

THE BEHAVIOR OF THE HORNED GREBE IN SPRING

ROBERT W. STORER

Museum of Zoology
University of Michigan
Ann Arbor, Michigan 48104

The Horned Grebe (*Podiceps auritus*) is a widespread and common breeding bird in the rolling pothole country of western North America and suitable parts of northern Europe and Asia, yet almost nothing has been written about its behavior. The purposes of this paper are to describe the behavior of this species on the breeding grounds prior to egg-laying, to compare the behavior of this species with that of related grebes, to offer suggestions concerning the evolution of some of the behavior patterns, and to compare behavioral with other kinds of evidence relating to the phylogeny of these birds.

The closest relatives of the Horned Grebe are the Red-necked Grebe (*Podiceps grise-gena*), Great Crested Grebe (*P. cristatus*), Eared Grebe (*P. nigricollis*), Silver Grebe (*P. occipitalis*), and Taczanowski's Grebe (*P. taczanowskii*). The head patterns of these species are shown in figure 1. Two other species, the Great Grebe ("*Podiceps*" *major*) and the Western Grebe (*Aechmophorus occidentalis*) are somewhat more distantly related to the Horned Grebe (Storer 1967) but are included in the discussion.

The Red-necked and Eared Grebes, like the Horned, have a Holarctic distribution, but the Eared also has isolated populations in Africa and, formerly, in the Andes of Colombia. The Great Crested Grebe is widely distributed in Eurasia, Africa, Australia, and New Zealand. The Silver Grebe is found in much of temperate South America, ranging north in the Andes to Ecuador; and Taczanowski's Grebe, a close relative of the Silver Grebe, is confined to Lake Junín at 13,400 ft elevation in Perú. The Great Grebe is widely distributed in South America from southern Brazil and Perú to Tierra del Fuego, but unlike the Silver Grebe, it is not found at high elevations. The Western Grebe is found in western North America, ranging south to the Mexican Plateau. Thus the Horned, Red-necked, and Eared Grebes are sympatric in varying combinations with the Great Crested Grebe in Eurasia and with the Western Grebe in North America. In South America, both the Silver and Taczanowski's Grebes occur on Lake Junín, and the Silver Grebe is widely sympatric with the

Great Grebe. The sympatry, particularly in the Northern Hemisphere, has presumably resulted in the evolution of specific differences in the nuptial plumage and courtship patterns which are effective in preventing hybridization and also differences in size, gregariousness, and feeding habits which may have resulted in reduced competition.

The behavior of the Great Crested Grebe is well known through the pioneering paper of Huxley (1914) and Simmons' monograph (1955). Papers by Wobus (1964) on the Red-necked Grebe, by Mrs. McAllister (1958) on the Eared Grebe, by Nero (1959 and in Palmer 1962) on the Western Grebe, and by me (1963b) on the Great Grebe provide some basis for comparison, although none approaches Simmons' study in completeness. Having had some field experience with all eight of the species concerned, I am fortunate in being able to make firsthand comparisons and to interpret the published work on these species.

Although my interest in the Horned Grebe dates from the 1930s when I first watched transients displaying in New Jersey, most of the observations on which this paper is based were made at potholes above the Qu'Appelle Valley of Saskatchewan in May and June 1959 and from 10 to 27 May 1966, and in the Minnedosa pothole country of Manitoba from 4 to 16 May 1967. These data were supplemented by observations made in several other years since 1953 in North Dakota and Alberta and by notes on wintering birds in California and transients in Michigan.

Most of the observations were made from a parked car, which proved a satisfactory blind and was sufficiently large for operating both a motion picture camera and sound equipment. Motion pictures have proved particularly valuable in describing complex behavior and in preparing the figures.

For ease in analysis, the complex courtship ceremonies are broken down into simple postures, movements, vocalizations, and displays. The terms "posture" and "movement" are used for the simpler elements of more complex patterns. "Display" and "ceremony" are used in the sense of Simmons (1955:182), who adapted

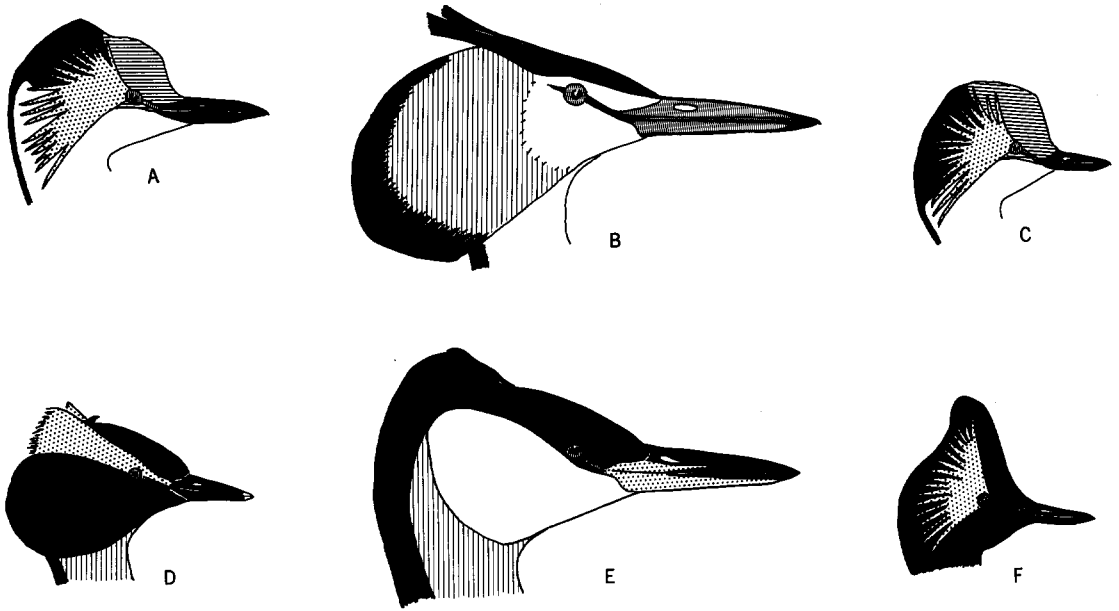


FIGURE 1. Heads of the six species of *Podiceps*, *sensu stricto*, in nuptial plumage. A. *P. taczanowskii*, B. *P. cristatus*, C. *P. occipitalis*, D. *P. auritus*, E. *P. grisegena*, F. *P. nigricollis*. Vertical hatching, rufous (coarse) or red (fine); horizontal hatching, gray; stippling, yellow or buff.

Huxley's usage (1914). The names used for the courtship movements are taken from McKinney (1965) because these movements in grebes are in general homologous with those in waterfowl and probably many other birds. The other names for behavior patterns are largely taken from the works of Simmons and Huxley. In a few cases I have coined new names, hopefully using words which aptly describe the behavior without implying purpose.

Of all kinds of behavior, courtship differs most from one species to another. I have therefore concentrated on studying and describing this aspect. But because elements of courtship patterns were probably derived from day-to-day behavior, discussion of the latter is needed background for any discussion of the origins of courtship displays.

THE NUPTIAL PLUMES AND DISPLAY

In nuptial plumage Horned Grebes are striking birds. The neck and sides are bright chestnut, and three groups of plumes adorn the head: the rounded, black tippets, the buffy lateral crests or "horns," and the small, medial, black "duck-tail" on the crown. Males and females are similar, but the females are smaller, their nuptial plumes are shorter than those of the males, and the chestnut of the neck and flanks often is paler and duller. Thus, while it often is difficult to tell the sex

of a lone bird, members of a pair can usually be distinguished when they are together.

The head plumes are conspicuous in displays and the positions of these plumes are integral parts of the displays. In the Ceremonial Turning Away and the posture preceding the Weed Trick, all the plumes are flattened against the head. The Furtive posture is similar, except that the duck-tail is raised; the raising of the duck-tail may thus be an expression of appeasement or anxiety. In Advertising, the tippets and horns are fully spread vertically but little flared out, whereas in Rearing and before, during, and dismounting after copulation, the tippets are fully spread and flared out so that they are almost at right angles with the sides of the head. At the height of the Penguin Dance and in the Weed Rush, the horns and tippets are held in a posture intermediate between those during Advertising and copulation. From this it seems likely that flaring of the horns and tippets expresses a strong sexual component in displays.

The function of the chestnut color of the neck and sides is not clear. In part, it may be cryptic, for birds in nuptial plumage are far less conspicuous on the potholes where they breed than birds in winter plumage would be. It also may be part of the pattern which functions in species recognition, for the Eared Grebe, the species which most resembles the Horned on the breeding grounds, has

a black neck. The position of the line of demarcation between the chestnut of the neck and the white of the breast is probably significant. At most times, the white of the underparts remains below the waterline, but in Advertising, when conspicuousness is advantageous, the head is stretched upward and the white of the somewhat puffed-out breast is prominent below the chestnut of the neck.

LOCOMOTION

Flying. On the breeding grounds, Horned Grebes fly more than one might expect. I have observed them flying under at least four sets of circumstances: approaching their mate after a separation, attacking another bird, flying away from a pothole in the evening, and flying upwind. Flying to the mate occurs occasionally when members of a pair are separated and one of them Advertises loudly. Such a flight may result in a Discovery Ceremony in both the Horned and Red-necked Grebes. In attacking another bird, a Horned Grebe, usually a male, first uses an intense threat posture, then flies low over the water at the other bird, pattering with his feet. On landing, he may engage his opponent on the surface or, more frequently, both dive and the pursuit continues under water.

Flight occasioned by the other two sets of circumstances is characteristically preceded by a special pre-flight posture (fig. 2). In this posture, the head is held high, about as in the Advertising posture, but the crests and neck feathers are "slicked down." The bill is pointed somewhat above the horizontal, and the head is held back but the neck is more nearly vertical than in the Z-neck posture. Birds in the pre-flight posture swim about "nervously" for from several seconds to a minute or two before taking off. Before the grebes settle down to nest, they may visit potholes for a day or more and then leave. I do not know whether these are transients on their way north or local birds visiting several potholes before selecting one for nesting, or both. The birds leave the potholes well after sunset. For example, on 15 May 1959 all nine birds which spent the day on a pothole near Fort Qu'Appelle, Saskatchewan, left between 20:55 and 21:21 MST, the apparently unmated bird leaving first and landing on a pothole across the road, and the others leaving in pairs at 21:05, 21:16, 21:20, and 21:21. The pairs circled the pothole gaining altitude before flying off, and none landed on the pond across the road, although the lone bird which had landed there earlier Advertised loudly while the last two pairs were circling.

Pre-flight behavior and taking-off were observed at the same two potholes on the evenings of 15 and 16 May 1966 between 20:30 and 22:00. I have also seen this behavior on the Huron River, near Ann Arbor, Michigan. Three Horned Grebes were on the river shortly after sunset on 20 April 1961. Two of the birds, possibly paired, remained close together on the water. About 19:27 EST the lone bird assumed the pre-flight posture and swam about, turning this way and that in a "nervous" fashion. Twice it dove, I thought with the wings slightly spread, wing-flapped, did at least two swimming-shakes, and once flapped across the water toward the pair before taking off at 19:37. It did not circle but flew directly east over a railroad bridge, possibly landing beyond on the river.

Upwind flights are seen on very windy days and serve to take the bird from the lee side of a pothole to the windward one. I saw one male make such flights, once on the afternoon of 16 May 1966 and twice within 6 min on the following afternoon. The last flight was filmed. The pre-flight posture resembled that of the evening flights except that the head was held somewhat lower and more forward, probably because of the strong wind; and the bird remained facing the wind the whole time the attitude was used. The female of another pair made a flight of 20 to 30 ft against a wind which was strong enough to make whitecaps on the pothole. Before landing, this bird hovered briefly with her feet in the water.

Swimming and diving. Horned Grebes swim on the surface with alternate strokes of the feet, but when resting they usually keep one foot shipped under the wing and maneuver with the other. Under water, simultaneous strokes of the two feet are the rule. The two commoner types of dive, the "feeding dive" and the "springing dive," described by Lawrence for the Western Grebe (1950:3), are also the common types for the Horned Grebe, but in the latter species the two types grade into each other. Shortly before submerging, the feathers of the head, neck, and body are "slicked down," expelling most of the air between them and the skin and thereby increasing the bird's specific gravity (fig. 2). When an Eared Grebe is on the surface, the body feathers, especially those near the tail, are erected more than those of a Horned Grebe, and they give the bird a characteristic high-sterned look. The slicking-down movement before diving has thus become exaggerated and probably has assumed a signal function as well as that of reducing the bird's specific gravity.

