Condor 84:370–380

DISPLAYS, VOCALIZATIONS AND BREEDING BIOLOGY OF THE GREAT GREBE (*PODICEPS MAJOR*)

ERIC A. GREENQUIST

ABSTRACT.—In studying the Great Grebe (*Podiceps major*) in Chile, I identified 14 displays and 8 adult vocalizations. The courtship displays were performed throughout the year, indicating maintenance of the pair bond after nesting ends, and suggesting that the grebes form long-term pairs. Breeding was not confined to any season; pair bond maintenance may be an adaptation that permits reproduction whenever environmental conditions are favorable. The "mutual" courtship displays—displays performed only by two grebes—were performed in significantly more ceremonies than were certain courtship displays performed by individuals. Shaking the closed wings during the rearing display was associated with copulation. The number of eggs on a nest platform was positively correlated with the degree to which the grebe covered the eggs with vegetation before leaving the nest. Both adults cared for the young, in some cases until the young were fully grown.

The Great Grebe (*Podiceps major*) is widely distributed in South America from coastal Peru, Paraguay and southeastern Brazil, south to Tierra del Fuego. It is a large grebe (length: 675–775 mm), similar in appearance to the Western Grebe (*Aechmophorus occidentalis*) of North America except that its bill, head and lower throat are black, the foreneck and the sides of the neck and chest are rufous, and the flanks are tinged with rufous or brown (Blake 1977). In the only previous account of Great Grebe behavior, Storer (1963a) described aggressive behavior and the courtship and the platform displays.

In this paper I amplify Storer's account, reporting additional forms of behavior, including the "gunner's" display and six adult vocalizations, for the first time. I attempt to analyze the message of the displays and the vocalizations and to describe the situations in which they are performed. I also quantify aspects of the courtship ceremony and the platform displays, and include information on nest building and brooding.

Throughout this paper I refer to grebe "consorts" or "pairs" even though I could neither recognize individuals from one observation period to the next, nor distinguish the sexes in the field. In these instances I assumed the existence of a pair bond based on the mutual behaviors of two grebes and on their movements to remain together during an observation period.

When describing Great Grebe platform behavior I refer to the active and the passive birds instead of to the male and the female. In at least five grebe species, the active and the passive roles are taken by either pair member (McAllister and Storer 1963:166, Storer 1969: 200). Great Grebes may exhibit similar behavior.

METHODS

I studied Great Grebes on the Gol-Gol River delta, which forms the eastern shore of Lake Puyehue (153 km^2 at 212 m), Osorno Province, Chile. Heusser (1974) and Veblen and Ashton (1978) described the region geographically, including the Valdivian Rain Forest plant community. The delta (approx. 200 ha) is characterized by unstable scoria flats, annual floods, and extensive wet meadows and marshlands. *Baccharis concava, Myrceugenia exsucca* and *Rubus constrictus* dominate the shrub layer; the herbaceous layer is primarily *Holcus lantus, Phragmites communis, Plantago lanceolata* and *Rumex* spp. *Pteris semiadnata* is the principal fern and *Hydrocotyle poepeggie* and *Juncus leseurii* dominate the aquatic vegetation. I previously described the delta and its wildlife community (Greenquist 1978). Except when stated, approximately 250 Great Grebes occupied the open water and the marshes of the delta throughout the investigation.

I observed Great Grebes on 102 days (approximately 440 h) from September 1977 until February 1979. I made observations during all months of the study; the majority were made during the drier months, October to February. I studied the grebes from the shore and from a rowboat on the open water. Owing to the grebes' tendency to approach me, I often found binoculars (10×50) unnecessary. I observed nest building and platform behavior from the shore of the largest nesting area. I used no blind; the shrubs that covered about 80% of the shoreline provided sufficient cover

for observation and still photography. I used a measuring pole, nailed to a partially submerged tree trunk, to measure relative changes in lake water level. Illustrations for this paper were copied from field sketches and photographs, and were checked for accuracy in the field. Sokal and Rohlf (1969) was the source of all parametric statistical analyses. All means are accompanied by their SD.

RESULTS

VOCALIZATIONS

I discerned eight adult Great Grebe vocalizations; of these the "huala" call was the most common. This call, issued with the bill opened widely, consists of a high, melancholy-sounding moan that lasts longer than 1 s before trailing off. The huala call carries well across water and is heard frequently, at times almost continually, on large sections of the lake. Great Grebes are gregarious birds and the huala call may be issued to maintain acoustic contact with conspecifics; it may be especially important at night. It is also the species-typical call issued during "advertising" (Storer 1963a:284). Huala calls are issued by Great Grebes that are alone, with consorts, and in groups.

The "soft" call consists of an irregular series of soft notes: *a,a . . . a,a,a . . .*; each note lasts about one-half second. This call is issued with the bill closed and does not carry as well as the huala call; I never heard it given by a lone grebe. It appears to be directed at the consort and it may help pair members remain proximal. I have heard grebes cease soft calling when their consorts dive to feed and resume soft calling when they reappear. As individuals that apparently are separated pair members approach each other, they issue a few soft calls before joining with a sudden, rapid exchange.

The "staccato" call is composed of loud, abrupt notes: *AP-AP-AP . . .*, uttered about twice per second. The bill is opened on each note. This call may be irregular or it may consist of one note. The staccato call appears to be used in alarm situations; it is issued by grebes when they flee from attacking conspecifics. It was also given when I surprised grebes in areas where they did not have immediate access to open water.

