise, stereotyped movements	x	x
primaries and breast used mostly	x	x
preens whole body	x	?
seen alone or with head shaking	x	x
Head Shaking:		
neck erect, medium stretched	x	x
crest up	x	x
neck feathers down, body feathers media	ım x	x
bill: forward	x	
slightly down		x
facing: forward	x	
each other		x
done swimming	x	
done stationary		x
done between battles		x
used by pair as threat or courtship	x	X
Penguin Dance:		
head turning	x	x
crest up, bill forward	x	x
neck medium stretched	x	x
body and neck fluffed	x	x
standing position	x	x
leaning		x
not leaning	x	
chitter call	x	?
elicited: by diving for weed		x
by penguin	x	
from surface	x	
by cat attitude	x	
turn forward while shaking	x	
stay facing each other	x	x
tollowed by head shaking	x	x

COURTSHIP PATTERNS COMPARED

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Cat A	ttitude:		
he	ad withdrawn, crest raised	x	x
bo	ody feathers raised	x	x
w	ings out, tipped forward	x	x
fa	ced partner	x	x
eli	icited by penguin	x	x
el	icited by mate approaching on surface	x	
fe	male may do it when threatened		x
fo	llowed by: penguin dance	x	
	head shaking		x

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pairs and were either driven off or accepted by one of the courting birds while the other swam away. Later, during nest establishment, the birds owning and defending nest platforms threatened and drove away any Eared Grebes approaching within about two feet of the platforms. Throughout the nesting season nests were defended in this way. But during courtship and on open water during nesting, threat was rare. While there is complete overlap from the highest to the lowest intensities of threat, three arbitrary divisions can be made on the basis of the elements included. The higher intensities were more characteristic of nest defence, and the lower of courtship.

At low intensity the angle of the neck was forty-five degrees forward, the bill straight forward and open (fig. 1). The feathers of the neck were laid down and those of the crest raised. The threatened bird usually just swam away. At middle intensity the birds swam slowly toward the threatened bird in the low intensity threat attitude. In high intensity threat the low intensity threat attitude was taken first. Then the wings were raised and the bird flapped over the water toward the other bird. The threatened bird escaped by diving, was sometimes followed a short distance, and might be struck or bitten before it had a chance to get away by diving. The striking motion involved drawing the head back and then thrusting it forward. The movement seemed to be the same as that performed in diving, and the dive was sometimes actually completed at the end of the rush. The threatened bird turned away as the rush began and took the blow, or most frequently the bite, on the side or wing. Threat seemed always to be successful in driving the intruder off. The Eared Grebe had moving attack-escape sequences instead of the stationary fighting and upright threat of the Great Crested Grebe (Simmons, 1955).

The threat call was almost always associated with the middle and high intensity threat, rarely with the low. The call is a loud chitter, the two notes about a musical fifth apart and alternated rapidly. In spite of the speed, each syllable is individually accented.

The forward threat and attack of the Eared Grebe appear to be the same as those used by the Great Crested Grebe (Simmons, 1955), and the Great Crested's bark call seems to be homologous with the chitter of the Eared. It is interesting that Simmons reported in the Great Crested Grebe so many variations of the threat call. This may be associated with its apparently greater use of threat behavior. I have observed no upright threat posture in the Eared Grebe, perhaps because two Eared Grebes never seem evenly matched. The Eared Grebe had no large territory boundary, for the only territory defended was the nest itself, and there one pair was always dominant.

In the fighting of the Great Crested Grebe, Simmons said, "both grebes leap at each other and clash vertically breast to breast." It is not clear whether this was the upright swimming posture of the upright threat or the standing posture of the penguin dance (fig. 1). This standing position, I have never seen in the Eared Grebe. Dubois (1918) described the Horned Grebe, *Podiceps auritus*, as having a lunging attack similar to what I saw in the Eared Grebe. Wetmore (1920) spoke of a female Pied-billed Grebe, *Podilymbus podiceps*, with young as "rising threateningly on the water, made a great boiling noise by treading rapidly with her feet." As the presence or absence of the standing fighting or threat behavior may have importance in tracing the evolution of some of the courtship patterns, it should be more thoroughly investigated.

During the courtship period a pair of Eared Grebes may use the head shaking courtship pattern as threat.