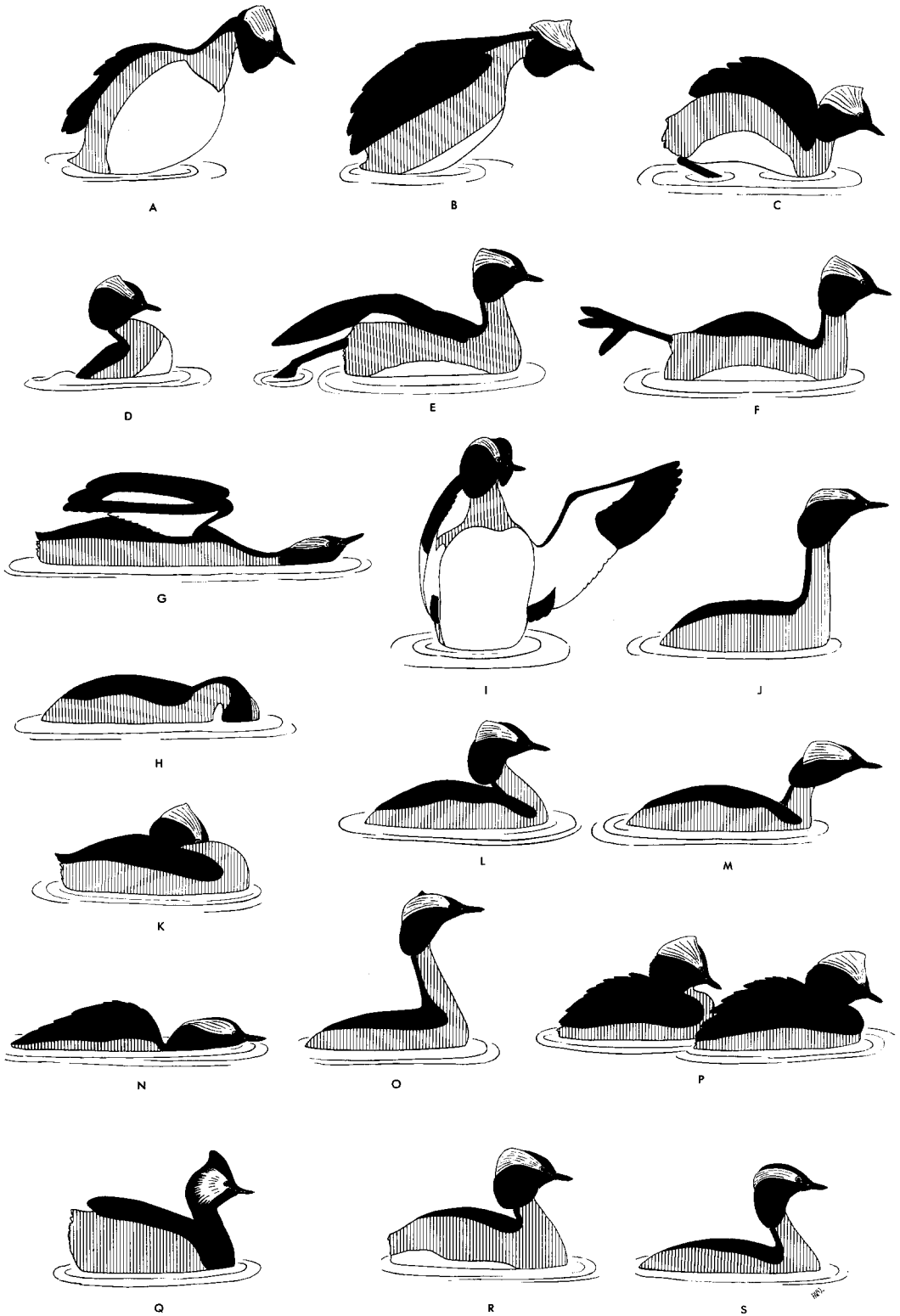


FIGURE 2. Day-to-day behavior of the Horned Grebe. A, B, and C. stages of the swimming-shake, D. bathing, E and F. wing-and-leg-stretch, G. both-wings-stretch, H. looking under water, I. wing-flapping, J. pre-flight posture, K. resting posture ("pork-pie"), L and M. head-bobbing, N. threat, O. appeasing posture, P. Triumph Ceremony, Q. Eared Grebe in normal posture before slicking down, R. Horned Grebe in same posture, and S. slicked down.

I have no detailed notes on "alarm dives" or "surface dives" (Lawrence 1950:4), but they may also be used by Horned Grebes. These birds may attack members of their own or other species by threatening and diving or by flying and diving. In the latter case at least, the wings may be used in submerging. I have not seen Horned Grebes use Ripple Dives like those used by Great Crested Grebes in the Discovery Ceremony (Huxley 1914: 512; Simmons 1955:190) or by Pied-billed Grebes (*Podilymbus podiceps*). The other ritualized dives employed in courtship are discussed elsewhere.

Resting. Horned Grebes, like other members of the family, rest in the well-known "pork-pie" attitude with the head directed forward and lying to one side of the neck (fig. 2). While in this posture, one foot is often shipped under the wing. When one foot is so shipped, the opposite side of the body rests somewhat lower in the water. In seven of eight observations, the grebes were seen to keep the head to the right (or high) side of the neck when the right foot was shipped, and vice versa. According to Simmons (in litt.), Great Crested Grebes also rest with the head on the high side.

FORAGING AND FEATHER-EATING

Studies by Wetmore (1924) and Munro (1941) have shown that Horned Grebes take a considerable variety of animal food. Crustaceans and fish predominate in stomachs of birds taken on salt water during the winter, and aquatic insects make up the bulk of the food taken on the breeding grounds. The methods of foraging are also diverse. On 26 October 1953 I watched a Horned Grebe diving in shallow water near a pier at Monterey, California. While on the surface, the grebe moved its feet alternately, but while under water used them simultaneously, and even when pursuing a fish it kept both wings folded against the body. The bird chased several schools of small fish (approximately three inches long). The schools successfully evaded the bird by circling sharply to the left or to the right or by dividing into two groups, one circling in each direction and both coming together after the bird passed between them. These chases were repeated several times, the bird making two or three attempts in one dive. Finally, after making an unsuccessful pass at a school, the bird found a fish which had become separated from the school and without surfacing, swam it down. The fish swam rapidly near the surface but made no attempt to dodge or circle. Just as the grebe

was about to catch it, both swam under the wharf. A few second later, the grebe swam out with the fish, worked it around in its beak, and swallowed it head first.

At all seasons, most of the food is obtained by diving. As in the above instance, large prey such as fish or amphibians is brought to the surface and pinched and shaken before it is eaten. Small items are evidently swallowed under water, for I have not seen foraging grebes surface with small insects in the beak or make swallowing motions when I did not see food in the beak. Wetmore (1924:13) mentions Horned Grebes feeding on insects cast on the surface of the water, and I have several times watched these birds picking up insects from the surface or from emergent vegetation, especially when there was a large hatch of midges. Like Great Crested Grebes (Simmons 1955:98), Horned Grebes occasionally look for food by dipping the head so that the eyes are below the surface (fig. 2), but on potholes where small invertebrates are abundant, the birds evidently find their food while they move about under the water.

Periods of foraging usually alternate with periods of preening, and for the several days prior to incubation, periods of nest-building and sexual behavior are interspersed with these. Observations on a pair of Horned Grebes near Fort Qu'Appelle indicate that in the period prior to egg-laying the female spends more time foraging than the male. The female of this pair laid the first two eggs of her clutch between 16:37, 17 May, and 14:13, 19 May 1966. On 14 May between 10:00 and 15:32, she spent approximately 172 min foraging; the male spent 86 min. Between 8:50 and 11:30 the following day, she spent 112 min foraging and the male 80; and between 12:27 and 16:27 on 16 May she foraged 112 min, the male 95. This greater amount of foraging is probably correlated with the production of eggs.

Since describing pellet-casting in the Horned Grebe (1961), I have observed the process at least three times and collected two of the birds at known times after they cast pellets. I was not able to retrieve the pellets. On 26 May 1966 D. E. Gill and I watched the pair mentioned above. The male, after being relieved at the nest, preened for 5 min or so and began a series of approximately 15 drinking motions. Then leaning his head forward, he shook it several times and coughed up an irregularly-shaped pellet about two inches long. He dove and started foraging almost immediately. When I collected him 2 hr later,

there was a mass of insect remains and one or two feathers in the large chamber of the stomach and a plug of feathers wedged tightly in the pyloric lobe. On 6 May 1967 J. A. Feduccia and I watched pellet-casting by another male Horned Grebe. This was preceded by at least 10 drinking motions and followed by the bird's looking under the water as though for the pellet. Shortly afterwards he started feeding and was collected 23 min later. The large chamber of his stomach contained 9 leeches, at least 197 caddis-fly larvae, 1 water boatman (*Corixidae*), 7 beetles (2 *Dytiscidae*, 5 *Gyrinidae*), 3 fruit flies (*Drosophilidae*), 6 large or medium-sized feathers, and 17 very small feathers or parts of feathers. The pyloric lobe contained a plug of 260 hair-like feather fragments. Assuming that no food items remained in the stomach after the pellet was cast, the bird caught and ate food items at the rate of 9.4 per min. Where food is this abundant and easily taken, the time spent foraging is probably a good indication of the amount of food taken.

The function of feather-eating by grebes has been discussed by many authors, but with few conclusions. Wetmore (1924:4) noted that the pyloric lobe of the stomach is almost invariably plugged with feathers and "that feathers occur in greatest abundance and most commonly in stomachs containing remains of fishes and hard-bodied insects, and that they are less abundant (or are even occasionally absent) in gizzards containing soft-bodied larvae or crustaceans that are easy of digestion and assimilation." He went on to suggest that the feathers act as a strainer to prevent fish bones or large pieces of chitin from entering the intestine.

In examining the intestines of grebes for parasites, I have found the contents quite free from bits of chitin or other "roughage," even when the only feathers in the stomach were those of the pyloric plug. From this, I conclude that the plug is an efficient strainer. Furthermore, the fact that adult grebes feed feathers to their newly hatched young suggests that early establishment of such a plug may be important. The masses of feathers in the large chamber of the stomach are a different matter. As I have mentioned in an earlier account of pellet-casting (1961), grebes living on fishless bodies of water and depending on arthropods for much of their diet rapidly accumulate indigestible chitin in the stomach. This requires rather frequent pellet-casting, and feathers do not accumulate in the stomach, although they remain in the

pyloric lobe even during the casting process. On the other hand, when grebes are feeding on fish, feathers may function to hold the bones in the center of the stomach and in this way may protect the walls while the bones are being dissolved by stomach acid. The fact that the bones are dissolved makes frequent pellet-casting unnecessary and permits the accumulation of feathers in the stomach.

COMFORT MOVEMENTS

In birds, comfort movements tend to be conservative, and homologous movements are often easily recognizable in birds of widely separate orders. Hence for these movements, I think it best to use a nomenclature which may be applied to all or most birds. To date, McKinney's analysis of the comfort movements in waterfowl (1965) appears to be the closest approach to this ideal, and I have followed it where possible. Because the tail of grebes is minute, motions associated with it are reduced, lost, or overlooked. Thus they are not mentioned in the descriptions which follow.

Swimming-shakes (McKinney 1965:132-133) are commonly observed in Horned Grebes (fig. 2). The movements are essentially like those of the Anatidae. They are frequent in bouts of preening and often terminate such bouts. They occasionally appear, I think, as displacement activities (in the sense of Tinbergen 1951:113), as when members of a pair meet and pass each other while foraging, before mounting, or before taking flight. I have no evidence that these swimming-shakes have become ritualized or that they have a special signal function. I have not seen grebes perform body-shakes, the corresponding movement on land (McKinney 1965:126).

Rapid head-shakes, similar to those of the waterfowl (McKinney *op. cit.*:135), are performed by Horned Grebes as a comfort movement, often in bouts of preening and after bill-dipping. Ritualized head-shaking has become a part of the Head-shaking and Discovery ceremonies (which see).

I once recorded a Horned Grebe in what may correspond with the wing-shake of the Anatidae (*op. cit.*:130-132). The feathers of the closed wings were ruffled and the wings shaken simultaneously in a motion which reminded me of a swimming-shake. This may be the evolutionary source of Wing Quivering (see p. 199).