The "drawl" call, which I heard less frequently than the previous calls, consists of a drawn out "*aw*" that meanders down, then up, and ends with a slight accent. It is issued with the bill closed and may last several seconds. The call appears to be used in distress situations, as when a grebe is being followed, but not attacked, by a threatening grebe. The four remaining vocalizations are described in their appropriate sections.

POSTURES AND LOCOMOTION

The positions of the crest (Fig. 1A–C) and of the short tail feathers are characteristic components of the Great Grebe postures and displays. (Storer [1963a:280] reported two crests. I did not see the second crest, which is a small projection in front of and between the eyes.) Normally, the crest is lowered and the tail feathers are relaxed (Fig. 1D). Great Grebes gave huala and soft calls, and occasionally staccato calls while in this posture.

I prefer the term "alert" posture to "investigating" named by Storer (1963a:Fig. 1). Although this posture was assumed by "investigating" grebes it more commonly was adopted by grebes that were about to flee. The typical posture that I saw (Fig. 1E) differed slightly from Storer's description: the head was higher, the crest was usually semi-raised, and the tail feathers were erected. In situations where a grebe normally escaped by rapidly submerging chest-first, the upper back and the lower neck were underwater (Fig. 1G) and the bird was stationary. Great Grebes gave huala calls, soft calls, staccato calls and drawl calls while in alert postures.

When fleeing over the water's surface (Fig. 1F) a grebe's crest and tail feathers were lowered and staccato calls commonly were issued. This was the usual method of escape when a grebe was attacked by a conspecific; a bird generally fled 5–20 m. Flapping the wings raised the body higher in the water (at times the grebe appeared to run across the surface) and propelled it faster; birds might travel more than 50 m with wing-flapping.

Submerging chest-first appeared to be a less urgent form of escape: fleeing to avoid an encounter with another grebe rather than to escape a direct attack. Groups of ten or more grebes, swimming on the open water, adopted alert stationary postures and rapidly submerged upon encountering a pair of grebes that were directing threat displays at them. The individuals of the group scattered underwater, surfaced several seconds later and swam away in alert postures. Grebes also submerged when they had no clear escape route, as in marshes and river mouths.

Great Grebes rarely flew. They became airborne by running across the water into the wind. The grebes covered distances of 5–10 m in the air, and they flew with the neck extended low in front and the legs hanging.

AGGRESSIVE ENCOUNTERS

Storer (1963a:281–282) described the Great Grebe "threat" display but he referred only briefly to its uses and to the aggressive encounters in which it appears. I saw the threat display

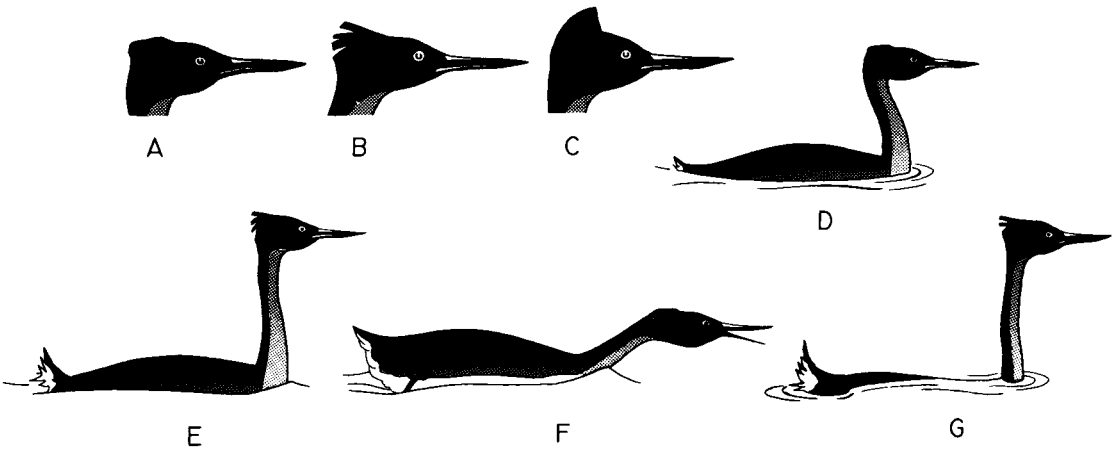

FIGURE 1. Typical forms of some Great Grebe postures: the crest in the (A) lowered, (B) semi-raised and (C) raised positions; (D) the normal posture, (E) the swimming alert posture, (F) the fleeing posture, and (G) the stationary alert posture.

used to force the intruder(s) away from a grebe's consort, nest platform, or young. The display also appeared to have a defensive function, as when a grebe pair threatened a group of conspecifics, or when an individual threatened a series of grebes while searching a group for its consort. The recipient of the display appeared to be "singled out" from the group. Consorts threatened each other when rejoining after feeding or after courtship. (Threat displays between consorts however, may result from a brief period of non-recognition; once the grebes approach to within a few meters they stop displaying and exchange soft calls.) Great Grebes threatened and attacked other species of waterbirds.

The threatening grebe (Fig. 2A) swam toward the recipient at a normal pace; the crest was lowered—occasionally it was semi-raised as illustrated by Storer (1963a:Fig. 1E, F)—and the tail feathers were relaxed. In some cases the body of the displaying grebe was submerged and only the head and the bill were visible.

The recipient of the threat display—usually less than 10 m away—swam away in an alert posture at a slightly faster rate and might periodically "glance back" at its pursuer or utter a low drawl call. Following might continue in this manner for three minutes or more but usually lasted only a few seconds. The threatening grebe might stop and turn away—continuing to display for several seconds—or it might attack the recipient.