Escape Attitudes

The alarm posture (fig. 1) was seen during courtship when the birds were disturbed by man. No other animal or natural phenomenon was seen to produce it. During nesting the alarm attitude was the usual one for birds on open water. They were shy and constantly alert during this time. When the eggs were hatched, the grebes returned to the former resting posture.

In the alarm attitude the feathers of the body, neck, and crest were all laid down. The neck was extended vertically, and the bill was straight forward. The wings were tightly closed. The grebe was ready to escape by diving, submarine diving, or flapping across the water. The alarm attitude is probably part of the intention movements of escape. The posture seems to be the same as that of the Great Crested Grebe (Simmons, 1955) but I do not find it described for any other species.

I have heard no call in alarm or escape behavior. This is particularly

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noticeable in the nesting colony, where, even with the most silent approach, I seldom saw and never heard a grebe; only the empty nests were found.

Simmons (1955) did not mention whether or not the Great Crested Grebe had an alarm call. Gross (1949) described the Least Grebe, *Podiceps dominicus*, male as having an excited call, *yeep-yeep-yeep*, followed by a rattled *ye-ye-ye-ye-e-e-e-e-e-e*. The female and young all dove "in a wild splash at this signal." Deusing (1943) said that the Pied-billed Grebe had a hu,hu,hu,hu call continued for several seconds, which he said might be an alarm call.

When a person or boat or other strange object appeared close to a grebe, it first assumed the alarm posture, and then escaped. When another grebe attacked it, however, it escaped without using the alarm posture. Escape may be made by pattering over the surface, by diving, or by the submarine dive. The crash dive was only seen in extreme circumstances, and was a combination of diving and pattering over the water. The wings were raised as if for flight, but the bird dived and used its wings a short distance under water. The submarine dive was almost as common as the ordinary escape dive and pattering. Unlike these, it was never seen except in an alarm situation. In this pattern the grebe sank out of sight from the alarm attitude, body first, then neck, then head.

NESTING

Beginning of Nest Establishment

In the course of one week, the behavior of the grebes changed abruptly. Late arrivals were conspicuous exceptions, keeping apart in a little group until they finished their courtship. When they began nest establishment behavior, these late arrivals were absorbed into the larger group. Before May 16, 1956 none of the elements of nest establishment was seen; after May 20 none of the courtship patterns was seen. The situation was the same and the dates were almost identical in 1955. The change is evident even to the casual observer. In the first period feeding and resting are closely intermingled with courtship; there is almost always a pair courting somewhere in sight. The birds are scattered all over the open water. The number of calls of the advertising courtship pattern makes the lake seem noisy all day, and the birds are very tame when approached.

In contrast, nest establishment behavior is seen each day for short periods only, and the whole colony is usually involved. These mating parties are always in the reeds or floating vegetation, and show platform building, platform defense, soliciting, and copulation. Between parties the birds spend most of their time resting in large groups near the reed area where they last built nest platforms. They scatter to feed periodically but always return to the group. While on open water they are silent and increasingly shy.

The change from courtship to nest establishment depends on the date the ice goes out and the temperature in the early part of May. The birds almost all arrive in the first three days after the ice breaks up on the breeding lakes. The warmer and sunnier it is in May (it seldom exceeds 85° F.) the greater the degree of courting activity. Presumably a certain amount of courtship must be done before the birds begin to change to nesting behavior. This is suggested by the observation that late flocks continue to court after the early flocks have already started nesting activities.

Soliciting

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Soliciting is the first behavior pattern of nest establishment seen each spring. In a soliciting grebe, the body is low in the water, neck forward, and head and bill laid straight out on the surface of the water. The neck is not unduly extended, and the crest is down. Both sexes may solicit and both call. This position is the same as the position of the female in copulation except that in copulation her bill is usually pointed slightly down. One call is associated with both soliciting and copulation. It is an eerie note somewhat similar in quality to the scream of the Red-shouldered Hawk, *Buteo lineatus*. It does not, however, change in pitch. The soliciting bird may be answered by its mate with the same call. Later in the season both birds solicit on the nest platform and copulation follows.

Simmons (1955) states that the Great Crested Grebe rarely solicits on the water, and does not start soliciting until the platform is at least partly built. The position taken is the same as that of the Eared Grebe, except that the neck is somewhat stretched. Simmons does not mention that any call accompanies this pattern as in the Eared Grebe.