A common motion in Horned Grebes may correspond with the wing-shuffle of ducks (*op. cit.*:147-149). In this, the closed wings remain in their usual position on the back but are moved forward and back in an undulating

motion. This may be kept up for several minutes, and, as in the wing-shuffle of ducks, occurs after bouts of preening.

Wing-flapping in grebes (fig. 2) closely resembles that in the Anatidae (op. cit.:141-142). It is a usual sequel to bathing and less often to preening. I once observed it, possibly as a displacement activity, prior to flight.

Foot-shaking is commonly performed by grebes. In the Horned Grebe, the motion resembles that described for ducks on the water (op. cit.:147). The motion regularly precedes "shipping" the foot under the wing and has been well described by Sim (1904:71) for the Red-necked Grebe. In the Horned Grebe the motion is very rapid and the foot is not held up like a flag for several seconds as it frequently is in the Western Grebe. The function of the motion appears to be removal of water from the foot.

The three stretching movements, wing-and-leg-stretch, both-wings-stretch, and jaw-stretch, described by McKinney (1965:150-152) for the Anatidae are all commonly performed by grebes (fig. 2). In the wing-and-leg-stretch, one foot is extended backward over the water and the toes spread. The wing of the same side is then spread and held back for a second or two after which it is folded, and finally, the foot is brought forward. This stretch is often seen in bouts of preening. Both-wings-stretches are less common in the Horned Grebe than wing-and-leg-stretches. In the former (fig. 2), the neck is held low, on or near the surface of the water and stretched forward, the bill is pointed upward at an angle, and the folded wings are raised, much as in McKinney's photograph of the Mallard in this attitude (1965:pl. I). In contrast to the Pied-billed and Western Grebes (personal observations), the Red-necked Grebe (Wobus 1964:29), and the Great Crested Grebe (Simmons 1955:100), the raised wings are not spread, nor have I seen the stretch prolonged beyond a second or two, or given repeatedly as is frequently the case in Western Grebes. The posture of the head and neck in the four species is similar. The both-wings-stretch is the only comfort movement of grebes in which I have found appreciable interspecific differences, and I have no explanations to offer for the origin and significance of these differences.

I have seen Horned Grebes jaw-stretch both while on the nest and while on the water. Neither it nor the other two stretching movements appear to have become ritualized or incorporated into the displays of grebes.

Of the cleaning movements described for

the Anatidae by McKinney (1965:152-158), scratching is the most obvious in the Horned Grebe. As in the ducks and the Great Crested Grebe (Simmons 1955:100), scratching is direct, that is, over the closed wing. I have no certain observations of foot-pecking, although I once watched a grebe with one foot shipped under the wing raise the wing and make motions which could have been directed at either the foot or the underside of the wing.

Bill-cleaning movements like those of the Anatidae may be completely replaced by bill-dipping in the grebes. The latter movement is frequently seen and is usually followed by head-shaking movements. The two movements have become ritualized into the Dip-shake of the Western Grebe (Nero 1959:294). I once saw a Horned Grebe bill-dip and then head-shake among a series of aggressive actions, a situation in which the combined movements appeared to be a displacement activity.

Of the bathing motions described by McKinney for the Anatidae (1965:171-176), head-dipping and wing-thrashing are commonly performed by grebes (fig. 2). During bathing, Horned Grebes puff out the breast more, hold the head lower, and keep the body more nearly upright than ducks do. Wing-flapping and preening usually follow bathing. A grebe may dive several times while bathing, each time emerging in the bathing posture.

Oiling and a great variety of nibbling motions are common preening activities of grebes. I have made no attempt to analyze them and doubt that there are many interspecific differences in these movements. The motion of turning the head back and running the bill through the remiges or scapulars has become ritualized as Habit Preening (see p. 193).

AGONISTIC BEHAVIOR

While Horned Grebes during migration may remain together in flocks with little apparent aggressive behavior, on the breeding grounds they become pugnacious, defending their territories vigorously against others of their species and at times even putting ducks to rout. The common form of threat (fig. 2) corresponds to the Forward Display of the Great Crested Grebe (Simmons 1955:138-139). Threatening birds may make short dashes at rivals, swimming very rapidly and stopping suddenly, or they may rush their rivals more vigorously, half flying and half pattering over the water. If the rival holds its ground, breast to breast fighting may follow. In this the wings are held open and may be used to raise the bird above its opponent. Although it is difficult to determine just how the feet are

used, it is my impression that they are used for combat as well as for keeping the bird upright. If an attacked or threatened bird dives, the attacker almost always dives and continues the pursuit under water. If an attacking bird catches another by the head or neck, both may dive and come up with the attacker still holding on. Drawing an analogy from waterfowl behavior, several authors have incorrectly described similar behavior in Pied-billed Grebes as forced copulation (see McAllister and Storer 1963).

Token Diving is a well-known threat display in the Great Crested (Simmons 1955:139) and Red-necked Grebes (Wobus 1964:54). I have seen it performed by the former species and by both the European and American races of the latter, but never by the Horned Grebe or any other species.

The appeasing posture of the Horned Grebe in general resembles the "furtive-posture" of the Great Crested Grebe (Simmons 1955:142). In it, the Horned Grebe holds the head high and the crests and tippets flattened against the head and neck, but it raises the duck-tail and holds the head back so that the posture of the bird resembles the letter "Z" (fig. 2).

In territorial encounters, it is usually the male who attacks intruders. After driving off his opponent, the male returns to his mate and the two assume the Hunched Posture (?Cat Display) and swim side by side for a foot or two, trilling (fig. 2). This I have called the Triumph Ceremony in my notes, although the term may not be entirely appropriate because the ceremony is sometimes used when there has been no aggressive encounter. It is quite unlike the "swimming-together" of Great Crested Grebes described by Simmons (1955:188), but it might be an evolutionary forerunner of the use of the Cat Display by the latter species in aggressive situations (op. cit.:144).

That Horned Grebes defend their nests vigorously has been mentioned by several authors. Of these DuBois' account (1919:171-173) is one of the most detailed. While observing Horned Grebes from a parked car, I occasionally saw them become uneasy and bob their heads forward and back as a coot does, but with a slower, smoother motion (fig. 2). Greater uneasiness, especially when the mate was not near, more often resulted in Advertising, and when still more alarmed, they often swam away in the Furtive Posture.

COURTSHIP

The displays and ceremonies which result in the formation and strengthening of the pair

bond, as opposed to those which are directly related to the act of mating, are here considered courtship. In grebes, mating usually takes place on the nest or on a similar platform built by the pair. Thus a strong pair bond must be established before building and, in turn, mating can take place. It is therefore not surprising that the courtship and mating behavior should be quite different. The species-specific elements of the behavior which prevent the formation of mixed species pairs are thus largely found in courtship behavior. The mating behavior varies much less from species to species.

Upright Posture. The neck is stretched upward to nearly its full length, the body axis remains horizontal, and the bill is most often held horizontal. Variants of this posture occur in Advertising and several other displays, including agonistic ones. The tail is frequently cocked when this posture is used in courtship displays.

The use of this term stems from Simmons' (1955:141) description and illustration of an "upright pre-attack posture." The term "upright threat posture" is in common use in behavior studies of the Herring Gull (e.g. Tinbergen 1953:53-54) and its relatives; no homology with this behavior of gulls is intended by the use of the term "Upright Posture" in grebes.

Penguin Posture. The neck is stretched upward and the body held nearly vertically. This posture is maintained by vigorous motion of the feet under water. Thus, while it appears to the observer as a posture and is here so classified, it could also be classified as a movement. The Penguin Posture appears to be related to the Upright Posture, and in some displays may grade into it. I believe that the degree to which the body is held vertically, and hence the height of the head above the water, is directly correlated with the intensity of the display. As evidence for this view, I can point out that as Horned Grebes approach each other for a Penguin Dance or for a Weed Rush, they rise higher and higher in the water, and as they move away from each other after these displays, they gradually settle into the swimming posture, and that the Penguin Posture is rarely assumed unless one bird is close to or touching another and rarely maintained for more than a few seconds unless a second bird responds by making an appropriate display. The expression "Penguin position" was used by Huxley (1914:500) for this posture.

Hunched Posture. The bird appears to ride high in the water because the body feathers are partly erected. The head is held close to the body and the ornamental plumes are spread. This term and Spread-wing Posture were suggested to me by Simmons (in litt.) and serve to break down the Cat Display of such species as the Great Crested Grebe into its components. The Hunched Posture is probably derived from agonistic behavior. It is used by Horned Grebes in situations in which the impulse to attack appears to be slightly stronger than that to flee, and in the Triumph Ceremony of a pair after an aggressive encounter with another bird or birds. Its effectiveness in agonistic situations probably results from the apparently larger size of the bird when the feathers are raised.

Bouncy Posture. The head is held low over the back, the bill directed forward, and the breast puffed out and raised. The tail is cocked and the posterior part of the body held low in the water (fig. 3). This posture bears a striking resemblance to the Bridling of the Chestnut-breasted Teal (*Anas castanea*) as figured by Lorenz (1941:257, fig. 31).

The name was suggested by the round, taut appearance of the bird and by its sudden swinging into the dive which immediately follows. The Bouncy Posture is a component of the Bouncy Dive Display, which in turn forms part of the Discovery Ceremony of all but the Great Crested Grebe.

There seems no reason for homologizing this posture with the post-copulatory Bridling of ducks, which Daanje (1950:79-80) believed to be "an intention movement indicating rapid swimming." Once, while watching a Horned Grebe bathing, I saw it dive two or three times, each time coming up in the same place in a posture which I could not distinguish from the Bouncy Posture. Future observations may show that this is a regular part of the bathing routine, and therefore the probable source of the display.

Spread-wing Posture. The wings are partially spread and the upper surface directed forward so that the plane of the wings forms an angle of approximately 45° with the horizontal (fig. 3). This posture is used while the bird is in the Hunched Posture and greatly accentuates the apparent size of the bird. Birds in this posture face the bird to which they are displaying. As far as I am aware, the Spread-wing Posture is only used as a component of the Cat Display (see below).

Daanje (1950) considers this action a ritualization of an intention movement of flight and

remarks on its similarity to displays of birds of several unrelated groups. Not mentioned by Daanje are the very similar defensive displays of several species of owls (e.g. *Asio otus* and *Bubo virginianus*, figured in Bent 1938, pls. 35 and 75, respectively). As in the Hunched Attitude, the apparently increased size of the bird enhances the aggressive effect of a display in which the wings are spread.

Barging. I first used this term in my field notes to describe slow forward motion in the Penguin Posture. The shape of the blunt bodies, especially those of the smaller species, in this posture suggests barges, and the slow motion produced by an obviously great expenditure of effort emphasizes the similarity. In low-intensity Barging when the body is not raised vertically to its full height, it can often be seen that the tail is cocked. Barging is a component of the Barge-and-Dive Ceremony of the Silver and Taczanowski's Grebes (Storer, MS) and appears as a variation in the Weed Dance of some species. It also forms part of a courtship ceremony of the Western Grebe, in which species it has been called "water treading" by Nero (*in* Palmer 1962:101). The latter term, however, does not convey the idea of forward motion and might more appropriately have been applied to the Penguin Posture.

On the one hand, Barging is closely related to the Penguin Dance, as in the Weed Dances mentioned above, and on the other hand, it may grade into Rushing (see below).

Rushing. This term is used here for rapid motion in the Penguin Posture. It is a component of the Weed Rush of the Horned Grebe and a display of the Western Grebe (the "Race" of Nero, *in* Palmer 1962:100). I have selected the term "Rushing" because it describes the motion without implying the competitive or esthetic motivation of such terms as "racing" or "dancing."

In the Barge-and-Dive Ceremony, Barging and Rushing may intergrade (Storer, MS). The increase in speed as Horned Grebes approach each other, rise higher into the Penguin Posture, and perform the Weed Rush suggests that the speed of Rushing may be directly correlated with the intensity of the display.