Attacks were made by diving, coming up beneath the recipient, and jabbing it with the bill. If the recipient was within 2–3 m the attacker might swim rapidly over the water's surface and jab it, with the bill opened slightly, in the upper back or neck. When attacked, a conspecific usually fled over the water's surface (rarely it dove head first) before physical contact was made.

After fleeing across the water, the recipient either dived and reappeared some distance away or it continued to swim away in an alert posture. The attacking grebe, upon surfacing, often continued to threaten the recipient, follow, and attack again. One grebe attacked another in this manner 10 consecutive times. I observed token diving (Storer 1963a:281–282) by the threatening grebe.

In cases of "intense" threat (Fig. 2B) the wings were raised in an apparent intention movement of an attack over the water's surface. The chin was held near the water; the bill was pointed upward slightly, toward the recipient. The crest was relaxed or semi-raised and might be fully raised immediately before attacking. The intense threat display was less common than the normal form. I saw it performed most often inside the nesting area where the opponents were at close quarters. The recipient of this display was almost always attacked. In disputes where the recipient returned the display, the opponents faced off 1–2 m apart and, if one of the grebes did not flee, an attack, and commonly a fight, followed within moments. Occasionally, one of the opponents arched its neck, raised its chest in the water and, with its bill opened wide, issued a loud "*AW*" just before attacking.

Fighting among Great Grebes was uncommon and generally lasted less than 5 s. All of the fights I witnessed were between two opponents—although consorts occasionally joined in attacking vanquished opponents—and did not result in noticeable injuries. The opponents usually attacked over the water's surface and met in upright, almost vertical, positions,

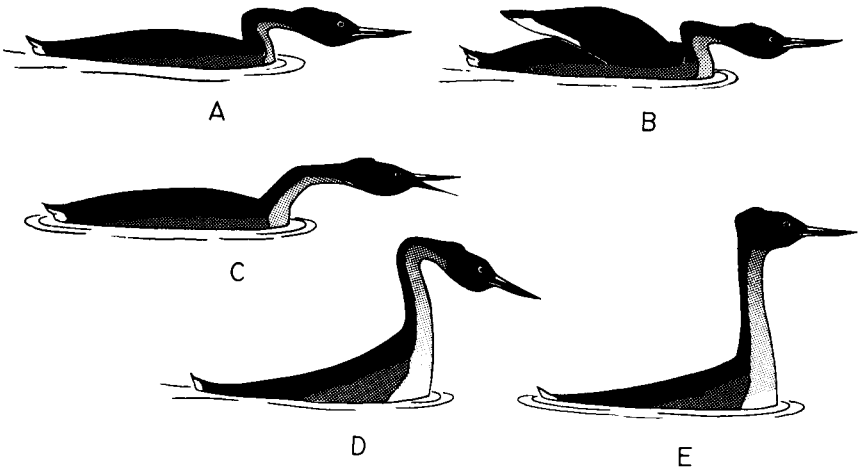

FIGURE 2. Typical forms of some Great Grebe displays: (A) the normal and (B) the intense forms of the threat display, (C) the gunner's display, (D) the S-neck display, and (E) the Z-neck display.

kicking the legs in the water, and jabbing at each other with the slightly open bills. The longest fight I observed occurred outside the nesting areas and lasted over 45 s. The consorts of the opponents remained close by but, except for one consort directing a threat display at the other, remained outside the conflict. On another occasion one grebe bit its opponent on the neck and held on for over 20 s as the opponent issued staccato calls and tried to flee across the water.

GUNNER'S DISPLAY

In the "gunner's" display, a grebe extends its neck to the front and holds its head low over the water (Fig. 2C); the tail plumage and the crest are relaxed. A call always accompanies the display: a soft, regular, "machine gun-like" vocalization of 2–4 notes/s: *a-a-a-a* . . . . During the call the bill is held open slightly. The display and the call generally last 3–5 s and grebes commonly rotate slowly or swim forward when performing the display on the open water. This display was performed throughout the year by both pair members.

I cannot interpret the meaning of this display, which has no apparent direction or objective. Except for simple investigation, I noticed no reaction to the display by consorts or by other grebes. The display was performed by grebes that were over 50 m away from conspecifics. The only similar form of behavior I found in the literature is McAllister's (1958:301) account of "soliciting" by Eared Grebes (*Podiceps nigricollis*), a behavior she related to nest establishment. The Great Grebe gunner's display might have a similar function: I commonly heard the gunner's display call during platform building, coming from the emergent vegetation of the main nesting area. On two occasions I watched Great Grebes display while lying on nest platforms. Another grebe displayed at the side of its nest platform and consort. The gunner's display was performed by grebes that had just threatened and driven off conspecifics, and it accompanied feeding and preening. Once it immediately preceded courtship.

PAIR BOND-RELATED BEHAVIOR

Storer (1969:187) defined courtship as those displays and ceremonies that result in the formation and in the strengthening of the pair bond; he outlined the Great Grebe courtship ceremony (Storer 1963a:282–286). Here I add to his account and quantify components of the courtship displays.

I witnessed the courtship ceremony during all months of the year, indicating that the pair bond was maintained after nesting ended and suggesting that Great Grebes formed long-term pairs. Any of the courtship displays might be repeated during a ceremony and the duration and the order of the displays varied among pairs and among successive performances by the same pair. Courting pairs might interrupt the ceremony at any time to drive off intruding conspecifics.