The Great Crested Grebe has another soliciting display in which it stands on the nest and arches its head as though to peer at its feet. Simmons (1955) refers to this as rearing. Hosking (1949) describes a similar pattern in the Horned Grebe, *Podiceps auritus*. Buddle (1939) gives a photograph of the New Zealand Dabchick, *Podiceps rufopectus*, in the rearing attitude. I have not seen this in the Eared Grebe, although it may occur. Perhaps rearing is the ritualized intention movement of sitting down on the nest. Motion pictures of both rearing and sitting down on the nest would be helpful in deciding this question. Rearing also resembles the copulation posture of the male and the posture of both birds in turning the eggs.

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Development of Platform Building

Nest or platform building begins at a very low intensity a few days after the first soliciting. The birds begin to drift all together into the reeds. Almost any place may be chosen, but some floating algae or reeds must be present. Isolated tufts and sparse floating pondweeds totally unsuitable for finished nests may be used for these early platforms. As the birds swim slowly around in the chosen area, a single female may pull a broken reed over and lay it across another reed caught between two upright stalks. Then the whole group swims away and resumes feeding.

With each occasion of group activity the intensity of the behavior increases and more pairs become involved. On Sorensen Lake the evening of June 9, 1955, this sequence was seen: At sunset the birds were all feeding on open water. A pair drifted into the entrance to the marsh, and the birds swam to opposite sides of a reed tuft in the middle of the channel. This tuft was one of a group of three each containing less than a dozen reed stalks. The female pulled at a long floating reed and added some floating algae to that already caught in the reed tuft. Several pairs swam by and were driven off, the area defended being only a foot or two around the platform. This pair held the tuft until dark at eleven P.M. and copulated on it about a dozen times. Several other pairs could be heard similarly occupied in the marsh, but the majority of the birds had not yet chosen tufts and trouped up and down in a body, heads down in resting posture. These early platforms are shown in Plate 13.

More and more pairs became involved, until on May 18, 1955 an active party was seen on Westwick Lake. The day was warm and sunny, and the grebes were feeding all over the lake. At four P.M. a disturbance on the far shore caused the grebes to drift toward me. In the next half hour they were all in the reed fringe in front of my canoe. The eerie trilling of the copulation call began and increased as pair after pair joined in. Six pairs solicited and copulated on old nests. Pairs rushed at each other, wings raised and beaks open in threat. A dozen small battles raged at once and the threat calls of fifty individuals were so continuous that I could not distinguish the birds which were calling. Six single birds tried to attract mates but were dealt with violently by both members of each pair they approached. American Coots (*Fulica americana*) and Ruddy Ducks (*Oxyura jamaicensis*) swam by and were not bothered by the grebes.

These parties start spontaneously and may take place in a different area each time. There is a tendency to use one reed bed for several days and then to move to another. The moves took place both on the THE AUK, VOL. 75



Eared Grebe. *Above:* An area of sparse reeds showing five unfinished nests used for copulation. *Below:* An early unfinished nest used for copulation.



Nests of Eared Grebe. *Above:* A nest not yet complete. *Below:* A finished nest with abandoned egg. The egg has been pecked by a grebe.

lake that I was watching from the canoe and on the lake which I watched only from a distant hillside. I doubt, then, that my presence disturbed the birds and caused them to move. The moves may have been connected with the increasing maturity of the nesting patterns.

In each of the two summers the grebes at one time chose an area of reeds far too sparse to support nests. On June 21, 1955 the grebes were in an area of new reeds in the center of Westwick Lake. The tufts each contained less than a dozen stalks and were several feet apart. I could see in this open area the beginnings of nearly fifty nests. The grebes were alternately soliciting on the new platforms and adding new material to them. Five nests had one egg; one nest had two. A thundershower accompanied by strong winds the next night destroyed the nests, and activity switched to a new area.

Nest Building Patterns

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All the building seemed to be done by the female. The male followed the female but was not seen to handle nest material. Since it was difficult to tell the sexes apart, some errors may have been made here. If only the female builds, this is the only pattern besides copulation in which the roles of the sexes are not the same. The female dives near the nest site and comes up about two feet from it with a large beakful of algae, lays it on the edge of the heap with a quick reaching movement, and dives again. The nest is set on a foundation of several bentover reeds. It may be in the center of a small clump of reeds or at the side of a large clump. The heap of debris finally makes a more or less pyramid-shaped pile reaching from a foot or two from the bottom of the lake to slightly above the surface. Three hours is sufficient time for the construction of a nest. Additional material may be added to the sides of the nest during the egg-laying period.