Porpoising. A bird in the Bouncy Posture suddenly leaps into the air, its body arched, and dives into the water (fig. 3). This is performed by Silver Grebes, and in a somewhat less exaggerated form by Taczanowski's Grebes, in the Discovery Ceremony. This type of dive appears to be a ritualization of

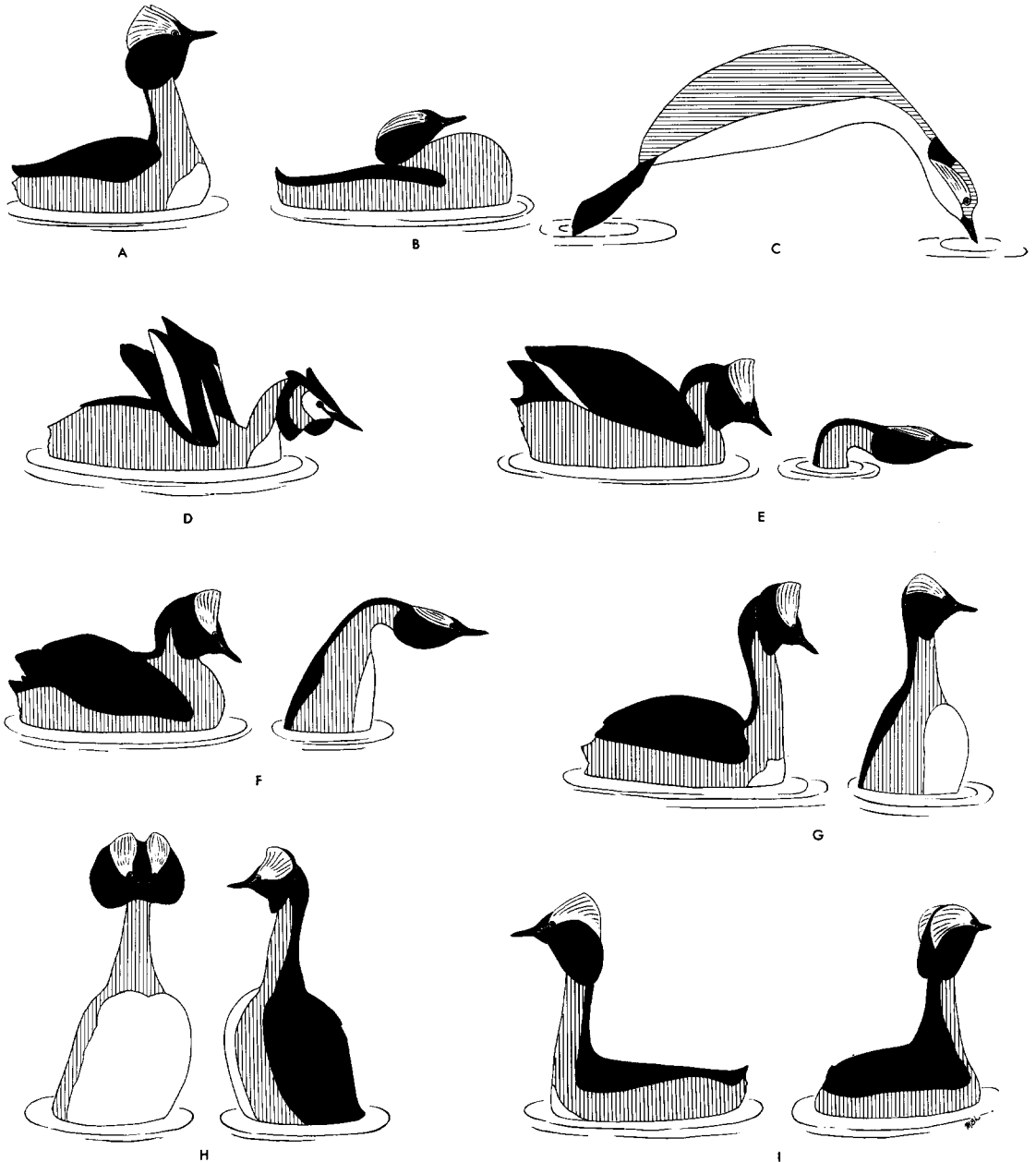


FIGURE 3. Courtship behavior of the Horned Grebe (and other species). A. Advertising, B. Bouncy Posture, C. Porpoising (Silver Grebe), D. Cat Display, with Spread-wing Posture (Great Crested Grebe, after Berg 1916), E, F, G, and H. successive stages in the Discovery Ceremony from the Cat Display and the Ghostly Penguin Display (E) to the Penguin Dance (H), I. Ceremonial Turning Away.

what Lawrence in his paper on the Western Grebe (1950:3) called the "springing dive," a kind of dive which I have seen used by grebes of several species in rough water.

Ripple Dive. Huxley (1914:512) described, but did not name, this type of underwater progression as a part of the Discovery Ceremony of the Great Crested Grebe. This dive is characterized by the bird's remaining so near the surface that a telltale ripple marks

its progress. Silver and Taczanowski's Grebes sometimes use Ripple Dives in this ceremony.

Because Great Crested Grebes also use shallow dives like these when not engaged in courtship, Simmons (1959:218) has referred to them as "travelling dives." He now agrees with me (in litt.) that "the actual underwater progression in the Discovery Ceremony needs a name and that 'Ripple-dive' is most suitable." Pied-billed Grebes (*Podilymbus podiceps*)

and probably other species regularly use shallow dives in which ripples are produced. When one can see only the ripples, it is impossible to tell if ripple dives used under different circumstances are performed similarly and also to tell to what extent, if any, such dives have become ritualized. I would assume, however, that a regular component of so complex a ceremony as the Discovery Ceremony would be ritualized.

An obvious function of a Ripple Dive is to make the location of the bird performing it clear to a bird observing it from the surface, a function also accomplished by a Horned Grebe's performing a series of Bouncy Dives.

Advertising Display. In a full Advertising Display, a Horned Grebe assumes an Upright Posture with the base of the neck or the anterior part of the body puffed out. This area is white, contrasting with the rufous color of the neck and sides. The body feathers are partly erected and the tippets and crests spread but not flared laterally (fig. 3). The Advertising call (see p. 200) is given from time to time as part of this display.

Advertising is best described as an expression of "anxiety" or "unrest," but there is a strong sexual element in the motivation as Simmons (1954:55) has stated in the case of the Great Crested Grebe. It is a common display from early in the courtship season at least until the start of incubation. It may be used still later; Great Crested Grebes (Simmons 1959:217) and Eared Grebes Advertise well after the young are hatched.

When members of a pair have been out of sight of each other for several minutes, one may Advertise. A lone bird is strongly attracted to a playback of recorded Advertising calls and will swim toward the source of these calls, Advertising repeatedly. This response is that of a bird seeking a mate and thus is not primarily related to territory. I have seen Advertising elicited by other stimuli: a lone bird foraging near the shore suddenly became aware of our presence, gave two weak Advertising calls, then swam away. (This suggests a possible connection between the Advertising call and an alarm note.) Another Horned Grebe Advertised when a Pied-billed Grebe made an upwind flight across the pothole. Horned Grebes also Advertised when a Red-necked Grebe took flight and circled over them. Similar responses to other Horned Grebes which had left a pothole and were circling it were noted several times.

The most frequent results of Advertising appear to be the attracting of a potential mate

and the bringing together of a pair which has been temporarily separated. In either case a Discovery Ceremony may follow. In the case of mated pairs, the frequency with which the Discovery Ceremony results decreases as the pair bond becomes stronger. The strongest response to Advertising is flying to the mate followed by a Discovery Ceremony and a Weed Rush and, in decreasing order of strength, swimming to the mate followed by a Discovery Ceremony and a Weed Rush, a Discovery Ceremony without a Weed Rush, a Head Shaking Ceremony, (?normal) preening, and merely swimming slowly together.

Simmons' note on Advertising in the Great Crested Grebe (1954) appears to be the first good description of this display in grebes and, I believe, the first use of this term in studies of grebe behavior. I have used this term, although it does not convey the strong element of anxiety present in the motivation for the display. Mrs. McAllister (1958) has figured and described this display in the Eared Grebe, and I have observed it in all five American species of *Podiceps*, *sensu stricto*. The postures used by these species and the Great Crested Grebe are all very much alike, but there are differences in the degree to which the head plumes are raised. In the Great Crested Grebe, "the conspicuous tippets are not spread appreciably and the crest is depressed" (Simmons 1954:54); in the Eared Grebe, "both crest and neck feathers are raised" (McAllister 1958:291); and in the Red-necked Grebe, the crests and the feathers on the back of the neck are almost fully erected. Advertising is similar in the Great Grebe, "*Podiceps*" *major* (Storer 1963b:283-284), and the well known *cree cree* call of the Western Grebe appears to be comparable, although the posture used by the latter species when giving the call is less stereotyped than it is in the species of *Podiceps*.

There are considerable interspecific differences in the frequency with which Advertising is performed. On the breeding grounds, I have recorded it infrequently in the Red-necked Grebe. Judging from Simmons' account (1954), it is more commonly given by the Great Crested Grebe, and I have found it more commonly used by Horned Grebes than by Red-necks. Wobus (1964) does not describe Advertising in the Red-necked Grebe, but the second call he described (p. 21), "waak," may be the Advertising call. In the Eared Grebe, Advertising is an extremely common form of behavior and is frequently used even after the young have hatched. In this species, the Ad-

vertising call is, to my ears, somewhat variable, and it may be that individuals come to recognize their mates and neighbors by their particular variation of this call. The recognition of individual birds and the appeasing rather than aggressive nature of this call are presumably advantageous in reducing aggressive behavior in colonial species like this one, which nest in thick emergent vegetation where approaching birds cannot be seen until they are close at hand. This variation is a step toward the striking variation in the corresponding call of the Western Grebe (Nero, *in* Palmer 1962:96; personal observations), which almost certainly functions in individual recognition.

The resemblance of the Advertising posture to certain agonistic postures (e.g. the Upright Pre-attack and Furtive Postures of the Great Crested Grebe, Simmons 1955:141-142) suggests a possible derivation from agonistic behavior. In general, the Upright Posture appears to have strong sexual and appeasement elements, and the spreading of the tippets and crests, strong sexual and aggressive elements. Thus the aggressive aspect of the spread head plumes may partially balance the appeasing nature of the posture and the call, allowing the sexual elements to predominate.

Cat Display. A Horned Grebe performing this display assumes the Hunched Posture and droops the wings slightly and then lowers the wrists; the leading edges usually remain between the flank feathers and the bird's sides (fig. 3). The display is used as part of the Discovery Ceremony, by the female in aggressive situations, and by members of a pair in Triumph Ceremonies after aggressive encounters.

The homologous display, which includes the Spread-wing Posture, is well known in the Great Crested Grebe, having been described and figured by both Huxley (1914) and Simmons (1955) and beautifully shown in an early photograph by Berg (1916:133). In her paper on the Eared Grebe, Mrs. McAllister (1958) has described this display and pointed out its similarity to that of the Great Crested Grebe. Her figure, however, does not show the wings spread as fully as had been the rule in my observations. Silver and Taczanowski's Grebes also perform Cat Displays of this type. The Red-necked Grebe has a Cat Display intermediate between the two types but more like that of the Horned Grebe; Wobus figures it (1964:43) and calls it the Swan Attitude ("Schwanenstellung") because of its resemblance to the common aggressive posture of

TABLE 1. Time taken by the phases of a series of Bouncy Dives by a Horned Grebe (expressed as number of motion picture frames at 16 per second).

Emerging	Bouncy Posture	Submerging	Under water
	23	7	57
15	15	8	48
9	17	8	41
7	12	7	26
9	8	8	12*

* Emerges in Ghostly Penguin display.

the Mute Swan. The S-neck posture of the Great Grebe may correspond with this display (Storer 1963b:283).

The Spread-wing Posture is such a conspicuous feature of the Cat Display of the Great Crested and Eared Grebes that, expecting to see a similar posture in the Horned Grebe, I was slow to recognize its Cat Display. Its relative inconspicuousness compared with the homologous display of the other two species may also account for the infrequency with which I have recorded it in situations other than the Discovery Ceremony.

Whether or not the Spread-wing Posture is part of the Cat Display is a conspicuous difference in the Discovery Ceremonies of the northern species and is probably a factor in preventing the formation of mixed pairs. Of the two large species, both of which have white cheeks, and the two small species, both of which have black cheeks and tufts of pale feathers behind the eye, the Spread-wing Posture is used by one and not by the other.

Diving Displays. In the early stages of a Discovery Ceremony, one member of a pair of Horned Grebes performs a series of "Bouncy Dives" (short dives from which it emerges in the Bouncy Posture). In making this series of dives, the bird does not travel in a straight line, but zig-zags somewhat, changing its direction with each dive. On coming up in the Bouncy Posture, it may face the other bird or may be oriented with its side toward it. Most frequently, however, it is in an intermediate position. I have never seen it face away from the other bird while in the Bouncy Posture. As the diving bird approaches the bird which is in the Cat Display, the duration of both the dives and the time it remains on the surface decreases. A tabulation of the time taken by the phases of one series of Bouncy Dives is shown in table 1.