Upright mohawk display. A grebe solicited courtship by performing the "upright mohawk" display (Storer 1963a:282). In many instances, especially those preceding the "mutual" courtship displays, the soliciting grebe issued huala calls (termed "advertising" by Storer [1963a: 283]). The second grebe, and occasionally an intruder, responded with the same display when as much as 30 m away from the first grebe. The birds might simply swim about at a normal pace displaying for several seconds, frequently turning their heads as if looking around,

before resuming normal postures; thus ending courtship, they might perform "ghostly-penguin" or "ceremonial flying-away" displays as described below, or, after any intruder had been driven away, they might join and perform the "mutual" courtship displays.

Mutual courtship displays. Unsynchronized "nodding" (Storer 1963a:284) was the first of the "mutual" courtship displays; i.e., three displays—nodding, turning and turning-away—which were performed only by two grebes. On two occasions I watched grebes perform the mutual displays with different partners. Nodding began when the grebes were up to 12 m apart; still in the upright mohawk posture, they faced each other and dipped their bills about 55° below the horizontal, rhythmically or unrhythmically, at a usual rate of 1 to 2 nods/s. Each nod was a quick down-up movement followed by a momentary pause in the upright mohawk posture. While nodding, the grebes generally approached to within 1 m. Individuals that performed the first nod of a nodding bout averaged 13.4 nods ± 7.9/bout ($n = 43$; range = 3–41) while second grebes averaged 8.4 nods ± 5.7/bout ($n = 36$; range = 0–20). Only once did the second grebe perform more nods than did the initiator. I found a positive relationship between the number of nods/bout performed by each grebe of a pair ($r_{(34)} = 0.77$, $P < 0.01$).

Nodding was followed by the "turning" display (Storer 1963a:284). The grebes, now separated by less than 1 m and still facing in the upright mohawk posture, performed rigid, synchronized, 90° turns to the same side. Occasionally, only the heads were turned. They swam side by side in the upright mohawk posture for <2 s, faced for about 1 s, and then turned again, to either the left or the right (they did not always turn to the opposite side as reported by Storer [1963a:284, 1963b:566]). If one grebe turned ahead of its partner it either waited for the other to catch up or it quickly refaced its partner so that the two could turn together. At the end of turning one grebe often performed an extra turn. Pairs averaged 5.8 turns ± 4.3/bout ($n = 42$; range = 1–18). I found no correlation between the number of nods performed by a grebe that initiated nodding and the number of turns subsequently performed by the pair during the same courtship bout ($r_{(37)} = -0.06$, ns).

The "turning-away" display (Storer 1963a: 284) was performed at a normal swimming pace. Storer (1963a:284, 1963b:566) called this display "ceremonial turning-away"; I shortened this term so the reader will not confuse it in later discussions with the "ceremonial flying-away" display. While separating, the grebes gave soft calls and periodically "glanced" at each other. They might separate 30 m or more before continuing courtship or rejoining in normal postures.

Solo courtship displays. Unlike the three mutual displays, the "ghostly penguin" display and the "ceremonial flying-away" display were performed by individuals. My observations of the surface portion of the ghostly penguin display differ from Storer's (1963a:284–285, Fig. 2B) account. Upon surfacing, a grebe quickly rose in the water; the chest was swollen, the neck was extended upward, the bill was dipped about 45° below the horizontal and the crest was raised. The upper throat might be slightly distended (at times the plumage of the upper neck appeared to be erected) and, occasionally the base of the neck was slightly swollen. When the grebe had fully surfaced the bill was quickly yet deliberately raised and the neck was relaxed; the bird resumed the upright mohawk posture. In 10% of the ghostly penguin displays ($n = 40$) bill raising was followed immediately by a quick, pronounced nod in which the neck was bent slightly. During the display the grebes swam an estimated 11.5 ± 8.3 m underwater ($n = 19$). Of 13 recorded displays the displaying grebe swam toward the second bird 10 times and surfaced on the opposite side of the second bird 7 times. Courting pair members might perform ghostly penguin displays at the same time.

When performing the ceremonial flying-away display (Storer 1963a:284) grebes "ran" an estimated 4–50 m across the water, generally away from the second bird, while flapping the wings. Unlike Storer (1963a), I never saw a grebe become airborne while performing this display. The bird stopped suddenly in a posture similar to the upright mohawk display except that the bill was dipped about 45° below the horizontal. The crest was raised; the plumage of the upper neck was erect. The grebe immediately raised the bill and relaxed the neck plumage, resuming the upright mohawk posture.

The courtship ceremony. Of 62 courtship ceremonies recorded during January and February 1979, 35 were interrupted by conspecifics who either threatened courting pairs or approached so closely that courting grebes interrupted ceremonies to drive them off. During the 27 uninterrupted ceremonies—if the upright mohawk display, which initiated all ceremonies, is not considered—the turning-away display was the most fixed behavior, performed in 23 ceremonies. Nodding and turning each occurred in 19 ceremonies; the ghostly

penguin display and the ceremonial flying-away display occurred in 12 and 8 ceremonies, respectively. A replicated goodness of fit test revealed a significant difference in the number of ceremonies in which these five courtship displays were performed ($G_{H(4)} = 23.52$, $P < 0.005$). A posteriori STP tests (1) found no significant difference in the number of ceremonies in which the mutual displays (nodding, turning and turning-away) were performed ($G_{H(4)} = 2.26$, ns), (2) showed that the three mutual displays were performed in significantly more ceremonies than was the ghostly penguin display ($G_{H(4)} = 10.68$, $P < 0.05$), and (3) found no significant difference in the number of ceremonies in which the ghostly-penguin display and the ceremonial flying-away display were performed ($G_{H(4)} = 1.28$, ns).