The center of the nest is cupped, but the rim is never more than an inch above the center. The whole nest is soggy, and the center may be slightly below water level even when the adult is not on it. The lower half of each egg is always wet.

The nest material depends on the lake bottom in the immediate vicinity of the nest. Nests built in a new reed bed were bright green, completely constructed of living algae; those in old reed beds were nearly black with rotting reeds and algae. All the nests had the appearance of being molded of wet clay, smooth and soft.

The colonies were compact units in the densest part of the reed bed and visible neither from the shore nor from open water. The final nests on other lakes, however, are often built much more in the open. Nests are from one foot to three feet apart and are in water one to three and a half feet deep. Places where there are surface algae are avoided. The first nests in the final colony are in a group and form a nucleus for the development of the colony. Darling (1938) suggested that a central nucleus and concentric rings is the usual colony form in gulls. The colony is compact, using every available reed tuft in the area.

When nest building, the females assume a shy attitude that continues through egg-laying and incubation. Their crests and neck feathers are sleeked down in a low intensity alarm attitude. The males do not seem to adopt the alarm attitude until the middle of egg laying.

Nest material was never seen used ritually in courtship or as an invitation to nest.

Copulation

Copulation occurs frequently from the time the first platforms are made until the end of egg laying. The female hops up on the platform with a thrust of her legs, wings closed. She stands on it with her legs out like props for a few seconds and then drops down on her belly. She stretches her neck forward and holds her bill pointed down at a forty-five degree angle. Her head and neck feathers are flattened. The male swims around behind the nest and hops up on her back without opening his wings. He stands at an angle slightly forward of vertical with crest and neck feathers down. His neck is curved and his bill pointed down. Both birds are motionless. The male gives the copulation call. The female does not join in the call and may even threaten passing birds. After about half a minute the male slides into the water over the head of the female. There is no post-copulatory display.

The female Great Crested Grebe (Simmons, 1955) holds her head and beak straight out, probably because of her long neck. The male takes the same position as seen in the male Eared Grebe, but the closed wings are quivered as in the rearing soliciting attitude. The call is a harsh rattle "sounding like a creaking *ee eee"* (Simmons, 1955, quotation of Hanzak). As the male slides off the nest, he takes the escape bathing position except with the crest and head up. He settles and begins head shaking with his back to the female. The female raises her head to head shake with him.

"Escape bathing" was so named by Simmons (1955) because he thought it was a real escape pattern. It is a particularly violent version of the bathing behavior which ends with a peculiar attitude. The body is held upright but half submerged, that is, half the white breast feathers are showing above the water. The neck is arched and the crest down; the chin is on the breast. I have seen this only three times in the Eared Grebe, and Simmons (1955) only five in the Great Crested Grebe. In all of my Eared Grebe records the pattern followed defeat in a nest establishing encounter. In three of Simmons' records, escape bathing followed aggressive encounters with other grebes; in the other two, it followed an escape dive. Following escape bathing, the Great Crested Grebe puts its head under water and looks around as if looking for something; I did not see Eared Grebes do this. Simmons felt that the grebes were looking for fish predators and that the whole pattern was one of escape. He says that the assumption of this attitude after copulation is a return to escape behavior after this unusually close contact with another bird. I do not doubt that post-copulatory attitude and the escape bathing posture are related. But the upright posture, the arched neck, and the lowered bill are never seen, even separately, in escape behavior. Escape bathing may be derived from the male copulation posture or from the rearing soliciting attitude, but it is probably a carry-over of sexual motivation.

Abandoned Eggs

When most of the pairs were involved in nest establishment, eggs began to appear. At first they were not brooded but simply abandoned on flimsy platforms. These were "yard eggs" in the same sense as those of galliforms and show readiness of the gonads before maturation of the incubation behavior. The hormonal basis of maturation of incubation behavior in grebes is not known, but it may well be related to increased production of the anterior pituitary hormone prolactin which is known to stimulate broodiness in pigeons and chickens (reviewed in Sturkie, 1954).