In the final dive of the series, the diver goes beyond the bird in the Cat Display, which turns, evidently watching the progress of the diving bird. The diver then emerges in the Ghostly Penguin Display. A frequent varia-

tion is for the diver to circle the bird in the Cat Display with a series of short Bouncy Dives before coming up in the Ghostly Penguin.

I have found Bouncy Dives to be a regular feature of the Discovery Ceremonies of the Red-necked, Horned, and Eared Grebes. In his work on the Red-necked Grebe, Wobus (1964:46) mentions a short emergence, often of only the head, in the Discovery Ceremony; this almost certainly refers to Bouncy Dives. According to Huxley (1914:512) and Simmons (1955:190), Great Crested Grebes use Ripple Dives in this phase of the Discovery Ceremony. Huxley (1914:512-513) mentions that a Ripple Dive may be interrupted by the diving bird's putting its head and neck briefly above the surface "merely to reconnoitre his position." It would be interesting to find out if Great Crested Grebes assume the Bouncy Posture in this situation. In the Silver and Taczanowski's Grebes, this part of the Discovery Ceremony is not fixed; either Ripple Dives or Bouncy Dives may be used, and the latter may be performed with or without Porpoising.

Ghostly Penguin Display. In this component of the Discovery Ceremony, a Horned Grebe emerges from the last of a series of Bouncy Dives facing away from the bird to which it has been displaying. As it emerges, its body is nearly vertical but its head and neck are nearly parallel to the surface of the water though arched downward (fig. 3). The horns and tippets are appressed to the head, but otherwise the posture of the head and neck resembles that assumed during Rearing. (This posture also resembles that of Western Grebes during the Rushing Display.) When the bird has risen to nearly its full height, the head is raised and held almost at right angles to the now vertical neck, and the horns and tippets are spread. While in this position, the bird then turns slowly toward the second bird. No call is uttered during this display.

So far as is known, this display occurs only as a component of the Discovery Ceremony. It is essentially similar in the five species in which I have observed it (the Red-necked, Horned, Eared, Silver, and Taczanowski's Grebes). Neither Huxley (1914) nor Simmons (1955) mentioned the rising with the head in the forward position in their descriptions of the Ghostly Penguin Display of the Great Crested Grebe and Mrs. McAllister (1958) evidently failed to notice it in the Eared Grebe. In response to my inquiry, Simmons made some further observations and

informed me that the Great Crested Grebe does indeed emerge with its head forward like the other species.

In one motion picture sequence of the Horned Grebe in the Ghostly Penguin Display taken at 16 frames per second, 11 frames elapsed from the time the bird first broke water until its head snapped back and the plumes were spread, and nine more while the displaying bird turned to face the second bird. Although I have no film of the Red-necked Grebe in this display, it is my impression that these birds emerge more slowly than do either the Horned or Eared Grebes. Huxley (1914:498) describes the slowness with which a Great Crested Grebe emerges in this display.

The Penguin Dance Display. In this display, two Horned Grebes rise up in the water face to face (fig. 3). The axis of the body is not quite vertical, the breast feathers are puffed out, and the back feathers may also be somewhat raised. The neck is stretched up, the bill is pointed somewhat below the horizontal, the horns are raised to a nearly vertical position, and the tippets are partially spread.

In the Horned Grebe, the Penguin Dance occurs, alternating with Habit Preening, at the climax of the Discovery Ceremony. In particularly intense bouts of Head Shaking, the birds may rise up in a Penguin Dance. In this species, I have never seen the Penguin Dance as part of a Weed Ceremony.

The Penguin Dance is found in essentially similar form in the Eared, Red-necked, and Great Crested Grebes. The remarkable photograph of Great Crested Grebes in this display by J. H. Drenth (Brit. Birds, 50:pl. 48, 1957) and the accompanying text by Simmons (1957) supplement the earlier descriptions by Huxley (1914) and Simmons (1955). In this species, the breast feathers are less puffed out than those of the smaller species, the bill is held horizontal, and while the tippets are expanded, the crest is lowered. In contrast to other species, this display is used only in a Weed Ceremony and never in the Discovery Ceremony. In the Eared Grebe, the Penguin Dance is very similar to that in the Horned, even to the puffing out of the breast feathers. This is not shown in Mrs. McAllister's figure (1958: fig. 1) although it is quite clear from my motion picture films. In this species, it is a component of the Discovery Ceremony and may occur as a separate ceremony, but as far as known, never with weeds. As in the Horned, the Penguin Dance may accompany intense bouts of Head Shaking. In the Red-necked

Grebe, the Penguin Dance is in general similar to that of the Horned, but it is used in a Weed Ceremony as well as in the Discovery Ceremony.

The evolution of the Penguin Dance appears to be closely connected with that of Rushing and will be discussed under that display and under Weed Ceremonies.

The Rushing Display. In Rushing, Horned Grebes rise in a way similar to that of the Penguin Dance, but they orient side-by-side, and move forward rapidly in the water. In this species, I have seen it only in connection with the Weed Ceremony.

Rushing appears as a rare variant in the Penguin Dance in the Eared Grebe (McAllister 1958:295), and I once saw a pair of Red-necked Grebes use it instead of the Penguin Dance in a Discovery Ceremony. (This case was unusual in that a third bird interrupted the ceremony during the Rushing.) There appears to be no record of Rushing by Great Crested Grebes.

Rushing and the Penguin Dance seem to be very closely related. This is indicated by the similarities of the postures used, by the occasional use of Rushing in place of the Penguin Dance by Eared and Red-necked Grebes, as mentioned above, and also by the fact that the Weed Ceremony of the Horned Grebe involves Rushing whereas the Penguin Dance is used in the comparable displays of the Red-necked, Great Crested, and Western Grebes. The upright position on the water in both these displays and in the Ghostly Penguin are characteristic of displays of high intensity. Indeed, the height to which birds rise in the water in displays may prove useful as one means of estimating the intensity of the motivation producing the display.

Head Shaking Display. In Horned Grebes, this display, a rapid turning of the head from side to side, occurs rather frequently. One or two Head Shakes are usually given as a pair comes together for a Triumph Ceremony. This display is most conspicuous in Head Shaking Ceremonies and is also seen as a postcopulatory display. In this display, the crests and tippets are usually somewhat spread, and the displaying bird may face toward or away from the bird to which it is displaying, or the two may be side by side.

Head Shaking is a common type of display in grebes. Simmons (1955:182) describes both rapid and slow variants of Head Shaking in the Great Crested Grebe. Huxley (1914) used the term "shaking" for this display, which he later (1924) called "head-shaking." In describ-

ing Head Shaking in the Eared Grebe Mrs. McAllister (1958:293-294) stated that the "tempo was military, precise but not hurried" in the Head Shaking Ceremony, but fast during the Penguin Dance. Wobus (1964:39-40) distinguishes between rapid ("Kopfschütteln") and slow ("Wegsehen") Head Shaking in the Red-necked Grebe. I have seen slow Head Shaking in the Great Grebe (Storer 1963b:283), and I have observed more rapid Head Shaking in the Silver and Taczanowski's Grebes. I have filmed Head Shaking in at least three different forms in the Western Grebe: a rapid shaking in the Bob-Shake Display, a slow turning in the Barging Display, and Dip-Shaking. (The last two are described by Nero, in Palmer 1962:101.)

When, as in the case of the last species, both fast and slow variants of Head Shaking occur in the behavior repertoire of a species and are used in different situations, I have limited the term "Head Shaking" to the more rapid motion and have referred to the slower one as "Head Turning." The use of these terms is intended merely as descriptive; no homologies are implied.

Rapid Head Shaking is thought to be derived from the common head shaking comfort movement used in removing dirt, water, etc., from the head and bill. (See McKinney's discussion [1965:135-137] of this behavior in ducks.) Whether Head Turning has the same derivation is open to question. It may even have arisen more than once. Dipping the bill in the water followed by raising and shaking the head is a related and not uncommon comfort movement in Horned Grebes. This movement is seen in a highly ritualized form in the Dip-Shaking Display of the Western Grebe (Nero, in Palmer 1962:101). Although ritualization of this movement has not been reported for any other grebe, I have seen it used, probably as a displacement activity, by Horned Grebes in aggressive situations.

Habit Preening Display. This ritualized type of preening is a simple motion, the grebe bringing its head down over the back and running the bill through or near the feathers of the back or wing. In Horned Grebes, it is a feature of the climax of the Discovery Ceremony and high-intensity Head Shaking Ceremonies.

The term was coined by Huxley (1914:497) in his work on the Great Crested Grebe and also discussed by Simmons (1955:185-188) in his work on the same species. Mrs. McAllister (1958:293) describes under the same name a less localized preening by Eared Grebes.

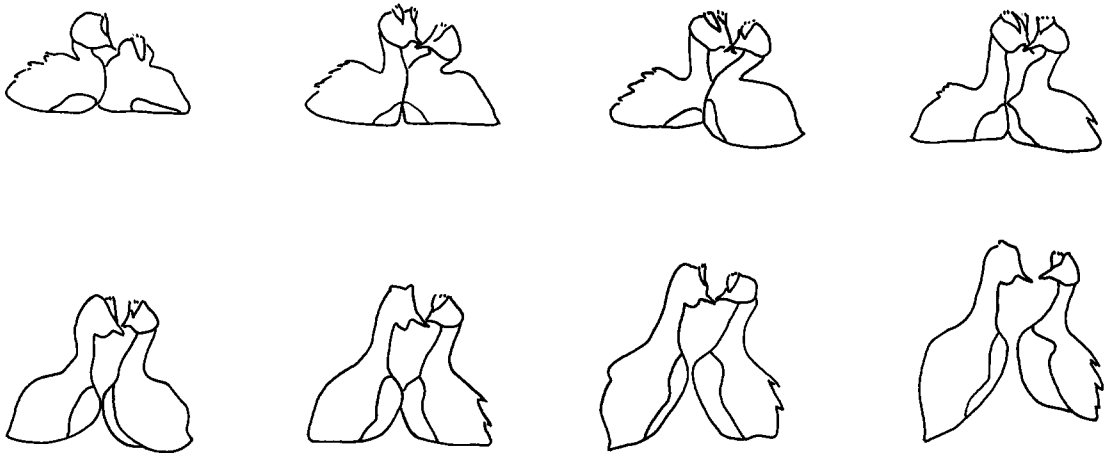


FIGURE 4. Tracings of a motion picture film of Horned Grebes showing the transition from Habit Preening to the Penguin Dance at the climax of a Discovery Ceremony.

Habit Preening has not been reported for the Red-necked or Great Grebes, but I have observed it in Silver and Taczanowski's Grebes. The latter two resemble the Horned and Great Crested Grebes rather than the Eared Grebe in this display. Bob-Preening, an exaggerated form of Habit Preening, is seen in the Western Grebe (Nero, *in* Palmer 1962:100; personal observations). It is generally agreed that Habit Preening is derived from ordinary preening.

Weed Trick Display. A Horned Grebe dives, comes up with a beakful of aquatic vegetation and, with head plumes spread, swims toward a second bird. This display was described and named by Huxley (1914:499-500) in his study of the Great Crested Grebe and discussed by Simmons (1955:189-190). It is also performed by the Red-necked Grebe ("Pflanzenbalz" of Wobus 1964:40; personal observations). It is unrecorded for the Eared Grebe, and I have failed to see it performed by that species or by the Silver or Taczanowski's Grebes.

This display is usually performed by two birds and is usually (possibly regularly) preceded by the birds' assuming a posture like the furtive upright posture used in the Ceremonial Turning Away. Indeed, Turning Away may be immediately followed by Weed Tricks, especially if the birds do not turn directly away from each other but swim more nearly side by side.

Discovery Ceremony. Once triggered, the Discovery Ceremony of the Horned Grebe proceeds almost mechanically, one step following the next in a precisely predictable form. Such a ceremony is usually preceded

by Advertising, and appears to be set off by one bird's diving and then the second's assuming the Cat Posture. The diving bird then emerges in a series of Bouncy Dives. In the case of the Great Crested Grebe (Simmons 1955:191), the Cat Display or the Ripple Dive may come first. However, in the few complete records which I have of the initiation of this ceremony in the Horned Grebe (made by two persons, each watching one bird), the Cat Display was assumed after the approaching bird had dived and before it emerged in the Bouncy Posture.