Even though one or more of the mutual courtship displays were omitted, nodding, turning and turning-away always were performed in the stated order and in immediate succession, uninterrupted by other displays. During the 27 uninterrupted ceremonies, the mutual displays were performed no more than once per ceremony; previously however, I saw the displays repeated during courtship bouts. The three displays were performed together in 13 ceremonies, nodding was omitted in 6 ceremonies, turning was omitted in 4 ceremonies and nodding was performed alone in 2 ceremonies.

The ghostly penguin display was performed 38 times during the 27 uninterrupted ceremonies (range = 0–11 displays/ceremony). The frequency of the number of displays per ceremony did not follow a Poisson distribution (chi-square goodness of fit test: $\chi^2_{(3)} = 8.04$, $P < 0.05$); clumping occurred (C.D. = 6.30). There was no significant difference in the number of ghostly penguin displays performed before and after the mutual displays ($\chi^2_{(1)} = 1.32$, ns). During the 62 recorded ceremonies there was no significant difference in the number of ghostly penguin displays performed by grebes that initiated courtship, and their partners ($\chi^2_{(1)} = 0.20$, ns; $n = 10$), nor in the number performed by grebes that initiated nodding, and their partners ($\chi^2_{(1)} = 0.05$, ns; $n = 42$).

The ceremonial flying-away display was performed 10 times during the 27 uninterrupted ceremonies (range = 0–2 displays/ceremony). The frequency of the number of performances per ceremony followed a Poisson distribution (chi-square goodness of fit test: $\chi^2_{(1)} = 0.20$, ns).

S-neck and Z-neck displays. Although the "S-neck" and the "Z-neck" displays (Storer 1963a:282–284) appear to be related to the pair bond, I do not consider them to be true components of courtship. They were performed in situations that seemed to pertain to the aggressive disruption of a pair bond by an intruder, or to its defense by a pair member. When performing the S-neck display (Fig. 2D) a grebe curved its neck forward—typically holding the head higher than described by Storer (1963a:Fig. 1G, H)—and pointed its bill downward slightly. In the Z-neck display (Fig. 2E) the neck was held vertically and the bill was horizontal. The chest was raised slightly, although not as high as during the upright mohawk display. The tail plumage in each display was relaxed and above water and the crest was lowered, becoming semi- or fully raised in "alarm" situations. Pair members, performing these displays, commonly exchanged soft calls.

The S-neck display often was accompanied by the "S-neck display" call: a soft, *a-a-a-a-OW-OW* uttered with the bill closed. Like the soft call, the S-neck display call was exchanged only between pair members; it was given only by grebes in the S-neck posture. Apparently, a grebe issues the call in aggressive or defensive situations to solicit its mate or to identify itself to its mate, so the two birds can join and support each other.

The S-neck display is related to the pair bond. Like Storer (1963a:283) I watched grebes, in the S-neck posture, face each other and perform courtship turns, which were performed only by two grebes in the same posture. It is also the aggressive display reported by Storer (1963a). Displaying grebes followed conspecifics and attacked them, either from beneath the water or over the water's surface. Unlike the threat display however, I saw neither the S-neck display nor the Z-neck display directed at consorts or at birds of another species. When the formation or the defense of a pair bond did not appear to be the purpose of an aggressive encounter, grebes performed the threat display. A paired grebe, performing the S-neck display and following an intruder, immediately assumed the threat display when the displaying grebe and the recipient of its display moved away from the displaying grebe's consort.

Pair members performed S-neck displays when grouped with conspecifics. As they displayed they usually turned their heads from side to side as if looking around, issued S-neck display calls and either drove off a conspecific or moved away from the area together. Courting pair members performed S-neck displays when interrupted by a conspecific. If the pair members were separated by a few meters they

gave S-neck display calls, turned to rejoin, and then drove off the intruder together. Frequently, one member of a courting pair assumed the display alone to drive off what I believed to be a grebe of the same sex, since not all intruders were driven off. In these situations courtship behavior often was resumed. Lone Great Grebes performed S-neck displays when their courtship activities were interrupted by a conspecific.

I found no evidence supporting Storer's (1963a:282) assessment of the Z-neck display as an appeasement posture. The Z-neck display appeared to be a mildly aggressive or defensive behavior that was closely related to, and often preceded or followed, the S-neck display. An intruder changed back and forth from the S-neck posture to the Z-neck posture as it moved away from an aggressive pair member, and it occasionally turned and attacked its pursuer. A paired grebe might direct an S-neck display at, and then follow, an intruder while its consort followed closely behind in the Z-neck posture. The slight chest raising of both displays suggested a sexual motivation, similar to that of the courtship displays.

NESTING ACTIVITY

I observed platform building in early October 1977, and I first found a completed nest platform on 23 October. I recorded a pair with downy young on 18 October but did not find another pair with downy young until 30 November. I noted copulation from the third week of October 1977 until the end of January 1978, and egg laying from 2 November 1977 until 21 January 1978. The end of nesting activity coincided with a sharp decrease in the maximum water level in the nesting areas from 1.6 m in mid-January to 0.8 m one month later. The drop in water level exposed scoria flats at the mouths of the nesting areas which the grebes apparently were reluctant to cross. Great Grebes do not venture onto dry land and, in those areas where the flats were submerged, the water was too shallow for escape diving. The grebes abandoned nests with eggs.

I did not record nesting activity again until the final week of July 1978; platform building and copulation followed a rise in water level which brought maximum depth in the nesting areas from 0.9 m to 2.4 m in only 52 days. The grebes abandoned the nests however, when, during the same month, the Chilean military occupied the section of land adjacent to the southern edge of the delta and began gunnery practice. Until that time the delta had been undisturbed. Intermittent shooting continued until late November 1978; approximately 150 Great Grebes returned to the delta by mid-January 1979. Nesting activity, however, did not resume on the delta following their return. By mid-February the nesting areas were again isolated due to low water; none of the Great Grebes in the delta area had downy young.