The first few days these eggs were not pecked, but after this all eggs found had a hole pecked in the top. Presumably a grebe pair may fight for and gain a platform with an egg, peck the egg, and push it off the nest. Just before final clutches were started on Westwick Lake in 1956 there was a broken egg under nearly every platform, and two under some. I never saw the grebes peck an egg, but the pecks were clearly those of small bills, and pecking was done when no other birds were around the area. The contents were not eaten. As the season progressed, the birds became more and more vigorous in guarding their platforms, and they began to incubate the eggs as they laid them. These incubated eggs were the eggs of the final clutch.

Two clutches of pecked eggs were found in the last week of incubation. One bird of each pair may have died or deserted the nest. Plate shows an abandoned egg that has been pecked.

Nest-establishment behavior begins about the same time, but it may end as early as May 20 or as late as July 16. On Westwick and Soren-

sen lakes in 1955 clutches were not begun until June 27 and June 22 respectively. 1956 was similar. If June is warm, the tempo of nest establishment rises gradually to a culmination in the laying of final clutches in the early part of June. But usually June is cold and rainy in the study area, and the birds stop all reproductive activity and rest and feed until good weather in July. When good weather returns, a burst of nest establishment activity leads to incubation.

Lack (1933) and Kendeigh (1934) give a number of examples of delay in nesting with unusually cold or wet weather. These delays may be in nest building, laying, or beginning incubation. They are apparently caused by inhibition of nervous mechanisms, because the changes are too sudden to be explained by changes in hormone balance. The selective mechanism presumably works in such a way that young are hatched when food is abundant, according to Kendeigh (1934). Cold weather did not seem to affect the supply of food for the Eared Grebe or its young, as the grebes fed on plentiful insect larvae in the water. But many young died of exposure during the first few days after hatching. If the birds started to incubate during inclement weather, these losses would probably increase.

Clutch Size

Full clutches varied from one to six eggs, but clutches of one, two, five, and six were relatively rare. The mean clutch size for all nests observed, except those robbed experimentally, was 3.48. Table 2 gives data for all nests where sufficient observations were made to ascertain full clutch size.

TABLE 2

ACTUAL FULL CLUTCH SIZE

	Total of Clutches	c/1	c/2	c/3	c/4	c/5	c/6	M ean
Westwick Lake, 1955 (Marsh colony)	113	1	8	47	45	9	3	3.48
Sorensen Lake, 1955	37	0	0	13	22	2	0	3.70
Total	150	1	8	60	67	11	3	3.59
Westwick Lake, 1956 (Marsh colony, undisturbed nests)	106	0	0	6 9	33	2	2	3.40
Westwick Lake, 1956 (Willows colony)	15	0	0	14	0	0	1	3.42
Sorensen Lake, 1956	22	0	1	16	4	1	0	3.22
Total	143	0	1	99	37	3	3	3.36

There is a significant difference (P = .01) between the distribution of clutch sizes for all nests observed in 1955 and for nests observed in 1956. Sorensen Lake, when the two years are compared, shows a less significant difference (P = .05). Westwick Marsh 1956 when compared with Westwick Marsh 1955, shows a significant difference (P = .01). The Westwick colonies had many more nests than the Sorensen colonies, so the total figure for the year approaches that for the comparison of the two large Westwick colonies. Significant differences between the clutch sizes of one lake from year to year are indicated.

When two colonies are compared in the same year, there is less difference between them. Westwick compared to Sorensen in 1955 shows no significant difference (P = .30). Westwick Marsh 1956 when compared to Sorensen 1956 and to Westwick Willows 1956 shows a slight difference (P = .05). Two colonies of birds under the same environmental conditions may, then, have clutch sizes which are significantly different, but the differences are not as great as those between two years of the same colony. The marsh colony was higher in mean clutch size than Sorensen Lake in 1955 and lower in 1956.

Indeterminate Clutch Size

One fresh egg was taken from each of thirty-two nests within the Westwick Marsh colony in 1956. The environmental conditions (except for the robbing) were exactly the same for robbed and undisturbed nests. Clutch sizes for the robbed nests are shown in Table 3.

TABLE 3.