As the bird performing the Bouncy Dives moves past or around the bird in the Cat Display and finally emerges in the Ghostly Penguin Display, the latter raises its head, somewhat as in Advertising. The bird in the Ghostly Penguin Display turns to face it, and the two swim together, rising in the Penguin Dance with head plumes widely spread (fig. 3). From the Penguin Posture, one or (usually) both make Habit Preening motions, which may or may not be synchronous, and again rise in the Penguin Dance (fig. 4). This alternation of Habit Preening and the Penguin Dance continues perhaps 10 times and forms the climax of the ceremony. After this, the birds turn slowly away from each other (Ceremonial Turning Away) and swim a short distance in opposite directions with the head and neck feathers depressed. As they move apart, the rigid posture of this display gradually is relaxed. Comfort movements or further courtship activities, such as the Weed Rush, may follow, but the lack of stereotyped behavior beyond this point indicates that the Discovery Ceremony ends here. Occasionally the birds

TABLE 2. Components of the Discovery Ceremony in six species of *Podiceps*.

	Species					
	<i>griseogen</i>	<i>cristatus</i>	<i>auritus</i>	<i>nigricollis</i>	<i>occipitalis</i>	<i>taczanowski</i>
Cat Display						
Hunched Attitude	+	+	+	+	+	+
Wing Spreading		+		+	+	+
Display Dives						
Bouncy Dive	+		+	+	+	+
Porpoising					+	+
Ripple Dive		+			+	+
Ghostly Penguin	+	+	+	+	+	+
Climax						
Penguin Dance	+		+	+	+	+
Head Shaking	+	+		+	+	+
Habit Preening			+		+	+
Head Flicking					+	+
Ending						
Turning-away	+	?	+	+	+	?
Barging					+	+

do not turn directly away from each other but swim more or less side by side. When they do this, the rigid posture is not relaxed and a Weed Display often follows.

The Discovery Ceremony is performed in spring usually prior to egg-laying. On the breeding grounds, which the Horned Grebes often reach at least temporarily paired, it usually occurs when members of a pair have been separated for a long time or by a considerable distance. Briefer separations more often result in bouts of Head Shaking, from which I would conclude that a Discovery Ceremony results from a more intense motivation than a bout of Head Shaking. I have seen the Discovery Ceremony performed by birds along their migration route south of the breeding grounds, and I suspect that it may also be performed before the birds leave their wintering grounds. Although I have not to my knowledge witnessed actual pair formation, I suspect that Advertising followed by a Discovery Ceremony is a prime factor both in forming and later in strengthening the pair bond.

That a disturbance may also trigger a Discovery Ceremony is well illustrated by the following observation. On 28 April 1959 near Fort Qu'Appelle, a Red-necked Grebe left its mate in a large opening in a marsh and swam under a bridge to a large lake across a road from the marsh. At this point, R. W. Nero, F. W. Lahrman, and I drove up and stopped on the road between the two birds. Almost immediately, the bird on the marsh Advertised loudly, and the other bird flew across the road to it. The first bird assumed the Cat Posture while its mate was still in the air and a Discovery Ceremony followed.

Huxley (1914:512-513) was the first to describe this ceremony, which he called the "Ceremony of Discovery." Simmons shortened the name to "Discovery-Ceremony" (1955:190). The studies of these two men on the Great Crested Grebe, that of Wobus (1964:46-47) on the Red-necked Grebe, and my own observations on the Red-necked, Eared, Silver, and Taczanowski's Grebes indicate that in its general pattern, as well as the circumstances under which it is given, the Discovery Ceremony of these species resembles that of the Horned Grebe (table 2). (Mrs. McAllister's belief that the Discovery Ceremony of the Eared Grebe "is an incomplete form of the penguin dance" [1958:295] evidently resulted from her failure to recognize the full ceremony.) There are important differences among the species in the details of the ceremony. The presence or absence of Spread-wing Posture in the Cat Displays and the different types of Diving Displays have already been mentioned. Even more striking are differences in the climax of the ceremony. Great Crested Grebes simply have a bout of Head Shaking in the Upright Posture. Eared Grebes combine the Penguin Dance with Head Shaking, and Red-necked Grebes combine it with Head Turning (slow swaying, Wobus 1964:46). Silver and Taczanowski's Grebes use the Penguin Dance with varying combinations of Head Shaking, Head Flicking, and Habit Preening. The Great Crested Grebe apparently lacks a ritualized ending for the Discovery Ceremony, whereas the Silver Grebe may either Turn-away or Barge, and in my limited observations on Taczanowski's Grebe, I have only seen Barging as an ending. Eared and Red-necked Grebes use the Turning Away

like the Horned Grebe. In the Diving Displays, the climax, and the ending of the ceremony, the displays of the Silver Grebe are far less fixed than are those of the northern species.

If, as I suspect, the Discovery Ceremony is a major element in the pair-formation process and later serves to strengthen the pair bond, it must provide a means whereby a bird will find a mate of the same species and the opposite sex. Specific differences in the shape and color of the bill and the head plumes must be important in a grebe's recognition of a member of its own species, as are also interspecific differences in the Advertising Call and in the details of the Discovery Ceremonies. The last can be likened to a maze wherein a bird must make a series of correct responses to achieve a goal. The similarity of the sexes and the interchangeability of the roles in the Discovery Ceremony and other courtship behavior make the question of how a bird chooses a mate of the proper sex somewhat more difficult. The smaller bills and overall size, the shorter ornamental plumes, and the slightly duller plumage of the females may be factors, but I suspect that the slightly greater height of the males in displays which involve the Penguin Dance may be the deciding one. These are questions on which experimentation and further observations would be most valuable.

In attempting to analyze the components in the Discovery Ceremony, I am impressed by the apparent balance between attack and escape elements in the parts of the ceremony in which the two birds use different displays. In the case of mutual displays like the Penguin Dance, a balance is maintained largely by the similar actions of the two birds, a small sexual component being responsible for counteracting such minor differences as the relative heights of the birds' heads. I do not believe that early in the cycle when the Discovery Ceremony starts, the sexual component can be strong enough to overcome any but minor differences in aggressive components during this ceremony. To me the Cat Display is best described as derived from a defensive act. The feathers and wings are spread to increase the bird's apparent size and the head is drawn back to a position from which a thrust of the beak can be made. The dives made by the approaching bird are very likely, as Simmons (1955:199) suggests, "a form of 'symbolic' attack." However, the "dangerous" element of the act, that is, the diving bird's being hidden from view, is counteracted in

the actions of the Great Crested Grebe by the Ripple Dive during which the bird's progress can be (and is) followed by its mate, and in the actions of the other three species by the Bouncy Display (derived from the agonistically neutral act of bathing, quite likely through its use as a displacement activity, during this period when attack and escape drives are balanced). It is particularly interesting in this connection to note that as the diver approaches the second bird, the duration of the dives becomes shorter and the Bouncy Display more frequent, though of shorter duration. Thus, as we would expect the impulse to flee would increase in the waiting bird as it is approached under the water, we find the diving bird indicating its position with greater frequency. Simmons (1955:199) expressed the idea that the Ghostly Penguin emergence is "based on the movements for attacking from under-water." Unfortunately, we do not know what the underwater postures of an attacking bird are, but it is likely that the head is drawn back and not extended in the odd posture so characteristic of the Ghostly Penguin, and of Rearing and the Rushing Ceremony of the Western Grebe. Although I have no suggestions as to how this display may have originated, I think it is highly significant that the bird performing the display always does so while *facing away* from the second bird. Thus we can postulate that a balance or near-balance in agonistic components is achieved by the bird in the more defensive posture (Cat) facing toward, and the bird in the more aggressive posture (Ghostly Penguin) facing away, from the bird with which it is performing the ceremony. From this point on in the ceremony, the two birds perform the same displays, but it is worth noting that the more aggressive postures are used when the birds are face to face and the more appeasing ones when the birds turn away.

Head Shaking Ceremony. Two Horned Grebes meet face to face and start a series of rapid Head Shakes. The ceremony may end with but one or two shakes by each bird, or Head Shaking may gain in intensity until the birds rise in a Penguin Dance, in which case Habit Preening usually follows. Very high-intensity ceremonies may be followed by Ceremonial Turning Away and a Weed Rush.

Head Shaking Ceremonies may occur in situations which might set off a Discovery Ceremony but in which the motivation is not as strong. They become more frequent for a time after pair formation, as the pair bond

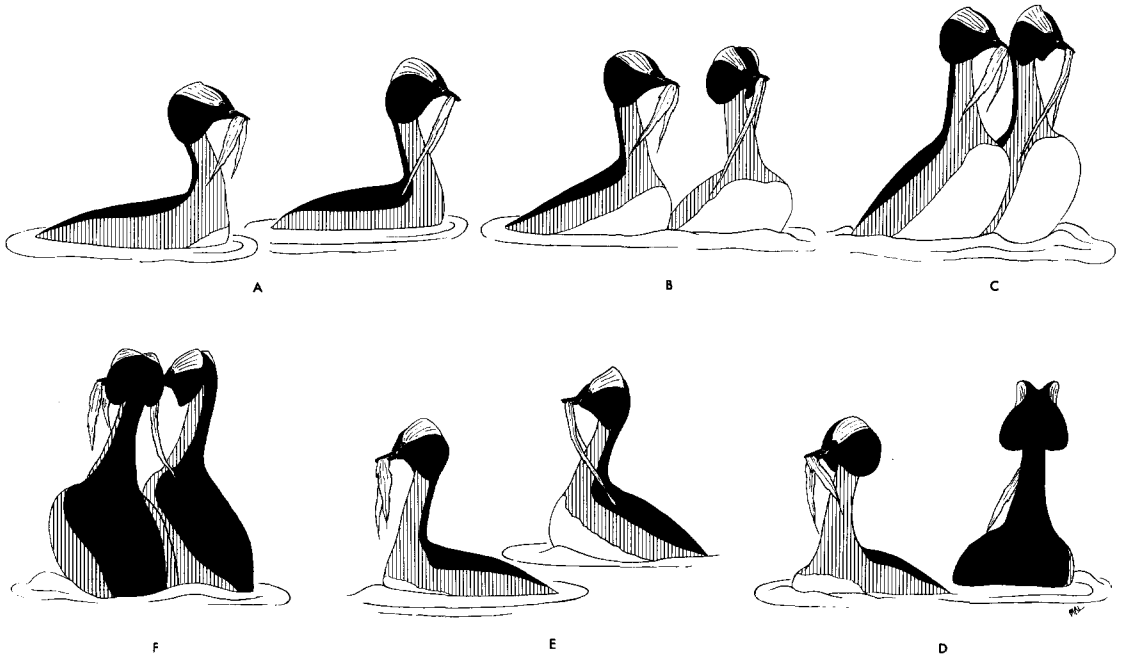


FIGURE 5. Part of a Weed Rush by Horned Grebes.

becomes stronger, and they are in turn used less frequently as the nest becomes the center of attention of the pair. The similarity of the second part of this ceremony to the Discovery Ceremony suggests a close evolutionary relationship between them. They differ, however, in that Head Shaking Ceremonies appear to start at a low intensity, which may increase through the first part of the ceremony, whereas there appears to be much more tension at the start of a Discovery Ceremony. Head Shaking Ceremonies also differ from Discovery Ceremonies in that the roles of the two birds are the same throughout, the "symbolic" attack and retreat of the first part of the Discovery Ceremony being replaced by Head Shaking. This, and the use of Head Shaking Ceremonies when a male returns to his mate after driving off an intruder, suggests that the aggressive element in Head Shaking Ceremonies is weaker than that in Discovery Ceremonies.

Head Shaking Ceremonies are reported in the Great Crested Grebe (Simmons 1955:184-189), the Eared Grebe (McAllister 1958:293-294), the Red-necked Grebe (Wobus 1964:39-40), and the Great Grebe (Storer 1963b:283). What Mrs. McAllister (1958:294-295) described as the "Penguin Dance" probably includes high-intensity Head Shaking and Discovery ceremonies; the relationship to Weed Ceremonies in this species is not clear. The more exaggerated motions of Bob-Shaking

and Bob-Preening are used in the comparable ceremony of the Western Grebe (personal observations), but in this species the birds most often swim side by side during the ceremony. As in the Head Shaking Ceremonies of at least the Horned and Great Crested Grebes, Head Shaking (Bob-Shaking) is regularly followed with a form of Habit Preening (Bob-Preening), and indicates an approaching end to the ceremony.