Nesting behavior began at a low intensity. During early October 1977, pairs of grebes rarely spent more than 2 h constructing nest platforms before abandoning the sites. They often built in unprotected areas; I watched several pairs collect and place vegetation on a sludge of organic debris that had been flushed from a river mouth and was floating on the lake, a location where platforms could neither be anchored nor completed.

I found completed platforms in three delta marshes. Each marsh was connected to the lake, affording the grebes access to deep water. It also possessed gently sloping shorelines that allowed moderately dense emergent vegetation to extend several meters from shore, and had a clearing or channel at the center which led to open water. The grebes built nest platforms away from currents and excessive wave action. Many platforms were built in highly visible locations; most however, were located back in the emergent vegetation that occupied about 60% of the surface area of each marsh. The main nesting area ($\sim$2,000 m^2) contained about 500 nest platforms; 150–200 of these were used for egg laying.

Great Grebe nest platforms resembled those described for other grebe species: sodden masses of emergent vegetation—in this case mainly rushes (*Juncus leseurii*) and marsh pennyworts (*Hydrocotyle poepeggie*)—floating on the water. The platforms generally measured 0.8–1.1 m in diameter; some platforms however, were $<$0.5 m in diameter, so small that their eggs, in some instances, rested in 5–10 mm of water. The nest territory extended $<$1 m from the platform edge; eggs were brooded on platforms only 1.3 m apart.

Both pair members defended the platform territory as construction began. Working individually, and generally within 10 m of the platform site, the grebes either collected vegetation from below the surface or clipped living emergent vegetation with the bill and carried it to the platform. I saw no stealing of nest material from other grebe platforms, even when those platforms were abandoned and breaking apart. As the grebes paused near the platform to preen, they flicked the bill in a slight circular motion to one side. My observations of nest building and platform behavior, and Storer's (1963a: 285) observations of courtship, suggest that "bill-flicking" is a ritualized behavior.

FIGURE 3. Forms of some Great Grebe copulatory displays: (A) the passive invitation display, (B) the active copulatory display with the eyes rolled forward, (C) the active post-copulatory display and (D) the passive post-copulatory display.

PLATFORM BEHAVIOR

Here I add to Storer's (1963a:286) brief description of Great Grebe platform behavior and quantify some display components.

Rearing display. The passive grebe initiated platform behavior by leaping onto the nest platform feet first to a standing position and performing either the "rearing" or the "invitation" displays described by Storer (1963a: 286). When rearing, the grebe's crest was generally semi-raised, and bill flicks were performed. Occasionally, the passive grebe raised its head, extending its neck vertically, while bill-flicking. The active grebe positioned itself in the water about 1 m directly behind the passive grebe; it waited in a normal posture, also bill-flicking.

Wing-shaking. Shaking the closed wings (Storer 1963a:286) during the rearing display lasted 1–2 s; bill-flicking was not performed during a wing-shaking bout. Rearing grebes averaged 1.3 wing-shaking bouts ± 1.7 each time they mounted the nest platform ($n = 82$; range = 0–9). Considering only those platform mountings which led to copulation however, rearing grebes averaged 2.0 wing-shaking bouts ± 1.7 per platform mounting ($n = 21$; range = 0–7). An R×C test of independence indicated that wing-shaking and copulation were positively associated ($G_{(8)} = 16.97$, $P < 0.05$).

Invitation display. My observations differ from Storer's (1963a:Fig. 3B) illustration of the bent neck and the raised crest components of the invitation display. The grebes that I saw lay with the neck extended low in front (Fig. 3A) and the crest relaxed. I observed passive grebes invite only when the active grebe was in a position to mount; once, when the active grebe swam to the front of the passive grebe to threaten conspecifics, the passive grebe raised its head and did not repeat the invitation display until the active grebe had returned to the pre-mounting position. Ten to twenty seconds passed before the active grebe mounted. During this period the active grebe moved its head slightly from side to side as if aiming the leap or judging the distance. The passive grebe often stopped inviting before mounting occurred. Grebes that did not perform this display were not mounted.

Copulatory display. The active grebe mounted by leaping from the water and landing feet first on the passive grebe's back. It stood with neck arched forward and crest raised (Storer 1963a:286). Its eyes were rolled forward (Fig. 3B) so that the whites showed in the rear and the active bird performed a left-right mark time movement on the passive bird's back; four to seven audible steps were performed during the 4–6 s copulation. The passive grebe maintained the invitation posture during copulation.

Post-copulatory displays. After copulating, the active grebe immediately leaped forward over the passive grebe's head, or occasionally over its shoulder, hit the water in a vertical position and rapidly undulated the lower body—this is the false bathing posture reported by Storer (1963a:286). This display was stereotyped (Fig. 3C); the neck was straighter than described by Storer, the crest was semi- or fully raised and the chest was swollen. The active grebe treaded water for about 4 s while moving forward, away from the nest platform. After water-treading ceased the active grebe maintained this post-copulatory posture for several seconds, adding irregular bill flicks and soft calls. As the active grebe leaped, the passive grebe immediately stood on the nest platform (Fig. 3D), its bill pointed downward and its crest semi-raised. Its neck was bent sharply

and the plumage of its upper neck was erect. After about 3 s the passive grebe performed irregular bill flicks, commonly raising its head back while doing so. After performing the display for about 15 s it slipped forward, into the water, in a normal posture.