INDUCED CLUTCH SIZE (BY ROBBING)

Westwick Lake 1956 (Marsh colony)	No. of Clutches	c/1	c/2	c/3	c/4	c/5	c/6	c/7	Mean
Second egg removed	15	0	5	7	2	1	0	0	2.93
Third egg removed	14	0	5	7	1	0	1	0	2.92
Fourth egg removed Total eggs	3	0	0	2	1	0	0	0	
in robbed nests	32	0	10	16	4	1	1	0	2.97
Total eggs laid	32	0	0	10	16	4	1	1	3.97

The total number of eggs laid in the experimental clutches is significantly different (P = .01) from the control clutches in the same colony. In the absence of environmental differences the birds responded to the loss of an egg by replacing it, making up fifty percent of the loss. The same percentage of loss was made up whether the third or the

second egg was taken. The first egg could not be taken because the nest would have been abandoned, and the data for the fourth egg removed are too few for analysis. Lack (1947) and Davis (1955) reviewed the incidence of determinate and indeterminate laying in birds. Columbidae, some Passerines, and many Charadriiformes are strictly determinate. Only the fixed number of oocytes are formed and these are laid whether eggs are taken from the nest or added to it. Many passerines, Anatidae, and Galliformes are indeterminate layers and keep laying until a predetermined number of eggs are in the nest. In these birds laying may not be suppressed by the addition of eggs to the nest. All indeterminate layers and the determinate passerines are to a certain extent variable in their clutch sizes. The Eared Grebe fits into the indeterminate group with those of the passerines which replace only a limited number of lost eggs. The mechanism for controlling the end of laying in indeterminate layers which have not been robbed is apparently not known for any species.

Synchronization of and Intervals between Egg Laying

Clutches of one colony were all started very close together in time. In the Westwick Willows colony 1956, the first eggs for all 22 clutches started were laid within a four day period. (Only 15 of these lend themselves to clutch size analysis.) Laying of first eggs in the larger colonies was more spread out; in 180 clutches started in Westwick Marsh 1956, all first eggs were laid in a thirteen day period. Darling (1938) found that in gulls larger colonies had a smaller span of first egg dates than smaller colonies. He felt that the greater the number of birds, the greater the stimulating effect of the group courtship, and therefore the greater the synchronization of egg laying. Nest establishment activities must be highly stimulating and those birds which are not yet involved swim back and forth watching. Also egg pecking would seem to hold back the first birds to lay until the whole group is ready. The resulting synchrony, while striking, is not so striking as that seen in Darling's gulls. Perhaps late migrants laid late in the large colony, or possibly the large colony had more young birds which laid late. The clutch size average of late layers was the same as that of early lavers.

Darling showed that synchronization in gulls reduced the percentage loss of young by predation. The Eared Grebe seemed to have no predators in the lakes studied, and therefore colonialism and synchronized laying for them serves no purpose in protection of eggs and young.

Data on the interval between eggs in a single clutch are difficult to obtain. In order to get large numbers of records, work was concentrated in the Westwick Marsh colony. Counts took nearly two hours and could not be made more than once a day for fear of disturbing incubation too much. On cold rainy days they had to be omitted altogether because of the danger of the eggs being chilled. Further studies should include more intensive study of fewer nests. In one four-day period before clutches in these nests were complete, fourteen nests held four fresh eggs, fifteen three, and three nests five. I have three records of two days skipped between eggs and two of three days between eggs. If the normal laying is every day, as it is in most passerines, skipped days occurred in 50% of the clutches. Lunk (1955 unpub.) showed that while Rough-winged Swallows (*Stelgidopteryx ruficollis*) regularly lay every day, 20% of the clutches showed skipped days.

In one instance I made counts in the evening, and the morning and evening of the next day. The following were noted:

1 egg laid between:	no. nests
8:00 р.м. and 10:00 л.м.	15
10:00 A.M. and 8:00 P.M.	13
no eggs whole 22 hours	21

All of these birds laid at least one more egg after this period. Skutch (1952) showed that most of the passerines he studied laid shortly after dawn. A few laid in late morning or very early afternoon. A caprimulgid laid in the afternoon. More detailed data on fewer nests would clarify the situation for the grebes.

SUMMARY

The behavior of the Eared Grebe was studied in 1955 and 1956 in the Cariboo Region of British Columbia.