Weed Ceremonies. If both members of a pair of Horned Grebes perform the Weed Trick at nearly the same time, a Weed Rush usually ensues. The birds, coming together, turn and Rush side by side for a few to perhaps 30 ft. Then they move apart, move together and Rush, move apart, and so on. Successive Rushes may be in the same or in different directions. Sometimes the birds Rush back and forth, while at other times the directions of the Rushes appear to be random. The number of Rushes in a ceremony varies from one to 10 or more and is usually at least four or five. The ceremony ends when one or both birds drop the weeds. As the birds separate at the end of each Rush, they subside into the Upright Posture and often swim about briefly before coming together for another Rush, again rising to the Penguin Posture as they meet and Rush (fig. 5). If one bird comes up with weeds before the second dives or if both dive and only one comes up with weeds, the bird

with weeds usually swims about for several seconds before dropping the weeds in the water. On rare occasions, the second bird may dive after the first has come up with weeds, may also come up with weeds, and join the first bird in a Weed Rush. Occasionally, if one bird fails to bring up weeds, both may dive again and both bring up weeds, and a Weed Rush may ensue. Usually, however, synchrony in the Weed Trick appears a requirement for the Weed Rush.

In the Great Crested, Red-necked, and Western Grebes, the Weed Ceremony is performed as a Penguin Dance rather than a Rush. In fact, it was called the "Penguin Dance" by both Huxley (1914) and Simmons (1955, 1957). I prefer to use the term "Weed Dance" for this ceremony and to limit the term "Penguin Dance" to similar ceremonies in which no weeds are carried (see below). Simmons (1965) now also uses this terminology.

Weed ceremonies were probably derived from nest-building activities. Two observations on Horned Grebes support this view. I once saw a pair of these birds, each carrying nesting material, approach their partially built nest from the same side. As they came near each other, they rose part way out of the water and Rushed to the nest on which they then deposited the material. On another occasion two birds performing a Weed Rush chanced to end the ceremony near their nest, whereupon they deposited the weeds they were carrying on it. If, as these observations suggest, the Weed Rush was derived from nest-building activities, the Weed Dance was probably derived from the Weed Rush rather than the reverse. A hypothetical evolutionary sequence of displays might be: obtaining and carrying nesting material, Rushing side by side (the addition of sexual and/or hostile motivation), standing face to face in the Weed Dance, performing the Penguin Dance (without weeds), and finally the use of the Penguin Dance in new ceremonies. The first two phases may be seen in the behavior of the Horned Grebe as described here, the third may be seen in the Weed Dances of the Great Crested, Red-necked, and Western Grebes, the fourth in the Penguin Dance of the Eared Grebe, and the fifth in the use of the Penguin Dance as a component of the Discovery Ceremony in all but the Great Crested Grebe. A different view, that the Penguin Dance was derived from breast-to-breast battle, has been expressed by Wobus (1964:45), but I find it difficult to understand by what means active

conflict like this could evolve into part of the courtship ritual.

PLATFORM BEHAVIOR

Inviting. As I have pointed out earlier (Storer 1963a), the precopulatory behavior of all grebes, so far as known, is quite similar. Of the three soliciting displays, Inviting, Rearing, and Wing-quivering, the first is the most frequently performed. Even before a platform is built, a Horned Grebe may Invite on the water, putting the head forward just over the surface and flattening the nuptial plumes. The neck is kinked so that the head is lower than the posterior end of the neck. After a platform is built, the birds usually Invite on it, and in doing so, they usually hold the head lower than the body. The Inviting posture is also that of the "passive" bird during copulation. Hosking and Newberry (1946) published photographs of female (pls. 73-75) and male (pl. 77) Horned Grebes Inviting. These photographs were published earlier, but with less successful reproduction, by Hosking (1939).

Huxley (1914:502) referred to the corresponding display of the Great Crested Grebe as the "passive pairing attitude," and Simmons (1955:243) called it the "invitation-display" or "inviting." I prefer "Inviting" as the simpler of Simmons' terms, both of which have the advantage over Huxley's in indicating the soliciting function of the display. The illustrations in Simmons' paper (1955:244, 247), show the Inviting bird with the neck straight out, but the photographs in a later paper (Simmons 1965:228) show the neck kinked, somewhat as in the Horned Grebe. Inviting is essentially similar in the Red-necked (Wobus 1964:49-53; personal observations), Eared, and Silver Grebes. The copulatory behavior of Taczanowski's Grebe has not been described but doubtless is similar to that of the Silver Grebe.

I have seen a male Horned Grebe Inviting on the water near a clump of emergent vegetation and then nest-building by both members of the pair at the same place. From this I infer that Inviting is also associated with selection of a nest site. Inviting and building may occur at several sites before the final one is selected. Male Western Grebes use the comparable Inviting Display (Low Arch) in similar situations.

Rearing. A Horned Grebe Inviting on a platform may rise to its feet, kinking its neck and holding its head downward at an angle of approximately 45°. The crests and especially the tippets are spread and flared out.



FIGURE 6. Platform behavior of the Horned Grebe and related species. A. Rearing, B. Wing-quivering, and C. Inviting, (all Horned Grebes). D, E, and F. Rearing by Eared, Red-necked, and Great Crested Grebes, respectively, (the last after an outline drawing by Robert Gillmor from a photograph by W. N. Charles).

This attitude is maintained rigidly, unless interrupted by Wing-quivering, for several seconds, after which the displaying bird usually resumes Inviting. This soliciting display is less frequent than Inviting and more frequent than Wing-quivering. It also appears to be intermediate between these two displays in intensity, Inviting being the least and Wing-quivering the most intense form of soliciting. A photograph of a male Horned Grebe Rearing appears in Hosking and Newberry (1946: pl. 78), but the authors do not comment on it as a display.

Simmons (1955:244-246) described Rearing in the Great Crested Grebe and appears to have coined the term. He also summarized the earlier accounts of this display. His figure (p. 245) does not represent the usual form of Rearing, which is shown in his later paper (1965:228) and still better in a photograph by W. N. Charles from which an outline drawing has kindly been prepared for my use by Robert Gillmor. Wobus (1960:62) figured Rearing by the Red-necked Grebe, but he did not show the characteristic kink in the neck. Hanzák (1952:16) mentioned that Eared Grebes "use this peculiar position" (Rearing), but Mrs. McAllister (1958:301) stated that she did not observe it. I have motion pictures of Rearing by Eared and Red-necked Grebes,

which show that the display in these species is essentially similar to Rearing in the Horned Grebe (fig. 6).

The derivation of Rearing is not clear. Mrs. McAllister (loc. cit.) suggested that it may be "the ritualized intention movement of sitting down on the nest." She also pointed out resemblances to the posture of the active bird during copulation and the posture used when turning the eggs. As I have pointed out earlier, the odd posture of the head and neck in Rearing resembles that in the first phase of the Ghostly Penguin Display and in the Western Grebe's Rushing Display.

Wing-quivering. While Rearing, a Horned Grebe may suddenly raise its body to a more nearly vertical position, at the same time keeping its head down, and quiver its nearly closed wings rapidly, usually showing the white in the secondaries. After Wing-quivering, the bird may continue Rearing or may subside into the Inviting posture.

This most intense form of soliciting has been well discussed by Simmons (1955:246) and like the other soliciting displays is probably essentially similar in all grebes. I have recorded it in the Red-necked and Eared Grebes, as well as in the Great (Storer 1963b), Pied-billed (McAllister and Storer 1963), and Western Grebes. This display may be derived

from the "wing-shake," which in my experience is a rather rare comfort movement in grebes.

Copulation and associated displays. In the Horned Grebe, I have only observed copulation on platforms built by the birds. These platforms are not necessarily those subsequently used as nests or even in the pothole on which the birds eventually nest. Before and during copulation the passive bird remains in the Inviting posture. The active bird moves about behind the passive bird for some time before mounting. It may make a variety of motions, including comfort movements, head-bobbing, and the "display" shown by Hosking and Newberry (1946:pl. 76, p. 112); but to date, I have not been able to discern a regular pattern for such motions. Mounting is immediately preceded by Copulation Trills, which are continued, with increasing intensity, by the active bird until just before it dismounts, waddling over the head of the passive bird and paddling rapidly as it slowly subsides into the Upright posture. Meanwhile the passive bird raises its head and the two may give one or two quick Head Shakes. The active bird may preen a bit and turn toward its mate. This may be followed by a few Head Shakes and preening by both birds. The postcopulatory behavior appears to be rather variable.

Reverse mounting occurs not infrequently early in the cycle of platform behavior; later, it is rare. I have recorded it in at least the Horned, Eared, Red-necked, Western, and Pied-billed Grebes.

According to Simmons (1955:248), Head Shaking, with the active bird in front of and facing away from the passive bird, is a regular feature of the postcopulatory behavior of the Great Crested Grebe, although the length of such Head Shaking Ceremonies is quite variable. Wobus (1964:49) described and figured (fig. 27, p. 52) a postcopulatory pose of the Red-necked Grebe which he termed an ecstatic posture. This, he says, is followed by slow Head Shaking ("Wegsehen"). I have a film sequence taken in Saskatchewan showing the same displays. I also have a sequence showing Habit Preening after reverse mounting in the Eared Grebe. Rapid postcopulatory water treading appears to be usual in all species studied.

SOME VOCALIZATIONS OF THE ADULTS

Advertising call. The Advertising call of the Horned Grebe consists of a single syllable, to which I have referred in my notes as

"AAANRRH." As Advertising appears to be the first step in pair-formation, it is important that the accompanying note should be species-specific. Because it is later used as a location note, individual recognition is also important, although more so in species like the Eared and Western Grebes, which nest in colonies, than in the more solitary Horned Grebe. The accompanying sonagrams (fig. 7) show that the call is a single note, usually descending in pitch and ending in a rattle or harsh trill. As can also be seen from the sonagrams of Advertising calls of four different birds, there is considerable variation in the length of the note, in the relative lengths of the rattle and the rest of the note, and in the timbre of the voice, as shown in the number and strength of the overtones. These notes are usually given in bursts of several calls, the intervals between the calls usually being between one and two times the length of the call. The individual calls in a burst may vary somewhat, but probably not in any regular pattern. (A burst of six consecutive calls is shown in fig. 7.)

The Advertising call of the Great Crested Grebe has been described by Simmons (1954: 53) as "a loud, drawn-out 'grr-owp' . . . followed by a secondary note, a moaning purr, 'row-ah'." Mrs. McAllister has rendered that of the Eared Grebe (1958:291) as "poo-eee-chk," from which it is easily recognized in the field. (Sonagrams of this call are shown in fig. 7.) In the Silver Grebe, I have recorded the Advertising call in my notes as "chook" and noted that upon closer hearing, it might prove to be more complex. Taczanowski's Grebe has a similar note, but I did not hear the two species near enough in time to make a meaningful comparison.

Platform call. While at or near a platform, Horned Grebes frequently give a two- or three-syllable call which I transcribed in my notes as "ga ga." Often when one bird is off foraging, its mate may remain near the nest giving this call repeatedly for several minutes at a time. This call is also given while a bird is Rearing or Inviting and by the passive bird during mounting. Both males and females use it, but I think males use it more frequently and give the call more loudly than females.

The intensity with which the call is given varies considerably. As the bird becomes more excited, this note grades into a loud, goose-like honking note, which may function, at least in part, as an alarm call. (This transition is illustrated in fig. 8.)