As the active grebe performed the mark time copulatory movement on the passive grebe's back it issued a call composed of three or four double notes: *A-AAAA, A-AAAA, A-AAAA,* which lasted 5–7 s. The call was given with the bill closed and it continued with a louder *AAAA-A-A-A-A* . . . , as the grebe leaped from the passive grebe and treaded water.

The nest platform alone was apparently sufficient to stimulate copulatory behavior by the active grebe. Twice I watched the same grebe mount an empty platform and perform the active copulatory and post-copulatory displays, complete with copulation calls. The displays in both cases however, were shorter than usual and the calls were softer. Although grebes reared on platforms when their consorts were absent, I did not see any other passive platform displays performed by lone grebes.

Great Grebes approached nest platforms that were occupied by copulating pairs. The intruders were driven away with a threat display by the active grebe before mounting or with an S-neck display by either pair member immediately after the active grebe dismounted. Once, a member of an intruding pair attempted to mount a passive grebe behind the already mounted active grebe, disrupting copulation. I saw no evidence, however, that copulation by one pair stimulated copulation on adjacent platforms by other pairs.

BROODING BEHAVIOR

Using a small, inflatable rowboat, I marked and examined 40 nest platforms in the main nesting area from 30 November until 16 December 1977. I entered the area slowly from the direction of the lake at each examination, allowing the grebes ample time to cover their nests and leave. Eleven platforms, examined regularly for two weeks, averaged 2.6 eggs $\pm$ 0.8 each (range = 1–4). In one case a platform was used for a second brood; I could not determine however, if these eggs belonged to the pair that originally had occupied the nest. The eggs of Great Grebes have a chalky texture; they are white when laid but after one to three days acquire a blotchy mustard-brown coloration. Of 113 nest examinations, 49.6% of the clutches were completely covered with vegetation; 22.1% were partially covered so that one or more of the eggs were visible. An R $\times$ C test of independence revealed a positive relationship between the number of eggs in a clutch and the degree to which the clutch was covered with vegetation ($G_{(6)} = 45.19$, $P < 0.005$).

I observed downy Great Grebes (described by Storer 1967) until the end of March 1978 and I recorded juveniles from the first week of December 1977 until late October 1978. The juveniles were slightly paler than the adults; the white area of the anterior chest extended well up the foreneck and the face was grey with dark lateral stripes. In some cases, immature grebes remained with the adults for nine months after nesting ended and were fed by the adults when fully grown.

I observed up to three downy grebes with adult pairs. One adult predominated in carrying the young. (Gibson [1920:83–84] described natural hollows beneath the wings of adult Great Grebes for transporting the young.) The other adult threatened or attacked conspecifics who ventured near. The adult presented food to the young with the bill tip. The downy grebes begged by issuing high-pitched calls: *CE-chuI,* which they continued to use until fully grown.

The adult that carried the young threatened intruders but rarely attacked. When approached, this adult assumed an alert posture and issued a "muted" call: *a-GAB, a-GAB, a-GAB,* a sound that was reminiscent of a duck quack. The bill opened slightly on each note; the call did not carry far. The muted call presumably serves to gather the downy young together or to warn them that the adult is changing location. It is not, however, a muted form of the staccato call, muted to draw less attention to the family while still alerting the young. The staccato call is issued by both parents in alarm situations.

In alarm situations the downy grebes pressed low to the back of the adult. If the adult dived, the young normally remained on the surface. Upon surfacing the adult uttered muted calls and was joined by the downy grebes. The young grebes, however, sometimes became confused, and on one occasion a lost downy grebe made several unsuccessful attempts to mount a third adult. In another instance a pair of adult Great Grebes drove off a lost downy grebe with threat displays. In both cases, the parents found their young.

DISCUSSION

Long-term maintenance of the pair bond may increase Great Grebe reproductive fitness. Reproduction is not confined to any season: in addition to October–January egg-laying, Gibson (1920:84) reported nesting during the final week of August, and I observed platform behavior in late July (austral winter). Great Crested Grebes (*Podiceps cristatus*) in South

Africa nest every month of the year (Dean 1977: 45), and Simmons (1974:416) suggested that in Britain local factors—water level, weather and the availability of cover—are of prime importance in determining the onset of nesting by this species. Environmental cues also appear to influence the onset of nesting by Great Grebes, and paired grebes are prepared to nest whenever environmental conditions are favorable. Pair bond maintenance may also aid survival of the young which are cared for by both adults for several months.

The mutual courtship displays—nodding, turning and turning-away—are performed in significantly more ceremonies than are the ceremonial flying-away or the ghostly penguin displays. The mutual displays also appear to form a separate unit within the courtship ceremony. These are the only displays that are performed exclusively by two grebes, and where frequent or continual communication occurs between grebe partners: the number of courtship nods performed by partners are positively correlated, and partners always perform synchronous courtship turns to the same side. The solo behaviors, which also include the upright mohawk display and advertising, frequently are performed by lone grebes. Although one or more of the mutual displays may be omitted during a ceremony, these displays are performed in an established order, and in immediate succession, uninterrupted by other displays. With the exception of the upright mohawk display, which is performed to solicit courtship, the solo displays occur in no apparent order. The mutual displays may serve to define the members of a breeding pair or to synchronize hormonal changes of the male and the female.