The Eared Grebe has five courtship patterns: an advertising display, habit preening, head shaking, the standing penguin dance, and the peculiar cat attitude. Comparison is made with the courtship patterns of the European Great Crested Grebe, as reported by Simmons. Both sexes have the same displays.

Threat and escape attitudes are described.

Eared Grebes are colonial birds, with remarkable synchronization in the transition of the colony from courtship behavior in early May to nesting behavior in the latter part of the month. When nest-building begins courtship ceases.

During nest establishment groups of birds frequent areas with reeds and floating vegetation, there is a soliciting display, and temporary platforms are made and abandoned. The females appear to do the actual nest building, but the lack of any striking sexual dimorphism leaves room for error. The nest is a floating heap of debris, on a

foundation of reeds, with the slightly rimmed cup rising only an inch or two above the water, so that the eggs are constantly damp. Nests are from one to three feet apart, in water one to three and a half feet deep.

Copulation occurs on the nest from the time the first platforms are made until the end of egg laying.

Eggs are laid and abandoned before the nest is fully built. Full clutches varied from one to six, three or four being usual; mean clutch size was 3.48.

Experiments in the removal of eggs indicate that the Eared Grebe is an indeterminate layer, but replaces only a limited number of lost eggs.

There is considerable synchronization in the beginning of egg laying among birds of a colony, particularly in the smaller colonies. The usual interval between egg laying was not definitely established, but in about 50 per cent of the clutches there was one day skipped, and in some cases two or even three days elapsed between eggs.

LITERATURE CITED

- BUDDLE, G. A. 1939. Some notes on the breeding habits of the Dabchick. Emu, **39**(2): 77-84.
- DARLING, F. F. 1938. Bird flocks and the breeding cycle. Cambridge.
- DEUSING, M. 1943. Nesting habits of the Pied-billed Grebe. Auk, 56: 367-373.
- DUBOIS, A. D. 1918. An experience with Horned Grebes (Colymbus auritus). Auk, 36: 170-180.
- GROSS, A. G. 1949. The Antillean Grebe at Central Soledad, Cuba. Auk, 66: 42-52.
- Hosking, E. J. 1949. Horned Grebe—courtship and display. Canadian Nature, 11: 150-153.
- HUXLEY, J. S. 1914. The courtship habits of the Great Crested Grebe; with an addition to the theory of natural selection. Proc. Zool. Soc. London, 25: 491-562.
- KENDEIGH, S. C. 1934. The role of environment in the life of birds. Ecol. Mono., 4: 299-417.
- KILHAM, L. 1954. Courtship behavior of the Pied-billed Grebe. Wilson Bull., 66: 65.
- LAWRENCE, G. E. 1950. The diving and feeding activity of the Western Grebe on the breeding grounds. Condor, **52**: 3-16.
- LACK, D. 1933. Nesting conditions as a factor controlling breeding time in birds. Proc. Zool. Soc. London, **1933**: 231-237.
- LACK, D. 1947. The significance of clutch-size. Ibis 89: 302-352.
- LUNK, W. A. 1955. The Rough-winged Swallow: a comparative study based on its breeding biology in southern Michigan. Ph.D. thesis for U. of Michigan. Unpubl.
- MUNRO, J. A. 1941. The grebes. Occas. Papers B. C. Prov. Mus., no. 3.
- MUNRO, J. A. and I. MCT. COWAN. 1947. A review of the bird fauna of British Columbia. B. C. Prov. Mus. Special Pub., no. 2.

SIMMONS, K. E. L. 1955. Studies on Great Crested Grebes. Avicult. Mag., 61: 3-13, 93-102, 131-146, 181-201, 235-253, 294-316.

SKUTCH, A. F. 1952. On the hour of laying and hatching of bird's eggs. Ibis, 94(1): 49-61.

STURKE, P. D. 1954. Avian Physiology. Cornell U. Press, New York.

SUFFERN, C. 1950. Note of Little Grebe. Brit. Birds, 43: 90.

TINBERGEN, C. 1942. An objectivistic study of the innate behaviour of animals. Bibliotheca Biotheoretica, ser. D, 1: 39-98.

TINBERGEN, N. 1951. The study of instinct. Clarendon Press, Oxford.

WETMORE, A. 1920. Observations on the habits of birds at Lake Burford, New Mexico. Auk, 38: 221-247.

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