On at least one occasion, I heard a male give this call while Inviting on the water at a place where shortly later he and his mate

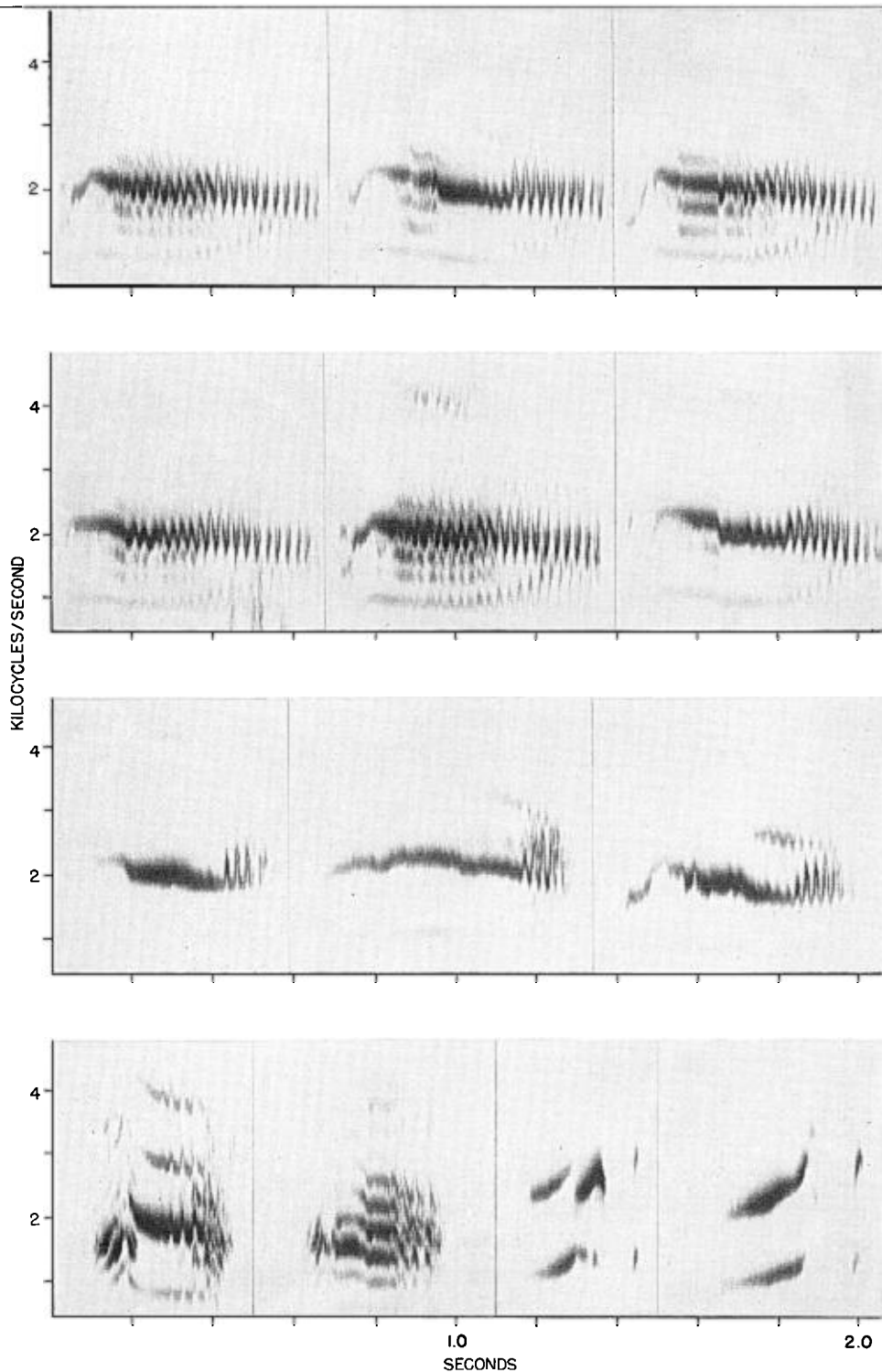


FIGURE 7. Advertising calls of Horned and Eared Grebes. Two top rows: a burst of six calls given by a Horned Grebe near Bethany, Manitoba, 11 May 1967. (The intervals between calls ranged from 0.3 to 0.6 sec.) Third row, left and center: two calls of a Horned Grebe recorded near Minnedosa, Manitoba, 11 May 1967; and right: a Horned Grebe recorded near Fort Qu'Appelle, Saskatchewan, 16 May 1966. Bottom row, two left calls: a Horned Grebe recorded near Moline, Manitoba, 14 May 1967; and two right calls: Eared Grebes recorded at the Lower Souris National Wildlife Refuge, North Dakota, 26 June 1965.

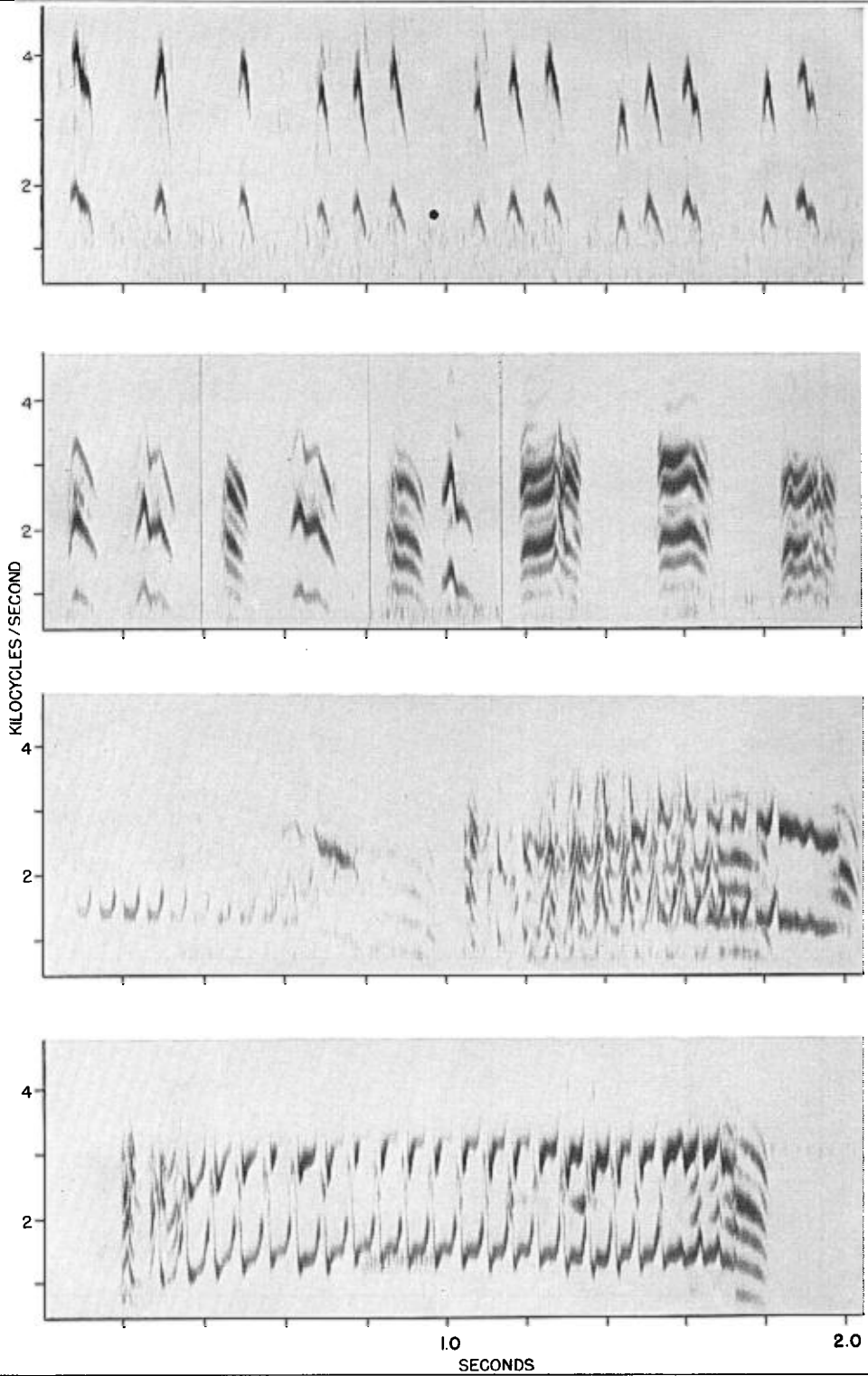


FIGURE 8. Calls of the Horned Grebe. Top row: Platform calls. Second row: transition from Platform calls to single honk-like note. Third row: Duet trill. Bottom row: Copulation trill.

did some building. Thus, it may be part of the behavior involved in selecting a platform site.

This call apparently directs the mate's attention to both the bird which is calling *and* the place whence it is calling. In contrast, the Advertising call directs another bird's attention solely to the calling bird. I have recorded a male Red-necked Grebe giving a comparable call which I transcribed as soft, repeated "guh" notes. This probably corresponds with the third call, ("ga") listed by Wobus (1964:21) for the same species.

Trill. This call is most commonly heard as a greeting duet (fig. 8). After an aggressive encounter, a male may swim to his mate and the two birds may briefly swim side by side in a Triumph Ceremony, both calling. A pair may also swim side by side and Trill after being separated. An intense form of the Trill is uttered before and during mounting by the active bird (male or female).

This call corresponds to the eerie whinny-like call of the Red-necked Grebe (the "uööh"-Gebrüll of Wobus 1964:22). In this species, the call is given more frequently than in the Horned Grebe and is often heard at night and on migration. In an intense form, this call is associated with copulation, as is the corresponding note in the Horned Grebe. Loud copulation notes have been described by Simons (1955:248) for the Great Crested Grebe and by Mrs. McAllister (1958:301) for the Eared Grebe, but the relationship of these notes to others in the repertoire are not discussed. I have heard loud copulation notes from Western and Pied-billed Grebes; such notes may prove characteristic of all grebes.

Pre-dive call. A very soft call, somewhere between a squeak and a grunt, is sometimes given immediately before diving. I described it in my notes as a "wheel" and was unable to record it. It could be heard from a distance of 25 ft but probably not much farther. When a pair near us was diving for food, only the male was heard to give the note and not before all dives. A male also gave this note when diving alone. I have no evidence that this call is used as a signal, nor can I see any relationship between it and others in the repertoire.

CONCLUSIONS

I think it more likely that a common ancestor of the six species (Horned, Red-necked, Great Crested, Eared, Silver, and Taczanowski's Grebes) performed the Discovery Ceremony than that this complex ceremony evolved in-

dependently more than once. This implies close relationship of these species, which is borne out by the pattern of the downy young (Storer 1967). These six species can be divided into those which use weed ceremonies (Horned, Red-necked, and Great Crested) and those in which such ceremonies are unknown (Eared, Silver, and Taczanowski's). The patterns of the downy young also confirm this subdivision, as do the type of nuptial plumes behind the eye and the birds' gregariousness in the latter group.

The Horned Grebe's closest relative is probably the Red-necked Grebe. The Advertising call, Trill, and conversational notes are quite similar. Unlike the Great Crested Grebe, neither uses Wing-spreading in the Cat Display, both use a Penguin Dance at the climax of the Discovery Ceremony, and the display dives of both are Bouncy Dives. On the other hand, the Horned Grebe's nuptial plumes are more like those of the Great Crested Grebe than those of the Red-necked, and the Red-necked and Great Crested share Token Diving and the Weed Dance. The Horned Grebe appears unique in its Weed Rush and in not spreading its wings in the two-wing-stretch.

Both the Great Grebe and the Western Grebe share courtship ceremonies with at least two of the six species of *Podiceps*, *sensu stricto*: the Great Grebe has a Retreat Ceremony like that of the Great Crested and Silver Grebes, and the Western Grebe has a Weed Dance like that of the Great Crested and Red-necked Grebes. On the other hand, the Great and Western Grebes lack the Discovery Ceremony, which appears to be replaced by the quite different Nodding and Turning Ceremony of the former and the Rushing Ceremony of the latter. This body of evidence suggests that these two species stand apart from the other six, but are no closer to each other than either is to the six. Again there is accord with the evidence from the pattern of the downy young.

Except at Lake Junín, the Silver Grebe is not sympatric with any other species which performs the Discovery Ceremony. Hence selection for reduced variability in the ceremony is not strong, the Discovery Ceremony itself being distinct enough from the ceremonies of the grebes with which the Silver Grebe occurs to prevent the formation of mixed pairs. This probably accounts for the variation in the display dives and in the climax of the Discovery Ceremony in that species. On Lake Junín, the Silver Grebe has been reported rarely with its very recent offshoot, Taczanowski's Grebe, which is confined to

that lake. From my limited experience there, it appears that the Discovery Ceremonies of these two species are similar. What keeps the two from hybridizing remains to be determined.

SUMMARY

The behavior of the Horned Grebe on the breeding grounds prior to egg-laying is described and compared with that of seven related species. Distinctive features of the behavior of the Horned Grebe include keeping the wings folded during the two-wing-stretch, the Weed Rush, the Advertising call, and several details of the complex Discovery Ceremony.

On the basis of behavioral evidence, the Horned Grebe appears more closely related to the Red-necked and Great Crested Grebes than to the Eared, Silver, and Taczanowski's Grebes. The Western and Great Grebes are distantly related to the other six and to each other. The behavioral evidence thus agrees with that from the patterns of the downy young.

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