Because the mutual displays are performed by only two grebes, however, the solo displays may initially be critical for mate selection. Huxley (1919:155) distinguished two forms of courtship activity by Great Crested Grebes: those displays performed during "pairing-up," and self-exhausting ceremonies performed by two grebes. These forms appear to be analogous to the solo displays and to the courtship ceremony, respectively, of the Great Grebe. I have no evidence that courtship in these birds has a true pairing-up phase; perhaps this "phase" may be extremely short-lived to prevent a lone grebe from extensively courting a paired grebe, or it may have been performed infrequently during the period when I collected the statistical data. The greater number of ceremonies in which mutual displays were performed however, may reflect a longer "mutual" courtship phase in which the ghostly penguin display and ceremonial flying-away perform a secondary role. They perhaps aid in the reinforcement and the maintenance of the pair bond, or serve as displacement activities as suggested by Storer (1963a:286). This latter possibility could explain the statistical clumping in the frequency with which the ghostly penguin displays were performed.

My statistical analyses, however, reveal little about the physiological mechanisms underlying courtship. The clumping of the ghostly penguin display performances does not appear for the ceremonial flying-away display, and I cannot account for the difference. I found no significant difference either in the number of ghostly penguin displays performed by grebes that initiate courtship, and their partners, or by grebes that initiate nodding, and their partners. Furthermore, I found no correlation between the number of nods performed by the grebe that initiates nodding and the number of turns subsequently performed by the pair during the same courtship ceremony.

Several meanings have been proposed for the closed wing-shakes performed by several species of grebes (Deusing 1939:369, Storer 1969:199, Chamberlin 1977:39). Simmons (1974:Plate 63) and Wiechmann (1974) observed female Great Crested Grebes wing-shake immediately before and after laying an egg. My data indicate that Great Grebe wing-shaking is a behavior associated with copulation; it appears to be a ritualized form of behavior to invite copulation and it may have additional functions.

The greater the number of eggs on a platform, the greater is the tendency of the grebe to cover the eggs with vegetation before leaving. I have evidence of bird predation on Great Grebe eggs, and the selective advantage of egg concealment, and of the eggs acquiring a coloration that blends with the platform, is obvious. Based on my observations however, and on my knowledge of local fauna, I think that predation is not a principal cause of egg loss in the delta area. Since a grebe has more invested in an egg than the cost of concealing it, if predation were high, selection would encourage the concealment of even single eggs. I do not believe that the correlation is an artifact; i.e., that my approaches to the nesting area were so sudden as to alarm grebes into quickly abandoning one or two eggs. Egg concealment in the delta area appears to strike a selective balance with the cost of replacing a clutch in an environment where predation is low.

ACKNOWLEDGMENTS

I thank Connie M. Armstrong for her suggestions on the initial manuscript and her aid in obtaining the references,

Claudio Briones R. for identifying the plants, and Anne LaBastille, Jerome S. Rovner, Robert W. Storer, Gerald E. Svendsen and an anonymous reviewer for their criticisms and suggestions on earlier drafts of this paper. I also thank the Smithsonian Institution/Peace Corps Environmental Program, and the Corporación Nacional Forestal, Osorno, Chile, for their support. I am grateful to the people of Puyehue National Park who aided in the study.

LITERATURE CITED

BLAKE, E. R. 1977. Manual of Neotropical birds. Vol. 1. Univ. of Chicago Press, Chicago.

CHAMBERLIN, M. L. 1977. Observations on the Red-necked Grebe nesting in Michigan. Wilson Bull. 89: 33–46.

DEAN, W. R. J. 1977. Breeding of the Great Crested Grebe at Barberspan. Ostrich Suppl. 12:43–48.

DEUSING, M. 1939. Nesting habits of the Pied-billed Grebe. Auk 56:367–373.

GIBSON, E. 1920. Further ornithological notes from the neighborhood of Cape San Antonio, Province of Buenos Ayres. Part 3. Phoenicopteridae-Rheidae. Ibis (Ser. 11)2:1–97.

GREENQUIST, E. A. 1978. La comunidad de vida silvestre del delta del Rio Gol-Gol con recomendaciónes para su manejo y desarrollo. Corporación Nacional Forestal, Santiago, Chile.

HEUSSER, C. J. 1974. Vegetation and climate of the southern Chilean Lake District during and since the last interglaciation. Quat. Res. 4:290–315.

HUXLEY, J. S. 1919. Some points in the sexual habits of the Little Grebe, with a note on the occurrence of vocal duets in birds. Br. Birds 13:155–158.

MCALLISTER, N. M. 1958. Courtship, hostile behavior, nest-establishment and egg laying in the Eared Grebe (*Podiceps caspicus*). Auk 75:290–311.

MCALLISTER, N. M., AND R. W. STORER. 1963. Copulation in the Pied-billed Grebe. Wilson Bull. 75:166–173.

SIMMONS, K. E. L. 1974. Adaptations in the reproductive biology of the Great Crested Grebe. Br. Birds 67:413–437.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman, San Francisco.

STORER, R. W. 1963a. Observations on the Great Grebe. Condor 65:279–288.

STORER, R.W. 1963b. Courtship and mating behavior and the phylogeny of the grebes. Proc. XIII Int. Ornithol. Congr. (1962):562–569.

STORER, R. W. 1967. The patterns of downy grebes. Condor 69:469–478.

STORER, R. W. 1969. The behavior of the Horned Grebe in spring. Condor 71:180–205.

VEBLEN, T. T. AND D. H. ASHTON. 1978. Catastrophic influences on the vegetation of the Valdivian Andes, Chile. Vegetatio 36:149–167.

WIECHMANN, M. 1974. Egg-laying by the Great Crested Grebe. Br. Birds 67:438.

Corporación Nacional Forestal, Casilla 813, Osorno, Chile. Present address: U.S. Bureau of Land Management, P.O. Box 670, Rawlins, Wyoming 82301. Received 26 May 1981. Final acceptance 1 June 1982.